

TWENTY-YEAR WOODY VEGETATION CHANGES
IN NORTHEASTERN ILLINOIS UPLAND FORESTS

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Marlin Bowles, Michael Jones, Jenny McBride, Tim Bell, & Christopher Dunn
The Morton Arboretum, Lisle, IL

Summary

Conservationists are concerned that forest fragmentation and loss of natural fire processes are allowing an increase in shade-tolerant fire-intolerant maples and causing decline of fire-adapted oaks and forest biodiversity. In 1997-98, we tested whether such changes are occurring in upland forests of the Chicago region of northeastern Illinois. To do so, we resampled trees and shrubs, aged trees, and measured canopy cover in 28 old growth or old second growth forest stands originally studied by the Illinois Natural Areas Inventory (INAI) in 1976.

The 28 stands were classified into maple ($n = 10$), red oak ($n = 9$), and white oak ($n = 9$) dominated stand types. Maple stands had greater % canopy cover and lower shrub layer species richness and density than oak stands. Maple stem densities and basal area also increased over time in all stands, although maples were present only in smaller size-classes in white oak stands. Substantial declines occurred across all stand types for density and basal area of large cohorts of mid size-class oaks, and for density and species richness of shrub layer vegetation. Ages of these oak cohorts indicate they originated in the mid-1800's, probably soon after European settlement reduced fire frequencies; however old-growth canopy oaks and maples are of presettlement age. Causes of oak mortality and shrub decline, even in stands with few maples, appear to be increasing shade from canopy closure associated with oak forest development and maturation, maple invasion, and a shift from wide-scale disturbance to canopy gap-dynamics in old-growth stands. Over-browsing by white-tail deer was apparently contributed to loss of shrub layer species on some sites.

These changes indicate that woody vegetation structural and compositional diversity have declined in maple and oak stands in the past 20 years. This decline also may be more advanced in maple stands and is apparently linked to changes in forest structure that began when post-settlement fire protection allowed oak regeneration in formerly open stands. Because these stands have linkage with pre-settlement conditions, they provide potential for restoring former structure and biodiversity. A high management priority should be to prevent further decline in oak stands by restoring natural disturbance processes and stand dynamics. Research is needed to determine if canopy-level disturbance is needed to maintain openings that will allow maintenance of shrub layer species and oak regeneration in these forests. Fire appears to be the principal tool, but it may have positive and negative effects without supplemental control of alien species and fire-resistant vegetation.

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INTRODUCTION AND PROBLEM

Few published quantitative data are available on the structural composition of upland forests of the Chicago region of northeastern Illinois and temporal change in these forests. Replacement of shade-intolerant fire-resistant oak (*Quercus*) species by the shade-tolerant fire-intolerant sugar maple (*Acer saccharum*) is a well known process in Midwestern forests (McIntosh 1957, Schlesinger 1976, Miceli *et al.* 1977, Pallardy *et al.* 1991, Roovers & Shifley 1997). This successional change is often attributed to fire suppression (Larsen 1953, Curtis 1959, Lorimer 1985, Abrams 1992), which is also thought to contribute to loss of biodiversity through decline of understory plants (McIntosh 1957, Curtis 1959, Wilhelm 1991, Bowles *et al.* 2000). Oak forest maturation and canopy closure also can contribute to failed oak reproduction and losses of lower and mid size-class oaks, and lower tree species diversity (Curtis, 1959, Christensen 1977, Lorimer 1984, McGee 1986). Change in woody understory composition and structure is also related to browsing by white-tailed deer (Anderson 1994, Strole & Anderson 1992) and invasion by the alien buckthorns *Rhamnus cathartica* and *R. frangula* (Apfelbaum & Haney 1991).

We determined whether changes that may be related to these processes are occurring in 28 maple- or oak-dominated forest stands located at 23 sites in the Chicago region of northeastern Illinois. These stands were identified and sampled by the Illinois Natural Areas Inventory (INAI) in 1976, and found to have grade A (old growth) or grade B (old second growth) stand structure (*sensu* White & Madany 1978). Our objectives were to assess twenty-year changes in woody vegetation composition and structure in these stands by analyzing changes in tree size-class distribution and basal area, and in shrub layer density and species richness. We also supplemented these data by quantifying canopy cover in relation to stand types and by aging dominant tree species from increment cores. These findings should help conservationists understand how to develop management and restoration objectives for maintaining biodiversity and representative natural vegetation types.

STUDY AREAS

The INAI classified the 28 stands into 14 dry-mesic upland sites, 12 mesic upland sites, and two flatwoods (Table 1). Most sites are located on fine-textured glacial tills in the Morainal Natural Division or the Grand Prairie Natural Division; one site (Edgebrook Flatwoods) is on lake plain sediment in the Lake Plain Natural Division (Figure 1). Dry-mesic sites are well drained, mesic sites are moderately well drained, and flatwoods are seasonally flooded due to an impermeable soil layer (White & Madany 1978). Sites classified as dry-mesic were *Quercus alba*-*Q. rubra*-*Q. velutina* dominated, mesic sites were *Acer saccharum*-*Q. rubra* dominated, and flatwoods were *Q. rubra*-*Q. palustris*-*A. rubrum* dominated at Edgebrook, and *Q. bicolor*-*Q. alba*-*Q. ellipsoidalis*¹ dominated at Ryerson (unpublished INAI data). In addition, most mesic sites are in landscape positions such as ravines or east of rivers that would have

¹Nomenclature follows Swink & Wilhelm (1994), in which *Q. ellipsoidalis* = *Q. coccinea*.

provided for greater fire protection and survivorship of *A. saccharum* than dry-mesic sites (Leitner *et al.*, 1991, Bowles *et al.* 1994).

METHODS

Historic data collection

The INAI sampled each forest stand in 1976 with nested plots at 20 sampling points equally spaced along randomly located transect lines (Table 2). These transects were not permanent, but were marked on aerial photo overlays. Overstory trees were sampled for basal area (BA) with a 3-BA factor metric wedge prism, and for density by 1 dm size-classes in circular 0.025 hectare (radius = 8.92 m) plots. Understory trees and shrubs >1m high but <1 dm diameter were sampled in ten circular 0.001 hectare (radius = 1.78 m) plots at alternating sampling points. The 0.025 hectare plot sampling methods limit analysis because data were tallied by size-class rather than by actual diameter measures per plot.

Data collection in 1997

All sampling transects were relocated as precisely as possible and marked with conduit stakes. As in 1976, tree species basal area (BA) was sampled from 20 points in each stand using a 3 BAF metric wedge prism (Table 2). Tree diameter at 1.4 m was measured in 20 circular 0.025 ha plots, while shrub and sapling densities were recorded from 20 nested 0.001 ha circular plots. Because of problematic separation of *Quercus bicolor* and *Q. macrocarpa* (which hybridize), and juvenile *Fraxinus americana* and *F. pennsylvanica*, these species were combined for data analysis in some sites. To age the most frequently sampled tree species in each stand, we extracted an increment core, at 1.4 m above ground level from at least one individual representing each size-class in which the species was sampled. The number of useful cores from larger trees was limited by failure to hit the tree pith, and by heart rot in many *Q. rubra*. This reduced total sample size and prevented precise determination of individual stand age structures. The canopy cover over each sampling plot was photographed on color transparency film with a 35mm camera mounted with a 180° fish-eye lens. The camera was held with its lens axis positioned vertically at 2.0 m above ground level.

Data analysis

To compare relationships among stands we first calculated BA and dominance from the 1997 wedge prism sampling data for each tree species, where $BA = [(no. \text{ of trees tallied}/no. \text{ points}) \times 3]$, and dominance is relative BA. Because the probability of prism-sampling each tree is proportional to its diameter, small trees are most likely sampled when close to the observer and data are biased toward larger size-class trees. Such data thus reduce the importance of smaller size-class species for ordination and classification, and may include large trees that occur in different habitats beyond the range of fixed-size plots. We classified and ordinated stands using the BA dominance data on PCORD software program (McCune & Mefford 1999). The data were first modified by eliminating all hybrid

Quercus macrocarpa-bicolor data because they were not consistent among stands. The resulting matrix was clustered using Ward's linkage method and a relative Euclidean distance measure, and ordinated using the Bray-Curtis technique with a Euclidean distance measure and the Variance-Regression endpoint selection. This analysis produced three stand types dominated by either *Acer saccharum*, *Q. rubra*, or *Q. alba*, which were used to compare data in subsequent analyses.

Twenty-year changes in woody vegetation structure within stand cluster groups were determined by comparing size-class distribution patterns and stem numbers sampled by 1-dm size-classes in the .025 ha tree plots in 1976 and 1997. For example, an increase in maples would be indicated by increasing size-class numbers in a negative exponential size-class distribution, while oak decline would be indicated by modal distribution patterns with lower size-class numbers corresponding to years of mortality and failed reproduction (e.g., Johnson & Bell 1975, Lorimer & Krug 1983). Two statistical procedures were used to assess temporal change and stand differences. A two-factor ANOVA was used to test for significant differences in mean size-class stem density between years (1976 vs 1997) and among stand type, and chi-square analysis was used to determine whether significant shifts in stem numbers occurred among size-classes over time.

To establish dominant tree cohort chronologies, ages of tree species based on tree ring counts were regressed against corresponding tree diameters (including bark) at 1.4m in height, using linear regression and power functions. Essentially no oaks were available for aging in the 1-<2 dm size-class. To compensate for this absence, one age-diameter correlate was randomly selected from the inner 5 cm core length (= up to 10 cm diameter) of each core and added to the data set. Bark width was unavailable for these data, so only values of <10 cm diameter were used because their bark thickness would be negligible within this diameter range. Species linear regression slopes were tested for differences among stand types with analysis of co-variance (ANCOVA) and a Fisher PLSD post hoc test. Because tree growth rates differed over time, non-linear age-diameter regressions had higher correlations than linear regressions, and power functions (Lorimer & Frelich 1998) were used to predict tree age at core height. For maple, red and white oak, ash, and basswood, linear regression slopes differed only among stands for maple in white oak stands (stand x maple dbh $F = 5.899$, $P = .0037$). Age-diameter power functions were determined by pooling species data across stands, while maple age was estimated exclusive of white oak stands. *Quercus macrocarpa* and *Q. bicolor* data were pooled because they had a small sample size and nearly identical linear regressions, and because their hybrids could not be clearly separated. Age-diameter power functions were also calculated for *Ulmus rubra* and *Carya ovata*, which also had small sample sizes.

Basal area was calculated for three tree species groups: maples (*Acer saccharum*, and *A. rubrum*), oaks, and all other species combined within each stand type by using size-class medians as estimates of tree diameters. Thus, BA was calculated as $BA = \text{number of stems per size-class} \times \text{size-class median}$, summed across all size-classes for each species group and stand type. Dominance was calculated as the percentage of BA in each species group or stand type. Percent change between 1976

and 1997 was calculated for each of these measures.

To analyze temporal change in shrub layer data, we partitioned species into: 1) true shrubs, 2) understory tree species that do not enter the tree canopy, and 3) tree saplings that also represent potential canopy trees. We then compared mean number of stems and species present per plot for shrubs and understory trees between 1976 and 1997 with a 2-factorial ANOVA partitioning time vs stand types. We also used 2 x 3 Chi-square contingency tables to test for proportional differences among shrubs, understory trees, and saplings in each stand type between 1976 and 1997.

