Ash Yellows, Drought, and Decline in Radial Growth of White Ash

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ABSTRACT

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The effect of MLO infection and drought on the radial growth of white ash trees was measured using standard dendrochronological techniques. Both MLO infection and drought stress caused reductions in the radial growth of white ash, but not all MLO-infected trees declined in radial growth. The effect of regional drought on the radial growth of white ash was investigated on 15 of 41 permanent research plots by comparing summary tree ring indices of the white ash within these plots with mean Palmer Drought Severity Indices for April through September. Growth decline associated with drought stress was reversible when drought stress abated. Growth decline associated with drought stress and MLO infection was more severe than that associated with MLO infection alone and did not appear to be reversible. Both ash yellows and growth decline were related to stand age, becoming less prevalent in older stands.

White ash (*Fraxinus americana* L.) died along roadsides and hedgerows (22) from unknown causes during the early 1900s in the northeastern United States and eastern Canada (18). In New York State, dying of white ash was extensive between 1942 and 1957 (21). The dieback and subsequent mortality were reported initially from woodlots and hedgerows, then from forested areas. Brandt (1) reported a dieback of white ash in all age classes from 15 to more than 150 yr. The term "ash dieback" (13) describes the syndrome consisting of small, chlorotic foliage tufted at the ends of slow-growing shoots, premature fall coloration, cankers on the trunks and branches, progressive dieback of twigs and branches, epicormic sprouts and occasional witches'-broom formation, and tree death 2–10 yr after onset of symptoms.

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The cause of ash dieback is unknown. Drought may be a predisposing factor (3,20,28), but the influence of drought on the growth of white ash and the role of drought in ash dieback are not understood because this disease has not been investigated with standard dendrochronological analyses. These analyses standardize tree ring measurements and permit removal of shared environmental effects, which may confound the interpretation of the effects of biotic agents.

In 1971, Hibben and Wolanski (11) first associated mycoplasmalike organisms (MLOs) with witches'-brooms on white ash. Symptoms of ash yellows (AshY), the disease caused by MLO infection, are similar to those of ash dieback and include reduced apical and radial growth, early onset of radial growth in the spring, elevated diffusive resistance of the foliage, formation of abortive sprouts and cankers, dieback, and death (13,14). The formation of witches'-brooms is diagnostic (13). In New York State, AshY is probably the primary cause of ash dieback (14). The objectives of this research were to: 1) compare the radial growth of MLO-infected and noninfected white ash trees in the northeastern United States, using dendrochronological analyses; 2) evaluate the interaction, if any, of MLO infection and regional drought on radial growth of white ash; and 3) evaluate radial growth of white ash in relation to stand age.

MATERIALS AND METHODS

Plots. Fifty plots were established in forest stands with a relative density of white ash (= percentage of white ash stems relative to number of stems of all other species) greater than 10%. Details of plot establishment and vegetation in the plots were described previously (25). We used 41 of the 50 plots; five of the remaining nine plots contained green ash (*F. pennsylvanica* Marsh.), and increment cores from four plots were lost. Three of the 41 plots were located in Connecticut, 1 in Massachusetts, 2 in New Jersey, 29 in New York, 4 in Pennsylvania, and 2 in Vermont. Two increment cores were extracted from each of 336 ash, representing seven to 12 dominant or codominant trees on each plot. In addition, 68 dominant or codominant sugar maple (*Acer saccharum* Marsh.) trees were cored (two cores per tree) in 19 of the plots as a control for growth fluctuations associated with drought alone. The trees were ≥5 cm at dbh (diameter at breast height = 1.4 m aboveground), and the cores were extracted 50 cm above the ground, as close to the pith as possible, and parallel to the slope contour if a noticeable slope existed (17). The dbh and the presence or absence of witches'-brooms were recorded for each tree. Because ash is among the first tree species to colonize old fields, stand age was calculated from ash increment cores.

MLO detection. The phloem from a living root of each of three to five ash trees on each plot (143 of the 336 trees) were tested by the DAPI (4′,6-diamidino-2-phenylindole) fluorescence test (23) for the presence of MLOs. A positive rating for AshY (= MLO infection) in a plot was the detection of the organism in at least one tree. Trees with witches'-brooms were selected for the DAPI test; if no such trees were found on a plot, then evenly spaced trees were tested.

