# A STUDY OF UNCONGENIALITY BETWEEN VARIETIES OF PEACHES AS SCIONS AND THE MARIANNA PLUM AS A STOCK

by

James A. McClintock

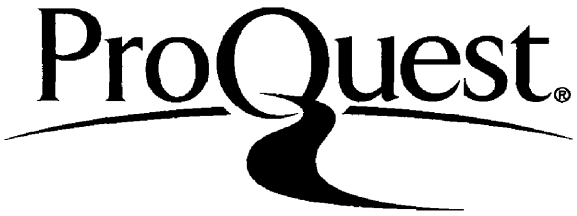
A THESIS

Submitted to the Graduate School of Michigan State College of Agriculture and Applied Science in partial fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Horticulture

1944



## Acknowledgments

This paper is the result of studies conducted over a period of years at state experiment stations in Georgia, Tennessee, Michigan and Indiana. Credit is due to each of these institutions for land and equipment used in advancing the solution of this problem.

These studies have been benefitted by the helpful suggestions of a number of men working in the sciences of Botany, Chemistry and Horticulture. To each of these the writer expresses his acknowledgment of assistance rendered.

For their continued interest in guiding the writer in various angles of these studies he expresses his personal indebtedness to Messrs. V. R. Gardner, F. C. Bradford, J. W. Crist, E. A. Bessey, E. F. Woodcock, E. J. Kohl, H. R. Kraybill, C. D. Ball and V. G. Grove.

# A Study of Uncongeniality Between Varieties of Peaches as Scions and the Marianna Plum as a Stock

by

J. A. McClintock

## Introduction

Quality, a human desire, is not essential to plants for their natural reproduction. This quest for quality is not entirely a new departure in the realm of horticulture but began as early as the science itself. It lead man to select individual fruit trees from their parent species. To these selections varietal names were given. Often a family name was given to the new selection as in the case of an early cherry, Richmond's Early. Or, to make it more personal, the varietal name given was that of some member of a family, as Elberta peach.

To perpetuate these varietal selections it is obvious that man had to change from nature's method of sexual reproduction by seed. Suckers, layers, and cuttings afforded means to assure vegetative continuity of some selections, but these methods were not uniformly successful and in many cases were slower than nature's methods of seed reproduction. In an effort to take advantage of nature's methods and yet retain what he had gained through selection for quality, man developed methods of raising root stocks from seed and then introducing a top of the desired variety by grafting or budding.

The original technique by which such unions were accomplished was probably suggested to man by natural grafts which he observed in the wild. Once the idea of such plant unions was grasped, the techniques were varied to suit man's purpose. Regardless of the fact that

many attempts made were unsuccessful, because of the wide botanical differences between stock and scion, by a process of "cut and try" completely incompatible combinations were gradually eliminated. With the working out of family relationships by systematic botanists information was obtained which greatly helped in selecting suitable stocks for the varieties man desired to propagate.

With this botanical classification as a background, however, propagators found that close relationships were not an assurance of successful union of stock and scion.

## History and Review of Literature

It is interesting to note that problems of affinity have existed ever since propagators began using a root stock of one plant and a scion of another plant. This is evidenced by Chang (5) who states that Chia in 500A.D. noted that plum, Prunus salicina Lindl., could successfully be grafted on peach stocks, Prunus persica (L) Batsch, whereas the peach usually failed to grow on plum stocks. Obviously this is a case of incompatibility which is not reciprocal. Further evidence that generalizations cannot be made regarding compatibility is furnished by the observation of Knight (11) in 1812, that plum stocks are best adapted to the peach. Horticultural literature yet abounds with such general statements. While problems of compatibility have been avoided in practice, relatively little has been done to determine why certain combinations are not congenial.

Since Argeles (1) has done an excellent piece of work in reviewing the literature on this subject for pome and stone fruits, the literature referred to in this study will be confined to that

which has a bearing only on the problem under consideration. Even within the limited field of peach-plum affinity published records vary as to the compatibility of stock-scion combinations.

In the writer's studies, primary interest is centered on one stock, namely the Marianna plum, and its compatibility with varieties of peaches. According to Hedrick (8) Marianna "is from either a self or a cross-fertilized seed of Prunus cerasifera Ehrh. If the latter the other parent must have been some native species, the particular variety possibly being Wild Goose, one of the Munsoniana plums." As evidence of its hybrid parentage Hedrick records its vegetative robustness and its semi-sterility. While he records the fact that the Marianna "grows very readily from cuttings," Hedrick does not offer this characteristic as evidence of its hybrid parentage. As he makes no mention of either Prunus cerasifera (Myrobalan) or Prunus munsoniana (Wild Goose) being readily propagated by cuttings it is evident that the Mafianna differs from these "parents" in that respect, thus indicating that it is a true hybrid.

Hedrick's statements regarding the parentage of the Marianna were evidently based on the earlier work of Bailey (2) who draws upon horticultural tests to show that the Marianna plum is a hybrid. Bailey found that less than 10 per cent of the hard wood cuttings of Myrobalan plums rooted and grew; while 70 per cent rooted and grew in the case of Marianna.

Waugh (21) agrees with Bailey and Hedrick regarding the hybrid origin of Marianna, but he believes it is a Myrobalan-Chicasa hybrid. He states "The spreading, half-thorny habit of the tree, the flowers borne several in a cluster, and the short stem of the fruit are all

characters not common to Myrobalan plums, but always found in the Chicasa." While Waugh does not mention the use of Marianna as a stock for peaches his experiments indicate that it proved to be a satisfactory stock for plums, for he states: "The best average growth has been made on Marianna." No mention is made of any lack of affinity between the Marianna plum stock and various plum varieties which he tested in his extensive experiments.

The readiness with which Marianna roots from hard wood cuttings probably accounts for its rather wide dissemination and early use as an understock. We find it introduced to fruit growers by Charles N. Eley in 1884 at Smith Point, Texas, and used as an understock for peaches in Georgia and Maryland in 1888-89, as reported by Smith (20). In both these states, mention is made of the fact that the Marianna stocks used were well-rooted cuttings. Attention is called to this point as evidence that the Marianna stocks discussed by Smith were clonal stocks, and thus of the same genetic make up as the original parent tree in Texas.

Smith (20) records in connection with his peach yellows studies that of 124 peach trees of Old Mixon, Early Crawford, Late Crawford, Mountain Rose, and Beer's Smock budded on Marianna stocks in August 1889, "24 were dead, 53 were dwarfed and yellowish as though suffering from defective nutrition" on September 18, 1890. "None, however, showed any signs of yellows.....They had been set very deep, and I was at a loss to account for the appearance of the sickly ones, unless this might have to do with it....Later I discovered that in all of the dwarfed and yellowish trees the tops had overgrown the stocks, and that in all the vigorous trees the growth of the stocks had kept even pace

with that of the tops." Although he did not record this as a case of incompatibility, Smith gave an excellent description, one of the first which the writer has found, of uncongeniality between the Marianna plum stock and various peach varieties. Smith records other experiments in which peaches grew poorly on Marianna stocks, but as his attention was concentrated on virus disease problems he did not follow up the affinity problems he encountered.

Booth (3) appears to be the next research worker to record difficulties with the Marianna plum as a rootstock for peaches. He reports that the peaches grew much more rapidly than the plums, and at the end of two years the trunks of the trees were twice as large above the point of union as below. He reports that during hot, dry weather of the second season the peach tops wilted for several days, but revived during the night, then finally dried out and died. He states: "This was evidently due to the lack of sufficient moisture furnished by these slow growing roots to supply the demands from above, during a period of excessive transpiration." Booth's statement implies that the slow growth of roots is a characteristic of the Marianna plum stock instead of retarded root growth caused by failure to obtain elaborated food from the peach tops. Though Booth gave a good description of a union lacking in affinity he apparently did not interpret the enlargement of the scion trunks above the unions as evidence that elaborated food was not passing down across the graft bridge.