Canopy cover for each plot was quantified by projecting it's corresponding canopy transparency photo through a video camera to a Delta-T Area Meter, which measured the area of canopy cover as a percent in contrast to transmitted light. A dark magenta filter was used to increase contrast and reduce color band width, and the area meter was calibrated for 66%. We tested for differences in mean percent canopy cover among maple, red oak, and white oak stands in a single factor ANOVA, using arcsine-transformed percentage values. Canopy cover values were tested for significant correlations with subcanopy oak densities.

RESULTS

Forest stand types

In 1997, 30 native tree species were prism sampled, with only red oak (*Quercus rubra*), white oak (*Q. alba*), and Maple (*Acer saccharum*) having >20% mean dominance, and other species with < .05% dominance. In 1976, 26 native trees were sampled, with nearly identical patterns of dominance (Bowles 2000). Cluster analysis and ordination of the 1997 tree dominance produced maple, red oak, or white oak stand types in which either *Acer saccharum*, *Quercus rubra*, or *Q. alba* attained greatest mean dominance (Figure 2). All but two of the stands classified by the INAI as mesic clustered as maple stands, while all but one of the original dry-mesic stands clustered as red oak or white oak stands. *Acer saccharum* had < 10% dominance in oak-dominated stands, while *Q. rubra* had < 20% dominance in white oak and maple stands, and *Q. alba* had < 20% dominance in red oak stands and < 10% dominance in maple stands. Among sub-dominant species, *Fraxinus americana* and *Tilia americana* tended to be less important in white oak stands, while *Ulmus rubra* had little variation among stand types. *Q. velutina*, *Q. macrocarpa*, and *Carya ovata* were infrequent and most abundant in white oak stands.

The Edgebrook Flatwoods stand clustered with *Q. rubra* stands due to dominance of this species at Edgebrook, and the Ryerson flatwoods stand classified with white oak stands, although *Quercus bicolor* dominance exceeded that of *Q. alba*. The Johnson's Mound dry-mesic stand classified with white oak stands, although *Ulmus rubra* and *Juglans nigra* dominance exceeded that of *Q. alba*. The Busse Woods dry-mesic stand clustered with white oak stands, which was problematic because it clustered with red oak stands in a classification of 1976 prism-data (Bowles *et al.* 2000). This probably occurred for multiple reasons. This large tract was difficult to survey and precisely resample along the original transect location. The transects also crossed irregular topography having both flatwoods dominated by *Q. macrocarpa-bicolor* hybrids, and an adjacent upland habitat gradient dominated by *Q. rubra* and by *Q. alba*. Prism sampling also included trees from adjacent habitats beyond the range of tree and shrub plots. We retained classification of this stand with red oaks to avoid confounding analysis of tree and shrub layer data between 1976 and 1997.

Age-diameter relationships

Power function estimates of the ages of the most common tree species (Figure 3) indicate that, excluding *Tilia americana*, forest-grown trees exceeding 0.75 m diameter are of pre-settlement (pre-1820) origin, and individuals reaching 1 m originated prior to 1700 (Table 3). More precise age estimates would include the number of years required for trees to achieve tree-coring height. This is probably < 10 years for oaks (G. Ware pers. comm.), and longer for *Acer saccharum*, which can persist as a shrub-layer species for 30 years (Hett 1971, Marks & Gardescu 1998). Ages of oak genets that formerly persisted as post-fire sprouting grubs would be much older than our age-class estimates.

Stand structure and temporal change

The size-class distribution patterns of *Acer saccharum*, as well as *Tilia americana* and *Fraxinus americana*, resembled expected negative exponential curves in all stands (Figure 4). Although maple size-class density did not change significantly over time, its size-class distribution shifted within stands, primarily due to a > 50% increase in stem numbers in the smallest size-class of all stand types in 1997 (Figure 4). In mid size-classes, maple stem numbers dropped slightly in maple stands and had little change in oak stands, although they appeared in larger size-classes in red oak stands, from which they were essentially absent in 1976. Neither *T. americana* nor *F. americana* stem densities changed over time or differed among stands (Table 4). However, in smaller size classes, ash declined in maple and red oak stands and increased in white oak stands, while basswood declined in maple stands and increased in red and white oak stands (Figure 4).

As expected, size-class distribution patterns of oaks were modal for lower mid size-classes and were skewed toward higher size classes, with nearly identical patterns in red oak and white oak stands (Figure 5). *Quercus rubra* and *Q. alba* stem densities also differed among stand types and declined about 50% over time, with significant 1-dm shifts in size-class distributions for oak stands (Table 4). *Q. alba* also declined slightly in mid size-classes in maple stands. *Q. macrocarpa/bicolor* stem densities also differed among stands and declined over time in white oak stands (Figure 5). Although oak stem numbers declined in lower and mid size-classes in all stands, they had either gains or no losses in larger size-classes.

The large cohorts of red and white oaks represented by mid-size-class peaks appear to have originated in the mid-1800s, or earlier, and lost about half their individuals as the cohort peaks shifted to one larger size-class between 1976-97 (Figure 5). Larger oaks dating to the mid 1700's are present in old growth stands, while the oldest maples may date to the late 1700's (Figure 4).

Basal area and temporal change

Basal area of maples was highest in maple stands, with about 14m²/ha and almost 50% dominance, as opposed to < 4m²/ha BA and 15% or lower dominance in most oak stands (Table 5). Oaks had < 10m²/ha BA and < 30% dominance in maple stands, as opposed to >20m²/ha BA and 70-80% dominance in oak stands. Other species, primarily smaller size-class *Ulmus americana* and *U. rubra*, and larger *Tilia americana*, and *Fraxinus* species, were equal in abundance to oaks in maple stands, but were less important in oak stands. The primary changes across all stands were increases in maple BA and dominance and declines in oak BA and dominance. As a result of these opposing changes, maples had more substantial increases in dominance than in basal area. For example, maples increased 6.9% in BA and 17.7% in dominance in maple stands, 100% BA and 225% dominance in red oak stands, and 29% BA and 38% dominance in white oak stands. Oaks decreased >10% in BA, but <10% in dominance in all stands. Grade A oak-dominated stands also had 22.3% of their basal in size classes above 60 cm and 5.2% above 80 cm, while grade B stands had 17% basal

area above 60 cm, and none above 80 cm.

The size-class distribution patterns of BA shifts also differed between maples and oaks and among stand types (Figure 6). In maple stands, maples increased in BA in lower and upper size-classes and lost BA in mid size-classes. Maples increased in BA in all but the largest size-class in red oak stands, and increased primarily in the smallest size-class in white oak stands. In contrast, oaks lost BA in smaller size-classes and gained BA in larger size-classes in all stands.

Shrub layer composition and temporal change

Shrub layer composition and structure differed between maple and oak stands. In 1976, *Acer saccharum* was the dominant sapling in maple and red oak stands, while *Fraxinus americana* and *Prunus serotina* were dominant saplings in white oak stands. *Carpinus caroliniana* and *Ostrya virginiana* were the most abundant understory trees in maple stands, while there was a greater abundance of *Crataegus* species in white oak stands. The most abundant shrubs in 1997 included *Hamamelis virginiana* and *Viburnum acerifolium* in maple stands, *Prunus virginiana* in red oak stands, and *Viburnum rafinesquianum* and *Cornus racemosa* in red and white oak stands.

Stem numbers of shrubs and understory trees, and their species richness, declined significantly over time, with the greatest change in white oak stands, and less decline in the already depauperate maple stands (Figure 7). An inverse relationship in sapling, understory tree, and true shrub densities also occurred among stand types, and this structure changed over time over time. Maple stands had higher sapling densities but lower species richness and lower densities of shrubs and understory trees than white oak stands, while red oak stands were intermediate (Figure 8). Important structural shifts also occurred within stand types over time. In 1976, shrub species dominated oak stand shrub layers; but, by 1997, tree saplings were most important in red oak stands and had increased in importance in white oak stands (Figure 8). All of the most abundant shrub species had declined in all stands by 1997, with losses of about 1000 stems/ha in *Viburnum acerifolium* and *V. rafinesquianum* (Figure 9).

Canopy cover

The range in percent canopy cover measured by canopy photographs was narrow, extending from 70% in white and red oak stands to > 71% in maple stands (Figure 10). However, percent cover was significantly higher in maple than in oak stands, and was significantly negatively correlated with 1997 densities of oaks in the 1-< 2 cm and 2-< 3 cm size-classes (Figure 10). This difference in canopy cover also corresponded to differences in shrub-layer species richness among stand types (Figure 5).

DISCUSSION

Differences among stand types

Dry-mesic and mesic northeastern Illinois forests differ along a tree species gradient, in which either *Acer saccharum*, *Quercus rubra*, or *Q. alba* are dominant overstory species. This species gradient is similar to the upland forest continuum in Wisconsin (Curtis & McIntosh 1951) and elsewhere in Illinois, where dominant species tend to occupy narrow portions of the environmental gradient (Adams & Anderson 1980). In northeastern Illinois, *Q. alba* also occurs with *Q. velutina* on dry sites underlain by gravel, while *Acer saccharum* also extends into wet-mesic sites along streams with greater abundance of *Ulmus rubra* *U. americana* (formerly), *Celtis occidentalis* and *Q. macrocarpa* (Madany & White 1976).

The inverse relationship between sapling and shrub densities across stand types may be affected by many factors, but the strong negative correspondence of shrub layer stem densities and species richness with differences in canopy cover suggests that canopy light levels are very important. The negative correlation between canopy cover and oak sapling densities also supports this hypothesis, as oaks are strongly light dependent. We measured an extremely small but significant difference in percent canopy cover between maple (> 71%) and oak forests (70%). Whether or not > 71% represents a threshold for negatively affecting shrublayer vegetation is not clear. However, Pubanz & Lorimer (1992) and Lorimer *et al.* (1994) found that a reduction from about 95% to 85% canopy cover, measured as a % of total Photosynthetically Active Radiation (PAR), significantly enhanced oak seedling survivorship in oak forests. This indicates that change in a narrow range of canopy cover can significantly affect shade-intolerant understory vegetation. Our measures used different instrumentation with a fixed calibration point, and may not be linear nor directly comparable to measures of PAR.

Change in maples and maple stands

Acer saccharum has increased in dominance in all stand types since 1976, and the proportions of these increases have been size-class dependent and have varied among stand types. The most apparent changes include a 50% or more increase in the 1-<2 dm size-class across all stand types, and increases in mid- to upper-size-classes in maple and red oak stands. Although these changes corresponded to small increases in BA, the maple cohorts now appear poised to gain further dominance in all stands. The large gain in 1-2 dm maples appears to have come from the relatively high number of saplings represented in the shrub layer in 1976 (Figure 8), which were primarily maples (Bowles *et al.* 2000). The much lower shrub layer sapling densities in 1997 may place a limit on further recruitment of maples (and other tree species). Despite small BA gains for oaks in upper size-classes of maple stands, their losses in mid size-classes and lack of reproduction is leading toward more complete maple dominance in maple stands. When this increasing maple dominance is coupled with the significant declines in shrub layer stems and species, maple stands appear to be shifting towards lower structural and compositional diversity.

