MYCOPLASMA-ASSOCIATED DISEASES OF TREES

by Charles L. Wilson and Carl E. Seliskar[1]

Abstract
A review is presented of tree diseases that may be caused by mycoplasmas. The symptoms of some mycoplasma-associated diseases of trees are discussed. Current need for research in this area is appraised.

Although mycoplasma-caused diseases of animals have been known since 1898, it was not until 1967 (11) that anyone suspected that mycoplasmas caused plant diseases. Because a number of important tree diseases may be caused by mycoplasmas, foresters and other arborists should become aware of developments in this field. This article presents a review of tree diseases that may be mycoplasma-caused and an appraisal of the current status of research in this area.

There are several reasons why mycoplasmas have been overlooked as possible causal agents of tree diseases. First, mycoplasmas are the smallest known living cells (Fig. 1), and they are very nondescript in form. Their cells are surrounded by an elastic membrane, but lack a cell wall. Internally, small, dark-staining bodies are present, which are assumed to be ribosomes or sites of protein synthesis. Instead of a distinct nucleus, mycoplasmas have strands of DNA that apparently serve as the genetic material of the cell. Mycoplasmas usually take on yeast-like shapes or form long filaments. We are not sure how plant mycoplasmas reproduce, but one theory is that most divide by binary fission like bacteria.

A number of tree diseases have been assumed to be caused by viruses because their symptoms were typical of virus diseases, no other organisms could be found, and transmission could be demonstrated by grafting.

To prove that a virus is the definite disease-causing agent, it is necessary to find the virus in the plant or isolate the virus from it and be able to reproduce the disease by inoculation with pure preparations of the virus.

Uncertainty in determining whether mycoplasmas cause plant diseases stems from the difficulty in culturing them in cell-free media. There are a number of reports that plant mycoplasmas have been maintained in pure culture (16, 31, 51), but many are so far inconclusive because of other researcher's inability to duplicate the results (8). Currently, the most accepted reports of the successful culturing of plant mycoplasmas are those of citrus stubborn disease and of corn stunt (4, 56). These organisms, however, called Spiroplasmas, may be different from the organisms commonly considered as mycoplasmas.

Tetracycline antibiotics have been known for some time to be active against animal mycoplasmas. Symptom remission has been obtained in plants that have mycoplasma-associated diseases by treating them with tetracyclines (15, 28, 38, 49). This is good circumstantial evidence that mycoplasmas are indeed the cause of these diseases. In addition, mycoplasma-like bodies in treated plants become disrupted as a result of the treatment. Mycoplasmas have been found in the tissue of suspected insect vectors (7, 25). Some vectors treated with tetracyclines have been "cleaned up" and are unable to transmit an infectious agent.

The fact that mycoplasma diseases, such as pear decline (21, 22, 26, 33, 39, 40), are susceptible to control with tetracycline antibiotics is encouraging. There is no known control of virus diseases of trees.

Symptoms of Mycoplasma-Associated Tree Diseases

There is no one set of symptoms that typify mycoplasma-associated diseases of trees. The most recurrent symptom, so far, is a "witches'-broom" type of growth (Fig. 5). Brooms are commonly formed because of a shortening of stem and leaf internodes, resulting from a loss in apical dominance. Also, terminal growth may be-

