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an illustrated review of

Apple virus diseases



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APPLE VIRUS DISEASES AN ILLUSTRATED REVIEW¹

R. C. MCCRUM, J. G. BARRAT, M. T. HILBORN, AND A. E. RICH

INTRODUCTION

Although comparatively little is known about apple viruses, they have received considerable attention in recent years. The literature is widely scattered in many journals, and often it is very confusing. The writers have attempted to review the available literature on the subject and to organize it in an orderly fashion. The name, symptomatology, host range, and geographic distribution are given for each virus disease. Where it was possible illustrations of each disorder have also been included.

No attempt has been made to designate specific names of the viruses in this publication. Rudimentary information is available on the etiology of only a few of the apple viruses. Some virus entities found in apple are transmissible to hosts other than apple. In such cases different names have been given to the causal viruses. To give separate binomial names to viruses of which little is known at this time would only lead to increased confusion and needless taxonomic classification.

An effort was made by the authors to see the original publications. Where the original publications were not seen the literature citation is followed by a citation to an abstracting journal. The writers are deeply grateful to the many persons who furnished illustrations and suggestions for this bulletin.

GENERAL

Apple virus research has recently attained an active status. It received this impetus only when it was realized that apples, like other crop plants, can and do suffer economic losses due to viruses.

All apple viruses are transmissible by budding and grafting operations. Different varieties of apples, when inoculated with identical virus material, develop diverse disease reactions; and a specific apple variety may respond differently to the same virus inoculum depending upon environmental conditions. As mentioned previously, viruses found in apples have also been transmitted to other hosts. In such hosts they

¹ Some of this information is based on a dissertation presented to the Graduate School, University of New Hampshire, by J. G. Barrat in partial fulfillment of the requirements of the Ph.D. degree.

frequently cause varying symptoms unlike those produced in apple, and the reverse is also true. Realizing these facts it should be evident that many of the apple diseases now classified as separate entities may in the future turn out to be only manifestations of a common causal agent. In a similar manner, they could be produced by the combined reaction of two or more different viruses in one host.

It becomes apparent as information accumulates that virus infections result in considerable losses in revenue to the apple grower. Reports reveal that trees infected with apple mosaic have suffered reductions in yield and in some cases have yielded 55 per cent less than trees free of the virus (76, 84, 114, 151, 152).² Observations in Nova Scotia (2), New Zealand (7), Holland (186) and the United States (10) indicate that several apple virus diseases are increasing in importance and spread. Some viruses exist in a latent form in apples and produce no visible symptoms on the host that carries them. In this form they have been spread to an unknown extent only to be observed when sensitive varieties succumb to these hidden viruses in the course of budding and grafting operations. Whether these symptomless carriers actually sustain reduced yields and vigor from such masked viruses needs to be determined.

It has been found in England (78) that many of the apple viruses may be spread by propagation through the use of infected scions and rootstocks. Eventually all commercial varieties will have to go through a screening test to select bud wood free of these latent viruses. Certified virus-free propagating material is one of the major objectives in apple virus research. Such a program has recently been initiated and should be of great benefit to the industry. Propagating material, however, will continue to need periodic inspection and indexing to maintain a source of disease-free material for nursery men and those interested in increasing orchard plantings. An interesting fact in this regard is mentioned by Posnette and Cropley (149) which should be of concern to all who work with apples, namely, that an apple clone can no longer be considered uniform when it is once infected with a virus.

Apple viruses that are found to be transmitted only by budding and grafting can be easily controlled by the use of virus-free stocks. Some apple viruses will undoubtedly be found to be insect transmitted. It is expected that such viruses will raise new problems in insect control. In some cases tolerant or resistant apple varieties will serve as the only means of control against viruses that are found to be rapidly disseminated. Properly timed insecticides would offer another possible means of control for certain insect vectored viruses. Surely in both present and

² Numbers in parentheses refer to literature cited, page 54.

future searches for new apple varieties, resistance to and freedom from apple viruses must be considered before any distribution of stock is considered.

APPLE MOSAIC

Apple mosaic is probably the most familiar virus disease of apples. It was described early in the nineteenth century. Bradford and Joley (39), in their review of the history of this disease, point out that *transmission of mosaic in apples* was accomplished in France by two workers in the years of 1825 and 1836. Stewart (175) observed a variegated foliage on apple trees on Long Island, New York in 1896 and at several other locations up to 1910. Morse (135) described a variegation of apple leaves in Maine orchards in 1916 and published photographs clearly depicting the mottled leaves (see cover). Blodgett (27) in 1923 found that mosaic could be transmitted by means of grafts. Since the official recognition of viruses as causal agents of disease did not occur until 1896, following Beijerinck's classic work on tobacco mosaic, Blodgett's report may be the first record of a transmissible virus disease of apples. It was often called infectious variegation.

Symptoms

Visibly infected trees often bear leaves that contain cream-colored areas. Sometimes these areas coalesce and produce large sections of non-green tissue (figure 1). Occasionally a leaf mosaic characterized by light and dark green areas may result instead of the cream-colored symptoms.



FIGURE 1. Individual apple leaves showing variations in "chlorotic" effect. Photo, W. J. Morse, Maine Agr. Expt. Sta. 1916.

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All leaves on a tree do not show symptoms, and different types of mosaic leaf patterns may be interspersed between normal leaves on single shoots. Leaves that exhibit severe symptoms early in the season may later develop large necrotic areas and prematurely drop from the tree. In this way tree vigor and potential yield are reduced. Loss of leaves also exposes the fruits to sunburn.

Temperature plays an important role in symptom development; temperatures above 80° F. tend to mask the mosaic pattern on leaves. Consequently leaves that develop during periods of high temperature do not appear to be diseased (68).

Graft and bud inoculation experiments demonstrate the incubation period (interval of time from inoculation to development of symptoms) to be fairly short, the minimum being 34 days (14, 105, 177, 200). Apparently the vigor of the tree is involved. When spring budded seedlings are cut back to stimulate new growth, mosaic will develop the same year as inoculated; otherwise, symptom expression will not take place until the following growing season. High temperatures during the growing season tend to mask symptoms and may play an important role in this delay of symptom development.

Mosaic increases the sensitivity of apple leaves to sprays applied to foliage for scab control (135). It was found that mosaic leaves suffered severe burn injury from the sprays as compared to normal leaves.

In general, fruit on mosaic infected trees develop no specific diagnostic symptoms. Posnette & Cropley (151), however, report that severely infected trees of the red fruited variety Lord Lambourne may develop conspicuous cream-colored patches on the fruit as well as reddish-brown streaks on the bark of young shoots. Christow (47), in a comprehensive early report on apple mosaic, found phloem necrosis in root tips as well as in the tap root and stems of trees inoculated with infected material.

Reduction in tree growth and yields is sustained by trees infected with apple mosaic. Golden Delicious nursery trees experimentally infected with mosaic are smaller and produce less foliage than uninoculated trees (56). Young orchard trees also suffer a reduction in girth development when infected with mosaic (7, 114). Many reports show that mosaic depresses yields, varying from slight reductions to as high as 55 per cent (76, 82, 84, 114, 147, 151, 152).

Etiology

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More is known about the virus factor responsible for mosaic than about other apple virus disorders. Natural spread of mosaic occurs in the field (7, 25). Blodgett (28) observed that the increase in spread of mosaic in a certain orchard seemed to follow the path of pruning operations and suggested that it might have occurred in this manner. In most instances attempts to transmit apple mosaic by mechanical means have failed (68, 84, 94, 105). However an atypical strain of apple mosaic reported by Yarwood (199) appears to be readily sap transmitted to tobacco and other herbaceous hosts. Fulton (65) found that clear infective preparations of apple mosaic could be obtained by grinding apple leaf tissue in calcium phosphate paste in 0.03 M phosphate buffer and centrifuging for one minute or less. Preliminary tests to transmit the virus with insects such as *Myzus persicae*, *Macrosiphum eriosoma*, *Aphis pomi*, and *Anaraphis roseus* have yielded negative results (28, 73, 84, 87) except for a brief Russian report (145) which records the occurrence of apple mosaic in the Latvian Republic "transmitted by *Aphis pomi* and *Psylla mali.*"

There is an interesting comment in regard to insect transmission furnished by Luckwill (12) who reported that occasionally mosaic appeared among seedlings in the nursery row. Although the seedlings in question originated from seed of mosaic-infected Jonathan trees, mosaic symptoms did not occur early in the life of the seedlings. A possible explanation was offered to suggest that infection occurred through the action of an occasional insect vector. However, such an implication was considered unsatisfactory. Posnette (151) considers that field spread of mosaic in England occurs only through root contact. The virus has been found to pass through natural root grafts in young nursery stock in New Zealand (87).

In many cases the virus has not been found to be fully systemic in affected trees (74, 75, 89, 109, 151). It has been shown, however, that shield buds taken from leaves showing no mosaic symptoms have transmitted the virus (45, 104).

