Structure and Composition of Forest Stands Affected and Unaffected by Ash Yellows

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ABSTRACT

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The incidence and effect of the mycoplasmal disease ash yellows in forest stands were evaluated in 50 plots located in six northeastern states. Three forest types identified by a vegetation analysis were dominated by *Fraxinus americana, Acer saccharum*, or *F. pennsylvanica*. The density of dead *F. americana* was greatest on sites dominated by this species, and the height of dead *F. americana* relative to live trees, or vertical distribution, differed among the forest types. Total tree mortality was generally greater in yellows-affected plots than in unaffected plots because of greater *F. americana* mortality. Live tree species composition was similar between yellows-affected and unaffected plots. The density and basal area of dead overstory *F. americana* were greater in yellows-affected than in unaffected plots dominated by *F. americana*. Mortality in plots dominated by *F. pennsylvanica* was minimal and restricted to individuals below the main tree canopy. Only one of 15 plots dominated by *A. saccharum* contained ash infected with mycoplasmalike organisms. A significant association was detected between the occurrence of ash yellows and both herbs characteristic of exposed conditions and areas classified as exposed. This association may explain the high levels of mortality in previous studies.

Fraxinus americana L. (white ash) is an economically and ecologically important species in the northeastern United States (7). High levels of dieback, retarded growth of living diseased trees, and mortality reported for this and congeneric species (6,11,14,22,26,33) are potentially serious problems for forest management. Early work linked the decline of *F. americana* to environmental stress (11), but recent work implicates the disease ash yellows (AshY) as one of the primary causes of dieback and mortality (14).

Ash yellows is caused by an uncharacterized mycoplasmalike organism (MLO) (12,14). Slow growth, crown dieback, witches'-brooms, and mortality have been attributed to this pathogen (9,12,14). Ash yellows and dieback occur in all size and age classes of *F. americana* and in many different habitats (6,11, 14,22,26,29). Indeed, ash dieback and AshY may be synonymous (14). Previous studies, however, emphasized *F. americana* that were less than 15 cm in diameter at 1.37 m (6,26) or that occurred in hedgerows, old fields, and coniferous plantations (14). Characteristics of forest stands affected by AshY have largely been ignored. We hypothesize that the incidence of AshY is related to stand level variables and that AshY will alter the structure and composition of the stands it affects.

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Objectives of this study were to: 1) characterize the structure and composition of selected forests in Connecticut, Massachusetts, New Jersey, New York, Pennsylvania, and Vermont that have a large component of *F. americana*, 2) evaluate mortality in relation to the presence of AshY, and 3) evaluate the effects of AshY on forest composition and structure.

MATERIALS AND METHODS

Plot establishment and measurements. Fifty plots 15 × 30 m were established in Connecticut, Massachusetts, New Jersey, New York, Pennsylvania, and Vermont in 1987 and 1988. Nondisturbed stands in all stages of development in which at least 10% of the trees were *F. americana* or *F. pennsylvanica* Marsh. were sampled. Eight of the 50 plots were systematically centered on continuous forest inventory plots maintained by the New York State Department of Environmental Conservation. The remaining plots were established to include as many trees with symptoms of AshY as possible or, in the absence of AshY symptoms, to be representative of stand structure and composition. In dense stands that were homogeneous with respect to structure and composition (n = three), plot size was reduced to 10 × 20 m. Each plot was classified as either exposed or nonexposed based on the degree of landscape heterogeneity (21), i.e., a nonexposed plot was one situated within a contiguous forest. A list of plots and their categorical variables is available (30).

