RESEARCH ARTICLE

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Forest Succession in an Oak-Hickory Dominated Stand During a 40-Year Period at the Ross Biological Reserve, Indiana

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ABSTRACT: Deciduous forests in the eastern United States have been dynamic over both geological and historical time scales, particularly since humans have modified the landscape. Historically, the central hardwood forest has been subject to considerable human disturbance, especially fire, and these anthropogenic disturbances have contributed to the dominance of shade-intolerant oak (*Quercus*) and hickory (*Carya*) species within the central hardwood region. Current research indicates that many of these forests are changing to dominance by shade-tolerant species, mainly sugar maple (*Acer saccharum* Marsh.). This change has been attributed to a lack of disturbance. The objective of this study was to document long-term changes in structure and composition of a mature oak-hickory stand at the Ross Biological Reserve in Indiana. There has been little disturbance at the Ross Biological Reserve in the past 55 years, and a similar trend of increased shade-tolerant species was expected. Results of decadal tree censuses suggest that a successional change toward the dominance of sugar maple has been occurring during the 40-year study period, and an abundance of sugar maple saplings suggests that the increasing importance of sugar maple will continue with a lack of disturbance. The increased abundance of sugar maple may be having a negative effect on regeneration of oak-hickory species as well as on understory species such as flowering dogwood (*Cornus florida* L.). Such changes in the plant community also suggest changes in resources for animals. Management of the Ross Biological Reserve, and similar areas, requires an appreciation of forest dynamics on a variety of time scales.

Index terms: central hardwood region, disturbance, forest succession, sugar maple

INTRODUCTION

Changes in the species composition of plant communities are the result of individual and population-level changes on variable time scales due to disturbance, dispersal, interspecific interactions, and/or biological modification of the site. Historically, midwestern and eastern United States hardwood forests have been subject to considerable human disturbance. Native Americans began using fire to alter forest communities long before European settlement (Parker 1989, Delcourt and Delcourt 1997). Charcoal records indicate that fire was a regular ingredient of the deciduous forest community on the Allegheny plateau for thousands of years (Delcourt and Delcourt 1997). During the 1600-1800s, Europeans invaded North America and used fire to manage the landscape, in addition to introducing disturbances from livestock grazing, logging, and large-scale agriculture. These combined effects contributed to the reduction of the central hardwood forest from more than 140 million hectares to a highly fragmented 4 million hectares (Parker 1989). The remaining forest was dominated by oak (*Quercus* spp.), chestnut (*Castanea* spp.) and hickory (*Carya* spp.) (Schlessinger 1976, Parker 1989, Ward and Parker 1989, Boerner 1991, McGee 1996). Low-intensity fires cleared out shade-tolerant species of mesic forests, such as maples (*Acer* spp.), reducing competition and promoting sprouting of more fire-tolerant species. Oaks and hickories are more tolerant of fires because of their thick bark and active resprouting of seedlings and saplings (Harrod et al. 1998). Human disturbance thereby maintained forests (Bormann and Likens 1979) consisting of oak, hickory, chestnut, ash (*Fraxinus*), poplar (*Liroidendron*), sassafras (*Sassafras*), and dogwood (*Cornus*) (Goebel and Hix 1996).

Currently, the central hardwood region is undergoing another change, this time due to a lack of disturbance. In the early 1900s, forest management practices shifted to fire suppression as a principal goal, causing a dramatic shift in forest dynamics throughout eastern and midwestern North America (Spetich and Parker 1998). Hardwood forests in this region are going through a successional change from dominance by oaks and hickories to dominance by shade-tolerant and mid-tolerant tree species.

Throughout the central hardwood region, shade-tolerant sugar maple (*Acer saccharum* Marsh.) is increasing in abundance and expanding throughout hardwood forests. The increase of sugar maple has been documented in several areas including Illinois (Lindsey 1962, Clapp and Ebinger 1988, Shotola et al. 1992), Ohio (Cho and Boerner 1991), Central Missouri (Pallardy et al. 1988), West Virginia (Gilliam et al. 1995), and Indiana (Johnson et al. 1973, Jenkins and Parker 1998, Spetich and Parker 1998). The widespread increase in sugar maple is attributed mostly to fire suppression (Gilliam et al. 1995, Barton and Gleeson 1996, Spetich and Parker 1998).

Although several studies have documented an increase of sugar maple throughout the central hardwood region, few studies have monitored permanent plots over a long-term period (Schlesinger 1976, Shotola et al. 1992, Spetich and Parker 1998). The objective of this study was to document long-term changes in structure and composition of a mature oak-hickory stand at the Ross Biological Reserve in Indiana. We used detailed decadal forest surveys at permanent plots of both the canopy and understory to describe tree species composition and abundance. The data reveal successional trends in this hardwood forest during a 40-year period. Based on regional trends and a lack of major disturbance in the forest for 55 years, we expected a shift in dominance from oak and hickory species to the shade tolerant species, especially sugar maple. We also expected that sapling data would show greater regeneration of sugar maple and poor regeneration of oak and hickory species, because of the lack of disturbance within this forest stand.

