Ash Yellows: Geographic Range and Association with Decline of White Ash

W. A. SINCLAIR, R. J. IULI, and A. T. DYER, Department of Plant Pathology, Cornell University, Ithaca, NY 14853-5908; P. T. MARSHALL, Indiana Department of Natural Resources, Vallonia 47281; J. A. MATTEONI, Agriculture Canada Research Station, Vineland Station, Ontario L0R 2E0, Canada; C. R. HIBBEN, Brooklyn Botanic Garden Research Center, Ossining, NY 10562; G. R. STANOSZ, Pennsylvania Department of Environmental Resources, Middletown 17057; and B. S. BURNS, Vermont Agency of Environmental Conservation, North Springfield 05150

ABSTRACT

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Ash yellows, a disease of *Fraxinus* spp. putatively caused by mycoplasmalike organisms (MLOs), was found to occur from Iowa and Missouri eastward to the Ottawa Valley of Canada and the Atlantic Coast in southern New England, as well as in scattered localities outside this range. New distribution areas recorded include Connecticut, Kentucky, Michigan, Missouri, Ohio, Pennsylvania, Utah, and the province of Quebec. In Utah, velvet ash (*F. velutina*) was affected, a new host record. The association of MLOs with decline in white ash (*F. americana*) was studied on 88 sites in four states (Indiana, New York, Pennsylvania, and Vermont) and southern Ontario. MLOs were detected by fluorescence microscopy in ash at 35 of 51 sites where severe dieback was common but at only five of 37 sites where dieback was scarce or absent. On sites where MLOs occurred, they could not be detected in all declining trees. Dieback at sites without MLOs was often associated with adverse soil conditions or evidence of prior injury. Thin canopies and slow growth of white ash were common on sites with and without MLOs.

Dieback and other symptoms of decline have been noticed in ash trees (*Fraxinus* spp.) in parts of the northeastern United States and eastern Canada since 1925 (20,22). White ash (*F. americana* L.) has been most commonly affected, but green ash (*F. pennsylvanica* Marsh.) and black ash (*F. nigra* Marsh.) also have symptoms.

The causes of these symptoms, to the extent known, are diverse. Black ash in Quebec showed dieback after a severe winter in 1925, and freeze damage to roots was suggested as the primary cause (22). In northern Minnesota, where *F. nigra* inhabits wet, poorly drained sites, it sustains chlorosis and twig dieback when the water table falls during drought (D. W. French, *personal communication;* W. Sinclair, *unpublished*). In Nova Scotia and coastal New England, white ash has died back after severe outbreaks of rust (*Puccinia sparganioides* Ell. & Barth.) (5,18).

In New York State, a decline of white ash, called "ash dieback," was for a time thought to be caused primarily by drought (15,24,35), but continuing mortality of ash was unrelated to weather fluctuations (4). Viruses were detected (3,7,11,14), but they occurred in vigorous as well as declining ash and were not conclusively shown to cause significant growth reductions (3,8,13).

Mycoplasmalike organisms (MLOs) may play a major causal role in ash decline (8,21). The syndrome of the mycoplasmal disease ash yellows (21) includes most of the symptoms of "ash dieback" (24) plus witches'-brooms (16) and foliar symptoms of the sort that MLOs cause in diverse plants.

In 1985–1989, ash yellows was reported from a variety of locations in the East (2,12,21) and Midwest (10,12,23, 32). White ash had been observed declining for 7–20 yr in Iowa and Indiana on sites where yellows was later diagnosed (19; J. Kemperman and L. Lichtsinn, *personal communications*). On the sites where ash yellows was studied in New York State, however, not all declining trees were found to be infected with MLOs (21,30). Therefore, the occurrence of MLOs in ash had to be assessed in relation to the occurrence of decline.

The present study had four objectives: to ascertain the geographic range of ash yellows and the region(s) where it is most common; to learn whether MLOs occur in nondeclining populations of white ash; to determine, on diverse sites where MLOs occur in ash, whether many declining trees are apparently not infected with these organisms; and to find out if there exists a widespread decline syndrome of white ash that is not associated with MLOs. An abstract has been published (31).