The virus may occur in a latent form in some stocks and be entirely overlooked due to little or no symptom development (39, 148). Strains of mosaic virus have been reported. Mutual antagonism exists between strains where mild strains seem to offer cross protection against the more severe strains (7, 12, 74, 148, 151). This type of reaction suggests that immunization with weak strains might offer a practical control in protecting trees from damage due to the more severe strains should the virus be found to be insect-transmitted. Posnette (147), however, found that mild strains of the virus can cause serious reductions in yields.

Attempts to associate virus particles with apple mosaic infections in apple and herbaceous plants by means of electron microscopy were attempted by Yarwood (200). However, no consistent particles were detected nor were any found using the conventional microscope.

Heat therapy of budwood to inactivate the virus has for the most

part yielded negative results (105, 177). Young plants held at 37° C. for extended periods of time seem to offer the most promising form of therapy (75, 147, 151). Hunter *et al.* (88) found that mosaic-infected buds inserted into young seedlings will withstand such heat treatments, begining one-half hour after budding. Correct temperature inactivation of the virus, according to Kegler (94), can be accurately determined only by the hot water method, as differences of 10-25° C. can exist between the shoot and the surrounding air when the hot air method is used.

Chemical treatment of infected material with di-nitro-ortho-cresol, elgetol, hydroquinone, sodium salicylate and urea failed to inactivate the virus (105).

Host Range

Many commercial varieties of apple show visible symptoms when infected with apple mosaic virus. Atkinson (12) cites at least 39 varieties and 3 rootstocks observed with mosaic symptoms. Apple seedlings in general are quite sensitive to mosaic. The absence of mosaic in apple varieties growing in warm climates could result from the masking effect due to high temperatures encountered during the growing season. Kegler (94) found considerable variation to exist among *Malus* sp. in regard to susceptibility.

Other plants of related genera which react to the virus factor that causes mosaic in apple include plum, peach, quince, pear, loquat, *Cotoneaster*, *Photinia*, and *Sorbus* sp.

Yarwood (200) obtained mechanical transmission of an atypical mosaic isolate from apple to tobacco, *Nicotiana glutinosa*, tomato, cucumber, globe amaranth, sunflower, broad bean, and other herbaceous hosts. Although mechanical transmission from apple to apple was not obtained, transmission from tobacco to apple by means of dodder produced symptoms on apple typical of the original natural infection. Other apple mosaic isolates do not produce this host index reaction.

Yarwood suggested that this mosaic isolate might be a strain of tobacco streak virus. Fulton (64) however could not obtain cross protection between tobacco streak virus and Yarwood's isolate. Attempts to produce infection on apple seedlings by transmitting tobacco streak through *Cuscuta campestris* Yunck. were also unsuccessful. Gilmer (68) has given this particular isolate the name of Tulare Apple Mosaic Virus and sets it apart from other known isolates of apple mosaic virus.

Apple Mosaic and Plum Line Pattern Complex

References in the literature suggesting the similarity of plum line pattern disease to that of apple mosaic are numerous (1, 44, 108, 115, 141, 182, 197). A coidentity of the two diseases as far as causal agent

is concerned is indicated by reciprocal inoculations of infected material between the two hosts. Apple mosaic has been transmitted to stone fruits in which it produced plum line pattern symptoms, and the reverse is true where plum line pattern was transmitted to apple causing mosaic symptoms in apple (56, 67, 74, 76, 95, 146). Posnette and Ellenberger (154) call attention to the fact that Christoff (49) was the first to demonstrate that "plum mosaic" could be transmitted to apple. Plum line pattern, like apple mosaic, is masked by high temperatures. An extensive list of host plants of plum line pattern virus is given by Baumann (22).

Peach Ring Spot and Apple Mottle

Cochran (53) reported the following interesting correlation between peach and apple. A mottle was produced on apple foliage when budded with peach ring spot-infected buds. Buds from these same apple seedlings when budded back to peach gave ring spot symptoms on peach. This virus entity, however, does not appear to be synonymous with apple mosaic as buds from four apple mosaic sources failed to give ring spot symptoms when budded to peach.

Geographical Distribution

Apple mosaic has been reported from many apple growing areas of the world. These include Australia (54, 79), Belgium (165), Brazil (89), British Columbia (107), Bulgaria (48, 97), England (189), Finland (90), France (165), Germany (114), Holland (183), India (26, 18), Italy (51), Nova Scotia (82), New Zealand (14), Norway (158), Sweden (103), Switzerland (170), South Africa (104), United States (142), and Yugoslavia (176). From the above list it can be seen that mosaic is probably present wherever apples are grown as a commercial crop. Due to the apparent coidentity with plum line pattern it is present in many stone fruit areas as well.

FLAT LIMB

Flat limb is not a newly discovered abnormality of apples. It has been noticed for a considerable period of time. Hockey (84), in his review of the disease, cites its presence in Nova Scotia in 1887 and in the United States in 1907 (52). McAlpine (118) described symptoms similar to flat limb and published two excellent illustrations of Gravenstein affected trees in Australia in 1912 (figure 2). Thomas (178) considered flat limb to be a virus disorder and placed it in the rough bark class due to its effect when transmitted to *Pyracantha gibbsi yunnanensis*. The syndrome complex of this disease is similar in many respects to that which occurs with stem pitting.



FIGURE 2. Copy print from McAlpine 1912, showing gnarling and twisting on Gravenstein apple limbs. Photo, Biology Branch, Department of Agriculture, Victoria.

Symptoms

Infected trees show an abnormal flattening of the branches which becomes more pronounced as the branches increase in size (figure 3). Not only do limbs have this flattened look but they may develop large

longitudinal grooves and pockets due to irregularities in growth. The advanced symptoms frequently produce a twisting of the limbs; consequently, in Australia the disease has been given the name of "twisting" (41).



FIGURE 3. Flat limb symptoms on young branches of the Gravenstein apple. Photo, Courtesy J. F. Hockey, Research Station, Canada Department of Agriculture, Kentville, N. S.

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Cross sections of stems through affected areas reveal a lack of wood development in the flat portions, although the bark is continuous over these flat areas. Apparently the cambial activity is arrested and wood initials do not develop. Pitting of the wood is apparent in such areas. As the limbs continue to increase in size the affected areas frequently succumb to secondary decays and large cankered areas may develop (86). No distinct fruit or leaf symptoms have been associated with flat limb. However, a decrease in foliage and fruit production occurs on affected trees (35).

Symptom development in this disease is very slow and varied, although characteristic irregularities usually appear 2 to 3 years after inoculation. Hockey (85) has found that it takes from 4 to 8 years for indisputable visible symptoms to appear in Nova Scotia transmission tests. The incubation period in Norway varies from 6 months to 5 years (98). Several investigators have noticed that the disease is more severe on sensitive varieties when they are grafted above ground to stem pieces than when they are grafted to root pieces of the same stock (41, 84, 85, 118). Scion rooting of the susceptible variety by deep planting of the stock on nurse roots has been suggested to minimize flat limb damage (41). Such treatment has not prevented Gravensteins from developing flat limb (8). Atkinson (13) reported that scion rooted Gravensteins still develop gnarling. In Nova Scotia (85) budded Gravenstein trees do not develop as much flat limb as young stem-grafted trees. This is also true when the susceptible Gravenstein variety has been propagated on Spy rootstocks (118, 85, 41).

Etiology

The virus responsible for flat limb can be carried in a latent form in apple (99). It has been shown to pass from infected apple material through intermediate varieties, in which it produces no symptoms, into healthy stocks where flat limb results (98). The fact that the virus can thus exist in a symptomless condition in some stocks would help to explain why healthy scions become infected on certain clonal rootstocks but not on others. In such a situation the virus could be carried in a latent form in varieties used as rootstocks and its presence demonstrated only when combined with sensitive varieties like Gravenstein.

Host Range

The variety Gravenstein and its bud sports are particularly sensitive to flat limb. It has also been noticed in the varieties Wagener, Abbodanza, Rambour Franco, Schneider, Tobiasler, Ontario, Golden Pearmain, James Grieve, Fillippa, Signe Tillisch, and Lord Lambourne. Symptoms similar to flat limb also have been observed on pear and quince (29, 30). *Pyracantha* sp. develops symptoms as noted earlier (178).

Geographical Distribution

Flat limb of apple has been reported from Australia (41, 42), British Columbia (60), Denmark (100), England (110, 189), Italy (35), New Zealand (125), Norway (158), Nova Scotia (82), Sweden (103), Switzerland (31), United Arab Republic (139), the United States (19, 52, 178), and Yugoslavia (92).

RUBBERY WOOD

Wallace *et al.* (189) reported this peculiar rubbery condition on the variety Lord Lambourne in England in 1944 and suggested its apparent transmission by grafts. Later observations made by others again drew attention to its possible virus nature (24, 57, 59). Transmission was demonstrated in 1950 by Luckwill and Crowdy (113), and Prentice (157).