Tree ring measurements and analyses. Dried cores were glued onto grooved wooden mounts and planed to make the rings distinct. Widths of annual rings were measured to the nearest 0.01 mm with a Bannister Incremental Measuring Machine (Fred C. Henson Co., Mission Viejo, CA) interfaced with an Apple IIe microcomputer and the program Compu TA (5,19). This software provided a graphic representation of annual growth (skeleton plot) from each core. Cores from approximately 30% of the ash trees were randomly chosen for remeasurement, and differences between the first and second measurements were evaluated by the *t* test. Remeasurements were not significantly different at $P \leq 0.05$. To minimize errors in counting and measuring rings, skeleton plots of the two cores per tree were compared. Skeleton plots from all the cored ash trees on a plot then were grouped to allow a comparison between plots with and without AshY. Similarities among the grouped skeleton plots then were determined by comparing their patterns. All rings for any given year fell on the same vertical line (26).

All tree ring data were transferred to the Syracuse University Mainframe computer, where INDEX and SUMAC programs were used to generate standardized tree ring series and their descriptive statistics (7–10). In the INDEX program, ring width measurements were converted into indices; growth curves were fitted to the ring width series with a least-squares technique, and then each ring width value was divided by the value from the growth curve for the year. The resulting ring width indices have a mean value of 1.0, with a minimum of 0.0 and maximum of 4.0. A negative exponential curve fit was chosen because valuable climatic information might have been removed by choosing a polynomial function (7). In the program SUMAC, the tree ring chronologies from individual trees and all of the trees in a plot(s) were averaged (summary indices) and then evaluated with an analysis of variance (ANOVA) and a cross-correlation analysis (8,27).

Evaluation of drought. Monthly data for the Palmer Drought Severity Index (PDSI) for each of 11 climatic divisions (representing all 41 plots) from 1895 to 1987 were purchased from the National Climatic Historic Data Center (U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Environmental Satellite, Data, and Information Service, Federal Building, Asheville, NC). PDSI data for each growing season (April–September) for each year from 1895 through 1987 were evaluated. PDSI, a measure of soil moisture deficits and surpluses, is based on precipitation and air temperature

