
Temporal Instability in Chicago's Upland Old Growth Forests

Marlin Bowles, The Morton Arboretum

Michael Jones, Christopher B. Burke Engineering

Jenny McBride, The Morton Arboretum

Tim Bell, Chicago State University

Christopher Dunn, Chicago Botanic Garden

As maples and oaks battle for control of the Chicago region forests, learn what several researchers discovered when they tested their assumption that maples are winning.

Abstract

We tested the assumption that sugar maple is replacing oaks in Chicago region forests by re-sampling 28 old growth upland forests that were first sampled in 1976. These stands were dominated by sugar maple, red oak, or white oak. Maple basal area increased over time, and its stem densities increased in smaller size classes in maple and red oak stands. Oaks decreased in basal area and in stem densities in all stands, with the greatest loss in lower to mid size-classes. In the shrub layer, these changes were accompanied by declines in dominant shrubs and a shift toward dominance by tree saplings in maple and red oak stands. Ages of declining oak cohorts indicate they originated in the mid-1800s, probably soon after European settlement reduced fire frequencies; however old-growth canopy oaks and maples are of pre-settlement origin. Causes of oak mortality and shrub decline appear to be increasing shade from canopy closure associated with forest succession and stand maturation. Maple has played a role in these processes in maple and red oak stands, but not yet in white oak stands. We attribute these changes to loss of landscape-scale fires that maintained more open forests in the early 1800's, although over-browsing by white-tailed deer has recently contributed to loss of shrub layer vegetation on some sites. As these stands shift to canopy gap replacement processes, oaks are likely to decline further, as maples that now dominate the sapling layer in most stands will most likely replace canopy oaks. A high priority for management and research should be to understand how to restore natural fire processes that will maintain oak dominance and shrub layer diversity in these stands.

Background

Replacement of shade-intolerant fire-resistant oak (*Quercus*) species by shade-tolerant fire-intolerant sugar maple (*Acer saccharum*) is a well-known successional process in midwestern upland oak forests (McIntosh 1957; Pallardy et al. 1991; Roovers & Shifley 1997). It is usually attributed to fire suppression (Curtis 1959; Lorimer 1985; Abrams 1992) and linked with loss of biodiversity through decline of light and fire adapted

understory plants (McIntosh 1957; Curtis 1959; Wilhelm 1991; Bowles et al. 2000). Other potential causes of structural change in oak forests include self-thinning of smaller size classes as forest canopies mature (Christensen 1977; Johnson et al. 2002), over-browsing by eastern white-tailed deer (Strole & Anderson 1992; Anderson 1994), and invasion by alien species such as common buckthorn (*Rhamnus cathartica*) and the honeysuckle *Lonicera maackii* (Apfelbaum & Haney 1991; Swink & Wilhelm 1994).

Despite concerns about deteriorating forest structure and composition, few studies have documented such changes in Chicago region forests, nor clarified possible cause and effect relationships. In this paper, we describe woody vegetation changes in 28 maple-or-oak dominated old growth forests in the Chicago region of northeastern Illinois (see Table 1 & Figure 1 in Bowles et al. 2000). The Illinois Natural Areas Inventory (INAI) described these remnants as the last remaining old growth (Grade A) or old second growth (Grade B) upland forests in this region (White 1978), and sampled them in 1976. We re-sampled them in 1997, and assessed twenty-year changes in tree species basal area (BA), dominance (relative BA), size-class distribution, and changes in shrub layer stem densities and species richness.

The INAI classified 26 of the 28 forest stands into 12 sugar maple/red oak (*Acer saccharum*-*Q. rubra*) dominated mesic stands and 14 white oak/red oak/black oak (*Quercus alba*-*Q. rubra*-*Q. velutina*) dominated dry-mesic stands. Two additional stands were flatwoods; one was red oak/pin oak/red maple (*Q. rubra*-*Q. palustris*-*A. rubrum*) dominated and the second was swamp white oak/white oak/scarlet oak (*Q. bicolor*-*Q. alba* *Q. ellipsoidalis*) dominated. Flatwoods are difficult to classify because they occupy poorly drained uplands that retain water during much of the growing season and support species that occupy a wide range of moisture conditions. Exclusive of the flatwoods, we classified the sites into maple-dominated, red oak-dominated and white oak-dominated stands, with red oak stands occupying an intermediate drainage position between mesic and dry-mesic (Bowles et al. 2000). For this paper, we include the first flatwoods with red oak stands, and the second with white oak stands.

Methods

The INAI sampled each forest stand with 20 nested plots, which we re-sampled in 1997 (Bowles et al. 2000). Data used to compare temporal change included density of trees by 1-dm size-class in 0.025 hectare plots and density of shrub layer stems in circular 0.001 hectare plots. We also aged dominant tree species with increment cores. Twenty-year changes in basal area, dominance and size class distribution were compared within each stand type. For this analysis, we used dominant and sub-dominant tree species that occurred in all stand types and exceeded 5% dominance in at least one stand type. This group includes sugar maple, basswood (*Tilia americana*), white ash (*Fraxinus americana*), red oak, white oak and bur oak (*Q. macrocarpa*). Because swamp white oak and bur oak can hybridize when they co-occur, these species were combined as "bur oak." Basal area was calculated by using size-class medians as estimates of tree diameters, and dominance was calculated as the percentage of total basal area for each species within stand types (Bowles et al. 2000). To analyze temporal change in the shrub layer, we partitioned species data into three life-form groups: true shrubs, understory tree species (which do not enter forest tree canopies) and tree saplings representing potential canopy