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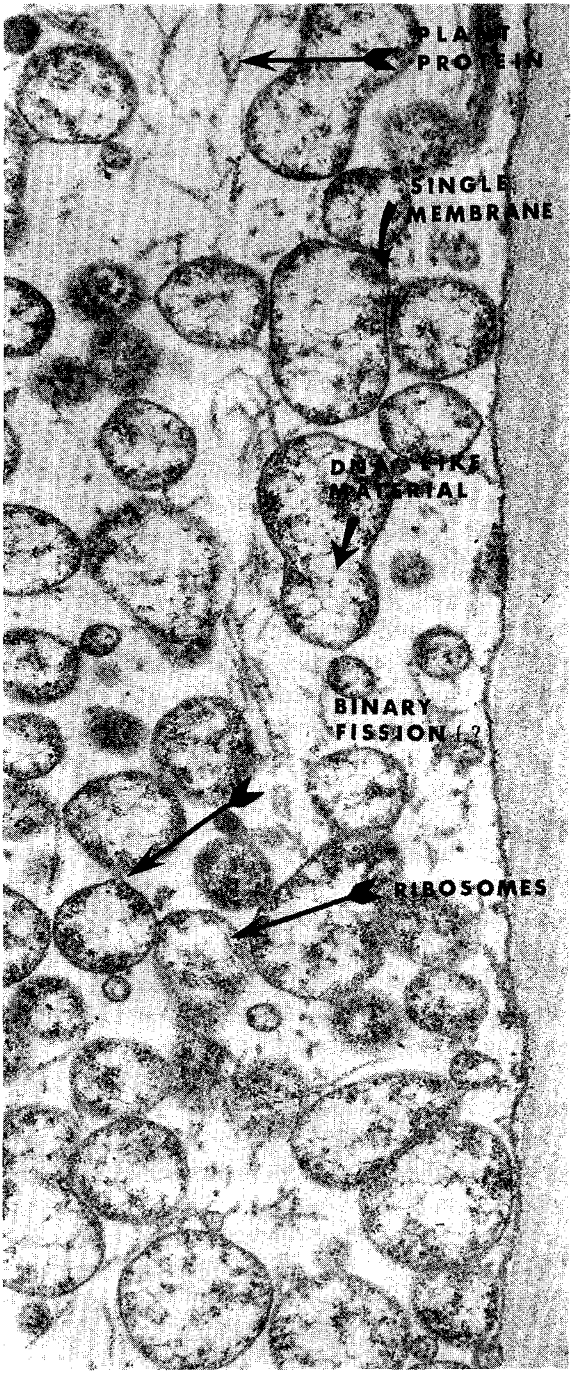

Figure 1.

come more upright; there may be overgrowth of the stem; and leaves and roots, as well as stems, may form brooms.

Depending on the particular disease, foliage may become yellow or reddish and dwarfed, and in some cases, even greener. Some foliage may become wrinkled or strap-shaped. Death of the phloem may occur, and there may be dieback of either terminal branches or roots. Starvation and decline symptoms may appear. Flowers may revert to leaves (phyllody), drop, proliferate, become dwarfed, or even enlarge.

To date, mycoplasmas are implicated as the possible cause of at least 23 tree diseases, as shown in the following table:

MYCOPLASMA-ASSOCIATED DISEASES OF TREES

DISEASE	VECTOR	REFERENCE
Areca catechu Yellow Leaf (India)	—	(36)
Apple Chat Fruit (France)	—	(2)
Apple Proliferation (France)	—	(1,16)
Apple Rubbery Wood (England)	—	(2)
Ash Witches' Broom (USA)	—	(2)
Black Locust Witches' Broom (USA, Europe)	—	(49)
Citrus Greening (South Africa)	psyllid	(28,30)
Citrus Likubin (USA)	psyllid	(5,7)
Citrus Littleleaf (Israel, Brazil, USA)	psyllid	(52,58)
Citrus Stubborn (USA)	—	(13,14,15,25,29,34)
Coconut Palm Lethal Yellowing (USA, Jamaica)	—	(3,19,33,42)
Dodonaca viscosa Spike (India)	—	(unpublished)
Elm Phloem Necrosis (USA)	leafhopper	(57)
Mulberry Dwarf (Japan)	leafhopper	(11,26)
Papaya Bunchy Top (Puerto Rico)	leafhopper	(53)
Paulownia Witches' Broom (Japan)	—	(11)
Peach Western X (USA)	leafhopper	(17,18,32,35,39)
Pear Decline (USA)	psyllid	(21,22,39,40)
Pecan Bunch (USA)	—	(27,48)
Prunus X Disease (USA)	leafhopper	(18)
Sandal Spike (India)	leafhopper	(9,10,24,37,38,44)
Walnut Bunch (USA)	—	(47)
Willow Witches' Broom (USA)	—	(23)

In this paper, we will discuss briefly those diseases affecting forest and ornamental trees.