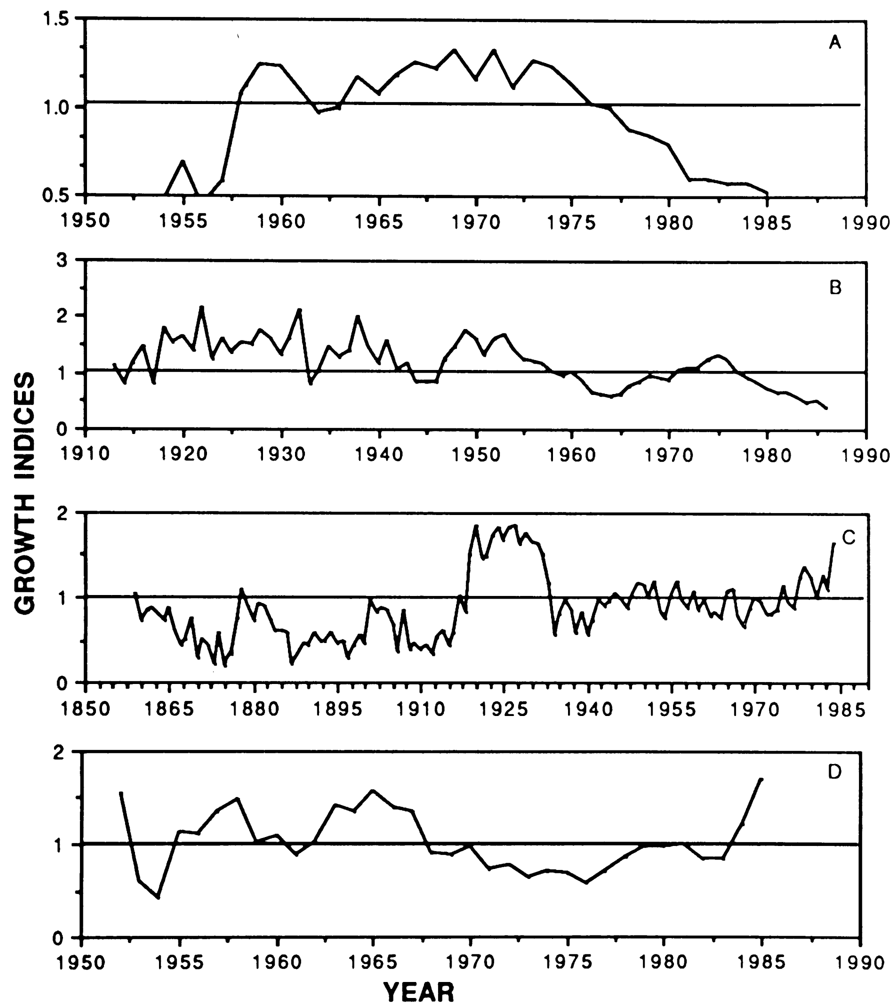

Fig. 1. Examples of summary white ash tree ring indices (generated by the computer program SUMAC) representing plots in New York with or without growth decline (diagnosed when the indices were consistently below 1.0 and showed no recovery since 1970): **(A)** Growth decline in the apparent absence of MLOs on a plot in Otsego County, **(B)** growth decline on seven plots affected by ash yellows in Ulster County, **(C)** no decline on a plot in Tompkins County where MLOs apparently were absent, and **(D)** no decline on a plot in Dutchess County where MLOs were detected.

(16). Values of 0.0 to −0.5 = normal, −0.5 to −1.0 = incipient drought, −1.0 to −2.0 = mild drought, −2.0 to −3.0 = moderate drought, −3.0 to −4.0 = severe drought, and greater than −4.0 = extreme drought. The same descriptives with + signs are used to describe wet spells.

Nineteen of the 41 plots were located in climatic divisions 2 and 5 in New York, where AshY is prevalent. In addition, these divisions were subjected to a severe regionwide drought between 1962 and 1967 (4). Therefore, these two divisions were chosen to evaluate the relationships among drought, MLO infection, and growth.

Evaluation of current growth decline. A plot was classified as a site of growth decline if the summary indices of growth were consistently below 1.0 and had not recovered (positive slope) since 1970, the year selected for the base to avoid the potentially confounding influence of the widespread regional drought of the mid-1960s. The ash on a plot were placed in the nondecline category if the summary indices of growth fluctuated since 1970 and were recently above or close to 1.0.

Evaluation of growth effects attributed to MLO infection. The computer program TRMCLM was used to remove environmental effects common to growth response of both MLO-infected and noninfected trees. The growth data (ring chronology) of one infected tree were compared with those for one noninfected tree in the same plot. Only four of the 41 plots contained both infected and noninfected trees as assessed by the DAPI procedure. Therefore, TRMCLM analysis was conducted on only four plots (i.e, for only four pairs of trees). In the program, PRI = [SDEV (I)/SDEV (NI)] × [INDEX (NI) − MEAN (NI)] and CI = INDEX (I) − PRI, where PRI = predicted residual indices, SDEV (I) = the standard deviation for ring indices of the infected tree, SDEV (NI) = the standard deviation for ring indices of the noninfected tree, INDEX (NI) = the index values of the noninfected tree, MEAN (NI) = the mean index value of the noninfected tree (about 1.0), CI = the corrected indices of the infected tree, and INDEX (I) = the index values of the infected tree (27).