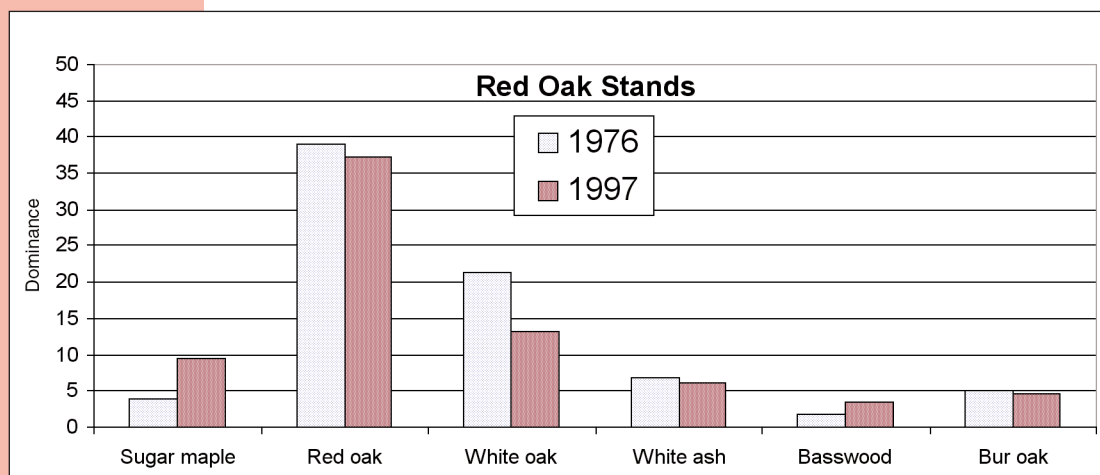
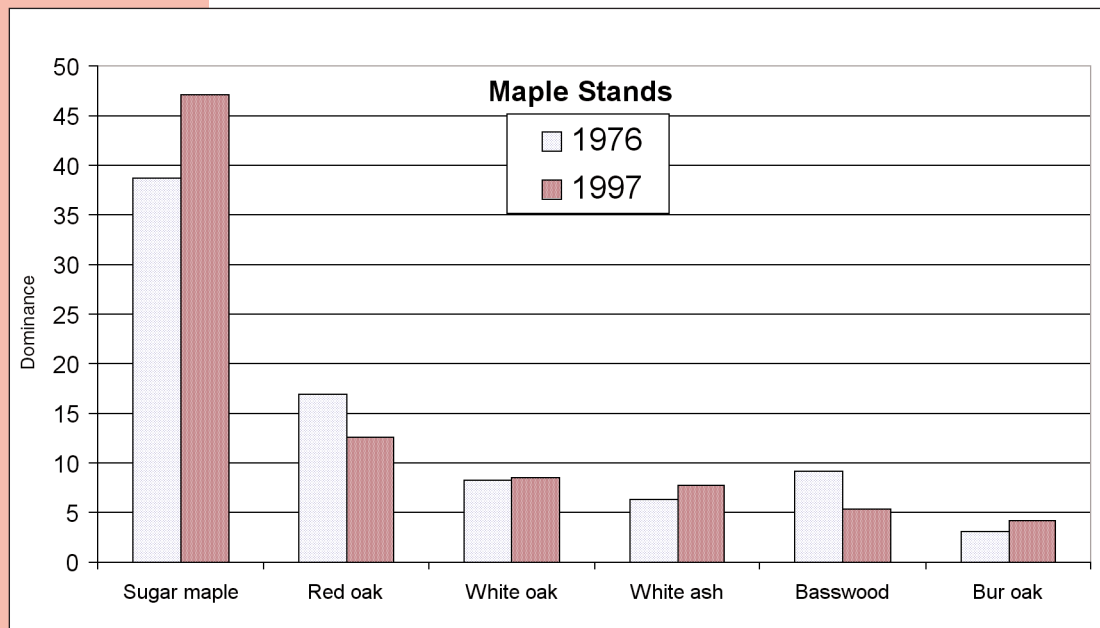
trees. Percent change in stems/ha was calculated for life-form groups as well as for dominant species.

Results

Change in canopy structure

The three stand types differed in canopy structure primarily among single dominant and subdominant species (Figure 1). In sugar maple stands, red oak was sub-dominant over other secondary species, while red oak stands had sub-dominance of white oak, and white oak stands had sub-dominance of red oak. White oak stands also tended to have lower dominance of white ash and basswood, and greater dominance of bur oak. Across all stands, BA of sugar maple increased significantly ($P = 0.017$) over time, while BA of oaks dropped significantly ($P = 0.013$). In all three stand types, maple gained from 6-9 % in dominance (Figure 1).

Figure 1. Temporal change in dominance (relative basal area) of dominant and sub-dominant trees among maple, red oak and white oak forest stand types sampled by the Illinois Natural Areas Inventory. (Figure 1 continued on page 8.)