METHODS

Study Area

This study was conducted at the Ross Biological Reserve, Tippecanoe County, Indiana (40° 24' N 87° 04' W). The Ross Biological Reserve of Purdue University is a 30 ha forest along the Wabash River. It is a mix of forest types, due to patchy soils from the river's edge to the glacial till plain and selective logging and grazing in the early 1900s until the Reserve was established in 1949. Since this time, no extensive cutting has occurred, resulting in a patchy distribution of oak-hickory dominated mature forest and second-growth forest.

Forest Survey

Complete inventories of all trees greater than 10 cm diameter at breast height (dbh) have been conducted at the Ross Reserve every 10 years since 1960 on a 5.4-ha plot within the mature oak-hickory slope. During Spring 2000, we re-sampled the previously established 5.4-ha plot. Data from previous surveys were taken from Delanglade (1961), Von Culin (1973), and from unpublished reports of surveys done by S. Austad and S. Wissinger in 1980 and by J. VanKley in 1990.

For each individual that was 10 cm dbh or greater, species and dbh were recorded, along with tag number if previously marked. Previously unmarked recruits into this size class were marked with numbered aluminum tags. Importance values were calculated as the sum of relative frequency, relative density, and relative dominance (Krebs 1994), and were calculated for all sampling years. Only species with 20 or more individuals in at least one survey were analyzed. Species were divided into groups based on stature (canopy or understory species). Canopy species were then grouped by population trends (increasing or decreasing abundance) since 1980. Diameter distributions were also generated by species for each survey year. The three-parameter Weibull probability density function was used to describe each diameter distribution (Shifley and Lentz 1985). Confidence intervals were also constructed for each Weibull shape parameter to determine if distributions were significantly skewed or normally distributed (Thoman et al. 1969).

Sapling Survey

A 2.6-ha sapling study plot was established which overlaps the forest survey plot. During the fall of 2000, we sampled every tree with a dbh of 2.5 cm or greater. For each individual, we recorded dbh, species, and tag number when possible. Sapling survey data was used to determine size class distributions of canopy species; understory species were not included in this analysis. Diameter distributions of trees sampled in the sapling study plot were also described using the Weibull probability function.

RESULTS

Forest Survey

The total number of individuals sampled was fairly consistent during the 40-year period, ranging from a low of 1700 in 1960 to a high of 1933 in 1980. The number of tree species recorded ranged from 25 to 28 species. The forest community included 14 canopy species with at least 20 individuals in at least one survey year. Five of these 14 species increased in abundance and nine decreased. Diameter distributions of all canopy species for all survey years (Figures 1 and 2) were all either positively skewed or normally distributed (shape parameter ranged from 1.35 to 3.06 for all species).

The canopy species increasing in abundance were tulip-poplar (*Liriodendron tulipifera* L.), sugar maple, American elm (*Ulmus Americana* L.), slippery elm (*Ulmus rubra* Muhl.), and hackberry (*Celtis occidentalis* L.). This group comprised 10% of total individuals in1960, 9% in 1970, 15% in 1980, 26% in 1990, and 42% in 2000. Each species in this group had its highest abundance in 2000, and all species increased in importance as well (Table 1).

Sugar maple increased in abundance more than any other species, from 34 individuals in 1960 and 39 in 1970, to 372 individuals in 2000, when it was the most abundant species. Sugar maple increased dramatically in importance (10.4 in 1980 to 34.1 in 2000), more than any other species, but was still less important than white oak (*Quercus alba*) (56.3 in 2000) (Table 1). Sugar maple increased steadily in rank of importance during the 40-year period, from 12th in 1960 to 2nd in 2000. The diameter distribution of sugar maple (Figure 1a) shows that the number of individuals in the smallest size class (10-19.9 cm dbh) increased greatly from 1980 to 2000, which was the primary reason for its increase in abundance and importance within the forest.

Other species increasing in abundance showed less dramatic change. Abundance of tulip poplar doubled over the 40 years,

Table 1. Importance values for canopy species for five sampling decades within the study plot. Importance values are the sum of relative frequency, relative density and relative abundance for trees > 10 cm dbh. First five species (bold) increased in abundance since 1980. Species ordered by group (increasing or decreasing abundance) and their importance rank in 2000.

