Virus Diseases of Trees and Shrubs

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The photograph on the front cover is of Red Flowering Horse Chestnut (*Aesculus carnea Hayne*). The branch on the left is healthy whereas that at the right has leaves with a yellow mosaic symptom associated with an ilar virus ressembling apple mosaic. Reproduced by kind permission of Long Ashton Research Station.

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To Audrey, Wendy and Elaine

VIRUS DISEASES OF TREES AND SHRUBS

Introduction

In the 1840s potato crops failed in many European countries with Ireland being the worst affected. The scourge, potato blight, was not new to farmers nor to scientists, but its cause was unknown until the Rev. M. J. Berkeley (1803–1889) argued that it was caused by the fungus *Phytophthora infestans*; the potato malady was the result of the fungus, and not the cause as had previously been believed. Berkeley's work was significant, for it heralded major advances in plant pathology. Subsequently, plant diseases have been attributed to a diverse array of microbes including algae, bacteria, fungi, nematodes and viruses. This work is concerned with viruses affecting trees and shrubs.

During the last fifty years, viruses have been increasingly recognized as major threats to agricultural and horticultural crops. They affect plants in many ways. Sometimes they cause obvious variations in leaf colour, occasionally inciting abnormal development of branches and stems, for example, potato mop top (Plate 1). In other instances, losses of vigour, yield and competitive ability occur in the absence of obvious blemishes. Potato viruses were among the first to be recognized because 'degeneration' (yield decline), attributable to viruses, increased in prevalence with the use of seed tubers from successive diseased crops. Johnson (1925) observed that apparently healthy potatoes could be symptomless carriers potentially jeopardizing adjacent plants. Interestingly, many virus-infected trees show symptoms for only a few weeks in a year and often only part of the foliage is affected. In many instances viruses have been isolated from superficially healthy trees and shrubs.

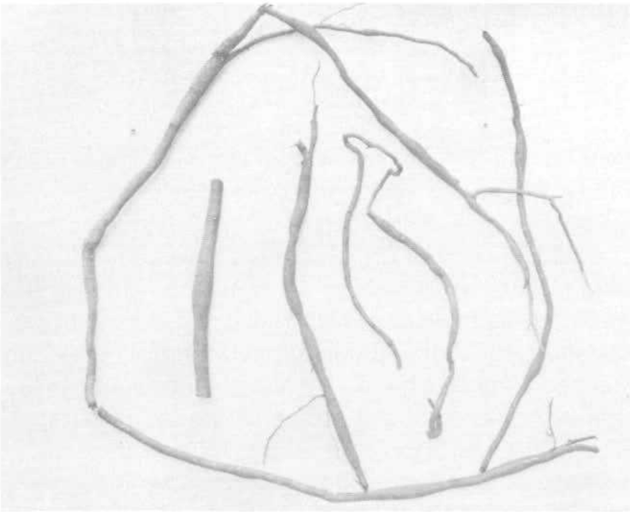
Plate 1—Potato mop-top. In naturally infected potato (cv Pentland Hawk) the virus caused one stem (at right) to be very short while another from the same tuber developed normally.

Photograph by courtesy of Scottish Horticultural Research Institute

With the development of the certified seed potato industry, viruses, which had previously been widespread, largely disappeared. Crop yields increased dramatically from a British national average of 7 tons/acre (17.8t/ha) in 1908 to 10 tons/acre (25.2t/ha) in 1965, an increase to which the development of new varieties and changed agricultural practices also contributed. The elimination of the more damaging viruses unmasked an additional range of viruses in potatoes. A similar chain of events might occur if vegetatively propagated stocks of woody perennials were freed from known viruses. For many years, the transmission of viruses through seed was considered unimportant because seed embryos characteristically resist invasion by viruses from the surrounding material tissue. Now, however, many viruses are known to be seed-transmitted, though transmission is usually infrequent. However, seed transmission of some viruses threatens the production of woody nursery stock; prunus necrotic ringspot virus is widespread in the seed of *Prunus* spp. (up to 40%), although subsequent infection is difficult to detect by visually inspecting foliage (Gilmer, 1955). The presence of this virus is sometimes shown by graft incompatibilities (a brown zone and pitting of wood at the union) developing when using infected but symptomless root-stocks (Plate 2).

See plate 2 a and b (Colour)

The spread of most viruses is dependent upon a variety of agencies, including man who has increased their occurrence by his predilection for vegetative propagation. Viruses are widespread in the plant kingdom, having been recorded in non-flowering (algae, fungi, mosses and ferns) as well as flowering plants. Viruses affecting non-woody flowering plants have already been adequately considered in text books and reviews, but those affecting woody prennials have been neglected. Numerous fragmentary records exist, but they have rarely been collated, excepting those dealing with fruit trees, e.g. *Malus* (Posnette and Cropley, 1963) and *Prunus* (Anon, 1976). Martin (1925), Peace (1962) and Hepting (1971), while concentrating on bacterial and fungal diseases, gave scant attention to the reported occurrence of virus-like diseases. To some extent, these deficiencies were corrected (Brierley, 1944; Seliskar, 1966; Schmelzer, 1968), but the recent 'flood' of published observations suggested the need to reappraise the situation. Because trees probably react in the same way as other woody perennials, it was decided to extend this review to include viruses and virus-like diseases of trees and shrubs, the range of hosts being restricted to those hardy in the UK. To avoid repeating the review collated by Frazier and others (1970), it was decided to omit viruses and virus-like diseases of orchard crops, excepting those also grown for amenity. Together, these limits exclude descriptions



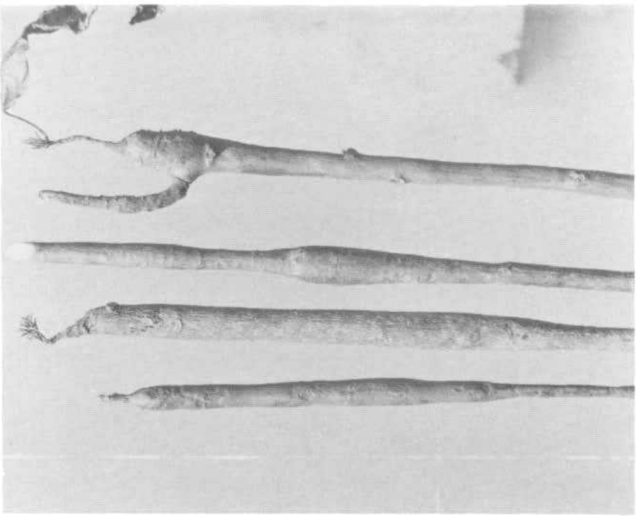


Plate 3 —Cocoa swollen shoot. *At left*, roots and *at right*, branches of *Theobroma cacao*. L. naturally infected with the virus.
Photograph by courtesy of Major J. Dade

of some of the well-documented conditions of tropical trees—swollen shoot/mottle leaf of cocoa (*Theobroma cacoa* L.) (Plate 3), spike disease of sandalwood (*Santalum album* L.), lethal yellowing of coconut (*Cocos nucifera* L.) (Maramorosch *et al*, 1970; Hull, 1971; Dijkstra and Lee, 1972; Brunt and Kenten, 1971; Grylls and Hunt, 1971). In considering the descriptions of viruses and virus-like diseases given in this work, the reader should be aware that the amount of detail largely reflects the numbers and location of trained virologists, and not necessarily the importance of either viruses or hosts.

Virus names

Plant viruses have often been given names that describe symptoms found in the first of their hosts to be identified (see Martyn, 1968 and 1971). Thus, it is now known that cherry leaf roll virus (CLRV), which was first characterized when shown to cause the upward rolling of bronzed leaves of cherry (*Prunus avium* L.) (Plate 4),

Plate 4—Prunus avium F12/1 showing (*at left*) leaf rolling premature defoliation and terminal dieback in the year following mechanical inoculation with an isolate of cherry leaf roll virus from birch. *At right*, healthy plant of the same clone for comparison.
Photograph by courtesy of Natural Environment Research Council

had earlier been associated with a disease of American elm (*Ulmus americana*), and subsequently with leaf vein yellowing in elder (*Sambucus* spp.) and yellowish ring and line pattern in silver birch (*Betula pendula* L. syn. *B. verrucosa* Ehrh.) and walnut (*Juglans regia* L.). Many viruses have some properties in common, such as shape and size, and these have been used in attempts to classify them. Other properties like host range, are useful in identifying and distinguishing significantly different groups of viruses (Harrison *et al*, 1971; Fenner, 1976).

Viruses and the diseases they cause

Although some viruses kill cells and, in rare instances, whole plants, the effects (symptoms) are usually less drastic (Corbett and Sisler, 1964; Bos, 1970; Smith, 1972). Symptoms vary, responding to changing environmental conditions, to differing isolates of the same virus, and other factors.

(a) *Foliage symptoms*

The colour of virus-infected foliage is typically yellow or pale-green (chlorotic) in part or completely, and sometimes red. The colour change may be distributed more or less evenly within a leaf, or be restricted to:

- (i) veins
- (ii) localized patches (mottling, mosaics)
- (iii) lines or rings

In a few instances, viruses affect leaf shape and, on rare occasions, wilting is a consequence of infection. In other instances, virus infections stimulate the development of outgrowths (enations) (Plate 5), often from lower leaf surfaces and commonly near veins, where they may be mistaken for insect galls. Virus infections of trees and shrubs are also associated with changes in branch colour, but, for part of the year, these are masked by foliage.

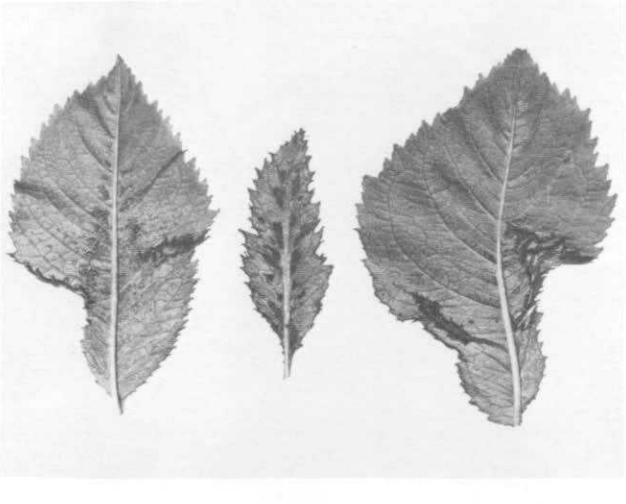


Plate 5—Cherry (cv Bing) leaves experimentally infected with raspberry ringspot and prune dwarf viruses and showing enations and distortion of the laminae.

Photograph by courtesy of East Malling Research Station

(b) *Stem and branch symptoms*

Distortions are more continuously obvious than colour changes. Three main types can be distinguished:—

(i) virus-associated death (necrosis) of bark cells allowing entry of secondary invaders (bacteria or fungi) themselves causing more generalized decay and ulceration (cankers).

(ii) an unnatural increase in cell number (hyperplasia) (Plate 6) and/or cell size (hypertrophy) may produce a tumour capable of erupting through bark and which, in turn, may be colonized by organisms causing secondary cankers.

(iii) local under-production of cells (hypoplasia) and/or cessation of cell division (atrophy) may produce pits and grooves with affected stems appearing to be flattened. When a flap of bark is raised, depressions in wood tissues are sometimes found to be matched by protrusions from the inner surface of bark.

General properties of viruses

Virus particles are composed of two parts, a nucleic acid core and a proteinaceous coat. Although some plant viruses have complex shapes, most are either tubular or spherical. Many are carried from one host to another by specific vectors, such as insects. Some are carried in pollen and transferred to seeds and seedlings. Commercial vegetative propagation is an important means of dissemination in cultivated woody plants. Because viruses infect all host tissues and can migrate across graft unions, healthy scions soon become infected when grafted to a diseased rootstock and *vice versa*.

Mechanisms of natural dispersal

Viruses can be naturally dispersed by:—

(a) parasitic animals, such as arthropods, nematodes, arachnids
(b) parasitic plants, such as root-infecting fungi, dodder (*Cuscuta* spp. Plate 7)
(c) seed
(d) pollen
(e) grafting
(f) contact
(g) vegetative propagation

Plant cell walls and cuticles are impermeable to viruses and, as a result, the walls must be damaged (punctured), for example by arthropod feeding, before the virus particles, that the vectors carry, can contact cell protoplasm. This process is obviated by those viruses that infect pollen and seeds. In general, a virus having vectors in one major taxonomic group will not be transmitted by organisms of another group. Some 400 insects are known to transmit about 250 different viruses; the peach potato aphid (*Myzus persicae* Sulz.),

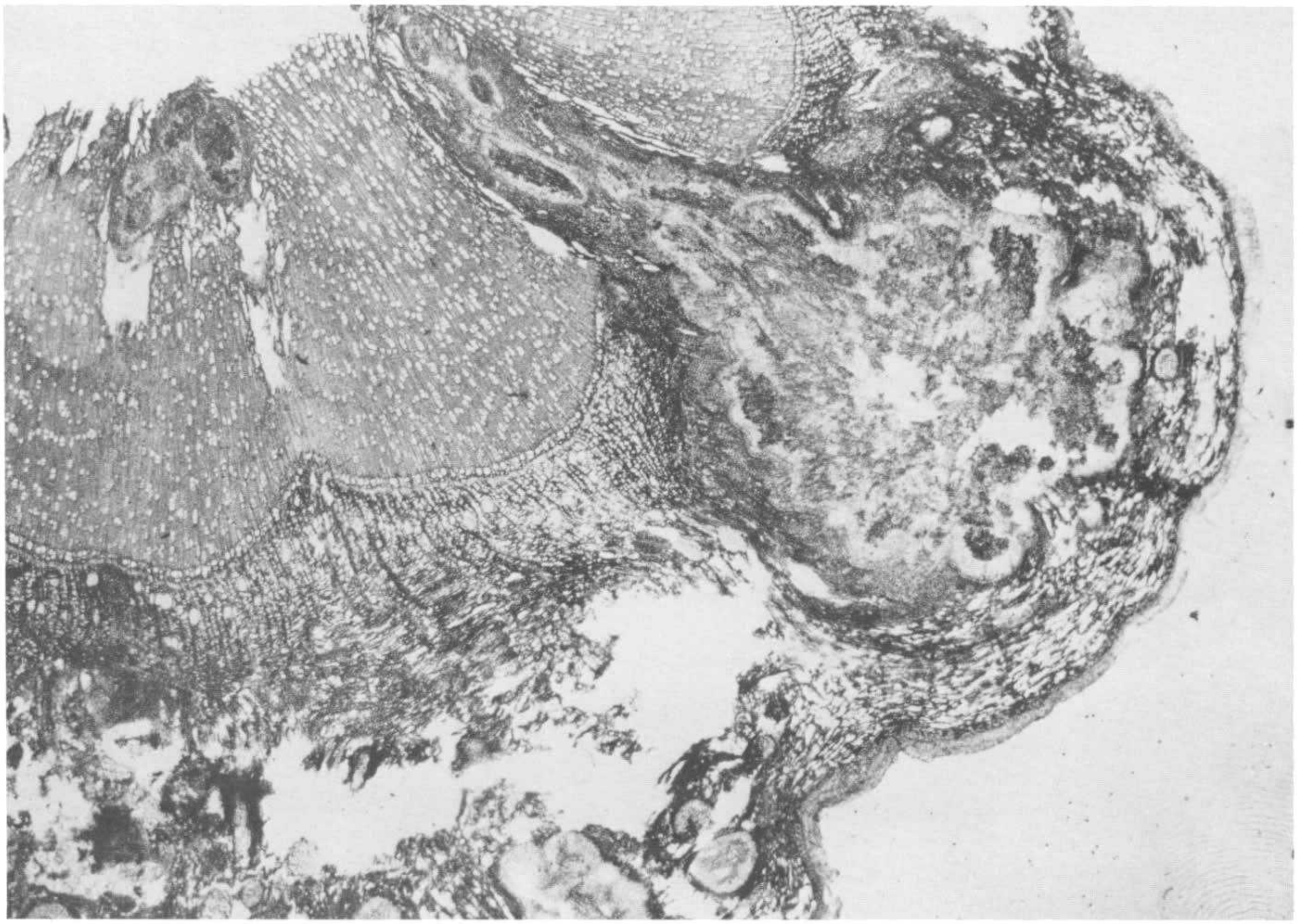


Plate 6—Populus x euramericana cv Rap branch sectioned to show hyperplasia of extra cambial tissue causing swellings. The cause of this condition is unknown but the swellings develop progressively and systemically; bacteria and fungi have not been associated.

Photograph by courtesy of Natural Environment Research Council

Plate 7—Dodder (*Cuscuta europea*) a parasitic flowering plant used to transmit viruses experimentally. The fine stems of the parasite have encircled and then established vascular connections with the host (*Chenopodium quinoa* Willd.) Some viruses (e.g. tobraviruses and cucumoviruses) infect and cause symptoms in dodder. Many others seem to be carried passively in the parasite when it bridges a healthy and a virus-infected host. *Photograph by courtesy of Natural Environment Research Council*

transmitting about seventy viruses, is probably the most important in temperate regions of the world. Aphid vectors of non-persistent viruses generally belong to species that produce migrant winged forms (alatae) which disperse the insects to, or from, primary and secondary hosts. The migrants tend to fly in short hops, landing periodically to feed by probing plant tissues. Viruses transmitted by aphids (Arthropoda; Aphidoidae) are conveniently grouped into:—

(i) *Non-persistent viruses*: efficiently acquired from, and inoculated to, hosts during probes of 30 seconds duration. Their ability to transmit is typically lost within minutes.

(ii) *Semi-persistent viruses*: an ill-defined group, probably best considered as having anomalous non-persistent relationships with their vectors, i.e. having the ability to be retained for two or three hours.

(iii) *Persistent viruses*: require minimum periods of acquisition feeding. Twelve hours or more must usually elapse before vectors can transmit an acquired virus and then only after inoculation feeding periods of at least one hour. Typically persistent viruses are transmitted by a very few aphid species; they are retained when insects moult and, in some instances, are transmitted to young via eggs.

Although the only well-characterized viruses yet detected in conifers have soil-inhabiting vectors, others with aerial vectors will doubtless be found. Three polyphagous aphid species capable of transmitting numerous viruses (Kennedy *et al*, 1962) have been recorded on conifers: *Aphis fabae* Scop, feeds and reproduces on species of *Larix*, *Picea*, *Tsuga* and *Pinus*; *Aulocorthum circumflexum* (Buckton) on seedlings of *Picea sitchensis* Carr. (Carter and Eastop, 1973); and *Aphis cracivora* Koch on *Cupressus funebris* Endl. (Eastop, 1958).

The first plant virus (rice dwarf) shown to be insect-transmitted had a leaf hopper vector (Fukushi, 1969). These insects are second only to aphids in their importance, transmitting not only viruses (mostly in the persistent manner) but also mycoplasma and rickettsia-like organisms, e.g. those consistently associated with sandal spike. Vector leaf hoppers include Chermoidea, Cicadelloidea, Fulgoroidea (plant hoppers), Membracoidae (tree hoppers) and Jassoidea. Leaf hopper-transmitted viruses commonly multiply in their vectors and, possibly because they need to be inoculated (Hopkins, 1977; Hull, 1971; Maramorosch, *et al*, 1970; Maramorosch, 1974) directly to internal food-conducting plant tissue, are not usually mechanically transmissible.

Although aphids and leaf hoppers are of over-riding importance in temperate regions of the world, other insects may be more important virus vectors elsewhere, e.g. white flies (Aleyrodoidea), the vectors of the Abutilon mosaic infectious agent in hot countries. Relatively little is know about white fly-transmitted agents. In contrast, Chrysomelid beetle-transmitted viruses (tymoviruses), which reach large concentrations in some plants, have been intensively studied—the isolation of a tymovirus is mentioned later when describing a virus-like condition in *Abelia*. Although chrysomelids retain the ability to transmit tymoviruses for about a week, the viruses are not known to multiply in their vectors. Other groups of insects including mealy bugs (Coccoidea), the vectors of cocoa swollen shoot virus, leaf miner flies (*Lirimyza langei* Frick) (Costa *et al*, 1958), and, exceptionally, grasshoppers (Walters, 1952), some butterfly and moth larvae, can transmit viruses, as can eriophyid mites (Arachnida; Aracina). Mites transmit viruses but feeding itself sometimes induces damage (see Carter, 1973; Matthews, 1970).

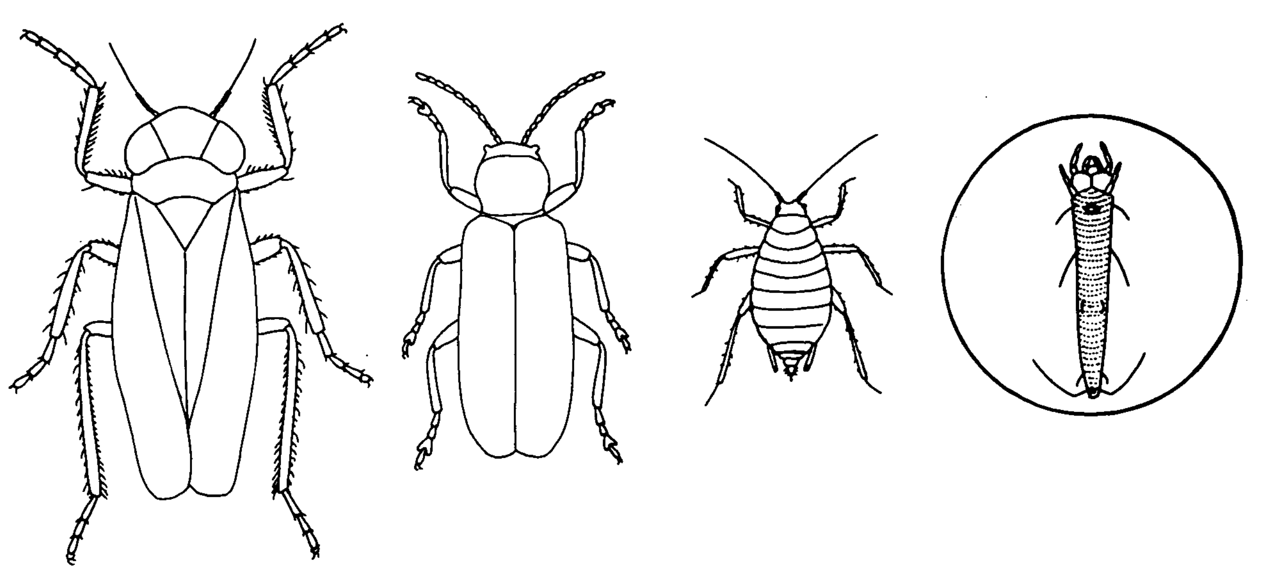


Plate 8—The size range of arthropod vectors of plant viruses illustrated with four examples (left to right): Leaf hoppers (*Nephatettix* sp., length c. 5mm); Beetle (*Oulema melanopa*, length c. 4mm); Aphid (*Aphis fabae*); at a greater magnification Eriophyid mite (*Vasetes tulipae*, length c. 0.2mm). *Photograph by courtesy of Natural Environment Research Council*

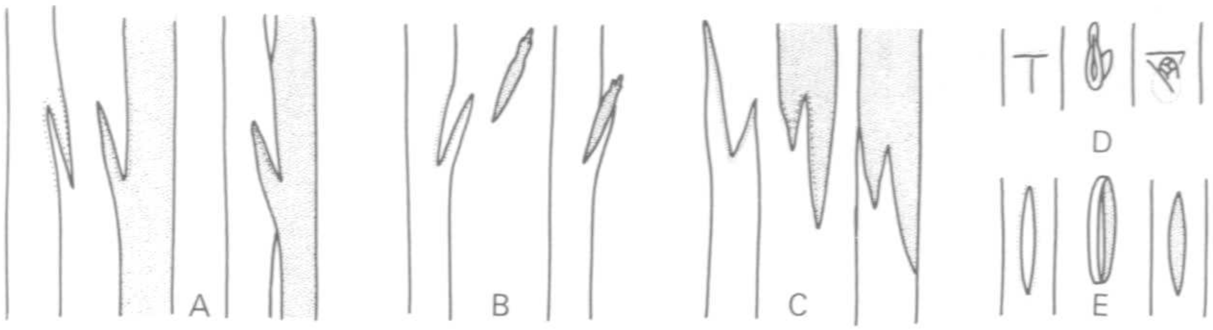


Plate 9—Five commonly used grafting methods facilitating experimental virus transmission. The scion is stippled. A. Approach; B. Wedge; C. Tongue; D. Budding; E. Tissue implantation.

Although aerially dispersed vectors (Plate 8) are of world-wide importance, the three known types of 'soil' transmission are not unimportant especially locally:—

(a) transmission to abraded roots of stable viruses surviving in plant debris (Smith *et al*, 1969).
(b) transmission by vagrant soil-living nematodes.
(c) transmission by soil fungi.

Because of their longevity, woody perennials are vulnerable to infection for protracted periods. Very few of the many pests and pathogens that colonize, sometimes transitorily, trees and shrubs have been tested for their abilities to spread viruses. Even if most of them were inefficient, the feeding damage done to plant cell walls might allow incidental transmission of viruses. For example, it was found that aphids can inoculate plants with viruses when clawing (scratching) leaf surfaces (Bradley and Harris, 1972). Filamentous fungi which develop mycorrhizal associations with roots of trees and shrubs remain untested, yet seem well placed to act as agents of virus spread. Similarly, mistletoe (*Viscum* spp.) and root parasites such as *Orobanche* spp. are untested, but are possible vectors of viruses affecting trees. Dodders (*Cuscuta* spp.) are a group of parasitic flowering plants first shown in 1940 to transmit viruses (Bennett, 1940), and these parasites are now used routinely for transmitting viruses which are not readily transmitted mechanically, by other vectors or via normal grafts (Plate 9). Although probably much less important as virus vectors than aphids, nematodes, etc., species such as *Cuscuta gronovii* Willd. parasitizing trees in the USA may, in rare instances, introduce viruses into their hosts. Even animals with restricted breeding or normal host ranges will probe into a convenient host before deciding whether or not it merits more prolonged attention and may transmit viruses at the same time. The feeding activities of birds may similarly offer occasional opportunities for incidental virus transmission. Alternatively, viruses may in some instances spread via natural root grafts or leaf contact, and it is possible that virus-carrying pollen may contaminate flowers of other plant species. Conceivably, mechanical transmission occurs naturally when adjacent pollen-coated leaves rub one against the other. It is commonplace in laboratory tests to transmit viruses by rubbing leaf surfaces of healthy receptors (Plate 10) with sap from diseased plants.

Serology

Plant viruses introduced into animals act as antigens. These provoke immune responses detectable after a latent period by the appearance of antibodies in blood and other body fluids. Because antibodies are highly specific and can be used for *in vitro* assays (Plate 11a and Plate 11b, colour), serological tests provide plant virologists with rapid means of unambiguously identifying viruses (Gibbs and Harrison, 1976; Matthews, 1957; Wetter, 1965; Ball, 1974).

Groups of viruses infecting woody perennials

About twelve of the 22 established groups of higher plant viruses have been detected in trees and shrubs (Plate 12). Until now, the commonest are those with spherical particles, 30 nm in diameter, and with wide

Plate 10—Mechanical transmission: usually preferred method by which viruses are transmitted in laboratory conditions so that the agent under scrutiny can be maintained in an insect-proofed glasshouse all the year round. An abrasive facilitates infection: celite which is incorporated into the inoculum (the sap) from the sugar dispenser (left) or carborundum typically dusted onto the leaves from muslin covered bottle (centre). Infection is initiated when a finger moistened with inoculum is gently rubbed over the upper leaf surfaces of the healthy receptor plant. Clean newspaper provides a cheap 'tablecloth' which can be discarded after each test, thereby minimising the risk of contaminating the bench with inoculum. *Photograph by courtesy of Natural Environment Research Council*

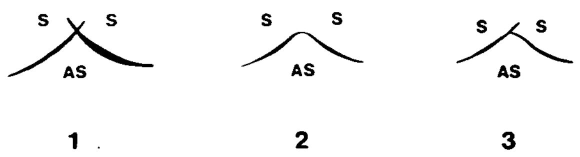


Plate 11a—Diagrammatic representation illustrating the range of precipitation reactions observable in a commonly used *in vitro* serological test. S, well containing virus (the antigen, often sap from infected plants) AS, well containing antiserum.
1. Non-identity. Two precipitin lines cross occuring when two antigen wells contain distinct antigens which react with two different antibodies present together in the antiserum well (AS).
2. Identity. Fusion of precipitin lines occuring when the antigens in the two wells combine with the same antibodies.
3. Partial-identity. Fusion of precipitin lines but with one showing the formation of a spur. Such reactions give rise to speculation concerning the degrees of similarity possessed by the two viral antigens. *Photograph by courtesy of Natural Environment Research Council*

host ranges (the opportunists). Future investigations are likely to show that ranges of 'specialist' viruses, resembling poplar mosaic and robinia true mosaic, and which naturally infect few hosts, are also common in woody perennials.

(a) Viruses with spherical particles
1. Nepoviruses
2. Ilarviruses
3. Cucumoviruses
4. Tobacco necrosis viruses

(b) Viruses with rod-shaped particles
5. Tobraviruses
6. Tobamoviruses
7. Potexviruses
8. Carlaviruses
9. Potyviruses
10. Closteroviruses

(c) Viruses with other shapes (e.g. bacilliform, sausage-shaped, particles)
11. Alfalfa mosaic
12. Rhabdoviruses

1. *Nepoviruses* have wide host ranges (their soil-inhabiting nematode vectors feed on the roots of many different plants) and are opportunists which have been frequently detected in trees and shrubs, e.g. arabis mosaic in ash (*Fraxinus excelsior* L., *F. americana* L.) and cherry leaf roll virus in birch and walnut. Although their soil-inhabiting nematode vectors are slow moving (30cm/yr), nepoviruses may spread rapidly because they are additionally transmitted in pollen and seed.

2. *Ilarviruses* are economically important and widespread in fruit trees, and have been recorded in amenity trees, such as elm mottle in lilac (*Syringa vulgaris* L.) and elm (*Ulmus glabra* L.); apple/rose mosaic in rose (*Rosa* spp. generally); prunus necrotic ringspot in horse chestnut (*Aesculus hippocastanum* L.); tulare apple mosaic and apple mosaic viruses in hazel (*Corylus avellana* L.). Ilarviruses tend to be host specific, being transferred from host to host via pollen. Other means of transmission are at present unknown.

3. *Cucumoviruses* infect plants in more than forty plant families. They are among the commonest opportunists found in cultivated plants, such as cucumber mosaic in honeysuckle (*Lonicera periclymenum* L.); privet (*Ligustrum* spp.) and *Paulownia tomentosa* (Thunb) Steud. Cucumoviruses are transmitted in seed, and non-persistently by at least sixty species of polyphagous aphid vectors.

4. *Tobacco necrosis virus* (TNV) is a group composed of many variants, capable of infecting species in at least 37 plant families. Unlike nepo-, ilar-, and cucumo-viruses which permeate roots, shoots and foliage, TNV is typically confined to roots, being transmitted by root-infecting fungi.

5. *Tobraviruses* are transmitted by vagrant soil-inhabiting nematodes (*Trichodorus* and *Paratrichodorus*) to more than 400 species in fifty plant families. Tobraviruses resemble TNV in that they

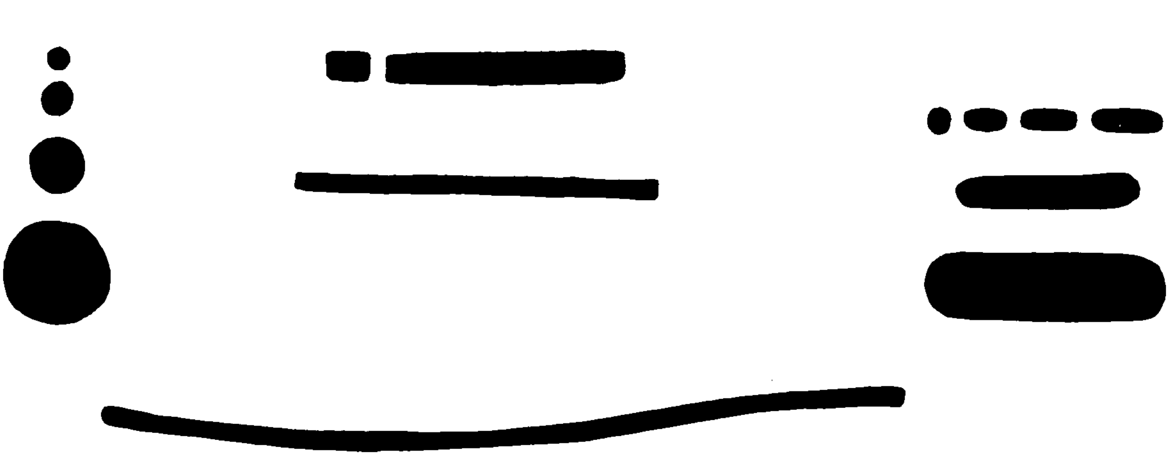


Plate 12—Spectrum of shapes and sizes of virus particles detected in trees and shrubs.

Photograph by courtesy of Natural Environment Research Council

are often restricted to roots. Tobacco rattle virus, the more prevalent member of the group, damages many agricultural and horticultural crops and has been associated with foliage symptoms in *Chinonanthus virginica* L. and was detected in poplar roots (Cooper and Sweet, 1976).

6. *Tobamoviruses* occur in large concentrations in infected plants and can be spread by contact (when healthy plants rub against infected specimens). Although they infect many hosts when artificially inoculated, the type member of the group (tobacco mosaic virus, TMV) has been infrequently isolated from trees. Virus particles resembling TMV, however, were detected in *Quercus* spp. in conditions that suggest that natural spread might have occurred with the aid of the powdery mildew fungus (*Sphaerotheca lanestris* Harkin). Other possible members of the group, such as potato mop-top virus, are transmitted by root-infecting fungi (Plasmodiophorales: *Spongospora subterranea* Lagerh.)

7. *Potexviruses* generally spread by contact when healthy plants rub against infected specimens yet tend to have restricted natural host ranges. A potexvirus is widely distributed in stocks of hydrangea.

8. *Carlaviruses* are specialist viruses, infections often being symptomless. Some members of the group are transmitted non-persistently by aphids, others have been (i) associated with diseases in woody plants, such as poplar mosaic, or (ii) recorded as latent, as in American elder (*Sambucus canadensis* L.).

9. *Potyviruses* are specialists, transmitted by aphids in the non-persistent manner and sometimes transferred in seeds. The economically damaging disease of fruit trees, plum pox, is readily perpetuated by vegetative propagation which also favours the perpetuation of Wisteria vein mosaic.

10. *Closteroviruses* have the longest particles yet detected in trees and shrubs. They have a semi-persistent relationship with their aphid vectors. Tristeza (sorrow) virus in citrus has destroyed seven million orange trees in Brazil alone. Apple stem grooving and the widespread but frequently inconspicuous apple chlorotic leafspot are less devastating. Closterovirus-like particles have been noted in lilac and *Crataegus* spp.

11. *Alfalfa mosaic viruses* are opportunists, widespread in woody plants such as *Daphne* spp., *Viburnum* opulus L., *Caryopteris incana* L., and *Philadelphus* spp. They are capable of infecting more than 300 species in 47 plant families. Although their bacilliform particles are morphologically distinctive, alfalfa mosaic resembles cucumoviruses in being transmitted non-persistently by aphids.

12. *Rhabdoviruses* have relatively large bacilliform or bullet-shaped particles resembling some viruses naturally infecting insects and others associated with diseases of fish and mammals. Some are persistently transmitted by aphids or leaf hoppers. Of those which infect plants, few have been studied in detail. Rhabdovirus-like particles have been found in tissues of woody plants, e.g. laburnums with foliar vein clearing.

The twelve groups of viruses briefly described account for about 10 per cent of the known plant pathogenic viruses. For further information, reference should be made to the AAB/CMI Descriptions of Plant Viruses and to other texts (Matthews, 1970; Gibbs and Harrison, 1976; Kado and Agrawal, 1972; Maramorosch, 1969).

Control (Prevention is better than cure)
Except for eliminating affected and unthrifty trees, it is usually impractical to prevent the spread of viruses after planting into 'the field'. Attention is inevitably focused on the nursery production of planting stock where critical examination and assessment of vigour can be practised routinely. Nurserymen should be aware that viruses may (i) increase production costs because of the possibly decreased growth of infected stock plants; and (ii) damage subsequent field performance. Nationally, attempts are made to control the introduction and spread of viruses by adopting quarantine measures designed to exclude non-indigenous pests and pathogens. Exclusion is particularly important for viruses because they are difficult to eradicate even when host ranges, rates of spread, and types of vector are fully understood. Nevertheless, there are many measures that arboriculturists can take to diminish the spread of viruses, particularly in hardy stock nurseries. By minimizing the unnecessary importation of rooted plants, the risk of introducing virus-transmitting soil-inhabiting pests, such as eelworms, will be lessened, a measure emphasising the desirability of producing home-grown planting stocks. Foliar insecticidal sprays can minimise existing populations of insect vectors and retard their build-up, but they may have little effect upon the incidence of virus diseases caused by non-persistent viruses because incoming vectors can transmit before being killed by insecticidal residues. By contrast, insecticides diminish infections caused by viruses spread in the persistent manner.