Changes in oaks and oak stands

In contrast to maples, oaks in oak stands have decreased in stem densities, basal area, and dominance since 1976. These changes have also been size- class dependent, but with the greatest losses in low and mid size-classes, and slight gains in large size-classes. The modal size- and age- class distribution patterns for oaks are also skewed toward older age classes, indicating that the forests are of presettlement origin. However, most individuals belong to a few cohorts that originated during the early- to mid-1800s, probably soon after settlement-caused landscape fragmentation began to reduce fire frequencies. For example, oaks up to 50 cm dbh probably originated soon after settlement, trees > 60-70 cm dbh originated prior to settlement, and larger oaks appear to date back to the late 1700s. The presence of a large mid size-class cohorts also suggests that the structure of oak forests were formerly open, which would have allowed oak establishment from seedlings or from post-fire sprouts that were present as grubs or woody undergrowth (Bowles *et al.* 1994, Bowles & McBride 1998). Red oak, for example, has potential for rapid growth, which would have allowed establishment after stand-level disturbances such as fire (Curtis 1959, 1988).

Differences in cohort ages suggest that fire protection effects may have occurred at different times among stand types, or that species may have responded differently. For example, the oak cohort in maple stands, which is primarily red oak, has a broad peak, and appears to have originated between 1821-1847. In contrast, the red oak cohort in red oak stands has a more narrow peak indicating most stems originated in 1847. However, white oaks have a 1862 peak in both red oak and white oak stands. One explanation for this is that fire suppression effects may operated on a temporal gradient across stand types, with earlier protection in maple stands because of their greater landscape fire protection. However, because red oaks are capable of rapid growth, they may have responded more quickly to fire protection than white oaks. This hypothesis is further supported by similar years for white oak cohort peaks in red and white oak stand types.

A maturation-successional model for forest change

The temporal pattern of increasing maple dominance and decline of oaks fits a stand maturation model of decreased oak density, reduction of dominant trees in lower size-classes, and oak replacement by shade-tolerant maples if present in the stand (*e.g.* Christensen 1977, Abrams & Downs 1990, Oliver & Larson 1990, Abrams 1992). These changes occur because oaks are relatively shade-intolerant and fire-tolerant (Lorimer 1983, Abrams 1992). This promotes oak establishment after disturbances such as fire open canopies. Survivorship of oak seedlings and saplings is reduced as forest canopies and subcanopies close (Lorimer 1983, Lorimer 1985, Crow 1988, Crow 1992), and because of natural demographic losses within cohorts. Oak forests thus appear unstable or transitional without recurring disturbance (McCune & Cottam 1985, Abrams 1992). The decline in shrub layer species would also appear to fit the same model because many shrubs sprout after fire and are relatively shade-intolerant, declining with increasing tree basal area (Loucks & Schnur 1976). The significant decline of oaks and

shrub layer species in white oak stands has occurred without significant maple invasion. This indicates that declining biodiversity in oak stands is necessarily caused by maple invasion, but by the natural process of canopy closure of oaks.

Changing land use and forest structure

A changing land use hypothesis helps explain the changes in Chicago region forests in relation to a maturation-successional model. Midwestern oak forests were apparently shaped by dynamic fire regimes prior to settlement (Gleason 1913, McAndrews 1966, Moran 1978, 1980; Grimm 1983, 1984, Anderson 1991, Leitner et al. 1991, Bowles et al. 1994). These fire regimes declined after settlement, which accelerated in the 1830's, allowing generation of the large oak cohorts. Although fire disturbance was replaced by other types of human disturbances that continued into the early 1900s (e.g. Mendelson 1998, Nowacki & Abrams 1997), the ages of oak cohorts in these old growth stands establishes a linkage with immediate post-settlement changes. Subsequent human disturbances included occasional burning, tree cutting, and possibly grazing by sheep and cattle, and were most severe during the 1880-1925 period (Mendelson 1998). Such disturbances probably maintained more open canopies and understories than at present in second-growth stands, and when reduced would have allowed release or establishment of new oak cohorts in these stands (Lorimer 1992, Abrams 1992, Mendelson 1998). With increasing fragmentation and conversion to urban land use, the old growth stands have shifted toward an internal canopy gap-phase process characteristic of maple forests (Bray 1956, Curtis 1959), which has increased average canopy shade from oaks and maples. This change has apparently led to the mortality of large numbers of mid-size-class oaks, which are shade intolerant and vulnerable to this process (Lorimer 1981).

Deer are present throughout most of the study areas (Witham & Jones 1990). Although not precisely quantified, browsing was almost always evident, and probably contributed to reduced shrub layer species richness. Past deer browsing has decimated ground layer plants in maple stands at Busse Woods (Bowles et al. 1997a) and at Ryerson Forest Preserve (e.g. Anderson 1994, Bowles et al. 1998). Deer browsing is also known to be impacting ground layer vegetation at Thorn Creek Woods (Bowles et al. 1995, 1996). In 1997, we found that browsing had also eliminated the shrub *Viburnum rafinesquianum* from the shrub layer of transects at Thorn Creek, reducing it to ground layer sampling plots (M.L. Bowles, pers. obs.). Deer browsing also contributes to seedling oak mortality (Buckley et al. 1998), and probably has limited oak recruitment, but not loss of mid-size-class trees.

Other factors, such as disease, also could be contributing to local oak mortality. For example, oak wilt would affect primarily the red oak group, but outbreaks usually occur within stands (Menges & Loucks 1984). Root disease caused by the fungus *Armillaria* sp. is more widespread and can cause mortality of different oak species, especially when trees are stressed, possibly by shade or by fire (Kile et al. 1991).

MANAGEMENT ISSUES AND NEEDS

Implications of temporal change

Although the INAI described these forests as old growth or old second growth, their structure and canopy dynamics indicate that they differ from the more stable old growth beech-maple forests (Poulson & Platt 1996) and are similar to other central hardwood oak forests. In oak forests, most workers have found that shade-tolerant maples are most abundant in small size classes, indicating recurring reproduction, while shade-intolerant oaks are usually restricted to larger size classes, indicating lack of reproduction under canopy shade. These observations have led to almost universal conclusions that in the absence of fire, formerly more open oak forests are shifting toward canopy closure and gap-phase reproduction processes, in which shade-intolerant oaks will not reproduce in the face of increasing maple dominance (e.g. Bray 1956, Boggess 1964, Boggess & Bailey 1964, Boggess & Geis 1966, McClain & Ebinger 1968, Schlesinger 1976, Christensen 1977, Miceli *et al* 1977, Anderson & Adams 1978, Adams & Anderson 1980, McGee, 1986, Abrams & Downs 1990, Pallardy *et al.* 1991, Abrams 1992, Roovers & Shifley 1997).

Setting research objectives

Maintenance of forest biodiversity is a primary management objective for oak forests (Leach & Ross 1995). Research is needed to determine how woody species composition and structure can be managed or restored, and the effects of such management on native and alien ground layer vegetation. Because of the large amount of historic evidence for either natural or anthropogenic fire as a critical factor in development and maintenance of oak forests (Crow 1988, Lorimer 1992, Abrams 1992), prescribed fire should be a critical factor in this research, possibly replicating past fire regimes. Maple dominated stands presumably had infrequent fires, possibly only during optimum conditions, such as during drought periods. However, fire will reduced densities of maple seedlings (Bowles *et. al.* 2000)

A strategy for maintaining forest biodiversity must set clear objectives and consider multiple experimental factors and questions that address structure and composition of forest canopy, subcanopy, shrub, and ground layer vegetation. For example, at what scale do canopy gap dynamics in forest fragments maintain sufficient light levels for woody understory reproduction, and for maintenance of ground layer vegetation? Bowles & McBride (1998) found that canopy light controlled the distribution of graminoid and herbaceous vegetation in savanna, and recommended subcanopy thinning to restore savanna ground layer structure. Crow (1992) found that reduction of overstory and understory vegetation density increased survivorship and growth of *Q. rubra* seedlings relative to full canopy cover. Pubanz & Lorimer (1992) and Lorimer *et al.* (1994) showed that reducing canopy cover to 85% and removal of competing understory saplings enhanced oak seedling survivorship and growth, but suggested fire as a more natural alternative. These results from midwestern oak stands raise relevant questions for Chicago region oak forests. Can fire be used to cause sufficient change in canopy and subcanopy structure so as to affect light-levels reaching ground-layer vegetation, given that much of the

canopy shade may be from larger fire-resistant trees? Also, what is the direct impact of different fire frequencies and intensities on ground layer vegetation, and does it interact with reduced canopy cover to further enhance herbaceous responses to increased light levels?

Issues and concerns

There are important differences between presettlement fires and prescribed burns that raise several concerns. Presettlement fires may have been temporally and spatially patchy in relation to vegetation pattern, and management fires may not occur in a landscape-scale context. As a result, they may not attain the intensity of large-scale fires, and may have different effects. There are also potential damaging or conflicting effects of fire management. For example, garlic mustard may persist in fire-managed tracts (Bowles *et al.* 2000). This species is a disturbance-adapted biennial, and fires may expose seed beds that enhance its establishment and spread (Anderson *et al.* 1996). Although repeated annual burns may deplete seed banks and reduce its populations sizes, they may negatively affect other plants or animals. Shrublayer management is of particular concern because this forest structural component provides the nesting substrate for forest interior birds, and alien shrubs enhance nest predation (Whelan & Dilger 1985, 1992, Schmidt & Whelan 1999). However the frequency and intensity of fires needed to maintain shrublayer diversity while managing for herbaceous groundlayer vegetation is unknown. Finally, almost no information is available on the status of forest invertebrate species and the potential effects of fire on their populations (but, see Wolf 1990, & Newman & Wolf 1990).

Stand histories are also important in structuring species size class distributions and the overall condition of stands, and in understanding management or restoration needs. For example, the maple stand at the Ryerson Conservation Area had a large component of old-growth *Ulmus americana* that was destroyed by Dutch elm disease in the 1960's (Bowles *et al.* 1998). Elm death reduced elms to small size classes in central Illinois (Johnson & Bell 1975), and allowed increased shrub growth in Wisconsin (Dunn 1986, 1987). At Ryerson, recent elm mortality may have been more important than absence of fire in promoting establishment of the large cohorts of 1- < 2 dm size-class of maples that are now present. Thus the current structure of this stand is not necessarily directly related to fire history.

Although restoring natural processes, such as burning, would be preferable, fragmentation of forest tracts prevents fire management on a landscape basis. Alternatives may require artificial reduction of canopy cover by removal of sub-canopy trees and selective removal of larger maple saplings that would quickly fill canopy gaps created by management. Control of deer herds is apparently critical, as continued over-grazing may prevent recovery of woody and herbaceous species such as *Trillium grandiflorum* (Anderson 1994), and deer browsing can affect bird nesting habitat (DeCalesta 1994). These are difficult management decisions that should be tested by sound experimental approaches and more frequent monitoring than at 20-year intervals.

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Table 1. Community classification, quality, and size of Chicago region forest stands sampled by the INAI. Letter codes: A = old growth and B = old second growth or selectively logged, C = second growth.