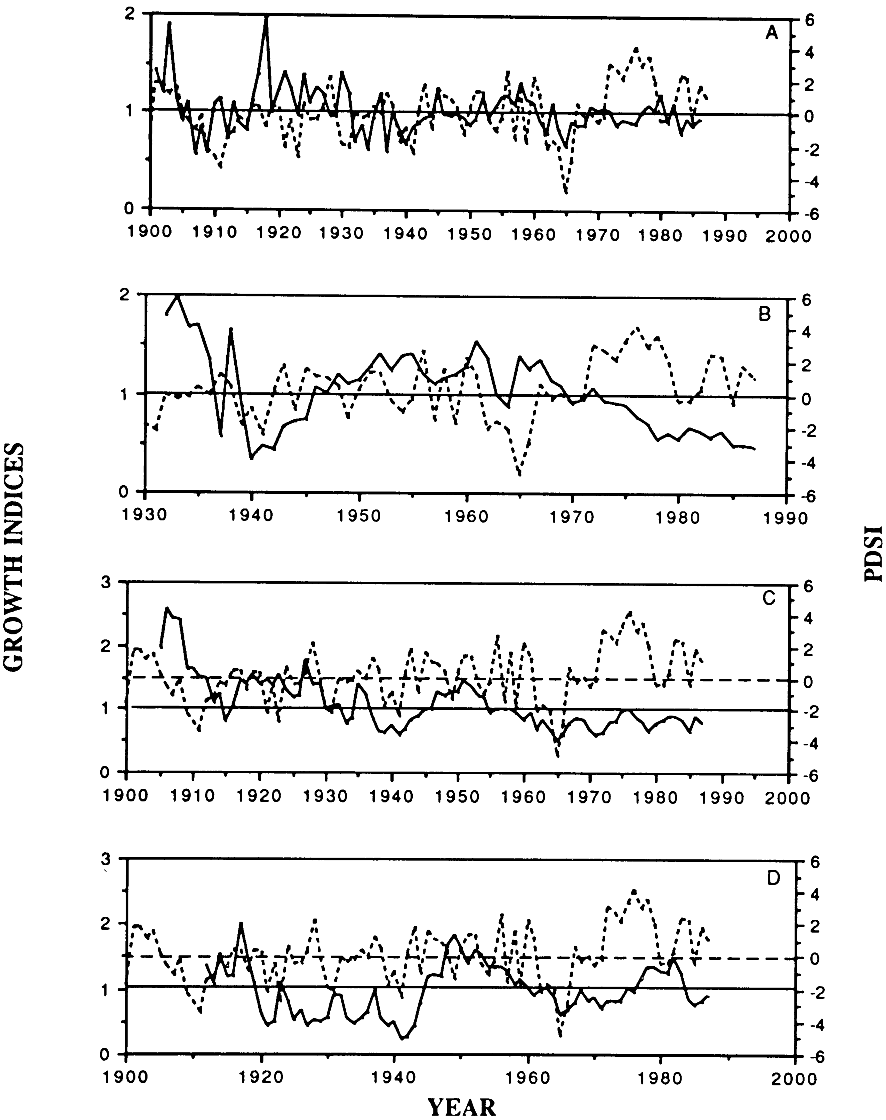

Fig. 2. Mean values (dashed lines; dashed horizontal lines = normal moisture) of the Palmer Drought Severity Index (PDSI) for each growing season (April through September) and summary tree ring indices (solid lines; solid horizontal lines = normal growth) of: **(A)** 14 sugar maple trees on six plots, **(B)** 15 MLO-infected white ash on four plots in Tully, Onondaga County, **(C)** five noninfected white ash trees on one plot in Broome County, and **(D)** six noninfected white ash on one plot in Chenango County. All plots are located in climatic division 2 in New York State. Normal growth and moisture axes are superimposed in A and B.

RESULTS

MLOs were detected in 51 ash trees located in 20 of the 41 plots, and 92 trees were scored as noninfected. Radial growth decline was detected on 20 plots, including 16 that were positive for the MLO (Fig. 1). Four of the 21 plots in the nondecline category were positive for the MLO. Mean age of stands (± standard error) of plots in the nondecline vs. decline category was 52 ± 4.1 yr vs. 41 ± 3.1 yr ($P > 0.05$). MLOs were detected in trees 18–80 yr old; the average age was approximately 40 yr.

Relationship of drought and MLO infection to growth decline. An extremely severe regionwide drought occurred in the 1960s, with climatic divisions 2 and 5 in New York State among the most severely affected. Over the period from 1900 to 1987, repeated episodes of slight to moderate drought of short duration occurred in both divisions (Figs. 2 and 3) and a moderate drought occurred between 1979 and 1981 in division 5 (Fig. 3) but not in division 2 (Fig. 2).