Experiments with food crops have shown that the spread of non-persistent viruses can be lessened by using reflecting 'mulches' (aluminium foil (Plate 13)) to deter aphids from landing (Smith and Webb, 1969), and by planting within protective barriers of tall-growing crops which physically impede incoming vectors while they loose their ability to transmit. For this reason, bananas are grown with coconuts, so decreasing the incidence of banana bunchy-top carried by the aphid *Pentolonia nigro nervosa* Coq (Magee, 1967). In Britain, rye (*Secale cereale* L.) is grown by some nurserymen as a packing material for their plants.

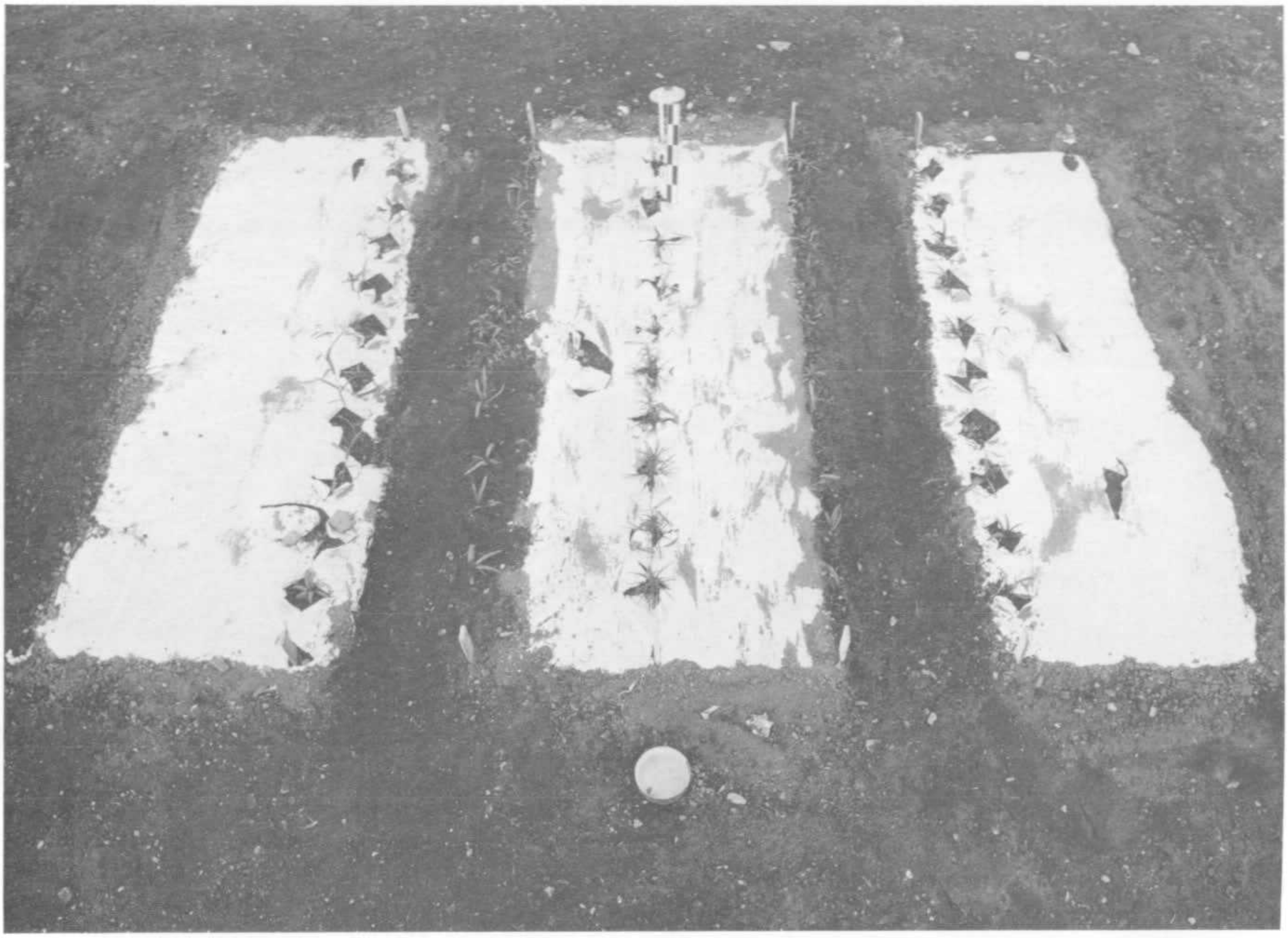


Plate 13—Experimental use of a reflective mulch (1 metre wide strips of aluminium foil laminated on kraft paper) to curtail the spread of viruses transmitted non-persistently by aphids. To achieve maximum aphid repellency, half the ground should be covered with the foil. In this photograph the effectiveness was being assessed on a *Lilium* crop. *Photograph by courtesy of Scottish Horticultural Research Institute*

The tall cereal might diminish rates of non-persistent virus transmission to low growing shrubs.

Soil-inhabiting vectors can be effectively controlled by treating nursery soils with partial sterilants, such as methyl bromide and dichloropropane-dichloropropene. Although these substances minimize the transmission of viruses, it should be remembered that most must be applied some weeks before planting, to facilitate the dispersal of plant damaging (phytotoxic) residues. These chemicals do not inactivate viruses. Instead, they kill their vectors and, in so doing, may diminish populations of beneficial fungi, such as those forming mycorrhizas with tree roots.

Plant nurseries are, for convenient management, typically sited on open-textured soils favouring infestations with soil-inhabiting virus-vector nematodes which are also commonly abundant in hedgerow soils. Trees and shrubs growing in the latter are commonly virus-infected. It is therefore prudent (a) to leave wide headlands and (b) to avoid planting recently cleared hedgerows for at least three years, unless the soil is partially sterilized. Alternatively, these risks can be obviated by propagating trees in steam-sterilized horticultural soil-mixes.

Virus-like symptoms not associated with viruses

Virus-like symptoms sometimes occur in the absence of viruses. In these instances, they may be attributed to :—

(i) feeding damage, e.g. foliar mosaics and shoot proliferation associated with the feeding of eriophyid mites (Carter, 1973; Kado and Agrawal, 1972; Maramorosch, 1969; Pirone *et al*, 1960);

(ii) genetic abnormalities and chimeras;

(iii) nutrient imbalances (Wallace, 1961; Hacskylo *et al*, 1969); and, as recently discovered;

(iv) mycoplasma (MLO) and rickettsia (RLO)-like organisms.

A group of 'yellows' diseases, typically associated with :

(i) foliar yellowing;
(ii) stunted and proliferating axillary shoots with abnormally erect habits (witches' brooms);
(iii) conversion of petals to leafy structures (phyllody Plate 14, Colour).

was, until 1967, thought to be caused by viruses (Doi *et al*, 1967). Although not normally transmissible by mechanically inoculating sap, the infectious agents of "yellows" diseases were transmitted by leaf hoppers, by grafting and some, at least, by dodders (*Cuscuta* spp.). When ultra-thin sections of affected tissues were examined in electron microscopes, rounded or elongated bodies were observed. These bodies, encompassed by unit membranes, seem to contain ribosomes and vary in size (100–1000 nm). Together with helical spiroplasma bodies, 250 nm wide and up to 12,000 nm long, associated with the 'stubborn' disease of citrus (Davis and Worley, 1973; Saglio *et al*, 1973), they are classified as mycoplasma-like organisms (MLOs). All plant MLOs seem to multiply in their insect vectors. Perhaps because high temperatures favour the build-up of leaf-hopper populations it is not surprising that diseases of mulberry, walnut, pecan and ash, attributed to MLOs are frequently reported when and where temperatures are high. While symptoms attributed to viruses are unaffected, symptoms of MLO diseases are suppressed by tetra- and chlortetra-cycline antibiotics.

Rickettsia-like organisms (RLOs) which have relatively thick outer membranes occur in the water-conducting channels (xylem vessels) of their plant hosts in contrast to MLOs which abound in food conducting phloem. Understandably therefore, RLOs tend to be associated with symptoms of wilt, particularly in young tissues. Whereas RLOs are graft transmissible, this method of dissemination is only successful when the source material includes woody tissues. In common with MLOs, they have leaf-hopper vectors but, in contrast, RLOs tolerate tetracycline antibiotics. Characteristically, diseases associated with RLOs are sensitive to differing penicillins which do not seem to affect either viruses or MLOs.

Classically it was assumed that viruses were the causes of disease if infectious agents could not be separated by filtration from extracts of diseased plants. Now, however, the list must be extended to include both MLOs and RLOs which are capable of passing through filters that retain bacteria.

The development of "witches' brooms" in coniferous and broadleaved trees—some affected conifers are retained as commercially desirable dwarf stocks (Waxman, 1975)—has been associated with a variety of pests and pathogens including fungi, insects, mites and, in the USA, dwarf mistletoe (*Arceuthobium* spp). (Gill and Hawksworth, 1961; Gill, 1935; Hawksworth, 1961; Hawksworth and Hines, 1964). However, in some instances, pests and pathogens do not seem to be involved.

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Table 1. **Viruses and graft-transmitted conditions recorded from trees and shrubs**

Genus	Page	Viruses Described (C.M.I./ A.A.B.)	Viruses Detected: Others	Viruses Detected: Graft trans-mission	MLO/ RLO
Abelia	20				
Abeliophyllum	20	j			
Abutilon	20		1		1M
Acacia	20	(a)			
Acer	21	b*(c)	2	2	
Aesculus	21	df		1	
Amelanchier	22	(z)?		1	
Aristolochia	22	be			
Berberis	22	e			
Betula	22	(a)? fghm*	2	1	
Buddleia	25	de			
Buxus	25	b			
Camellia	25			2	
Caragena	25		1		
Carpinus	26			1	
Carya	26				1M
Caryopteris	26	ij			
Castanea	26		1	2	
Catalpa	26	k			
Celastrus	27	j			
Celtis	27	g?			
Chimonanthus	27		1		
Chionanthus	28	ehj			
Cistus	28	i			
Clematis	28	eh			
Conifers	28	b*j*l*m*	2+		1R
Cornus	29	bcegkls			1M
Corylus	30	fx			
Crataegus	30	(f)z			
Daphne	31	bceij	6+		
Diospyros	31		1	1	
Escallonia	32	e			
Eucalyptus	32		1	1	
Euonymus	32	dem	2		
Fagus	33	j			
Ficus	33			1	
Forestiera	33	j			
Forsythia	33	bchijo(p)			
Fraxinus	34	bc	1+1?	4	1M
Fuchsia	37			1	
Galvezia	37	k			
Gleditsia	37				
Hebe	37	i(p)			
Hedera	37	bd	1		
Hydrangea	37	bcehijlmq			1M
Ilex	38	c			
Jasminum	39	bce	1	1	
Juglans	39	g			1M
Laburnum	41	bj	1	1	
Lavandula	41	i			
Leycesteria	41	e			
Ligustrum	42	begrs*	3	1	
Lonicera	42	e	1	1	
Lycium	42	e(p)			
Maclura	43		2		
Magnolia	43	e			
Morus	43	y	1	1	1M
Myrica	44			1	
Nandina	44	e			
Passiflora	44	et	1		
Paulownia	45	e(p)			1M
Philadelphus	45	eip			
Pittosporum	45		1	3	
Populus	46	b*um*o*			
Ptelea	48	bg			
Pyracantha	48	f?			
Quercus	48		2	1	
Rhamnus	50	ei			
Rhododendron	50			1	
Robinia	51	(a)djw	2		1M
Rosa	52	bcdflrv	2+	2+	1M
Romneya	55	e			
Salix	55	(u)			1R
Sambucus	56	bdegjlm	4+1?		
Skimmia	57	c			
Solanum	57	e			
Sorbus	57	z?		2	
Spiraea	58	b			
Staphylea	58	bj			
Symphoricarpus	58	d			
Syringa	58	bdhgjps	3	3	
Taxus	60			1	
Tilia	60			2	
Ulmus	61	gp	1	2+	2M
Viburnum	66	i			
Wistaria	67		1		

Symbols in parentheses indicate viruses to which the host was susceptible by inoculation.

Symbols marked with an asterisk indicate viruses detected in roots but not foliage.

a bean yellow mosaic (Bos. 1970; C.M.I./A.A.B. Descr. Plant Viruses no. 40)
b arabis mosaic (Murant, 1970; C.M.I./A.A.B. Descr. Plant Viruses no. 16)
c tobacco ringspot (Stace-Smith, 1970; C.M.I./A.A.B. Descr. Plant Viruses no. 17)
d strawberry latent ringspot (Murant, 1974; C.M.I./A.A.B. Descr. Plant Viruses no. 126)
e cucumber mosaic (Gibbs and Harrison, 1970; C.M.I./A.A.B. Descr. Plant Viruses no. 1)
f apple mosaic (Fulton, 1972; C.M.I./A.A.B. Descr. Plant Viruses no. 83)
g cherry leaf roll (Cropley and Tomlinson, 1971. C.M.I./A.A.B. Descr. Plant Viruses no. 80)
h tobacco rattle (Harrison, 1970; C.M.I./A.A.B. Descr. Plant Viruses no. 12)
i alfalfa mosaic (Bos and Jaspars, 1971; C.M.I./A A.B. Descr Plant Viruses no. 46)
j tomato black ring (Murant, 1970; C.M.I./A A.B. Descr Plant Viruses no. 38)
k broad bean wilt (Taylor and Stubbs, 1972; C.M.I./A A B. Descr. Plant Viruses no. 81)
l tomato ringspot (Stace-Smith, 1970; C.M.I./A.A B. Descr. Plant Viruses no. 18)
m tobacco necrosis (Kassanis, 1970; C.M.I./A.A.B. Descr Plant Viruses no. 14)
n elderberry latent (Jones, 1974; C.M.I./A.A.B. Descr. Plant Viruses no. 127)
o raspberry ringspot (Murant, 1970; C.M.I./A.A.B. Descr. Plant Viruses no. 6)
p elm mottle (Jones, 1974; C.M.I./A.A.B. Descr. Plant Viruses no. 139)
q hydrangea ringspot (Koenig, 1973; C.M.I./A.A.B. Descr. Plant Viruses no. 114)
r prunus necrotic ringspot (Fulton, 1970; C.M.I./A.A.B. Descr. Plant Viruses no. 5)
s tomato bushy stunt (Martelli *et al.*, 1971; C.M.I./A.A.B. Descr. Plant Viruses no. 69)
t passion fruit woodiness (Taylor and Greber, 1973; C.M.I./A.A.B. Descr. Plant Viruses no. 122)
u poplar mosaic (Biddle and Tinsley, 1971; C.M.I./A.A.B. Descr. Plant Viruses no. 75)
v tobacco streak (Fulton, 1971; C.M.I./A.A.B. Descr. Plant Viruses no. 44)
w robina true mosaic (Schmelzer, 1971; C.M.I./A.A.B. Descr. Plant Viruses no. 65)
x tulare apple mosaic (Fulton, 1971; C.M.I./A.A.B. Descr. Plant Viruses no. 42)
y mulberry ringspot (Tsuchizak, 1975; C.M.I./A.A.B. Descr. Plant Viruses no. 112)
z apple chlorotic leaf spot (Lister, 1970; C.M.I./A.A.B. Descr. Plant Viruses no. 30)

Note added in proof

When preparing this conspectus, the author endeavored to be comprehensive but anticipated that some relevant data would be omitted accidentally. He is now aware that in the U.S.A. bean yellow mosaic virus naturally infects *Cladrastis lutea* Koch and that the virus caused leaf deformation and veinal chlorosis (Provvidenti, R. and Hunter, J.E. *Pl. Dis. Reptr.* 1975, **59**, 86–7).

Furthermore, following the recent presentation to the University of Bristol of a thesis for the degree of Doctor of Philosophy, it is apparent that Dr J. B. Sweet has isolated raspberry ringspot virus from *Daphne* "Somerset" having in some instances foliar chlorotic spots and has implicated graft transmissible agents resembling apple stem grooving virus (Lister, 1970; C.M.I./A.A.B. Descr. Plant Viruses No. 31) with stunting and chlorotic flecking in leaves of *Sorbus "mitchellii"*.

The author will appreciate being told of any errors of fact or interpretation and would like to be informed of all relevant new data.

ABELIA—*Caprifoliaceae*

Waterworth *et al.*, (1975) isolated a virus from "herbaceous hosts" inoculated with sap extracts of petals from symptomless *Abelia grandiflora* Rehd. Judged by host range, symptoms in "herbaceous hosts" and serological properties, the virus seemed closely related to, but not identical with, two tymoviruses (eggplant mosaic and andian potato latent viruses).

COMMENT: When inoculated to *Acer palmatum* Thunb., an isolate of Abelia virus caused mild chlorotic vein banding patterns. The virus infected *Rhododendron sp* without causing visible symptoms.

Reference
Waterworth, H.E., Kaper, J.M. and Koenig, R. (1975). Purification and properties of a tymovirus from *Abelia*. Phytopathology **65**, 891–896.

ABELIOPHYLLUM—*Oleaceae*

Foliage disease

SYMPTOMS: Diffuse mottling along veins in immature leaves with chlorotic patches and later white or red discolourations near veins. Visible only in spring.

Distribution: In *Abeliophyllum distichum* Nakai in an East German botanic garden.

Transmission: Mechanically by inoculating infectious sap to "herbaceous hosts."

Causal agent/Relationship: Tomato blackring virus was identified but not proved to be the cause of the disease in *A. distichum* (Schmelzer, 1974).

Reference
Schmelzer, K. (1974). Untersuchungen an Viren der Zier-und Wildegeholze 8. Mitteilung Neue Befunde an *Forsythia. Hydrangea* und *Philadelphus* sowie Viren und Virosen an *Rhamnus, Centaurea, Galvezia, Cistus, Forestiera, Abeliophyllum, Celastrus, Staphylea* und *Crambe*. *Zbl. Bakt. Parasit Kde* **129** *Abt. II*, 139-68.

ABUTILON—*Malvaceae*

Foliage disease

SYMPTOMS: Bright yellow-green variegation; witches broom may occur later (Flores and Silberschmidt, 1967).

Distribution: Probably worldwide in horticulturally desirable and vegetatively propagated *Abutilon thompsonii* (*A. striatum* Dickson var Thomsonii Veitch) and *A. megapotamium* St. Hilaire and Noral.

Transmission: By grafting variegated with healthy *Abutilon* spp. (Baur, 1904) and in 14–24% seed (Keur, 1934). In Brazil, natural vectors are whiteflies, *Bemisia tabaci* Genn (Orlando and Silberschmidt, 1946). In rare instances mechanical transmission in sap to "herbaceous hosts" has been obtained (Costa and Carvalho, 1960).

Plate 15—Leaf of *Abutilon* sp. showing discrete patches of yellow and shades of green; a mosaic symptom associated with a graft-transmissible agent.

Photograph by courtesy of Natural Environment Research Council

Causal agent/Relationship: Unknown; mycoplasma-like organisms were associated in some instances with variegation in *A. striatum* (de Leeuw, cited in Costa, 1976).

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ACACIA—*Leguminosae*

Acacia sp. (unnamed) were stated (Atanasoff, 1967) to be susceptible to natural infection with bean yellow mosaic virus but unfortunately the symptoms were not described, so it is impossible to judge whether there was any similarity with the yellow ring-like spots, affecting *A. saligna* Wendl., which in Italy were reportedly associated with an agent transmissible by grafting (Marras, 1962).

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Atanasoff, D. (1967). Virus stem pitting of Birch. *Z. Pflkrankh. PflPath. PflSchutz*, **74**, 205–08.
Marras, F. (1962). La Maculatura Anulaire dell *Acacia saligna*. *Riv. Patol. Veg., Padova* **2**, 275–80.

ACER—*Aceraceae*

Foliage diseases

SYMPTOMS: Yellow mottle-mosaic (Atanasoff, 1935; for others see Brierley, 1944).

Distribution: In horticultural forms of *Acer negundo* L. and Sycamore (*A. pseudoplatanus* L.) in Europe and Japan.

Transmission: By grafting.

Causal agent/Relationship: Unknown.

SYMPTOMS: Chlorotic or ring mottle.

Distribution: In *A. saccharum* Marsh in North America (Brierley, 1944) and in Roumania (Ploaie and Macovei, 1968).

Transmission: No information.

Causal agent/Relationship: Unknown.

SYMPTOMS: Severe stunting and dense green foliage preceding decline and death.

Distribution: In *A. rubrum* L. in USA (Kenknight, 1960).

Transmission: By grafting from Acer to rosaceous hosts e.g. *Prunus angustifolia* Marsh.

Causal agent/Relationship: Unknown.

SYMPTOMS: Shortening of internodes, terminal bud failure, changes in leaf outline and mosaic mottling with chlorotic (tending to yellow ochre) spots (Szirmai, 1972).

Distribution: In *A. negundo* and *A. pseudoplatanus* in Hungary (Szirmai, 1972) and UK (Cooper, unpublished data).

Transmission: Leaf symptoms are the only part of the syndrome which have been 'transmitted' (to eleven of twenty seedlings by chip budding). Whiteflies, *Trialeurodes vapoariorum* West, were vectors in two of three tests which have not been attempted with aphids.

Causal agent/Relationship: Unknown.

SYMPTOMS: Vein chlorosis, leaf blade perforation—"tatter leaf" (Smolak, 1949; Blattny, 1950).

Distribution: In *A. pseudoplatanus* and *A. negundo* in Czechoslovakia.

Transmission: In sap using charcoal or bentonite to aid transmission (Subikova, 1973).

Causal agent/Relationship: Unknown; symptoms in test plants resembled those due to tobacco necrosis virus.

COMMENTS: Mosaic and narrowing of leaf laminae in *A. negundo* and mild mosaic in *A. ginnata* Mich. developed when these plants were inoculated with tobacco ringspot virus (Wilkinson, 1952).

Arabis mosaic virus was detected in roots of *A. pseudoplatanus* but was not associated with leaf symptoms (Thomas, 1970).

References
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Wilkinson, R.E. (1952). Woody plant hosts of the tobacco ringspot virus. *Phytopathology* **42**, 478.

AESCULUS—*Hippocastanaceae*

See Plate 16 & 17.. Colour & Cover

Foliage diseases

SYMPTOMS: Yellow mosaic.

Distribution: Affecting *A. hippocastaneum* L. from Czechoslovakia, East Germany, Roumania and UK (Timpi, 1907 cited in Brierley, 1944, Sweet, 1976). Propagated commercially and widely distributed in UK because of attractive foliage.

Transmission: By budding and grafting between *A. hippocastaneum*, also when budded into woody indicators of apple viruses, to cause symptoms resembling those associated with prunus necrotic ring spot virus (Sweet, 1976). No infection detected in 50 seedlings from seed of infected *A. hippocastaneum* (Sweet *et al*, 1978).

Causal agent/Relationship: Unknown; but serological tests on yellowed *Aesculus* leaves revealed infection with the apple mosaic serotype of prunus necrotic ringspot virus (Sweet *et al*, 1978).

SYMPTOMS: Tatter leaf syndrome called 'necrosis' (Smolak, 1963) associated with diminished growth, clustered branches, few or no flowers and inviable seed.

Distribution: In *A. hippocastaneum* in Czechoslovakia.

Transmission: By grafting, even though no union established. Uncertain whether the whole syndrome developed in grafted plants.

Causal agent/Relationship: Unknown; syndrome somewhat resembles incipient witches broom.

SYMPTOMS: Chlorotic or necrotic ring and line patterns.

Distribution: In *A. carnea* Hayne in East Germany (Schmelzer and Schmidt, 1968).

Transmission: Mechanically, by inoculating infectious sap to "herbaceous hosts".

Causal agent/Relationship: Strawberry latent ringspot virus isolated from diseased specimens but not confirmed as causal agent (Schmelzer, 1969).

References

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AMELANCHIER—*Rosaceae*

Foliage disease

SYMPTOMS: Yellow ring and line patterns.

Distribution: In *A. vulgaris* Moench in Netherlands.

Transmission: By grafting between *A. vulgaris* (van Katwijk, 1957).

Causal agent/Relationship: Unknown.

COMMENT: When *A. canadensis* (L.) Med. was grafted with *Sorbus aucuparia* L. showing yellow rings and lines in the foliage, chlorotic ring and line patterns developed in the *A. canadensis* (Kralikova, 1961). For associated virus—see under Sorbus (p 58).

References

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ARISTOLOCHIA—*Aristolochiaceae*

Foliage disease

SYMPTOMS: Chlorotic ring and line patterns.

Distribution: Affecting *A. durior* Hill and *A. clematis* L. throughout Northern Europe.

Transmission: Mechanically, by inoculating infectious sap to "herbaceous hosts".

Causal agent/Relationship: Cucumber mosaic (Lihnell, 1951) and arabis mosaic viruses (Schmelzer and Schmidt, 1968) have been isolated singly and together, but their effects on healthy *Aristolochia* seem not to have been tested.

References

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BERBERIS—*Berberidaceae*

Foliage disease

SYMPTOMS: (a) Leaf mosaic characterized by reddish blotches;
(b) varying degrees of foliar distortion and
(c) restriction of leaf area.

Distribution: New York State, USA, affecting *B. thunbergii* DC (Wilkinson, 1953).

Transmission: Mechanically, when sap from diseased host was inoculated to "herbaceous hosts". The virus identified as cucumber mosaic virus.

Causal agent/Relationship: Characteristic symptoms developed when *Berberis* seedlings were inoculated and systemically infected with an isolate of cucumber mosaic virus.

Reference:

Wilkinson, R.E. (1953). *Berberis thunbergii*, a host of cucumber mosaic virus. *Phytopathology* **43**, 489.

BETULA—*Betulaceae*

See plate 18, 19, 22 (Colour)

Foliage diseases

SYMPTOMS: Chlorotic (or in summer, white) lines forming "oak leaf" designs, irregular rings or linear flecks, together with, in rare instances, mild mosaic. Symptoms erratic and usually restricted to a few fully expanded leaves on some branches.

Distribution: On *Betula papyrifera* Marsh and *B. alleghaniensis* Britton in Eastern Canada and in the

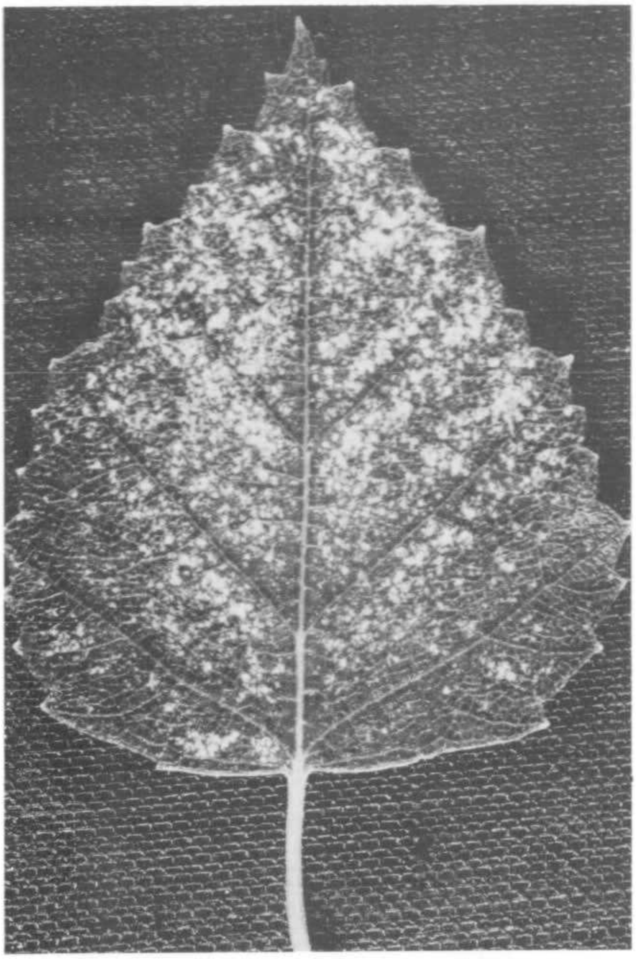

Plate 20—Betula verrucosa experimentally infected with apple mosaic virus and showing chlorotic white spots in a later formed leaf. *Photograph by courtesy of The State Plant Pathology Institute Denmark*

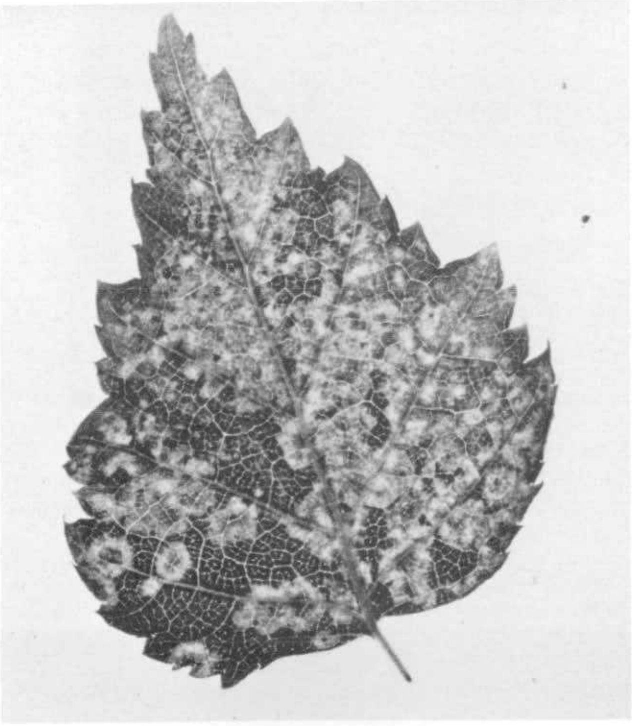

Plate 21—Betula verrucosa experimentally infected with cherry leaf roll virus and showing yellow ring and blotch patterns in later formed leaves. *Photograph by courtesy of Natural Environment Research Council*

North-eastern USA (Hansbrough, 1953; Berbee, 1957; Gotlieb and Berbee, 1973).

Transmission: Ten of twelve *B. alleghaniensis*, patch grafted from diseased plants, developed symptoms (Berbee, 1959). Line patterns observed in *B. papyrifera* and *B. alleghaniensis* budded with diseased *B. papyrifera*. However, by the fourth growing season, the inoculated plants were symptomless (Gotlieb and Berbee, 1973). Attempts to transmit the infectious agent with leafhoppers (unnamed) were inconclusive (Berbee, 1957). It was transmitted to "herbaceous hosts" but not *Betula* spp. in sap from newly expanded leaves of *B. papyrifera* (Gotlieb and Berbee, 1973) and *B. alleghaniensis* (Gotlieb, 1975).

Causal agent/Relationship: In serological (gel diffusion) tests, a virus isolated from *B. papyrifera* had many antigens in common with a rose isolate of apple mosaic virus but few if any determinants in common with an isolate of prunus necrotic ringspot (Gotlieb and Berbee, 1973). An isolate from *B. alleghaniensis* was serologically similar to, but not necessarily identical with, a *B. papyrifera* isolate of apple mosaic virus (Gotlieb, 1975).

COMMENTS: Experimental graft transmission of apple mosaic virus from infected apple induced small white spots to form in leaves of *B. verrucosa* (Kristensen and Thomsen, 1962). The virus was recovered two years later from the birch when grafted to apple (Thomson, pers. comm.).

SYMPTOMS: Diffuse mottle with chlorotic spots or lines in spring/summer, changing to yellow line patterns, rings and patches in autumn. Symptom expression erratic and partial in affected trees.

Distribution: Eastern Germany (Schmelzer, 1972) and UK (Cooper and Atkinson, 1975) affecting *B. verrucosa* Ehrh. and *B. pubescens* L.

Transmission: Mechanically in extracts of pollen, roots or leaves of affected birches to infect "herbaceous hosts". Virus occurring naturally in pollen infects up to 75% birch seed. There is no evidence suggesting that the virus is naturally transmitted between birches by soil-inhabiting nematodes (Cooper, 1976).

Causal agent/Relationship: The infectious agent has antigenic properties in common with cherry leaf roll virus (CLRV), and although three birch CLRV isolates had many antigenic determinants in common, each was distinguishable from isolates of the virus from other genera, eg. *Prunus*, *Sambucus*. Cherry, elder and birch isolates of CLRV, propagated in "herbaceous hosts", induced the formation of yellow ring and line patterns one year after being inoculated to *B. verrucosa* seedlings (Cooper and Atkinson, 1975); a birch isolate induced 'leaf roll' when inoculated to *Prunus avium* L. (Cooper, 1976).

SYMPTOMS: Yellow chevrons, oak leaf patterns and ringspots.

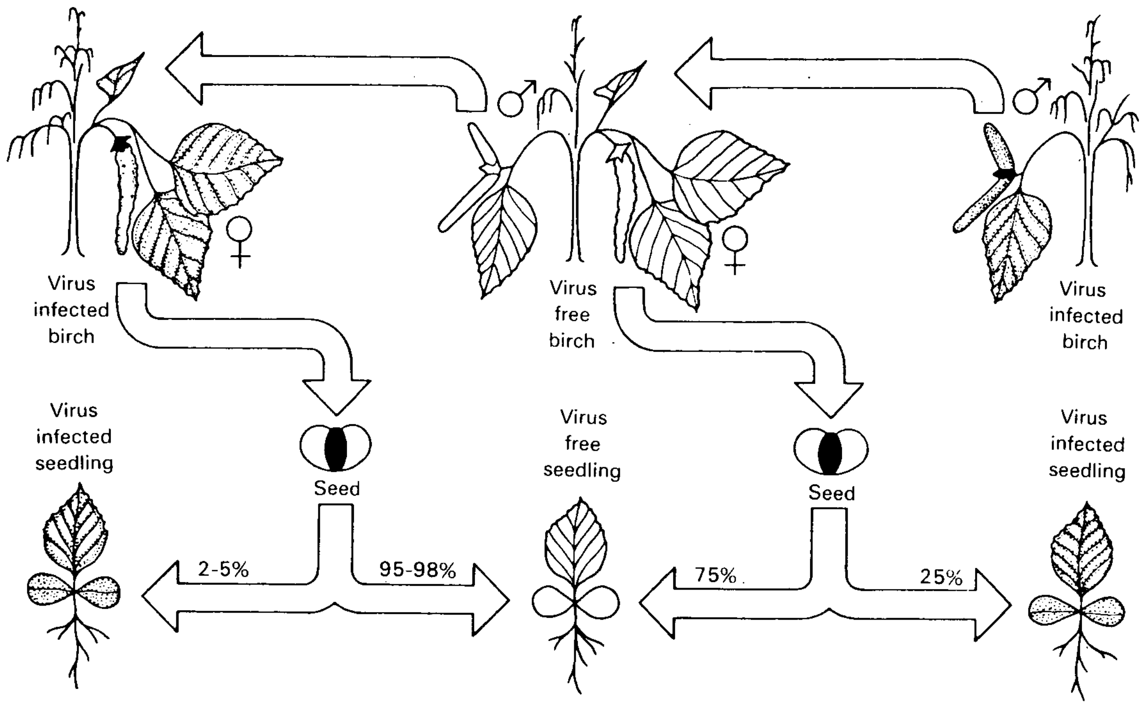

Plate 23—Diagram showing maternal and paternal factors influencing the transmission of cherry leaf roll virus to seeds of *Betula verrucosa*. Fewer seeds were infected when female flowers on infected trees were fertilized with healthy pollen than when virus-carrying pollen was applied to healthy trees. In these experiments, four maternal birch trees remained healthy during two seasons even though part of the seed produced carried cherry leaf roll virus. *Photograph by courtesy of Natural Environment Research Council*

Distribution: Experimentally incited in Bulgaria (Atanasoff, 1967).

Transmission: By grafting birch (species not given) with bark from *Acacia* sp. naturally infected with bean yellow mosaic virus.

Causal agent/Relationship: Not known. Unfortunately, Atanasoff did not assay foliage showing symptoms after grafting.

SYMPTOMS: Chlorotic vein banding pattern.

Distribution: Unknown. One seedling of *B. pubescens* from about 500 growing in sterilized compost in UK showed symptoms for the first season of growth in a cool glasshouse.

Transmission: Transmitted to *B. pubescens* neither by budding nor by parasitizing dodder *Cuscuta europeaus* L. Not sap transmitted to "herbaceous hosts".

Causal agent/Relationship: Two types of virus-like particles (tubular and spherical, c 30nm diameter) were found when sap from a leaf with symptoms was examined (J.I. Cooper, unpublished data).

COMMENTS: When assaying *B. verrucosa* roots, naturally occurring tobacco necrosis virus was detected (Cooper, 1976). Cadman (cited in Schmelzer, 1972) detected tobacco rattle virus in *B. verrucosa* foliage with chlorotic symptoms but did not prove that the virus caused the disease.

Stem disease

SYMPTOMS: Stem grooving, pitting and figuring in wood.

Distribution: Locally in Northern Europe and U.S.S.R.

Transmission: By grafting from *B. verrucosa* forma carelica (Peterson and Vitola, 1971). Also in soil (Sakss and Banders, 1974). The characteristic anatomy developed in wood three years after seedlings of healthy *B. verrucosa* were grown in soil taken from the root regions of natural Karelian birch in the U.S.S.R.