## Allied Investigations

In 1919 the writer became interested in the Marianna plum as a stock while investigating the spread of peach rosette in commercial

orchards in the Fort Valley, and Marshallville sections of Georgia. Resulting studies (13) confirmed Smith's findings regarding the resistance of the Marianna plum to the rosette virus. Therefore it seemed desirable to investigate further, to determine why peach varieties in many cases failed to make satisfactory growth on this stock. The readiness with which Marianna stocks could be budded, and the apparently strong unions which resulted were not indicative of uncongeniality. In 1920 and 1921 when such peach-plum combinations showed sudden wilting of the tops the trees were dug and examined, and it was found that the plum roots had died while the peach tops were still alive. These tests were repeated at the Tennessee Agricultural Experiment Station in 1922, 1923 and 1924 with similar results on hundreds of trees. This indicated that soil organisms might have been attacking the roots. Detailed pathological studies failed to disclose any parasitic organisms associated with the dying or dead roots. The results of these studies (14, 15) indicated that the failure of these unions was caused by some type of uncongeniality between stock and scion. These investigations, as well as those of Smith and Booth, had all been conducted with Marianna stocks propagated vegetatively from hard wood cuttings. This therefore was a case of uncongeniality between a stock of uniform genetic make up and scions of varied genetic make up such as occured in the various peach varieties tested, and thus presented fewer genetic variables than if seedling plum stocks had been used. In no cases were peaches found by the writer which showed good affinity for this clonal stock, although varieties such as Arp, Belle, Elberta, J. H. Hale, Heath Cling, Hiley, Mayflower, and Truimph were repeatedly tested from 1919 to 1925.

In 1929 Howard and Heppner (10) presented the results of their studies with seedlings of Myrobalan and Marianna plums as stocks

for peaches. They reported that "On the whole seedlings of both Myrobalan and Marianna might be said to be unreliable as peach stocks because of the great variability in vigor and lack of uniformity in their affinity for the peach." Their studies of seedlings offered promise, however, for they recorded a wide range of difference in the affinity of the various seedling stocks. Some Myrobalan seedlings gave 100 per cent failures; one proved "almost perfect" as a stock for peaches. There were also all gradations between the two extremes. From these findings one was encouraged to believe that some Marianna seedlings might also prove more congenial to peaches than the original clonal strain, for Howard and Heppner state "Apparently there are similar variations among Marianna seedlings, although we have not tested them so extensively." The hope for congenial plum stocks which the studies of Howard and Heppner offered suffered a setback in later tests conducted at the East Malling Research Station in England by Chang (5), who reports that "when these California strains of Myrobalan were worked with Hale's Early peach scions, none of them showed any sign of compatibility with this Variety."

These findings brought the problem back to a study of the reasons why plum stocks are not satisfactory as understocks for peaches. According to Bradford and Sitton (4) and Proebsting (17, 19) such evidence of lack of compatibility as is manifested by peach on plum may be due to structural weaknesses resulting from failure of the stock and scion tissues to unite throughout the regions of the union. External symptoms, as indicated by overgrowth above the union, would seem to give the appearance of structural weakness, but such evidence is not substantiated by the breaking of the scion from the stock at the union, as

frequently occurs in the case of apricots on plum stocks. This is well illustrated and described by Proebsting (19) who shows that only parenchyma cells develop at the line of union between apricot and Myrobalan plum. Of the thousands of unions of peach on Marianna plum which the writer has made in Georgia, Tennessee and Indiana during the course of these studies, no cases of breaking at the union have been observed.

Examination of the accompanying figures of sections of these unions will disclose that the xylem tissues are fairly well developed in the cases of both the congenial and the uncongenial unions. Many similar unions have been cut longitudinally for less detailed study; there has been found good development of the woody tissues. In no cases examined to date has the writer found in peach or Marianna plum a union of parenchyma cells only, such as frequently develops in unions of pear on quince or apricot on plum. In some cases, as illustrated in Figures 3 and 4, phloem tissues have turned inward and occupied areas normally occupied by xylem tissues, as seen in Figures 1 and 2. In none of these cases however are the xylem unions sufficiently reduced in area or strength to cause breaking at the unions while growing in the nursery rows. This would indicate that uncongeniality in these obviously not normal unions is not due to or associated with any failure of the xylem tissues to unite.

Crafts (6) and Mendel (16), working with herbaceous and woody material respectively, came to similar conclusions, namely, that anatomical differences between the stock and scion are the real reasons for the observed lack of affinity. Their conclusions are not greatly different from the opinions of those who attribute lack of affinity to structural weaknesses, except that they hold that the symptoms may appear without

any associated structural weaknesses. Booth's (3) studies indicated that the graft union is a point or region of weakness even in unions which are considered congenial, but in the writer's experience such implied reduction in strength is not manifested by breaking at the union as it is in apricot on plum stocks and pear on quince stocks. It therefore would seem that manifestations of uncongeniality may take different forms in different stock-scion combinations. No one who has seen apricot shoots break from their bud unions with plum stocks or certain pears break from their union with quince stocks would deny that these are both incompatible and structurally weak. There might be less readiness in using the term incompatible for a peach budded on plum where the scion wilts and dies with no external evidence of structural weakness. In the writer's mind, however, this is equally strong evidence of lack of congeniality.

Other workers, as Haas and Halma (7), Kostoff (12), and Proebsting and Barger (18) suggest biochemical changes or the development of toxins as the causes of incompatibility; but the analogy is drawn from the field of animal physiology and the comparisons have not been entirely satisfactory when applied to plants. It is altogether probable that structural weaknesses are the result of abnormal anatomical development in the region of the union and that these abnormalities in anatomy may be due to chemical or physiological differences between the two components of an uncongenial union. However until more evidence on the chemical phases is available it seems desirable to add what we can to the evidence regarding observed anatomical differences which help to explain observed cases of uncongenality.

Howard and Heppner (10) used 29 varieties of peaches in their studies with Myrobalan, and Marianna seedling stocks and recorded some differences in affinity; however, no varieties of commercial value were found which they were willing to recommend for commercial propagation on either of these stocks.

## Procedure

The writer confined his study to varieties which would be likely to be grown on a commercial scale in the South and thus profit most from a stock which was known to be resistant to rosette virus which had until recently infected peaches only in the Southern states. No differences in affinity were observed by the writer such as those reported by Howard and Heppner. It is true that there were differences in the time which elapsed before individual trees developed symptoms of uncongeniality, though such differences were not correlated with varieties. In fact, there were as great differences between individuals of a given variety as there were between individuals of different varieties. These findings are in agreement with those of Proebsting (19) with other Prunus combinations.

More than usual care was taken in making the unions, therefore differences in technique probably were not very important factors. In no case was true grafting resorted to, because it is well established that wounding of Prunus xylem tissues results in excessive gum formation. If this gum exudes into the space between stock and scion, it may retard the growth of wound callus which first unites the two components of the graft. Propagation was confined to budding, and the buds were cut so that only phloem, cambium and undifferentiated xylem cells were lifted from the peach budstick. In nursery practice such buds are called

bark buds because all differentiated wood is left attached to the bud-stick. In no cases were true shield buds used, which contained differentiated xylem because it is recognized that such xylem tissues would not readily unite directly with the stock, but would remain as an area of structural weakness at the union.

In making the T-shaped opening in the stock, for the insertion of the bud, care was used not to cut into the xylem, thus reducing the possibility of gum formation from wounding of xylem tissues of the stock. Thus if gum formation subsequently developed, it is assumed that it was the result of physiological abnormalities.