In both divisions, the growth of sugar maple responded consistently to moisture availability (Figs. 2A and 3A). In division 2, growth of noninfected ash also responded, for the most part, to moisture availability (Fig. 2C and D). The growth of infected ash responded to moisture availability until the early 1970s (Fig. 2B), when growth continued to decline even in the presence of adequate moisture. In division 5, the growth of a group of noninfected ash in only their second decade of growth in the 1960s did not respond to the severe drought of that decade but did respond to moisture fluctuations thereafter (Fig. 3D). The growth of two groups of infected ash consistently responded to moisture availability until the early 1980s, after which growth continued to decline even in the presence of adequate moisture (Fig. 3B and C). Because the plots represented in Figures 2 and 3 are similar with respect to stand level characteristics (e.g., relative density of ash per hectare, average ash dbh, stand age) (25), the differences in the response of ash to moisture availability are not likely to be attributed to stand level variables.

TRMCLM analysis illustrates the effects of MLO infection on the growth of white ash (Fig. 4). The corrected index of the infected tree depicted in Figure 4A shows a radial growth decline during 1949–1954 and 1964–1965 and again during the early 1970s but greater relative growth in recent years. The corrected index of the infected tree depicted in Figure 4B shows a severe radial growth decline in 1972 and again in 1981. The corrected index of the infected tree depicted in Figure 4C shows a radial growth decline during 1960–1961 and again in the mid-1960s but not since the late 1970s. The corrected index of the infected tree depicted in Figure 4D shows radial growth decline between 1965 and 1975, then subsequent recovery. The use of alternative uninfected trees in each plot, where possible, did not significantly alter the results.

A relationship among the incidence of AshY, growth decline, and stand age became apparent when plots were grouped according to stand age (Table 1). The incidence of growth decline decreased with increasing stand age. The incidence of AshY peaked in the 40- to 49-yr age category, then decreased. The observed vs. expected frequencies of both AshY and growth decline across four stand age classes were significantly different (chi-square, $P < 0.001$).

DISCUSSION

Responses to MLO infection in the field among trees of different ages are confounded by differences in the initial year of infection. Therefore, our interpretations of the data presented here were based on the following intuitive and empirical assumptions: 1) Once a tree was infected with MLO, it remained infected; 2) some infected trees may live many years; 3) MLO infection does not necessarily result in a marked growth decline; and 4) if dendrochronological techniques are used, growth decline associated with infection is detectable against the background of other growth-suppressing influences.

In general, the growth of sugar maple and noninfected ash responded consistently to moisture availability (Figs. 2 and 3). There were some exceptions, however. For example, the growth of one group of young noninfected ash increased throughout the early 1960s, a period of extreme drought (Fig. 3D). In the 1920s, another group of young noninfected ash grew poorly even in the presence of adequate moisture (Fig. 2D). Perhaps these trees were for a time suppressed in the understory.

Castello et al (3) reported that the relationship between drought and mortality of white ash was not distinct. Drought in the early 1960s was associated with increased mortality, and the number of declining and dead trees leveled off when the drought ended in 1967. The mortality rate during the drought period was twice that during the subsequent wet period. However, ash mortality also was common during the 1940s and 1950s, a period of generally normal to above-normal moisture (3). Ash mortality increased, but at a slower rate, in the 1970s, even though this was a wet period. Castello et al (3) evaluated mortality, not radial growth. Matteoni and Sinclair (13) evaluated radial growth, although not with dendrochronological methods, and determined that the year of onset of growth decline varied among trees on any site and among sites where MLO infection occurred. Therefore, it seemed unlikely that a common causal abiotic factor such as drought was alone responsible for growth decline.

MLO infection may interact additively or synergistically with drought stress to cause a decline in growth. There was a moderate drought during the late 1970s in division 5 (Fig. 3) that did not occur in division 2 (Fig. 2). MLO-infected ash in both divisions declined in growth rate during that time period, but the rate of decline was much steeper among drought-stressed trees (Fig. 3B and C) than among trees with adequate moisture (Fig. 2B). The infected ash in both divisions were located in plots with similar stand characteristics (25).