MATERIALS AND METHODS

Detection of MLOs. The 4′,6-diamidino-2-phenylindole·2HCl (DAPI) fluorescence technique (25,26), as adapted for diagnosis of ash yellows (30), was

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used. Briefly, for trees without witches'-brooms, one root 2–6 mm in diameter was collected from each tree, stored in a plastic bag on ice for up to 12 hr, washed, and cut to obtain two or three segments 8–10 mm long. These segments were stored in vials containing 2.5% glutaraldehyde in 0.1 M phosphate buffer, pH 7.0, at 2 C for up to 6 mo. Sections from one segment per tree were cut, treated with aqueous DAPI (0.4 $\mu g \cdot g^{-1}$ in buffer as above), and examined by epifluorescence microscopy to detect fluorescent particles in phloem sieve tubes. The particles were presumed to be the DNA of MLOs. Twigs from witches'-brooms were treated in the same manner as roots.

Geographic range. We gathered information about the geographic range of ash yellows from a survey in four states and the province of Ontario, as described below, and from microscopic examination of ash specimens that we collected or that were sent to us from outside the survey region. This information, supplemented by published reports, was used to compile a distribution map.

Survey of the association of ash yellows with decline. Between June 1986 and September 1988, we examined 903 ash trees on 88 sites in four states (Indiana, New York, Pennsylvania, and Vermont) and southern Ontario. This survey dealt primarily with white ash but included some green ash on four sites in northern New York and Ontario. The sample was composed as follows: Indiana, 125 trees on 13 sites in 12 counties; New York, 504 trees on 28 sites in 12 counties; Pennsylvania, 112 trees on 22 sites in 12 counties; Vermont, 80 trees on 12 sites in three counties; Ontario, 82 trees on 13 sites in eight counties. The sites were located along field edges, in hedgerows, in woodlots interspersed with agricultural land, and in forests. Sites were selected either because of prior knowledge of declining ash or because ash were noticed in locations that were convenient to examine. Dieback and other symptoms of decline were prominent at 51 of the selected sites and scarce or absent at the remaining 37 sites. Sites with standing water were not examined.

We searched for witches'-brooms, which are diagnostic for ash yellows (21), on and in some cases adjacent to each site. If brooms were found, twigs or growing shoots were collected from one or two of them and examined by means of the DAPI technique to corroborate the diagnosis. Trees with brooms, although included in the totals above, were not counted for the data summary, because we were interested primarily in the occurrence of MLOs in trees without diagnostic symptoms of yellows.

On 68 sites (31 with and 37 without prominent dieback of ash), the incidence of MLO infection of ash was assessed by sampling and examining the roots of trees (usually 10 or more) that lacked witches'-brooms and that represented the range of health and debilitation of ash on each site. On the remaining 20 sites, all of which had ash with prominent dieback, sampling was restricted to one to three symptomatic trees, and preference was given to trees with witches'-brooms.

The trees examined were between 4 and 75 cm in diameter at 1.4 m above ground, and those in woodlots and forests occupied intermediate to dominant positions in the canopy. Each selected tree was tallied in one of three health categories: normal, slow-growing, or dying back. It was not possible, however, to choose equal numbers of trees representing each health class on each site. Young trees on all sites and trees up to sawtimber size (about 45 cm in diameter) on sites believed to be conducive to vigorous growth were classified as growing normally if they displayed no dieback other than of shaded branches beneath the canopy (considered to be normal) and if their apical twigs were elongating more than approximately 25 cm per year as estimated by the unaided eye from the ground. All other trees without dieback of canopy branches were classed as slow-growing. For large old trees (more than 45 cm in diameter), the 25-cm standard was not applied; rather, normal versus abnormally slow growth was judged subjectively.

For many of the trees observed during the growing season, twigs of the canopy were obscured by foliage, and their growth rates could not be estimated. In these cases canopy density was used as a surrogate for twig growth: normal growth was recorded if the canopy was dense, and slow growth was recorded if the canopy was abnormally thin. Any tree with dieback of canopy branches, regardless of current growth rate, was classified as dying back.