Causal agent/Relationship: Not known.

COMMENTS: The figuring in wood enhances timber value for veneers. Somewhat similar syndromes of untested aetiology are reportedly widespread in Europe (Gardiner, 1965). Atanasoff (1967) speculated on the possible virus aetiology of *B. verrucosa* forma carelica, forma gibbosa, forma callosa and forma maseria.

References

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Hansbrough, J.R. (1953). The significance of the fungi and viruses associated with birch dieback. *Report of the symposium*

on birch dieback. Ottawa, 1952, 128–135. Dept Agriculture, Canada.
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Peterson, L. and Vitola, R. (1971). (The occurrence of stem pitting in Birch). *Trudy LSKhA Latvijas Lauksaimniecivas Akademijas Raskstí* **40**, 20–24.
Sakss, K. and Banders, V. (1974). (Studies on growing the figure wood of Karelian Birch) For. Abstr. **38**, 5928.
Schmelzer, K. (1972). Das Kirchenblattroll-virus aus der Birke (*Betula pendula* Roth.) *Zentbl. Bakt. ParasitKde Abt. II*, **127**, 10–12.

BUDDLEIA—*Loganiaceae*

Foliage disease

SYMPTOMS: Narrowing of leaf lamina; arc and ring patterns.

Distribution: In the UK (Smith, 1952), the Netherlands (Bouwman and Noordam, 1955) and Eastern Germany (Schmelzer and Schmidt, 1968) and in France (Signoret, 1969) affecting *Buddleia davidii* Franchet.

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationship: Cucumber mosaic virus was identified and Koch's postulates satisfied by Schmelzer and Schmidt (1968).

COMMENTS: With few details, van Hoof and Carron (1975) reported that strawberry latent ringspot virus was detected in foliage of *B. davidii* and that the virus was seed borne in this plant.

References
Bouwman, L.W.M. and Noordam, D. (1955). Komkommermosaickvirus in *Buddleia davidii* Franch. *Tijdschr. PlZiekt.* **61**, 79–81.
Schmelzer, K. and Schmidt, H.E. (1968). Untersuchungen an Viren der Zier- und Wildegeholze. 6. Mitteilung: Erganzende Befunde and *Caryopteris* sowie Virosen an *Philadelphus, Aristolochia, Buddleja, Lycium* und *Aesculus*. Phytopath. Z. **62**, 105–126.
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van Hoof, H.A. and Carron, J.E.A. (1975). Strawberry latent ringspot virus-infected fields of *Rosa rugosa* produce healthy cuttings but diseased rootstocks for standard roses. *Meded. Fac. Landbouw. RijksUniv. Gent* **40**, 759–763.

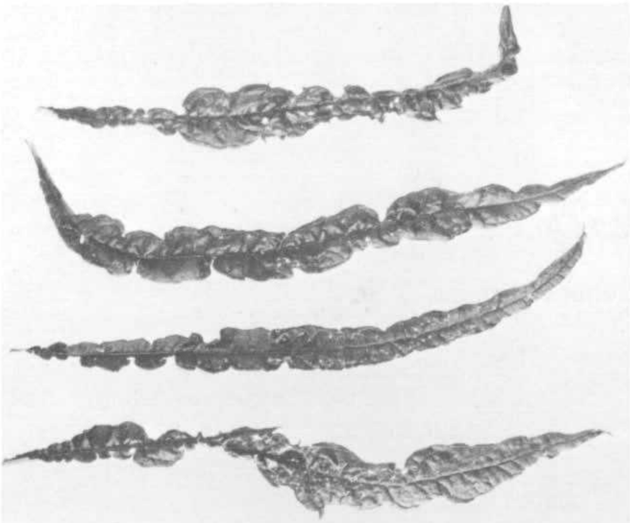

Plate 24—Leaves of *Buddleia variabilis* showing mottle and distortion symptoms when infected with cucumber mosaic virus.
Photograph by courtesy of Glasshouse Crops Research Institute

BUXUS—*Buxaceae*

In a brief statement without details, *Buxus simpervirens* L. was said to be a natural host of arabis mosaic virus (Lister in Frazier *et al*, 1970).

Reference
Frazier, N.W., Fulton, J.P., Thresh, J.M., Converse, R.H., Varney, E.H. and Hewitt, W.B. (1970). p.38. *Virus diseases of small fruits and grape vines.* Berkeley: University of California, Division of Agricultural Sciences.

CAMELLIA—*Ternstroemiaceae*

Flower break symptoms and irregular chlorotic or yellow foliar blotches have been repeatedly observed in *Camellia japonica* L., hence the appellation 'variegated' in horticultural publications. Plakidas (1954) recognised another syndrome including yellow foliar ringspot patterns, in addition to the symptoms already described. These and a severe chlorosis in new growth developed when agents were transmitted by cleft grafting techniques to and from cultivars of *C. japonica* and seedlings of *C. sasanqua* Thun. (Plakidas, 1954). Unequivocal proof of a virus origin is still lacking.

Reference
Plakidas, A.G. (1954). Transmission of leaf and flower variegation in Camellias by grafting. *Phytopathology* **44**, 14–18.

CARAGENA—*Leguminosae*

Foliage disease

SYMPTOMS: Chlorotic, eventually yellow spots appearing to spread from the point of insertion of petiole into lamina to give an oak leaf vein banding effect.

Distribution: In Poland affecting *Caragena arborescens* Lam. (Kochman and Sikora, 1968).

Transmission: In sap to "herbaceous hosts" Attempts to transmit the infectious agent from herbaceous plants to *C. arborescens* or between *C. arborescens* seem to have been unsuccessful (Kochman and Sikora, 1968).

Causal agent/Relationship: Unknown.

Reference
Kochman, J. and Sikora, A. (1968). Experiments with a new virus disease of the pea tree (*Caragena arborescens* Lam.). *Phytopath. Z.* **61**, 147–156.

CARPINUS—*Betulaceae*

A chlorotic line pattern on foliage has been reported on *Carpinus betulus* L. growing in Italy: an agent was reportedly transmitted to *Ostrya carpinifolia* Scop. by budding and chip-grafting (Gualaccini, cited in Seliskar, 1966). Unfortunately, very scant details were provided.

Reference
Seliskar, C.E. (1966). FAO/IUFRO Symposium on internationally dangerous forest diseases & insects. 44, Oxford 1964. (FAO/FORPEST 64–5, 1966).

CARYA—*Juglandaceae*

See plate 25 (Colour)

Stem disease: Pecan bunch.

SYMPTOMS: Branch dieback and witches' broom.

Distribution: Frequent in *Carya pecan* (Marsh) Eng. and Graebn. and *C. illioensis* (Wang) K. Koch in the USA (Selsikar *et al.*, 1974; Dale, 1977).

Transmission: By grafting affected and healthy *C. pecan*. (Cole, 1937).

Causal agent/Relationship: Mycoplasma like organisms detected by electron microscopy (Seliskar *et al.*, 1974; Dale, 1977).

COMMENT: A somewhat similar witches' broom disease, with which grafting tests do not seem to have been done, was reported in *C. ovata* (Mill) K. Koch (Seliskar, 1966).

References
Cole, J.R. (1937). Bunch disease of pecans. *Phytopathology* **27**, 604–612.
Dale, J.L. (1977). Mycoplasma like organism observed in pecan with bunch disease in Arkansas. *Pl. Dis. Reptr* **61**, 319–321.
Seliskar, C.E. (1966). FAO/IUFRO Symposium on internationally dangerous forest diseases & insects. 44, Oxford 1964. (FAO/FORPEST 64–5, 1966).
Seliskar, C.E., Kenknight, G.E. and Bourne, C.E. (1974). Mycoplasma like organisms associated with pecan bunch disease. *Phytopathology* **64**, 1269–1272.

CARYOPTERIS—*Verbenaceae*

Two viruses, alfalfa mosaic and tomato black ring, were transmitted to "herbaceous hosts" from *C. incana* Miquel showing large interveinal chlorotic or yellow patches in leaves (Schmelzer, 1962–63; Schmelzer, 1968). Neither virus seems to have been reintroduced into healthy *C. incana*.

References
Schmelzer, K. (1962–63). Untersuchungen an Viren der Zier und Wildgeholze 3. Mitteilung: Virosen an *Robinia, Caryopteris, Ptelea* und anderen Gattungen. *Phytopath. Z.* **46**, 235–268.
Schmelzer, K. (1968). Zier-, Forst- und Wildgeholze. In: *Pflanzliche* Virologie edited by M. Klinkowski. vol. 2 part 2, 232–303. Berlin: Akademie-Verlag.

CASTANEA—*Fagaceae*

Foliage diseases

SYMPTOMS: Leaves, apparently healthy in spring, albeit possibly smaller than usual, become chlorotic or yellow in summer and fall prematurely in autumn. Affected trees with possibly bunched and spindly branches produce few fruits.

Distribution: Affecting *Castanea crenata* Sieb. and Zucc. and *C. mollissima* Blume in Japan (Shimada, 1962).

Transmission: By grafting but not by seed.

Causal agent/Relationship: Unknown.

COMMENTS: Chlorotic flecking, oak-leaf, line pattern and irregular spotting were observed in *Castanea* spp. in Italy. Agents were apparently transmitted by grafting (Gualaccini, 1959).

SYMPTOMS: Narrow crescent shaped and otherwise deformed leaves.

Distribution: In Hungary affecting *Castanea sativa* Mill. (Horvath *et al.*, 1975).

Transmission: Not transmitted following mechanical inoculation of herbaceous test plants (seven families), or seedlings of *Quercus cerris* L. or *C. sativa*. No transmission between *C. sativa* with aphids (*Myzocallis* sp.).

Causal agent/Relationship: Unknown; virus-like rod-shaped particles (300 x 20nm)—characteristic of the tobamovirus group—were found by electron microscopy in affected *C. sativa* foliage.

References
Guallaccini, F. (1959). Atti del primo Convegno sulle malattie da virus dei fruttiferi e della Vite, Pavia, 7–8 Giugno 1958. *Notiz. Mal. Piante* 1959, 47–48 (N.S. 26–27), 155–161.
Horvath, J., Eke, I., Gal, T. and Dezsery, M. (1975). Demonstration of virus-like particles in sweet chestnut and oak with leaf deformation in Hungary. *Z. PflKrankh. PflPath. PflSchutz.* **82**, 489–502.
Shimada, S. (1962). Chestnut yellows. *Pl. Prot., Tokyo*, **16**, 253–254.

CATALPA—*Bignoniaceae*

Foliage disease

SYMPTOMS: Chlorotic leaf spotting.

Distribution: Affecting *Catalpa bignoniodes* Walt. in Eastern Europe (Schmelzer, 1970).

Transmission: Mechanically in leaf sap to "herbaceous hosts".

Causal agent/Relationship: Broad bean wilt virus (Taylor and Stubbs, 1972) was identified and proved to be a causal agent, Koch's postulates having been satisfied (Schmelzer, 1970).

References

Schmelzer, K. (1970). Untersuchungen an Viren der Zier-und Wildgeholze. 7. Mitteilung: Weitere Befunde an *Buddleja, Viburnum, Caryopteris* und *Philadelphus* sowie Viren an *Leycesteria, Chionanthus, Ribes, Hydrangea, Syringa, Spiraea* und *Catalpa*. *Phytopath. Z.* **67**, 285–326.

Taylor, R.H. and Stubbs, L.L. (1972). Broad bean wilt virus. *C.M.I./A.A.B. Descr. Plant Viruses*. no. 81.

CELASTRUS—*Celastraceae*

Foliage disease

SYMPTOMS: Chlorotic mottle and rings.

Distribution: Affecting *Celastrus orbiculatus* Thunb. in an arboretum in East Germany.

Transmission: In leaf sap to "herbaceous hosts".

Causal agent/Relationship: The potato bouquet serotype of tomato blackring virus was identified, but not proved to have caused the disease with which it was associated (Schmelzer, 1974).

References

Schmelzer, K. (1974). Untersuchungen an Viren der Zier-und Wildegeholze 8. Mitteilung Neue Befunde an *Forsythia. Hydrangea* und *Philadelphus* sowie Viren und Virosen an *Rhamnus, Centaurea, Galvezia, Cistus, Forestiera, Abeliophyllum, Celastrus, Staphylea* und *Crambe*. *Zbl. Bakt. ParasitKde* **129** *Abt II*, 139–168.

CELTIS—*Ulmaceae*

Foliage disease

SYMPTOMS: Chlorotic-yellow blotches somewhat more apparent in summer after cold spring weather and on young branches produced following pruning.

Distribution: Affecting *Celtis australis* L. in Italy and Yugoslavia (Anselmi and Saric, unpublished data).

Transmission: In sap.

Causal agent/Relationship: Unknown, but elm mosaic virus (cherry leaf roll virus) has been transmitted to "herbaceous hosts" from Celtis with symptoms (Saric, unpublished data).

COMMENT: Using *Celtis* foliage from Italy, repeated attempts failed to detect sap transmissible virus (Cooper, unpublished data).

CHIMONANTHUS—*Calycanthaceae*

Foister (1961) reported with few details the transmission of a virus (not identified) to *Nicotiana* (species not given) from *Chimonanthus fragrans* Lindl. showing chlorotic mottle symptoms in the leaves.

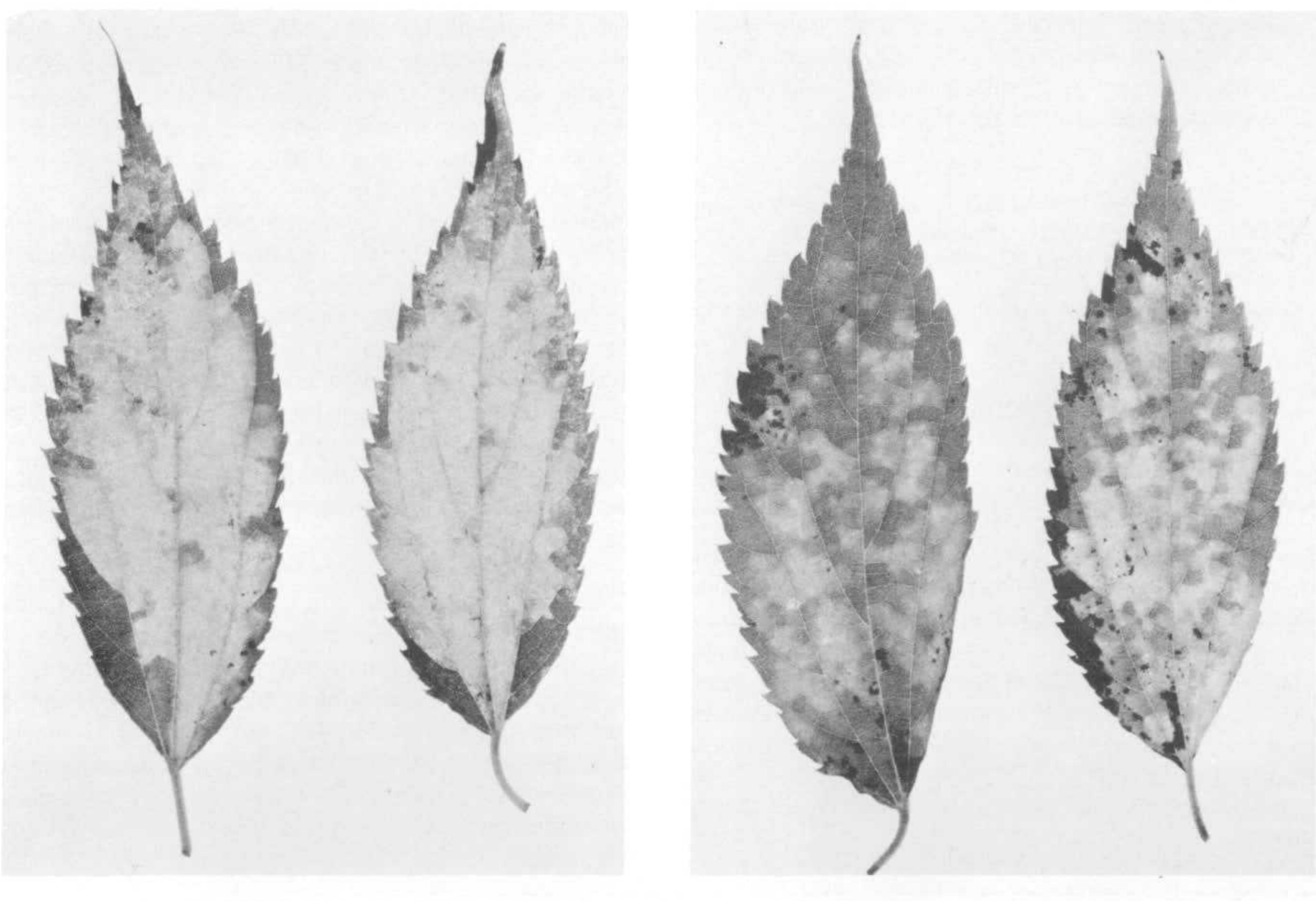

Plate 26—Celtis australis leaves showing chlorotic mosaic symptom associated in a few instances with cherry leaf roll virus.

Photograph by courtesy of Natural Environment Research Council

Reference
Foister, C. E. (1961). The economic plant diseases of Scotland. Tech. Bull. No. 1. Department of Fisheries for Scotland, Published by H.M.S.O., Edinburgh, 209 pp.

CHIONANTHUS—*Oleaceae*

See plate 42a (Colour)

Mixtures of the following viruses: tomato black ring, tobacco rattle and cucumber mosaic were detected in "herbaceous hosts" inoculated with sap from leaves of *Chionanthus virginicus* (*virginica*) L. showing chlorotic or necrotic ring and line patterns Schmelzer (1970).

Reference
Schmelzer, K. (1970). Untersuchungen an Viren der Zier-und Wildgeholze. 7. Mitteilung: Weitere Befunde an *Buddleja, Viburnum, Caryopteris* und *Philadelphus* sowie Viren an *Leycesteria, Chionanthus, Ribes, Hydrangea, Syringa, Spiraea* und *Catalpa*. *Phytopath. Z.* **67**, 285–326.

CISTUS—*Cistaceae*

Foliage disease

SYMPTOM: Yellow mottling, lines and rings in some but not all leaves.

Distribution: In a botanic garden in East Germany affecting *Cistus populifolis* L. and *C. monspeliensis* L.

Transmission: Not obtained in sap.

Causal agent/Relationship: Using sap from naturally affected leaves of *Cistus* spp. in serological tests, reactions with alfalfa mosaic virus serum were observed (Schmelzer, 1974).

Reference
Schmelzer, K. (1974). Untersuchungen an Viren der Zier-und Wildegeholze 8. Mitteilung Neue Befunde an *Forsythia. Hydrangea* und *Philadelphus* sowie Viren und Virosen an *Rhamnus, Centaurea, Galvezia, Cistus, Forestiera, Abeliophyllum, Celastrus, Staphylea* und *Crambe*. *Zbl. Bakt. Parasit Kde* **129** *Abt II*, 139–168

CLEMATIS—*Ranunculaceae*

See plate 27 (Colour)

In a brief report, Thomas (1975) recorded the isolation in "herbaceous hosts" of cucumber mosaic virus from *Clematis x jackmanii* 'superba' with chlorotic leaf vein banding and from clematis 'Vyvyan Pennel' with diffuse chlorotic flecks around the veins. Brunt and Thomas (1975) also recorded the isolation of tobacco rattle virus from *Clematis x heracleifolia* showing chlorotic lesions in its foliage.

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CONIFERS—*Pinaceae; Cupressaceae*

Although soil-borne viruses have been detected in the roots of conifers;

(a) tobacco necrosis virus in *Pinus sylvestris* L. (Yarwood, 1959).
(b) tomato blackring virus in *Picea sitchensis* (Bong) Carr. (Harrison, 1964).
(c) arabis mosaic virus in *Chamaecyparis lawsonsiana* Murray (Harrison, 1964; Thomas, 1970).
(d) tomato ringspot virus in *Cupressus arizonica* Greene (Fulton, 1969). None has been found in foliage.

Foliage diseases: The information on foliar conditions ascribed to viruses is inconclusive but some of the salient points are discussed below.

'Virosis' or 'growth' asymmetry of *Picea* spp. was described by Blattny (1939) and studied in greater detail by Smolak (1948), Cech *et al*, (1961). Pintera (1955, 1960), Pintera *et al.* (1964) and others. In *Picea excelsa* (=*P. abies* (L) Karsten) growing in Czechoslovakia, affected specimens reportedly have yellow-white foliage on some branches (tending to be most apparent in autumn and in spring) shortened needles, asymmetrically growing lateral branches and premature needle fall. Virosis was reportedly transmitted by fundatrix but not alate aphids (*Saccipantes abietis* L. and *Cinaropsis pilicornis*) (Pintera, 1955; Pintera *et al.* 1964). Similar symptoms were reported in *P. sylvestris, Picea sitchensis* and *Picea pungens* Lambert (Schmelzer *et al.* 1966, Biddle, 1968 and Biddle and Tinsley, 1968 and Schmelzer, 1968) growing in Czechoslovakia, Roumania, UK and USSR. Rod-shaped particles of varying length (many *c* 625 nm) were reported in needle exudates (Cech *et al.* 1961); the particle diameters ranged from 22 nm (Cech and Kralik, 1958) to 49 ± 3 nm (Cech *et al.* 1961). Sap from needles of affected *P. sitchensis* growing in UK contained rod-shaped particles up to 6μ long, the cores of the particles being penetrated by the negative stain used during preparation for viewing with an electron microscope. From needles of *P. sitchensis* with vivid yellow-white patches, sap contained rod-shaped structures, 25 nm in diameter and up to 2μ in length or particles 35 nm in diameter by up to 5μ long. Biddle concluded that these particles from *Picea sitchensis* and others detected in *Pinus sylvestris* and *P. monticola* Dougl. were more likely to be crystalline storage products than virus particles.

Schmelzer *et al.* (1966) and Schmelzer (1968) identi- identified a condition which they named Kiefernscheck-nug (pine mottling) but its infectious nature remains to be established. Extracts of mottled needles contained rod-shaped particles 300–600 nm long and 15 nm in diameter—somewhat similar to the particles associated with virosis. However, Schmelzer and his colleagues were careful not to suggest that these were virus particles.

An association between irregularly spherical 'virus-sized' particles and a defoliation syndrome in *Pinus* *densiflora* Sieb. and Zucc. has been described from Japan (Koyama, 1970).

In West Germany, severe stunting, excessive branching and diminished needle size affecting *Larix decidua* Miller have been associated with rickettsia-like organisms (Nienhaus *et al.* 1976). Transmission of these organisms through soil occurred when washed chopped roots of diseased trees were mixed with sterilized soil which was planted with tree seedlings. Following tests of this type, rickettsia-like organisms were detected by electron microscopy in root cells of *L. decidua, Quercus robor* L. *Pseudotsuga taxifolia* (Lam.) Britt. and herbaceous plants including *Vinca rosea* L. and *Chenopodium* spp. There is no direct proof of the pathogenicity of these organisms.

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CORNUS—*Cornaceae*

See plate 28 (Colour)

Foliage disease

SYMPTOMS: In leaves, faint chlorosis near main veins and terminal dieback.

Distribution: In USA affecting *Cornus florida* L. (Waterworth and Povish, 1972).

Transmission: Mechanically in leaf sap to 'herbaceous hosts'.

Causal agent/Relationship: Has affinities with cherry leaf roll virus (CLRV) which when mechanically inoculated to seedlings of an unnamed *Cornus* sp. incited chlorotic flecking along veins and transient chlorotic ringspots (Waterworth and Lawson, 1973).

COMMENTS: Six viruses; arabis mosaic, broad bean wilt, cucumber mosaic, cherry leaf roll, tobacco ringspot and tomato ringspot have been detected in *C. florida* in the U.S.A. (Waterworth and Povish, 1972; Waterworth and Lawson, 1973; Barnett and Baxter, 1973; Reddick *et al*, 1977). Arabis mosaic virus was associated with white or chlorotic mosaic in some but not all leaves (Barnett and Baxter, 1976) but in dogwood the other viruses were typically latent.

A serologically distinct isolate of CLRV was obtained from *Cornus* sp. in U.S.A. by J.P. Fulton but the condition of the host was not described (see Walkey *et al*, 1973).

In Europe, two syndromes have been described. Atanasoff (1935) commented on abnormally shaped fruits in *Cornus mas* L. and speculated about the cause. Additionally, Schmelzer observed yellow ring and line patterns in leaves of *C. sanguinea* L. without being able to detect mechanically transmissible virus in the plants. However, in a brief report, Brunt and Stace-Smith (1971) recorded the isolation of tomato bushy stunt virus from an unnamed dogwood with similar symptoms. Furthermore, Sweet and Campbell, (1975) detected cherry leaf roll with tomato bushy stunt viruses in foliage of *C. sanguinea* with yellow line patterns.

Stem disease

SYMPTOMS: Witches' broom, proliferation of axillary branches, phyllody and chlorosis of newly emerging leaves which remained small.

Distribution: In New Jersey and New Brunswick, USA affecting *Cornus amomum* Mill. and *C. stolonifera* Michx. (Ruja *et al.* 1976).

Transmission: Not reported.

Causal agent/Relationship: Mycoplasma-like organisms varying in diameter from 160–20 nm were found in phloem tissue of *C. amomum*. The further development of symptoms was suppressed temporarily when tetracycline hydrochloride solutions were sprayed onto leaf surfaces.

References

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Waterworth, H.E. and Povish, W.R. (1972). Tobacco ringspot virus from naturally infected dogwood, autumn crocus and Forsythia. *Pl. Dis. Reptr.* **56**, 336–337.

CORYLUS—*Betulaceae*

See plate 29 (Colour)

Foliage disease

SYMPTOMS: Yellow line pattern and yellow or chlorotic interveinal mosaic associated with ringspot and vein banding.

Distribution: Affecting *Corylus avellana* L. in Italy (Scaramuzzi and Ciferri, 1957) Bulgaria (Atanasoff, 1935) Turkey, France (Marenaud and Germain, 1975) and probably wherever *Corylus* is widely propagated.

Transmission: By chip budding (Scaramuzzi and Ciferri, 1957).

Causal agent/Relationship: Not proven, but, in the second season after grafting diseased *Corylus* from Turkey to *Malus* sp., foliage of the latter developed chlorosis (Marenaud, unpublished data). A virus with serological and other properties in common with tulare apple mosaic virus (Fulton, 1971) was isolated from *Prunus persicae* seedlings which had been inoculated with sap from the chlorotic *Malus* foliage. A hazel with similar symptoms in U.K. contained apple mosaic virus which was detected serologically (J.I. Cooper, D. Barbara, unpublished data). However, Sweet, *et al* (1978) failed to detect virus in this tree despite numerous inoculations to "woody indicators".

COMMENTS: A distinct syndrome in *C. avellana* characterized in Italy by premature defoliation and dieback was described by Corte and Pesante (1963). Although they detected a probable virus which they did not identify when "herbaceous hosts" were mechanically inoculated with hazel leaf sap, they were unable to re-establish the condition in *C. avellana*.

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CRATEAGUS—*Rosaceae*

See plate 30 (Colour)

Foliage disease

SYMPTOMS: Chlorotic ring and vein banding patterns.

Distribution: Throughout U.K. affecting *Crataegus oxyacantha* Jacq. Of 97 *C. oxyacantha* tested by bud inoculation to 'woody indicators', Sweet (unpublished data) detected 28 infections with a virus presumed to be CLSV; only 5 of the 28 plants showed symptoms.

Transmission: When double budded with affected material of *Crataegus*, symptoms developed in 'woody indicators' including: *Malus platycarpa* (Posnette and Cropley, 1954, 1961; Anon, 1966).

Causal agent/Relationship: The symptoms in 'woody indicators' resembled the disease attributed to pear ring pattern mosaic virus (syn. apple chlorotic leaf spot virus; CLSV) (Posnette, 1957). However, the symptoms in *Crataegus* were not always associated with the presumed CLSV (Sweet and Campbell, 1976). When inoculated to *C. prunifolia* Pers., *Crataegus* isolates of the presumed CLSV induced the formation of chlorotic rings and line patterns but these symptoms did not develop in *C. oxyacantha* (Sweet, 1976).

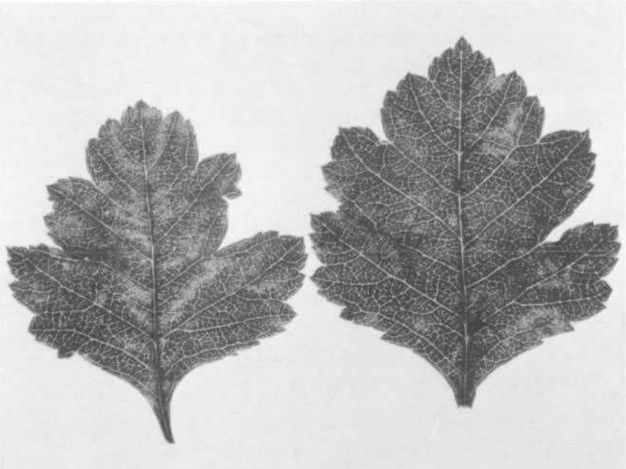

Plate 31—Leaves of *Crataegus oxyacantha* naturally infected with a graft transmissible agent resembling apple chlorotic leaf spot virus. Symptoms are chlorotic vein-banding.

Photograph by courtesy of Long Ashton Research Station

COMMENTS: When budded to 'woody indicators', an individual of *C. korolkowi* (Syn. *C. wattiana* Hemsl. and Lace) which had foliar chlorotic ring and line patterns induced symptoms which Sweet and Campbell (1976) considered atypical of any known virus of pome fruit (ie. fruit with a 'core' eg. apple, quince, pear etc.).

Yellow spots with mottling of foliage were experimentally induced when buds of apple infected with apple mosaic virus were grafted to *C. oxyacantha* (Kristensen and Thomsen, 1962).

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DAPHNE—*Thymelaeceae*

See plate 32 (Colour)

Foliage disease

SYMPTOMS: Yellow ring and line patterns in leaves associated with defoliation or dieback.

Distribution: Worldwide in *Daphne mezereum* L. and *D. odora* Thunb.

Transmission: In sap to 'herbaceous hosts'.

Causal agent/Relationship: Whereas cucumber mosaic virus was frequently associated with these symptoms (Boning, 1963; Smith, 1972) the virus was also isolated from forty five symptomless plants of *D. odora*, fifteen of which also contained alfalfa mosaic virus (Milbrath and Young, 1956). Following a different series of observations, Hollings (1961 a and b) suggested that the slight mottling in leaves of *D. mezereum* associated with alfalfa mosaic virus was greatly aggravated by the presence of cucumber mosaic virus.

COMMENTS: The genus is liable to frequent virus infection, complex mixtures seem common and knowledge of disease aetiology lacking. A survey of thirteen Daphne species in New Zealand (Forster and Milne, 1975) revealed arabis mosaic virus (it was previously reported in Daphne in U.K., see Lister, in Frazier *et al*, 1970), tobacco ringspot as well as cucumber and alfalfa mosaic and three viruses, two of which were subsequently (Morris-Krsinich, 1976) identified with carnation mottle (Hollings and Stone, 1970) and isolates of cucumber mosaic having unusual host range properties in herbaceous test plants. Four distinct viruses having rod-shaped particles of different modal length but of unproven pathogenicity have been detected in Daphne plants in New Zealand (Forster and Milne, 1975). Because of their superficial similarities to members of the tobamo, potex, carla and potyvirus groups respectively, these were named Daphne-TMV, Daphne viruses X, S and Y. (Forster and Milne, 1975). Foliar chlorotic mosaic symptoms with distortion in *D. odora* "Leucanthe" or "Rubra" and necrotic flecks in "Leucanthe Alba" were associated with Daphne virus Y (Forster and Milne, 1976).
In the U.K., Thomas (1975) isolated a potyvirus from *D. mezereum* with yellowish rings and general leaf chlorosis but did not present proof that the virus caused the associated symptoms. In the U.K., tomato black ring virus has been isolated from symptomless *D. retusa* Hemsl. (Forster, unpublished data).

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DIOSPYROS—*Ebenaceae*

A range of symptoms has been observed in *Diospyros*, including leaf mottling, veinal necrosis, leaf malformation, premature defoliation and flower fall, necrosis in the wood, internal necrotic spots in the fruit and dieback. Mezzetti (1950) in Italy reported transmission: some of these symptoms formed in healthy plants after grafting with diseased scions. An unidentified virus has been transmitted mechanically to "herbaceous hosts" from an affected Diospyros sp. in Brazil (Herbas, 1969).

References
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ESCALLONIA—*Saxifragaceae*

In a brief report, Thomas (1975) recorded the isolation in herbaceous hosts of cucumber mosaic virus from *E. rosea* Griseb. with severe leaf chlorosis.

Reference
Thomas, B.J. (1975). Miscellaneous hardy nursery stock. *Rep. Glasshouse Crops Res. Inst.* 1974, 119–120.

EUCALYPTUS—*Myrtaceae*

In 1963, Foddai and Marras working in Italy (see Schmelzer, 1968) reported a graft transmissible witches' broom type disease in *E. rostrata* Schlecht. The witches' broom was associated with leaf malformation chlorosis and vein yellowing but the causal agent has not been determined.
In India, Sastry *et al.* (1971) detected in *E. citriodora* Hock. a virus resembling tobacco mosaic; its significance is unknown.

References
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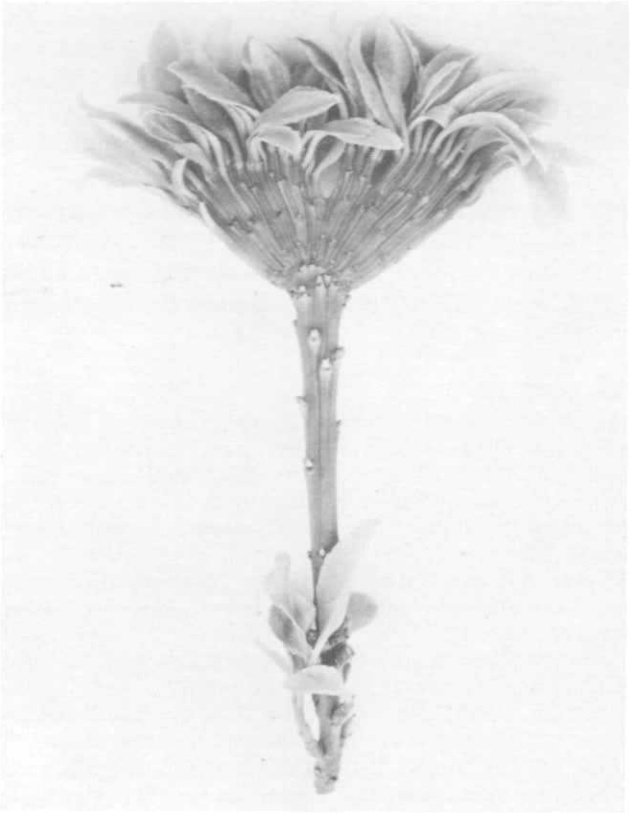

Plate 34—Euonymus japonicus fasciation reportedly associated in some instances with rhabdovirus-like particles.

Photograph by courtesy of G. Jonsson

EUONYMUS—*Celestraceae*

See plate 33 (Colour)

Foliage diseases

SYMPTOMS: Vein clearing.

Distribution: Widespread in Europe affecting the cultivated *Euonymus fortunei*; (*E. radicans* Sieb.) and *E. japonicus* Thunb. (Baur, 1908) and the native *E. europaeus* L. (Schmelzer, 1969).

Transmission: By grafting from affected to healthy *E. europaeus* (Schmelzer, 1969). The symptoms were associated with a virus transmitted mechanically when *Euonymus* leaf sap was inoculated to "herbaceous hosts".

Causal agent/Relationship: Not proven. Schmelzer, (1969) associated strawberry latent ringspot virus.

COMMENTS: Bojansky and Kosljarova (1968) tentatively associated green-yellow spotting and leaf vein banding in *E. europaeus* with a virus transmitted by aphids (*Aphis euonymi* F.). Subikova *et al.* (1974), using the same source material, identified tobacco necrosis virus (Kassanis, 1970) which is normally transmitted by soil-inhabiting fungi.

SYMPTOMS: Chlorotic rings and oak leaf patterns in young leaves.

Distribution: In USA affecting *E. kiautschovica* Loesner and *E. fortunei* var vegeta.

Transmission: Mechanically in foliar sap inoculated to "herbaceous hosts", by dodder (*Cuscuta campestris*), grafting and nematodes (*Xiphinema* spp.) but not in seed (Puffinberger and Corbett, 1973).

Causal agent/Relationship: Not proven; an isolate named euonymus ringspot virus had properties in common with nepoviruses but was not serologically related to those (unnamed) tested.

SYMPTOMS: Bright yellow blotches and rings.

Distribution: In USA (Barnett and Baxter, 1973) UK and the Netherlands (Cooper, unpublished) affecting *E. japonicus* cv microphyllus Hort. Probably widespread in this cultivar.

Transmission: Mechanically, in sap to "herbaceous hosts".

Causal agent/Relationship: In all tested plants, cucumber mosaic virus was associated with the disease but not shown to be its cause.