Site No.	Site name	County	Dry-mesic	Mesic	Flat-woods	Size in Hectares
1)	Bloomingtondale (Meacham) Grove F. P.	DuPage Co.	B			17
2)	Busse Woods F. P.	Cook Co.	B	A		262
3)	Crabtree Farm Woods	Lake Co.	A			15
4)	Elburn F. P.	Kane Co.	B			23
5)	Glen A. Lloyd Woods Nature Preserve	Lake Co.		B		54
6)	Helm's Woods F. P.	Kane Co.	B			28
7)	Herrman's Woods	Lake Co.	A			15
8)	Johnson's Mound F. P.	Kane Co.	B	B		43
9)	Maple Grove F. P.	DuPage Co.		B		21
10)	MacArthur Woods F. P.	Lake Co.		B		157
11)	McCormick Ravine Preserve	Lake Co.	A	A		45
12)	Messenger Woods F. P.	Will Co.	B	A		68
13)	Mooseheart Ravine	Kane Co.	B			17
14)	Morton Arboretum	DuPage Co.		B		50
15)	Norris (Jones) Woods	Kane Co.	B			33
16)	Paw Paw Woods F. P.	Cook	B			55
17)	Pilcher Park	Will Co.		A		120
18)	Raccoon Grove F. P.	Will Co.	B			38
19)	River Road Woods F. P.	Lake Co.		A		8
20)	Ryerson Conservation Area	Lake Co.		B	B	133
21)	St. Francis Boy's Camp F. P.	Lake Co.	A			27
22)	Thorn Creek Woods N. P.	Will Co.	B			33
23)	Edgebrook Flatwoods	Cook Co.			C	70

Table 2. Comparison of INAI sampling methodologies and those used in the current study.

Category	INAI (1976)	Current study methods
All trees	20 prism sampling points	20 prism sampling points
Basal Area	yes	yes
Relative dominance	yes	yes
Trees (\geq 1dm dbh)	20 plots (each 0.025 ha)	20 plots (each 0.025 ha)
Frequency	no	yes
Density	no	yes
Exact diameter (dbh)	no	yes
Size class distribution	yes (1-dm size classes)	yes (1-dm size classes)
Shrubs & trees (>1m high)	10 plots (each 0.001 ha)	20 plots (each 0.001 ha)
Frequency	yes	yes
Density	yes	yes
Ground layer	none	20 plots (each 1m ²)
Frequency	no	yes
Cover	no	yes (by 1dm ² intercept)

Table 3. Predicted tree species ages in 1997 at different diameter classes basen on poter funtions. N = number of age-diameter samples. Maple age estimates exclude white oak stands; others are based on total samples. Species are ranked by the age estimate at 100 cm.

Species	N	Power funtion	R ²	Diameter in cm at 1.4m			
				25	50	75	100
<i>Tilia americana</i>	45	age = 4.0199 x diam. (.8396)	0.8857	59.97	107.32	150.84	192.05
<i>Fraxinus americana</i>	71	age = 5.662 x daim. (.8035)	0.867	75.20	131.25	181.79	229.07
<i>Acer saccharum</i>	93	age = 4.8941 x diam. (.8498)	0.8987	75.44	135.97	191.91	245.06
<i>Quercus bicolor/macrocarpa</i>	15	age = 2.8488 x diam. (.9752)	0.8976	65.76	129.27	191.96	254.13
<i>Ulmus rubra</i>	14	age = 4.157 x diam. (.892)	0.7511	73.41	136.23	195.58	252.80
<i>Quercus rubra</i>	77	age = 4.2045 x diam. (.898)	0.8746	75.69	141.06	203.01	262.85
<i>Carya ovata</i>	19	age = 10.145 x diam. (.716)	0.7625	101.66	167.00	223.25	274.31
<i>Quercus alba</i>	84	age = 4.4839 x diam. (.9114)	0.8661	84.28	158.52	229.40	298.16

Table 4. Probabilities that tree species mean size-class densities did not differ (two-factor ANOVA) between year (1976 & 1997) and among stand type, and that size-class distribution of stem numbers did not differ (Chi-square Contingency Table Analysis) between 1976 and 1997 (see Figures 4 & 5). Significance levels: * = <.05, ** = <.01, *** = <.001. *Quercus macrocarpa* and *Q. bicolor* are comined because they have comparatively low sample sizes and hybridize when they co-occur.

Species	---Mean density---		-----Size-class distribution-----		
	Year	Stand type	Maple stands	Red oak stands	White oak stands
<i>Acer saccharum</i>	0.674	0.007**	<.001***	0.004**	<.001***
<i>Tilia americana</i>	0.949	0.478	0.471	0.604	0.122
<i>Fraxinus americana</i>	0.339	0.137	<.001***	0.020*	0.028*
<i>Quercus rubra</i>	0.022*	<.001***	0.187	<.001***	0.006**
<i>Q. alba</i>	0.006**	<.001***	<.001***	0.015**	<.001***
<i>Q. macrocarpa/bicolor</i>	0.033*	<.001***	0.259	0.119	0.022*

Table 5: Temporal change in basal area (BA = m2/ha) and dominance (DOM = % of BA) of maples, oaks, and other species among 28 maple-, red oak-, and white oak-dominated Chicago region forest stands.

Species group	Measure	Maple stands			Red oak stands			White oak stands		
		1976	1997	Percent change	1976	1997	Percent change	1976	1997	Percent change
Maple	BA	13.46	14.39	+6.9	1.58	3.23	+100.4	1.06	1.37	+29.2
	DOM	40.30	47.44	+17.7	4.66	15.18	+225.7	3.5	4.83	+38.0
Oak	BA	9.96	8.24	-17.3	25.63	21.28	-17.0	24.90	21.83	-12.3
	DOM	29.82	27.17	-8.9	75.52	68.18	-9.7	82.26	76.92	-6.5
Others	BA	9.98	7.70	-22.8	6.73	6.70	-.01	4.31	5.18	+20.2
	DOM	29.88	25.39	-15.0	19.82	16.64	-16.0	14.24	18.25	+28.2
Total	BA	33.40	30.33	-9.2	33.94	31.21	-8.0	30.27	28.38	-4.5
	DOM	100.0	100.0	0.0	100.0	100.0	0.0	100.0	100.0	0.0

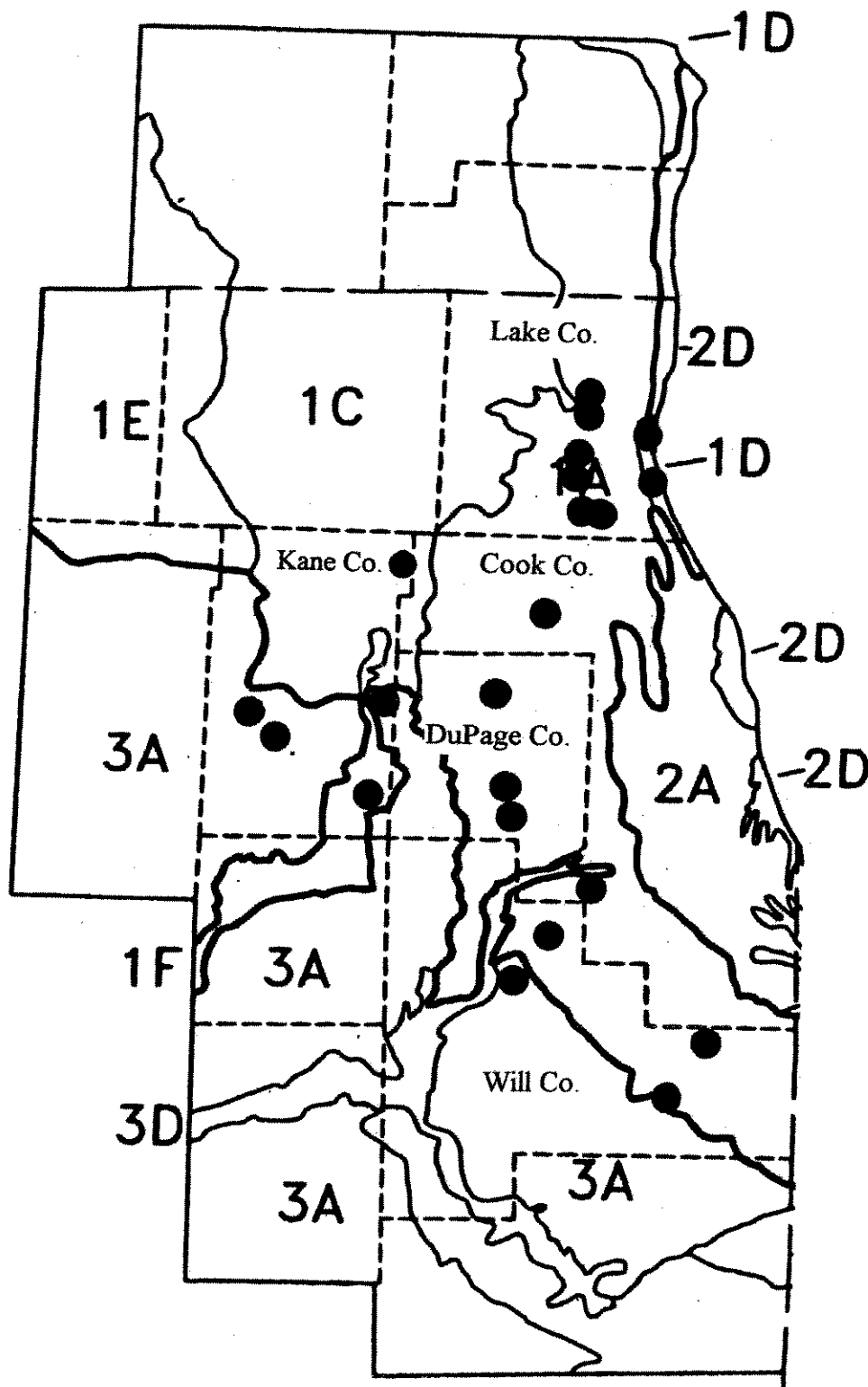


Figure 1. Study site locations in Natural Divisions of the Chicago Region (Swink & Wilhelm 1994).