Earlier observations in the literature mention the willowy type of growth occasionally obtained when scion varieties were top-worked on certain under-stocks and suggest that the virus causing rubbery wood has been present in apples for many years (117, 118). At least 18 apple varieties that were widespread before the dispersion of the sensitive variety Lord Lambourne have been found to carry this virus in a latent condition (150). Malling clonal rootstocks planted in 1920 have also been found to carry rubbery wood virus (150), and such plantings predate the introduction of Lord Lambourne as a new seedling variety in 1922 (16). One wonders what would have happened if this variety had been propagated on infected stocks during its early trials. It probably would have received an unfavorable rating and thus been discarded. Certainly many promising earlier varieties must have met this fate due to latent apple viruses.

Symptoms

The most characteristic symptom of this disease is the unusual flexibility imparted to apple stems and branches (figure 4). In young nursery trees the weight of the branches alone is sufficient to cause the young whips to assume a horizontal position. In mature trees the weight of the fruit accentuates this bending and the tree assumes a willowy habit of growth. Wood from severely affected rubbery branches has a cheese-like texture. Microscopic examinations of this wood reveal a lack of lignification in the xylem elements (23, 168). Xylem vessels have irregular walls, and some are found in a collapsed condition similar to gelatinous

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fibers found in tension wood. This lack of lignification can be seen by eye when cross sections of infected stems are treated with a phloroglucinol stain (0.5% phloroglucinol in conc. HCl acid) (23). This is a negative stain reaction where the unlignified tissues remain colorless while normal wood elements stain red.



FIGURE 4. Rubbery wood symptoms in Lord Lambourne. Photo, Canada Agriculture, Summerland, B. C.

Infected trees tend to be smaller in size, and consequently yields are reduced. Young trees infected with rubbery wood may fruit at an early age (figure 5). The figure shows Lord Lambourne trees bearing fruit while still in the nursery row.

No diagnostic fruit or leaf symptoms have been associated with this disease. Detection therefore is dependent upon the lack of rigidity in branches and tree growth. Since this is a qualitative measurement and symptoms do not occur on many varieties, positive identification is possible only with the use of the sensitive Lord Lambourne variety.

An efficient method of indexing apple stocks for the presence of rubbery wood virus has been described by Posnette and Cropley (150). This method has also been used for other viruses. Essentially it consists of inserting two buds, one above the other, on young clonal rootstocks. The top bud serves as the indicator variety, in this case Lord Lambourne, and the lower bud is taken from the material to be indexed. The clonal



FIGURE 5. Lord Lambourne on M.II rootstocks. Left, normal; right, infected with rubbery wood virus. Note precocious fruiting. Photo, East Malling Research Station.

rootstock is cut back and only the indicator bud is allowed to grow. Care should be used in the selection of virus-free rootstock material. Malling 11, previously indexed for rubbery wood, was used for the rootstock by Posnette and Cropley. Readings for the transmission of rubbery wood to the Lord Lambourne indicator should extend over a period of at least two years as considerable variation exists in disease development (40, 140). Posnette and Cropley (150) found that a considerable degree of variation existed in indexing for rubbery wood even when a common clonal rootstock was used. This led them to suggest that strains of the virus may exist in natural infections.

Degrees of rubberiness range from slight, where known qualitative hand bending techniques are necessary, to severe cases where the young shoots are unable to remain upright.

Etiology

As mentioned above, strains of the virus apparently exist. Diversity in field expression of the disease is no doubt attributed to this virus variation, although environmental conditions can also influence this aspect (16).

No insect transmission has been reported. Natural spread of the virus, if it occurs, is very slow and probably takes place only through root grafts. Brase and Gilmer (40) indexed clones of Malling rootstocks planted in 1928 at Geneva, New York, and found that although 6 per cent of the Malling 1 clones contained rubbery wood virus it had not spread to other clones over a considerable period of time.

The virus occurs in a latent form in many rootstock and scion varieties (113, 155, 168, 196). In this form it has undoubtedly been spread throughout the world. Posnette and Cropley (150) found the virus to be latent in 18 of 43 different apple varieties when they were indexed on Lord Lambourne. Although rubbery wood virus was found in several of the Malling rootstock clones, other clones of the Merton series indexed negative for the virus.

Preliminary experiments indicate that rubbery wood virus is quite heat stable. It was not inactivated in young Golden Delicious trees kept at a temperature of 99° plus/minus 2° F. for a period of 40 days although the trees survived such treatment (16).

Host Range

Lord Lambourne is extremely sensitive to rubbery wood virus and is now used as the standard indicator for this virus. Golden Delicious is also quite sensitive to this virus although field-infected trees do not always develop symptoms. Other varieties reported to show rubbery wood symptoms include Dartmouth Crab, James Grieve, Miller's seedling, Sturmer Pippin, and Kingston Black (108).

Geographical Distribution

Rubbery wood virus disease of apple has been reported from many apple growing areas in the world including Australia (16), British Columbia (196), Denmark (70), England (190), Holland (185), Italy (51), Norway (158), Sweden (103), Switzerland (4, 29, 38), and several locations in the United States (40, 156, 161). Because the inciting virus is carried in a latent form in many of the old apple varieties, it is expected that its detection by indexing will reveal further distribution of this virus.

STEM PITTING

Stem pitting is a virus disorder primarily affecting the developing wood and bark tissues of certain apple stocks. It is now a major problem in the production of winter-hardy apple trees.

Attention was drawn to this disease due to incompatibilities which arose when certain scion varieties were top-worked to winter-hardy apple stocks. Many plantings of hardy stock trees were made in the early 1940's in the United States using the variety Virginia Crab as a bodyforming stock. This variety was selected because of its previous outstanding performance in midwestern plantings. Although incompatibility of certain scion clones with this variety had been reported earlier (102, 116, 119), they were considered at the time to be of a horticultural nature as were other incompatibilities among apple varieties. It remained for Smith (172), and others (126, 129, 180), to suggest that this disorder was of a virus nature. Guengerich and Millikan (71) in 1956 obtained transmission of the stem pitting virus factor with buds and bark patches thus proving its virus nature.

Symptoms

Susceptible varieties such as Virginia Crab and other crab apple types when top-worked with varieties containing the pitting factor appear to grow normally at first and show no obvious external symptoms. However, if the bark on these susceptible trees is peeled back, wood pitting symptoms can be seen on the developing wood. Deep longitudinal pits or furrows become evident on the wood surface into which fit corresponding "pegs" or wedges of the peeled bark. Stem cross sections show abnormal radially ribbed growth rings. Virginia Crab is now used as an indicator variety for stem pitting. Symptom development is rapid and pitting appears on one-year old wood. Bark patches of healthy Virginia Crab grafted in early spring to trees containing the virus will develop pitting in the wood laid down by the Virginia Crab patches during the current growing season (121) (figure 6).



FIGURE 6. Wood pitting which developed under bark patches of Virginia Crab. Left, Virginia Crab on Virginia Crab; right, Virginia Crab on Cortland. Photo, Maine Agr. Expt. Sta.

Histological sections of infected wood show multinucleate cambial initials and distorted nuclei. Certain areas of cambial derivatives become abnormal giving rise to disoriented xylem elements and phloem rays. Large parenchyma "islands" are found in the xylem along with wide xylem rays. Degenerate sieve tubes and the absence of sieve areas and companion cells are also characteristic of infected phloem tissue (81).

Once trees are infected they continue to decline. During this stage they tend to produce heavy crops of fruit. Gross morphological symptoms can be seen on older trees in the form of ridged and twisted trunks. Frequently diseased trees develop an over-growth or "knobby knee" condition where the interstock and top-worked varieties meet. Such unions are weak, and branch failures occur with the heavy fruit load usually found on infected trees. Generally pitting is not found on the scion variety top-worked on these trees. However, some pitting has been found in Red Delicious, Spartan, Winesap, and McIntosh varieties growing on pitted Virginia Crab at the union of stock and scion (19, 196).



FIGURE 7. Stem pitting symptoms on Virginia Crab apple trunk top-worked to Baldwin. Note only three seedling roots remain to support the tree. Photo, Maine Agr. Exp. Sta.

The disorganized wood in the intermediate framework portion of the trees has a detrimental effect on the seedling rootstock due to the im-

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paired downward translocation to the roots (figure 7). Consequently these trees have a very poor root system. Trees which have been infected for several years tend to lean as the tops continue to fruit while the root systems decline.

No diagnostic leaf symptoms have been associated with apple varieties top-worked on diseased trees although several rosaceous woody plants develop leaf symptoms when inoculated with infected material. Seedlings of *Amelanchier* spp. (figure 8), *Malus floribunda, Crataegus* crusgalli, Crataegus mollis and Prunus tomentosa all show marked foliage symptoms in the year following August budding (130, 132, 196).