COMMENTS: Rhabdovirus-like particles were found in fasciated but not symptomless specimens of *E. japonica* (probably *E. japonicus*) (Jonsson, 1974).

With few details, Codaccioni and Cossard (1977) reported that the virus-like particles were transmitted and infectious for *Euonymus* but did not prove that they caused fasciation.

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FAGUS—*Fagaceae*

Rankin (1928) reported that beech (*Fagus sylvatica* L.) in the USA was liable to show chlorotic symptoms which did not disappear when solutions of mineral nutrients were applied. In East Germany, chlorotic or yellow rings and flecks were observed in leaves of *F. sylvatica* (Schmelzer *et al.* 1966). These workers did not report attempts to detect viruses in this material but cited an unpublished observation by Cadman who transmitted tomato black ring virus from leaves with these symptoms collected in Scotland.

Reference

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FICUS—*Moraceae*

See plate 35 (Colour)

Foliage disease

SYMPTOMS: Mosaic irregular green-yellow blotches some with red margins and premature leaf fall (Ainsworth, 1935) also fruit spotting (Condit and Horne, 1933; 1941).

Distribution: Although first reported from California, USA, the disease seems prevalent wherever *Ficus carica* L., *F. stipulata* Thunb. *F. altissima* Blume and *F. krisna* DC are grown.

Transmission: By grafting in conditions reportedly free of eryiophyid mites (*Aceria ficus* Cotte) thought to be natural vectors (Flock and Wallace, 1955). Successful spread via seeds has not been recorded. Sowbane mosaic virus (Kado, 1971) was detected following mechanical transmission of fig sap to 'herbaceous' hosts (*Quacquarelli*, 1971).

Causal agent/Relationship: Unknown.

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FORESTIERA—*Oleaceae*

Foliage disease

SYMPTOMS: In spring, light and dark green mottling and distortion; later formed leaves were larger and had fewer symptoms.

Distribution: In a botanic garden in East Germany affecting *Forestiera acuminata* (Michx.) Poir.

Transmission: In sap to "herbaceous hosts" inoculated with foliar sap from young (but not old) leaves in summer.

Causal agent/Relationship: The potato bouquet serotype of tomato black ring virus was associated, but not proved to cause the disease (Schmelzer, 1974).

References

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FORSYTHIA—*Oleaceae*

Foliage disease

SYMPTOMS: Vein yellowing, yellow net.

Distribution: Widespread in Europe and recorded from the USA affecting *Forsythia intermedia* Zabel, *F. suspensa* (Thunb.) Vahl. and *F. europaea* Deg et Bald.

Transmission: By grafting and by mechanical inoculation of "herbaceous hosts" with sap from affected *Forsythia* leaves (Schmelzer and Schmidt, 1959; Tiangco and Varney, 1970; Schmelzer, 1957; 1962/63; 1974).

Causal agent/Relationship: In East Germany the causal association of arabis mosaic virus (AMV) with yellow net was proved by inoculating cotyledons of *F. intermedia* with AMV-containing sap from "herbaceous hosts" (Schmelzer, 1962/63; 1964). In other tests done in the USA, Tiangco and Varney (1970) showed tobacco ringspot virus to be a cause of yellow net. However, this virus has also been detected in symptomless *Forsythia* (Waterworth and Povish, 1972).

COMMENTS: In UK, raspberry ringspot virus was detected in leaves of *F. sybaldii suspensa* Hort. and *F. intermedia* with bright yellow ring patterns plus vein, yellow net (Cooper, in litt.). In East Germany tomato blackring, alfalfa mosaic and tobacco rattle viruses were detected in *F. intermedia* (Schmelzer, 1957; 1962/63; 1974) and arabis mosaic virus in *F. europea* (Schmelzer, 1974) but their relationship with disease in *Forsythia* has not been determined.

White mosaic or chlorotic ringspot symptoms developed in leaves when *F. intermedia* was mechanically inoculated with sap containing elm mottle virus (Schmelzer, 1969).

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Schmelzer, K. and Schmidt, H.O. (1959). Die gelbenetz Krankheit der Forsythie. *Phytopath. Z.* **36**, 97–99.
Tiangco, E.S. and Varney, E.H. (1970). A vein chlorosis or yellow net disease of Forsythia caused by tobacco ringspot virus. *Phytopathology* **60**, 579.
Waterworth, H.E. and Povish, W.R. (1972). Tobacco ringspot virus from naturally infected dogwood, autumn crocus and Forsythia. *Pl. Dis. Reptr* **56**, 336–337.

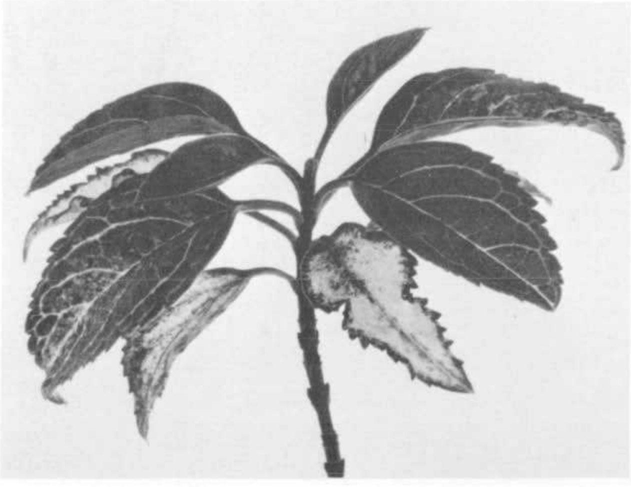

Plate 36—Forsythia x intermedia leaves showing the range of symptoms (from yellow-white to almost normal green) when naturally infected with raspberry ringspot virus.

Photograph by courtesy of Natural Environment Research Council

FRAXINUS—*Oleaceae*

See plate 37, 42 (Colour)

Several distinct syndromes of probable virus aetiology have been recognized in species of *Fraxinus* but only four have received detailed attention. Atanasoff (1935) listed many of the very early horticultural observations which showed that the golden-variegation characteristic of forms designated *F. americana L. aucubaefolia* Hort. and *F. pubescens* Lam. *aucubifolia* Hort. (= *F. pennsylvanica* Marsh.) was graft transmissible. However, although suitable material is extant, nothing is known of the agents causing this condition. A distinct group of symptoms, which included diminished leaf size and interveinal chlorosis, were observed on ash (species not recorded) in Bulgaria (Atanasoff, 1935). He reported that the disease was transmitted within one month of budding but the symptoms which were described as developing on the stock after budding were appreciably more severe, including premature leaf fall, than those noted on the budwood. There is no information on the properties of this agent or its possible relationships. Mosaic mottling with distortion of leaflet laminae has been reported from Bulgaria (Atanasoff, 1935), Italy (leaf marbling, marmoreggiatura; Ciferri *et al*, 1961), East Germany (grunmosaik, Schmelzer, 1962/63) and the UK (personal observation). Attempts in East Germany and UK to transmit the condition by sap inoculation from infected leaves to leaves of other plants including *F. ornus* L. failed. Strangely, there are no reports of efforts having been made to show graft transmission.

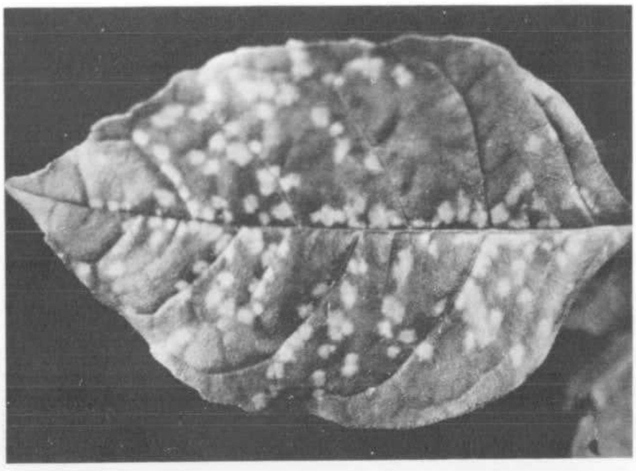

Plate 38—Leaf of *Fraxinus americana* seedling showing chlorotic spots (local lesions) which formed following mechanical inoculation with tobacco ringspot virus.

Photograph by courtesy of C. R. Hibben

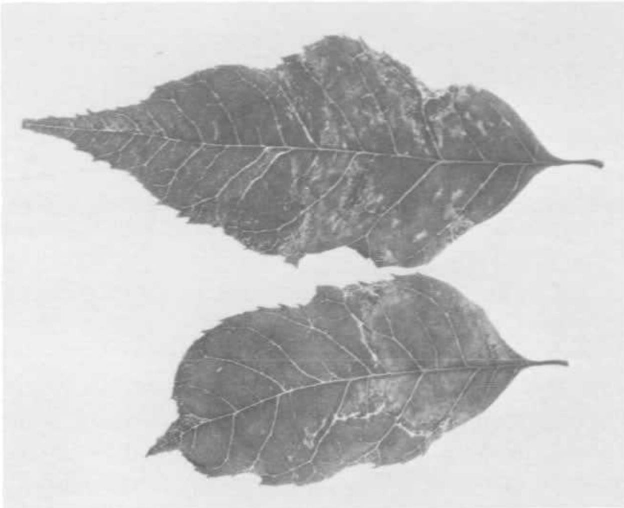

Plate 39—Fraxinus americana on *F. excelsior* rootstock naturally infected with arabis mosaic virus. Leaves showing malformation, chlorotic ring and line patterns.

Photograph by courtesy of Natural Environment Research Council

Foliage diseases

SYMPTOMS: Chlorotic vein banding, oak leaf patterns and chevrons or mild mottle; symptoms erratically and partially expressed.

Distribution: In UK (Cooper, 1975) affecting *Fraxinus excelsior* L.

Transmission: In foliar sap to "herbaceous hosts".

Causal agent/Relationship: Arabis mosaic virus, having few if any antigenic determinants not possessed by a sugar beet isolate AB10 (Harrison, 1958), was detected in leaves with symptoms but also in leaflets without symptoms on the same trees. The virus caused chlorotic symptoms in foliage of inoculated *F. excelsior* seedlings which it infected systemically (Cooper and Sweet, 1976).

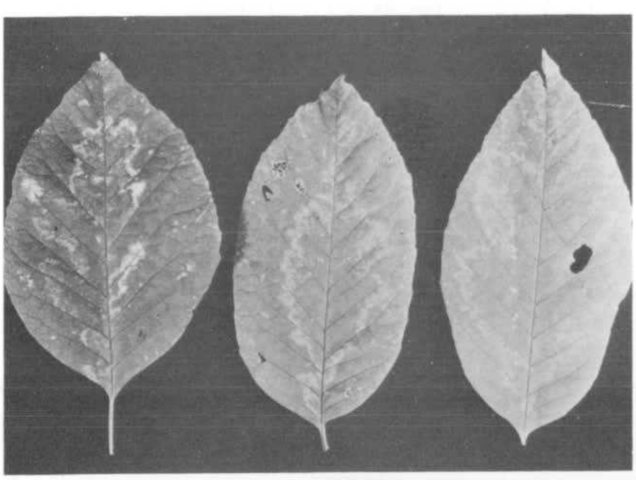

Plate 40—Leaflets of *Fraxinus americana* showing chlorotic ring and line patterns when naturally infected with a virus resembling tobacco mosaic. *Photograph by courtesy of G. N. Agrios*

COMMENTS: One *F. excelsior* tree showing yellow oak leaf patterns in its leaves was observed in Kent (Thresh, unpublished data) but not tested. Novak (1969) showed that *Syringa* with ringspot disease caused chlorotic oak leaf patterns to form in leaves of *F. excelsior* and *F. americana* seedlings into which the material was grafted. When ungraded *F. excelsior* rootstocks were budded with *F. americana* and half of the rootstocks infected by budding with arabis mosaic virus-infected *F. americana* there was, in the first year, a significant ($P < 0{\cdot}05$) diminishing in extension growth and in cross-sectional area of shoots measured 10 cm above the graft union (Sweet, unpublished data).

SYMPTOMS: Chlorotic spots, rings, vein banding patterns, red coloured spots and rings; symptom expression very variable and always partial (Hibben, 1973).

Distribution: In Northeastern states of USA affecting *F. americana* L. and *F. pennsylvania* March var lanceolata Sarg. (Hibben, 1966 b).

Transmission: By grafting and following sap inoculation of "herbaceous hosts". (Hibben, 1966 a and b).

Causal agent/Relationship: An isolate from *F. americana* possessed antigenic determinants in common with tobacco ringspot virus (Hibben and Bozarth, 1972) but the extent of the relationship could not be determined from this work (Scott, 1973).

COMMENTS: In common with tobacco ringspot virus isolates from other hosts, ash isolates are spread in soil by nematodes, *Xiphinema americanum* Cobb. (Hibben and Walker, 1971 a and b). Although it is probable that ash isolates of the virus are translocated from roots to leaves, this is not proven and Kochs postulates have not been fully satisfied. Following manual inoculation, tobacco ringspot virus infected leaves of *F. pennsylvanica* causing a mosaic and narrowing of leaflets (Wilkinson, 1952).

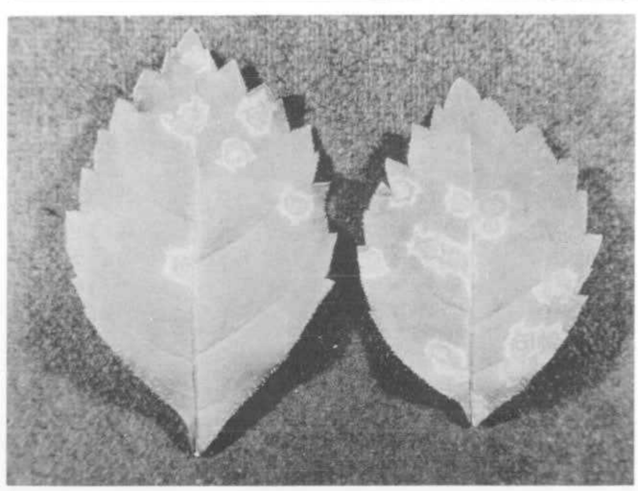

Plate 41—Leaves of *Fraxinus excelsior* showing concentric chlorotic local lesions which formed following mechanical inoculation with the virus resembling tobacco mosaic.

Photograph by courtesy of G. N. Agrios

SYMPTOMS: Chlorotic ring and line patterns with leaf distortion.

Distribution: In one nursery in UK affecting *Fraxinus americana* on *F. excelsior* rootstocks (Cooper and Sweet, 1976).

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationship: Arabis mosaic virus possessing few if any serological determinants not held in common with sugar beet and *F. excelsior* isolates was indentified and caused puckering with chlorotic line pattern symptoms in systemically infected foliage of inoculated *F. americana* seedlings.

COMMENTS: Ring and line pattern symptoms were observed in *F. americana* in Massachusetts, USA (Lana and Agrios, 1973, 1974) and the syndrome developed in *F. americana* and *F. pennsylvanica* seedlings budded with the diseased material. A virus having serological and other properties in common with tobacco mosaic virus was detected in "herbaceous hosts" inoculated with leaf sap from the diseased *Fraxinus*. Furthermore, rod-shaped virus-like particles "some of which were similar in shape and size to tobacco mosaic virus" were revealed when partially clarified sap from diseased ash foliage was examined in an electron microscope. Attempts to reintroduce the virus in sap from "herbaceous hosts" into healthy *F. americana* and *F. pennsylvanica* were reportedly unsuccessful although chlorotic local lesions formed in inoculated leaves of *F. excelsior*. This "target" symptom is somewhat similar to a syndrome noted in Italy on *F. excelsior* and described as "punteffiatura chlor-necrotica" (Casalicchio, 1965). Although a sap transmissible virus having properties in common with tobacco necrosis virus was apparently associated with the disease in Italy, no unambiguous identification was made and attempts to examine the effect of the isolate on healthy *F. excelsior* were not reported.

Stem disease

SYMPTOMS: Witches' broom. In *Fraxinus americana*, diseased foliage was simple rather than pinnate, chlorotic and borne on abnormally erect branches some derived from precocious axillary and terminal bud growth.

Distribution: The syndrome was probably first described (1947) from USSR (Kuprevicz, cited in Schmelzer, 1968) but more intensively studied in the USA where it was observed in New York State (Hibben and Wolanski, 1971).

Transmission: By dodder (*Cuscuta subinclusa* Dur. and Hilg. and *C. campestris* Yuncker) from affected *F. americana* to *Vinca rosea* L. cv Little Pinkie.

Causal agent/Relationship: Elongated ovoid and filamentous MLO were observed in the phloem tissue of roots and mid veins of leaves of *F. americana* and also in *C. campestris* parasitizing the diseased *V. rosea* into which transmission was first observed. Although attempts to satisfy Kochs postulates have not been reported, circumstantial evidence favours the view that MLO may play a part in both the witches' broom and in the dieback syndromes described in *F. americana*.

COMMENTS: Plakidas (1949) observed a witches' broom syndrome in *F. berlandierana* DC and reported transmission between *F. berlandieiana* by grafting but the published data suggest that it was a dieback rather than a witches' broom which developed and then in only one of an unspecified number of plants.
A somewhat similar syndrome was observed in *F. ornus* growing in Italy (Ciferri *et al*, 1961) although vein clearing followed by vein necrosis seemed the more common symptom. The agent was reportedly transmitted to *F. excelsior* and *F. ornus* by chip budding but few details of the experiment were given.

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FUCHSIA—*Onagraceae*

Uschdraweit (1955) reported anthocyanescence and narrowing of leaves, stunting and impaired flower formation in *Fuchsia spp.* from South America and that symptoms developed in stocks (unspecified) grafted with diseased scions.

Reference
Uschdraweit, H.A. (1955). Eine Viruskrankheit bei dar Gattung Fuchsia. *Gartenwelt Berl.* **55**, 147–148.

GALVEZIA—*Scrophulariaceae*

Foliage disease

SYMPTOMS: Leaves on some shoots were mottled and curled with slight necrosis.

Distribution: An individual of *Galvezia speciosa* A. Gray from Chile in an East German botanic garden.

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationship: Virus identified as broad bean wilt but not proved to be the cause of the symptom (Schmelzer, 1974).

Reference
Schmelzer, K. (1974). Untersuchungen an Viren der Zier-und Wildegeholze 8. Mitteilung Neue Befunde an *Forsythia. Hydrangea* und *Philadelphus* sowie Viren and Virosen an *Rhamnus, Centaurea, Galvezia, Cistus, Forestiera, Abeliophyllum, Celastrus, Staphylea* und *Crambe. Zbl. Bakt. Parasit Kde* **129**, 139–168.

GLEDITSIA—*Leguminosae*

A witches' broom syndrome is reported to affect *G. triacantos* L. in the U.S.A. (Grant and Hartley, 1938) and Atanasoff (1935) recorded a deforming mosaic symptom without witches' broom in Bulgaria. Neither disease has been studied in detail and their relationship if any to conditions reported in *Robinia pseudoacacia* L. remains to be established.

Reference
Atanasoff, D. (1935). Old and new virus diseases of trees and shrubs. *Phytopath. Z.* **8**, 197–223.
Grant, T.J. and Hartley, C. (1938). A witches' broom on black locust and a similar disease on honeylocust. *Pl. Dis. Reptr* **22**, 28–31.

HEBE—*Scrophulariaceae*

In a brief report Schwenk *et al*, (1969) recorded the isolation of alfalfa mosaic virus from *Hebe sp.* The authors did not state whether or not symptoms were associated with the infection. Schmelzer (1974) reported that *Hebe bolonsii* CKn was susceptible to experimental infection with elm mottle virus.

References
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Schwenk, F.W., Williams, H.E. and Smith, H.S. (1969). Alfalfa mosaic virus from *Hebe, Ilex* and *Viburnum. Phytopathology* **59**, 1048–1049.

HEDERA—*Araliaceae*

See plate 43 (Colour)

Foliage diseases

SYMPTOMS: Chlorotic-yellow vein banding, blotches or broad ring patterns.

Distribution: Affecting *H. helix* L. in several counties of the UK.

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationship: Arabis mosaic virus (AMV) was consistently associated but in one instance occurred with strawberry latent ringspot virus (SLRV). Although both viruses systemically infected *H. helix* seedlings, yellow symptoms were caused by neither AMV alone nor mixtures with SLRV (Cooper and Sweet, 1976).

COMMENTS: The foliar symptoms in *H. helix* resemble those described as ivy ringspot virus, a disease recorded but not apparently studied in Roumania (Ploaie and Macovei, 1968).

In France, tubular rod-shaped virus-like particles were found when fasciated *H. helix* was examined; the presumed virus was not shown to cause the abnormality (Witz *et al*, 1972).

References
Cooper, J.I. and Sweet, J.B. (1976). The detection of viruses with nematode vectors in six woody hosts. *Forestry* **49**, 73–78.
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HYDRANGEA—*Saxifragaceae*

Foliage disease

SYMPTOMS: Leaves crinkled, rolled or asymmetric (distorted), fewer and smaller florets on short stalks in the cymes (Brierley and Smith, 1952; Brierley and Lorentz, 1957).

Distribution: Affected *H. macrophylla Thunb.* are found worldwide.

Transmission: Several distinct viruses transmitted mechanically in leaf sap to "herbaceous hosts".

Causal agent/Relationship: Hydrangea ringspot virus (Koenig, 1973), which is only recorded from hydrangea and which is spread on pruning knives and mechanically by leaf contact, but neither in seed (Brierley and Lorentz, 1957) nor by aphids (Hollings, 1958), caused the development of chlorotic or brown spots or rings in distorted leaves (Brierley and Smith, 1952). In the USA, Brierley (1954) transmitted tomato ringspot virus from chlorotic hydrangeas and considered it somewhat more damaging than hydrangea ringspot virus. Tobacco ringspot has also been recorded in the USA from hydrangea (Anderson, 1958), whereas in Europe, Schmelzer (1970) detected tomato blackring, arabis mosaic and tobacco rattle viruses associating foliar mosaic symptoms in *H. macrophylla* with TRV and AMV when present together. Viruses having aphid vectors have also been associated with the syndrome.

Foliar mosaic and leaf distortions have been attributed to cucumber mosaic virus in Japan (Tamura and Komuro, 1967) whereas alfalfa mosaic virus is a probable cause in Italy of foliar vein clearing (Belli, 1968). Irrespective of the associated virus, symptoms expressed differ with cultivar and are dependent on environmental conditions.

COMMENTS: Kristensen (1962/64) recorded the isolation in "herbaceous hosts" of tobacco necrosis virus. Neither details of the associated symptoms in *Hydrangea* sp nor the properties of the virus were given.

Stem disease

SYMPTOMS: Witches' broom / phyllody. Cymes (heads) of flowers dwarfed with the individual flowers or florets green instead of pink, white or blue; leaf-like structures originating from the female parts of flowers (pistils). In some instances leaves have vein yellowing and may be unusually small.

Distribution: Widespread in florists' hydrangea Diseased *H. macrophylla* noted in West Germany Anon, 1933), the USA (Brierley and Smith, 1954) and France (Dunez, 1963).

Transmission: By grafting from diseased to previously healthy hydrangeas (Dunez, 1963; Hearon *et al*, 1976). Welvaert *et al.* (1975) induced phyllody in *Vinca rosea* L. joined to diseased hydrangea by the parasitic *Cuscuta subinclusa* but Hearon *et al.* (1976) did not transmit the agent of disease using *C. campestris* Yunck. to bridge diseased hydrangeas with a range of "herbaceous hosts" including *V. rosea*.
Whereas Brierley and Smith (1954) reported that leafhoppers that fed on diseased hydrangeas induced aster "yellows" in China aster (*Callistephus chinensis* (L.) Nus), Hearon *et al.* (1976) were unable to transmit witches' broom between hydrangeas using leafhoppers (*Macrosteles fascifrons* (Stal.).

Causal agent/Relationship: Mycoplasma-like organisms were observed in ultra-thin sections of diseased hydrangea foliage (Muller, 1971; Amici *et al.* 1972; Welvaert *et al.* 1975; Hearon *et al.* 1976).

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ILEX—*Aquifoliaceae*

Foliage disease

SYMPTOMS: Chlorotic-yellow spots in young leaves and irregular margins in older leaves.

Distribution: In Maryland, USA affecting *Ilex crenata* var rotundifolia (Waterworth and Povish 1977).

Transmission: To "herbaceous hosts" inoculated with sap from young leaves triturated with phosphate buffer. Disease developed in three of eight *I. crenata*, six months after inoculation with concentrated and partially purified virus.

Causal agent/Relationship: The isolates possessed antigenic determinants in common with tobacco ringspot virus.

Reference
Waterworth, H.E. and Povish, W.R. (1977). A yellow leafspot disease of *Ilex crenata* caused by tobacco ringspot virus. *Pl. Dis. Reptr* **61**, 104–105.

JASMINUM—*Oleaceae*

See plate 44 (Colour)

Foliage diseases

SYMPTOMS: Yellow rings and blotches.

Distribution: Widespread.

Transmission: Cane (1720) reported that yellow striped leaves developed on a green plant grafted with a variegated form of *Jasminum* sp. This very early report of graft transmission has subsequently been confirmed (Atanasoff, 1935; McLean, 1960, Waterworth, 1971). A virus was transmitted to "herbaceous hosts" inoculated with sap extracts from the yellow blotched leaves of *J. officinale* L. cv aureo-marmorata Hort. (Cooper and Sweet, 1976).

Causal agent/Relationship: Although arabis mosaic virus was transmitted from and identified serologically in yellow Jasminum foliage, this virus isolate systemically infected *J. officinale* seedlings but did not affect leaf colour during the ensuing year.

COMMENTS: Several viruses have been isolated from symptomless *Jasminum* plants; tobacco ringspot and cucumber mosaic viruses from *J. nudiflorum* Lindl., tobacco ringspot and arabis mosaic virus from *J. mesnyi* Hance. (*J. primulinum* Hemsl.). A previously undescribed virus, which Waterworth (1971) called jasmine latent virus 1, was transmitted from *J. odoratissimum* L. These viruses were more readily transmitted to "herbaceous hosts" when inoculated with petal rather than leaf sap extracts. Waterworth (1971) isolated an aphid-transmissible virus (which he provisionally named jasmine mild mosaic) from leaves of *J. multiflorum* Andr. with mild mosaic symptoms.

SYMPTOMS: General poor growth associated with yellow blotches in young foliage plus leaf drop and in older leaves, necrotic spots and interveinal chlorosis.

Distribution: Affecting *J. officinale* in South Carolina, U.S.A.

Transmission: In sap to 'herbaceous hosts'.

Causal agent/Relationship: Tobacco ringspot virus was associated and, in a brief report without details was said to cause the disease. (Barnett, personal communication in Morton *et al*, 1977).

COMMENTS: During a six month period, Morton *et al*, (1977) compared naturally infected and tobacco ringspot free clones of J. officinale and reported that the virus-infected plants had fewer flowers, shorter stems (50% of controls) and inferior root systems. Furthermore, whereas none of 25 healthy plants died, there was a 56% (14/25) mortality in the tobacco ringspot infected stocks.

References
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JUGLANS—*Juglandaceae*

See plate 45b/46 (Colour)

Foliage diseases

SYMPTOMS: Chlorotic discolourations of leaf laminae in the form of yellowish spots, rings and line patterns accompanied by occasional necrotic flecks or chrome yellow blotches on leaves and fruits (Savino *et al.*, 1976; Savino *et al.*, 1977; Quacquarelli and Savino, 1977). Symptoms first obvious in U.K. in June; rarely affecting more than 25% of the leaves on any tree.

Distribution: Although trees with foliage symptoms seem few, virus infection is widespread in *J. regia* L. in Southern Italy (Quacquarelli and Savino, 1977) and in U.K. where incidence parallels frequency of *J. regia*, being ten times greater in southern as compared to northern Britain (Cooper, unpublished data).

Transmission: In sap from leaves, fresh pollen or immature fruits to "herbaceous hosts" and in seed of naturally infected *J. regia*: the amounts of seed transmission to seedlings being 32% when seed was stored at 25 °C before germination (Quacquarelli and Savino, 1977). Four to six percent transmission occurs in Juglans seed stratified before commercial use in U.K. (Cooper, unpublished data). In Italy, virus infected seedlings had mild chlorotic mottle symptoms and smaller leaves than healthy (Quacquarelli and Savino, 1977). Although this was not observed in U.K. 3 year old virus infected seedlings were significantly ($P<0{\cdot}01$) shorter ($\frac{3}{4}$) and the mean diameter at one third total height was significantly ($P<0{\cdot}05$) less (4/5) than the dimensions of their healthy counterparts (Cooper, unpublished data).

Causal agent/Relationships: The isolates associated in Italy with the different syndromes and tentatively named walnut ringspot and walnut yellow mosaic

Plate 45a—Walnut bunch disease—brooms in *Juglans sieboldiani* in autumn when "normal" foliage had fallen.
Photograph by courtesy of C. E. Seliskar, U.S.D.A.

viruses (Savino *et al.*, 1976) differed slightly one from another but possessed antigenic determinants in common with cherry leaf roll virus isolates (Savino *et al.*, 1977). Cherry leaf roll virus isolates have been obtained from symptomless walnuts in U.K. (Cooper, unpublished data) and Italy (Quacquarelli and Savino, 1977). Indeed, this is the rule rather than the exception. Because seedling *J. regia* inoculated and systemically infected with a walnut isolate of cherry leaf roll virus failed to develop foliage symptoms during two subsequent seasons (Cooper, unpublished data), it is possible that other agents than cherry leaf roll virus may be causing the foliage symptoms.

COMMENTS: In Bulgaria, a similar syndrome (walnut line pattern) was noted but not studied (Christov, 1958).

OTHERS: A graft incompatibility of untested aetiology showing as a black line at the union between *J. regia* scions on *J. nigra* L. rootstocks and culminating in the death of bark and the trees was noted in the U.S.A. (Miller *et al.*, 1957) and in the U.K. (Glenn, 1966).

Stem disease

SYMPTOMS: Walnut bunch. Bunched, wiry shoots, dwarfed and chlorotic leaves diminished yield of nuts and of veneer quality timber and premature death.

Distribution: Widespread in the eastern USA (Hutchins and Wester, 1947; Miller and Thompson, 1949); not reported from Europe. The species most severely affected by the disease are: *J. nigra* L. *J. cinerea L.* and *J. sieboldiana* Maxim.

Transmission: By bark patch grafting between *J. nigra* and *J. sieboldiana* although symptoms took two years or more to show in the initially healthy wood (e.g. Carling and Millikan, 1974).

Causal agent/Relationship: Seliskar (1973) reported the presence of MLO (revealed by electron microscopy) in the petioles, roots and stems of diseased but not healthy trees. There has been no clear indication that the disease spreads and no vector is known.

References

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LABURNUM—*Leguminosae*

An infectious (graft transmissible) foliage variegation of *Laburnum* spp. with yellow chlorosis primarly alongside veins, has been known since the 1860's (Baur, 1907; van Katwijk, 1953). It has also been recorded from *L. vulgare* (probably = *L. anagyroides* Med.), *L. vossii* Hendr. (= *L.* x *watereri* Dipp. 'vossii'), L. alpinum (Mill.) Bercht. and Presl. (see Atanasoff, 1935) and *Cytisus hirsutus* L. (Baur, 1907). Arabis mosaic virus was identified following transmission to "herbaceous hosts" inoculated with sap from *L. vossii* Hendr. on *L. anagyroides* rootstocks (Cooper and Sweet, 1976). Leaves of the former, which was stunted, were chlorotic. Furthermore, the terminal buds were dead and some main shoots were dying-back. Hunter (1976) consistently associated *Fusarium avenaceum* (Corda ex Fr.) Sacc. with the bud death symptom and showed that this fungus caused bud death.
A graft transmissible chlorosis of *L. anagyroides*, *L. alpinum* cv aureum and *C. hirsutus* in which leaf laminae were more or less uniformly chlorotic (sometimes yellow) has been associated with two sap transmissible viruses; arabis mosaic and tomato black ring (Schmelzer, 1962/63; 1968). However *L. anagyroides* remained symptomless following inoculation with an isolate of arabis mosaic virus from *L. anagyroides* (Schmelzer, 1962/63). Schmelzer was unsuccessful in his attempts to transmit variegation to Laburnum using sap from affected specimens.

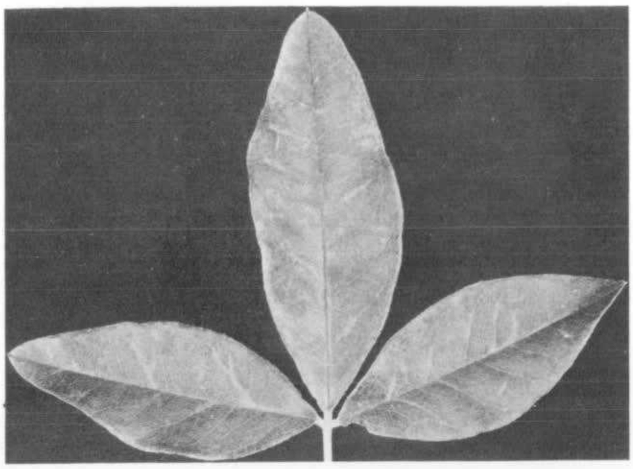

Plate 47—Laburnum anagyroides foliage showing chlorotic vein-clearing symptoms associated with rhabdovirus-like particles.
Photograph by courtesy of M. G. Schultz

Although a causal association has not been proved, rhabdovirus-like particles were detected in the yellow areas, but not in other parts of *L. anagyroides* leaves with vein clearing (Schultz, 1973; Schultz and Harrap 1975).

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LAVANDULA—*Labiatae*

Foliage disease

SYMPTOMS: Mosaic.

Distribution: Recorded in France affecting *Lavandula hybrida* Rev. (Marchoux and Rougier, 1974).
Transmission: In sap to "herbaceous hosts".
Causal agent/Relationship: Unknown but alfalfa mosaic virus was identified in "herbaceous hosts" inoculated with sap from affected lavender.

Reference

Marchoux, G. and Rougier, J. (1974). Virus de la mosaique de la luzerne: isolement a partir du lavendin (*Lavendula hybrida* Rev.) er da l'aubergine (*Solanum melongena* L.). *Ann. Phytopathol.* **6**, 191–196.

LEYCESTERIA—*Caprifoliaceae*

Chlorotic rings and flecks have been reported in *L. formosa* Wallich. growing in England. Somewhat more necrotic symptoms were observed in Romania (Savulescu and Ploaie, 1961, cited in Schmelzer, 1968). The symptoms in England were associated with cucumber mosaic virus (Hollings, 1961a and b).

References

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LIGUSTRUM—*Oleaceae*

Foliage diseases

SYMPTOMS: Chlorotic chevrons, rings or blotches.

Distribution: Widespread in Europe and North America affecting *Ligustrum vulgare* L. and *L. ovalifolium* Hass Karl.

Transmission: In foliar sap to "herbaceous hosts" (Kochman *et al*, 1964; Schmelzer, 1962/63; Smith, 1957; Cadman, 1960; Cooper, 1975) and by grafting (Baur, 1907; Hildebrand, 1953).

Causal agent/Relationships: A great many observations have been made on plants in several countries showing similar symptoms. There is therefore some doubt about whether the diseases were in fact the same. Smith (1957) identified cucumber mosaic virus in association with the symptoms in *L. vulgare* and, although Kochman *et al*, (1964) did not identify the isolates they obtained, their published data are not incompatible with having also obtained a cucumovirus. By contrast, arabis mosaic virus has been identified by Schmelzer (1962/63), Cadman (1960), Jankulova and Schmelzer (1974), Cooper (1975) and Brunt and Thomas (1975).

SYMPTOMS: Bright yellow rings and spots with chlorotic rings and, less frequently, depressed or necrotic lesions.

Distribution: In USA affecting *L. lucidum* Ait.

Transmission: By grafting to *L. lucidum* (Plakidas 1959).

Causal agent/Relationship: Not known.

COMMENTS: Similar syndromes occur in *L. vulgare* and *L. ovalifolium* in UK and in *L. japonicum* Thunb. in the USA.

Several viruses have been isolated following inoculations of foliar sap to "herbaceous hosts".

(1) Few details are available but Seymour (1965) detected prunus necrotic ringspot virus in *L. japonicum* Thunb.

(2) Schmelzer *et al*, (1969; cited in Schmelzer, 1972) reported cherry leaf roll virus.

(3) Tomato bushy stunt virus has been isolated from roots but not leaves of *L. vulgare* (Lovisolo *et al*, 1965).

(4) A virus having slightly flexuous rod-shaped particles about 650nm long has been reported by Brunt and Thomas (1975).

(5) Novak (1969) suggested that the virus he isolated from *L. vulgare* was probably tomato black ring.

References

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Cadman, C.H. (1960). Viruses with nematodes as vectors. *Rep. Scott. hort. Res. Inst.* 1960–1, 54.

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LONICERA—*Caprifoliaceae*

Lihnell (1951) reported the transmission of cucumber mosaic virus to 'herbaceous hosts' inoculated with sap from weakly growing plants of *Lonicera pericylmenum* L. having distorted leaves with ringspot symptoms but did not report the effect when this virus was inoculated into healthy plants. In a brief statement, Brunt and Thomas (1975) noted their detection of a virus they called 'lonicera latent' which had particles about 650nm long; its pathogenicity for honeysuckle was not reported.