Only living trees were examined in this study and, therefore, may represent those individuals that survived the effects of MLO infection and drought. Because they may be the more resistant individuals within the ash population, measurement of their response may not elucidate all of the interrelationships among infection, drought, and growth.

Ferris et al (6) provided evidence that MLO infection in white ash seedlings is associated with radial growth decline. In the field, however, not all infected trees

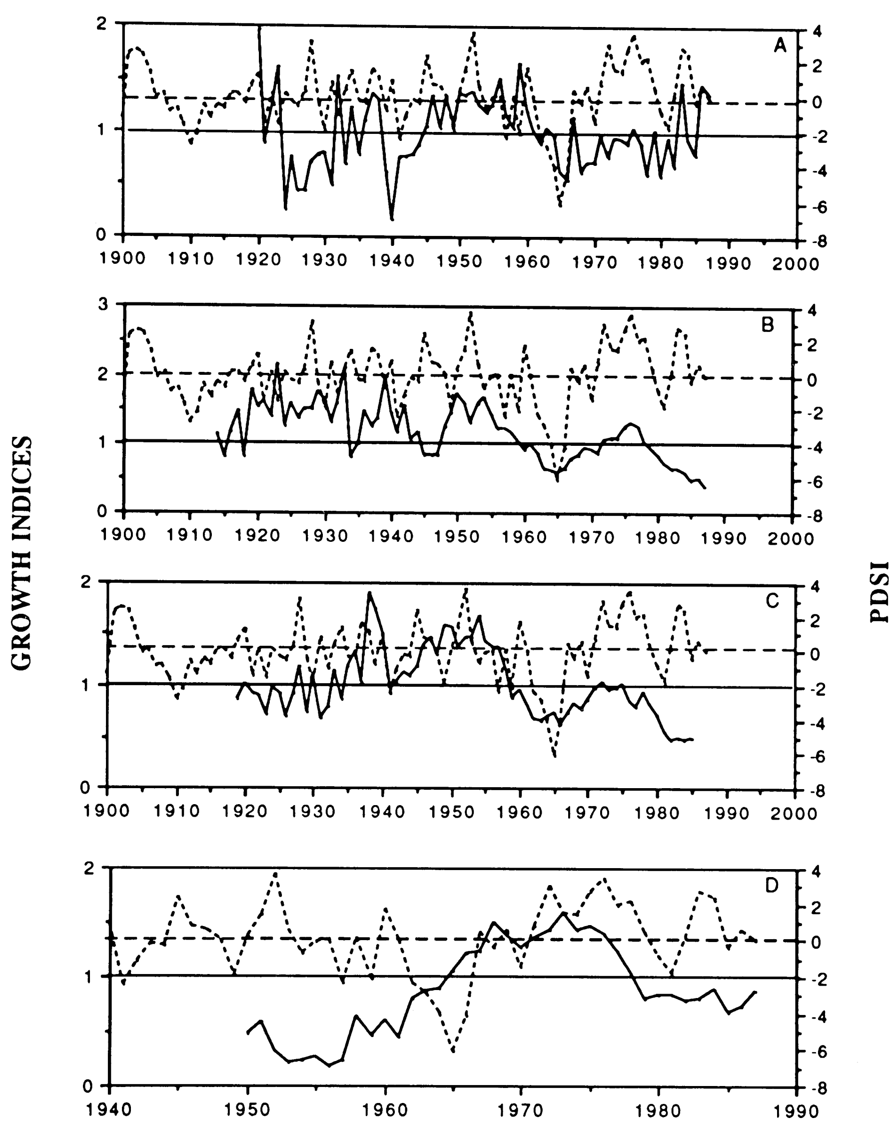

Fig. 3. Mean values (dashed lines; dashed horizontal lines = normal moisture) of the Palmer Drought Severity Index (PDSI) for each growing season (April through September) and summary tree ring indices (solid lines; solid horizontal lines = normal growth) of: **(A)** six sugar maple trees on six plots, **(B)** 41 MLO-infected white ash on seven plots in Ulster County, **(C)** six MLO-infected white ash on one plot in Rensselaer County, and **(D)** five noninfected white ash on one plot in Dutchess County. All plots are located in climatic division 5 in New York State.