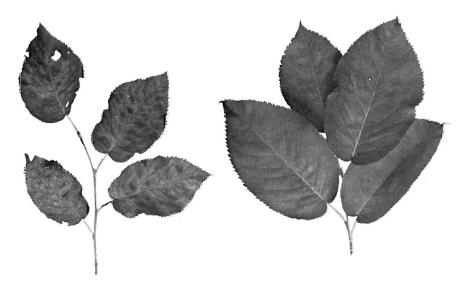


FIGURE 8. Amelanchier spp. foliage. Left, leaves from bush inoculated with stem pitting source; right, leaves from uninoculated control. Photo, Millikan and Guengerich, Phytopath. 46:130.

When fruiting branches occur on the pitted framework of varieties of Robin Crab, Virginia Crab, and Sugar Crab, the fruit formed is often prominently ribbed and dwarfed. In some cases Red Delicious develops a patchy fruit condition, and ripening is considerably retarded on scions top-worked to Virginia Crab (127). Maney (116) reported that Stayman fruit was injured in size, color and quality when growing on Virginia Crab.

Occasionally trees of Virginia Crab top-worked with standard commercial varieties are found that do not show pitting. In most cases these trees are found to be strongly scion-rooted on Virginia Crab roots. It has been suggested that scion-rooting might have prevented the development of pitting (120, 172). Scion-rooting of non-pitted Virginia Crab trees in some cases, however, appears to be a secondary effect manifested by the vigor of the Virginia Crab when combined with scion varieties that are free of the stem pitting virus factor (123).

Etiology

The virus entity responsible for stem pitting is carried in a latent form in commercial varieties (9, 134). Although it appears to be widespread, selections of Golden Delicious and Baldwin have been found that do not carry the virus (72, 123).

Mink and Shay (134) report an interesting occurrence of pitting symptoms on seedling trees that had never been united with other varieties. In a visual survey of nearly 900 seedlings 6 to 8 years old the range of pitting among different seedling crosses varied from 16 to 90 per cent. There appeared to be no difference in incidence or severity among crosses involving *Malus atrosanguinea* (Spaeth.) Schneid., *M. floribunda* Sieb., *M. prunifolia* (Willd) Barkh., and *M. pumila* Mill. Four out of 26 seedling progeny of a cross between Starking and *M. baccata jackii* Rehd. exhibited pitting symptoms. Pitting was most severe on triploid seedlings which resulted from crosses of diploid selections with tetraploid Mc-Intosh. Although the seedlings were not indexed for the presence of the virus, such information does indicate possible seed transmission or spread by other natural means.

Host Range

Stem pitting was first noticed on Virginia Crab interstocks but has since been found on many other varieties. Crab apple types seem to be very susceptible. Florence Crab, Red River Crab, Beauty Crab, Robin Crab, Sugar Crab, Columbia Crab, and Hyslop Crab develop severe stem pitting (19, 93). McCrum and Hilborn (122) reported that 39 of 53 different hardy stock varieties were found to have stem pitting symptoms. Several hardy stock varieties exist that are tolerant of the stem pitting virus (122, 131). It has been found in Red Delicious, Golden Delicious, and Rome Beauty that have had no contact with Virginia Crab. Spy 227, Malus sikkimensis, M. floribunda, M. platycarpa, and the Russian apple clone R12740-7 and its seedlings all developed pitting and appear to be good indicators for stem pitting (131, 132, 133). Recent information by Luckwill and Campbell (112) suggests that Malus platycarpa Rehd. may serve as an indicator for several other latent apple viruses. Line patterns, dwarfing, and possibly a scaly bark condition were produced on this clone when inoculated with buds from symptomless apple varieties. Datura *innoxia* has been reported to produce a local lesion reaction when inoculated with apple material from stem pitted trees (80).

Geographical Distribution

Stem pitting has been reported from many of the apple-growing areas in the United States. It has also been found in British Columbia (193), Quebec (55), and possibly occurs in a masked form in the variety Lord Lambourne in England (9).

THE SPY 227 APPLE REACTION

Gardner *et al.* (66), and others (181, 192, 201), describe a viruslike disease which occurs with the clonal U.S.D.A. apple selection Spy 227. Spy 227 was a seedling selected for its robust nature, ease of propagation, resistance to woolly aphid, etc. It also displays extreme incompatibility to selections made within commercial apple varieties. The reaction of Spy 227, dwarf fruit and decline of Hyslop Crab, and stem pitting may be synonymous in regard to the causal virus.

Symptoms

Buds of scion varieties containing the lethal virus entity, when inserted into young Spy 227 stock, appear to grow normally during the first spring and summer, but in the fall they begin to show signs of decline. Symptoms indicative of this decline include abnormal leaf color, early defoliation, frequent terminal blossom formation and dieback of young roots. Trees begin to die the second year and continue to do so up to the fourth year when all budded trees finally succumb.

Two curious lethal time factors occur with Rome Beauty apple when budded to Spy 227. If the Spy stock is cut back after bud set, the inserted Rome Beauty bud appears to grow normally the first year. Some of these budded trees begin to die in the spring of the second year and at the end of the third year all budded trees are dead. However if the budded Spy stem is not cut back, all trees die during the year of budding (66).

Guengerich and Millikan (72) noted a similar reaction to that produced by Rome Beauty when Golden Delicious buds containing the stem pitting virus factor were used on Spy 227. In addition they found stem pitting to occur on Spy 227. Thus they suggest that the factor responsible for this lethal incompatibility produced by some apples may be due to the stem-pitting virus. They also suggest that Spy 227 would serve as a good indicator for apple viruses if this assumption is true.

Etiology

The lethal factor can be filtered through varieties top-worked on Spy 227 thus proving its virus origin. When material containing the lethal virus entity is whip-grafted to healthy scions already top-worked on Spy 227 stock, death of the top-worked Spy tree results the second year following the double working.

Host Range

Incompatibility which results in death of clonal Spy 227 has been produced by buds from Yellow Newtown, Jonathan, Golden Delicious, Red Delicious, Winesap and McIntosh.

Geographical Distribution

This disease reaction has been reported only from the United States.

DWARF FRUIT AND DECLINE

Dwarf fruit and decline was reported by Cation and Gibson (43) as a virus disorder of Hyslop Crab. It was brought to their attention when this variety was used in extensive grafting operations. The disease may be associated with stem pitting.

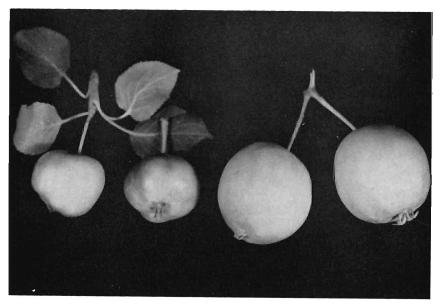


FIGURE 9. Dwarf fruit and decline symptoms on Hyslop Crab fruits. Left, infected apples showing dwarfed, deformed fruit; right, normal fruit. Photo, Donald Cation, Michigan State University.

Symptoms

Certain Jonathan apple scions, when combined with Hyslop Crab used as an intermediate stock, produce dead or worthless trees. However, this effect is not seen immediately. In fact the Jonathan scions appear to grow normally and may remain in this condition for several years. Eventually tree growth is reduced and decline becomes manifest.

Jonathan fruit produced on diseased Hyslop Crab trees is reduced in size. When Hyslop Crab branches are permitted to fruit on these Jonathan top-worked trees, the fruit is dwarfed, deeply lobed and sometimes exhibits prominent longitudinal five-ribbed forms (figure 9). When infected Hyslop Crab scions are grafted to healthy Hyslop Crab, fruit distortion is produced on the inoculated healthy trees, but less tree decline is noticed as compared to the Jonathan combinations.

Severe stem pitting is also evident on Hyslop Crab trees that show deformed fruit and decline symptoms according to recent information offered by Cation.³ He suggests that dwarf fruit and decline may be similar to stem pitting although comparisons of such virus sources need to be made to establish their relationship. McIntosh 106, the clone of apple that carries a virus lethal to Spy 227, also causes severe stem pitting on Hyslop Crab as well as fruit deformation.

Not all sources of Jonathan carry this fruit distortion and tree decline virus entity. Some Jonathan clones used in Michigan experiments gave rise to normal fruit trees when grafted to Hyslop Crab stocks. If the causal virus is related to that which causes stem pitting, then it occurs in a latent form in many commercial apple varieties.

Geographical Distribution

Although the disease has been described for only the Michigan experiments (43), stem pitting has been observed in Hyslop Crab when used as a framework variety in British Columbia (93).

CHAT FRUIT

Chat fruit, literally, means dwarf or small sized fruits. In 1944 Wallace *et al.* (189) reported a peculiar fruit condition on Lord Lambourne apple trees in England which was characterized by chat fruits. Its mode of occurrence suggested graft transmission. Luckwill and Crowdy (113) demonstrated its virus origin with transmission studies whereby chat fruit was conveyed to healthy scions top-worked on infected trees. Later confirmation by Luckwill (111) revealed that the

³ Personal correspondence from Donald Cation.

virus causing chat fruit was transmitted in buds and bark patches to healthy Lord Lambourne trees.