RESULTS AND DISCUSSION

Geographic range and a newly recorded suscept of ash yellows. We diagnosed MLO infection in specimens of white ash from sites of ash decline in six states and one Canadian province where the disease was not previously known. These records, and the collectors of specimens if other than the authors, are as follows: Connecticut (P. M. Wargo); northern Kentucky; central lower Michigan (R. O. Kapp [see reference 36]); three locations in Missouri (C. Luley); central and northern Ohio (S. Bonstedt); south-central and southeastern Pennsylvania; and Gatineau Park in southern Quebec. We also found yellows in velvet ash (*F. velutina* Torr.) in Utah. Other records of ash yellows based on both symptomatology and electron or light microscopy exist for various ash species in Illinois, Indiana, Iowa, Massachusetts, Minnesota, Nevada, New York, Vermont, Wisconsin (G. L. Worf, *personal communication*), and the province of Ontario (1,2,10,12,16,21,23,32). Thus, the disease occurs in at least 16 states and two provinces (Fig. 1).

The principal range of ash yellows, though still imperfectly known, is an east-west band lying between approximately 39 and 45 degrees north latitude. It extends on the north from northeastern Iowa to the Ottawa Valley of eastern Ontario and southern Quebec and thence to eastern Massachusetts, and on the south from west-central Missouri to southeastern New York State. The disease also occurs in scattered localities

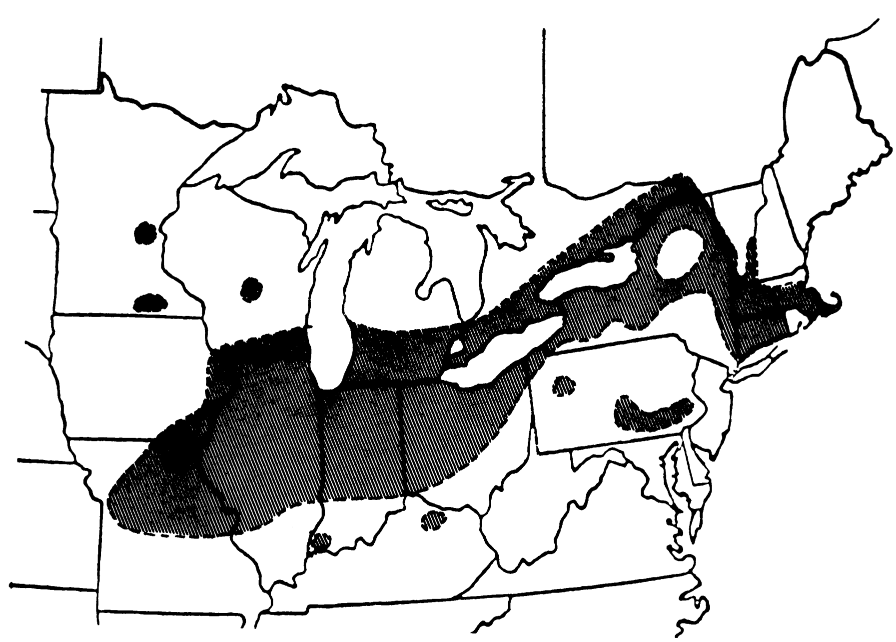

Fig. 1. The range of ash yellows in eastern North America. The boundaries of the range have been drawn to connect localities where the disease has been confirmed; ash yellows occurs discontinuously within this range. The disease has not been reported from New Hampshire or Rhode Island.

at the northern and southern fringes of the principal range and beyond it in the western Great Lakes region, southern Indiana, and northern Kentucky. The range of white ash (9) extends beyond that of ash yellows on the north, east, and south.

Yellows in white ash is more common and prominent where fields and woodlots are intermixed than where the land is primarily forested. Thirty-seven of the 40 sites where we found the disease were in areas of mixed land use or in forests on land formerly cleared for agriculture. The three sites in forested terrain were located in southern Vermont. Smallidge (33), in a study of the characteristics of forest stands affected by ash yellows, also noticed higher incidence of the disease in areas of mixed land use than in areas primarily forested. We did not find ash yellows in the heavily forested Knobs region of south-central Indiana, in the Adirondack region or the Delaware and Susquehanna watersheds of eastern New York, on the Allegheny Plateau, or in the Pocono Mountains of Pennsylvania.