The bark flaps of the stock were raised by inserting the tip of the bud at the top of the T-shaped cut through the phloem, and then pushing steadily on the bud until it moved downward and was entirely enclosed by the stock bark flaps. This brought the cambium and associated undifferentiated phloem and xylem cells of the scion bud into more or less immediate contact with similar cells of the stock, with a minimum of exposure to desiccation and its resultant cork formation. Here again the purpose was to bring about as normal a union as possible, so that any abnormalities which develop would be the manifestations of physiological influences.

During the earlier years of these studies the unions were wrapped with string and raffia. These wraps offered a greater opportunity for desiccation and subsequent abnormal cell formations, such as cork and gum. As the studies progressed rubber typing strips became available. With these the entire union could be covered with an overlapping rubber seal. This held the bud in close contact with the stock and excluded excess air and moisture, without exerting so much pressure

as to result in retardation of wound callus development to join the two graft components.

Most of the uncongenial unions of peach on Marianna plum stocks, not used for anatomical studies, died during the time they stood in the nursery rows. In cases where the peach buds failed to unite with the plum the Marianna stocks were pruned and allowed to grow for orchard studies.

Using similar technique in budding, other unions were made in which peaches served as the stocks, and Marianna plums as the scion buds. Such unions were the reciprocals of the uncongenial peach-plum combinations. Southern "natural" peach pits were planted to supply peach seedlings for budding to plums. In addition to Marianna plum, buds of the Methley variety were put in peach seedlings, because this had proved to be a vigorous growing variety when budded on Marianna plum stocks. Both the Marianna and the Methley plums made good unions with the peach stocks. Those not used for anatomical studies were transferred from the nursery rows and spaced for more extensive growth. These trees grew and produced fruit typical of each variety.

No symptoms of uncongeniality developed. At the end of six growing seasons in this location 73 of these trees were dug for detailed studies of the unions. Of 44 Marianna plums on seedling peach stocks the average diameter at the union was 5.8 inches. When random samples were sawed through the union lengthwise, there appeared to be normal development of both xylem and phloem, with no marked overgrowth of either stock or scion. That the peach stocks appeared to have a slightly stimulating effect on the Marianna plum scion is indicated by the fact that 12 Marianna stocks on their own roots averaged 4.2 inches in diameter at the same level

as the Marianna on peach stocks which averaged 5.8 inches. The 17 Methley plums on seedling peach roots averaged 7.0 inches in diameter at the union, indicating that this scion variety is equally vigorous whether on peach seedlings or on rooted Marianna cuttings, as previously mentioned. No overgrowth of Methley plum developed at the unions with the peach seedlings. The remaining trees of these reciprocal combinations were under observation for four growing seasons after the above measurements were taken. During that time none of these trees developed symptoms which indicate lack of affinity. These records would seem to confirm the anatomical studies which indicate that Marianna plum on peach stock is congenial, in contrast to the markedly uncongenial union of peach on Marianna plum stocks.

A third set of unions was made in which a vigorous growing variety of plum was budded into Marianna plum stocks. These trees made good growth in the nursery with no symptoms of uncongeniality developing. Some of these trees were retained and transferred to the orchard. They have made vigorous growth and have come into bearing without any abnormal symptoms developing. The results obtained with plum varieties on Marianna, as a stock, are in agreement with those obtained by Waugh (21) who early recorded the merits of the Marianna variety as a stock for cultivated plums.

The data above recorded indicate that peach on Marianna, as a root stock is the only truly uncongenial combination in these studies.

## Anatomical Studies

With external symptoms of uncongeniality confined to this anatomical differences which might explain the observed manifestations of one combination, material was propagated for investigation of uncongeniality. The stocks were grown from hardwood cuttings of Marianna plum and wherever

possible were budded to peaches during late summer of the first growing season. Satisfactory unions of buds of various varieties were obtained and these remained dormant until the following spring. Then the Marianna stocks were cut back to the inserted buds, thus making these peach buds the terminal buds of each plant. In most cases the inserted buds grew well during the early part of the summer, but by midsummer some of the peach tops began to show evidences of uncongeniality. After recording the symptoms on a number of these combinations, the region of the union of each was prepared for further study, by washing, to free the bark from soil particles. The cleaned stems were then pruned to remove all surplus stock and scion tissues above and below the unions. These unions were taken to the laboratory in the fresh condition, and stored in a moist refrigeration unit. From the storage unit the peach-plum unions were removed one at a time, and cut into sections from 40 microns down to 16 microns in thickness, using a sliding microtome. The unions cut at 20 to 30 microns in thickness gave more whole sections across the entire unions. After sectioning, each lot, in a separate watch glass, was washed in four changes of tap water. After washing, the water was drained off and the sections covered with Delafield's haematoxylin stain and allowed to stand from 24 to 48 hours. The stain was then drained off and the sections destained in acid alcohol. When the excess stain had been removed the acid alcohol was drained off and the sections covered with 50 percent, by volume, alcohol to rinse off surface particles of haematoxylin. The 50 percent alcohol was then drained off and the sections covered with safranin stain and left for 12-24 hours. The excess safranin was then removed by draining off the solution and destaining in acid alcohol for one to two minutes. The sections were then washed in

50 percent alcohol, and run up through 95 percent and absolute alcohol, and finally transferred to xylol. From xylol the sections were mounted on standard microscope slides and sealed in with balsam and cover glasses and allowed to dry for microscopic study.

Microscopic examination indicated that these fresh sections did not furnish suitable material for detailed study; therefore, additional material was prepared by placing similar unions in 46 to 48 percent hydrofluoric acid for a limited time before sectioning. While this treatment softened the tissues somewhat it did not enable the cutting of thin sections which retained their shape; therefore, details of tissue arrangement at the union could not be clearly detected under the microscope. A third lot of unions was therefore prepared, treated similarly with hydrofluoric acid, and then infiltrated with celloidin according to standard methods for woody materials. This material was soft enough to cut, yet did not crumble when sectioned at 20 microns.

Examination of sections of congenial unions, such as plum on Marianna plum stocks, under the microscope indicated that the unions were well developed throughout. Figure 1 is a section of congenial union of Methley plum scion above, and Marianna plum stock below. There is some evidence of gum formation in the dark colored areas at the union, but these gum pockets occupy a relatively small proportion of the union. The xylem strands are little distorted in their growth from the stock to the scion and are not weakened by admixtures of phloem as in the uncongenial unions. The medullary rays are seen to follow well defined courses across the union and should be able to serve for lateral food transport in a normal manner. The phloem of stock and scion is seen to have united in a

normal manner which insures ample sieve tissue development to transport elaborated foods. Such unions make vigorous growth of tops, and the root systems show no symptoms of starvation. Hundreds of sections of such congenial unions have been examined, and all show a normal development free from any signs of uncongeniality between the Marianna plum stocks and the Methley plum scions. In no section could one see evidence of serious gum formation. The wound callus had filled practically all of the area, and had differentiated into cambial regions that were producing new xylem and new phloem which was continuous. Figure 2 shows the remarkable completeness of the union of all tissues from the plum stock below to the plum scion above. There is no more distortion of the tissues than might be expected of any inserted bud as it oriented itself from the later position, where first inserted on the stock, to a more vertical position as it developed into a terminal shoot. The continuity of both xylem and phloem tissues from stock to scion, and the clear cut medullary rays extending all the way from the central pith region across the xylem and phloem, would seem to insure ready transport of water, mineral nutrients and elaborated food to all parts of this union, as readily as if this were one plant, instead of two plants joined at a bud union. The freedom from pockets of gum, or cork cells in the xylem, which might result in structural weakness, is worthy of note. With care used in budding, the stock xylem was not injured and therefore was not stimulated to produce gum. When the union was covered with a rubber strip, desiccation was reduced to a minimum, therefore gum and cork cells were not encouraged to develop. In all the congenial unions, neither gum nor cork were found interfering with normal tissue bridging the stock to scion.