Vein-yellowing which gives plants of *L. japonica* Thunb. cv aureo-reticulata horticultural value did not always develop when affected tissue was grafted to healthy Lonicera. The plants with vein yellowing did not yield viruses manually transmissible to "herbaceous hosts" (Schmelzer, 1962/3). However, Sweet (unpublished data) transmitted the disease agent by grafting and frequently isolated CMV from affected plants; he did not prove that CMV caused the disease.

References

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LYCIUM—*Solanaceae*

Foliage disease

SYMPTOMS: Chlorotic mottling with some necrosis.

Distribution: East Germany (Schmelzer and Schmidt, 1968) and Bulgaria (Kovachevsky 1965;

cited in Schmelzer, 1968) affecting *Lycium halimifolium* Mill.

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationship: Cucumber mosaic virus was identified and reproduced the syndrome when reintroduced into seedlings (Schmelzer and Schmidt, 1968).

COMMENTS: Schmelzer (1974) reported that *L. halimifolium* was susceptible to experimental infection with elm mottle virus.

References

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MACLURA—*Moraceae*

Foliage diseases

SYMPTOMS: Yellow mosaic associated with foliar distortion and interveinal yellowing which in turn causes local tissue translucency, is more obvious in spring than during summer periods of high temperature (Plese and Milicic, 1973).

Distribution: Only known from Yugoslavia affecting *Maclura pomifera* (Raf.) Robinson.

Transmission: Mechanically, to infect "herbaceous hosts" inoculated with sap from young or old leaves or from bark and from diseased to healthy *Maclura* seedlings by aphids (*Myzus persicae* Sulz.); it was non-persistent (Plese and Stefanac, 1976).

Causal agent/Relationship: Cylindrical and pinwheel inclusions, characteristic of potyviruses (Edwardson, 1966; 1974) were seen when infected *Maclura* leaf tissue was examined in an electron microscope. However, the flexuous rod-shaped virus-like particles seen were shorter (600–650nm) than those typical of potyviruses (Plese and Stefanac, 1976).

SYMPTOMS: In summer, some leaves have chlorotic ringspots up to 2cm (diameter), others have yellow-white spots and curved line patterns.

Distribution: Only known from Yugoslavia affecting *M. pomifera*.

Transmission: Mechanically in leaf sap to infect "herbaceous hosts".

Causal agent/Relationship: On the basis of serological tests and host symptoms, a member of the cucumovirus group was identified but not proven to cause the associated disease (Plese and Milicic, 1973).

References

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MAGNOLIA—*Magnoliaceae*

Foliage disease

SYMPTOMS: Chlorotic line patterns.

Distribution: In East Germany and Czechoslovakia affecting *Magnolia* sp. (Schmelzer and Schmelzer, 1968).

Transmission: Mechanically in magnolia leaf sap to "herbaceous hosts".

Causal agent/Relationship: The isolated virus was identified with cucumber mosaic virus but this was not proven to cause the associated disease.

Reference

Schmelzer, K. and Schmelzer, A. (1968). Virus befall an Magnolien (*Magnolia* spp.). *Acta phytopathol. Acad. Sci. Hung.* **3**, 411–413.

MORUS—*Moraceae*

Foliage disease

SYMPTOMS: Mosaic and (at temperatures below 30°C) enations (Ishiie and Kawakami, 1966).

Distribution: Japan.

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationship: Not known. A virus having spherical particles c 30nm in diameter and nematode (*Longidorus martini* Memy) vectors (Yagita and Komoro, 1972) was identified but did not cause symptoms in experimentally infected mulberries (Tsuchizaki *et al*, 1971).

COMMENTS: Virus-like particles having flexuous rod-shaped particles of undescribed relationships were observed with the aid of an electron microscope in diseased *Morus*, but their role in the pathology of mosaic disease remains obscure.
At temperatures of 30°C (but not below), Ishiie and Kawakami (1966) resolved a second component of the mosaic syndrome, the production of filliform leaves with mosaic. The cause is unknown. A mosaic disease of *Morus indica* L. was recorded in India and was re-

portedly transmitted by two aphid genera (Chatterjee and Raychaudhuri, 1965).
A distinct agent associated in India with a yellowing of leaf veins was graft transmissible and has been suggested but not proved to have whitefly vectors (Raychaudhuri *et al*, 1961).

Stem disease

SYMPTOMS: Witches' broom (mulberry dwarf.) Branch proliferation, leaf chlorosis and bud precocity.

Distribution: Japan.

Transmission: By grafting and by *Hishimonus sellatus* Uhler, leaf-hoppers (Ishiie and Matsumo, 1971 a and b).

Causal agent/Relationship: MLO observed in ultra-thin sections of phloem parenchyma cells (Doi, *et al*, 1967) : remission of symptoms followed tetracycline therapy (Ishiie and Matsumo, 1971 a and b).

References

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MYRICA—*Myricaceae*

Stem disease

SYMPTOMS: Leaf yellowing stunting and a "witches' broom" appearance.

Distribution: Recorded in New Jersey, USA affecting *Myrica carolinensis* Mill. (Raychaudhuri, 1952).

Transmission: By grafting (but not in sap) also by dodder (*Cuscuta campestris*) to *Vinca* sp. causing "yellows" symptoms and flower malformation. The leaf hopper *Macrosteles divisus* Uhler failed to transmit the disease to "herbaceous hosts".

Causal agent/Relationship: Not known; there are some similarities with diseases associated with mycoplasma-like organisms.

Reference

Raychaudhuri, S.P. (1952). Bayberry yellows. *Phytopathology* **42**, 17.

NANDINA—*Berberidaceae*

Foliage disease

SYMPTOMS: Reddening of petals and some (but not all) leaves seen in spring, although infected leaves tended to recover in hot summer weather. Additional symptoms included distortion and narrowing of leaf laminae, diminished flower number and poor fruit set (Barnett and Baxter, 1973a and b).

Distribution: In South Carolina and Mississippi, USA affecting *Nandina domestica* Thunb. (Brierley and Smith, 1960; Barnett and Baxter, 1973a and b).

Transmission: In sap to "herbaceous hosts" but no natural spread noted and not seed borne to seventy seedlings observed.

Causal agent/Relationship: Cucumber mosaic virus was identified and caused interveinal reddening and other symptoms similar to those seen in naturally infected plants.

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PASSIFLORA—*Passifloraceae*

Cucumber mosaic virus was detected in one plant of *Passiflora caerulea* L. showing chlorosis, curling and leaf deformation (Zschau, 1964) but the virus may not cause these symptoms. The only other virus identified from *P. caerulea* growing in Europe has not been associated with symptoms and was in the first instance detected when infected leaves were examined with an electron microscope (Schnepf and Brandes, 1961/62). Passiflora latent virus is readily transmitted to "herbaceous hosts" inoculated mechanically with foliar or petal sap but not by aphids (*Myzus persicae*; Brandes and Wetter, 1963/64).
Passiflora spp. (eg. *P. edulis* Sims) grown for fruit in semi-tropical regions are liable to infection with cucumber mosaic and/or passion fruit woodiness viruses (see Taylor and Greber, 1973 and others cited therein.)

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PAULOWNIA—*Scrophulariaceae*

Foliage disease

SYMPTOMS: Deforming mosaic, vein banding, chlorotic ringspot or oak-leaf symptoms (Horvath, 1973); 44% diminishment in height and 49% decrease in diameter growth as compared with healthy (Schmelzer, 1969).

Distribution: Hungary affecting *P. tomentosa*.

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationships: Cucumber mosaic virus (CMV) identified and in a series of tests Schmelzer (1969) inoculated seedlings of *P. tomentosa* with CMV to obtain systemic infection and chlorotic symptoms although not the full range reported by Horvath (1973).

COMMENT: Schmelzer (1974) reported that *Paulownia tomentosa* was susceptible to experimental infection with elm mottle virus.

Stem disease

SYMPTOMS: Axillary buds and shoots were precocious and grew almost throughout the year, branches tended to be erect, leaves were thin narrow chlorotic and tended to fall prematurely. Root growth tended to be poor and affected trees died within a few years of symptoms first showing.

Distribution: Widespread in South East Asia affecting *Paulownia tomentosa* (Thunb.) Steud. and *P. fortunei* Hensl. (Tokushige, 1951).

Transmission: Root or stem grafting.

Causal agent/Relationships: MLO associated with the syndrome (Doi *et al.*, 1967).

References

Doi, Y., Teranaka, M., Yora, K. and Asuyama, H. (1967). Mycoplasma- or PLT group-like microorganisms found in the phloem elements of plants infected with mulberry dwarf, potato witches' broom, aster yellows or Paulownia witches' broom. *Ann. phytopathol. Soc. Japan* **33**, 259–266.
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PHILADELPHUS—*Saxifragaceae*

Foliage diseases

SYMPTOMS: Chlorotic mottle or chevron patterns on leaves which, in some instances, were also twisted.

Distribution: In East Germany affecting *P. falconeri* Sarg.

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationship: Cucumber mosaic virus was identified in affected plants but not proved to be the cause of the disease (Schmelzer, 1970).

SYMPTOMS: Whitish rings/arcs/mottle or oak leaf patterns.

Distribution: In East Germany affecting *Philadelphus sp.* (Schmelzer and Schmidt, 1968).

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationship: Alfalfa mosaic virus was isolated and identified and shown to cause the syndrome (Schmelzer, 1970).

SYMPTOMS: Like those of white mottling associated with lucerne mosaic virus. Light green-dark green mosaic with blistering and increased indentations of the margins of leaves on some (but not all) branches.

Distribution: In East Germany affecting Philadelphus spp. (unspecified).

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationship: Isolates from Philadelphus were identified with elm mottle virus (Schmelzer, 1974) but although one of these isolates was inoculated and infected eighty two species (seventy four systemically) in twenty six families, Philadelphus was not one of these and the relationship of the virus with the disease therefore remains unproven.

References

Schmelzer, K. (1970). Untersuchungen an Viren der Zier- und Wildgeholze. 7. Mitteilung: Weitere Befunde an *Buddleja, Viburnum, Caryopteris* und *Philadelphus* sowie Viren an *Leycesteria, Chionanthus, Ribes, Hydrangea, Syringa, Spiraea* und *Catalpa*. *Phytopath. Z.* **67**, 285–326.
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Schmelzer, K. and Schmidt, H.E. (1968). Untersuchungen an Viren der Zier- und Wildegeholze. 6, Mitteilung: Erganzende Befunde an *Caryopteris* sowie Virosen an *Philadelphus, Aristolochia, Buddleja, Lycium* und *Aesculus*. *Phytopath. Z.* **62**, 105–126

PITTOSPORIUM—*Pittosporaceae*

Foliage disease

SYMPTOMS: The smaller downward rolling leaves of diseased plants have vein yellowing which mainly affects lateral veins (Plavsic-Banjac *et al.* 1976).

These symptoms are less obvious in summer than in other seasons—possibly an effect of high temperature (Corte, 1957).

Distribution: Affecting *P. tobira* (Thunb.) Ait. in Italy (Corte, 1957) and Yugoslavia (Horvath, 1973; Plavsic-Banjac *et al.* 1976).

Transmission: By grafting diseased and healthy *P. tobira* (Horvath, 1973) but apparently not by seeds, aphids or mites (Corte, 1957).

Causal agent/Relationship: Symptoms in *P. tobira* linked to rhabdovirus-like particles, measuring 245 x 18nm and associated with inner nuclear membranes of affected cells.

COMMENTS: Sparse evidence suggests that vein yellowing is distinct from (a) graft-transmissible variegation recorded in *P. tobira* in France (Carriere, 1887) and the USA (Brierley, 1944); (b) mosaic of *P. daphniphylloides* Hayata noted by Milbrath (1940).

Stem disease

SYMPTOMS: (a) Necrosis of outer bark which is shed.

(b) Death of branches.

Both symptoms have been associated with the following foliage defects; chlorotic blotches, ringspots, oak-leaf or watermark symptoms.

Distribution: Affecting *P. tobira*, *P. crassifolium Solander* and *P. viridiflorum* Sims and "variegated" *P. tobira* (Thomas and Baker, 1947).

Transmission: By grafting affected *P. crassifolium* or *P. tobira* to *P. tobira*. No transmission through seed observed (Thomas and Baker, 1947).

Causal agent/Relationship: Unknown.

COMMENTS: Slight swellings on dwarf stems with roughened bark have been noticed in Florida in vegetatively propagated planting stock (Alfieri and Seymour, 1970).

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POPULUS—*Salicaceae*

See plate 48 (Colour)

Foliage disease

SYMPTOMS: Mosaic. Yellow spots which tend to extend along the fine leaf veins (astroid spotting) typically appearing first in the oldest fully expanded leaves in late spring. Diminishment in height and diameter growth may occur during the first year or two after planting but the effect, which is greater in some clones (eg. *P. x euramericana* cv Eugenei 15 to 20%) than others (eg. *P. x euramericana* cv Gelrica—no significant decrease) is probably not maintained for more than a year or two (Navratil, 1963; van der Meiden, 1964, Milinko and Schmelzer, 1968, Mackay and Beaton, 1969; Biddle and Tinsley, 1971b). Specific gravity and the strength of branch wood (buttwood was not tested) can also be adversely affected (Biddle and Tinsley, 1971b). High temperatures tend to mask symptoms in foliage (Bertranet and Taris, 1971).

Distribution: In Bulgaria (Atanasoff, 1935), Yugoslavia (Perisic, 1951), Netherlands (Berg, 1962), Poland (Benben, 1957), Denmark (Kristensen, 1960), Italy (Corte, 1960), West Germany (Zycha, 1961; Brandes, 1963), Czechoslovakia (Blattny *et al.*, 1962; cited in Berg, 1964), East Germany (Schmelzer, 1964) and the Georgian SSR (Navratil, 1965). Berg (1964) cited authorities for the occurrence of the disease in all areas where poplars are grown commercially except South Africa and South America and reported that almost all clones of the Aigerios Duby and Tacamahaca Spach. sections (Anon, 1958) of the genus Populus were susceptible to the diseases; clones of the Turanga Bge., Leuce Duby and Leucoides Spach. sections were not. Although Brunt *et al.* (1976) reported the isolation of poplar mosaic virus from a hybrid *P. tremuloides* x *P. tremula*, the tree in question was a *P. euramericana* hybrid (Brunt, personal communication).

Transmission: By grafting and in sap to herbaceous hosts (Berg, 1962; 1964). There is no unequivocal evidence that the disease spreads from tree to tree. In poplar, the virus was not seed or pollen borne (Cooper, 1976) and was not experimentally transmitted by dodder (*Cuscuta californica* Choisy or *C. subinclusa* Dur. Hilg.; Schmelzer, 1966). Aphids have been tried as vectors but the following did not transmit the disease, *Chaitophorus versicolour* C. L. Koch, *Pterocomma populea* Kitb., *Myzus persicae* Sulz., *Aphis fabae*, *Aphis cracivora Koch*, *Chaitophorus leucomelas* Koch, *Macrosiphum euphorbiae* (Thom.) and *Hyperomyzus lactucae* L. (Berg, 1964; Blattny, 1965; Schmelzer, 1966; Boccardo, *et al.*, 1973; Cooper unpublished data). Eriophyid mites of the genus Acutops did not transmit the agent between poplars (Cooper, 1976) and experiments described by Berg (1964) indicated that pruning tools did not carry the disease agent.

Causal agent/Relationships: Different workers, using phenotypically and genotypically distinguishable sources have identified their isolates as poplar mosaic virus having flexuous rod-shaped particles with modal lengths ranging from 626nm to 735nm (Berg, 1962). Other data (Brcak and Blattny, 1962; Brandes, 1963; Biddle and Tinsley, 1971a; Kraus, 1973; Atkinson and Cooper, 1976; Brunt *et al*, 1976, Luisoni *et al*, 1976) strengthens the possibility that poplar mosaic virus has properties in common with members of the carlavirus group although no serological relationship to seven members of this group was detected by Berg (1964). Berg also failed to detect antigenic relationship between poplar mosaic virus and the type member of the potex virus group and four poty viruses.

COMMENTS: A great many different symptoms have been ascribed (often with little justification) to poplar mosaic disease. For example, Blattny (1965) suggested that the disease could be characterized by diminished rooting capacity and petiole necrosis and a group of more than seven symptoms; vein necrosis, top necrosis, premature leaf fall, tumour formation, stem cracking. Furthermore, increased flexibility of lower branches were recognized in *P. deltoides* Marsh cv. angulata and ascribed to poplar mosaic (Castellani, 1966). Unfortunately Kochs postulates have not been even partially satisfied for all of these.

The necrotic leaf spotting disease affecting *P. tremuloides* Michx. in Canada (Boyer, 1962), and in Eastern Europe, where *P. canescens* (Ait.) Sm. and *P. alba* L. are reported to have symptoms (Blattny, 1965), is probably not associated with poplar mosaic virus as was at first thought. Although an agent was reportedly transmissible in sap from *P. tremuloides*, (Boyer, 1962 detected infection in one of eight suspects), in seed (Boyer and Navratil, 1970), by budding (seven of ten attempts) and by insects (Boyer, 1962; two of three attempts), electron microscopic examination of diseased leaves, extracts and exudates did not reveal virus-like particles. Indeed, despite the fact that sap from affected aspen leaves passed through a bacteria-retaining filter and rubbed onto primary leaves of *Vigna sinensis* Endl. cv Black Eye caused red brown lesions to develop during three to six days (Boyer and Navratil, 1970), the virus aetiology of the syndrome will be more plausible if transmission by grafting between aspens can be achieved in conditions when the uninoculated control plants do not show "chlorotic symptoms not verified as necrotic leaf spot" (Boyer and Navratil, 1970). Boyer (1962) and Hepting (1971) both commented on the macroscopic similarities between necrotic leaf spotting in aspens and the disease shown to be caused by the fungus, *Plagiostoma populi* Cash and Waterman (Cash and Waterman, 1957) but it seems unlikely that this is the cause of symptoms observed by Boyer because he reported that no evidence of fungi was found in the leaf tissues he examined.

Tomato black ring, tobacco rattle, arabis mosaic and tobacco necrosis viruses were detected in roots but not leaves of *P. x euramericana* cv I–78 and Robusta within one year of planting in soil infested with these viruses (Cooper and Sweet, 1976).

OTHER: In a brief report Hibben *et al.* (1977) reported the isolation of tobacco necrosis virus from 'deteriorating' clones of *Populus tremuloides* Mich. in the U.S.A. Furthermore, Berbee *et al.* (1976) briefly noted the detection of a potyvirus-like agent from five Aigerios clones and from a 'deteriorating' aspen.

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PTELEA—*Rutaceae*

A leaf variegation of yellow colour detected in *Ptelea trifoliata* L. cv "fol variegatis" was reported graft transmissible by Baur (1907) but although the effect was sought after for horticultural purposes it was not until 1962 that sap transmission tests from the affected plants were tried (Uschdraweit cited in Schmelzer, 1962/63). A virus transmitted from *P. trifoliata* was tentatively identified as arabis mosaic but was not inoculated back to healthy *Ptelea* spp. (Schmelzer, 1962/1963). Subsequent tests allowed identification of this isolate with cherry leaf roll virus (Schmelzer, 1972) but other work (Schmelzer and Stahl, 1972) showed that arabis mosaic virus may also be detected in variegated *P. trifoliata*.

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PYRACANTHA—*Rosaceae*

Using the technique of double budding, Sweet (1974) observed yellow flecking in leaves of *Malus sylvestris* (*M. pumila*, Miller cv sylvestris) cv Lord Lambourne (on *M. sylvestris* cv Tremlett's Bitter rootstocks) inoculated with symptomless *Pyracantha rogersiana* Chittenden cv Roger Red. Similar symptoms in Lord Lambourne have been associated with apple mosaic virus (Fulton, 1972).

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QUERCUS—*Fagaceae*

Foliage diseases

SYMPTOMS: Chlorotic vein banding or ringspot symptoms associated with progressive dieback.

Distribution: Arkansas, USA, affecting *Quercus marilandica* Muench. (Barnett, 1971) and *Q. velutina* Lam. (Kim and Fulton, 1973).

Transmission: By grafting but not in sap.

Causal agent/Relationship: Not known; Kim and Fulton (1973) resolved virus-like flexuous rod-shaped particles of unspecified length in sectioned leaf tissue viewed with an electron microscope.

SYMPTOMS: Yellowing, rosetting, necrotic spotting and premature breaking of dormancy.

Distribution: In USA (California) affecting *Quercus agrifolia* Nee. and *Q. phellos* L. and *Lithocarpus densifolia* (possibly *L. densiflorus* Rehd.).

Transmission: Mechanically in partially purified foliage extracts but very infrequently (Yarwood and Hecht-Poiner, 1970; Neinhaus and Yarwood, 1972).

Causal agent/Relationship: Rod-shaped virus-like particles resembling those of tobacco mosaic were detected with an electron microscope in plants with symptoms but also in a range of symptomless *Quercus* spp.

COMMENTS: It has been proposed that the mildew fungus *Sphaerotheca lanestris* Harkin is a vector of the virus because conidia from *Quercus* induced lesions to form on "herbaceous hosts" onto which they were dusted (Yarwood, 1971).
Schmelzer, *et al.*, (1966) recognised in *Quercus* spp. three foliage diseases of possible virus aetiology but the symptoms on which they based their diagnosis did

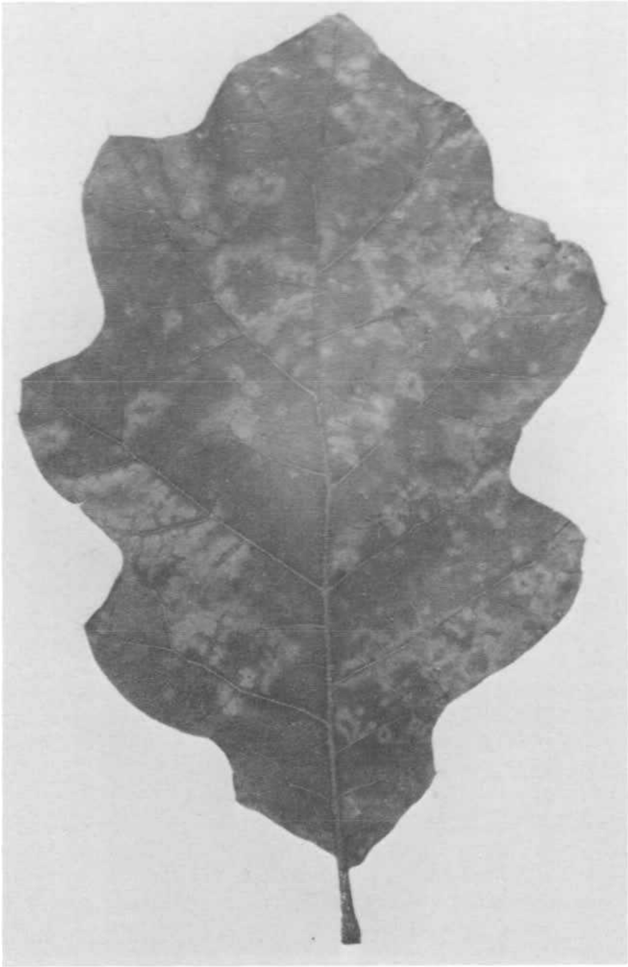
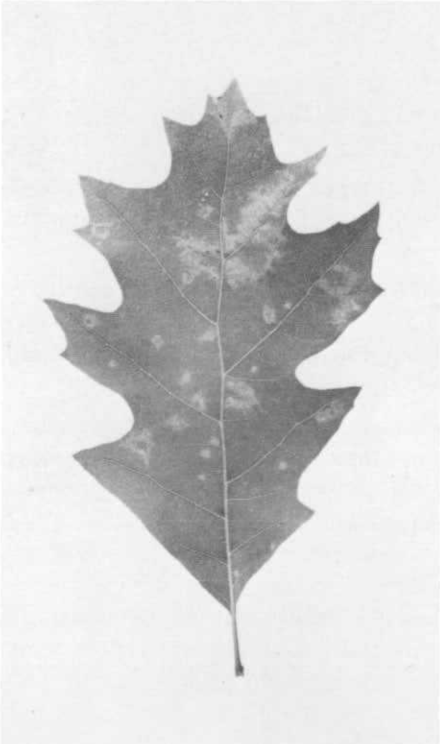


Plate 49—Leaf of *Quercus marilandica* seedling naturally infected with a graft-transmissible agent and showing chlorotic vein banding patterns.

Photograph by courtesy of O. W. Barnett

not greatly differ. Eichenfleckung had symptoms of chlorotic flecking without foliar deformation of *Q. petraea* Leiblin and *Q. robur* L. growing in Czechoslovakia and East Germany. Eichensheckung was delineated because the symptoms consisted of diffuse chlorotic star-shaped lesions in leaves of *Q. robur* which were deformed by partial underdevelopment of the laminae and twisting on the midveins. This disease was reported from East Germany and associated with rod-shaped virus-like particles about 300nm long resembling in this respect the observations of Yarwood and his co-workers. The other disease described by Schmelzer *et al.*, (1966) was termed Eichenmosaik, affected *Q. petraea* in Hungary and resembled witches' broom with an additional whitish mosaic symptom in leaves. Symptoms resembling Eichensheckung and Eichenfleckung are frequent in oak growing in Southern England and Sweden (Biddle, 1968).

Blattny (1964) briefly described a presumed virus disease of oak in Czechoslovakia which was transmitted by grafting and apparently (though few experimental details were published) by aphids (*Tuberculoides annulatus* Htg.). In Hungarian forests Horvath, *et al.* (1975) observed *Quercus cerris* L. with twisted or crescent-shaped leaves subsequently found to contain virus-like rigid rods (300 x 20nm) resembling tobamoviruses reported in oaks in the D.D.R., Czechoslovakia and California. The presumed virus was transmitted neither mechanically (to a wide range of herbaceous hosts) nor by aphids (*Myzocallis* sp.) given 24 hr. access to *Castanea sativa* with superficially similar foliage symptoms (see p. 26) before transfer to oak seedlings.



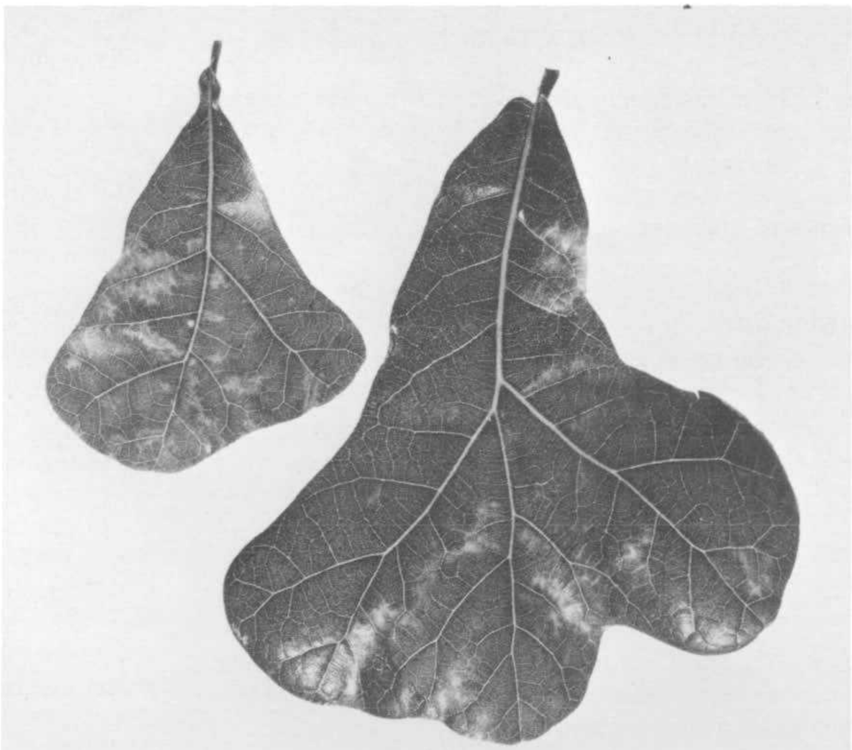


Plate 50—Leaf of *Quercus velutina* (left) and *Q. marilandica* (right) showing ringspot symptoms resulting from graft transmissions using *Q. marilandica* as inoculum. Virus-like flexuous rod-shaped particles were associated.

Photograph by courtesy of J. P. Fulton and O. W. Barnett

SYMPTOMS: Yellow or chlorotic leaf mottle.

Distribution: In Denmark affecting *Q. borealis* Mich. (syn. *Q. rubra*, Duroi) (Kristensen, 1963).

Transmission: By budding to *Q. borealis* which subsequently became stunted.

Causal agent/Relationship: Not known.

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RHAMNUS—*Rhamnaceae*

A graft transmissible variegation of *Rhamnus* sp. has been recorded but little studied (Brierley, 1944 cited one reference).

Foliage diseases

SYMPTOMS: Yellowish green mosaic or chlorotic bands, diminished leaf area and deformation.

Distribution: In USA (Quiaoit and Fulton, 1966) and East Germany (Schmelzer, 1974) affecting *Rhamnus cathartica* L.

Transmission: In sap with *Myzus persicae* from and to "herbaceous hosts".

Causal agent/Relationship: Cucumber mosaic virus was identified as a cause of the associated symptoms (Quiaoit and Fulton, 1966).

SYMPTOMS: Light green yellowish, reddish or white lines on both sides of main veins or with similarly coloured oak leaf patterns.

Distribution: In East Germany (Schmelzer, 1974).

Transmission: By budding to *R. frangula* but not in sap inoculated to "herbaceous hosts".

Causal agent/Relationship: Not known.

COMMENT: Schmelzer (1974) showed that *R. frangula* leaf sap mixed with extracts of plants infected with cucumber mosaic virus did not eliminate infectivity suggesting that an inhibitory property of the sap was not responsible for the failure to detect sap transmissible infectivity in the naturally affected *R. frangula.*

SYMPTOMS: Chlorotic rings, more obvious on young than older leaves.

Distribution: In Italy, affecting *Rhamnus fragula.*

Transmission: In sap to "herbaceous hosts" when immature leaf or root extracts were used as inoculum.

Causal agent/Relationship: Alfalfa mosaic virus was identified but not proved to be causing the symptoms (Marani and Giunchedi, 1976).

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RHODODENDRON—*Ericaceae*

Foliage disease

SYMPTOMS: Concentric necrotic ring patterns in two-year-old leaves.

Distribution: In horticultural cultivars of *Rhododendron* sp. in Oregon USA and British Colombia, Canada.

Transmission: By grafting from Rhodendron to *Kalmia latifolia* L on one occasion. Not in foliar sap mechanically inoculated to a range of "herbaceous hosts" (Coyier *et al.*, 1977).

Causal agent/Relationship: Unknown. Electron microscopy revealed flexuous rod-shaped virus-like particles 460–540nm long and about 13nm in diameter in leaves with symptoms.

COMMENTS: A similar syndrome in *Kalmia latifolia* was noted by Pearse (1968) who suggested that a virus might be the cause but did not report transmission tests.

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ROBINIA—*Leguminosae*

Mosaic and mottling symptoms have been reported in leaves of *Robinia* from many countries of Southern and Central Europe, in parts of the USA and in Asia. However, it is now known that several distinct viruses are capable of causing these symptoms when present alone. The different viruses which have been associated with mosaic in *Robinia* spp. are, with one, or perhaps two, exceptions, well known for the effects they cause in other hosts.

Foliage diseases

SYMPTOMS: Mosaic, mottling and deformation of foliage associated with 5 to 6 fold diminishing effect on wood production through effects on height and diameter growth; three-year-old nursery stock trees infected with robinia mosaic virus were said to be half the height of controls and less frost hardy (Schmelzer and Milinko, 1963; Milinko and Schmelzer, 1968).

Distribution: In the plains (but not mountainous regions) of Eastern Europe (Schmelzer, 1968) affecting up to 10% of *Robinia pseudoacacia* L., *R. pseudoacacia* forma umbriculifera Hort. and *R. viscosa* Ventenat.

Transmission: Experimentally in sap and via dodder to "herbaceous hosts". Naturally by *Aphis cracivora* Koch and experimentally by other aphids including *Myzus persicae* Sulz. (Schmelzer and Milicic, 1965, cited in Schmelzer, 1971; Milinko and Schmelzer, 1961; Milinko and Schmelzer, 1968). Propagation by top grafting to infected *R. pseudoacacia* stocks was said to be an important natural means whereby the virus was disseminated (Schmelzer and Milinko, 1963; Schmelzer, 1968).

Causal agent/Relationship: Robinia true mosaic virus (Echtes Robinienmosaik: Schmelzer, 1971) has been shown to cause mosaic symptoms but it is not the only virus which has been associated with this syndrome. Although bean yellow mosaic (Bos, 1970) infects *R. pseudoacacia* under experimental conditions to cause chlorotic mottle symptoms in leaves (Kovachevsky, 1968) and tobacco mosaic virus has been associated with a somewhat similar syndrome in Bulgarian *Robinia* (Atanasoff, 1965), Schmelzer's extensive work only revealed the following:—beet ringspot and potato bouquet serotypes of tomato blackring and strawberry latent ringspot viruses. Robinia true mosaic virus has some properties in common with cucumber mosaic virus and some with the unidentified virus associated with mosaic symptoms in *R. pseudoacacia* in the Chun-Chon area of South Korea (Kim, 1964; 1965) although the three viruses do not seem to have been compared in the same laboratory.

SYMPTOMS: Chlorotic blotches, spots and mosaic.

Distribution: In USA affecting *R. pseudoacacia*.

Transmission: By grafting but not following mechanical inoculation of sap to "herbaceous hosts" (Fulton and Kim, 1973).

Causal agent/Relstionship: Electron microscopy of thin sections of Robinia leaves revealed approximately spherical apparently membrane bound virus-like particles, distributed singly or in groups of two or three in the perinuclear space or within the cisternae of cell endoplasmic reticulum. Although these particles resemble those of tomato spotted wilt virus (Ie, 1970), their reported size is considerably greater.

Stem disease

SYMPTOMS: Shown most clearly in plants pruned to stimulate new growth. Single or multiple regions where buds and leaves proliferate brought about when all axillary (plus in rarer instances adventitious) buds develop into short succulent branches bearing leaves with greatly diminished area. Vein clearing may occur and leaf shape may be altered from bluntly rounded to pointed (Cullen, cited in Grant *et al.*, 1942). Petiole length may be one fifth of healthy, root proliferation may occur and the disease has been said to predispose affected plants to winter injury or death (Grant, 1939; Grant *et al.*, 1942).

Distribution: Waters (1898) first described the disease from *R. pseudoacacia* in Maryland, USA

Plate 51—Witches broom in *Robinia pseudoacacia* associated with mycoplasma-like organisms.

Photograph by courtesy of C. E. Seliskar, U.S.D.A.

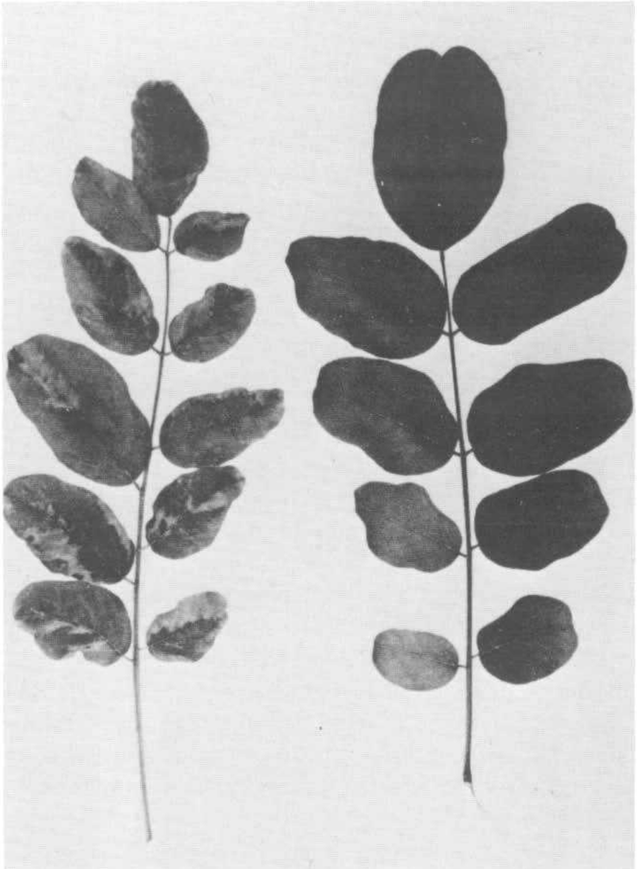

Plate 52—Leaves of *Robinia pseudoacacia* showing chlorotic blotches associated with a virus resembling tomato spotted wilt.
Photograph by courtesy of J. P. Fulton

but its occurrence in Georgia and Virginia before 1900 was indicated when herbarium specimens were examined (Hartley and Haasis, 1929). The disease has been reported in a region bounded by the Atlantic to the east, Pennsylvania to north and including Ohio, Kentucky, Arkansas, Tennessee and South Carolina (Grant, 1938a & b; Grant, 1939; Grant and Hartley, 1938). A witches broom syndrome has also been reported from Southern and Central Europe (Blattny, 1959; Ciferri and Corte, 1960).