Symptoms

Symptom expression is manifest in the production of small, dwarfed fruit (figure 10). Fruit on infected trees is green at maturity and the exposed sides are a dull red color. Pedicels on chat fruits are somewhat elongated. Premature fruit drop also occurs. Experimentally inoculated Lord Lambourne trees have produced chat fruit symptoms the year following inoculation. The mean fruit weight and percentage of fruits $2\frac{1}{4}$ inches or over on these young trees is considerably reduced.

Chat fruit affected trees tend to be more upright in growth habit in contrast to the normal spreading character observed in healthy trees. Chat fruit may occur on Lord Lambourne trees infected with rubbery wood but generally the two disorders occur separately.



FIGURE 10. Apples of the variety Lord Lambourne. Top, normal apples; bottom, apples from trees infected with chat fruit. Photo, L. C. Luckwill, Long Ashton Res. Sta. Bristol.

Etiology

Transmission of the virus occurs more readily when bud inoculations are used as opposed to bark chips. Strains of the virus may exist according to Luckwill (111) who found that transmission seemed to vary with different tree isolates. The virus occurs in a latent form in some apples. Malling stocks indexed at Long Ashton, England, for chat fruit revealed 22 per cent infection in M. IV, 6 per cent in M. XVI and 4 per cent in M. XII while other Malling stocks were free of the virus. Some natural spread of the virus has been observed (109).

Host Range

Lord Lambourne is used as the indicator variety for chat fruit virus. Other varieties observed with symptoms like chat fruit include Jonathan, Turley, and Golden Delicious (156).

Geographical Distribution

Chat fruit has been reported from England (58), Denmark, Switzerland (6), and the United States (156).

CHLOROTIC LEAF SPOT

Mink and Shay (133) report an apple leaf disorder occurring on the Russian apple clone R12740-7A to which they have given the name chlorotic leaf spot. Although in indexing trials a correlation exists



FIGURE 11. Chlorotic leaf spot disease symptoms on University of Illinois Russian seedling clone R12740-7A. Photo, Gaylord Mink, Department of Botany and Plant Pathology, Purdue University, Lafayette, Indiana. between the development of stem pitting symptoms and chlorotic leaf spot, it is described here as a separate virus disorder. Chlorotic leaf spot symptoms are not unlike leaf symptoms associated with the leaf-pucker-russet-ring complex (figures 12 and 13, pages 30 and 31).

Symptoms

Young leaves on infected trees show a unilateral distortion with pale yellow spots of varied size that persist throughout the growing season (figure 11). It appears that temperature tends to mask disease expression since symptom development is greatest on leaves formed early in the growing season. Late summer leaves are mostly symptomless.

A period of two years is required for symptoms to appear when five year old trees are used as indicators. When the double budding method is used, symptoms develop on the young indicator shoots during the first year's growth. Severe fruit symptoms have been observed in some cases where trees have shown chlorotic leaf spot.⁴

Stem pitting was associated with chlorotic leaf spot in 27 out of 36 trees indexed. Non-pitted Virginia Crab and Hyslop Crab apple varieties did not produce chlorotic leaf spot when indexed. Mosaic symptoms have also been associated, in some cases, with chlorotic leaf spot.

Host Range

The Russian apple variety R12740-7A, and seedlings from this clone, are the only known indicators of chlorotic leaf spot.

Geographical Distribution

Chlorotic leaf spot has been reported only from Indiana; however, it was observed on Russian seedlings of clone R12740-7A in Holland by Shay in 1955 (133).

LEAF PUCKER AND THE ASSOCIATED FRUIT SYMPTOMS RUSSET RING AND BLOTCH

Leaf pucker and associated fruit distortions were discovered to be graft transmissible as an outcome of screening several unknown apple disorders in British Columbia (195). Later, the name russet-ring was used by Reeves and Cheney (162) to describe a graft transmissible fruit disorder which was accompanied by foliage symptoms similar to those of leaf pucker. Fruit symptoms described as russet-ring have

⁴ Personal communication from Gaylord Mink.

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been observed since 1935 on orchard trees in the state of Washington (174). It appears that the above two disorders plus fruit blotch may form a single disease complex. For the sake of clarity these have been grouped under one heading.

Symptoms

Foliage symptoms appear on the first formed leaves in early spring. Leaves on the fruit spurs appear dwarfed and puckered (figure 12). In addition to the distortion, chlorotic flecking is apparent particularly bordering the mid vein (figure 13). The flecks assume a yellow-green color, not typical of apple mosaic symptoms which tend to be creamy white in color. Puckering and dwarfing of the leaves become less evident as the season progresses but chlorotic flecking may still occur. Suppression of symptoms continues until there is a complete masking of symptoms on leaves formed during hot weather.



FIGURE 12. Leaf pucker symptoms on McIntosh. Photo, Canada Agriculture, Summerland, B. C.

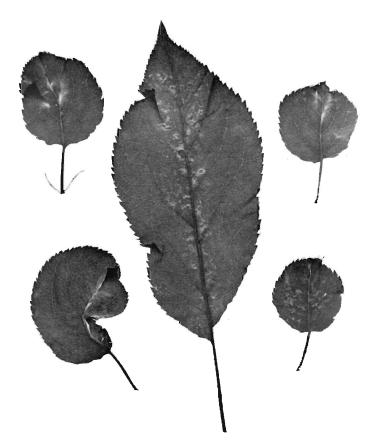


FIGURE 13. Leaf symptoms in Golden Delicious apple infected with the russet ring disease. Photo, Reeves and Cheney, Proc. Wash. State Hort. Assoc. 55.

Fruit symptoms in a single variety appear to vary from orchard to orchard and from tree to tree within orchards. The type of fruit symptom also varies with the variety. McIntosh affected fruit commonly exhibit small depressions within which the skin is abnormally pigmented. On some fruits this is accompanied by russet ring patterns on the skin. Golden Delicious is a good indicator for the russet ring symptom. On young infected Golden Delicious fruits, slightly sunken rings of a white or green color appear on the otherwise normal reddish colored fruits. Russeting of these rings occurs as the fruit matures. At harvest time these russeted areas appear as irregular ring-like configurations on the surface of the fruit (figure 14).

Yellow Newtown apples develop elaborate networks of ring russeting, usually covering most of the fruit surface (figure 15). In the

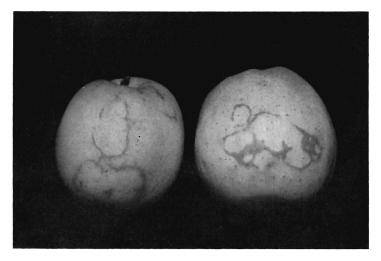


FIGURE 14. Fruit symptoms of russet ring in Golden Delicious apple. Photo, Reeves and Cheney, Proc. Wash. State Hort. Assoc. 55.

Spartan variety, irregular large depressions are formed on the cheek of the fruit near the calyx end. With Stayman apples, extensive super-ficial skin blotching occurs without russeting, and the blotches vary from purple to brown in color. With the Jubilee variety symptoms are not as extensive, and affected fruits develop no russeting but exhibit a purple skin blotch.⁵

Tree growth in the Spartan variety is affected. Inoculated trees emerge from dormancy four to five weeks later than uninoculated trees. Dieback of terminals occurs and a severe reduction in fruit set occurs on the inoculated trees.⁵

The severity of leaf pucker and fruit russeting on infected trees varies from season to season. Temperature appears to be an important factor. In seasons characterized by the early onset of warm sunny weather, no fruit symptoms occur, and only first-formed leaves develop puckering and flecking; in cool summers, severe fruit russeting occurs, and foliage symptoms continue to develop on leaves formed throughout the first half of the growing season.⁵ In this respect, where foliage symptoms are dependent upon temperature, leaf pucker with its associated fruit symptom complex is similar to that of apple mosaic and chlorotic leaf spot.

Whether foliage and fruit symptoms of leaf pucker and russet ring are caused by the same virus has not been proven.

⁵ Personal communication from Maurice Welsh.

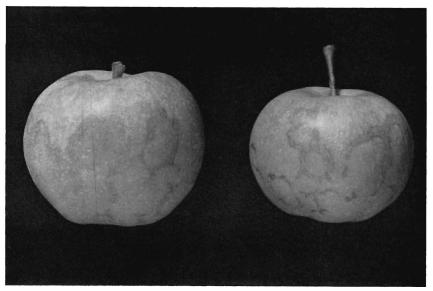


FIGURE 15. Russet ring symptoms with leaf pucker on Yellow Newtown apple. Photo, Canada Agriculture, Summerland, B. C.

Host Range

Fruit and foliage symptoms have been observed on Golden Delicious, McIntosh. Stayman, Yellow Newtown, Jubilee, and Spartan. Fruits of Red Delicious, Stayman Winesap, Black Ben Davis, and Rome Beauty have not shown symptoms although ring russeting occurs on Golden Delicious top-worked to these same trees. Foliage symptoms do, however, occur on the Rome Beauty and Stayman Winesap varieties (162). It appears that Red Delicious and Black Ben Davis could act as symptomless carriers of the virus entity.