Crown class—dominant, codominant, intermediate, and suppressed (31)—and the diameter at 1.37 m aboveground (dbh) of living stems of all woody species and standing dead *F. americana* and *F. pennsylvanica* stems >5.0 cm dbh were recorded in all plots. Standing dead stems of all species >5.0 cm dbh were included on 40 plots. Saplings and shrubs between 1.0 and 5.0 cm dbh at 1.0 m height were recorded by species and diameter in two subplots 5 × 5 m located in opposite corners of the main plot. Genera of herbaceous plants on each plot were recorded and, when possible, identified to species. Site characteristics included percent slope, position of the plot on the slope, aspect, and soil depth to an impermeable root-restricting layer and were measured in each plot. Aspect was transformed by the methods of Beers et al (2) and Stage (32). The texture of a composite soil sample from each plot was analyzed (4).

Pathogen detection. The presence or absence of MLOs in ash on each plot was tested by the DAPI DNA-staining technique (25) as applied to one root sample collected from each of three to five *F. americana* or, when dominant, *F. pennsylvanica* per plot (28). If one tree tested positive for MLOs, the plot was classified as DAPI-positive. Plots were classified as symptomatic if any *F. americana* or *F. pennsylvanica* in or near the plot had witches'-brooms. Hereinafter, plots that tested positive for MLOs will be referred to as POS and those that tested negative as NEG, and SYM and ASY will refer to plots with and without symptoms, respectively.

Data analysis. Data were analyzed using SAS (23,24). Stand level variables included mean dbh, basal area, density, and importance values (1) [importance value = (relative basal area + relative density)/2] and were calculated by species for each plot. Basal area was the area of a cross section of the tree stem at dbh and density was the number of stems per unit area. Relative basal area and density were calculated for each species as the percentage of the total basal area and density. Vertical distributions of *F. americana* and *F. pennsylvanica* were calculated using basal area for live and dead in each crown class. Comparisons of vertical distribution were made between POS and NEG plots. To reduce data set variability, plots were classified into forest types by TWINSPAN (two-way indicator species analysis [16]) based on the importance values of live overstory trees. Classification of understory types by sapling/shrub layer importance values was done similarly. Principal components analysis (PCA) ordinations using relative basal area, relative density, and importance value compared species in the live, dead, and sapling/shrub stratum. Discriminant analysis was used to determine if stand characteristics distinguished MLO-affected and unaffected plots. Summary statistics compared differences between diseased and healthy stands within each forest type, whereas chi-square and multivariate statistics compared differences between diseased and healthy plots among forest types.

Two indices were calculated to evaluate the vertical distribution, or crown class, of *F. americana*. Crown class refers to tree height relative to other trees in the immediate area. The first index, the crown class contribution of *F. americana* based on basal area, is a measure of the potential for forest change after mortality or disturbance. Crown class contribution is the percentage of *F. americana* basal area in a crown class relative to the sum of live and dead basal area for all species for that crown class. The second index is the canopy distribution of *F. americana* basal area within each crown class relative to the sum of live and dead basal area for all species in all crown classes. Vertical structure comparisons were made using both basal area and density, and the results were similar; thus, large diameter snags were infrequent. Basal area was used because of the close relationship of basal area to canopy size. Both crown class indices were calculated for each of the four crown classes: dominant, codominant, intermediate, and suppressed. Crown class contribution can only be evaluated within a crown class for each disease and vigor treatment. Canopy distribution values, however, can be compared among crown classes.

Table 1. Comparison of overstory species (live trees only) by forest type between DAPI-positive and DAPI-negative stands