Transmission: Most frequently by grafting (Jackson and Hartley, 1933), by budding but not in sap or with six named aphid species and "several unidentified leaf hoppers and aphids" (Grant *et al.*, 1942).

Causal agent/Relationship: Seliskar *et al.*, (1973) detected with an electron microscope, MLO in affected tissue.

COMMENT: It is interesting to note that witches' broom in Robinia has not been reported from the total geographic range of *R. pseudoacacia* in the USA and that the known distribution coincides quite closely with that of elm phloem necrosis.

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ROSA—*Rosaceae*

See plate 53, (Colour)

In common with other plant material which has been vegetatively propagated for many years, roses frequently contain mixtures of viruses.

There is an extensive literature relating to graft-transmissible agents of *Rosa* spp., hybrids and cultivars, but until recently very few viruses infecting these plants were characterized and their individual effects studied in roses. White (1932) reviewed many of the earliest observations on infectious chlorosis of roses in the USA and elsewhere and contrasted these symptoms with effects attributed to nutritional imbalance or insect feeding. Since then, a great number of observations have been reported and from these I have made a somewhat arbitrary selection of conditions, with, in some instances, unconfirmed but possible virus aetiology. The amount to which symptom expression differs in different cultivars infected with the same virus has not yet been fully assessed but it has been suggested that environmental conditions (e.g. temperature) affect symptom expression (Ikin, 1971).

Foliage diseases

SYMPTOMS: Mosaic; rose yellow mosaic. Chlorotic-yellow ringspot, oak-leaf or line patterns in leaves although a very large number of additional symptoms have been described (Thomas and Massey, 1939; Bos, 1976; Brierley and Smith, 1940).

Distribution: Most countries in Eastern and Western Europe (Schmelzer, 1968) in addition to the USA, Australia (Basit and Francki, 1970), New Zealand (Fry and Hunter, 1956), India (Sastry, 1966) and Norfolk Island (Ikin cited in Ikin and Frost, 1974) affecting horticultural roses.

Transmission: By grafting but, more significant, in sap to "herbaceous hosts" inoculated with leaf extracts of *Rosa setigera* Michx. (Fulton, 1952), other *Rosa* spp. and horticultural clones by which means Koch's postulates were satisfied. Natural dissemination in the USA is probably largely via vegetatively propagated virus-infected rootstocks (Brierley and Smith, 1940). In Europe, where seedling stocks are more widely used, dissemination is probably largely due to propagation of infected scions.

Causal agent/Relationship: Several workers using different techniques to overcome the problems of virus transmission have isolated similar viruses from *Rosa*, *Malus* and *Prunus* spp. Taken together, data from serological studies made by Halliwell and Milbrath (1962), Willison *et al.*, (1956), Fulton (1967; 1968) and Casper (1973) indicate that a continuous spectrum of viruses having different proportions of their antigenic determinants in common may be detected in association with rose mosaic disease. Some of the isolates within this group (Ilarviruses; Fulton, 1968) have been associated with recognizable diseases in hosts other than rose and the names apple mosaic or plum line pattern viruses have been widely publicized although Fulton (1967; 1968; 1972) considered these three viruses synonyms. Prunus necrotic ringspot virus has few antigenic determinants in common with the other members of the ilarvirus group although the disease this virus causes in *Rosa* sp. is not readily differentiated from that caused by apple/rose mosaic viruses (Fulton, 1967; 1972).

COMMENTS: In UK, arabis mosaic and tobacco streak viruses have been detected in mixture with apple/rose mosaic and prunus necrotic ringspot viruses (Farrar and Frost, cited in Ikin and Frost, 1974). However, Fulton (1970) recognized a distinct syndrome in *R. setigera* and showed that irregular chlorotic patches, vein chlorosis, leaf twisting and stunting of shoots was induced in this species by tobacco streak virus. Although arabis mosaic virus has been isolated from symptomless roses (Ikin and Frost, 1974), the virus was associated with chlorotic ring and vein mottling symptoms in the cultivar Masquerade (Cammack, 1966) and Sweet (1974) observed slight chlorosis in roses he experimentally infected with the virus. Two additional viruses, tomato ringspot (Halliwell and Milbrath, 1962) and tobacco ringspot (McDaniel *et al.*, 1971) have also been isolated from plants with symptoms of rose mosaic disease but whether they caused these symptoms remains to be established.

A previously undescribed disease, rose ring pattern, characterised by rings, fine line patterns and chlorotic flecking of the leaves and colour break rings in the petals was reported by Secor and Nyland (1978). The causal agent, which was transmissible to "woody indicators" by grafting has not been identified but was detected in *R. multiflora* Thunb. cv Burr. in California.

SYMPTOMS: Yellow net. Bright yellow chlorosis of veins of lower leaves in particular; often part of the mosaic syndrome (White, 1932; Brierley and Smith, 1940).

Distribution: Widespread in commercial rose cultivars throughout the world but recently recognized and studied in Wisconsin, USA, (Fulton, 1976).

Transmission: Using 2–5% polyvinyl pyrrolidone

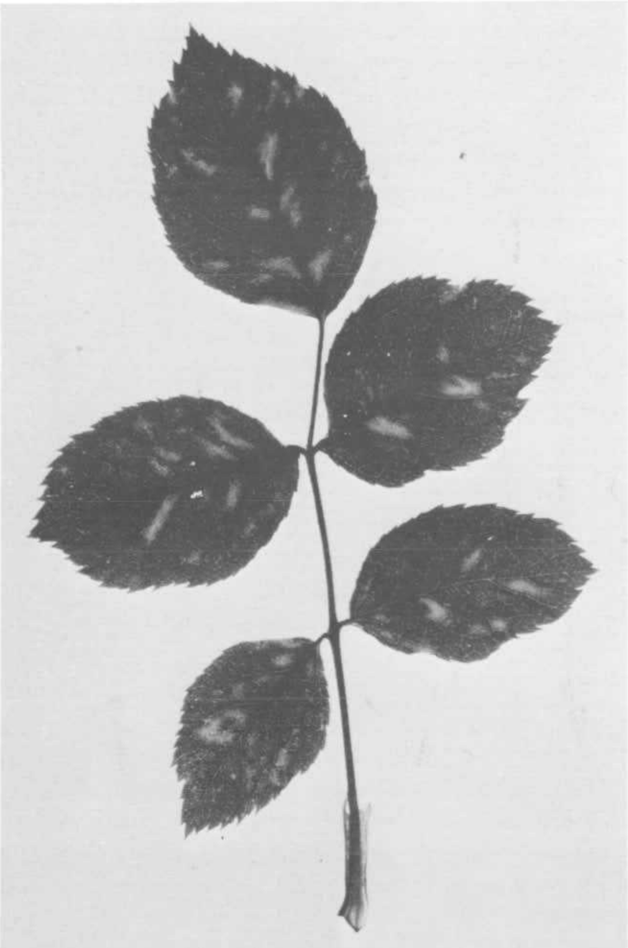

Plate 54—A leaf of the rose cultivar Baccarat showing interveinal chlorosis when naturally infected with strawberry latent ringspot virus.
Photograph by courtesy of Long Ashton Research Station

(PVP), 2-Mercaptoethanol and phosphate buffer pH 8·0, Fulton (1976) transmitted a virus to "herbaceous hosts" from affected roses. Fulton also transmitted the agent from roses by grafting with seedling *Prunus mahaleb* L., *P. persicae* Batsch. and *P. pennsylvanica* L. and hence from *Prunus* spp. to rose again.

Causal agent/Relationship: A variant of prunus necrotic ringspot virus having few, if any, serological determinants not held in common but differing in its requirements for PVP for mechanical transmission from rose. Other prunus necrotic ringspot and apple mosaic virus isolates were isolated from roses showing yellow net symptoms on lower and mosaic on upper leaves (Fulton, 1976).

COMMENTS: Most vein yellowing is undoubtedly associated with and probably caused by ilarviruses. However, in the Netherlands (van Hoof and Caron, 1975) and in UK (Cammack, 1966; Harrison, 1967; Ikin and Frost, 1974), some foliar flecking and vein yellowing has been associated with strawberry latent ringspot virus. This virus has also been associated with mosaic, mottling, strapping, puckering or twisting of leaves, diminished leaf size and a somewhat bushy habit (causing economic damage in standard roses; Ikin, 1971). Data are few but it seems noteworthy that diminished vigour and possibly some of the effects on leaves which have been attributed to this virus may, in glasshouse conditions, be partly caused by the feeding effects of high populations of *Xiphinema, Longidorus* and *Pratylenchus* nematodes (Brown, 1965; Winfield, 1974). Vein yellow net symptoms affecting *R. multiflora* in the USA with additional dwarfing and epinasty (rose spring dwarf) were due to graft-transmitted agents not studied in detail (Traylor *et al.*, 1971; Slack *et al.*, 1976a & b).

Stem diseases

SYMPTOMS: Shortening of internodes, precocious axillary bud break and anthocyanescence of leaves.

Distribution: In the Northern states of the USA affecting *R. eglanteria* L., *R. woodsii* Lindl., *R. multiflora* Thunb. and *R. rubrifolia* Vill.

Transmission: By grafting and apparently by eriophyid mites (*Phyllocoptes fructiphilus* Koch) but not *Tetranychus urticae* Koch (Allington, *et al.*, 1968).

Causal agent/Relationship: Not known.

SYMPTOMS: "Rose streak" discolouration (browning) of the bark. Less frequently the rachis, main veins or stipules of leaves may be similarly discoloured and fruits may show brown spots, arcs or concentric ring patterns.

Distribution: In the USA (Brierley, 1935), in East Germany (Schmelzer, 1967) and probably in the UK (Ikin and Frost, 1974).

Transmission: By budding to *R. multiflora* but not in sap to "herbaceous hosts" (Schmelzer, 1967).

Causal agent/Relationships: Not known.

OTHER: In Czechoslovakia, the cowl forming condition affecting leaves of *R. cervensia* Hudson, *R. moyesii* Hemsl. and Wilson and *R. rugosa* Thunb. noted by Klastersky (1951) was reportedly transmissible by grafting.

In the UK, Hollings (1961) recorded (without details) the occurrence of three graft-transmissible disorders affecting either the leaves or flowers of rose cultivars and Farrar and Frost (1972) recognized a distinct graft-transmissible flower break symptom which was associated with spherical virus-like particles visible with the aid of an electron microscope (Farrar and Frost cited in Ikin and Frost, 1974).

Somewhat more detailed research has been devoted to an investigation of the bud proliferation, wilt and die-back syndrome which was probably first noted in Australia (Grieve, 1931) although similar conditions have been reported from Italy, Czechoslovakia, New Zealand (Fry and Hammett, 1971 and others cited therein), the USA (Cheo, 1970), the UK (Hutton, 1970; Ikin and Frost, 1974; Hollings *et al.*, 1973; Sweet, 1974) and the Netherlands (Bos and Perquin, 1975). Although parts of the syndrome seem to have been transmitted by grafting (Fry and Hammett, 1971; Sweet, 1974; Slack *et al.*, 1976b) others have failed to achieve transmission of the agent(s) in this or in any other way (Ikin and Frost, 1974). Bos and Perquin (1975) reviewed most of the relevant literature and considered many of the alternate possibilities but without implicating any specific aetiological agent. It seems likely that the syndrome will be found to be due to a complex of interacting factors; physiological and environmental influences, perhaps virus, mycoplasma (MLO were reportedly observed in diseased but not healthy roses; Atkey and Thomas 1976) and/or incipient *Verticillium* wilt.

Roses with green petals are highly prized in horticulture; this effect is in some instances a symptom of disease. In the U.S.S.R. studies confirmed that the condition was transmissible by grafting and with dodder (*Cuscuta campestris*). MLO were associated with the symptom (Protsenko *et al.*, 1972; Protsenko and Surgucheva, 1975).

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ROMNEYA—*Papaveraceae*

Hollings (1961) detected cucumber mosaic virus in *Romneya coulteri* Harvey showing faint mottling of leaves but did not report tests to infect healthy *Romneya* with the virus.

Reference

Hollings, M. (1961). Virus and its effect on some ornamental shrubs. *Nurserym. Seedsm. Glasshouse Grower* **132**, 930–931.

SALIX—*Salicaceae*

Stem Disease

SYMPTOMS: Brooming, narrowing and chlorosis of leaves and predisposition to winter injury.

Distribution: In Czechoslovakia affecting *Salix triandra* L., *S. viminalis* L., *S. babylonica* (=*S. salmoni* Carriere Hort), *S. aurita* L., *S. caprea* L., *S. alba* L., *S. pentandra* L. (Svobodova *et al.*, 1962 cited in Schmelzer, 1968). In USA affecting *S. rigida* Muhlenberg (Holmes *et al.*, 1972).

Transmission: By grafting.

Causal agent/Relationship: Phloem of diseased (but not symptomless) trees in the USA contained micro-organisms bounded by walls rather than membranes thereby indicating their resemblance to rickettsia rather than mycoplasma-like organisms (Holmes *et al.*, 1972; Maramorosch, 1974).

COMMENT: *Salix caprea* L. became symptomlessly but systemically infected with poplar mosaic virus when grafted with *Pxeuramericana* 'OP226' scions as donors (Cooper, unpublished data).

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SAMBUCUS—*Caprifoliaceae*

See plate 55, 56 (Colour)

Foliage diseases

SYMPTOMS: Yellow net. A yellow-pale green colour in veins of some but not all leaves particularly in spring and autumn.

Distribution: Widespread in Europe affecting *Sambucus nigra* L. and reported on one occasion from the USA (Yarwood, 1959).

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationship: Koch's postulates have been satisfied by several authors using different viruses: arabis mosaic (Cadman, 1960; Harrison and Winslow, 1961; Schmelzer, 1966), tomato blackring and cherry leaf roll (Schmelzer, 1966). Stefanac (1969) also detected cherry leaf roll virus in *S. nigra* in Yugoslavia, as did Horvath *et al.* (1974) in Hungary, and Jones and Murant (1971) in Scotland. Strawberry latent ringspot virus was detected in *S. nigra* with yellow net symptoms (Lister, 1964) but no reports of reintroduction of the virus into this host have been published. Hansen (1967) and Hansen and Stace-Smith (1971) isolated a virus they called 'golden elderberry virus' from *S. nigra* L. aurea Sweet showing yellow areas and ring symptoms in their leaves. Jones and Murant (1971) showed that there were few if any serological determinants not held in common between golden elderberry virus and an isolate of cherry leaf roll virus from *S. nigra* in Scotland. In brief statements, Jones (1972) and Brunt and Stace-Smith (1971) reported the isolation from 'elder' in Scotland and England respectively of a virus having a modal length to its rod-shaped particles of 650nm. The english isolate was serologically related to carnation latent virus (Wetter 1971).

COMMENTS: Two distinct syndromes (agents) are reportedly graft transmissible from *S. nigra*. These are 'pseudolacinity' in which the leaflets tend to be narrowed and irregularly pointed and a condition termed "ornamental mosaic" which is characterized by yellow ringspot patterns with blistering (Blattny and Oswald, 1950). Further work will be needed to determine the aetiology of these diseases, the pseudolacinity in particular has features which suggest genetic abnormalities and Helebrant (1969) was unable to transfer the laciniate character either by grafting or in sap rubbed onto leaves of *S. nigra* or *S. racemosa* L. Unfortunately, Helebrant was not using the authentic material of Blattny and Oswald (1950) so the point remains unclear.

SYMPTOMS: Chlorotic blotching in leaves.

Distribution: In North America affecting *Sambucus canadensis* L.

Transmission: In sap to "herbaceous hosts".

Causal agent/Relationship: Golden elderberry virus (=cherry leaf roll virus). Other viruses isolated from *S. canadensis* but with unproven causal association with distinct symptoms are

Plate 57—Leaves of *Sambucus canadensis* showing chlorotic oak-leaf symptoms which formed following inoculation with elderberry latent virus.

Photograph by courtesy of Scottish Horticultural Research Institute tobacco mosaic (Mueller, 1967), tomato ringspot (Uyemoto, 1970), cucumber mosaic and tobacco necrosis plus its satellite virus (Uyemoto and Gilmer, 1971). A virus which Jones (1972) called 'elderberry virus A' was detected in *S. canadensis* imported into Scotland from the USA Its properties were not studied in detail but it had flexuous rod-shaped particles and may be similar to the carlavirus isolates from Sambucus sp. (presumably *S. nigra*) from England and Scotland. A virus with a similar morphology to elderberry virus A was obtained from *S. canadensis* in USA (Uyemoto and Gilmer, 1971). Jones (1972) isolated a different virus which he called 'elderberry latent' from *S. canadensis* cv Adams No. 2. This virus, which was not transmitted non-persistently by representatives of two aphid genera, had spherical particles of two main sizes and caused transient chlorotic ringspot and line patterns to form in some but not all leaves of *S. canadensis* cv Adams No. 2 systemically infected following experimental mechanical inoculation.

OTHER: Chlorotic blotching, in some instances associated with necrotic flecks or rings in *S. racemosa* L. has also been associated in the DDR and in Yugoslavia with isolates of cherry leaf roll virus (Schmelzer, 1966; Stefanac, 1969). In Southern Finland, *S. racemosa* infected with cherry leaf roll virus and an unidentified carlavirus, showed chlorotic blotching in spring foliage. However, in summer/autumn, leaves on infected plants had bright yellow ring patterns (Cooper, unpublished data).
Cherry leaf roll virus was also transmitted from *S. ebulus* L. in Yugoslavia. The infected Sambucus showed chlorotic foliage symptoms not proved to be due to the associated virus (Mamula and Milicic, 1975).

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SKIMMIA—*Rutaceae*

In a brief report, Varney (1965) stated that tobacco ringspot virus was detected in an unidentified plant of *Skimmia* with ringspot symptoms in its leaves. The isolate infected two *Skimmia* clones systemically but did not cause symptoms.

References

Varney, E.H. (1965). A ringspot virus disease of *Skimmia* sp. *Phytopathology*, **55**, 131.

SOLANUM—*Solanaceae*

Foliage disease

SYMPTOMS: Diffuse mottling, malformation and on some leaves severe mosaic.

Distribution: In *Solanum crispum* Ruiz and Pav. in U.K.

Transmission: Mechanically in leaf sap to "herbaceous hosts".

Causal agent/Relationship: Cucumber mosaic virus was identified but not proved to cause the disease (Cooper unpublished data).

COMMENT: Only one woody climber included. There are numerous additional viruses recorded from herbaceous species such as the potato.

SORBUS—*Rosaceae*

See plate 58a (Colour)

In East Germany, graft transmissible chlorosis and variegation of *Sorbus aucuparia* L. was noted by Baur (1907). Although the cause remains to be determined it may be significant that somewhat similar symptoms formed in leaves of *S. aucuparia* inoculated with apple mosaic virus (Kegler cited in Schmelzer, 1968). Kegler (1959/60) reported the graft transmissibility of a distinct agent causing yellow-whitish flecks, rings and lines in leaves of affected plants. This condition is frequent in *S. aucuparia* in UK and in Finland but has not to date yielded viruses transmissible in foliar sap to herbaceous hosts (Cooper, unpublished data). Although no virus was detected following inoculation of *Sorbus* leaf sap to herbaceous test plants, Sweet (pers. comm.) using a double budding technique and woody indicators, induced stunting and leaf chlorosis (symptoms typical of apple chlorotic leaf spot virus) in *Malus platycarpa* and the Russian clone R 12740–7A of *M. sylvestris* (both on rootstocks of *M. sylvestris* cv Tremlett's Bitter) following inoculation with buds either from a symptomless *Sorbus thianshanica* Ruprich or from *S. aucuparia* with yellowing and line patterns in the foliage. His observations confirmed and extended that of Kralikova (1961). An apple isolate of chlorotic leaf spot virus induced a stunt in some but not all *Sorbus aucuparia* seedlings which were experimentally infected following bud grafting (Sweet and Campbell, 1976).

References

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Sweet, J.B. and Campbell, A.I. (1976). Pome fruit virus infections of some woody ornamental and indigenous species of Rosaceae. *J. hort. Sci.* **51**, 91–9.

SPIRAEA—*Rosaceae*

See plate 58b (Colour)

Spiraea douglasii Hooker with leaves showing vein yellows and enations yielded arabis mosaic virus to herbaceous test plants. However, it seems unlikely that this virus caused these symptoms because AMV was also detected in symptomless *Spiraea x bumalda* Burr. cv Antony Waterer and *S. japonica alba* Nichols (*S. albiflora* (Mig.) Zab) (Sweet 1974). Schmelzer (1970) also isolated AMV from an unnamed cultivar of *S. x bumalda* showing vein yellow net symptoms.

References

Schmelzer, K. (1970). Untersuchungen an Viren der Zier- und Wildgeholze. 7. Mitteilung: Weitere Befunde an *Buddleja, Viburnum, Caryopteris* und *Philadelphus* sowie Viren an *Leycesteria, Chionanthus, Ribes, Hydrangea, Syringa, Spiraea* und *Catalpa*. *Phytopath. Z.* **67**, 285–326.

Sweet, J.B. (1974). *Virus infections of woody rosaceous ornamentals. M.Sc. Thesis*, University of Bath.

STAPHYLEA—*Staphyleaceae*

Following manual inoculation of "herbaceous hosts" inoculated with foliar sap from *Staphylea emodi* Wahl. (showing green mottle symptoms) arabis mosaic virus was identified. This virus, with the beet ringspot serotype of tomato blackring, was associated with diffuse-transparent yellowing in foliage of *S. trifolia* L. (Schmelzer, 1974). Neither virus was reported to have been reintroduced into healthy *Staphylea* plants.

Reference

Schmelzer, K. (1974). Untersuchungen an Viren der Zier- und Wildegeholze 8. Mitteilung Neue Befunde an *Forsythia. Hydrangea* und *Philadelphus* sowie Viren und Virosen an *Rhamnus, Centaurea, Galvezia, Cistus, Forestiera, Abeliophyllum, Celastrus, Staphylea* und *Crambe. Zbl. Bakt. ParasitKde* **129** *Abt. II*, 139–168.

SYMPHORICARPUS—*Caprifoliaceae*

In a brief report, van Hoof and Caron (1975) reported the isolation of strawberry latent ringspot virus from leaves of *S. albus* Blake: symptoms were not described.

Reference

van Hoof, H.A. and Caron, J.E.A. (1975). Strawberry latent ringspot virus-infected fields of *Rosa rugosa* produce healthy cuttings but diseased rootstocks for standard roses. *Meded. Fac. Landbouw. RijksUniv. Gent* **40**, 759–763.

SYRINGA—*Oleaceae*

Foliage diseases

SYMPTOMS: Diverse array including light green ring and line patterns with occasional distortion, leaf cracking, and "shot hole" effects. Symptoms sometimes transient or restricted to a few leaves. Ringspot (Atanasoff, 1935); ringspot mosaic (Smolak and Novak, 1950).

Distribution: Bulgaria (Atanasoff, 1935), The Netherlands (van Katwijk, 1955), many other European countries (Schmelzer and Schmidt, 1966; Novak, 1969) and the USA (Beale and Beale, 1952).

Transmission: Parts of the syndrome (agents) by grafting between 1) named *S. vulgaris* clones (Protsenko and Protsenko, 1950; Beale and Beale, 1952) and 2) lilac with symptoms of ringspot. Also agents when the latter was grafted to other Oleaceous genera (Novak, 1969).

Causal agent/Relationship: The main cause is unknown. A hitherto undescribed virus, lilac ring mottle, was transmitted mechanically to "herbaceous hosts" inoculated with sap from lilac foliage but was not consistently associated with ringspot symptoms (van der Meer, *et al.* 1976). Other viruses occasionally associated with ringspot disease include elm mottle (Schmelzer, 1969), strawbery latent ringspot (van der Meer, 1976) arabis mosaic (Cooper, 1975) and tobacco rattle (Huttinga, 1972). Bacteria (*Pseudomonas syringae* Van Hall) have also been implicated (Novak and Lanzova, 1975; 1977).

SYMPTOMS: Chlorotic watermark or "oak-leaf" banding patterns with interveinal chlorosis, "chlorotic ringspot" (Novak, 1969).

Distribution: Czechoslovakia and UK.

Transmission: Via stem grafts on one occasion and by root grafts on two (Novak, 1969). Mechanically in sap to "herbaceous hosts" (Brunt, 1978: Novak and Lanzova, 1975; 1977).

Causal agent/Relationship: Unknown but, because the syndrome resembles that studied by Beale and Beale (1952), Novak (1966; 1969) suggested that it may be a "strain" of the agent causing ringspot disease. More recently, Novak and Lanzova (1975; 1977) reported detecting arabis mosaic and cherry leaf roll viruses in lilac with chlorotic ringspot disease.

A hitherto undescribed virus having flexuous rod-shaped particles (10 x 1200nm) was associated with "chlorotic* leafspot" disease (Brunt, 1978). The pathogenicity of the virus for lilac was not recorded. In experimentally infected *Chenopodium quinoa* and *Phaseolus vulgaris* leaves, ultrastructural changes associated with lilac chlorotic leafspot virus were reported (Brunt and Stace-Smith, 1978).

SYMPTOMS: Distinct yellow blotches, (some centred on veins) surrounded by one or more concentric rings, "yellow ring" (Novak, 1969).

Distribution: Czechoslovakia and in Poland (Kochman *et al.*, 1964).

Transmission: By budding or grafting *S. vulgaris* (Novak, 1969). Unidentified viruses were detected in "herbaceous hosts" inoculated with sap from Syringa leaves (Kochman *et al.*, 1964; Novak, 1969; Schmelzer, 1970).

Causal agent/Relationship: Schmelzer (1970) detected mixed infections with tomato black ring (potato bouquet strain) and arabis mosaic viruses in seedlings budded with material from Poland/ Kochman. Furthermore, Novak and Lanzova (1977) detected tomato bushy stunt virus. Effects attributable to these viruses alone or in combination have not been recorded.

SYMPTOMS: Pale yellow to white mosaic patterns in *S. vulgaris* (white mosaic). Other symptoms include chlorotic, but not necrotic, rings or broad white chevron patterns and on occasions the affected white leaves become curled.

Distribution: East Germany (Schmelzer and Schmidt, 1966).

Transmission: By grafting (Schmelzer and Schmidt 1966). In tests done early in spring Schmelzer (1969) transmitted a virus from *S. vulgaris* to "herbaceous hosts" using leaf sap, transmission being aided when inocula were buffered with phosphate solutions. The virus was not transmitted via dodder (*Cuscuta californica* Choisy or *C. subinclusa* Dur. et Hilg.). Attempts to find aphid vectors have been unsuccessful, but Schmelzer (1969) detected virus in pollen of *S. vulgaris* with symptoms of white mosaic.

Causal agent/Relationship: Schmelzer (1969) found that viruses from *S. vulgaris* with white mosaic, were virtually identical with those isolated from *Ulmus* spp. with elm mottle disease. A lilac isolate of elm mottle virus caused white mosaic disease in 3 of 18 *S. vulgaris* seedlings. Schmelzer (1969) was subsequently able to recover virus from affected plants.

COMMENT: Symptoms of white mosaic resemble those of streak mosaic (necrotic ringspot) reported from Czechoslovakia (Smolak and Novak, 1950; Novak 1969) but attempts to transmit streak mosaic have not been noted.

SYMPTOMS: In a specimen, (25 years old) of *Syringa oblata affinis* (possibly *S. affinis* L. Henry or a hybrid) some leaves were (i) yellow mottled and (ii) smaller than usual (Waterworth, 1972).

Distribution: Maryland, USA.

Transmission: Characteristic leaf mottle symptoms developed in three of ten lilac plants (species not reported) four weeks after being mechanically inoculated with a concentrated virus-containing extract in phosphate buffer. In 18 out of 20 experiments, aphids, *M. persicae*, transmitted lilac mottle virus as if it was non-persistent.

Causal agent/Relationship: Particles of lilac mottle virus are flexuous, and 575 to 610nm long. The virus was serologically related to carnation latent virus (Wetter, 1971) and other (but not all) members of the carlavirus group.

SYMPTOMS: Blighting phenomena (including lilac mosaic). Among the symptoms of lilac mosaic disease, Atanasoff described angular pale spotting of leaves

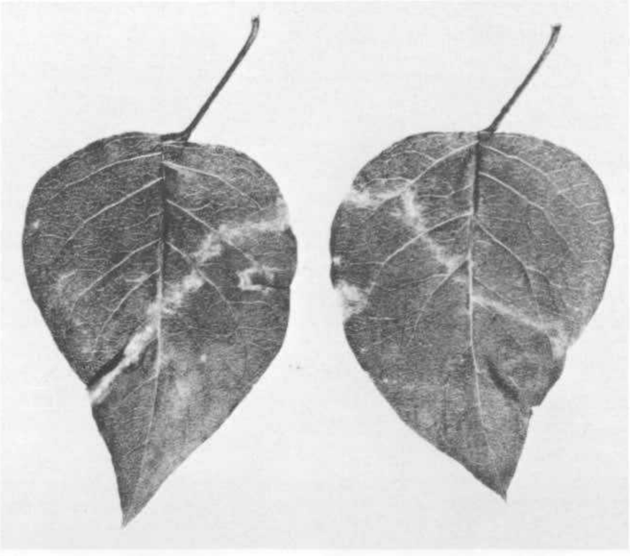

Plate 59—Leaves of *Syringa vulgaris* cv Michael Buchner inoculated by budding and showing chlorotic ring and line patterns. Although arabis mosaic virus has been transmitted from bushes with similar symptoms, other viruses have also been associated.

Photograph by courtesy of F. A. van der Meer

*The associated symptoms in lilac included chrome yellow rather than chlorotic line patterns.

which rolled at their margins, became brittle before dropping to expose stem apices which were then liable to early autumnal frost injury. Similarly complex arrays of symptoms including leaf rolling associated with dark coloured or necrotic etching were reported by Schmelzer, (1968).

Graft-blight (Chester, 1931; Cadman, 1940; Smith, 1940) occurs universally when *Syringa* spp. are grafted to *Ligustrum* rootstocks as was common in horticultural practice. Even though rootstocks appear normal, foliar blight tends to increase in severity as the grafted plants age, with mottling, inward rolling and foliar death occurring in the second and third years.

Distribution: Wherever *Syringa spp* are grown.

Transmission: Although Smith (1940) reported the transmission of graft blight between different *Syringa* spp., Cadman (1940) questioned Chester's (1931) earlier evidence because symptoms did not develop when *Syringa* scions grew away from their own sucker roots.

Causal agent/Relationship: Unknown but similar symptoms of leaf roll and necrosis have been attributed in the USA to atmospheric pollutants (Hibben and Walker, 1966; Hibben and Taylor, 1974). Bacteria might also be involved (see Novak and Lanzova, 1977).

Stem disease

SYMPTOMS: In *S. japonica* Decne witches' broom tending to occur in the upper parts of affected plants as abnormally slender, freely branching lateral shoots bearing leaves of about one quarter normal size. Leaves are additionally twisted, rolled or may show chlorotic flecks (Brierley, 1951). In *S. vulgaris*, thin lateral shoots develop at the expense of the main stems: the smaller leaves having additional vein clearing symptoms (Lorentz and Brierley, 1953).

Distribution: USA.

Transmission: By grafting but not by mechanical transmission in foliar sap.

Causal agent/Relationships: Unknown, possibly mycoplasma-like particles will be associated.

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TAXUS—*Taxaceae*

Taxus baccata L. cv Aurea in Czechoslovakia has leaves which are golden yellow when young but which change colour to a pale green in Autumn. Blattny (1960) reported transmitting the yellow leaf variegation agent by grafting but with few details.

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TILIA—*Tiliaceae*

Two virus-like conditions are reported to affect species of *Tilia* in Eastern Europe. Cowl-formation by leaves of *T. platyphyllos* Scop., *T. cordata* Mill., *T. macrophylla*

Plate 2a Graft incompatibility (cause unknown) showing as a brown line at the union between *Acer pseudoplatanus* seedling rootstock and an *A. rubrum* scion.

Plate 2b Graft incompatibility showing as stem pitting at the union between the scion R 12740/7A "Russian apple" (a 'woody indicator') and *Malus sylvestris* rootstock. At least two virus-like agents were present; Spy epinasty and apple stem pitting.

Plate 11b Double diffusion serology in agarose jelly. The central well contains antiserum to a birch isolate of cherry leaf roll virus. Surrounding this are wells containing sap from herbaceous hosts infected with birch (b) or elder (e) isolates. Wells at right (h) contain sap from healthy plants. The white precipitin lines show spur formation (arrowed).

Plate 14 Sunflower petals showing on the left that petals have been converted to leaf like structures—phyllody. This symptom is typically associated with mycoplasma-like organisms.

Plate 16 Distant view of a specimen *Aesculus hippocastaneum* showing the general yellow appearance; a symptom associated with an ilarvirus.

Plate 17 Close-up of one leaf from the affected tree showing a yellow 'oak leaf' vein-banding pattern.

Plate 18 *Betula alleghaniensis* leaves showing chlorotic vein banding and concentric ring patterns associated with apple mosaic virus.

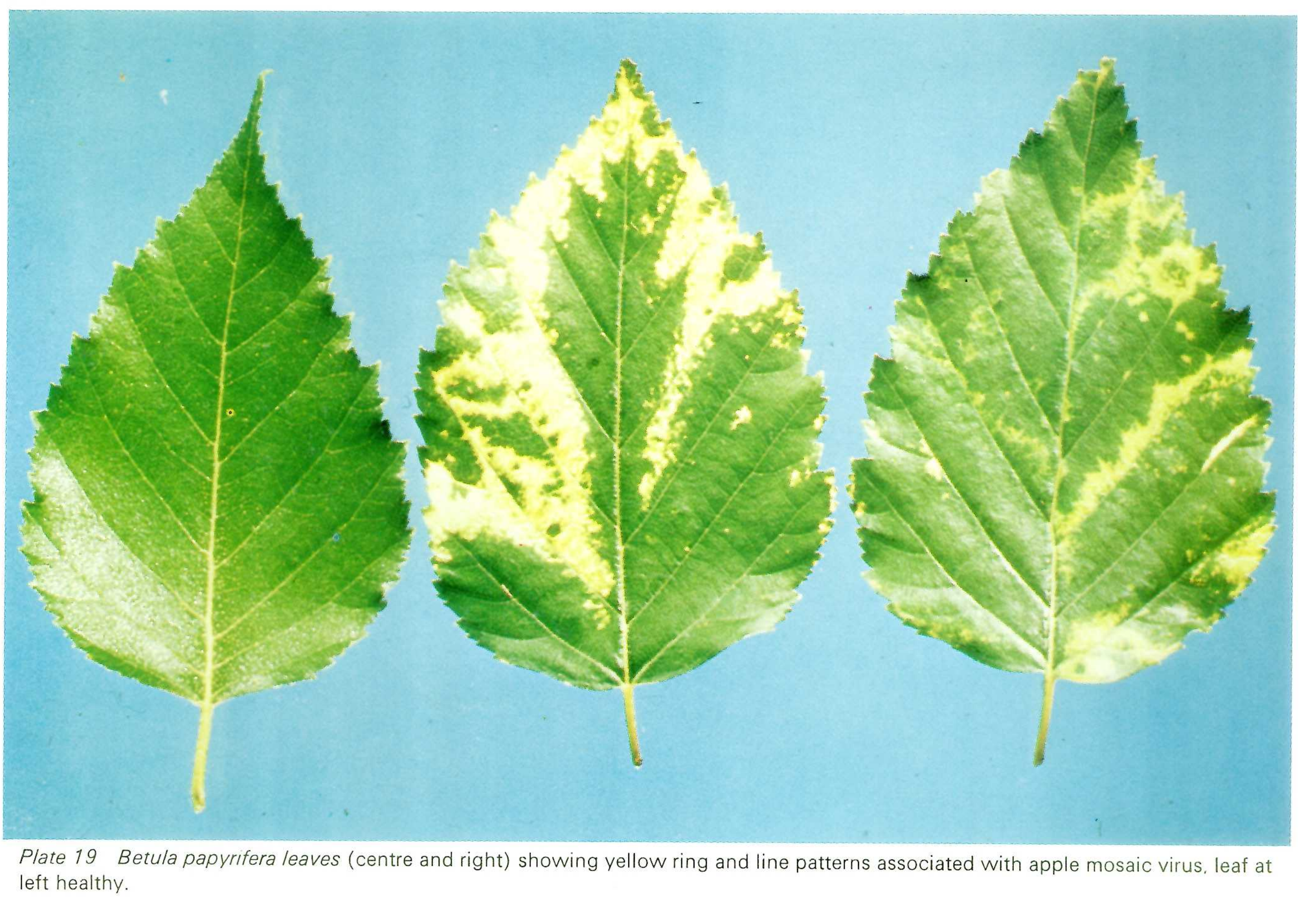

Plate 19 *Betula papyrifera leaves* (centre and right) showing yellow ring and line patterns associated with apple mosaic virus, leaf at left healthy.