Velvet ash is a previously unrecorded host of MLOs, although an undocumented report of the disease in its variety, Modesto ash (*F. velutina* var. *glabra* Rehd.), has been published (1). We found diseased and dead velvet ash in Zion National Park, UT, in May 1988. The affected trees displayed witches'-brooms, deliquescent branching, stunted twigs and foliage, and dieback. Infection by MLOs was confirmed by a positive reaction with DAPI in phloem of specimens from two witches'-brooms. We also provide documentation here for the earlier report of yellows in Modesto ash (1). The diagnosis was made by means of the DAPI test on specimens consisting of rosettes and portions of witches'-brooms submitted to W. Sinclair by W. Sheta from Las Vegas, NV.

Association of decline with MLOs. MLOs were detected in ash on 40 of the 88 sites in the survey, and decline was prominent on 35 of the 40 sites. Considering only the 68 sites where multiple trees were evaluated, MLOs were detected in more than half of all trees sampled where dieback was common, but in only nine trees (3% of those sampled) on sites where dieback was scarce or absent (Table 1). Only eight of the 236 trees that were classed as normal were found to be infected, and all of these were on sites where dieback was common. Based on previous field observations (21) and on the 1- to 3-yr incubation period of ash yellows in small trees graft-inoculated in the field (W. A. Sinclair, *unpublished*), we presume that the normal-appearing but diseased trees will display symptoms.

Of 497 white ash examined on the 40 sites where MLOs were detected, 75 were normal, 223 were growing slowly, and 199 displayed dieback. Within these groups, 11, 51, and 81%, respectively, were infected, as judged from results of the DAPI test. These trends were similar to those previously reported from New York State (21,30). When only data from sites outside New York were considered, of 154 trees on sites where MLOs were found, 5% of the 42 normal trees, 37% of the 59 slowly growing trees, and 75% of the 53 trees with dieback tested positive with DAPI. Based on previous work (30), we believe that very few of the trees that were scored negative for MLOs would have been scored positive if they had been resampled. Whether MLOs were present in such trees at levels below those detectable with DAPI or whether additional decline-inducing factors were present on sites of MLO infection is unknown.

The nine trees in which MLOs were detected where dieback was scarce to absent (Table 1) were located on five sites, four of which were within a few kilometers of severe outbreaks of MLO-associated ash decline. The ash on all five sites were growing slowly, and some trees on two of these sites showed dieback.

Witches'-brooms versus DAPI test for disease survey. Witches'-brooms were found on ash at 37 of the 40 sites where MLOs were detected by the DAPI technique. Therefore, searching for witches'-brooms was nearly as useful as microscopic analysis for diagnosing ash yellows on surveyed sites. At one of the three sites where the disease occurred but brooms were not found, few ash were present, and only one tree showed dieback; it tested positive with DAPI. At the other two sites, ash were growing slowly but not dying back. Because witches'-brooms form most commonly on severely debilitated trees (16,21; P. T. Marshall, *unpublished*), we presume that diseased trees on these sites had not yet progressed to the stage of broom formation.

Three of the 44 specimens from witches'-brooms were scored negative for MLOs in phloem. These results were disconcerting, because in previous examinations of brooms from ash, we had never encountered a negative result (21). The scores may have been negative because MLOs had not yet moved into the young shoots that were sampled. To test this idea, we performed the DAPI test on specimens collected from new shoots of three witches'-brooms about 2 wk after growth began in the spring in 1989. In all three cases, the results were negative, whereas tests on the same brooms in previous years had given positive results. Delays in the appearance of MLOs in current-year tissues have previously been reported for apple proliferation, pear decline, and X-disease of peach (6,27–29).