Forest type	DAPI-positive			DAPI-negative		
Species[a]	Density[b]	BA[c]	IV[d]	Density	BA	IV
White ash						
Fraxinus americana L.	614	14.8	60.1	935	14.9	60.1
Acer saccharum Marsh.	108	1.1	7.4	127	2.1	8.2
Prunus serotina Ehrh.	75	1.4	6.5	77	1.6	5.7
Quercus rubra L.	60	0.7	4.3	0	0	0
Acer rubrum L.	43	0.9	3.9	78	1.4	5.3
Carya glabra (Mill.) Sweet	29	0.8	3.1	0	0	0
Ulmus americana L.	30	0.6	2.7	53	0.8	3.4
Pinus strobus L.	6	0.4	1.1	87	2.3	7.4
Tilia americana L.	4	<0.1	0.2	31	0.6	2.1
Other ($n = 27$)	105	2.8	11.2	106	2.2	7.8
Total	1,074	23.5	100.3	1,494	25.9	100.0
Sugar maple						
Fraxinus americana	556	16.3	57.4	129	7.7	20.4
Acer rubrum	178	4.2	16.4	62	2.5	7.9
Acer saccharum	200	2.9	14.8	387	11.3	41.8
Tsuga canadensis (L.) Carr.	111	2.1	9.2	19	1.0	2.8
Acer pensylvanicum L.	0	0	0	32	0.1	2.1
Betula alleghaniensis Britt.	0	0	0	38	1.7	5.0
Fagus grandifolia Ehrh.	0	0	0	67	1.5	6.5
Prunus serotina	0	0	0	16	0.9	2.4
Quercus rubra	0	0	0	21	1.0	2.9
Tilia americana	0	0	0	10	0.9	2.0
Other ($n = 12$)	44	0.2	2.3	63	1.4	6.1
Total	1,089	25.7	100.1	844	30.1	99.9
Green ash						
Fraxinus pennsylvanica marsh.	881	20.9	73.1	933	22.4	65.2
Acer saccharinum L.	81	5.7	12.7	133	5.0	11.8
Carya cordiformis (Wang.) Koch	37	2.5	5.7	0	0	0
Acer saccharum	22	0.5	1.8	233	4.4	14.7
Populus deltoides Bartr. ex Marsh.	0	0	0	11	3.6	5.5
Other ($n = 7$)	73	2.2	6.7	66	0.4	2.9
Total	1,094	31.8	100.0	1,376	35.8	100.1

[a] Nomenclature according to Mitchell (17).
[b] Number of individuals·ha^{-1}.
[c] Basal area = $m^2 \cdot ha^{-1}$, measured at 1.37 m aboveground.
[d] Importance value = (relative basal area + relative density)/2.

RESULTS

Statistical analyses were run separately to compare plots on the basis of POS vs. NEG status and SYM vs. ASY. Conclusions generated by both analyses were identical (30), and only results based on DAPI DNA-staining are presented here.

Forest type classification. TWINSPAN identified three forest types characterized by the following dominant species: 1) *F. americana*/*Pinus strobus* L./*Acer saccharum* Marsh./*Prunus serotina* Ehrh. (19 of the 30 plots were NEG); 2) *A. saccharum*/*F. americana*/*A. rubrum* L./*Fagus grandifolia* Ehrh. (14 of the 15 plots were NEG); and 3) *F. pennsylvanica*/*A. saccharinum* L./*A. saccharum*/*Carya cordiformis* (Wang.) Koch (two of the five plots were NEG). These will be referred to as the white ash, sugar maple, and green ash forest types, respectively.

Species composition. The species composition of the living overstory of POS and NEG plots is compared in Table 1. *F. americana* and *F. pennsylvanica* dominated and had similar importance values for both disease classes within the forest type dominated by each species, respectively. In the sugar maple forest type, *F. americana* dominated the POS plot but not the NEG plots. Species ranks in the sapling/shrub layer varied between disease classes and among forest types (Table 2). Except in the white ash forest type, POS plots had greater total densities and basal areas than NEG plots. In the white ash forest type, the density of dead trees differed significantly between POS and NEG plots ($P < 0.05$, by nested ANOVA) (Table 3). The dominant live species of each forest type also dominated the importance values of dead trees. However, the second ranked dead species varied between disease classes and among forest types. In the white ash forest type, dead *F. americana* contributed more basal area and density in POS plots than in NEG plots.