MORAINAL NATURAL DIVISION

- 1A - Western Morainal Section
- 1B - Eastern Morainal Section
- 1C - Kettle Moraine Section
- 1D - Racine Till Plain Section
- 1E - Winnebago Drift Section
- 1F - Fox River Bluff Section

LAKE PLAIN NATURAL DIVISION

- 2A - Chicago Lake Plain Section
- 2D - Illinois Dunes Section

GRAND PRAIRIE NATURAL DIVISION

- 3A - Grand Prairie Section
- 3D - Bedrock Valley Section

Bray-Curtis Forest Stand Ordination

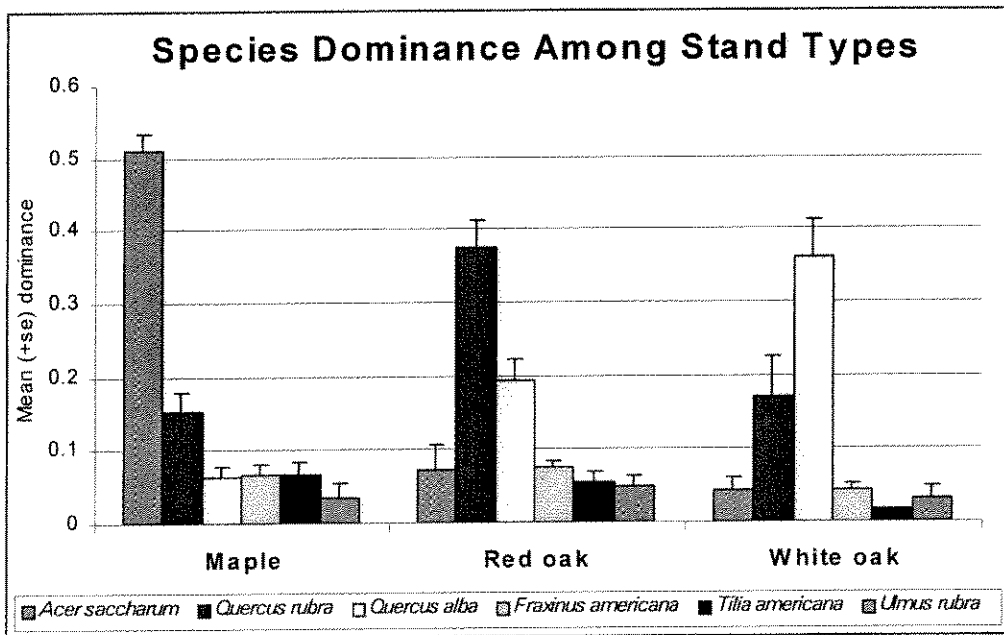
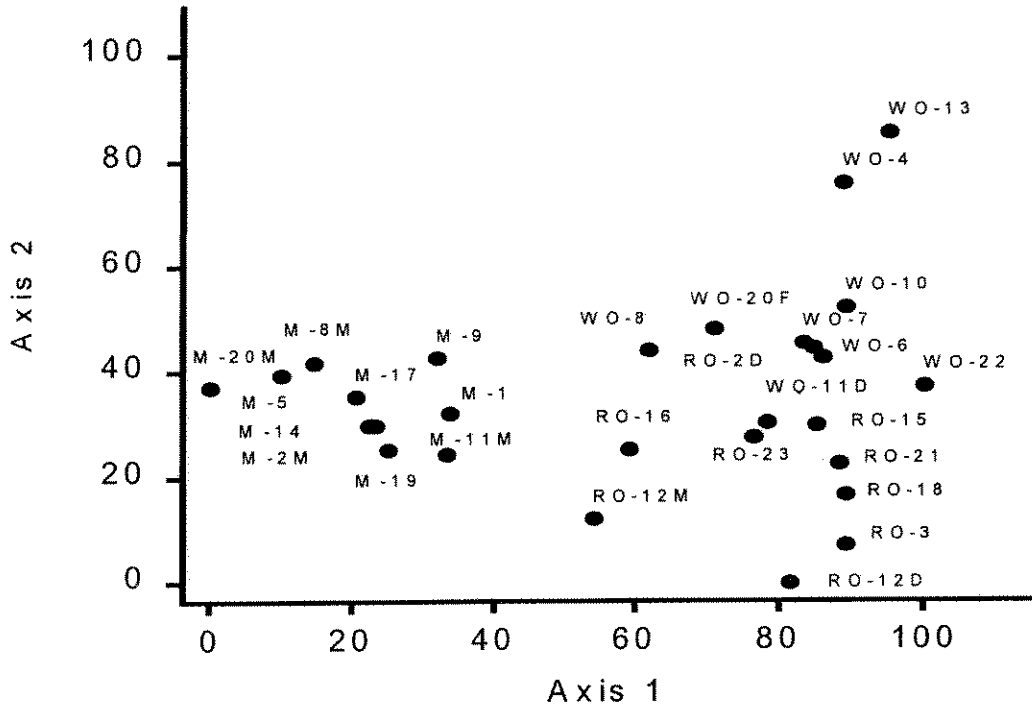


Figure 2. Bray-Curtis forest stand ordination (upper) and mean species dominance (relative basal area) of dominant species among forest stand types (lower). Ordination codes represent stand type clusters for: maple (M), red oak (RO) and white oak (WO) stand types. Numbers correspond to sites in Table 1; for multiple sites per stand, D = dry-mesic and M = mesic.

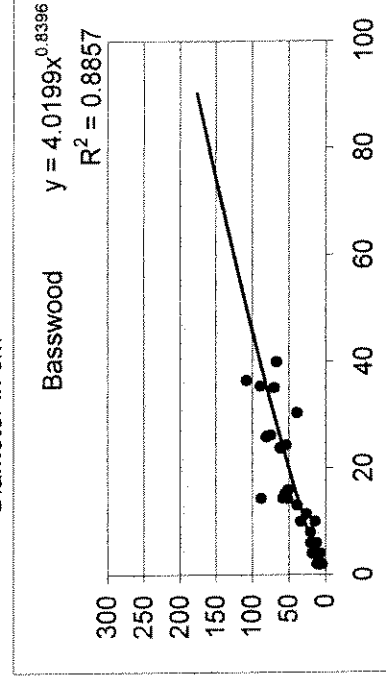
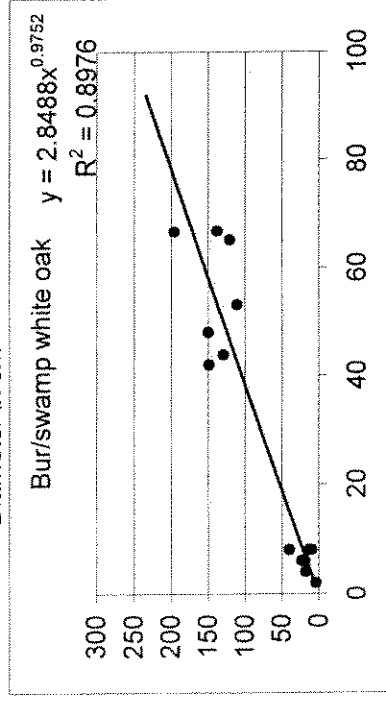
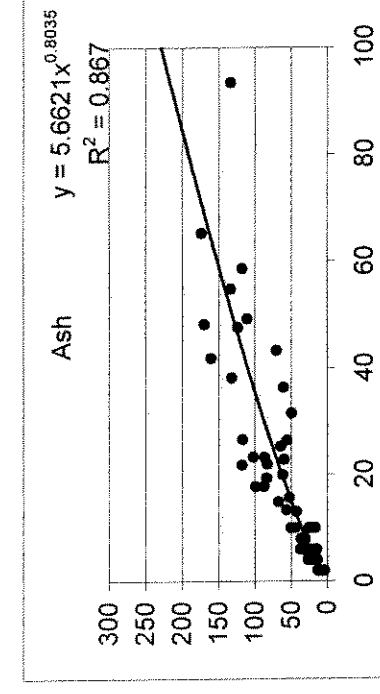
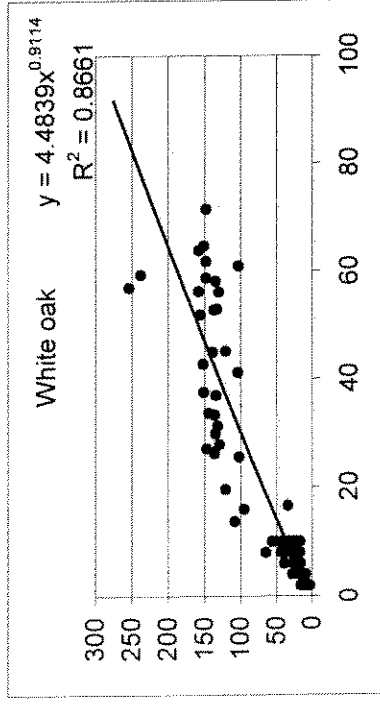
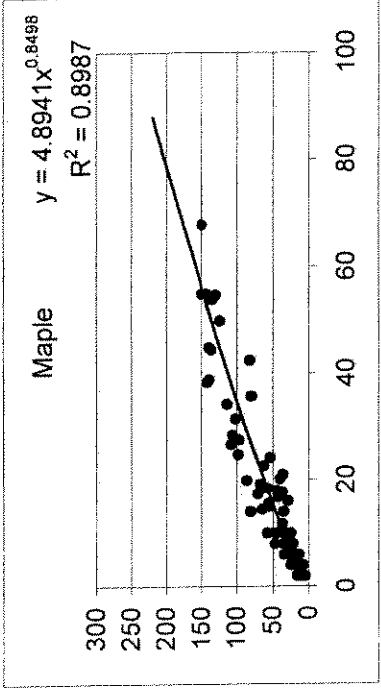
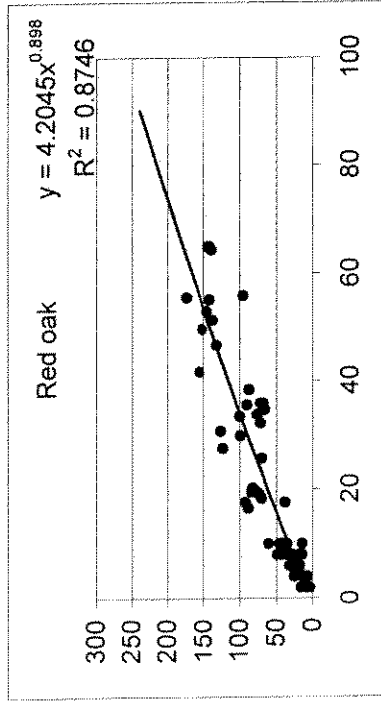


Figure 3. Age-diameter power functions of red oak, white oak, bur/swamp white oak, maple, ash, and basswood. Ages based on tree cores taken in 1998 from high quality Illinois Natural Areas Inventory forest stands.