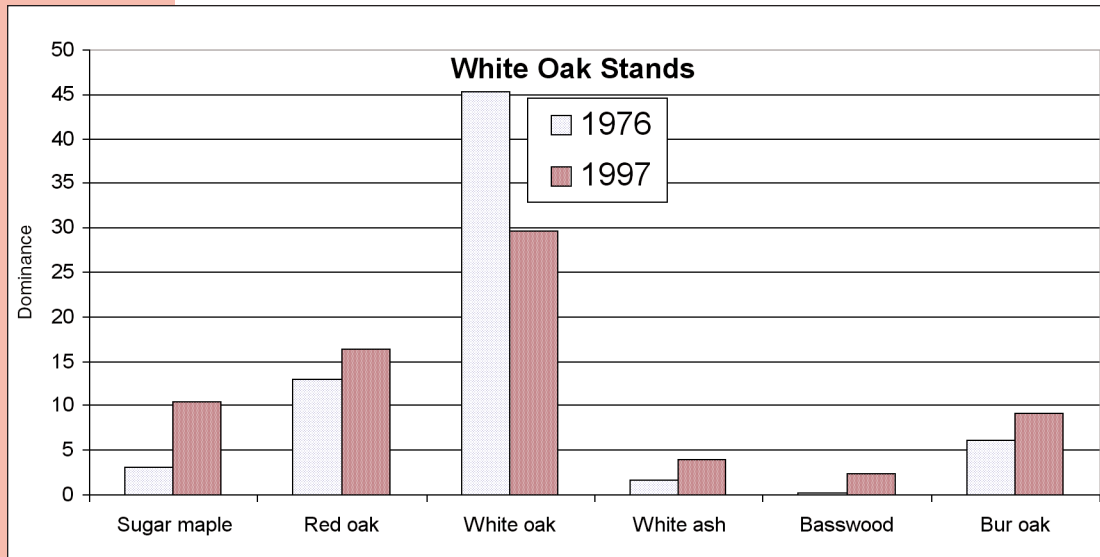


Figure 1. Temporal change in dominance (relative basal area) of dominant and sub-dominant trees among maple, red oak and white oak forest stand types sampled by the Illinois Natural Areas Inventory.

Red oaks decreased in dominance in maple and red oak stands, but increased in white oak stands. White oaks decreased in red oak and white oak stands. These changes were accompanied by a 100% or more increase in maple stem densities in the smallest size class, which was non-significant only in white oak stands (Figure 2). In contrast, oaks underwent a significant decline, dropping by 50% in mid-size classes.

Regression analyses of tree age vs. size indicate that, excluding basswood, forest-grown trees exceeding 0.75 m diameter are likely of pre-settlement (pre-1820) origin, and individuals reaching 1 m originated prior to 1800. These analyses also suggest that the large cohorts of maple appearing in the smallest size class in 1997 originated in about 1950, while declining oak cohorts in the > 3-4 and > 5-6 dm size classes appear to have originated between 1820-1880.

Change in shrub layer structure

The structure of shrub layer species groups differed among stand types and changed significantly over time, with the greatest decline among shrubs in oak stands (Figure 3). In 1976, shrub layer stem densities ranged from about 5,000 stems/ha in maple stands, which were dominated by tree saplings, to 9,000 stems/ha in white oak stands, which were dominated by shrubs. By 1997, total stem densities had declined significantly ($P < 0.0001$) to about 3,000 stems/ha across all stand types. This decline was accompanied by a significant ($P < 0.0001$) decrease from about 2.2 to 1.2 species/plot.

Figure 2. Change in size class distribution of sugar maple and oaks among maple, red oak and white oak stand types. ANOVA: Maple stands: maple ($P = 0.0106$), oaks ($P < 0.0001$), red oak stands maple ($P = 0.0188$), oaks ($P < 0.0001$), white oak stands: maple ($P = 0.2088$), oaks ($P < 0.0001$).