Vertical structure. Across all forest types, there was minimal *Fraxinus* spp. mortality in the upper crown classes in NEG plots (Fig. 1). Mortality of *Fraxinus* spp. in POS plots occurred in the upper crown classes only in the white ash forest type (Fig. 1A). This mortality was restricted to the lower crown classes in the other forest types (Fig. 1B and C). The crown class contribution of live *Fraxinus* spp. is similar in POS and NEG plots in the white ash and green ash forest types. In the white ash forest type, POS plots had a nearly uniform distribution of dead *F. americana* across crown classes, whereas live *F. americana* were concentrated in the upper crown classes (Fig. 2). Mortality of *F. americana* in NEG plots was restricted to the lower crown classes. Distribution of live *F. americana* was similar in NEG and POS plots. In the sugar maple forest type, the POS plot had dead *F. americana* only in the suppressed crown class (Table 3), but live *F. americana* occurred in all crown classes. Dead *F. americana* in NEG plots were uniformly distributed in the lower three crown classes but were absent from the dominant crown class. However, live *F. americana* basal area was concentrated in the upper two crown classes. In the green ash forest type (Fig. 2C), most dead *F. pennsylvanica* in both POS and NEG plots occurred in the suppressed crown class. Most live *F. pennsylvanica* in POS plots occurred in the upper two crown classes, whereas NEG plots had more *F. pennsylvanica* in the codominant class and nearly equal proportions in the three remaining crown classes.

Disease incidence related to environmental variables. Chi-square statistics (or Fisher exact test where appropriate) were calculated by forest type for the occurrence of each species in each stratum against the presence or absence of yellows. These statistics were calculated initially with the data separated by forest type, but because no significant relationships occurred, the data were grouped. Positive associations (in decreasing levels of significance from $P < 0.001$ to 0.09) were detected between AshY and the occurrence of *Geranium* spp., *Solidago* spp., *Berberis vulgaris* L., *Eupatorium* spp., *Parthenocissus quinquefolia* (L.) Planch., *Alliaria petiolata* (Bieb.) Cav. & Grande, and *Celastrus* spp. in the understory. Negative associations (in decreasing levels of significance from $P < 0.001$ to 0.12) were detected between AshY and *Trillium* spp., *Caulophyllum thalictroides* (L.) Michx., *Maianthemum canadense* Desf., and *Streptopus* spp. in the understory. A significant ($P < 0.05$) negative relationship was detected between AshY and the the occurrence of the sugar maple forest type.

Analysis to evaluate AshY incidence in relation to plot exposure showed a significant ($P < 0.001$) positive relationship between AshY and exposed plots but no significant relationship of the disease to plot position on the slope.

Discriminant analysis using site characteristics did not adequately separate POS and NEG plots. Fifteen of 50 plots (30%) were misclassified when stand characteristics were used. Specifically, five of 27 NEG plots (19%) were misclassified as POS and 10 of 23 POS plots (44%) were misclassified as NEG. Thus, discrimination of MLO by stand characteristics is less accurate in POS than in NEG plots.

DISCUSSION

Ash yellows apparently is related to some combination of site and/or stand conditions and is thus not a simple host-pathogen interaction. That most past studies were conducted in plots of sapling and pole-size trees typically in old-field settings (6,14,26) suggests that AshY is strongly associated with specific stand conditions. Results from the present

Table 2. Comparison of sapling/shrub species by forest type between DAPI-positive and DAPI-negative stands