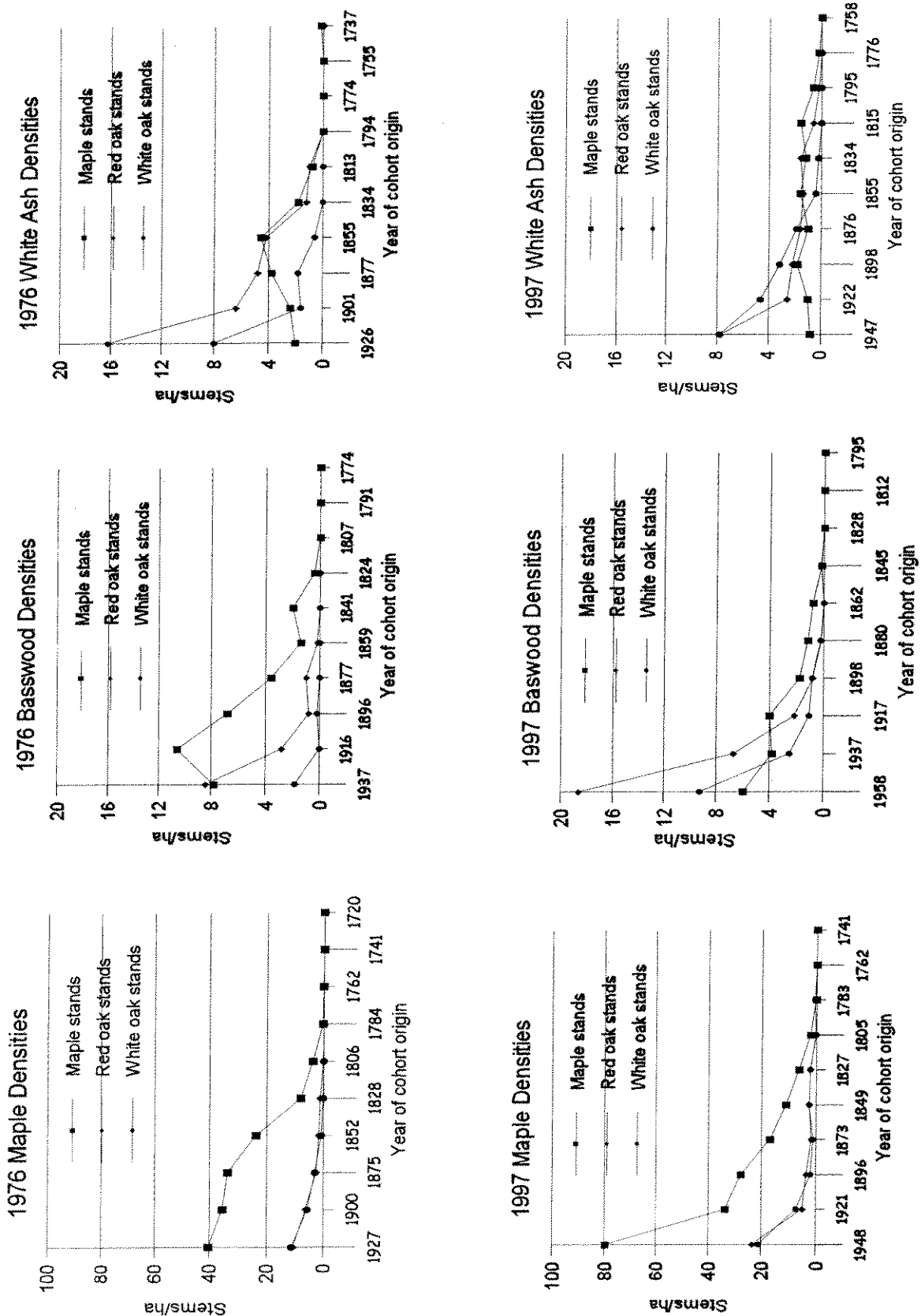


Figure 4. Temporal differences in age- and size-class densities of maple, basswood and white ash in maple (—■—), red oak (---●---), and white oak (---◆---) stands between 1976 and 1997. Classes indicate year of cohort origin based on tree age and diameter power functions (Figure 3) at 10-cm intervals between 10 and 110 cm.

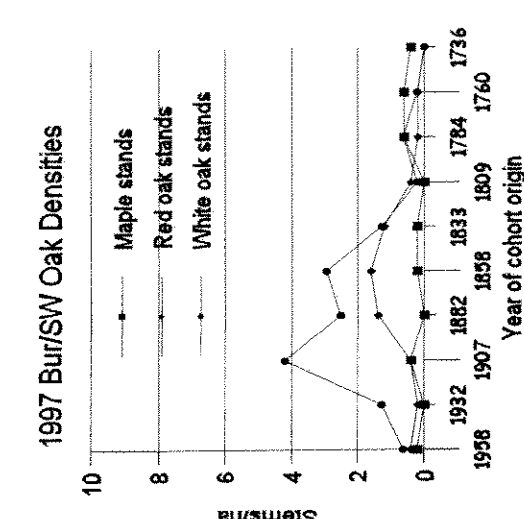
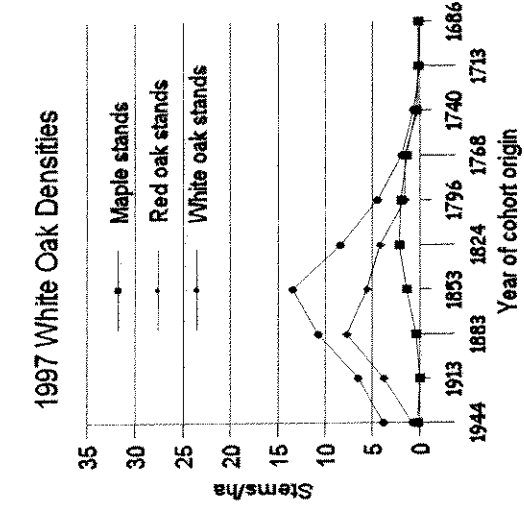
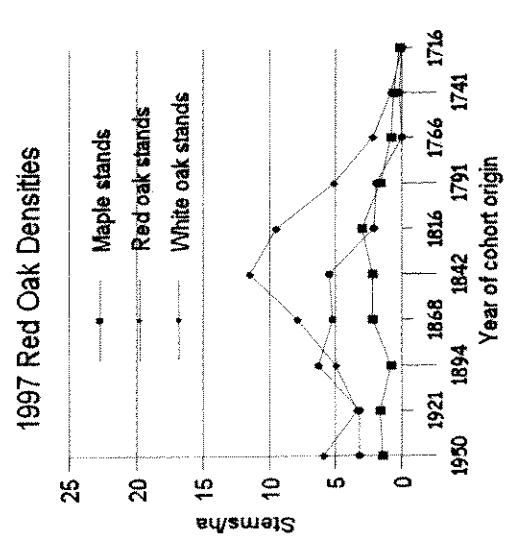
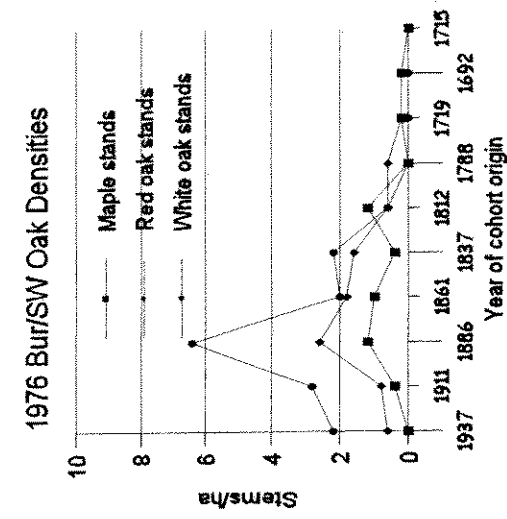
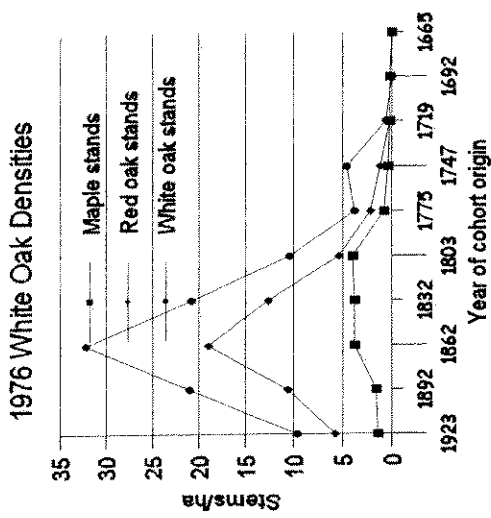
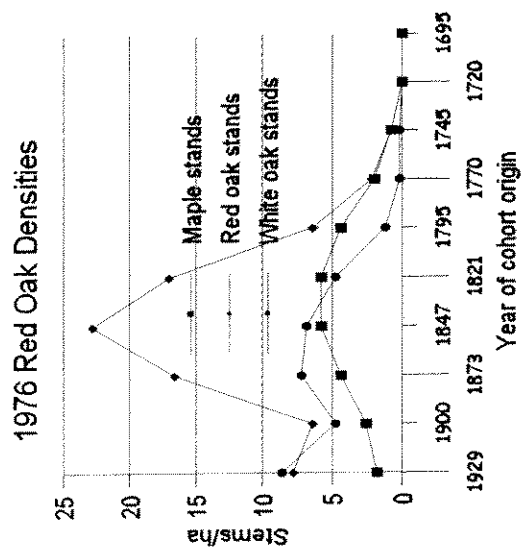


Figure 5. Temporal differences in age- and size-class densities of red oak, white oak, and bur/swamp white oak in maple (---◆---), red oak (---●---), and white oak (---○---) stands between 1976 and 1997. Classes indicate year of cohort origin based on tree age and diameter power functions (Figure 3) at 10-cm intervals between 10 and 110 cm.