Assuming that equal care is used in making all unions, the presence of sizable pockets of gum at the union is evidence that factors other than

the wounding of the stock xylem or the desiccation of cells near the cut edges of the stock and scion (bud) are responsible for gum formation. Sections of the uncongenial unions of peach on Marianna plum were conspicuous for the presence of gum in the region of the union. Figure 3 is a section of an uncongenial union of peach above, budded on Marianna plum stock, below. The mechanics of making the union were as carefully carried out as were those illustrated in figures 1 & 2, but the development was entirely different. Gum pockets are numerous throughout the xylem in the region of the union. The xylem strands do not show continuity from stock to scion. Some of the wound callus appears to have not yet differentiated. At the left side the phloem has failed to unite and instead, both the stock and scion phloems have grown inward and developed barriers to the union of the stock and scion xylems. The lack of continuity of the rays implies poor lateral conduction resulted. The enlargement of the scion in diameter, above the union, is evidence that elaborated food was stored there. Failure of the stock and scion phloems to unite, prevented the sieve tube continuity at the union, therefore the stock was not supplied with elaborated food and did not keep pace with the growth of the scion. Were the masses of gum continuous the unions would undoubtedly show weakness of structure that would manifest itself in separation of stock and scion under strain. The open spaces in the region of the union of figure 3 may be the result of gum deposits preventing complete xylem union. In these peach-plum unions, however, the gum pockets were generally separated from one another and served to direct the vasculars and their supporting cells into the most devious and distorted masses of tissues, as seen in the central position of the scion in figure 3. Such twisted masses of xylem appear to be mechanically strong because such combinations do not break at the union. While apparently

mechanically strong, such distorted xylem tissues cannot function normally as compared with xylem in unions of congenial combinations, such as those illustrated by figure 2. Certainly water transport upward must be seriously retarded into its passage across the uncongenial unions. The practically normal growth of the scion and stock tissues, and the absence of gum deposits in congenial unions, as seen in figure 2, is in contrast with the much distorted tissues and an abundance of gum in uncongenial combinations as shown in figure 3 and indicate that something more vital than external physical factors is influencing the success or failure of these unions.

## Discussion

The fundamental cause or causes underlying these observed structural differences are probably of a chemical nature. Such chemical differences as may exist have not as yet been investigated for the peach-plum combination in question. Materials for such studies are being accumulated. Progress has been made in obtaining interstocks which are mutually compatible with peach scions and Marianna plum stocks.

While the most striking symptom of uncongeniality between Marianna plum stocks and various varieties of peaches is the wilting of the scion as reported by Booth (3), Howard and Heppner (10) and the writer (14), this manifestation is a secondary response in the writer's opinion. Regardless of their distortion at the union, the xylem elements are structurally strong so they do not break under strains which frequently break structurally weak, incompatible unions such as apricot budded on plum stocks.

With such strength of xylem tissues as above recorded the peach on Marianna plum stocks would continue to function, even through more slowly

than normal, providing something did not occur to stop the intake of water by the roots which are still young enough to absorb water from the soil. Lack of soil moisture is not believed to be the basic reason for this. These uncongenial peach-plum combinations have been observed to wilt in soils sufficiently well supplied with moisture to support trees of similar but congenial combinations, in an actively growing condition with all leaves remaining continuously turgid. Lack of moisture and its resultant wilting of these uncongenial combinations, must then be sought in some conditions which inhibit the formation of new root hairs. Invasion of the roots, by soil inhabiting parasitic organisms, could bring about the death of the root hairs, but no such organisms were found associated with the roots of the Marianna stocks of the uncongenial combinations.

The failure of elaborated food to diffuse down across the graft union and provide for root growth, might bring about the condition where no further root production was possible. A hint that this may be the primary cause of the observed secondary manifestation of wilting is given in the enlargement of the peach scion just above the union, a symptom frequently observed associated with uncongenial peach-plum combinations.

The studies of Heinze, Parker and Borthwick (9) substantiate this theory of the inability of elaborated food to normally diffuse down across the graft union. When they grafted Red Kidney bean on Biloxi soybean a satisfactory union resulted, and water and mineral nutrient transport across the union appeared normal. The elaborated food produced by the Red Kidney bean scion did not, however, freely pass down across the graft union to the Biloxi soybean stock. This they proved by placing the grafted plants in a darkened location, and noting that the accumulated starch in the Red Kidney bean leaves was not lost even after many days. Control grafts of

Red Kidney bean scions on Red Kidney bean stocks lost most of the starch from their leaves the first night. In these studies the Red Kidney bean scions supplied only a portion of the total leaf surface, and the soy bean leaves on the stock plant supplied sufficient elaborated food to nourish the roots. Although it was outside the purpose of their studies it is interesting to surmise what the results would have been if the soybean stock had been entirely dependent upon elaborated food from Red Kidney bean scion leaves.

Similarly the writer has had no difficulty in prolonging the life and growth of peaches on Marianna plum stocks where the peach scions were budded into the plum scaffolds and thus became only part of a multiple top, the balance of which produced Marianna plum leaves. In such unions, the customary enlargements developed at the base of the peach scions, indicated failure of the elaborated food to cross the union. Such peach scions have been carried along until they produced fruit of normal size and flavor. This method of adapting the peach to the Marianna stocks was not practical, however, because the plum branches outgrew the peach branches and thus required more than average pruning to allow normal peach growth.

If the scion was entirely peach growth, and elaborated food was stored in the phloem at the base of the peach scion to the extent that a visible overgrowth was produced, as seen in figure 3, it was obvious that the roots were not getting all the elaborated food they could have used. In congenial combinations, which showed no abnormal symptoms, scion overgrowths at the union were rare.

Searching for a reason for the failure of the elaborated food to pass down across the graft union, the phloem region of the uncongenial peach-plum combinations was studied in detail in the celloidin-infiltrated sections. By following the phloem of stock and scion in section, throughout the extent of the unions, it was found that in many cases there was little or no union between stock and scion phloems, as seen in figures 3, 4 and 5. Phloem cells had been produced by the respective cambia, but instead of helping to complete the graft bridge by intermingling in a more or less continuous layer, the respective phloems seemed to remain unto themselves. In some cases the stock, and the scion phloems developed a certain distance toward one another and then stopped without uniting, thus leaving a distinct gap. In figure 4, an uncongenial union between Marianna plum stock below, and peach scion above, it will be seen that on both sides of the section, the phloem of the stock has not united with that of the scion. The increased thickness of the scion phloem above is also indicative of accumulation of elaborated food materials which probably would have diffused down to the plum stock, if the respective phloems had grown together and provided for sieve tissue continuity. In other cases the phloem of one or the other component had grown out for a certain distance and then curved inward, thus leaving an area of xylem without a covering of bark. In the uncongenial union illustrated in figure 5, the plum stock phloem at the lower left has grown inward and seemed to terminate between masses of developing stock and scion xylem tissues. Though the peach scion phloem is not complete in this section its direction of growth, where it leaves the xylem at the upper left, indicates that it did not unite with the stock phloem on this side of the union. The much greater thickness of the scion phloem above indicates that elaborated food materials are being stored at

the base of the scion because of their inability to get across the union to nourish the stock tissues. In some cases there appeared to be evidence of partial phloem union, and such cases would seem to explain the variation in the time of visual manifestation of uncongeniality. The more complete the phloem union the more delayed would be the manifestation of uncongeniality, because even partial union of the two phloems would insure some elaborated food materials reaching and nourishing the roots.