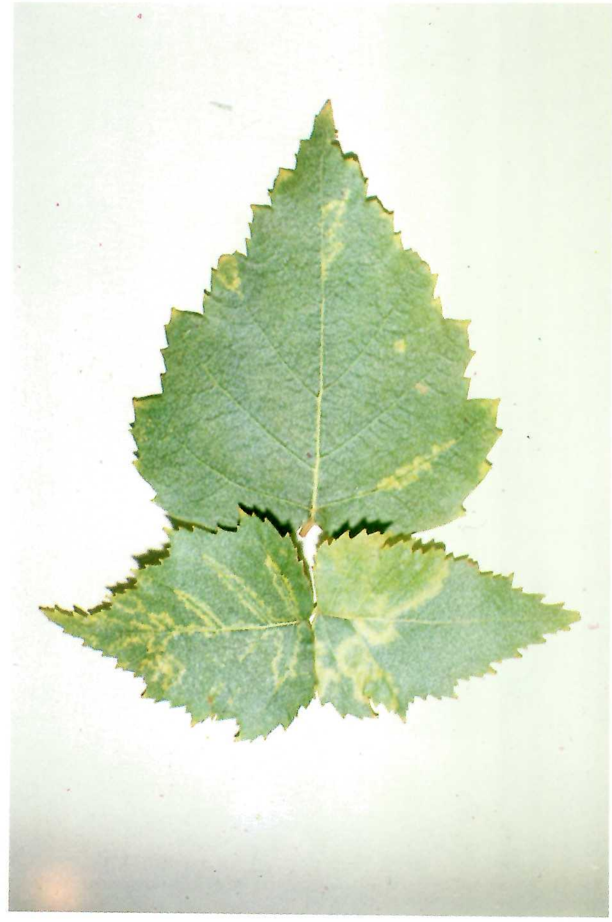

Plate 22 Leaves of *Betula verrucosa* naturally infected with cherry leaf roll virus and showing yellow ring and vein banding patterns.

Plate 25 Witches' broom in *Carya pecan* (Pecan bunch).

Plate 27 Clematis (unnamed cultivar) showing yellow ring and line patterns associated with cucumber mosaic virus.

Plate 28 *Cornus sanguinea* leaves showing yellow ring and line pattern symptoms associated but not consistently with mixtures of tomato bushy stunt and cherry leaf roll viruses.

Plate 29 *Corylus avellana* leaf showing yellow 'target' spot symptom associated with an ilarvirus serologically resembling apple mosaic. Somewhat similar symptoms have also been associated with the distinct tulare apple mosaic virus. However, in other instances hazel with these symptoms have consistently failed to yield any virus.

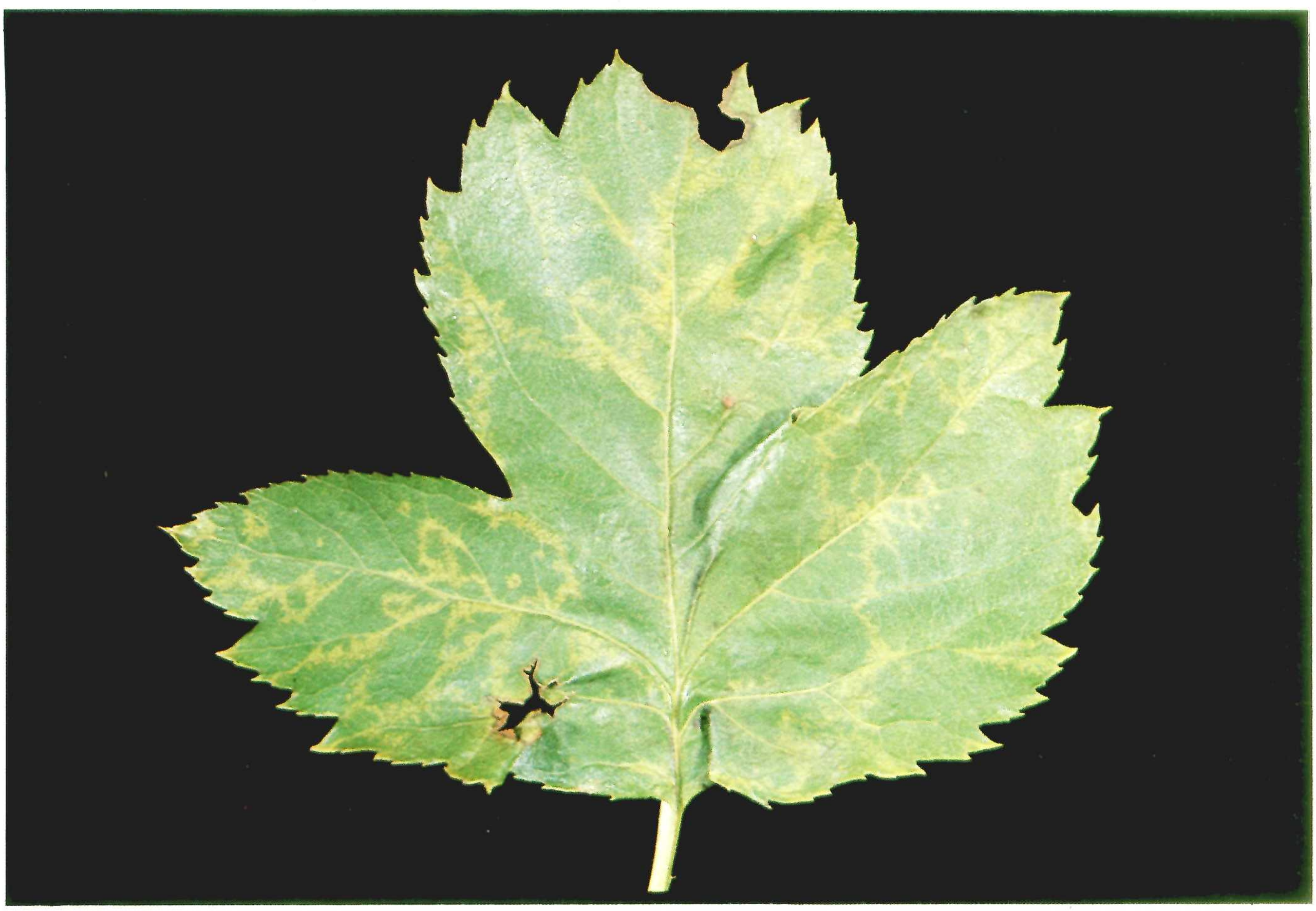

Plate 30 Leaf of *Crataegus wattiana* showing chlorotic ring and line patterns associated with a graft transmissible agent.

Plate 32 *Daphne odora* foliage showing general chlorosis associated with two viruses, arabis mosaic and cucumber mosaic.

Plate 33 *Euonymus microphyllus* foliage showing yellow blotch symptoms when infected with cucumber mosaic virus.

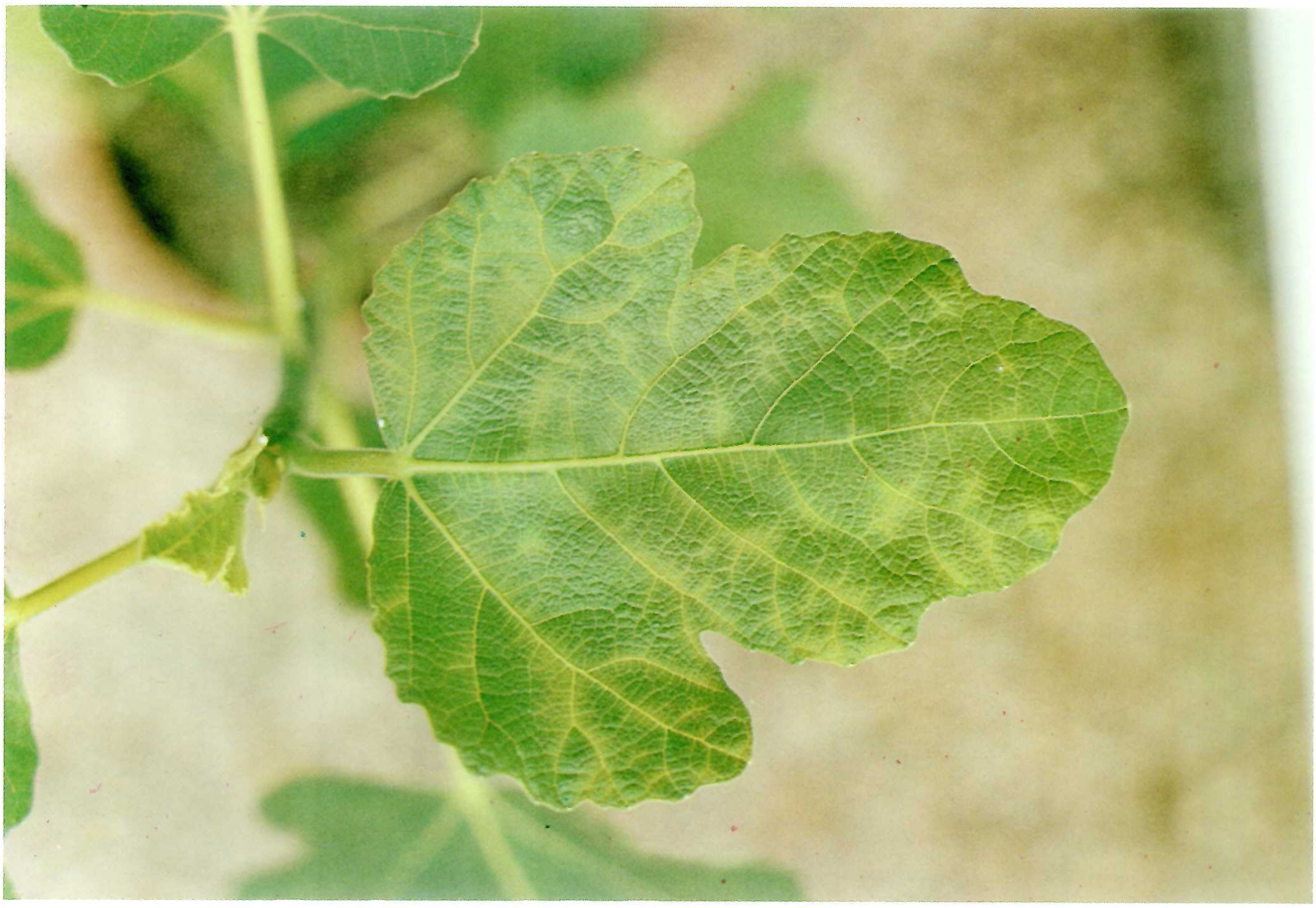

Plate 35 Fig mosaic disease ; symptom in a leaf of an unknown cultivar.

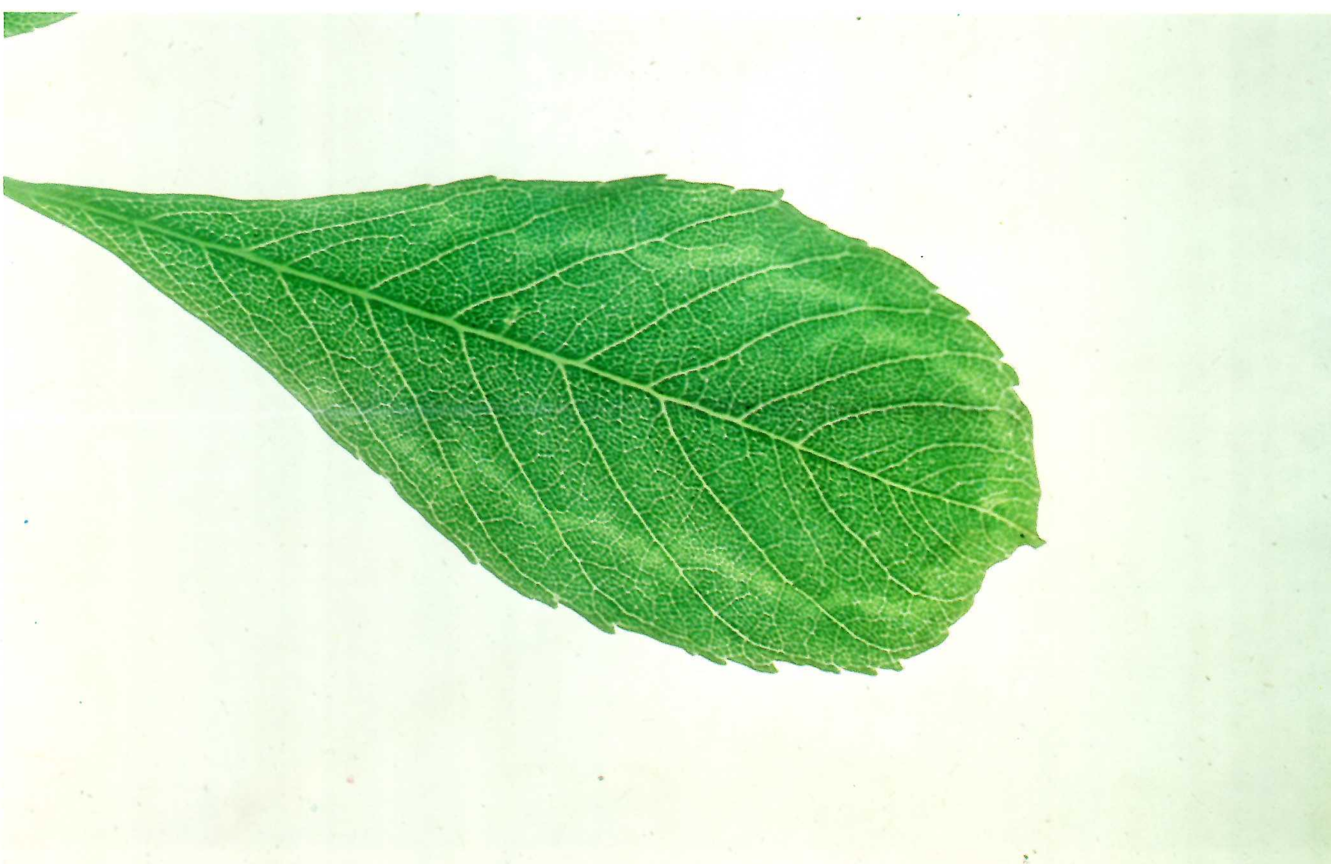

Plate 37 Leaflet of *Fraxinus excelsior* naturally infected with arabis mosaic virus and showing a chlorotic line pattern symptom.

Plate 42 Ash witches' broom. *Fraxinus americana* showing foliar chlorosis, diminished leaf size and branch proliferation. In background left, healthy leaf for comparison.

Plate 42a *Chionanthus virginica* on a *Fraxinus ornus* rootstock showing yellow ring symptoms in foliage; associated with tobacco rattle virus.

Plate 43 Leaves of *Hedera helix* showing yellow vein banding and blotch patterns when naturally infected with arabis mosaic in combination with strawberry latent ringspot viruses.

Plate 44 *Jasminum officinale* foliage showing yellow blotch patterns when naturally infected with arabis mosaic virus.

Plate 45a *Juglans regia* foliage showing in Southern Italy chrome yellow mottle associated with cherry leaf roll virus.

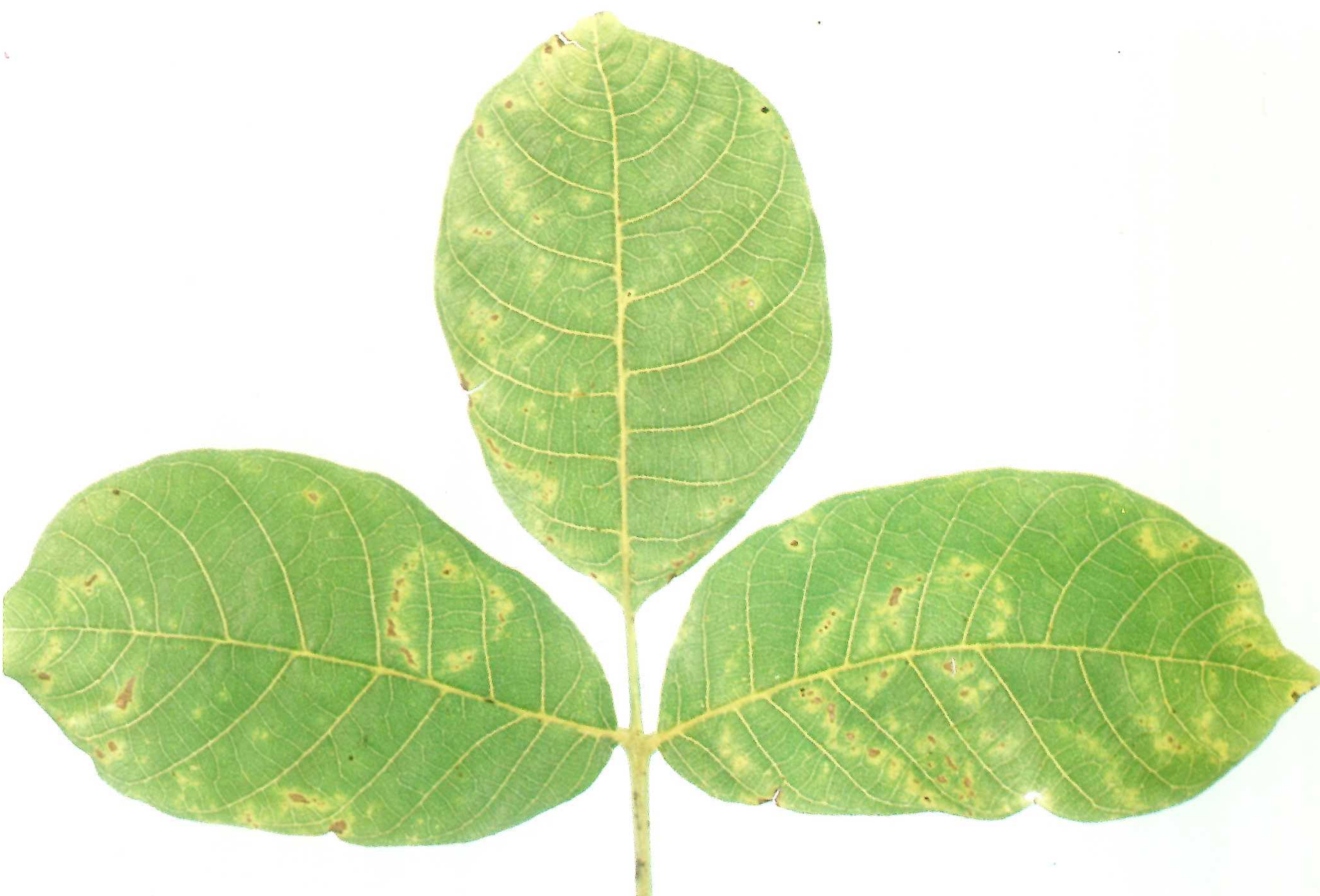

Plate 46 *Juglans regia* foliage showing chlorotic ring patterns when naturally infected with cherry leaf roll virus. The infected tree was a seedling originating from imported seed and it is noteworthy that this chlorotic syndrome is also frequent in walnuts growing in Italy.

Plate 48 Leaf of *Populus x euramericana* cv Robusta naturally infected with poplar mosaic virus and showing yellow ring and diffuse spot symptoms.

Plate 53 Leaves of the rose cultivar Queen Elizabeth showing yellow ring and line patterns of rose mosaic disease typically associated with ilarvirus infection.

Plate 55 *Sambucus nigra* foliage showing (*at right*) general pallor associated with arabis mosaic virus. Virus was not detected in the bush on the left with the darker green foliage.

Plate 56a Yellow ring and blotch patterns in *Sambucus nigra* foliage infected with arabis mosaic virus. Typically, symptoms are expressed on only part of the foliage but superficially healthy leaves contain virus.

Plate 56b Leaflet of *Sambucus nigra* naturally infected with arabis mosaic virus and showing yellow net symptoms. Yellow net has been associated with a range of different nepoviruses.

Plate 58a *Sorbus aucuparia* leaf showing fine yellow ring and line pattern symptoms when naturally infected with a graft transmissible agent resembling apple chlorotic leaf spot virus.

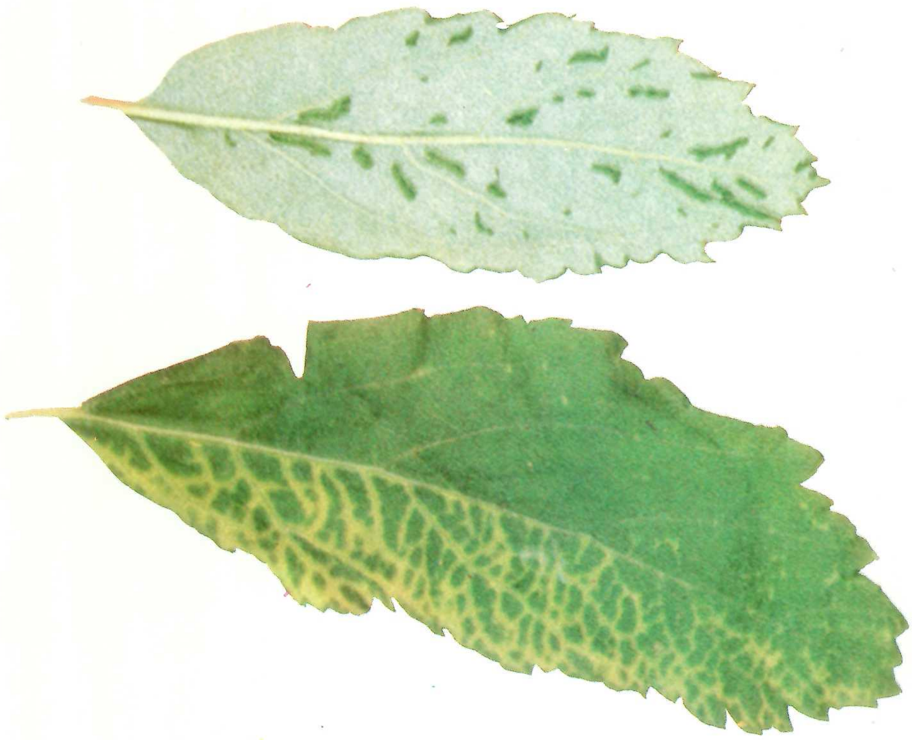

Plate 58b Leaves of *Spiraea douglasii* naturally infected with arabis mosaic virus and showing vein yellowing on the upper and outgrowths (enations) on the lower surfaces.

Plate 64 *Viburnum lantana* showing red tinged yellow line patterns in leaves; associated with alfalfa mosaic virus.

(=*T. americana* cv macrophylla hort.) and possibly *Ulmus* spp. is reportedly graft transmissible (Klastersky 1951). However, details of the experiments were few and, as noted elsewhere, (see cowl formation in *Ulmus*), other workers have failed to obtain transmission of the cowl condition by grafting. From Czechoslovakia, but also from Italy, it is reported that a condition affecting *T. cordata* (associated with dwarfed foliage, interveinal mottling and dieback) was transmitted by bark patch grafting (Blattny, 1938).

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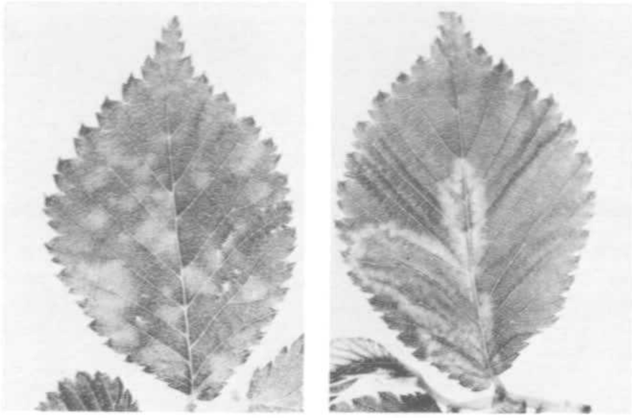

Plate 60—Leaves of *Ulmus glabra* naturally infected with elm mottle virus and showing (*at left*) blotches and (*at right*) line pattern symptoms.

Photograph by courtesy of Scottish Horticultural Research Institute

ULMUS—*Ulmaceae*

Foliage diseases

SYMPTOMS: Elm Mottle (Ulmenscheckung). Bright yellow spots, rings or stripes; no necrosis (Schmelzer, *et al*, 1966).

Distribution: Atanasoff (1935) described symptoms in unspecified *Ulmus* growing in Bulgaria. Schmelzer (1969) cited authorities who recorded elm mottle disease in Czechoslovakia, UK, and the U.S.S.R. and Bojansky (1969) reported that elm mottle was one of the symptoms occurring together with witches' broom in East Germany. Species affected include *Ulmus glabra* L. and *U. carpinifolia* Gled.

Transmission: In spring/summer, Schmelzer (1969) transmitted a virus to "herbaceous hosts" by mechanical inoculation but success was infrequent. Jones and Mayo (1973) similarly isolated virus from Scottish *U. glabra*. A Scottish isolate of elm mottle virus was returned to *U. glabra* seedlings by mechanical inoculation with sap from infected herbaceous hosts but the characteristic symptoms of the disease were not observed in these plants during a period of twelve months in a heated glasshouse (Jones and Mayo, 1973).
Elm mottle virus is seed-borne in naturally infected *U. glabra* and was detected in pollen from another naturally infected host (*Syringa vulgaris* L.). Although Schmelzer (1969) indicated that tests to assess whether elm mottle virus was transmitted in elm pollen were then in progress, the results have not been noticed.

Causal agent/Relationship: Both the Scottish and East German virus isolates had antigenic determinants in common but the extent of their serological relatedness was not assessed. Although serologically unrelated, the particle properties of a Scottish isolate were in some respects similar to those of tobacco streak (Fulton, 1971) and prunus necrotic ringspot viruses (Fulton, 1970; Jones and Mayo, 1973). Virus isolates from East German *Ulmus* and from white mosaic-affected *S. vulgaris* cross protected against one another but were distinguishable in other ways. Thus, an isolate from *S. vulgaris* caused oak-leaf chlorotic line patterns in leaves of *Buddleja davidii* Franch. after mechanical inoculation whereas one from *Ulmus* did not (Schmelzer, 1969). It is unfortunately not recorded whether this species was infected by *Ulmus* isolates.

SYMPTOMS: Elm stripe (Ulmenstreifung). As elm mottle but, in addition, chlorotic or necrotic oak leaf line patterns and stripes along the midrib of leaves may occur (Schmelzer *et al*, 1966).

Distribution: In East Germany affecting *U. glabra*.

Transmission: Not recorded. Sap transmission tests revealed elm mottle virus in material with these symptoms. Electron microscopic examination of elm sap showed flexuous rod-shaped virus-like particles about 750 nm in length (Schmelzer, 1969).

Causal agent/Relationship: Not known.

SYMPTOMS: Elm mosaic symptoms reportedly vary but it is probable that most observations have been made on trees simultaneously affected by several different pathogens. Whereas some leaves on an affected tree may be normal in size, colour and texture, others may be abnormally large and dark green or small, stiff, mottled and distorted. Smaller leaves may show yellow-green mottle or yellow mottling along midribs and in a few instances yellow or chlorotic ringspot symptoms. Subsequently, leaf buds may fail to expand leaving branches bare. Swingle *et al*, (1941; 1943) also commented that whereas elm mosaic disease was not associated with discolouration of bark or wood, these tissues on affected trees tend to be dry and brittle and difficult to separate one from another. In *U. americana* L. Ford *et al*, (1972) recognized an additional symptom—enations—associated with the disease. It is noteworthy that the original description of elm mosaic disease (Swingle *et al*, 1941) included the phrase "mild to moderate brooming of branches". This describes a symptom characteristic of MLO—associated elm witches' broom. Furthermore, about half (46·6%) of trees in which zonate canker was recognised to occur showed foliage symptoms attributed by Swingle

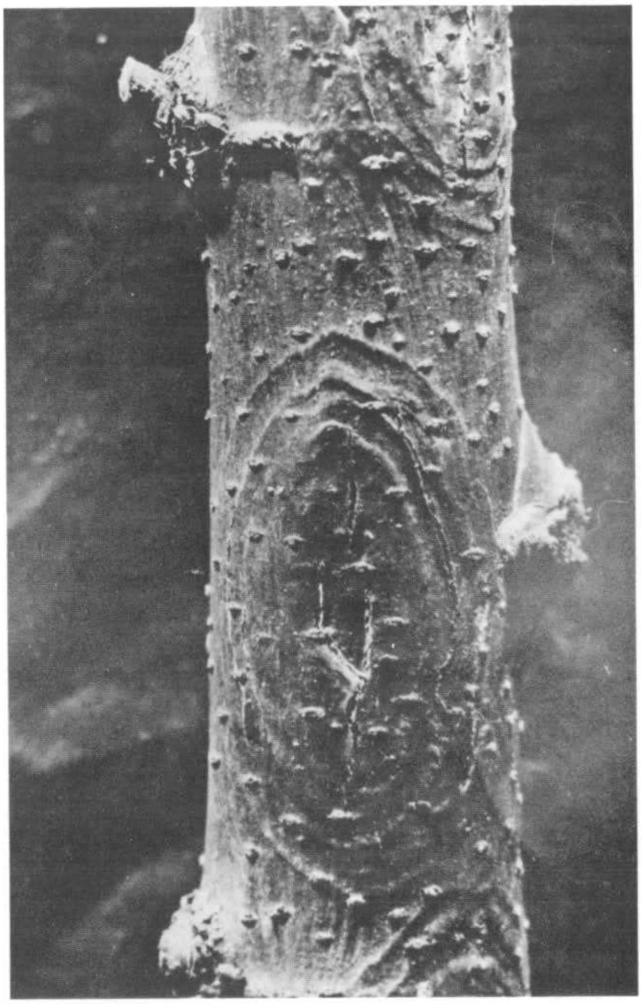

Plate 61—Elm zonate canker, symptom in *Ulmus americana* with (*left*) and without (*right*) bark removed. Concentric ridges are apparent on the bark.

Photograph by courtesy of Natural Environment Research Council after U.S.D.A. R. W. Swingle

et al, (1941) to elm mosaic disease. Parts of the syndrome described as elm mosaic closely resemble elm mottle and elm stripe diseases.

Distribution: Elm mosaic disease is recorded only from the U.S.A. (Iowa, Ohio, Kentucky, Michigan, New Jersey and Wisconsin) and affects *U. americana*.

Transmission: Swingle *et al*, (1941; 1943) demonstrated the graft transmissibility of the elm mosaic agent: whereas none of five attempts at transmission via root grafts (which united) was successful, twenty of twenty plants in which bark patch grafts were used became diseased. In some plants, the whole syndrome of elm mosaic developed, in others only the yellow or chlorotic ringspot symptom. The majority of host stocks developed a yellow-green mottle. Only one tree produced the witches' broom effect. These observations were unfortunately not recorded in detail but it is tempting to speculate that two (or indeed three) distinct agents may have been separated or partially separated by the grafting experiments.

In a short paper, Callahan (1963) reported the transmission by inoculation of sap of elm mosaic from diseased to healthy *Ulmus* spp. Earlier, Varney and Moore (1952) transmitted a virus from elm mosaic diseased trees to "herbaceous hosts". Although this virus was subsequently named elm mosaic virus, Varney and Moore were unable to infect elm seedlings when the seed coats were inoculated with sap from the infected herbaceous plants. However, Ford *et al*, (1972) induced symptoms they considered typical of elm mosaic disease in seedlings of *U. americana* inoculated with sap from "herbaceous hosts" containing a virus isolated from a Moline form of *U. americana* growing in Iowa.

Some natural spread of elm mosaic disease was reported in the early literature (Swingle *et al*, 1943) but since then, there have been no substantial data published on the pattern and extent of spread. Nevertheless, a considerable knowledge of possible vector agencies has accumulated. Bretz (1950) reported 1–3·5% seed transmission of elm mosaic disease and Callahan (1957a & b) showed that this could occur through pollen or ovules. However, there was no evidence that trees became infected by pollination with infected pollen.

Causal agent/Relationship: The elm mosaic virus isolate transmitted by Varney and Moore (1952) has general properties in common with tomato ringspot virus. In addition, leaves of tobacco plants systemically infected with tomato ringspot virus did not develop lesions when later inoculated with elm mosaic virus. However, this phenomenon of cross protection operated only in one way, i.e. the elm mosaic isolate did not protect against tomato ringspot virus. One way cross protection with tomato ringspot virus has been confirmed using elm mosaic virus isolates from Wisconsin (Fulton and Fulton, 1970; Jones, 1973) and Iowa (Ford *et al*, 1972). However, although the two viruses are similar in many properties they appear not to be related serologically (Fulton and Fulton, 1970; Ford *et al*, 1972; Jones, 1973). Furthermore, whereas isolates of tomato ringspot virus infecting plants singly, or together with a Wisconsin isolate of elm mosaic virus, were transmitted by nematodes (*X. americanum*), elm mosaic virus was not (Fulton and Fulton, 1970). More recent work has shown that the Wisconsin isolate of elm mosaic virus is serologically related to isolates of cherry leaf roll virus from different hosts (Jones and Murant, 1971; Schmelzer, 1972; Jones, 1973; Walkey *et al*, 1973).

SYMPTOMS: Elm scorch. Gradual crown decline associated in *U. americana* with necrosis of leaf margins, interveinal areas or the entire laminae (Wester and Jylkka, 1959).

Distribution: South eastern states of USA.

Transmission: When 213 chip bud inoculations were made to visually healthy *U. americana*, 18·3% of stocks showed symptoms after one year and a further 2·8% in the second year although none of sixty-seven healthy chip buds induced symptoms. When bark patch grafting was used, one of 170 diseased and one of 108 healthy grafts induced disease.

Causal agent/Relationship: The apparently greater transmission via bark patch grafts directed Wester and Jyllka to suggest that the causal "virus" was associated with xylem tissue as was known for Pierce's disease of grapevine (Hewitt *et al*, 1942). An alternative explanation equally compatible with the data reported is that the symptoms Wester and Jyllka described were caused by bacteria: foliage effects of *Erwinia nimipressuralis* Carter (1964). Some evidence in favour of the latter hypothesis may come from Wester and Jyllka's paper; they reported that bacteria were obtained in culture from their experimental material but were considered contaminants. Unfortunately, no data was given on the frequency that elm scorch disease was associated with the bacteria Wester and Jyllka cultured but further data on this foliage symptom and its cause seems desirable.

Plate 62—Ulmus americana dead and dying when affected by elm phloem necrosis; a disease associated with MLO.

Photograph by courtesy of C. E. Seliskar, U.S.D.A.

Stem diseases

SYMPTOMS: Elm zonate canker. This disease has not been seen in naturally affected trees and significantly was noted in grafted stock in which Swingle and Bretz (1950) recognized an additional syndrome which they attributed to elm mosaic. Therefore, it must be borne in mind that the observations they recorded may be the result of two or more pathogens in combination. Some affected plants showed mottling and necrotic spotting symptoms in their spring foliage.

In a few instances concentric, slightly raised rings of alternately light and dark tissue developed on the surface of bark in young branches. These enlarged into dry necrotic bark cankers which extended to affect cambium as well as xylem tissues, killing parts of the trees by girdling. On branches at levels below where grafts were inserted, leaves showed brown necrotic spots which coalesced to cause parts of the laminae to collapse.

Distribution: Although the zonate canker form of this disease has not been recorded at present outside the USA, it is noteworthy that leaf symptoms similar to the necrotic collapse, described and illustrated in *U. americana* by Swingle and Bretz (1950) have been noted in *U. glabra* and *U. carpinifolia* from Czechoslovakia (Svbodova, 1963; cited in Schmelzer, 1968).

Transmission: The disease developed in apparently healthy nursery trees to which bark patch grafts from trees showing abnormally severe symptoms of elm mosaic disease had been applied. There is evidence that the condition may be latent in *Ulmus* because cankers developed in trees grafted with bark patches from seven of fifteen symptomless trees.

The leaf necrosis reported to accompany zonate canker formation did not develop in foliage of twenty *U. americana* to which leaf sap had been manually inoculated.

Causal agent/Relationship: None known. Mycological investigations did not reveal any consistent association of the cankers with visible organisms. Swingle and Bretz (1950) commented on the similarities (having regard to the graft transmission via bark patches) with Pierce's disease of grapevines which is now associated with RLO (Goheen *et al*, 1973).

SYMPTOMS: Elm witches' broom. In *U. carpinifolia* they included chlorotic leaves of abnormally small size and which tend to be borne on twigs with short internodes: affected twigs dieback and trees may progressively wither and die (Bojansky 1969). In many instances, cowl-forming leaves (Klatersky, 1951) may be seen at the proximal ends of twigs on affected trees. Cowl-formation, the twisting of the lamina around the midrib to form a cone, has been reported in leaves of several trees and shrubs growing in Eastern Europe but only one attempt at transmission by grafting and none otherwise are reported. Bojansky (1969) suggested that cowl formation is a "teratological phenomenon" and supporting evidence for this view may come from Gualaccini (1963) who reported that agents causing cowl symptoms were not graft transmitted. Histological observations on twigs affected by witches' broom disease revealed greatly diminished phellogen and phelloderm and, when leaves were examined, the palisade cells were observed to be abnormally short and broad making difficult their distinction from spongy mesophyll.

Distribution: Czechoslovakia (where it is reportedly common, Bojansky, 1969), UK (Jones and Cooper, unpublished data) and from Italy (Gualaccini, 1963): However, symptom expression seems greatly affected by environmental factors (branches with symptoms at one time of the year may recover to show normal growth) and it seems probable that the disease is present elsewhere.