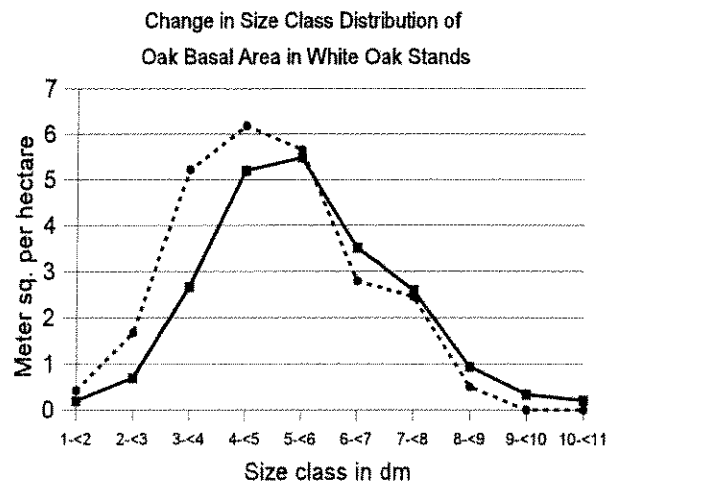
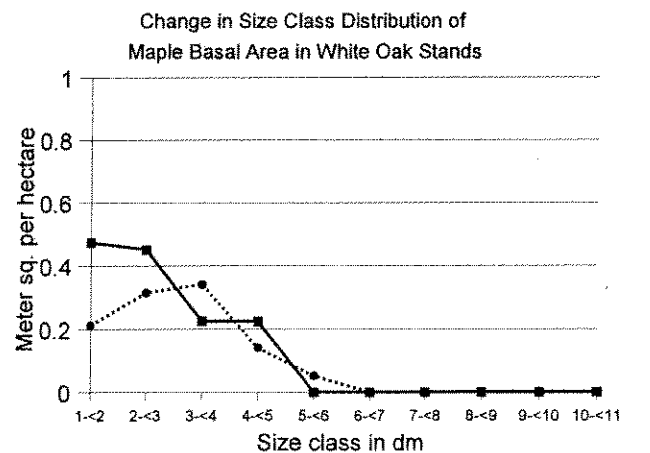
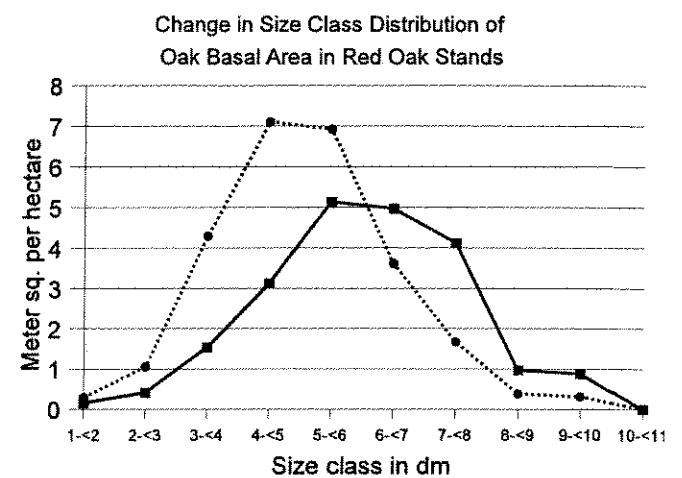
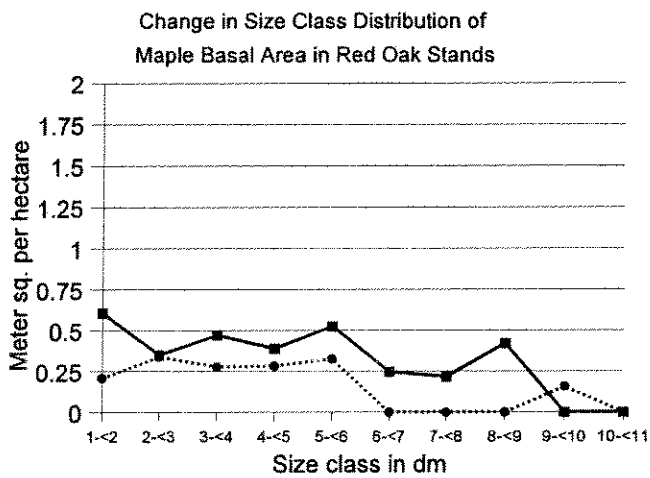
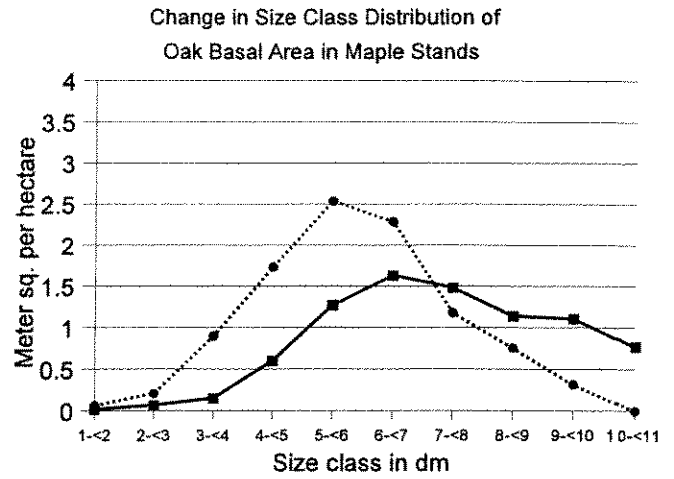
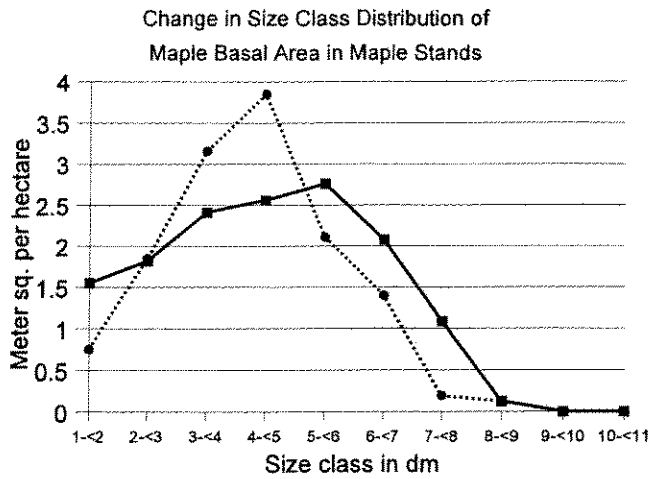
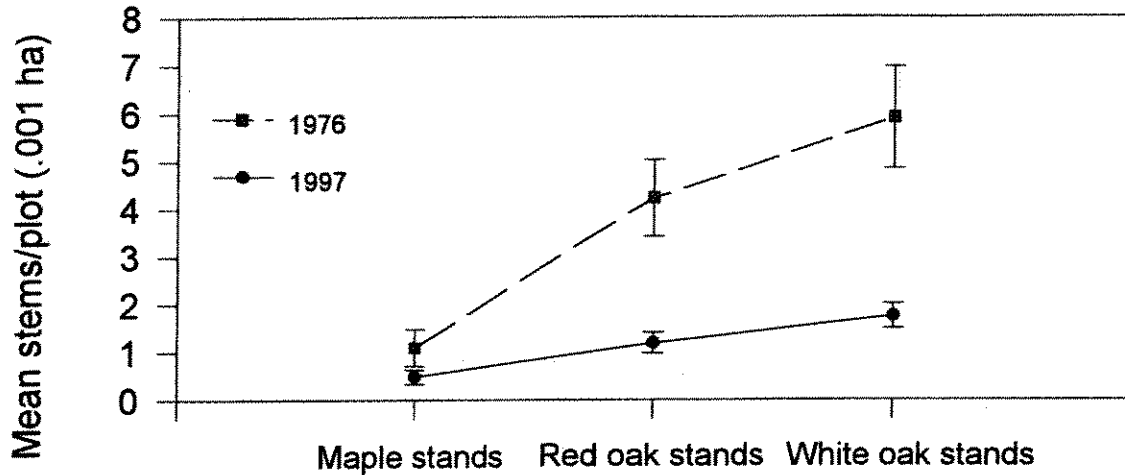
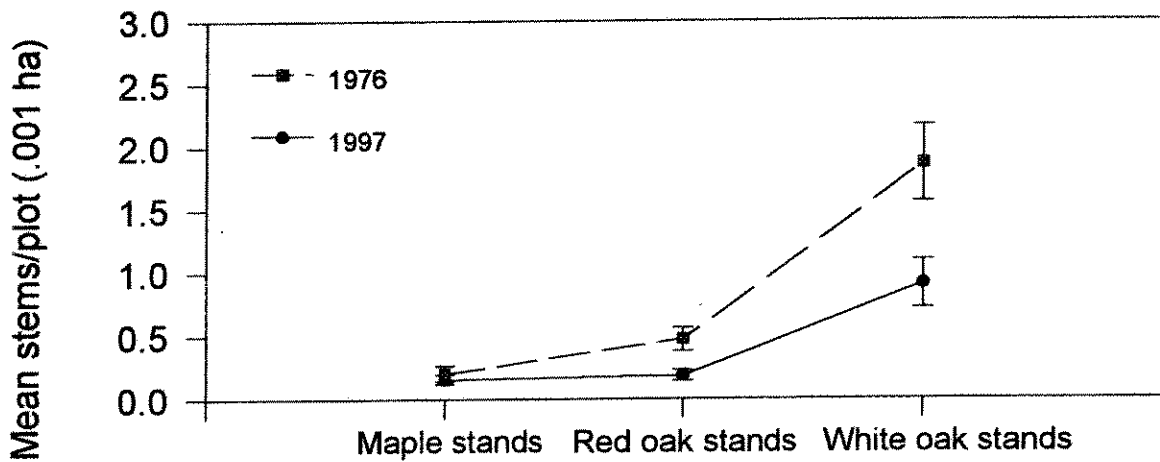


Figure 6. Temporal change and size-class distribution of maple and oak basal area in maple, red oak, and white oak stands. Areas below 1976 and above 1997 curves represent basal area loss. Area below 1997 curve and above 1976 curve represents basal area gain.

TEMPORAL CHANGE IN SHRUB STEM DENSITY



TEMPORAL CHANGE IN UNDERSTORY TREE STEM DENSITY



TEMPORAL CHANGE IN UNDERSTORY TREE & SHRUB RICHNESS

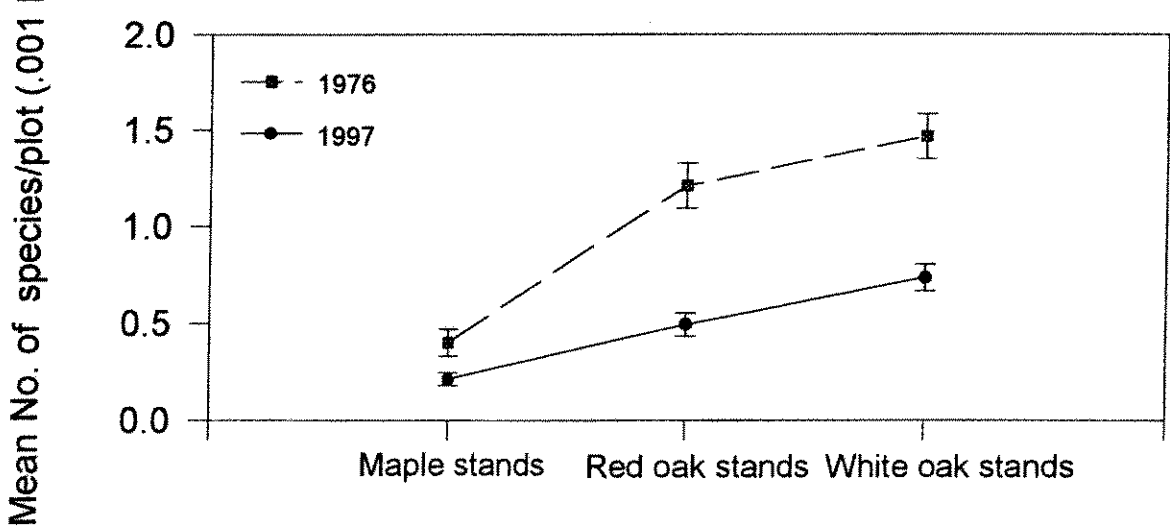


Figure 7. Temporal change in understory tree and shrub density and species richness. Shrub density ANOVA: year ($F = 50.65$, $P = .0001$), stand ($F = 14.21$, $P = .0002$), year x stand ($F = 8.16$, $P = .0003$); Tree density ANOVA: year ($F = 14.21$, $P = .0002$), stand ($F = 45.06$, $P = .0001$), year x stand ($F = 5.76$, $P = .0033$); Species richness ANOVA: year ($F = 79.18$, $P < .0001$), stand ($F = 58.79$, $P = .0001$), year x stand ($F = 8.48$, $P = .0002$).