Why union occurs between stock and scion xylem even though in a much distorted pattern, while stock and scion phloems unite only partially or not at all, is still an unsolved problem. Cambial activity must have been going on in both stock and scion at about the same time to produce the new xylem which resulted in a relatively strong physical union. It is suspected that the difference may be related to elaborated food materials. The failure of the phloems to unite offered an explanation of why the trees wilted and died. Kostoff (12) attributes the failure of the union of herbaceous plants to the formation of chemical substances which inhibit the passage of food materials across the union. The presence of such substances as precipitins, antigens, etc., have not been determined thus far in these studies, but, if present, they must be associated with the elaborated materials moving downward in the phloem, because it is the lack of phloem continuity which is responsible for elaborated food materials not reaching the roots, and thus for the failure of these peach-plum combinations.

If the phloem unions were as complete as those of the xylem, there might still have been some enlargement at the base of the scion just above the union, because of the distorted growth of the sieve tube elements; but when the respective phloems failed to bridge the union, as shown in figures 3, 4 and 5, there must have been areas where sieve tube connections

were entirely lacking. Under such conditions the roots were cut off from elaborated foods and therefore eventually died.

Uncongeniality Explained by Propagation Technique

The order in which the various steps in the manifestation of uncongeniality took place was not disclosed by the sections examined, but knowing the steps in the propagation processes one can theorize that the action is somewhat as follows: In the Northern States, stocks to be budded are allowed to grow at least an entire season in the nursery row. In so doing the stock produces a normal root system for a one year old tree, with a full sized top to manufacture food to maintain the root growth. Some time late in the summer, that is, in July, August or September, the bud of the scion variety is inserted in the stock. Wound callus is formed and the inserted bud is said to have united with the stock. In most cases such buds remain dormant; that is, the bud does not start into vegetative growth during the remainder of that growing season. In the spring of the next year, the top of the stock is cut off just above the inserted bud. This makes the inserted scion bud essentially the terminal bud of that particular plant. Having been so suddenly changed from a lateral position near the base of the stock to the terminal position at the top of what is left of the stock, due to the excision of all stock tissues above it, this inserted bud has had little opportunity to develop the particular hormone which is associated with buds which develop naturally in the terminal position. Without ample terminal bud hormone, this inserted scion bud is not able to function as a true terminal bud in inhibiting the growth of the lateral buds which are normally present on the stock below the inserted bud. The result is, that both the scion bud, and the stock buds start into vigorous growth in the spring of the second year. This uses up some of the food stored in that part of the

stock left after removing most of the top. As the lateral buds below the union are initiated from the stock, they undoubtedly have a more normal and completely established union with the stock vascular tissues than does the inserted scion bud. This advantage of better union, and the lack of retardation by terminal bud hormone, gives the lateral stock buds a stimulus which, if not artifically curtailed, would result in the stock shoots over-growing the shoot from the inserted terminal bud. Before these lateral stock shoots, commonly called suckers, have had time to produce much leaf surface and elaborate food materials to help nourish the stock roots, they are removed, allowing the inserted bud shoot to produce a single straight trunk of the desired variety. This removal of all stock shoots capable of producing elaborated food, throws the entire responsibility for food production onto the scion shoot. This causes the young tree to be temporarily in a very much unbalanced condition. For the time being it is a tree with a two year development of root system, and much less than a one year top. In a congenial union such an unbalanced condition adjusts itself through the rapid growth of the scion shoot into a top capable of furnishing elaborated food materials for its own growth and for that of the stock. This assures continuous production of new roots and root hairs. By mid-season of the second year in the nursery row, a congenial combination has generally produced sufficient top growth of the scion to re-establish a balance between top and root, or scion and stock.

In the case of uncongenial combinations, however, the sequence of development varies from the normal order outlined for the congenial growth, as follows: In the uncongenial union, the scion bud at first gets enough water and mineral nutrients by diffusion through the wound callus from the stock, to care for its meager needs. This might continue to

serve the needs of the inserted bud for sometime, even if true vascular tissue union was poorly established. With its immediate needs supplied the inserted bud produces a shoot and as new growth progresses the xylem union of the stock and scion continues to develop. Even though this xylem union is far from normal it does function for support and for the transport of water and mineral nutrient to the expanding scion shoot. It is not implied that food elaboration is the same in quantity as in a congenial combination, but with water and solutes available the scion of the uncongenial combination is able to produce elaborated food. Scion top growth generally shows no pronounced abnormal development until midseason of the second year or later. This can be explained on the basis that the elaborated food produced by the scion top provides for the growth needs of the scion component. The difficulty manifested from midseason on is the result of the failure of the elaborated food to move down to the stock roots. In congenial combinations, with normal phloem bridges across the unions, the elaborated food would diffuse on down through the united sieve tissues of the scion and stock and nourish the roots. The complete union of stock and scion phloems of the congenial union illustrated in figure 6 indicates how this occurs. But in the case of this particular uncongenial combinations of peach on Marianna plum, there is little or no phloem union between the peach scion and the plum stock. Figure 7 is a section of an uncongenial union which shows, at the right center, the ingrowing rolls of stock and scion phloems. A sizeable space is left between these masses of phloem. The unprotected xylem for some distance back from this opening appears to be filling up with gum. If these xylem tissues had been unprotected by a layer of bark and thus had been continuously exposed to desiccation, one might expect gum to form in such an area, as a protective medium. The extensive development

of scion phloem at the top of this figure indicates that considerable elaborated food was stored near the base of the scion, and just above the union with the uncongenial stock. As new root growth is dependent upon a supply of elaborated food materials, it is probable that the new rootlet growth develop more and more slowly as the food reserves in the stock below the union, and in the larger roots, are used up. Some time during early summer this reduction of food in the stock reaches a critical point where no further new root growth takes place. When this stage is reached, the roots cease to take up water and mineral nutrients and begin to die at the tops. This theory is substantiated by the evidence of Howard and Heppner (10) that death of the roots progresses backward from the tips in the case of uncongenial unions of Prunus. With the reduction in root development, a corresponding reduction in water and mineral nutrient intake probably occurs. This reduction in water intake is probably occurring at a time when the expanding scion top needs its greatest amount of moisture to provide for mid-summer transpiration. Booth's data gives a conception of these peach top demands for water. He records that "for several days the peaches on Marianna stocks wilted during the day and recovered at night, but finally dies." The writers studies (14) indicate that at the time when wilting of the top discloses the extreme manifestation of uncongeniality, death of the roots has generally progressed well up toward the union. On examination of such uncongenial combinations soon after wilting of the peach leaves occurs, it was found, on cutting through the union, that the peach tissues were alive and appeared normal in color and turgidity; while the plum tissues were dead, discolored and shrunken. The appearance was very similar to the condition which might occur, if a root rotting organism had invaded and killed the tissues of a susceptible root stock, up to the region of union with a resistant scion

variety. The fact that no such organism was found associated with these manifestations, indicated that the cause was not of parasitic nature. The further fact that Marianna roots nourished by their own tops, or by the tops of congenial varieties of plums, have never in the writer's studies shown any abnormal symptoms when grown side by side in the same soils, indicated that these peach-plum unions are uncongenial. Whatever the fundamental causes of this uncongeniality, its manifestations were brought about by lack of union between stock and scion phloems which resulted in starvation of the stock roots, and thus the wilting and finally, the death of the entire plant.

## Summary

In horticultural practice man makes use of budding and grafting as a means of propagating varieties which he has selected because of their superior qualities.

Budding and grafting involve the combining of a rootstock of one plant and a scion of a different plant.

Because of its ease of propagation from cuttings, the Marianna plum makes a desirable rootstock.