Forest type Species[a]	DAPI-positive			DAPI-negative		
	Density[b]	BA[c]	IV[d]	Density	BA	IV
White ash						
Acer saccharum Marsh.	856	0.5	43.0	109	0.1	5.3
Prunus serotina Ehrh.	550	0.2	23.3	145	0.1	5.9
Fraxinus americana L.	166	0.1	7.6	564	0.3	19.7
Lindera benzoin (L.) Blume	163	<0.1	5.5	655	0.2	17.5
Cornus foemina Mill. spp. *racemosa* (Lam.) J. Wilson	113	0.1	4.8	0	0	0
Prunus virginiana L.	113	<0.1	3.8	18	<0.1	0.6
Acer rubrum L.	63	0.1	3.7	0	0	0
Hamamelis virginiana L.	50	<0.1	3.3	0	0	0
Cornus amomum Mill.	0	0	0	1,136	0.2	25.1
Fraxinus pennsylvanica Marsh.	0	0	0	341	0.3	16.1
Ulmus americana L.	0	0	0	114	<0.1	5.4
Other ($n = 11$)	113	0.1	5.2	73	0.1	2.6
Total	2,187	1.1	100.2	3,155	1.4	98.2
Sugar maple						
Acer saccharum	3,200	1.3	85.9	614	0.4	47.5
Hamamelis virginiana	400	0.1	7.1	71	<0.1	4.1
Ostrya virginiana (Mill.) Koch	200	0.1	6.9	114	<0.1	6.2
Acer pensylvanicum L.	0	0	0	171	0.1	11.7
Betula alleghaniensis Britt.	0	0	0	43	<0.1	2.8
Carpinus caroliniana Walt.	0	0	0	71	0.1	7.6
Fagus grandifolia Ehrh.	0	0	0	314	0.1	16.4
Other ($n = 4$)	0	0	0	72	0.1	3.7
Total	3,800	1.5	99.9	1,470	0.8	100.1
Green ash						
Fraxinus pennsylvanica	800	0.8	32.9	400	0.1	23.7
Lindera benzoin	867	0.3	20.9	0	0	0
Viburnum recognitum Fern.	667	0.2	16.2	0	0	0
Sambucus canadensis L.	533	0.2	14.6	0	0	0
Acer saccharinum L.	200	0.3	11.5	200	0.3	27.1
Acer saccharum	67	<0.1	1.3	200	0.2	18.7
Amelanchier spp.	0	0	0	200	0.2	17.4
Viburnum lentago L.	0	0	0	300	<0.1	13.2
Other ($n = 2$)	134	0.1	2.7	0	0.0	0.0
Total	3,268	1.8	100.1	1,300	0.8	100.1

[a] Nomenclature according to Mitchell (17).
[b] Number of individuals·ha^{-1}.
[c] Basal area = $m^2 \cdot ha^{-1}$, measured at 1.37 m aboveground.
[d] Importance value = (relative basal area + relative density)/2.

study support this contention, specifically: 1) the different species composition and structure between MLO-affected and unaffected plots in the different forest types, 2) the different vertical distributions of live and dead *F. americana* and *F. pennsylvanica* in MLO-affected and unaffected plots, 3) the association between AshY and the presence (or absence) of certain species, 4) the negative association between AshY and the occurrence of the sugar maple forest type, and 5) the association between AshY and stand exposure.

The similarity in live species composition and stand structure between MLO-affected and unaffected forests dominated by *F. americana* indicates that AshY will have only a moderate impact on the future structure and composition of this forest type; this assumes that AshY is stable in these stands. Species composition of live trees differs from that of dead trees and involves different species, particularly in the white ash forest type (Tables 1 and 3). Thus, present species composition may be the result of longer infection periods and selective mortality associated with AshY.

The potential for shrub species as indicators of AshY infection in forest stands should be better evaluated. Shrubs dominate NEG plots in the white ash forest type and POS plots in the green ash forest type (Table 2). The sapling/shrub layer of the one POS plot in the sugar maple forest type is dominated by shrubs, but the 14 NEG plots are dominated by arborescent species. Although the potential for these shrubs as indicators of AshY should be better evaluated, the association does not imply causality. Shrub associations with AshY could be related to site characteristics such as soil, stage of stand development, and past or current stresses.

The greater basal area of dead *F. americana* in the upper canopy of MLO-affected plots than in that of unaffected plots, given the similar vertical distribution of live individuals (Figs. 1 and 2), suggests that mortality may be related to canopy position. Upper canopy trees, because of their position or growth characteristics, may be subjected to different stresses or susceptibilities to infection than lower canopy trees.

Differences in species composition between POS and NEG plots in the sugar maple forest type (Table 1) may be due to a small sample size. However, all separation by disease class and forest type was done objectively, after plots were sampled. The infrequent detection of MLOs in this forest type suggests a negative association between AshY and one or more characteristics of the sugar maple forest type.