Geographical Distribution

Leaf pucker and its associated fruit disorders have been reported from British Columbia (194) and the state of Washington (161). Similar russet ring symptoms have been observed in Indiana.⁶

DAPPLE APPLE

Smith *et al.* (173) observed this fruit spotting disease of apple in New Hampshire and gave the name dapple apple to the disorder. Barrat *et al.* (20) demonstrated that symptom development can be obtained in previously symptomless trees by transmission of the virus entities in buds and by grafts.

⁶ Personal communication from Gaylord Mink.

Symptoms

Only the fruits are affected. Maximum symptom expression occurs at fruit maturity in most varieties. Fruit spotting is first evident in mid-July. Small, pale, circular spots that stand out in contrast to the normal green color can be seen on young fruits. Early symptoms vary from tree to tree. As infected fruits mature, these spots enlarge and sometimes may coalesce to form large discolored areas. Usually the spots retain a circular pattern and are concentrated near the calyx end of the apple (figure 16). Dappling of the apple becomes more intense and easier to discern as fruit approaches maturity because the affected spots remain greenish and thus stand out against the developing red background. However, this is true only of fruit that is normally red at maturity. Symptoms in green and yellow fruited apple varieties are difficult to see except when a red blush occurs on the fruit.



FIGURE 16. Symptoms of dapple apple on Starking Delicious. Photo, A. E. Rich, New Hampshire Agr. Exp. Sta.

Although dappled fruits are normal in size, the surface over the spotted areas is somewhat flattened and a reduction of bloom is evident.

Dapple apple was initially observed on Cortland apples top worked to Virginia Crab body stocks. Barrat (19) postulates that disease development is dependent on two latent viruses and that both are necessary for dapple apple symptoms to occur. The basis for this assumption rests on the finding of dappled Cortland apples on limbs top-worked to Virginia Crab body stocks some of which had developed pitting while others had not. According to this hypothesis, one factor originally occurred in the Virginia Crab and the other was endemic with the single tree source of Cortland scion wood. He further postulates the presence of the virus factor for dapple apple in Virginia Crab occurs independently of the stem pitting virus. Dapple apple symptoms have since been observed on other varieties independent of Virginia Crab body stocks.

Host Range

Dapple apple symptoms have been observed on Cortland, Macoun⁷, McIntosh, Starking Delicious, Golden Delicious, Robin Crab⁸, Turley, Winesap, and Virginia Crab varieties.

Geographical Distribution

The disease has been reported only from the United States: Maine⁸, Massachusetts (19), possibly Missouri (156), and New Hampshire (21).

FALSE STING AND GREEN CRINKLE

False sting and green crinkle appear to be synonymous. These two separately described fruit disorders have been noticed in separate locales for many years. Hockey (83) adopted false sting as an appropriate name to describe affected fruit found in Nova Scotia because it was similar to sting injury produced by feeding punctures of various insects found there. Due to lack of noticeable capsid insect injury in New Zealand the name false sting does not carry the same connotation. Consequently the name green crinkle seemed more appropriate to describe the disease (11). McAlpine (118) considered fruit crinkle disorders of a similar nature found in Australian orchards to be a "confluent form of bitter pit." Illustrations from the latter's early 1912 report resemble somewhat the symptoms described for false sting and green crinkle virus diseases. Roberts (164) reported a fruit crinkle condition in Wisconsin in 1919 which he stated was apparently similar to the physiological crinkle reported earlier by McAlpine.

Symptoms

Distinguishing symptoms are observed only on apple fruits. No foliar or bark disorders have been consistently associated with this disease complex. There is, however, a report by Thomas and Raphael (179) of a disorder on fruits similar to false sting which was consid-

⁷ Rich, unpublished data.

⁸ McCrum, unpublished data.

ered to have a physiological origin. In this one case malformed wood and internal cork were found in conjunction with the fruit symptom.

Shortly after bloom, when the fruits are from $\frac{1}{2}$ to $\frac{3}{4}$ inch in diameter, small depressions or creases appear on the surface (figure 17). Frequently russeted and cracked areas develop in these depressions (figure 18). Disfigurement of infected fruit is magnified as the season advances. In addition to the above symptoms, fruit may occasionally show excessive bumpiness on the surface. In some cases these bumps or wart-like swellings may have a russeted surface.

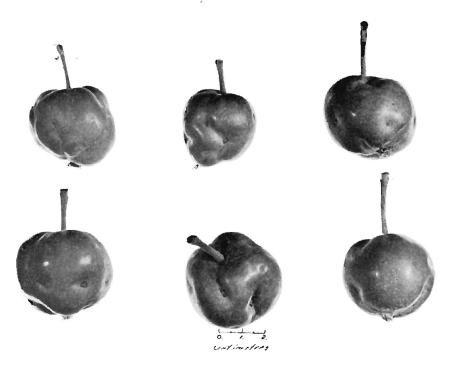


FIGURE 17. Symptoms of false sting on Gravenstein apple fruits collected five weeks after full bloom. Photo, J. F. Hockey, Research Station, Canada Department of Agriculture, Kentville, N. S.

Histological examination of tissue below the depressions or swellings reveals disoriented, abnormal vascular elements accompanied by an elongation of cortical cells. Apple tissue in these areas is also darker green than normal fruit flesh (84).

Affected fruits may appear only on one branch of a tree or they may be spread throughout the tree. In either case disfigured fruit is consistently produced year after year.

Etiology

Transmission occurs through the use of infected scions and buds. Healthy scions grafted to infected trees produce diseased fruits and the reverse also occurs. Double budding young Malling IX rootstocks with healthy and infected buds demonstrates bud transmission of the virus (17). No insect transmission has been observed, and field spread is restricted to the use of infected propagating material.

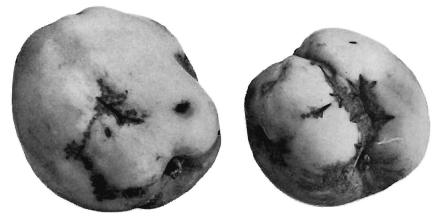


FIGURE 18. Russeting and cracking in depressions caused by green crinkle on Gravenstein apples. Photo, Atkinson and Robbins, N. Z. Journal Science & Technology 33.

A period of at least three years is required for symptoms to develop to prove transmission where bud indexing is employed (12).

Host Range

False sting and green crinkle symptoms have been observed on the following varieties: Baldwin, Ben Davis, Blenheim, Cox's Orange Pippin, Dunn's Fuhr, Granny Smith, Gravenstein, Guldborg, King of Tompkins, Lord Wolseley, McIntosh, Northern Spy, Statesman, Sturmer, Sweet Alfred, and Tolman Sweet.

Geographical Distribution

This virus fruit disorder has been reported in Australia (5), Denmark (101), England (189), Norway (158), New Zealand (11), Nova Scotia (82), and the United States (19).

GREEN MOTTLE

Graft transmission of a virus causing green mottle on apple fruits was demonstrated by Palmiter and Parker and reported in 1955 (143).

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Blemished fruit characteristic of this disease have been observed in New York State since 1938.

Symptoms

Symptoms of green mottle appear only on the fruit. Surfaces of affected fruits develop dark green rings that stand out against the normal lighter green skin color (figure 19). Symptom development is slow and field spread of the virus is slight. Small trees grafted with infected scions require three years to develop mottled fruit.



FIGURE 19. Green mottle symptoms on Duchess of Oldenburg apple. Photo, T. H. Barksdale and H. H. Lyon, Dept. of Plant Pathology, Cornell University, Ithaca, N. Y.

Host Range

Duchess of Oldenburg is the only variety reported to develop green mottle symptoms. McIntosh fruits produced from scions topworked to an affected tree several years earlier have not shown this disorder. It has been suggested that the virus may be present in a latent form in trees of other varieties as well (144).

Geographical Distribution

Green mottle has been observed only in a few trees in New York state.

APPLE VIRUS DISEASES

RING SPOT

Ring spot of apples has been observed in New Zealand orchards for 25 years. This fruit-blemishing disease has also been called "Henderson Spot" (3) and "Thumb Mark" (8). Ring spot was adopted by Atkinson *et al.* (15) to best describe the disease. Graft transmission tests to prove the virus nature of this disease have been disappointing.

Symptoms

Symptoms occur only on apple fruits. When affected apples reach approximately an inch in size (3 cm.), faint light brown areas can be seen through the downy covering of the young fruit. As the apples mature these areas develop a rough russeted surface with a scaly margin.