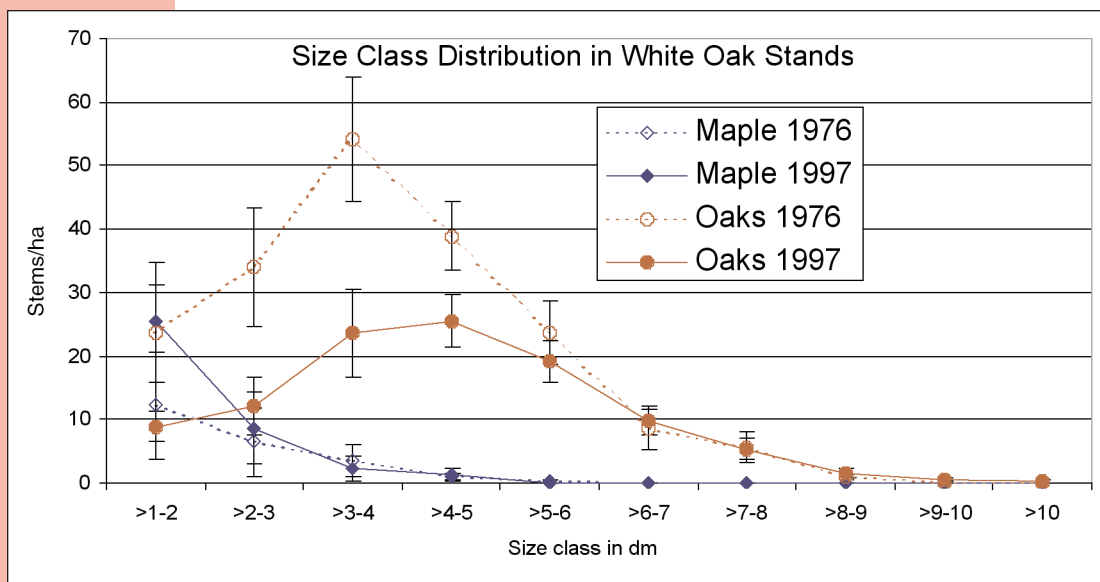
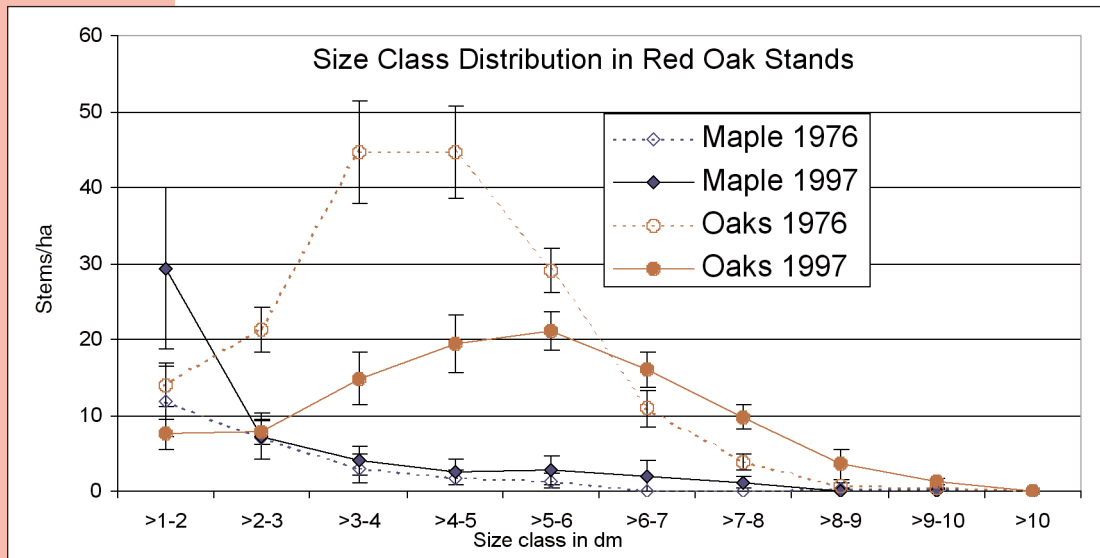
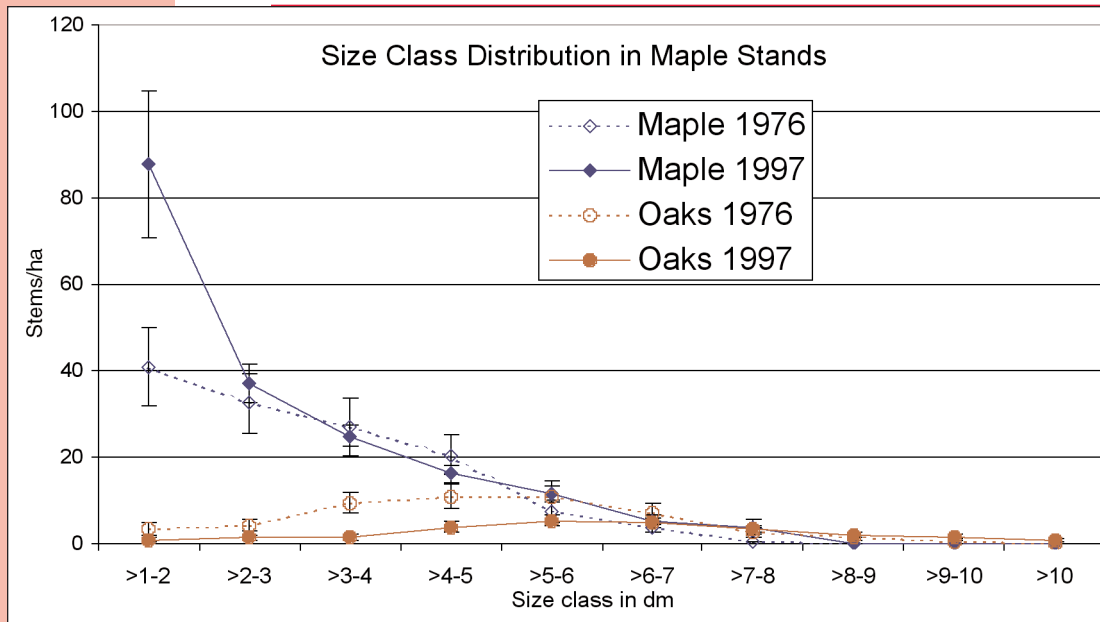
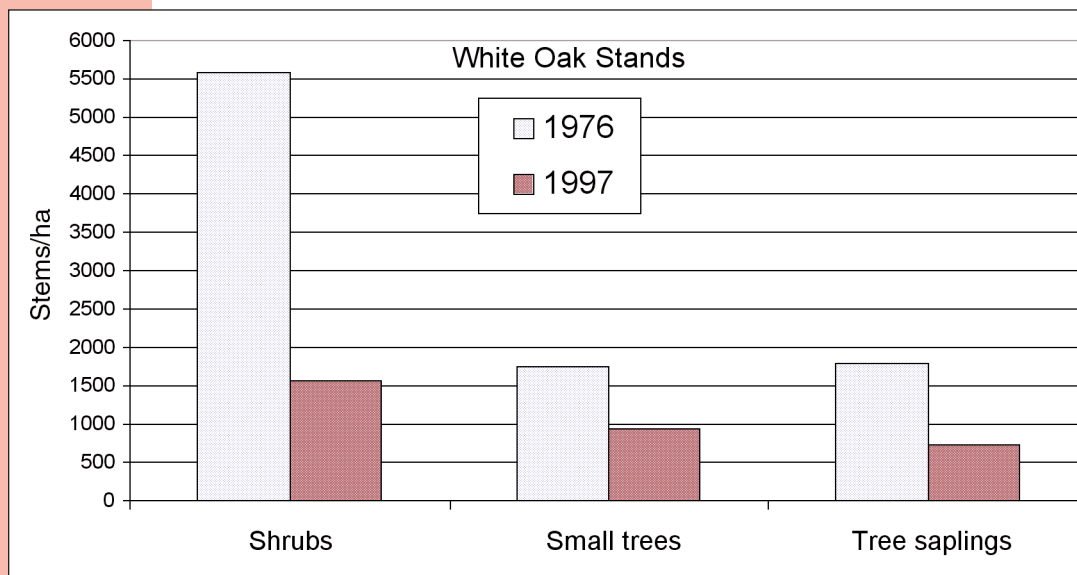
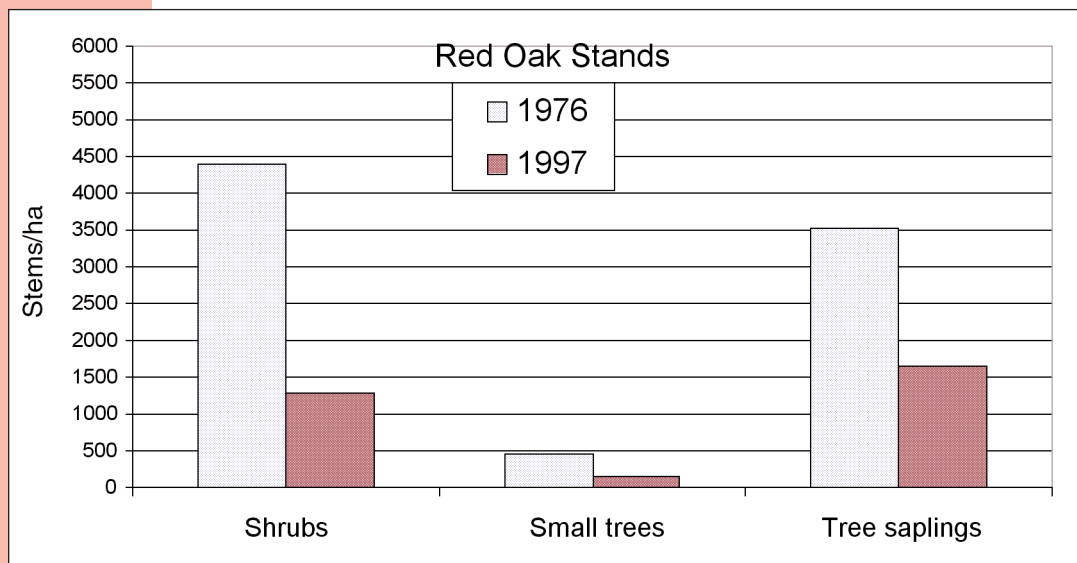
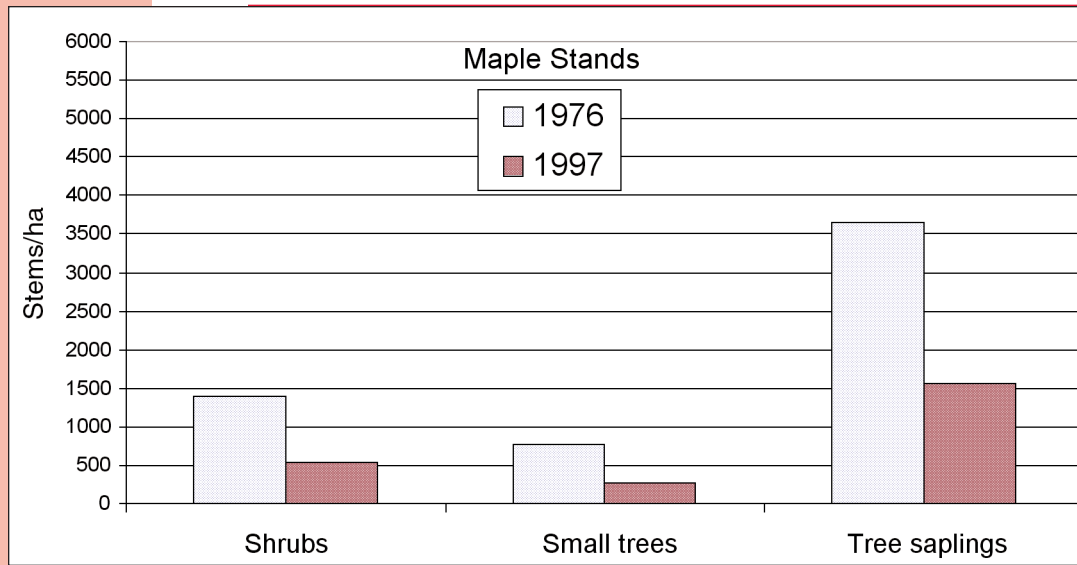