Dead trees in the green ash forest type, in both MLO-affected and unaffected plots, were predominantly *F. pennsylvanica* (Table 3). However, mortality of all species was low in this forest type (Table 3). Mortality of *F. pennsylvanica* was restricted to the suppressed crown class in NEG stands and predominantly to lower canopy positions in POS plots (Fig. 2C). Ash yellows apparently did not influence mortality in the plots studied in this forest type. Moreover, no stand-level response to AshY is expected because Ferris et al (9) found that *F. pennsylvanica* was less affected than *F. americana* by MLO infection.

Discriminant analyses indicated that stand level variables are, by themselves, inadequate to predict the presence of MLOs in these plots. However, unaffected plots were generally well described by the stand level variables. This suggests basal area and density are less variable in unaffected plots than in MLO-affected plots. Perhaps these plots, affected for varying time periods, are showing a time-dependent response.

Chi-square tests identified relationships between some characteristics of landscape pattern and MLO infection of ash. Understory species (e.g., *Lonicera, Solidago, B. vulgaris, Eupatorium*) that were positively associated with the occurrence of AshY are also characteristic of high light and, thus, exposed environments. Negatively associated vegetation (e.g., *Fagus grandifolia, Trillium, C. thalictroides, M. canadense*) are characteristic of more mature, shaded forest stands (3,10). The highly significant positive relationship between exposure and MLO detection is in accord with the relationship between understory vegetation and MLO detection.

The positive association of AshY with stand exposure suggests several possible explanations for disease epidemiology. Exposure may provide: 1) a habitat for a possible alternative plant host for MLOs that cause AshY, e.g., *Solidago* spp. (8); 2) a habitat for an insect vector of MLOs (1,12,15); 3) a biological corridor that spatially connects a susceptible host with a vector source (27); or 4) a stressful environment for dominant *F. americana*. Also, exposed stands may have a common, but heretofore unmeasured, variable that is related to the incidence of AshY. None of the above possibilities are mutually exclusive.

If AshY incidence depends on stand exposure, then edge forests may be most affected. The recent coalescence of forest stands in central New York and throughout the Northeast (18) may then reduce the occurrence of AshY in future dec-

Table 3. Comparison of overstory species (dead trees only) by forest type between DAPI-positive and DAPI-negative stands

Forest type Species[a]	DAPI-positive Density[b]	BA[c]	IV[d]	DAPI-negative Density	BA	IV
White ash						
Fraxinus americana L.	168	2.3	67.5	87	0.7	45.2
Prunus serotina Ehrh.	30	0.2	9.2	12	0.1	6.2
Quercus bicolor Willd.	14	0.2	5.8	0	0	0
Pinus strobus L.	5	0.1	3.0	12	0.2	8.7
Pinus sylvestris L.	4	0.1	2.9	0	0	0
Robinia pseudoacacia L.	6	0.1	2.9	0	0	0
Ulmus rubra Muhl.	2	0.1	2.4	0	0	0
Ulmus americana L.	5	0.1	1.9	12	0.2	9.0
Acer rubrum L.	0	0	0	6	0.1	5.8
Crataegus spp.	0	0	0	32	0.2	14.4
Juglans nigra L.	0	0	0	8	0.1	6.4
Other ($n = 5$)	10	0.2	4.4	8	0.1	4.4
Total	244	3.2	100.0	177	1.7	100.1
Sugar maple						
Acer saccharum Marsh.	44	11.4	50.7	25	0.5	41.2
Acer rubrum	67	3.6	33.0	2	<0.1	1.6
Prunus serotina	22	0.4	8.5	2	0.1	6.0
Fraxinus americana	22	0.2	7.8	11	0.2	19.0
Ostrya virginiana (Mill.) Koch	0	0	0	2	<0.1	2.0
Pinus strobus	0	0	0	5	0.1	7.7
Quercus rubra L.	0	0	0	6	0.1	8.8
Other ($n = 2$)	0	0	0	7	0.2	13.7
Total	155	15.6	100.0	59	1.2	100.0
Green ash						
Fraxinus pennsylvanica Marsh.	148	0.7	92.9	122	0.5	84.6
Ulmus americana	7	0.1	7.2	0	0	0
Amelanchier spp.	0	0	0	11	0.1	9.4
Other ($n = 1$)	0	0	0	11	<0.1	5.9
Total	155	0.8	100.1	144	0.6	99.9