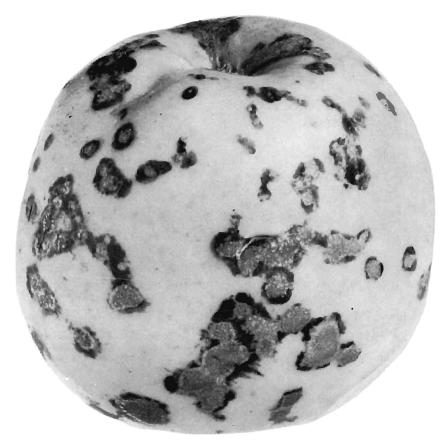


FIGURE 20. Ring spot symptoms on Granny Smith apple showing typical scaly, russet-like spots with smooth dark brown edges. Photo, Atkinson, et al., N. Z. Journal of Science and Technology 35.

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Shortly before harvest, narrow-dark bands with smooth surfaces appear surrounding the russeted spots. Development of the smooth-dark bands is regarded as a reliable diagnostic feature (figure 20). Further development of these bands may occur after harvest. Some fruits tend to form concentric circles of brown tissue from which the name thumb mark was derived (figure 21). However, this is the unusual condition as found in New Zealand. In some cases spots coalesce to form large patches of russeted skin surrounded by the smooth dark margins. In all types of spotting only the external fruit surface is involved. The flesh under the russeted areas appears normal. Flavor and keeping quality are not impaired. The market value of such fruit is considerably reduced.



FIGURE 21. Atypical symptoms of ring spot on Granny Smith apple showing concentric circles of brown tissue. Photo, Atkinson, *et al.*, N. Z. Journal of Science and Technology 35.

Symptom development varies from year to year and from tree to tree. Some trees may produce a few affected fruits one year and none the next. However, trees that produce a large percentage of marked fruit continue to bear ring spotted apples although the percentage of fruit affected varies from year to year. Inconsistency of disease development is noticed on single branches and even on single fruit spurs.

Attempts to transmit ring spot by grafting infected scions to healthy trees result in long erratic incubation periods. Symptoms were reproduced regularly on infected scions top-worked to healthy trees, but in eight trees so treated only seven out of 5667 apples developed ring spot symptoms on other branches of the inoculated trees in the first four years following grafting. Five years after inoculation one lateral branch was found to produce five ring spotted apples. The same branch also exhibited affected fruit the sixth year. Ring spot has not been found to move throughout a healthy tree following inoculation with infected scions.

Host Range

The apple variety Granny Smith seems to be the only consistent host of ring spot. Several odd fruits of Cox's Orange Pippin, Delicious, and Sturmer have been observed with symptoms similar to ring spot.

Geographical Distribution

This fruit blemishing disorder has been reported from New Zealand (12, 198). A virus-like condition resembling ring spot has been reported on Abbondanza fruits in Italy (124).

STAR CRACKING

Virus diseases are usually characterized by distinct symptoms produced in a host as a result of virus infections. In many cases only one diagnostic symptom occurs. The name star cracking refers to a characteristic symptom which occurs on fruit of Cox's Orange Pippin due to an apple virus infection. Star cracking, however, is only one of a complex of symptoms that occur on apple trees suffering from this particular virus disease.

Jenkins and Storey (91) observed that transmission of star cracking seemed to take place through natural grafts and suggested that the disorder was due to a virus or some part of a virus complex. Later Posnette and Cropley (153) demonstrated transmission which proved the virus nature of this disease and which also verified symptom development as observed earlier by Jenkins and Storey. The disease appears to be fairly widespread in England (9).

Symptoms

Symptom development in inoculated trees varies depending upon the source of virus inoculum. This variation tends to indicate that strains of the virus occur. However, star cracking of the fruits occurs in all cases (figure 22). Some isolates (scions taken from single, severely infected trees) produce wood and leaf irregularities when grafted to normal trees as well as star cracking of the fruit.

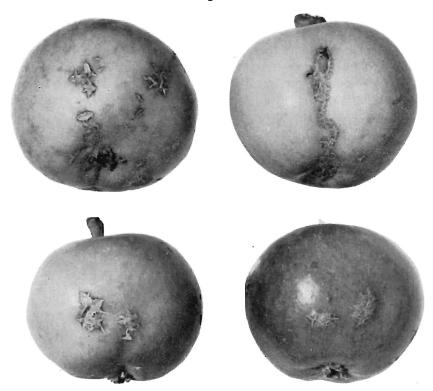


FIGURE 22. Star cracking on Cox's Orange Pippin. Photo, reproduced by permission of the editor of Journal of Horticultural Science.

Trees grafted with severely infected isolates break dormancy later than normal trees. Leafing and flowering may be delayed by as much as three weeks compared to uninoculated trees (figure 23). Flower bud production is also reduced. Tip dieback of young, one year old terminal leaders occurs. Following this winter dieback, axillary buds further down the affected shoots elongate, giving rise to a bushy or witches' broom type of growth. Blister-like lesions or cankers develop around buds on the one year old shoots as a result of inoculation with severe strains.



FIGURE 23. Delay in leafing and flowering on Cox's Orange Pippin caused by star cracking virus isolates. Left. control; center, mild isolate; right, severe. Photo, reproduced by permission of the editor of Journal of Horticultural Science.

In the fall young leaves produced on new terminals tend to be smaller in size, of a chlorotic color, and have curled edges giving a cupped or leaf-roll effect.

The relationship of star cracking to other apple virus diseases has been briefly mentioned by Posnette and Cropley (153) and is summarized as follows: trees of susceptible Cox's Orange Pippin when infected with different apple mosaic isolates and a separate vein-clearing virus do not show symptoms of star cracking. Star cracking material when grafted to Lord Lambourne does not cause chat fruit nor rubbery wood symptoms to occur on this variety, nor does star cracking appear on the Lord Lambourne fruit. Apparently star cracking can occur in a latent condition in the variety Lord Lambourne. Transmission studies with the variety Cox's Orange Pippin suggest that several viruses or strains may be involved (77).

Host Range

The apple variety Cox's Orange Pippin is most sensitive to this disease and serves as an indicator variety. Transmisson to Bramleys seedling causes dieback, canker symptoms and star cracking of fruit. Other varieties observed with fruit symptoms similar to star cracking include Early Victoria, Charles Ross, Laxton's Fortune, Monarch, and Golden Delicious.

Geographical Distribution

Star cracking has been reported to occur in England (77), Norway (159), Switzerland (171), and possibly in the United States (161).

SCAR SKIN

Recently two additional fruit disorders of a virus-like nature have been reported from the United States. Millikan (128) reported a scar skin disease of apples in Missouri, and Miller (127) described a patchy fruit condition of Delicious apples, top-worked to Virginia Crab, which was common in northern Missouri. These two reports appear to be descriptions of a single virus disease. Whether they are actually transmissible and, if so, whether they are caused by the same virus has not been indicated. Scar skin symptoms on some fruits (figure 25) closely resemble those of dapple apple (figure 16, page 34). However dapple apple virus produces no corky periderm as in scar skin. Further work may show this disorder to consist of a virus complex.

Symptoms

Scar skin serves to describe the effect of the disorder on mature fruit. However, development of scar skin first takes place in early June in Missouri orchards and appears as small light-green water-soaked areas on small, young fruit. Affected tissue is usually restricted to the calyx end of the apple in the early stages. As the fruit enlarges, scar tissue develops in the epidermis at the calyx end and later spreads to the sides of the fruit (figure 24). Scar tissue may cover up to 50 per cent of the fruit surface. Affected trees not only bear scarred apples but the apples produced also suffer a reduction in size compared to unaffected fruit of the same variety (figure 25).

Host Range

Scar skin has been observed on the following apple varieties: Red Delicious, Jonathan, and Turley. The Golden Delicious variety appears to be tolerant of scar skin.⁹

⁹ Personal communication from D. F. Millikan.



FIGURE 24. Scar skin symptoms on Red Delicious. Left, healthy; center, infected with scar skin; right, healthy. Photo, D. F. Millikan, Missouri Agricultural Experiment Station.

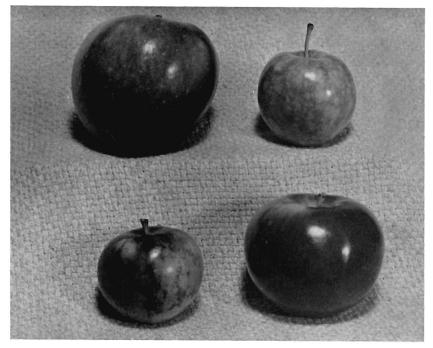


FIGURE 25. Scar skin symptoms on Red Delicious and Turley apples. Top left, healthy Delicious top-worked on healthy Turley (right, below); top right, diseased (scar skin) Delicious top-worked on scar skin infected Turley (left, below). Photo: D. F. Millikan, Missouri Agr. Exp. Sta.

Geographical Distribution

This fruit blemishing disease has been reported only in Missouri (127, 128).

ROUGH SKIN

Rough skin of apple causes considerable loss in revenue to Netherlands fruit growers (138, 186). Apples are graded on three points color, fruit finish, and size, all of which are affected by rough skin. Not only does this disease cause a reduction in size of fruit, it also produces markings on the fruit surface; thus affected fruit which are salable fall into the lowest commercial grade.