Because of its resistance to the virus disease, peach rosette, it would be desirable to use Marianna plum stocks as understocks for commercial peach culture, especially in the Southern states.

Attempts to propagate peaches on this plum stock have met with failure.

The peach buds unite readily with the plum stocks and preliminary growth of the peach scions appears satisfactory.

During the second growing season the trees generally manifest symptoms of uncongeniality.

An early symptom frequently overlooked, is the enlargement of the basal portion of the peach scion, just above the union.

Somewhat later in the same season the peach leaves begin to wilt and this symptom is generally followed by death of the entire tree.

Examination of the plum roots discloses that many of them are dead or dying, while above the union the peach woody tissues are still alive.

Pathological examination of the dying or dead roots disclosed the presence of no parasitic organisms.

Marianna plum roots on ungrafted stocks, as well as those budded to other plum varieties and growing in the same soils, remained healthy.

Neither plum varieties budded on Marianna stocks nor Marianna plums budded on peach seedlings roots, developed any abnormal symptoms in the nursery row, or up to a period of ten years after having been transferred to orchard plantings.

None of the various combinations broke at the union, as frequently occurs in apricot budded on plum stocks, or certain pears on quince stocks.

Peach-plum unions cut lengthwise with a small saw disclosed good union of the xylem tissues.

Cross sections of celloidin-infiltrated tissues in the region of the union verified the union of the xylem of stock and scion, but disclosed distortion of xylem strands, and invasion of the woody tissues by gum and distorted phloem.

The major defect, disclosed by microscopic examination of the sections, was the failure of the stock and scion phloems to unite.

Examination of sections of congenial unions disclosed both xylem and phloem continuity of stock and scion.

These anatomical differences indicate that the cause of uncongeniality between peach scions and Marianna plum stocks is the result of failure of the phloems to unite.

This lack of phloem union prevents sieve tissue continuity; therefore elaborated food materials cannot diffuse down to the stock roots, so remain at the base of the scion as an overgrowth of the tissues just above the union.

Shortage of elaborated food materials from the scion results in starvation of the stock tissues and failure of new roots to develop.

Death of the roots from starvation prevents the intake of water and mineral nutrients and this eventually results first, in wilting of the scion leaves, and later, in the death of the entire plant.

## Literature Cited

(1) Argles, G. K. A review of the literature on stock-scion incompatibility in fruit trees with particular reference to pome and stone fruits. Technical Communication No. 9 Imperial Bureau Fruit Production. 5-115. 1937.

(2) Bailey, L. H. The cultivated Native Plums and Cherries. Cornell Univ. Agr. Exp. Sta. Bul. 38: 1-73. 1892.

(3) Booth, N. O. Some investigations in grafting. Proc. Amer. Soc. Hort. Sci. 10:144-149. 1913.

(4) Bradford, F. C. and Sitton, B. J. Defective graft unions in the apple and the pear. Mich. Agr. Exp. Sta. Tech. Bul. 99:1-106. 1929.

(5) Chang, W. T. Studies in incompatibility between stock and scion, with special reference to certain deciduous fruit trees. Jour. Pom. and Hort. Sci. 15:267-325. 1938.

(6) Crafts, A. S. Phloem anatomy in two species of Nicotiana, with notes on the interspecific graft union. Bot. Gaz. 95:592-608. 1934.

(7) Haas, W. R. C. and Halma, F. F. Chemical relationship between scion and stock in citrus. Plant Physiology. 4:113-121. 1929.

(8) Hedrick, U. P. The plums of New York, State of New York Dept. of Agr. Eighteenth Ann. Rept. 3(11): 273-274. 1910.

(9) Heinze, P. H., Parker, M. W. and Borthwick, H. A. Floral initiation in Biloxi Soybean as influenced by grafting. Bot. Gaz. 103:518-530. 1942.

(10) Howard, W. L. and Heppner, M. J. Graft affinity tests with peach on myrobolan and marianna plums. Proc. Amer. Soc. Hort Sci. 25:178-180. 1929.

(11) Knight, T. A. On the proper stock for the Moor's Park Apricot. Transactions Hort. Soc. London. 2:19021. 1818.

(12) Kostoff, D. Acquired immunity in plants. Genetics 14:37-77. 1929.

(13) McClintock, J. A. Peach Rosette, an Infectious Mosaic. Jour. Agr. Res. 24:307-315. 1923.

(14) McClintock, J. A. Uncongeniality, a Limiting factor in the use of disease resistant stock. Proc. Amer. Soc. Hort. Sci. 21:319-320. 1924.

(15) McClintock, J. A. Further evidence of uncongeniality in disease resistant stocks. Proc. Amer. Soc. Hort. Sci. 22:231-232. 1925.

(16) Mendel, K. The anatomy and histology of the bud-union in Citrus. Rehovoth Agr. Exp. Sta. Bul. 19:3-46. 1936.

(17) Proebsting, E. L. Structural weaknesses in interspecific grafts of Pyrus. Bot. Gaz. 82:336-338. 1926.

(18) Proebsting, E. L. and Barger, E. H. The precipitation reaction as a means of determining the congeniality of grafts. Science. N.S. 65:573-574. 1927.

(19) Proebsting, E. L. Further observations on structural defects of the graft union. Bot. Gaz. 86:82-92. 1928.

(20) Smith, Erwin, F. Additional evidence on the communicability of peach yellows and peach rosette. U. S. Dept. of Agr. Div. Veg. Path. Bul. 1 45-54. 1891.

(21) Waugh, F. A. Hybrid Plums. Ver. Agr. Exp. Sta. Bul. 67:1-30. 1898.