Transmission: Transmission between *U. carpinifolia* by means of budding has been recorded but the range of symptoms which developed in inoculated trees have not been fully described. It is interesting to note that Gualaccini (1963) reported graft transmission of witches' broom agents to *Robinia pseudoacacia* L. in addition to *U. pumila* L.

Causal agent/Relationship: Not known.

SYMPTOMS: Elm phloem necrosis. Drooping and curling of leaves becoming yellow then brown before falling. In many instances, trees showing overt signs of the disease in spring died during the same summer. When exposed, the inner bark tissue reportedly exudes an odour of wintergreen and may show a butterscotch colour darkening to black-brown (Swingle *et al.*, 1949). Phloem necrosis affects root tissue too; fibrous roots die soon after infection, hypertrophy and hyperplasia of parenchyma occurring in the phloem of older roots and the stem (McLean, 1944).

Distribution: Elm phloem necrosis is not known to occur in countries other than USA where in some years and in some localities the disease has been implicated in the death of 75% of elms (Seliskar, 1966). Hepting (1971) stated that in some cities of the Midwestern states more elms are killed by phloem necrosis than by the closely similar Dutch elm disease which has a different cause, the fungus *Ceratocystis ulmi* (Buism.) C. Moreau.

Traditionally, elm phloem necrosis was observed only within the region of the Great Plains eastwards to West Virginia and south to the Mississippi (Bretz and Swingle, 1946; Swingle *et al.*, 1949), but the disease was more recently recorded from Pennsylvania (Sinclair *et al.*, 1971; Sinclair, 1972).

Transmission: Readily obtained by budding or grafting albeit with a somewhat variable incubation period before symptoms develop (1–24 months). Attempts to transmit the disease to herbaceous plants by mechanical inoculation of leaves with phloem exudates or leaf extracts were unsuccessful (Thornberry, 1958). In a series of papers, Baker (1948, 1949) and others showed that nymphal leafhoppers (*Scaphoides luteolus* Van Duzee) transmitted phloem necrosis to twenty two of 119 elm seedlings after acquisition access periods ranging from three to thirteen days. Although Peace (1962) suggested that localized spread of the disease may occur through root grafting it seems probable that this leafhopper species, which feeds primarily in the midrib and larger leaf veins, is the most important vector over large distances because the known distribution of *S. luteolus* parallels almost exactly that of phloem necrosis (Baker, 1949 and others). *S. luteolus* is locally abundant but was not recognized as such because adults particularly tend to occur for most of the year only in the inner crown of trees they infest where they cannot be readily detected. Consequently, the known vector (the abilities of other leafhoppers to transmit phloem necrosis appear not to be known) may occur in countries other than the USA and it is possible that phloem necrosis may occur in parts of the world where the progressive death of elms is attributed to Dutch elm disease.

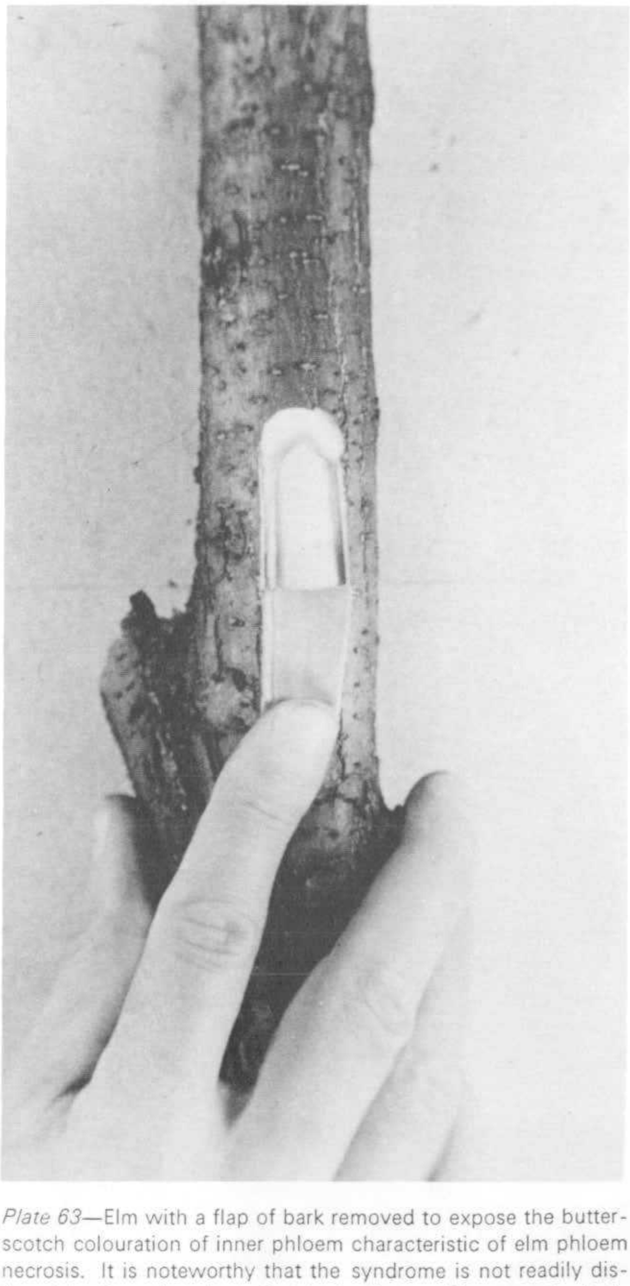

Plate 63—Elm with a flap of bark removed to expose the butterscotch colouration of inner phloem characteristic of elm phloem necrosis. It is noteworthy that the syndrome is not readily distinguished from that due to Dutch elm disease (*Ceratocystis ulmi*).

Photograph by courtesy of C. E. Seliskar, U.S.D.A.

Causal agent/Relationship: Despite the long period of time devoted to the study of phloem necrosis, attempts to characterize the causal agent have been few. Swingle *et al.* (1945) examined phloem extracts from diseased and healthy trees and Wilson *et al.* (1972) studied thin sections of phloem and other tissue, neither group observed virus-like particles. In contrast, Thornberry (1958) observed spherical virus-like particles of approximately 50nm diameter in extracts of foliage from *U. americana* affected with phloem necrosis but not from *S. luteolus*. Recent observations have indicated that graft but not sap transmissible diseases with "yellows" symptoms and leafhopper vectors are more likely to be associated with mycoplasma than viruses. Thus it was not surprising when ovoid and filamentous mycoplasma-like bodies were observed in some phloem cells of *U. americana* (Wilson *et al.* 1972).

COMMENTS: Swingle *et al.* (1945) noted degrees of resistance to phloem necrosis in some clones of *U. americana* and hybrids between *U. fulva* Michx. and *U. pumila* L. but did not determine whether this resistance was to the leafhopper vector or the causal agent.

In the past, removal of trees showing symptoms has been recommended to diminish inoculum and annual "protective" spraying with insecticides (two or more applications per year) has also been suggested (Swingle *et al.* 1949). More recent data indicated that tetracyclines injected into trees at a concentration of about 250mg/cm of diameter, caused remission of symptoms although these reappeared when treatment ceased (Filer, 1973).

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VIBURNUM—*Caprifoliaceae*

See plate 64 (Colour)

Foliage disease

SYMPTOMS: Variegation, light green to white patches, vein yellowing and necrosis.

Distribution: East Germany, Czechoslovakia and Hungary (Schmelzer and Schmidt, 1960) affecting *Viburnum opulus* L. Affecting *V. tinus* L. in Yugoslavia, Italy, France (Plese and Milicic, 1971), the USA. (Schwenk *et al.*, 1969) and the UK plus *V. lantana* L. in UK (Cooper, unpublished data) and East Germany (Schmelzer, 1966).

Transmission: In sap to "herbaceous hosts" and with aphids (*Myzus persicae* Sulz. and *Aphis viburni* Scop.).

Causal agent/Relationship: There are only two reports of tests to satisfy Koch's postulates; the diseases in *V. opulus* and *V. tinus* were reproduced following the inoculation of seedlings with alfalfa mosaic virus. An isolate of alfalfa mosaic virus from *V. tinus* possessed a protein coat with novel properties (Cooper, 1976).

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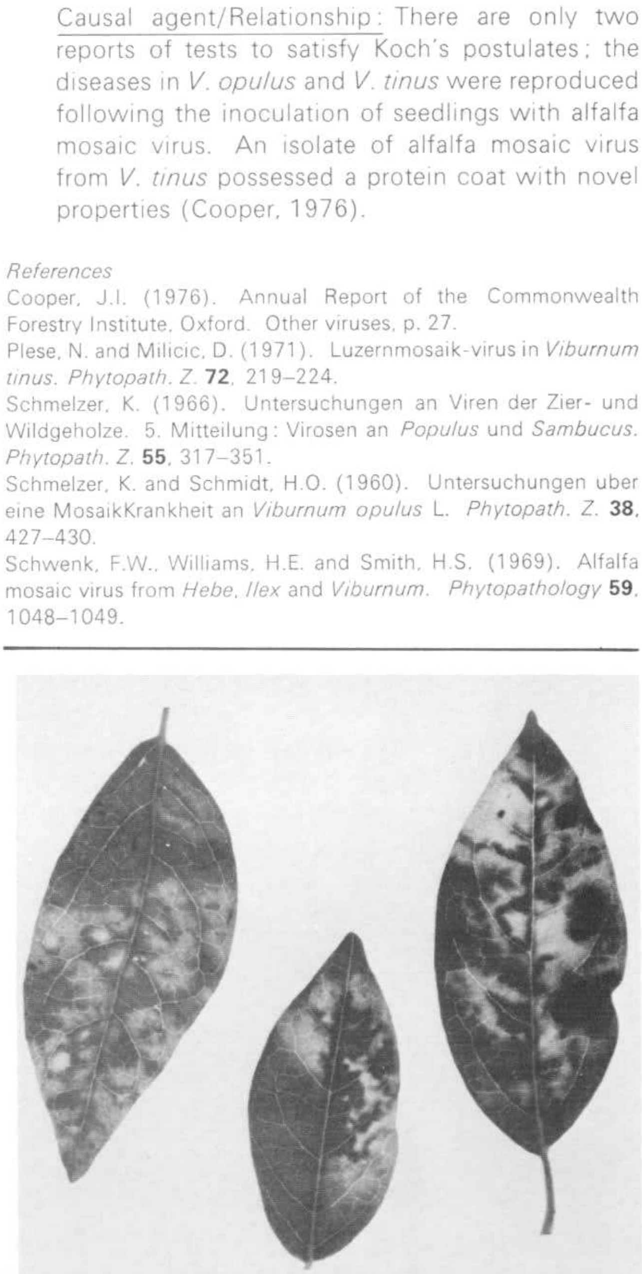

Plate 65—Viburnum tinus leaves showing chrome yellow line patterns associated with alfalfa mosaic virus. The virus infected healthy *V. tinus* seedlings but did not cause symptoms during a subsequent two year period.

Photograph by courtesy of Natural Environment Research Council

WISTARIA—*Leguminosae*

Foliage disease

SYMPTOMS: Yellow-pale green blotches, vein yellowing lateral twisting and malformation of leaves.

Distribution: In the USA (Brierley and Lorentz, 1957) in Italy, Bulgaria, East Germany and the Netherlands (Lovisolo, 1960, cited in Schmelzer, 1968) and probably whenever *Wistaria floribunda* D.C. is grown.

Transmission: By grafting to *W. sinensis* Sweet (Brierley and Lorentz, 1957) and in sap to "herbaceous hosts" (Bos, 1970).

Causal agent/Relationship: The isolates Bos obtained had properties in common with members of the potyvirus group. Mueller (1967) detected tobacco mosaic virus in *W. sinensis* with chlorotic leaf spotting symptoms but inoculation of healthy *Wistaria* spp. with the isolate did not cause symptoms.

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Conclusion

Until now, knowledge of viruses infecting trees and shrubs has been based on speculative investigations made after the accidental discovery of a virus-like disease which seemed to justify part-time research. Therefore, it is likely that the viruses detected represent only the tip of an iceberg; many others await discovery and it is premature to discuss in detail the significance of the available data. It is, however, noticeable in Table 1, p. 19, that trees/shrubs with 'sappy' leaves e.g. *Ulmus, Sambucus* and species in the Oleaceae are known hosts to more viruses than trees with thin, dry, brittle leaves, e.g. *Quercus, Fagus* and *Acer*. Perhaps this only reflects the greater ease of transmission from soft foliage. However, future work may show that this difference is not real, or is due to some other property. Similarly, data are too few to justify the assertion that plants in the families Caprifoliaceae, Leguminosae, Oleaceae and Saxifragaceae are more prone to infection by viruses than trees and shrubs in other families (Table 2, p. 68) but it is tempting to speculate that their leaves may be found to contain lesser amounts of chemicals which impede detection (usually mechanical transmission) of viruses which are present.

Examination of the available data does raise two questions. Why are 'specialist' tree viruses seemingly infrequent and why are 'opportunists' relatively common? There are probably many reasons but most important, the detection of virus-associated diseases depends on the availability of virologists and these may be in the wrong places. The study of viruses requires costly analytical and measuring instruments, consequently, most is known about viruses of plants grown in the countries of Western Europe, North America, and much more recently in Japan and Australasia.

It seems axiomatic that highly adapted pathogens such as viruses evolved through long association with their hosts. Thus, all but a few of the potato viruses (about thirty known) seem to have come with planting stock from the centres of species diversity in the Solananceae (namely the Andean regions of South America) to countries in which *S. tuberosum* is now cultivated as a food crop. The exceptions are the 'opportunists' alfalfa mosaic, cucumber mosaic, tomato black ring, tobacco necrosis and tobacco rattle viruses.

Amenity trees grow in greater variety in UK than almost anywhere else in the temperate world. However, the species diversity is artificial. Fewer than fifty are native to Britain (Clapham, Tutin and Warburg, 1962), and only a handful occur wild exclusively in the UK. Europe in general, the UK in particular and North America to a lesser extent, have a greatly enriched tree flora as a consequence of introductions made from diverse and often very restricted natural populations. A realistic estimate of potentially damaging viruses may only be obtained when detailed research into tree and shrub viruses is done in the remote regions of the Andes, China, the Himalayas, etc., from which the plants came. There are other possible explanations. Perhaps as Thresh (1974) implied, trees and shrubs are inherently more resistant to virus infection than other plants. Alternatively, the comparative scarcity of unusual and distinct viruses recorded to date in European and North American trees and shrubs may be due to the fact that when introductions were made, only a few specimens (by chance free from virus infections) formed the nucleus of the stock which now exists. In some instances this may have been because seed having a smaller risk of virus infection than growing plants was the foundation. In any event, the available information on virus incidence in trees and shrubs is consistent with the relatively recent exposure of initially healthy and for the most part widely scattered plants to a range of 'opportunist' viruses. One might anticipate that the effects of these and other viruses will become more apparent with the expansion of managed plantations/forests which are more suitable for rapid virus spread because they consist of one plant species in large numbers and all at a similar stage of growth. Thus, although it now seems likely that all but a few of the potato viruses were imported into Europe with planting stock, historical evidence, reviewed by Salaman (1949) and van der Plank (1949), suggests that the non-persistent aphid borne potato viruses Y and A became prevalent about 1770 whereas the contact—spread

Table 2. **Vector routes, where known, of some well characterized viruses detected in tree/shrub families.**

Host family	In the soil											In the air by aphids non-persistent					
	by Nematodes									other							
Aceraceae	AMV																
Aquifoliaceae				TobRSV													
Araliaceae	AMV	SLRV															
Aristolochiaceae	AMV											CMV					
Berberidaceae												CMV					
Betulaceae			CLRV						TRV	TNV							
Buxaceae	AMV																
Bignoniaceae														BBW			
Calycanthaceae																	
Caprifoliaceae	AMV	SLRV	CLRV	TobRSV	TomRSV		TBRV			TNV		CMV	LMV				
Celestraceae		SLRV					TBRV			TNV		CMV					
Cistaceae													LMV				
Cornaceae	AMV		CLRV	TobRSV	TomRSV						TBSV	CMV		BBW			
Fagaceae							TBRV										
Hippocastanaceae		SLRV															
Juglandaceae			CLRV														
Labiatae													LMV				
Leguminosae	AMV	SLRV					TBRV					CMV			RoMV		BYMV
Loganiaceae		SLRV										CMV					
Magnoliaceae												CMV					
Malvaceae																	
Moraceae								MulRSV									
Myrticeae																	
Oleaceae	AMV	SLRV	CLRV	TobRSV		RRV	TBRV		TRV		TBSV	CMV	LMV				
Onagranaceae																	
Papaveraceae												CMV					
Passifloraceae												CMV				PFW	
Pinaceae	AMV				TomRSV		TBRV			TNV							
Pittosporaceae																	
Ranunculaceae									TRV			CMV					
Rhamnaceae												CMV	LMV				
Rosaceae	AMV	SLRV		TobRSV	TomRSV												
Rutaceae	AMV		CLRV	TobRSV													
Salicaceae	AMV					RRV				TNV							
Saxifragaceae	AMV			TobRSV	TomRSV		TBRV		TRV	TNV		CMV	LMV				
Scrophulariaceae												CMV	LMV	BBW			
Solanaceae												CMV					
Staphyleaceae	AMV						TBRV										
Taxaceae																	
Thymelaeaceae	AMV			TobRSV			TBRV					CMV	LMV				
Tiliaceae																	
Ulmaceae			CLRV														
Verbenaceae							TBRV						LMV				

Nematode-borne viruses with polyhedral particles
AMV arabis mosaic virus
SLRV strawberry latent ringspot virus
CLRV cherry leaf roll virus
TobRSV tobacco ringspot virus
TomRSV tomato ringspot virus
RRV raspberry ringspot virus
TBRV tomato black ring virus
MulRSV mulberry ringspot virus
TRV tobacco rattle virus

Other soil-borne viruses
TNV tobacco necrosis virus
TBSV tomato bushy stunt virus

Aphid-borne viruses
CMV cucumber mosaic virus
LMV alfalfa (lucerne) mosaic virus
BBW broadbean wilt virus
RoMV robinia true mosaic
PFW passion fruit woodiness virus
BYMV bean yellow mosaic virus

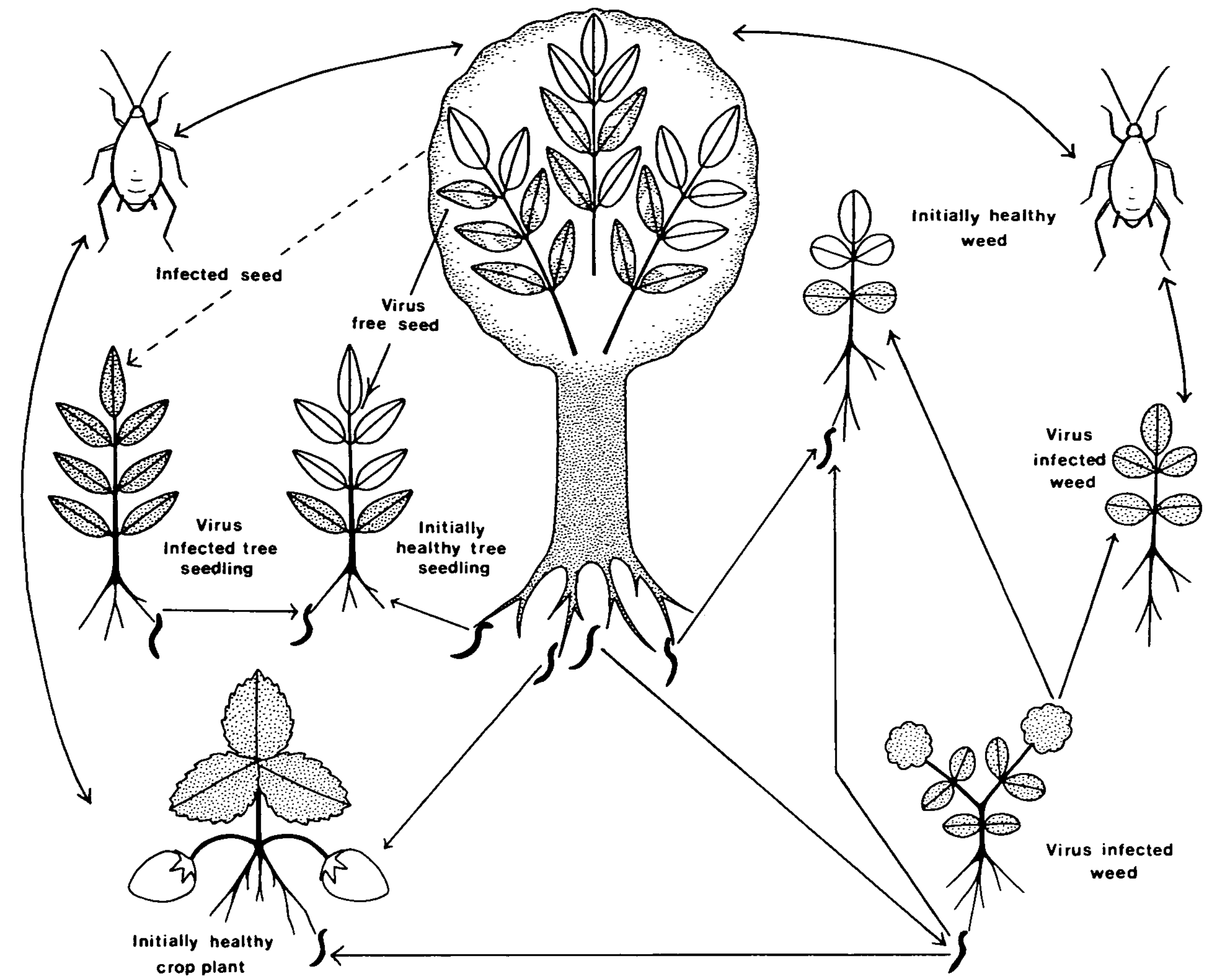

Plate 66—Diagram indicating some of the pathways of virus spread and the possible involvement of trees and shrubs.

potato virus X and the 'specialist' persistently aphid-transmitted leaf roll virus were not widespread until about 1904 even though probably locally important before this date. Perhaps this was because the potato crop was much more continuous in its distribution by this time, thereby facilitating epidemic virus spread. It is noteworthy that the incidence of infection with viruses having aerial vectors tends to diminish when susceptible crops are closely planted. Furthermore, individuals in mixed plant communities usually have a lower virus incidence than those in similar pure stands. The practice of growing hardy nursery stock in mono culture at wide spacing surrounded by soil kept weed free by herbicides or cultivation may tend to facilitate infection.

Although the incidence of 'specialist' tree viruses like poplar mosaic and robinia true mosaic is unexpectedly low, it is apparent from Tables 1 and 2 that viruses with polyhedral particles and nematode vectors have been detected very frequently in leaves of broadleaved trees and in the roots of conifers. Nepoviruses (Harrison and Murant, 1977) are readily mechanically transmitted in sap to "herbaceous hosts", being somewhat more stable and reaching higher concentrations than many others. This combination of properties has favoured their detection and, although *Xiphinema* spp. (e.g. *X. diversicaudatum* transmitting arabis mosaic virus) multiply relatively more on woody perennial hosts rather than weeds or herbaceous crops (Thomas, 1970), it is premature to deduce that nepoviruses generally have some intrinsic preference for woody hosts. Thus, tomato black ring and raspberry ringspot viruses, with *Longidorus* vectors, have to date been detected somewhat less frequently than arabis mosaic, tomato and tobacco ringspot. Perhaps this is because longidorids tend to be associated with shallow rooted herbaceous crops rather than tree roots (Lamberti, Taylor and Seinhorst, 1975).

Cherry leaf roll virus isolates have properties in common with nepoviruses but differ from other members of the group in being a collection of "specialists" with a predelection for woody hosts. Serological tests chiefly measure changes in one property of a virus particle, its protein coat, and in other circumstances might not be given undue weight. However, specific transmission by vectors is likely to require adsorption of virus particles to vector surfaces, and adsorption will be greatly affected by properties of the protein coat. Consequently, a brief discussion of comparative serology has ecological/epidemiological relevance. Antigenic variations between cherry leaf roll virus isolates from the same or closely related hosts have, but infrequently, been noted (Schmelzer, 1972; Walkey, Stace-Smith and Tremaine, 1973; Waterworth and Lawson, 1973; Savino *et al.*, 1977). Notwithstanding the report suggesting that two Yugoslavian isolates of cherry leaf roll virus from *Sambucus nigra* and *S. racemosa* had few, if any, of their antigenic determinants not held in common (Grbelja, 1972) somewhat greater serological differences are more typical, as when isolates including those from *Betula*, *Cornus*, *Juglans*, *Ligustrum*, *Ptelea*, *Prunus*, *Sambucus* and *Ulmus* were compared (Cooper and Atkinson, 1975; Jones, 1976; Schmelzer, 1972). Significantly, although *Prunus* isolates of cherry leaf roll virus have been reportedly transmitted by *Xiphinema* spp. (Fritzsche and Kegler, 1964; Flegg, 1969; McElroy and Jones, cited in Jones, 1976) the efficiency is low and, since Fulton and Fulton (1970) did not detect transmission of an elm isolate by *X. americanum* Cobb, it is tempting to suggest that a highly genus specific vector agency such as pollen may be the most important, possibly the only method of plant-to-plant spread in nature. Whereas in elm, walnut and birch, CLRV does not seem to spread with the aid of soil-inhabiting vectors, the virus is disseminated in seed (Callahan, 1957a, b; Lister and Murant, 1967; Tomlinson and Walkey, 1967; Schimanski and Schmelzer, 1972; Cooper, 1976 and Plate 23). When susceptible trees having numerous flowers may be exposed to wind-borne inoculum for several centuries, virus spread might well depend upon very rare events, perhaps including virus transmission following interspecific or intergeneric pollination.

Although viruses require a continuous supply of hosts in which they can grow and must frequently spread to infect new hosts if these are ephemeral, the pressure to find a new home is somewhat less strong when the host is perennial. The infrequency of observed differences between arabis mosaic and tomato ringspot virus isolates from different host genera/species and locations suggests that the mobility of highly polyphagous vectors is the most important factor, allowing frequent interchange of viral genetic material (out breeding) between diverse virus populations in weeds, crops, trees, etc. (Plate 66). The same is probably true for viruses such as cucumber and alfalfa mosaic which have non-persistent relationships with their omnivorous vector aphids. Seed and pollen transmission tends to stabilize (by inbreeding) virus populations, facilitating spread but at the expense of diversity. At all stages in virus replication, mutations may produce new types, differing from the parental viruses in properties having consequential effects on vector relationships. In some instances, the ability to be transmitted by vectors will only be diminished, in other instances lost, and the viruses will thereafter depend for their survival on seed, pollen and vegetative propagation of the infected host. Because of their longevity, trees and shrubs might well be repositories for numerous 'fossil' viruses having unusual properties. It will be interesting to see whether future research shows that woody perennials generally contain a greater range of distinct viruses than do plants with shorter life spans and in which vector transmission may be assumed to play a more essential role in virus survival.

Woody perennials are now being imported into the UK on an unprecedented scale. Trees and shrubs are entering the country, not only for amenity use by municipal authorities, but also for domestic garden planting. Sometimes rootstocks are imported, such as *Rosa rugosa*. In other instances, named varieties that have been grafted onto rootstocks are introduced complete. Many, perhaps all, horticultural forms of *Acer* and *Fraxinus* spp. are budded in the UK into *Acer pseudoplatanus* or *Fraxinus excelsior* rootstocks and, in most instances, these rootstocks are seedlings. In any event the plants are generally imported in a dormant condition when visual inspection to detect virus-like symptoms is impossible. Strange though it may seem, a great many indigenous species are not normally raised from seed collected in the UK. Indeed, the normal sources of rootstocks are rooted seedlings imported through, but not necessarily originating in, Denmark, the Netherlands or West Germany. Clearly, the importation of indigenous species is not essential and, even as seedlings, should be avoided because of the attendant risks. Seed is relatively, but not by any means completely (see Phatak, 1974; Neergaard, 1977), free from phytosanitary threat. By contrast, rooted seedlings inevitably bring with them soil in which they grew, thereby offering opportunities for the importation of non-indigenous soil-inhabiting pests and pathogens, such as types of the fungus *Syncytrium endobioticum* Worr. which are capable of causing wart disease in potato cultivars immune to the fungus present in UK. As far as is known, virus-vector nematodes occurring in the exporting countries also occur in the UK. However, it is worth noting that studies of nematode-transmitted viruses have shown that the reassortment of genetic material between two viruses present in one host can occur (Harrison *et al.*, 1974) and the possibility cannot be excluded that exotic virus strains may be introduced into the UK in woody planting stock.

Until planting stock free of known viruses is available for comparison, it will continue to be difficult to quantify loss due to virus infection of trees. However, it is not difficult to appraise the position that forest and shade trees occupy in virus ecology. It is apparent even in this rudimentary state of virology that woody perennials are potential reservoirs of pathogens for plants growing in their vicinity. Consequently, trees warrant more detailed attention than they have been awarded hitherto, the aim being to free them from viruses, thereby increasing their productivity and environmental benefit, and at the same time lessening the hazard they pose to adjacent crops.

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Glossary

AETIOLOGY: Study of the origins and causes of diseases.

ANTIGEN: A protein, or more rarely other types of molecules with large molecular weights, which when injected into living vertebrate animals cause the formation of 'new' specific proteins (antibodies).

ANTISERUM: Serum containing antibodies produced by a vertebrate injected with antigen.

BUDDING: A grafting method in which a bud is the scion.

CLONE: A genetically 'uniform' line of plants derived from an individual (mother plant) by vegetative propagation.

CROSS PROTECTION: The protection afforded when an earlier virus inoculation prevents the development of additional symptoms when followed by a second inoculation with a different virus. Cross protection is generally only given by closely related viruses, although somewhat less reliable when assessing relationships than serological tests (Fulton, 1978).*

CULTIVAR (cv): A genetically 'uniform' line of cultivated plants characterized by any agricultural/horticultural feature.

DIFFERENTIAL HOST: A plant producing distinctive and diagnostic symptoms when infected by a particular agent (e.g. virus).

FASCIATION: Incomplete separation of additional shoots (proliferation) giving the appearance of a flat bundle.

GRAFT TRANSMISSION: Transmission of infectious agents from rootstocks to scions or *vice versa* after grafting. Garner (1958)** described numerous methods of which 'approach' and 'detached scion' techniques are commonly used by virologists. In the former, the partners grow on their own roots whereas in the latter only one partner does.

HERBACEOUS HOSTS: Plant species commonly used to detect viruses in sap when mechanically inoculating. The following are worthwhile:

*Fulton, R.W. (1978). Superinfection by strains of tobacco streak virus. Virology **85**, 1–8.
**Garner, R.J. (1958). *The grafters handbook*. London: Faber & Faber.

(1) Chenopodiaceae — *C. quinoa* Willd.
C. amaranticolor Coste & Reyn.

(2)	Solanaceae	*Nicotiana tabacum* L. *N. clevelandii* Gray *N. glutinosa* L. *N. megalosiphon* Heurck & Muell.
(3)	Leguminosae	*Phaseolus vulgaris* L. *Vigna sinensis* L.
(4)	Cucurbitaceae	*Cucumis sativus* L.

IN VITRO: A term describing activities or experiments done in artificial conditions. Literally 'in glass' and generally used to describe laboratory experiments.

IN VIVO: A term describing activities or experiments done in living host plants. Literally, 'in something which lives'.

ISOLATE: The infectious preparation obtained from a susceptible host inoculated with sap from an infected plant. The term implies a functional unit that may contain more than one type of virus.

KOCH'S POSTULATES: There are three: (a) consistent associations of a suspected agent with a disease syndrome.
(b) isolation of the infectious agent
(c) reproduction of the disease syndrome (a) after transmitting the infectious agent (b) to healthy hosts.

N.B. The additional need to re-isolate the infectious agent (b) from the experimentally infected and diseased plant (c) was suggested by E. F. Smith.

MECHANICAL TRANSMISSION: The transfer of viruses from one plant to another by friction; the one rubbing against the other or more usually by artificially rubbing leaf sap, root extracts etc. from infectors to leaves of other hosts.

MODAL LENGTH: Most frequently observed length of virus particles: a criterion used when grouping viruses having rod-shaped particles.

NANOMETRE (nm): $=10^{-9}$ metre or 1/1,000,000 mm.

SEROLOGY: The study of reactions between antigens and antibodies in the aqueous part of blood (serum) from immunized animals (usually rabbits, rats, mice, guinea pigs). Antigens and their complementary antibodies react specifically. Antibodies may neutralize the infectivity of a virus with or without causing the virus particles to form a visible aggregate that precipitates.

SYSTEMIC SYMPTOMS: Symptoms occurring in parts of plants other than those actually inoculated.

VIRUSES: Specific aggregations of two or more types of chemicals (usually nucleic acid surrounded by a proteinaceous coat) which are infectious and potentially able to cause disease.

VIRUS NAMES: There is no universally accepted system of naming viruses. Fenner (1976)* defined twenty groups of viruses known only to multiply in vascular plants and a further two groups having members multiplying in both plants and invertebrates. Additionally there are many plant viruses that have not yet been categorized similarly.

WITCHES' BROOM: Unusually prolific groups of shoots.

WOODY HOSTS (Indicators): Species/cultivars of woody perennials commonly used for detecting graft-transmissible virus-like infectious agents. The following are sensitive and susceptible to appreciable ranges of infectious agents.

Cydonia oblonga Mill.	cv 7/1
Malus pumila Mill.	cv Lord Lamborne M 139 cv Spy 227 cv Virginia crab
Malus platycarpa Rehd.	
Prunus avium L.	cv Sam cv F 12/1
Prunus persicae (L.) Batsch.	cv GF 305
Prunus serrulata Lindl.	cv Shirofugen cv Kwanzan
Pyrus communis L.	cv A 20
Pyronia veitchii (Trabut.)	Guillaumin.

*Fenner, F. (1976). Classification and nomenclature of viruses. *Intervirology* **7**, pp 115.

Appendix

Some additional virus-like conditions with unknown or untested aetiology

Host	Syndrome	Reference
Acacia spp.	leaf mosaic	Wiehe (1948)
Acer sp.	leaf vein banding & ringspot	Schmelzer *et al.* (1966)
Acer sp.	leaf deforming mosaic & shothole necrosis	Smolak (1949)
Aesculus sp.	stem spindle tumour	Buchwald (1961)*
Ailanthus sp.	leaf mosaic & rolling	Svobodova (1963)*
Albizzia sp.	leaf mosaic	Wiehe (1948)
Alnus sp.	leaf vein clearing	Novak (1966)
Calluna sp.	dwarfing & proliferation	Svobodova (1963)*
Carpinus sp.	leaf deformation & mosaic	Ploaie & Macovei (1968)
Cassia spp.	leaf mosaic	Deighton & Tinsley (1958)
Castanea sp.	dieback	Kuhnholtz-Lordat (1944)
Celtis sp.	leaf curl	Sibilia (1947)
Cornus sp.	dimpled fruit	Atanasoff (1935)
Cystis sp.	leaf mosaic	Eliade (1965)*
Deuzia sp.	leaf distortion & mosaic	Eliade (1965)*
Erica sp.	dwarfing and proliferation	Svobodova (1963)*
Fagus sp.	stem pitting	Parker (1974)
Fagus sp.	leaf chlorosis, ring & line patterns	Schmelzer *et al.* (1966)
Fraxinus sp.	dwarfing & proliferation	Kuprevicz (1947)*
Ginkgo sp.	leaf interveinal yellowing and patterns	Smolak (1964)
Gleditsia sp.	leaf yellow ring & line patterns	Atanasoff (1935)
Mahonia sp.	leaf vein banding	Kochman & Styra (1957)*
Populus x euramericana	branch or stem (1) pitting & grooving (cv Gelrica & Eugeniei) (2) swelling (cv Rap & TT32)	Mackay (Bryant & May (Forestry) Ltd., Willington Beds. unpublished data)
Quercus spp.	(1) leaf mosaic or flecking	Schmelzer *et al.* (1966)
	(2) stunting mottling & bud precosity	Gregory and Seliskar (1970)
Rhododendron sp.	swollen internodes	Brooks (R.H.S. Wisley, Surrey unpublished data)
Rhododendron sp.	leaf distortion and mottle	Pape (1931)
Robinia sp.	leaf deformation	Hartel & Thaler (1959)*
Sarcoccocca sp.	leaf vein yellowing	Bestangno (1960)*
Ulmus sp.	leaf necrotic collapse	Svobodova (1963)*
Ulmus sp.	trunk "witches' brooms"	Atanasoff (1973)

*Authorities marked with an asterisk are cited in Schmelzer (1968)

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J. I. Cooper — Oxford, 1978

Abbreviations

AMV	=	arabis mosaic virus
CLRV	=	cherry leaf roll virus
CLSV	=	apple chlorotic leaf spot virus
CMV	=	cucumber mosaic virus
LMV	=	lucerne (alfalfa) mosaic virus
MLO	=	myco plasma-like organism
RLO	=	rickettsia-like organism
SLRV	=	strawberry latent ringspot virus
TBRV	=	tomato black ring virus
TMV	=	tobacco mosaic virus
TNV	=	tobacco necrosis virus
TobRSV	=	tobacco ringspot virus
TomRSV	=	tomato ringspot virus
TRV	=	tobacco rattle virus

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