Symptoms

Rough skin symptoms can be seen on young developing fruit. In certain areas on the fruit surface, epidermal cells die and corky tissue is formed beneath these cells. The corky areas which have a slightly sunken surface may develop on both green and colored parts of the apple skin. When the russeted areas are small in size they have a circular shape. Fruit are often found, however, on which russeted areas appear in the form of large, corky ring configurations and, in some cases, small circular patches may coalesce and form elongated strips of russeted tissue (figure 26). In some cases severe russeting covers a large part of the apple surface. Cracking, not unlike that found with the star cracking disease, often takes place under the russeted areas in certain fruit varieties (figure 27).



FIGURE 26. Rough skin disease of Glorie van Holland apples with corky spots in the form of rings. Photo, courtesy J. G. ten Houten, Institute for Phytopathological Research, Wageningen, The Netherlands.

Leaf symptoms occur with trees affected with rough skin. The top leaves of young shoots develop a type of vein clearing in which chlorotic areas appear in and around the leaf veins.

Not all fruits that show russeting are to be taken as showing symptoms of rough skin. Mulder (138) draws attention to genetic abnormali-



FIGURE 27. Golden Delicious apples with corky spots and cracks as symptoms of rough skin disease. Photo, courtesy J. G. ten Houten, Institute for Phytopathological Research, Wageningen, The Netherlands.

ties found in the Netherlands that produce symptoms quite similar to those of rough skin disease.

Chiu *et al.* (46) described a chemical test for the presence of rough skin. It is based on the fact that leaves from trees infected with rough skin virus have a higher arginine content than leaves free of the virus.

Host Range

Rough skin disease of apples has been found on Baldwin, Beauty of Boskoop, Canada Pippin, Dijkmanszoet, Glockenopfel, Glorie van Holland, Golden Delicious, Gravenstein, Henimuri, Jonathan, Laxton's Superb, Notaris, Ontario, and Reinette de Champagne. The same or a similar disorder has been observed in Virginia Crab.¹⁰

Geographical Distribution

Symptoms of rough skin on apples have been reported from Denmark (160), France (187), Germany (33), Holland (188, 187), Switzerland (62, 171), Peoples Republic of China (96), Union of South Africa (106), and the United States (156).

¹⁰ Rich, unpublished data.

APPLE PROLIFERATION

Apple proliferation is synonymous with apple witches' broom. Although this disease complex has been known for many years in Italian nurseries (169), suggestions as to its virus nature did not occur until the early 1950's. Mulder (137), in Holland, reported the disease to be of virus origin and suggested the name "proliferation disease." Rui (166), in 1950 in Italy, described the disease and called it "Scopazzi" or witches' broom. Since then over 30 references have accumulated in the literature in regard to this apple virus disorder. Transmission of the virus has been demonstrated by several workers (37, 137, 163, 169). Since proliferation disease is of the witches' broom type, it might be of interest to point out that Bos (34) has published an extensive review of witches' broom diseases.

Symptoms

There are several diagnostic symptoms produced by trees infected with proliferation virus. However, it must be pointed out that symptoms on mature trees vary considerably, not only among trees but from year to year. In some years infected trees show no symptoms.

Instead of developing long terminal shoots, which ordinarily occur with healthy trees, affected trees give rise to clusters of bushy shoots which resemble fagots or witches' brooms. This type of growth arises due to stimulation of axillary buds on young shoots by the virus. Proliferation occurs on old trees as well as on nursery stock. Experimentally infected trees are characterized by the premature growth of axillary and terminal buds in early spring (figure 28). Such trees may start to break dormancy 30 days earlier than healthy ones. Affected trees also show a retarded defoliation and go into dormancy later than normal trees.

Leaf shape, color, and development are affected by this virus. Leaves on secondary branches are smaller and tend to be more elongate than normal (figure 29). The edges of affected leaves are often more finely and deeply dentate. Another curious but characteristic symptom which occurs with this virus disease is the extreme enlargement of the leaf stipules (figures 29 and 30). Leaves on infected shoots may show a mild chlorosis of the leaf blade and veins varying in color from a light green to yellow and sometimes with a reddish color.

Other curious growth habits occur with this disease. Flowers may be produced late in the season on affected branches (35). Fruit is late in ripening and frequently smaller than that on normal trees. Yield losses due to dwarf fruit have been reported as high as 95 per cent (37). Yield reductions also occur as side shoots arise from buds which should



FIGURE 28. "a," proliferation symptoms on the variety Abundance experimentally infected; "b," a shoot from healthy tree. Photo taken in early spring. G. Scaramuzzi, E. Refatti e A. Corte: Gli "Scopazzi Virosici" del melo.

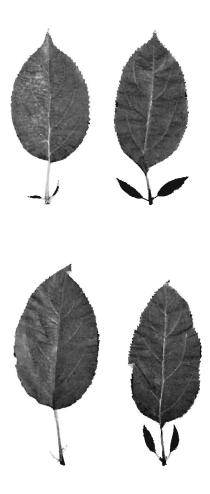


FIGURE 29. Enlargement of leaf stipules on trees experimentally infected with proliferation. Top right, Gravenstein and bottom right, Golden Delicious leaves from infected trees. Leaves at left represent same varieties from healthy trees. Photo, G. Scaramuzzi, E. Refatti e A. Corte: Gli "Scopazzi Virosici" del melo.

normally be fruit buds (36). Experimentally infected young trees show a steady reduction in vigor over a six year period. Symptom expression seems to be associated with tree vigor as the disease is more apparent on young nursery trees produced from infected mother trees that show little or no proliferation (32, 50).



FIGURE 30. Enlarged stipules due to infection with proliferation virus on a shoot of Beauty of Boskoop. Photo, courtesy J. G. ten Houten, Institute for Phytopathological Research, Wageningen, The Netherlands.

Etiology

Virus isolates from older trees seem to produce a greater intensity of symptoms than does the same type of inoculum from younger trees. Symptoms also appear earlier when buds from older trees are used. No information exists on insect transmission of the virus. It is apparently transmitted by budding and grafting. The disease has been seen to increase in orchards where the virus has apparently been spread through natural root grafts. Fogliani (61) noticed that Golden Delicious trees became infected or developed proliferations after scions were taken from them and suggested that transmission may have occurred through pruning operations. Pruning has been shown to increase the amount of symptom development (169).

Host Range

Apple varieties showing symptoms of proliferation include Beauty of Boskoop, Gravenstein, Abbondanza, Imperatore, Golden Delicious, Schneider, Champagne Pippin, Berlepsch, Golden Pearmain, Annurca, Canada Pippin, Landsberger Reinette, Laxton's Superb, Signe Tillisch, Cox's Orange Pippin, Blenheim, and Golden Pippin. Undoubtedly other varieties will be reported as hosts of this virus. Transmission of proliferation to pear has also been reported (51).

Geographical Distribution

Proliferation or witches' broom disease occurs in Austria (63), Denmark (98), France (136), Germany (63), Bavaria (115), Holland (183), Italy (167), and Switzerland (36). A disorder called big stem of apple which occurs in Iraq (191) may be related to apple proliferation although transmission of this disorder has not been demonstrated.

ROSETTE

This graft-transmissible, branch stunting, abnormality of apple trees was first reported from Holland by van Katwijk (184) in 1953. Since this disease could be mistaken for a nutritional disorder which produces similar symptoms, it is evident that transmission studies should be attempted before new occurrences of the virus type rosette are reported. Relationship of the causal virus to that which causes proliferation disease is not known.

Symptoms

Symptoms may occur on single limbs or be generally dispersed throughout the whole tree. Instead of developing along the young shoots, leaves occur as rosettes at the ends of terminals giving rise to curious rattle-like growths. Not only are leaves restricted to location on affected branches but the leaves produced in these rosettes are markedly different from normal leaves (figure 31). The leaves in these rosettes average $6 \times 4\frac{1}{2}$ cm. and are much smaller than normal leaves which average $10 \times 8\frac{1}{2}$ cm. Leaf shape is also affected by the virus entity. The bases

of affected leaves assume a wedge shaped pattern, and frequently the serrations along the margin of the blade become more intense, resembling the condition found with proliferation virus. Some leaf curl occurs with rosette infected leaves.



FIGURE 31. Symptoms of rosette on Beauty of Boskoop. Photo, courtesy Plant Protection Service, The Netherlands.

Tree growth appears to be affected as well as fruitfulness. Apple trees infected with this virus develop little if any fruit, and the trees in general have an upright type of growth.

Host Range

The disease has been observed on the variety Beauty of Boskoop. Jonathan shows some distortion of the leaves when inoculated but not to as great a degree as the former variety.

Geographical Distribution

Rosette has been reported from orchards and nurseries in two different provinces of Holland (184). It is suspected to occur in Denmark on the variety Beauty of Boskoop.

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