Figure 1

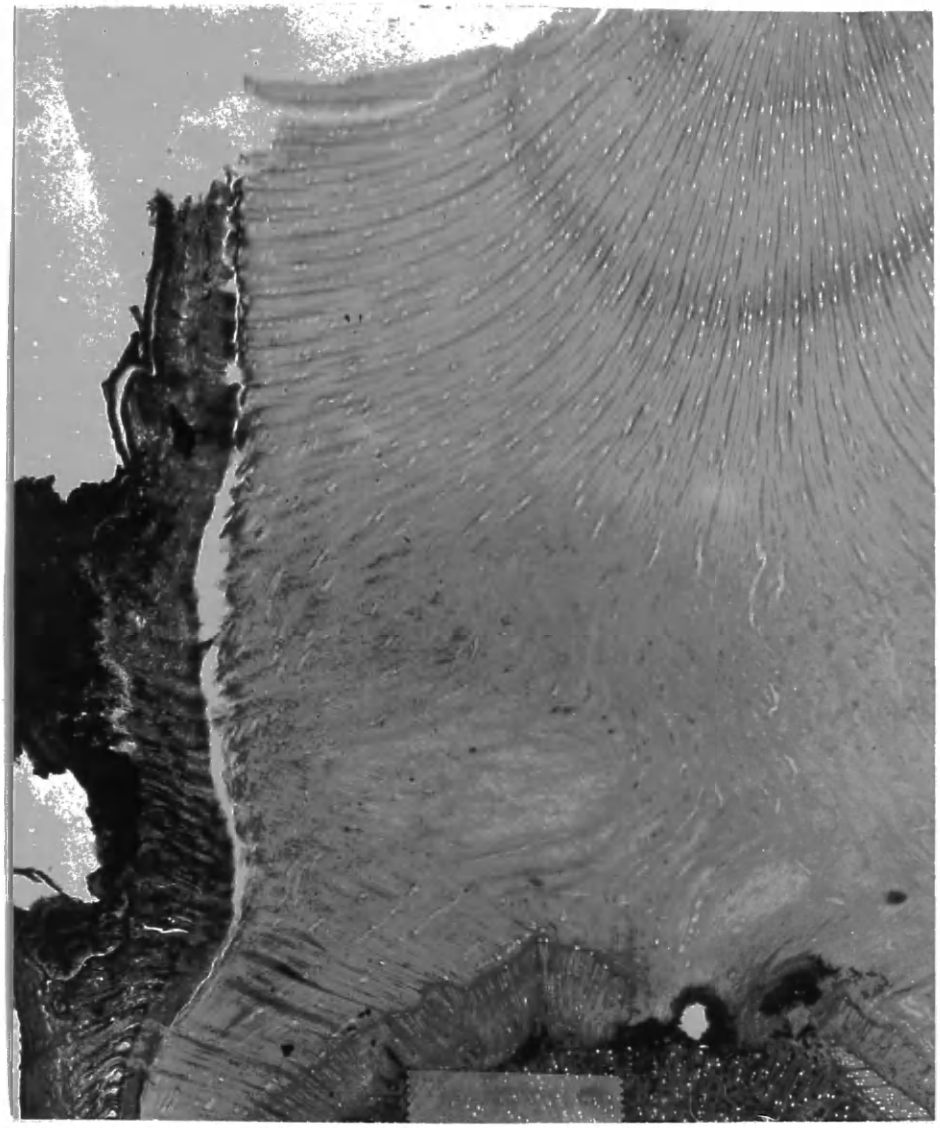


Figure 1 is a section of a congenial union of Methley plum scion above on Marianna plum stock below. The continuity of xylem and phloem from stock to scion indicates structural strength, and free movement of water, mineral nutrients and elaborated food materials. Note the uniformity in diameter above and below the union.

Figure 2

Figure 2 is a section of a congenial union of Methley plum scion above on Marianna plum stock below. The continuity of xylem and phloem from the stock to the scion is complete on both sides of the section. Note also the continuity of ray tissues from the central pith region across the entire xylem and phloem assuring free lateral transport as well as ample movement up through the xylem and down through the phloem.

Figure 3

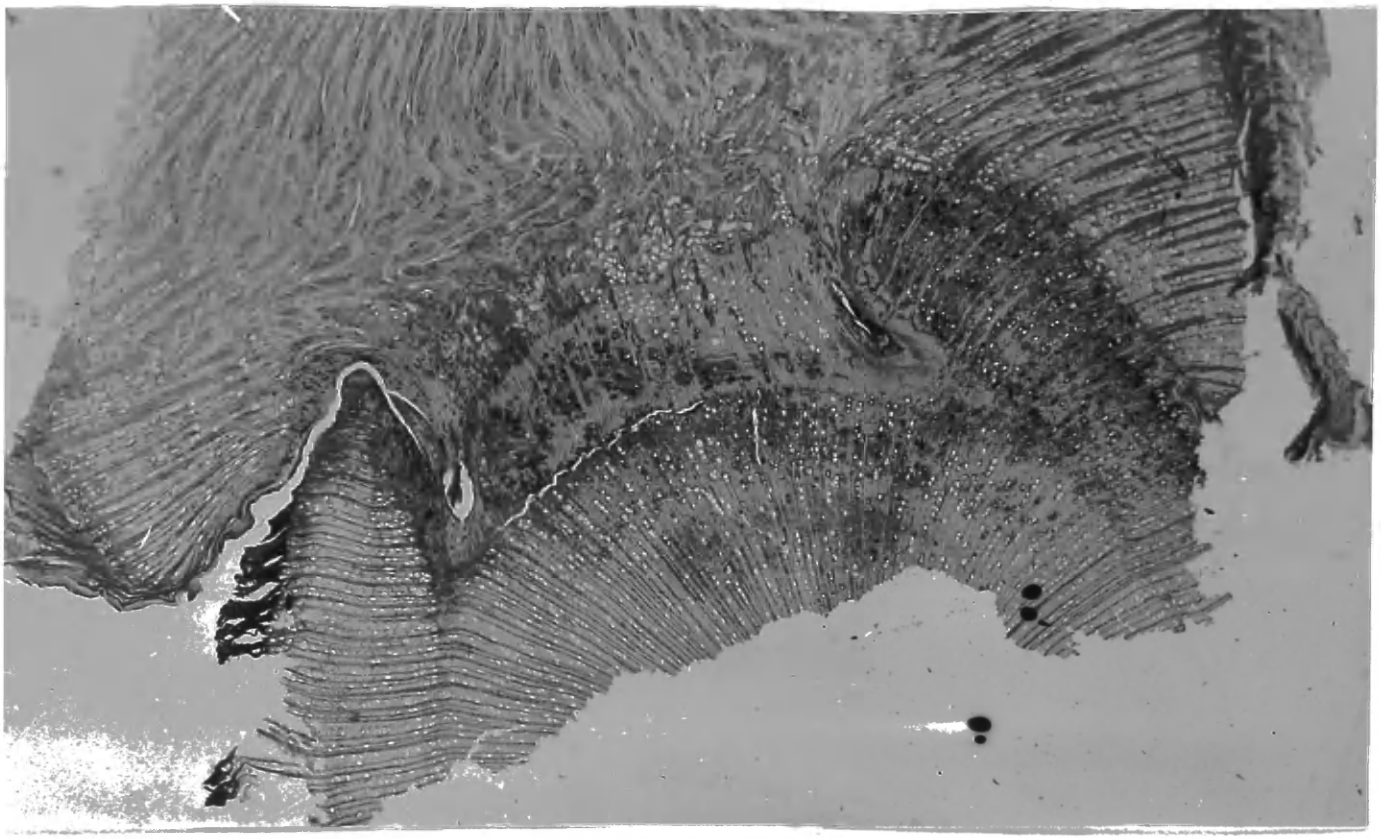


Figure 3 is a section of an uncongenial union of peach scion above on Marianna plum stock below. The xylem strands show sufficient continuity from stock to scion to provide for movement of water and mineral nutrients, and assure reasonable strength. The presence of gum and the invasion of the xylem region by the inward growing phloem prevents ray continuity. Failure of stock and scion phloems to unite, and overgrowth of the scion tissues just above the union indicates lack of continuity of the phloems and inability of elaborated food materials to be translocated from the scion to the stock.