Ash Witches'-Broom

Hibben & Wolanski (20) found witches'-brooms on declining white ash (*Fraxinus americana* L.) in New York State. Symptoms included small, chlorotic, sometimes deformed leaves that were often simple rather than pinnately compound, shortened internodes, abnormally erect branches, and shoot growth from axillary and terminal buds that normally remain dormant until the following year. The exact relationship between the witches'-broom and ash decline was not determined.

Hibben & Wolanski (20) found mycoplasmas associated with the brooms. They found no viruses associated with the affected tissue, and they were unable to transmit the infectious agent mechanically by sap inoculations. They were able to transmit the agent to *Vinca rosea* through dodder, from *V. rosea* to *V. rosea* by grafting, and from *V. rosea* to *Daucus carota* through dodder. Graft transmission of ash witches'-broom from ash to ash was reported in 1973 by Schall & Agrios (46).

Black Locust Witches'-Broom

Witches'-broom of black locust was first reported in 1898 and was assumed to be a virus disease. This disease occurs throughout the USA and several European countries.

Symptoms first appear when inflorescences emerge from the spathe with necrotic tips. Fruit trees. Occasionally the crowns of trees are affected. Brooms commonly develop late in the season from the growth of normally dormant axillary buds in leaf axils, grow into the fall, and frequently are winter-killed.

Seliskar et al. (49) found mycoplasma-like bodies associated with sieve elements and companion cells in phloem of stems, roots, and petioles of black locust showing witches'-broom symptoms.

Coconut Palm Lethal Yellowing

Lethal yellowing is a serious disease of coconut palm (*Cocos nucifera* L.). It has been known for some time in Jamaica and has recently become an important problem in southern Florida.

Symptoms first appear when infloresecenes emerge from the spathe with necrotic tips. Fruit drops in all stages of development, and yellowing begins in the lower fronds. The disease progresses until the bud becomes necrotic, and the tree dies. Cessation of symptom development and resumption of normal growth have been achieved through treatment with tetracycline antibiotics (33). Mycoplasmas were found in infected coconut palms by Beakbane et al. (3) and Parthasarathy (41).

Elm Phloem Necrosis

Elm phloem necrosis was described as a virus disease on *Ulmus americana* L. and *U. alata* Michx. in 1938 (54). After it was discovered in Ohio, elm phloem necrosis has subsequently been found in most of the central and southern United States. Recently, it has been found in Pennsylvania and New York (50,51). Epidemics of elm phloem necrosis have resulted in the death of thousands of trees within a community. Currently there are epidemics in New York (50), Pennsylvania (51), and Mississippi (12).

Symptoms of elm phloem necrosis appear as a general decline of the tree (Fig. 4). Leaves turn yellow or bronze and remain small. The entire crown is affected. Small feeder roots die, and in later stages of the disease the inner phloem at the base of the stem turns butterscotch brown (Fig. 2). If pieces of affected phloem are placed in a closed container and warmed, a distinctive wintergreen odor is emitted. Phloem necrosis can be transmitted by the whitebanded elm leafhopper (*Scaphoideus luteolus* (Fig. 3).

Wilson et al. (57) found mycoplasma-like bodies associated with elm tissue showing symptoms of elm phloem necrosis. Filer (12) has recently been able to get remission of symptoms of phloem necrosis by treating trees with tetracycline antibiotics. Some trees failed to show symptoms for three years after treatments.

Paulownia Witches'-Broom

Paulownia witches'-broom is the most serious disease of Paulownia in Japan, causing severe damage in plantations in central and southern sections.

Axillary buds and shoots grow from May or June into late fall on part or all of the tree. Twigs and branches become weak and brittle. Leaves on diseased branches become abnormally thin, narrow, rough, and chlorotic. One- and two-year-old trees usually die within two years; older trees may survive for several years.