Figure 3. Temporal change in shrub layer structure in maple, red oak and white oak stand types between 1976 and 1997.

Chi-square: maple stands ($X^2 = 5.886$, $P = 0.004$), red oak stands ($X^2 = 19.216$, $P < 0.001$), white oak stands ($X^2 = 26.507$, $P < 0.001$).



The distribution of dominant shrub layer species varied across stand types (Table 1). In 1976, maple stands were dominated by maple saplings, but also had a strong component of witch hazel (*Hamamelis virginiana*) and maple-leaved arrow-wood (*Viburnum acerifolium*). In 1976, red oak stands were also dominated by maple-leaved arrow-wood and maple saplings, as well as choke cherry (*Prunus virginiana*), and had minor representation of eastern hop-hornbeam (*Ostrya virginiana*). White oak stand shrub layers in 1976 were dominated by downy arrow-wood (*Viburnum rafinesquianum*), gray dogwood (*Cornus racemosa*) and American hazelnut (*Corylus americana*), with moderate representation of eastern hop-hornbeam and American hornbeam (*Carpinus caroliniana*). Almost all shrub layer species declined by 1997, with dominance shifting to maple saplings in both maple and red oak stands (Table 1). Most species retained their dominance in white oak stands, but underwent substantial declines. The alien buckthorn was rarely encountered in 1976; although it had increased by 1997, it remained a minor component of all stands.