[a] Nomenclature according to Mitchell (17).
[b] Number of individuals·ha^{-1}.
[c] Basal area = m^2·ha^{-1}, measured at 1.37 m aboveground.
[d] Importance value = (relative basal area + relative density)/2.

ades. In the present study, exposure is not an indication of whether a plot is on the forest edge, but rather is a qualitative assessment of landscape heterogeneity. Although homogeneity may facilitate disturbance because of uniformity of conditions, heterogeneity, as in the present situation of forest fragmentation, also may increase the amount of disturbance (21).

Land abandonment and reforestation have increased the prominence of *F. americana* since the 1930s. Although *F. americana* is a consistent component of numerous forest associations (10), it is not historically a dominant component of eastern deciduous forests (5,20). The proposed role of *F. americana* in presettlement eastern forests, regenerating from one disturbed area to another (13), suggests it is able to reseed and dominate many of the large areas made available by the recent increase in land abandonment (18,34). Therefore, perhaps the increased incidence of ash decline (6) is a result of the increased occurrence of *F. americana*, specifically a more contiguous host population.

During forest development after a major disturbance, forest stands undergo a stressful period of stem exclusion, or self-thinning (19). Given that many forest stands in the northeastern United States are even-aged stands originating within the last 60 yr, and that *F. americana* is a frequent dominant in old-field originated forests (7,18,34), stress associated with stem exclusion could be partially responsible for the intensification of *F. americana* mortality observed in recent decades (6). Although many of these forest stands have similar age distributions (18), the selectivity of AshY for a specific age, or the environmental conditions associated with a specific age structure, is unknown. The lower frequency of MLO infection in forests dominated by sugar maple, a characteristically dominant species in mature eastern forests, suggests that mortality due to AshY may facilitate the transition of a forest from the stem exclusion stage to that stage of forest development when late successional species begin to express dominance, or the stand reinitiation stage (19). This transition hypothesis is supported by the greater importance of *A. saccharum* in the understory of POS plots than in NEG plots in the white ash forest type.

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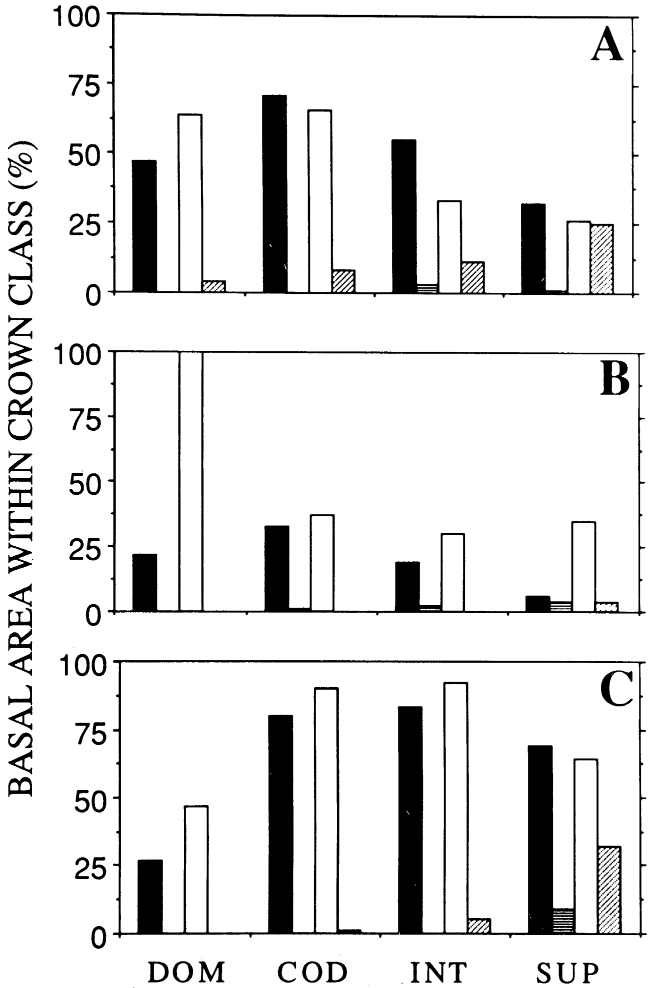