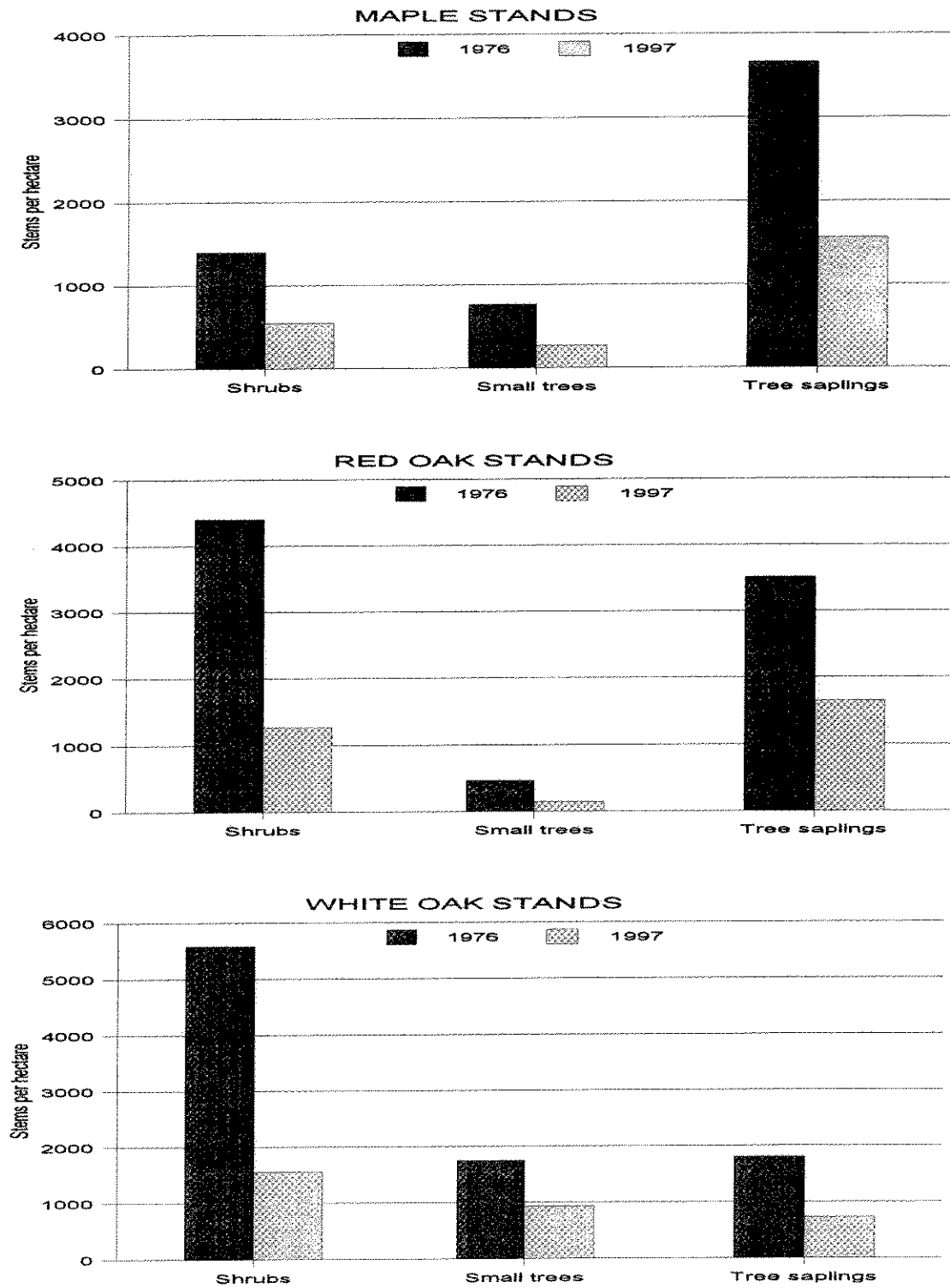


Figure 8, Temporal change in shrub layer structure. Chi-square: maple stands ($X^2 = 5.886$, $P = .004$), red oak stands ($X^2 = 19.216$, $P < .001$), white oak stands ($X^2 = 26.507$, $P < .001$).

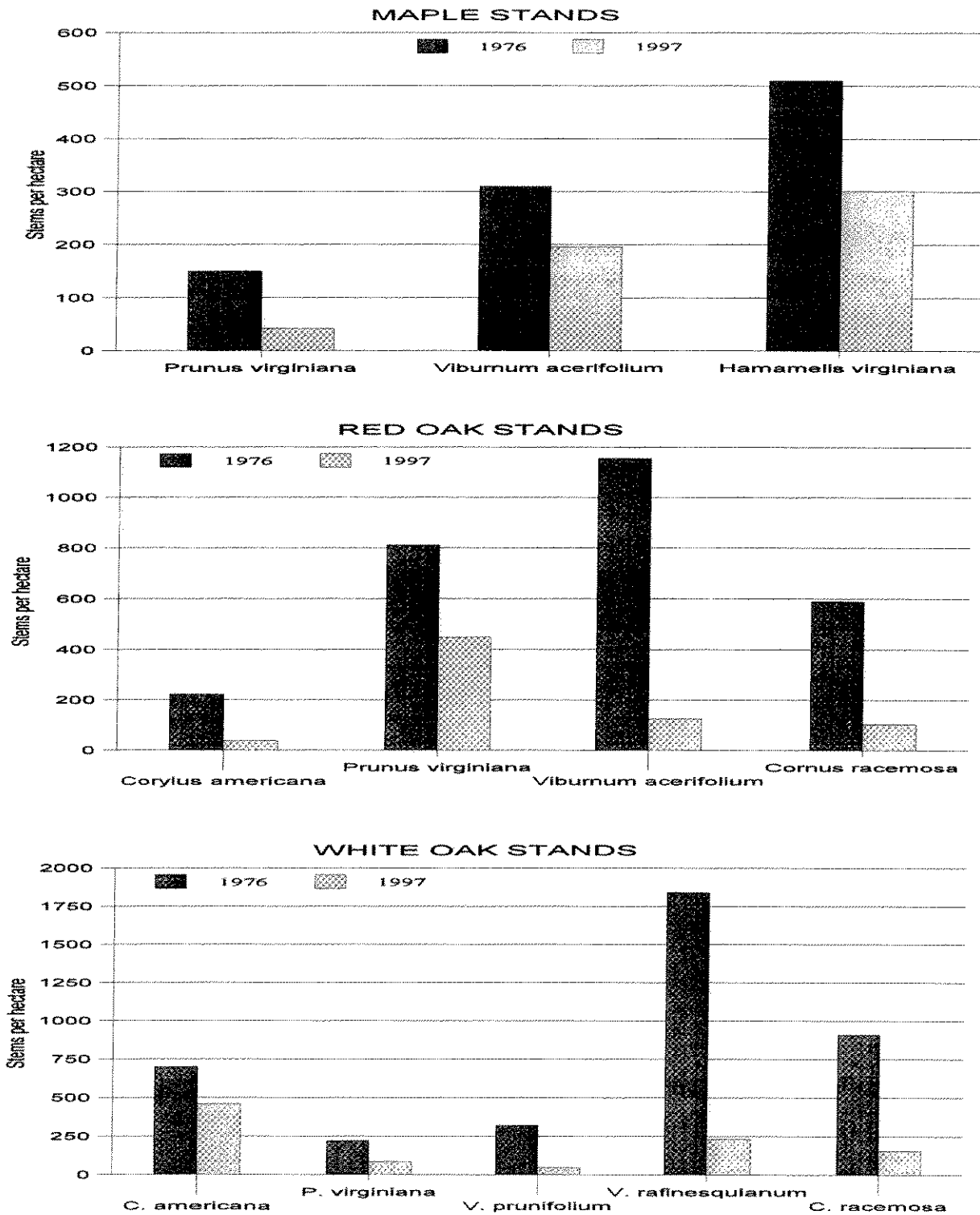


Figure 9. Temporal change in shrub layer species densities within stand types. Stems per hectare based on plot totals summed within stand types.

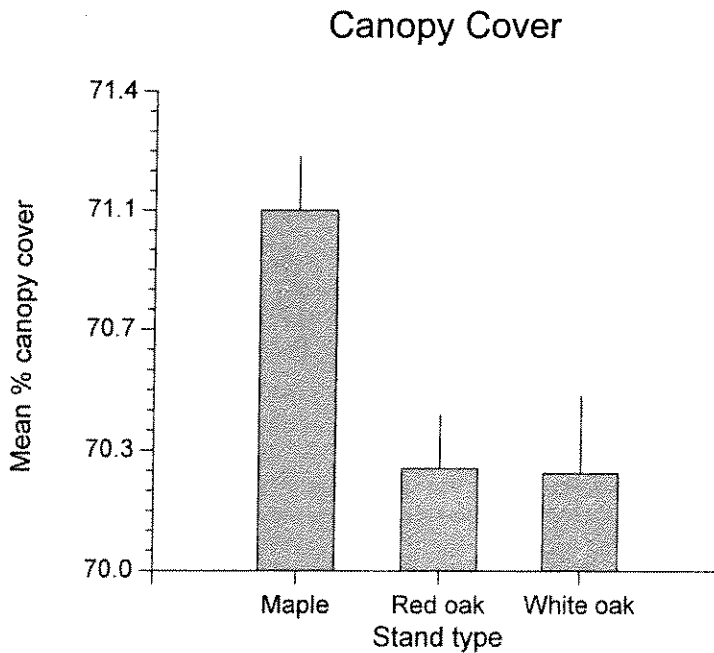
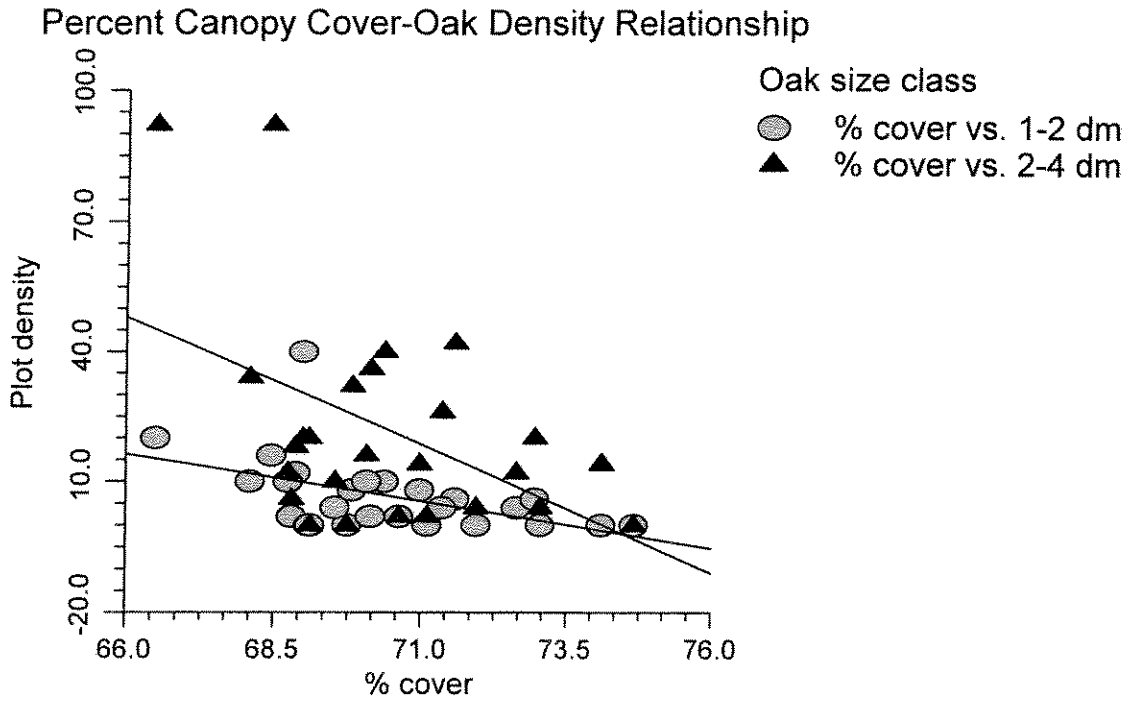


Figure 10. Relationships between stand type and percent canopy cover (lower graph), and percent canopy cover and plot density of 1-2 dm and 2-4 dm size class oaks (upper graph). Percent canopy cover ANOVA: $F = 6.37$, $P = .002$. Percent canopy cover-oak density correlations: 1-2 dm ($R^2 = .2336$, $P = .0124$) 2-4 dm ($r^2 = .2256$, $P = .0142$).