Species/type	Maple stands			Red oak stands			White oak stands		
	1976	1997	% change	1976	1997	% change	1976	1997	% change
True shrubs (total)	1400	545	-61.07	4400	1273	-71.07	5580	1555	-72.13
<i>Prunus virginiana</i>	150.00	42.33	-71.78	811.11	448.09	-44.76	220.00	85.00	-61.36
<i>Viburnum acerifolium</i>	310.00	195.77	-36.85	1155.55	125.68	-89.12	-----	-----	-----
<i>Hamamelis virginiana</i>	510.00	301.59	-40.86	-----	-----	-----	-----	-----	-----
<i>Corylus americana</i>	-----	-----	-----	222.22	38.25	-82.79	700.00	460.00	-34.29
<i>Cornus racemosa</i>	-----	-----	-----	588.89	103.93	-82.35	910.00	155.00	-82.97
<i>Viburnum prunifolium</i>	-----	-----	-----	-----	-----	-----	320.00	45.00	-85.94
<i>Viburnum rafinesquianum</i>	-----	-----	-----	-----	-----	-----	1840.00	230.00	-87.50
* <i>Rhamnus cathartica</i>	0.00	5.30	100.00	27.78	54.56	96.40	33.33	122.22	266.67
Small trees (total)	760	265	-65.13	467	148	-68.31	1750	935	-46.57
<i>Ostrya virginiana</i>	80.00	60.00	-25.00	188.89	89.33	-52.71	455.56	200.00	-56.10
<i>Carpinus caroliniana</i>	70.00	115.00	64.29	33.33	46.00	38.00	566.67	422.22	-25.49
Saplings (total)	3660	1561	-57.35	3511	1650	-53.00	1800	725	-59.72
<i>Acer sacchrum</i>	4080.00	1616.90	-60.37	1011.11	776.11	-23.24	166.67	122.22	-26.67
<i>Ulmus rubra</i>	230.00	15.00	-93.48	355.56	142.44	-59.94	266.67	50.00	-81.25
<i>Fraxinus sp</i>	70.00	95.60	36.57	455.56	98.00	-78.49	488.89	166.67	-65.91
<i>Tilia americana</i>	120.00	45.00	-62.50	611.11	128.67	-78.95	55.56	38.89	-30.00

Table 1. Density (in stems/ha) and percent change in total, dominant native, and alien (*) shrubs, small trees, and tree saplings in old growth forest stands sampled by the Illinois Natural Areas Inventory in the Chicago region of northeastern Illinois.

Discussion

Processes of forest change

The woody composition and structure of Chicago region old-growth forests is linked with historic pre-settlement and post settlement conditions. The pre-settlement ages of larger canopy trees indicates that these stands would have been exposed to natural fire processes occurring before European settlement. The large number of mid-size class oaks that originated during the early- to mid-1800s appears to have been released by reduced fire frequencies associated with landscape fragmentation that began after settlement (Anderson 1991). The appearance of these oaks also suggests that an open canopy structure in the mid-1800s allowed enough light to promote their regeneration from seedlings or grubs (Bowles & McBride 1998). Original fire processes appear to have been moderated by landscape fire breaks, as maples and smaller oak cohorts co-occurred in more mesic stands that would have received more fire protection (Bowles et al. 1994). Nevertheless, these smaller oak cohorts also declined over time.

In the narrow time frame of 20 years, these forests have undergone substantial losses of oak saplings and native shrubs, with increasing dominance by sugar maple in maple and red oak stands. This pattern of changing structure represents two interconnected processes of forest change that are closely linked with fire suppression. A successional process of increasing maple dominance and replacement of oaks characterizes changes in mesic stands, while a stand maturation process best describes the loss of subcanopy oaks in dry-mesic stands (e.g., Christensen 1977; Abrams & Downs 1990; Oliver & Larson 1990; Abrams 1992). These changes occur because oaks are relatively shade-intolerant and fire-tolerant, regenerating after disturbance and declining as closing forest canopies reduce shade and cause mortality of sub-canopy individuals (Crow 1988; Abrams 1992; Crow 1992; Will-Wolf & Roberts 1993). Successional replacement by more shade tolerant maples occurs as part of the maturation process when they are present or occur as adjacent seed sources (Schlesinger 1976; Pallardy et al. 1991). The decline in shrub layer species also appears to fit these models because many shrubs sprout after fire and are relatively shade-intolerant, declining with increasing tree basal area (Loucks & Schnur 1976). An important finding is that the significant decline of oaks and shrub layer species in white oak stands, and to some extent in red oak stands, has occurred without significant maple invasion and appears linked with increasing oak canopy cover. Oak forests are thus unstable without recurring disturbance (McCune & Cottam 1985; Abrams 1992; Will-Wolf & Roberts 1993).

These changes indicate that the stands we studied have shifted toward canopy gap tree replacement processes, in which shade-intolerant oaks will not reproduce in the face of increasing maple dominance and shade (e.g., Bray 1956; Schlesinger 1976; Christensen 1977; Anderson & Adams 1978; Canham 1985; Abrams & Downs 1990; Pallardy et al. 1991; Abrams 1992; Roovers & Shifley 1997). This process appears to be much further developed in maple stands, which have comparatively lower structural and compositional diversity, as well as greater percent canopy cover (Bowles et al. 2000).