Fig. 1. Proportion of basal area within each crown class and disease class contributed by live and dead *Fraxinus* spp. in the **(A)** white ash, **(B)** sugar maple, and **(C)** green ash forest types. Solid bars represent live, and horizontally hatched bars dead, *Fraxinus* spp. in plots that tested negative for MLOs; open bars represent live, and diagonally hatched bars dead, *Fraxinus* spp. in plots that tested positive for MLOs. DOM = dominant, COD = codominant, INT = intermediate, SUP = suppressed.

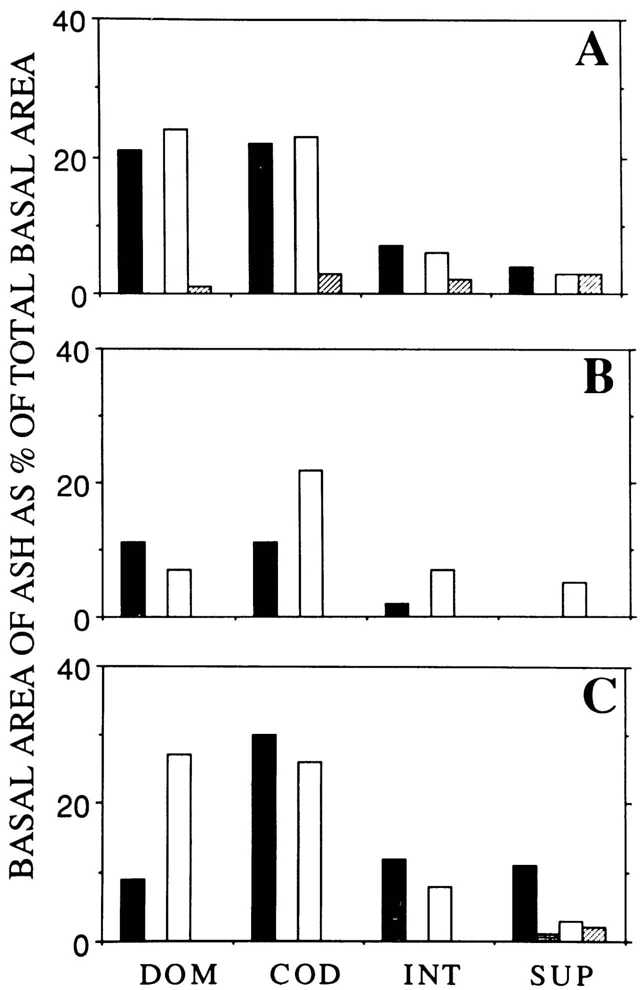

Fig. 2. Basal area of live and dead *Fraxinus* spp. as percentages of total basal area in each disease class in the **(A)** white ash, **(B)** sugar maple, and **(C)** green ash forest types. Solid bars represent live, and horizontally hatched bars dead, *Fraxinus* spp. in plots that tested negative for MLOs; open bars represent live, and diagonally hatched bars dead, *Fraxinus* spp. in plots that tested positive for MLOs. DOM = dominant, COD = codominant, INT = intermediate, SUP = suppressed.

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