display dieback or growth decline (2,13,14). MLO infection was associated with growth decline in some trees but not always with a sustained radial growth decline. Only one of four infected trees evaluated with TRMCLM was in a growth decline (Fig. 4B), which may indicate tolerance to MLO infection. Perhaps some of the noninfected trees used for TRMCLM analysis were infected with MLOs but at levels not detected by DAPI. Alternatively, some infected trees may be the result of recent infection or may not go into growth decline immediately after infection. Interaction with another factor (e.g., drought) may be needed before growth decline begins. Some white ash may have the ability to recover from MLO-induced growth decline (Fig. 4A, C, and D). MLO-infected American elm (*Ulmus americana* L.) die within several years of infection (14). Similarly, MLO-infected coconut palm (*Cocos nucifera* L.), mulberry (*Morus* spp.), and jujube tree (*Ziziphus jujuba* Mill.) die quickly (29,30). MLO infection and subsequent growth decline and recovery could have occurred in the 1960s, 1970s, and 1980s (Fig. 4B, C, and D) or perhaps as early as the 1950s (Fig. 4A). Therefore, if able to recover from MLO infection, infected ash may be unusual.

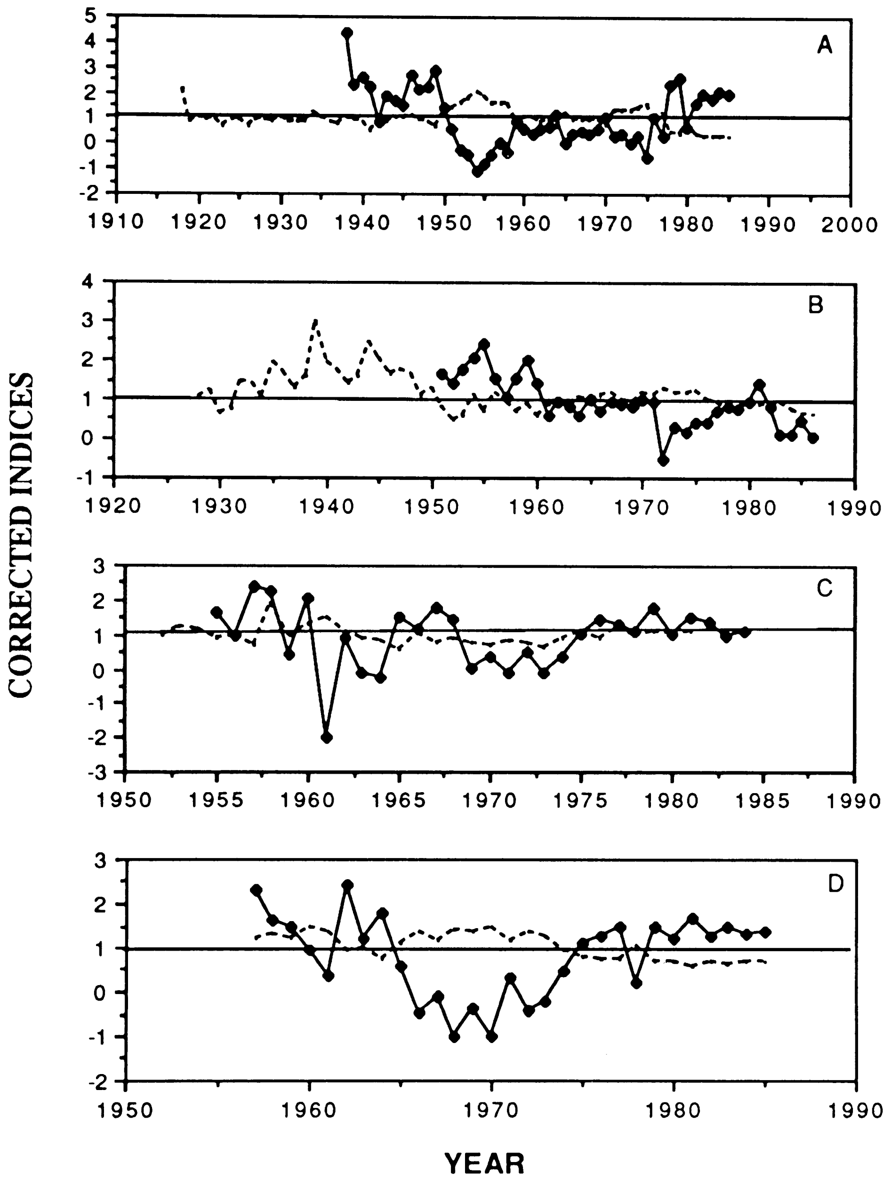

Fig. 4. Tree ring indices from one MLO-infected white ash (solid lines) and one noninfected white ash (dashed lines) from each of four plots, corrected for climate and site conditions common to both trees by the computer program TRMCLM: **(A)** Two trees on one plot in Rensselaer County. The infected tree showed growth decline in the 1950s but not currently. **(B)** Two trees on one plot in Ulster County. The infected tree showed a brief period of growth decline in the early 1970s, from which it recovered, and a second period of growth decline beginning in 1980, from which it has not recovered. **(C)** Two trees on one plot in Dutchess County. The infected tree showed a brief period of severe growth decline in the early 1960s and a longer but less severe growth decline in the late 1960s to early 1970s, from which it subsequently recovered. **(D)** Two trees on one plot in southeastern Pennsylvania. The infected tree showed a sustained growth decline in the 1960s and early 1970s, from which it has recovered. None of the noninfected trees showed evidence of growth decline.

The presence of radial growth decline in the four plots that were apparently unaffected by MLOs may be explained by other abiotic or biotic stresses, such as other diseases, insects, crown position, or stand development. White ash often decline without MLO infection that is detectable by the DAPI procedure (23,24). Conversely, MLO infection may have been present but undetected in these four plots.