The increasingly high population levels of eastern white-tailed deer in the Chicago region (Witham & Jones 1990) are no doubt contributing to loss of woody plant diversity in forest stands. Browsing was almost always evident in 1997, and probably

contributed to reduced densities of shrubs. It reduced height of arrow-wood stems from the shrub layer to the ground layer in one white oak stand; but, it also led to an increase in *Carpinus caroliniana* basal stem sprouts. Deer browsing also contributes to mortality of oak seedlings (Buckley et al. 1998), and consumption of acorns may also reduce oak recruitment. However, the significant losses of larger oak saplings is apparently not a direct result of deer browsing, but more likely an effect of decreasing light availability due to canopy closure. Although the alien buckthorn increased across all stand types, it remained at low densities and appears not to have caused the wide-scale loss of shrubs.

Management challenges

Although the INAI described these forests as “old growth” or “old second growth,” structural changes indicate that they are temporally unstable and will require fire management to prevent further decline and to restore former levels of structure and diversity. Effective fire management may be difficult because of the advanced degree of change in these forests and because we lack specific information on their pre-settlement structure and the fire processes that maintained them (Anderson 1991; Mendelson 1998). There is experimental evidence that reduction of canopy cover and competing saplings increases oak survival and regeneration (Crow 1992; Lorimer et al. 1994). However, larger trees that contribute to canopy shade may be fire-resistant, and modeling suggests that major fire disturbance may be needed for regeneration of oak stands (Will-Wolf & Roberts 1993). These results raise relevant questions for Chicago region old-growth forests—most importantly, can fire be used to maintain oak-dominated old-growth structure that promotes oak regeneration in canopy gaps and maintains a forest shrub-layer? The direct impact of different fire frequencies and intensities on forest ground layer vegetation is also unknown, and fire may promote the spread and persistence of the alien garlic mustard (*Alliaria petiolata*) in forests (Bowles et al. 2000; Luken & Shea 2000). The effect of fire on forest interior birds is an important concern, as some species appear to decline with increasing fire frequency—probably due to reduction of shrub layer and leaf litter habitats (Blake 2005). Potential fire effects on forest invertebrates are also an important concern, and there are almost no relevant data available from Midwest forests. For example, species richness of springtails (*Collembola*), which are forest litter dwelling arthropods, is reduced by burning, although some species may prefer burned areas (Brand 2002). Many factors other than fire can affect stand successional trajectories. For example, loss of American elm (*Ulmus americana*) to Dutch elm disease in wet-mesic stands may promote increases of either shrubs (Dunn 1986) or maple saplings (Bowles et al. 2003). Control of deer herds is apparently critical, as continued over-grazing may prevent recovery of woody and herbaceous species (Anderson 1994), and can reduce 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.

Marlin Bowles is a Plant Conservation Biologist at The Morton Arboretum. He can be reached at mbowles@mortonarb.org

Michael Jones is a Botanist with Christopher B. Burke Engineering, Ltd. He can be reached at ecobot@sbglobal.net

Jenny McBride is GIS specialist at The Morton Arboretum. She can be reached at jmcbride@mortonarb.org

Tim Bell is Professor of Botany at Chicago State University and Research Associate at The Morton Arboretum. He can be reached at tbell22@csu.edu

Christopher Dunn is Executive Director for Research Programs at the Chicago Botanic Garden. He can be reached at cdunn@chicagobotanic.org

Acknowledgements

We thank Chicago Wilderness, the Nancy Ryerson Ranney Leadership Grants Program, the Forest Preserve Districts of Cook, DuPage, Kane, and Will counties, and The Illinois Conservation Foundation for funding this work. We also thank the Illinois Department of Natural Resources for permission to use INAI data, and INAI director John White and staff for collecting original data. We also thank the Illinois Nature Preserves Commission and many landowners for permission to conduct this study, as well as agency personnel, site stewards, and volunteers for assistance with various aspects of this project. Finally, we thank John Dwyer, George Ware and reviewers for their thoughtful comments.

Literature Cited

- Apfelbaum, S.I. & A. W. Haney. 1991. Management of degraded oak savanna remnants in the upper Midwest, preliminary results from three years of study. Pp. 81-89 In: Burger, G.V., J.E. Ebinger, & G.S. Wilhelm (eds.) *Proceedings of the Oak Woods Management Workshop*. Eastern Illinois University, Charleston.
- Abrams, M.D. 1992. Fire and the development of oak forests. *BioScience* 42:346-353.
- Abrams, M.D. & J.A. Downs. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwest Pennsylvania. *Canadian Journal of Forest Research*. 20:1864-1870.
- Anderson, R.C. 1991. Presettlement forests of Illinois. Pp. 9-19 In: Burger, G.V., J.E. Ebinger, & G.S. Wilhelm (eds.) *Proceedings of the Oak Woods Management Workshop*. Eastern Illinois University, Charleston.
- Anderson, R.C. 1994. Height of white-flowered *Trillium* (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecological Applications* 4:104-109.
- Anderson, R.C. & D.E. Adams. 1978. Species replacement patterns in central Illinois white oak forest. Pp. 284-301 In: Pope, P.E. (ed) *Central Hardwood Forest Conference II*. Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana.
- Blake, J. G. 2005. Effects of prescribed burning on distribution and abundance of birds in a closed-canopy oak-dominated forest, Missouri, USA. *Biological Conservation* 121:519-53.
- Bowles, M.L., M.D. Hutchison, & J.L. McBride. 1994. Landscape pattern and structure of oak savanna, woodland, and barrens in northeastern Illinois at the time of European settlement. Pp. 65-73 In: Fralish, J.S., R.C. Anderson, J.E. Ebinger, & R. Szafoni (eds.) *Proceedings of the North American Conference on Savannas and Barrens*. Environmental Protection Agency, Chicago, Illinois.
- Bowles, M.L. & J.L. McBride. 1998. Vegetation composition, structure, and chronological change in a decadent midwestern North American savanna remnant. *Natural Areas Journal* 18: 14-27.