Doi et al. (11) found numerous mycoplasma-like bodies in sieve tubes severely affected by the disease. No bodies were found in new, healthy twigs that grew on branches infected by witches'-brooms the previous year.

Pecan Bunch Disease

Pecan bunch is a widespread yellows-type disease, occurring throughout the commercial range of native pecan, (*Carya illinoensis* (Wangehn.) K. Koch). First reported in 1937 in Louisiana, the disease has since been discovered in eight southern states and is serious on a number of widely planted horticultural cultivars and native hickory species.

Characteristically, infected trees produce one to many witches'-brooms in the crown (Fig. 5). Brooms arise from the indeterminate growth of normally dormant axillary buds. They come into leaf before normal foliage, continue growth late in the fall, and are often killed by winter cold.

Although pecan bunch has been assumed to be virus-caused, the consistent association of a mycoplasma with diseased, but not healthy, trees strongly points to a mycoplasma etiology (48).

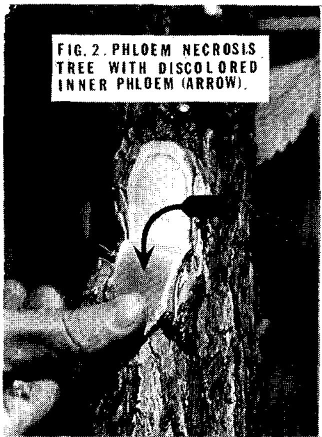

FIG. 2. PHLOEM NECROSIS TREE WITH DISCOLORED INNER PHLOEM (ARROW).

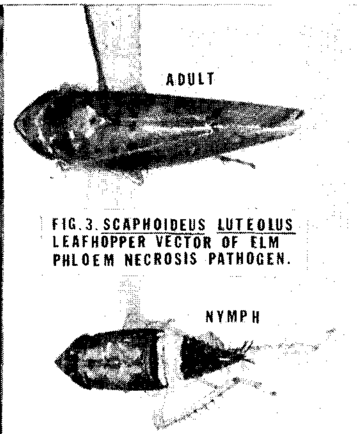

FIG. 3. SCAPHOIDEUS LUTEOLUS LEAFHOPPER VECTOR OF ELM PHLOEM NECROSIS PATHOGEN.

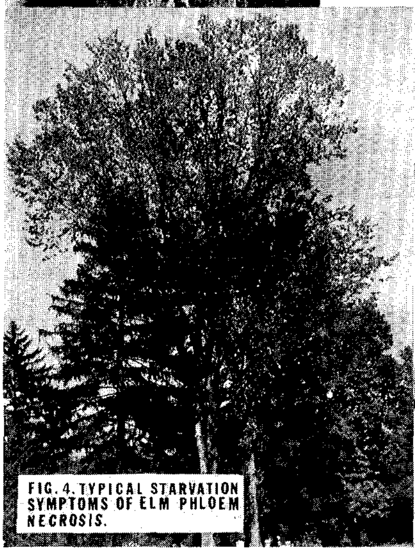

FIG. 4. TYPICAL STARVATION SYMPTOMS OF ELM PHLOEM NECROSIS.

FIG. 5. WITCHES' BROOMS ON PECAN AFFECTED WITH BUNCH DISEASE.

Mulberry Dwarf

This disease is of considerable economic importance in Japan, where the mulberry is a food source for silkworms. Early symptoms consist of a wrinkling of the leaf, whose surface becomes firmer to the touch, without any color change. Later leaves are smaller and more deeply indented, acquire a hard texture, and become yellowish-green. Internodes are shortened, and new shoots are weak and slender. Finally, the tree assumes a dwarfed witches'-broom appearance. Root development is less vigorous in affected trees.

Doi et al. (11) found various shapes of mycoplasma-like bodies in sieve tubes of diseased trees, and sometimes in the adjacent phloem parenchyma cells. Ishiie et al. (26) noted symptom remission of mulberry dwarf when plants were treated with tetracycline antibiotics.