Figure 4

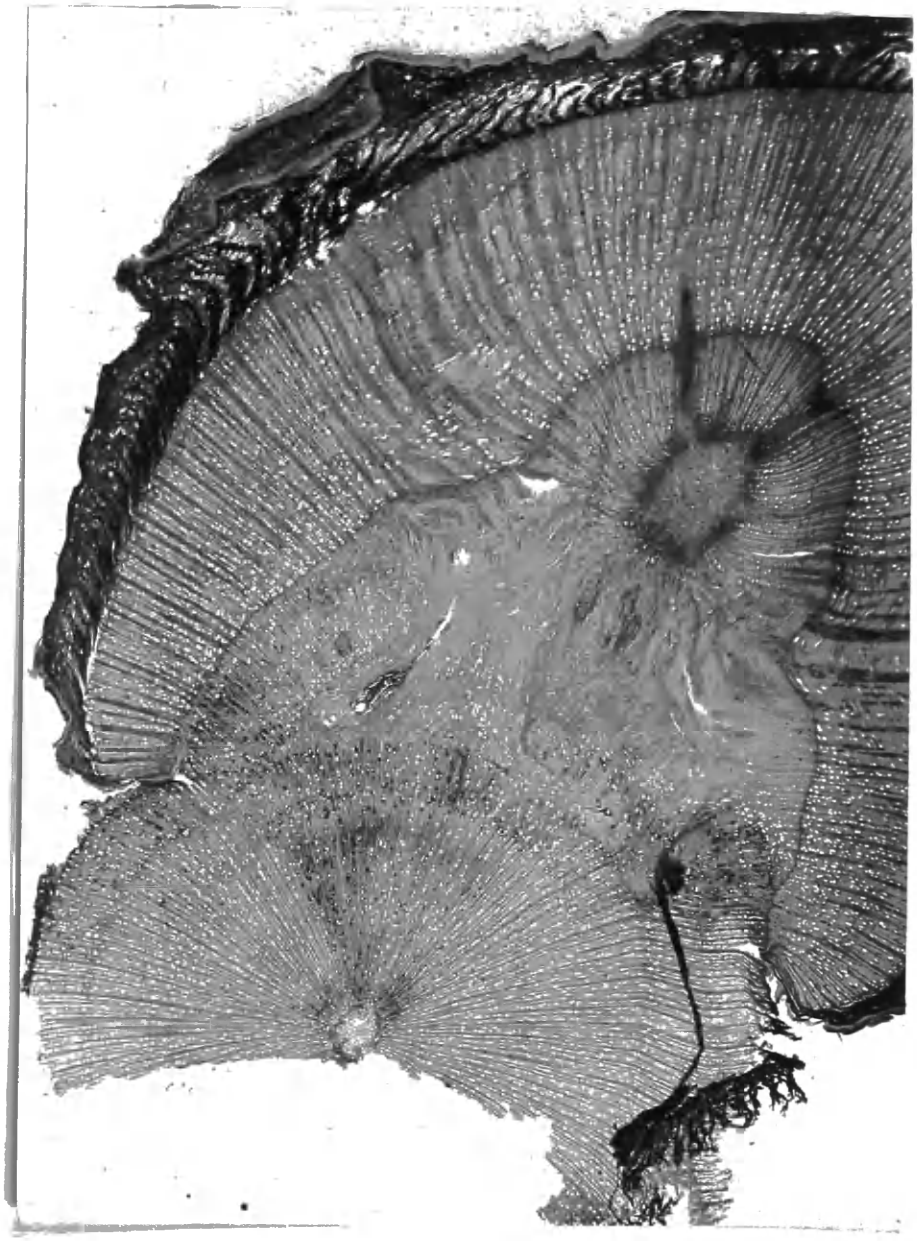


Figure 4 is a section of an uncongenial union of peach scion above on at Marianna plum stock below. While the union of stock and scion xylems is fairly continuous, the stock and scion phloems show little evidence of uniting and appear to be invading regions normally occupied by xylem. Ray continuity is also curtailed. Enlargement of the scion tissues above indicates that elaborated food materials are not diffusing from the scion to the stock.

Figure 5

Figure 5 is a section of an uncongenial union of peach scion above on Marianna plum stock below. Xylem union, although far from normal, is sufficiently complete for strength and for water and mineral nutrient transport. The inward curling of the stock phloem at the lower left and the wide area of exposed xylem and the relatively thick scion phloem above indicate entire failure of scion and stock phloems to unite. Elaborated food materials would have serious difficulty in moving from scion to stock in such a union.

Figure 6

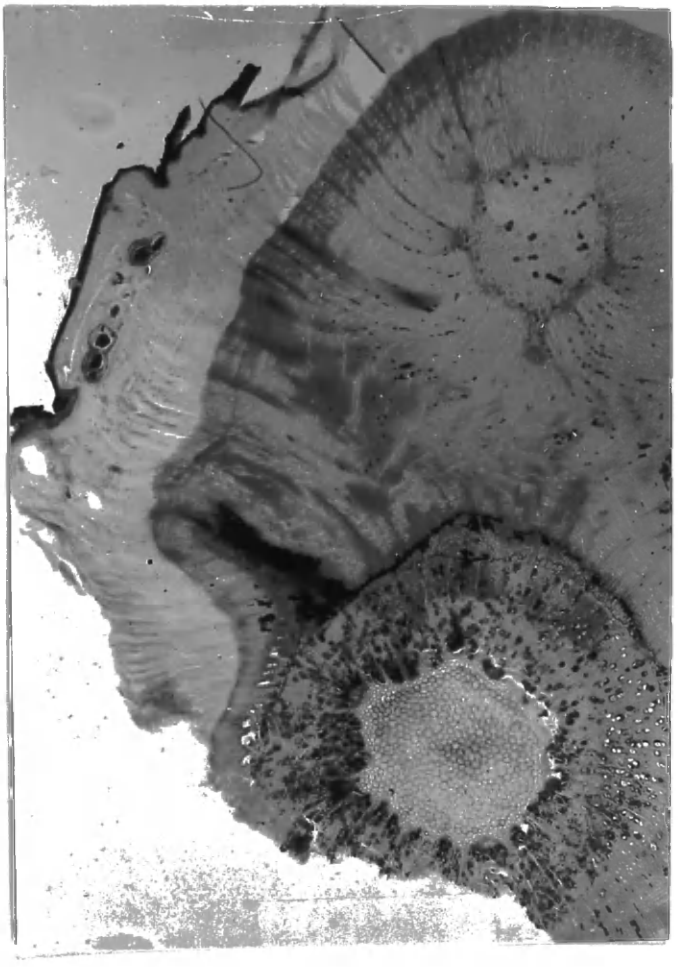


Figure 6 is a section of a congenial union of plum scion above on Marianna plum stock below. Continuity of both xylem and phloem from the stock to the scion assures strength of the union and free movement of water and mineral nutrients upward and elaborated food materials downward. Such unions never developed abnormalities of either the scion or stock.

Figure 7

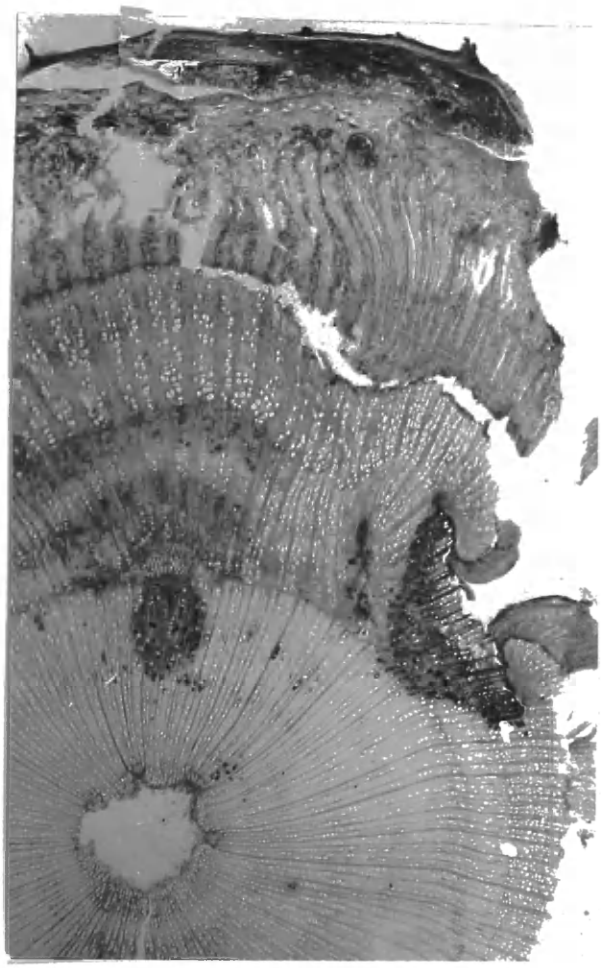


Figure 7 is a section of an uncongenial union of peach scion above on Marianna plum stock below. At the right center the two inrolling masses of stock and scion phloem appear to have avoided contact. The sizeable space left between the stock and scion phloems leaves exposed xylem which appears to be providing its own protection through the formation of gum which discolors the xylem in this region. The extensive development of phloem at the top of this figure indicates the piling up of elaborated food materials above the graft union.