-
- Bowles, M.L., C. Dunn, M. Jones, J. McBride, C. Bushey, & R. Moran. 2003. Twenty-year woody vegetation changes in northern flatwoods and mesic forest at the Ryerson Conservation Area, Lake County, IL. *Erigenia* 19: 31-51.
- Bowles, M., M. Jones, J. McBride, T. Bell & C. Dunn. 2000. Structural composition and species richness indices for dry-mesic and mesic forests of the Chicago region of northeastern Illinois. *Erigenia* 18: 30-57.
- Brand, H. R. 2002. The effect of prescribed burning on epigeic springtails (*Insecta: Collembola*) of woodland litter. *American Midland Naturalist* 148: 383-393.
- Bray, R. 1956. Gap phase replacement in a maple-basswood forest. *Ecology* 37: 598-600.
- Buckley, D.S., T.L. Sharik, & J.G. Isebrands. 1998. Regeneration of northern red oak: positive and negative effects of competitor removal. *Ecology* 79: 65-78.
- Canham, C. D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. *Bulletin of the Torrey Botanical Club* 114:134-145.
- Christensen, N.L. 1977. Changes in structure, pattern and diversity associated with climax forest maturation in Piedmont, North Carolina. *American Midland Naturalist* 97: 176-188.
- Crow, T.R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*): a review. *Forest Science* 34: 19-40.
- Crow, T.R. 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. *Oecologia* 91: 192-200.
- Curtis, J.T. 1959. *Vegetation of Wisconsin*. University of Wisconsin Press, Madison.
- DeCalesta, D. 1994. Effects of white-tailed deer on songbirds within managed forests in Pennsylvania. *Journal of Wildlife Management* 58: 711-718.
- Dunn, C. P. 1986. Shrub layer response to death of *Ulmus americana* in southeastern Wisconsin lowland forests. *Bulletin of the Torrey Botanical Club* 113: 142-148.
- Johnson, P.S., S.R. Shifley & R. Rogers. 2002. *The Ecology and Silviculture of Oaks*. CABI Publishing, UK.
- Lorimer, C.G., J.W. Chapman, & W.D. Lambert. 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology* 82: 227-237.
- Loucks, O.L. & B.J. Schnur III. 1976. A gradient in understory shrub composition in southern Wisconsin. Pp. 99-117 In: Fralish, J.S., G.T. Weaver, & R.C. Schlesinger (eds.) *Proceedings of the First Central Hardwood Forest Conference*. Southern Illinois University, Carbondale.
- Luken, J.O. & M. Shea. 2000. Repeated prescribed burning at Dinsmore Woods State Nature Preserve (Kentucky, USA): Responses of the understory community. *Natural Areas Journal* 20: 150-158.
- McCune, B. & G. Cottam. 1985. The successional status of a southern Wisconsin oak woods. *Ecology* 66: 1270-1278.
-

-
- McIntosh, R.P. 1957. The York Woods: a case history of forest succession in southern Wisconsin. *Ecology* 38: 29-37.
- Mendelson, J. 1998. Restoration from the perspective of recent forest history. *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters* 86: 137-147.
- Oliver, C.D. & B.C. Larson. 1990. *Forest stand dynamics*. McGraw Hill, New York.
- Pallardy, S.G., T.A. Night, & E.Garrett. 1991. Sugar maple invasion in oak forests of Missouri. Pp. 21-30 In: Burger, G.V., J.E. Ebinger, & G.S. Wilhelm (eds.) *Proceedings of the Oak Woods Management Workshop*. Eastern Illinois University, Charleston.
- Roovers, L.M. & S.R. Shifley. 1997. Composition and dynamics of Spitler Woods, an old-growth remnant forest in Illinois (USA). *Natural Areas Journal* 17: 219-232
- Schlesinger, R.C. 1976. Hard maples increasing in upland hardwood stands. Pp. 177-185 In: Fralish, J.S., G.T. Weaver, & R.C. Schlesinger (eds.) *Proceedings of the First Central Hardwood Forest Conference*. Southern Illinois University, Carbondale.
- Strole, T. A. & R. C. Anderson. 1992. White-tailed deer browsing: species preferences and implications for central Illinois forests. *Natural Areas Journal* 12: 139-144.
- Swink, F. & G. Wilhelm. 1994. *Plants of the Chicago Region*. The Morton Arboretum, Lisle, Ill.
- White, J. 1978. *Illinois Natural Areas Inventory Technical Report*. Illinois Natural Areas Inventory, Urbana, and Natural Land Institute, Rockford.
- Wilhelm, G. 1991. Implications of changes in floristic composition of the Morton Arboretum's East Woods. Pp. 31-54 In: Burger, G.V., J.E. Ebinger, & G.S. Wilhelm (eds.) *Proceedings of the Oak Woods Management Workshop*. Eastern Illinois University, Charleston.
- Will-Wolf, S. & D. W. Roberts. 1993. Fire and succession in oak-maple upland forests: a modelling approach based on vital attributes. Pp. 217-237 In: Fralish, R.S, R. P. McIntosh, & O.L. Loucks (eds.) *John T. Curtis, Fifty Years of Wisconsin Plant Ecology*. Wisconsin Academy of Sciences, Arts & Letters, Madison.
- Witham, J. H. & J. M. Jones. 1990. White-tailed deer abundance on metropolitan forest preserves during winter in northeastern Illinois. *Wildlife Society Bulletin* 18: 13-16.