Sandal Spike

Spike disease is the most serious disease of sandal (*Santalum album* L.) in South India. In its first stages, only parts of the tree may be affected, but in two to three years the entire tree will die. Leaves become very narrow and stand out stiffly from the branches, giving them a spike-like appearance. There is a shortening of the internodes. One of the first symptoms is a reversion of flowers to leaf-like structures (phyllody). There is a reduction in the perianth and stamen and a leaf-like enlargement of the pistil.

Mycoplasma-like bodies have been found associated with sandal spike disease (9,24). Tetracycline antibiotics have caused symptom remission (38,44). Mycoplasmas have been isolated from diseased tissues (37), but this work needs confirmation.

Walnut Bunch Disease

Bunch disease of walnut was first reported in 1932 in a nut orchard in Delaware. It was doubtless present long before this, however. Photographs of diseased trees taken in Georgia in 1914 (on file with the U.S. Dept. of Agriculture) clearly show bunch symptoms. The disease is widespread in the eastern United States and is found on Japanese walnut, butternut, English walnut, and native black walnut. Black walnut is the most resistant, and sometimes symptoms are masked in affected trees. Conversely, Japanese walnut is highly susceptible, and diseased trees die back over a period of several years.

Symptoms first appear as small brooms, which arise from the precocious development of axillary buds, which normally remain dormant. Like pecan bunch, brooms start growth early in the spring before normal foliage and continue late into the fall. As do a number of yellows-type diseases, walnut bunch causes a brittleness in the wood, which may affect the usefulness of the tree for veneer.

The disease can be transmitted by grafting, but no natural vector is known. The disease was once thought to be virus-caused, but the recent discovery of mycoplasmas in diseased trees (47) raises doubt as to a virus etiology. Seliskar (47) found mycoplasmas in the phloem tissues of petioles, roots, and stems of diseased, but not healthy trees. They were most abundant in petioles of highly symptomatic twigs in brooms and rarely found in nonsymptomatic portions of diseased trees.

Willow Witches'-Broom

A witches'-broom disease has recently been reported on scattered trees of *Salix rigida* Muhl. in New York, New Hampshire, and Massachusetts. Usually no more than one affected plant is found at each location. The disease is characterized by the early breaking of axillary buds and consequent growth of numerous spindly, erect branches. The leaves are stunted. The witches'-brooms commonly die in winter.

Holmes et al. (23) found typical mycoplasma-like bodies in phloem elements of diseased, but not healthy trees.

Current Status of Research

Current evidence that mycoplasmas cause tree diseases is circumstantial. The culturing of mycoplasmas that cause a few tree diseases has apparently been accomplished, but needs verification. Once we were able to fulfill Koch's postulates, the causal relationships of mycoplasmas can be delineated.

Assuming that we will soon be able to show that mycoplasmas do unequivocally cause tree diseases, more information is still needed to control these diseases effectively. What is the relationship of the various mycoplasmas? Are they host-specific? Do they have alternate hosts? Do they attack herbacious plants as well as trees? Other than by insects, how are they spread? Where do they overwinter? Are there saprophytic plant mycoplasmas? Are some trees attacked simultaneously by viruses and mycoplasmas (6)? We need answers to these questions in order to develop intelligent control procedures. Viruses have been found that are associated with mycoplasmas (43). We need to determine whether mycoplasmas are the disease-causing agents or sometimes only vectors of plant pathogenic virus.

Undoubtedly, mycoplasmas will be found associated with additional tree diseases. There are a number of prospects, such as boxelder witches'-broom and numerous other witches'-brooms of hardwoods and conifers. No mycoplasma has yet been found associated with a disease of coniferous trees.

The interaction of mycoplasmas with other disease-causing agents also needs to be determined. There is the possibility that mycoplasmas may serve as antagonists to other pathogens. They also might predispose trees to other diseases. The factors that predispose trees to mycoplasmal infections need to be determined.

It is obvious that our understanding of mycoplasma-associated diseases of trees is rudimentary. However, recently increased research in this area should soon provide us with answers to some of our questions.

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