Dieback in the absence of MLOs. Sixteen sites (one each in Indiana and New York, nine in Pennsylvania, and five in Ontario) were examined where many ash showed dieback but MLOs were not detected. Evidence of prior injury or environmental insult was apparent at eight of these sites. Ash at one site were growing in a shallow soil on a limestone outcrop and were apparently stressed by periodic water shortage and nutritional imbalance; all trees there were chlorotic. On another site with shallow soil overlying ledges, ash and maples had sustained dieback several years previous and were recovering when examined; we suspected prior drought stress. Root damage by hoofed animals was apparent at three sites, and we found evidence of prior water impoundment at another. Two sites in hedgerows were adjacent to cultivated fields, and root damage was suspected. At the remaining eight sites, seven of which were in northern Pennsylvania, no potential cause of decline was apparent. The survey did not reveal a widespread syndrome of dieback in ash other than that associated with MLOs.

Unexplained slow growth and thin canopies of white ash. Slow growth and thin canopies in the absence of detectable MLOs were widespread and were not confined to large trees. On the 31 sites where dieback was common, 218 of the

Table 1. Incidence of infection of white ash by mycoplasmalike organisms (MLOs) in relation to tree condition and frequency of dieback[a]

	Sites where dieback was common		Sites where dieback was scarce or absent	
Tree condition	Trees (no.)	MLO-infected trees[b] (%)	Trees (no.)	MLO-infected trees[b] (%)
Normal[c]	74	11	162	0
Growing slowly[c]	218	49	132	4
Showing dieback	252	65	27	15
Totals and means[d]	544	51	321	3

[a] A total of 865 white ash (excluding trees with witches'-brooms) were examined at 68 sites where trees in all health classes were sampled. Dieback was common at 31 sites and scarce or absent at 37 sites.

[b] Percentage of the number in the corresponding health category.

[c] Classification was based on observation of apical twigs or, if twigs were obscured by foliage, canopy density (normal or thin).

[d] Means were weighted according to numbers of trees in each category.

544 trees examined were classed as growing slowly (i.e., they showed slow twig growth and/or thin canopy), and 49% of the trees in this class were found to be infected with MLOs (Table 1). On sites where dieback was scarce or absent, 132 of the 321 trees examined were also classified as growing slowly, but only 4% of these trees were scored positive in the DAPI test.

The lack of vigor of the slowly growing ash that were infected with MLOs can be attributed to that infection, because direct as well as circumstantial evidence indicates that MLOs suppress ash growth dramatically (8,21). The slowly growing trees that tested negative with DAPI are enigmatic. Repeated sampling and testing of such trees would not often yield evidence of MLOs, because within the limits of detection by the DAPI technique, the error rate for diagnosis based on one root sample per tree is less than 5% (30). Moreover, when we resampled seven sites (70 trees, which are not counted in the totals mentioned above) on which ash growth was slow or ash were declining and from which the first sets of samples had tested negative for MLOs, the results were again uniformly negative. If the DAPI test is reliable for MLO detection, as is widely believed (17,25,26,30), our data reveal the widespread occurrence in white ash of slow growth that is not associated with MLOs and does not necessarily presage dieback. Tegethoff and Brandt (34) examined ash on forest inventory plots in six northeastern states in 1963 and found that the proportion with thin canopies but without dieback varied from 18.4% in Connecticut to 43.5% in Pennsylvania. We found no records of the fate of the trees they examined. Perhaps thin canopies, which presumably develop in response to unidentified stress-inducing stimuli, are transient phenomena in many ash not affected by MLOs.

Conclusions based on our survey and related observations are as follows. 1) Ash yellows is common but discontinuously distributed within a band that lies primarily between 39 and 45 degrees north latitude from Iowa and Missouri to the Ottawa Valley and the Atlantic Coast and also occurs in scattered localities beyond this range. 2) Dieback of white ash is usually prominent on sites where trees of this species are infected with MLOs. 3) On sites where MLOs occur in ash, they cannot be detected in all declining ash. 4) Thin canopies and slow growth of white ash are widespread and are often independent of the ash yellows syndrome. 5) Although a variety of biotic and environmental factors may induce decline of white ash, the only widespread decline syndrome detected up to now is that associated with infection by MLOs.

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