The incidence of MLO infection and growth decline apparently was related to stand age; stands where ash were categorized as nondeclining tended to be older than those where ash were declining (Table 1). Because infection was not always associated with growth decline, and because older stands were less likely to be declining (Table 1), some other age-related factor may be associated with decline. During forest development after a major disturbance, forest stands undergo a stressful period of stem exclusion, or self-thinning (15). Competition in white ash stands 30–50 yr old may be responsible for the high incidence of growth decline observed in this age group. The incidence of MLO infection also peaked in this age group, which implies some, as yet unknown, relationship between infection and either stand development or vector/host relationships. MLO infection may hasten thinning in young white ash stands of old-field origin in the Northeast because both the incidence of infection and growth decline peaked in stands of the same age (30–50 yr). Conversely, the observed peak in the incidence of infection and growth decline in the 30- to 50-yr age category may simply represent an artifact of sample size.

Hornbeck et al (12) reported that in New England, white ash older than 50 yr showed constant or increasing growth

Table 1. Relationships among stand age, presence or absence of MLO infection, and growth rate category[a]

		Plots with ash with:	
Stand age (yr)	No. of plots	Growth decline[b] (no.)	MLO infection[c] (no.)
30–39	14	9	8
40–49	9	5	6
50–59	4	2	2
>59	10	2	2

[a] Frequencies of plots with growth decline and, separately, with MLO infection were significantly unequal in the various stand age categories according to the results of chi-square analyses ($P < 0.001$); four plots less than 30 yr old were not included.

[b] Summary white ash tree ring indices were consistently below 1.0 and showed no recovery since 1970.

[c] Determined by DAPI test on three to five white ash per plot.

from 1950 to 1980 as measured by basal area increment. In the present study, both infection and growth decline occurred in all age categories but were less common in forest stands older than 60 yr (Table 1).

Both MLO infection and drought stress apparently caused a reduction in the radial growth of ash (Figs. 2 and 3). Not all infected trees were declining in growth (Fig. 4), however. Growth decline associated with drought stress appeared to disappear when drought stress abated (Figs. 2 and 3). Growth decline associated with drought stress and MLO infection was more severe than that associated with MLO infection alone and did not appear to be reversible (Fig. 3B and C). We support previous assessments of drought and MLO infection as separate causal factors in decline of white ash (3,13) and provide the first evidence that drought and MLO infection may interact in decline of this species. In addition, both the incidence of infection and growth decline were related to stand age, becoming less prevalent as stands aged.

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