Species Name	1960	1970	1980	1990	2000
Acer saccharum	8.10	8.81	10.66	20.30	33.67
Liriodendron tulipifera	19.72	19.35	20.90	24.47	24.76
Ulmus americana	8.99	6.04	10.21	13.61	17.32
Ulmus rubra	8.56	6.18	6.52	6.63	8.60
Celtis occidentalis	0.59	0.39	2.63	4.83	7.22
Quercus alba	64.26	66.29	63.68	59.46	55.86
Fraxinus americana	25.26	27.54	28.13	28.53	26.38
Quercus velutina	35.77	37.69	29.69	26.68	25.08
Carya glabra	30.27	23.92	24.39	21.55	20.58
Juglans nigra	23.58	24.75	21.58	21.09	20.13
Quercus rubra	18.48	17.81	20.61	18.53	16.96
Carya ovata	17.19	17.41	12.93	11.91	11.42
Carya cordiformis	8.47	13.07	13.85	11.80	11.31
Fraxinus pennsylvanica	7.63	6.43	1.93	1.36	1.41

but importance values changed little (Table 1). Increases in numbers of very small and very large tulip poplars were offset by declines in intermediate size classes (Figure 1b). American elm had the second highest increase in abundance of all species, increasing from 27 individuals in 1970 to 154 in 2000. American elm nearly doubled in importance over the 40 years (Table 1). Slippery elm was less abundant, with 43 individuals in 2000, and changed little in importance. Hackberry steadily increased in abundance to a high of 56 individuals in 2000 with a corresponding increase in importance (Table 1).

The canopy species decreasing in abundance since 1980 were white oak, red oak (*Quercus rubra* L.), black oak (*Quercus velutina* Lam.), shagbark hickory (*Carya ovata* (P.Mill) Koch), pignut hickory (*Carya glabra* (P.Mill) Sweet), bitternut hickory (*Carya cordiformis* (Wang) K.Koch), white ash (*Fraxinus Americana* L.), green ash (*Fraxinus pennsylvanica* Marsh.), and black walnut (*Juglans nigra* L.). This group comprised 85% of the total individuals in 1960, but decreased during the 40 years to a low of 54% in 2000.

White oak was the most abundant species from 1960 until 1990. In 2000, white oak (349 individuals) was surpassed by sugar maple with 372 individuals. White oak maintained its dominance in basal area throughout the study, having twice the basal area as the next highest species. White oak peaked in importance value in 1970 (Table 1). The diameter distribution of white oak (Figure 2a) shows a continual decrease in the number of individuals in the three smallest size classes during the 40-year period. Growth of established individuals is responsible for the increase in basal area of white oak during our study, with fewer individuals recruited into the smallest size classes.

Other canopy species declining in abundance also showed reduced recruitment. Red oak reached its highest abundance in 1980 with 98 individuals but declined to a low of 60 individuals in 2000; importance also declined since 1980 (Table 1). Black oak declined from a peak of 215 individuals in 1970 to 103 in 2000, and importance declined as well (Table 1). Black oak also showed reduced numbers in the smallest size classes, but growth in the largest (Figure 2b). Shagbark hickory reached a peak in abundance of 105 individuals in 1970, and since then continually declined to a low of 56 individuals in 2000. Its total basal area has remained fairly constant, and importance has changed little (Table 1). Pignut hickory had its highest abundance in 1960 with 198 individuals. Pignut hickory reached its peak in basal area in 1980, when it also peaked in importance, but has consistently declined since (Table 1). As in some of the oaks, the diameter distribution of pignut hickory showed a consistent decrease of individuals in the smallest size class since 1980 (Figure 2c). Diameter distributions of the other two hickory species were similar to that of pignut hickory. Bitternut hickory peaked in abundance, basal area, and importance in 1980 with 118 individuals declining to 73 in 2000 (Table 1).

White ash peaked in abundance in 1980 with 170 individuals, declining to 124 in 2000. However, white ash consistently increased in basal area, and its importance value changed little (Table 1). The diameter distribution of white ash (Figure 2d) showed a decrease in individuals for the three smallest size classes but growth in the three largest classes. Green ash peaked in abundance in 1960 with 37 individuals, and declined since in numbers, total basal area, and importance (Table 1). Black walnut reached its peak abundance in 1970 with 127 individuals, and declined to 82 individuals in 2000; importance declined slightly.

Understory tree species included sassafras (*Sassafras albidum* (Nutt.) Nees.), flowering dogwood (*Cornus florida* L.), redbud (*Cercis Canadensis* L.) and hophornbeam (*Ostrya virginiana* (P.Mill) K.Koch). These species contributed a maximum 7% of the total abundance in trees >10 cm dbh during the 40-year period. As a group, these understory species peaked in importance in 1980 and declined dramatically since (Table 2). Sassafras peaked in abundance in 1970 with 36 individuals, declining to

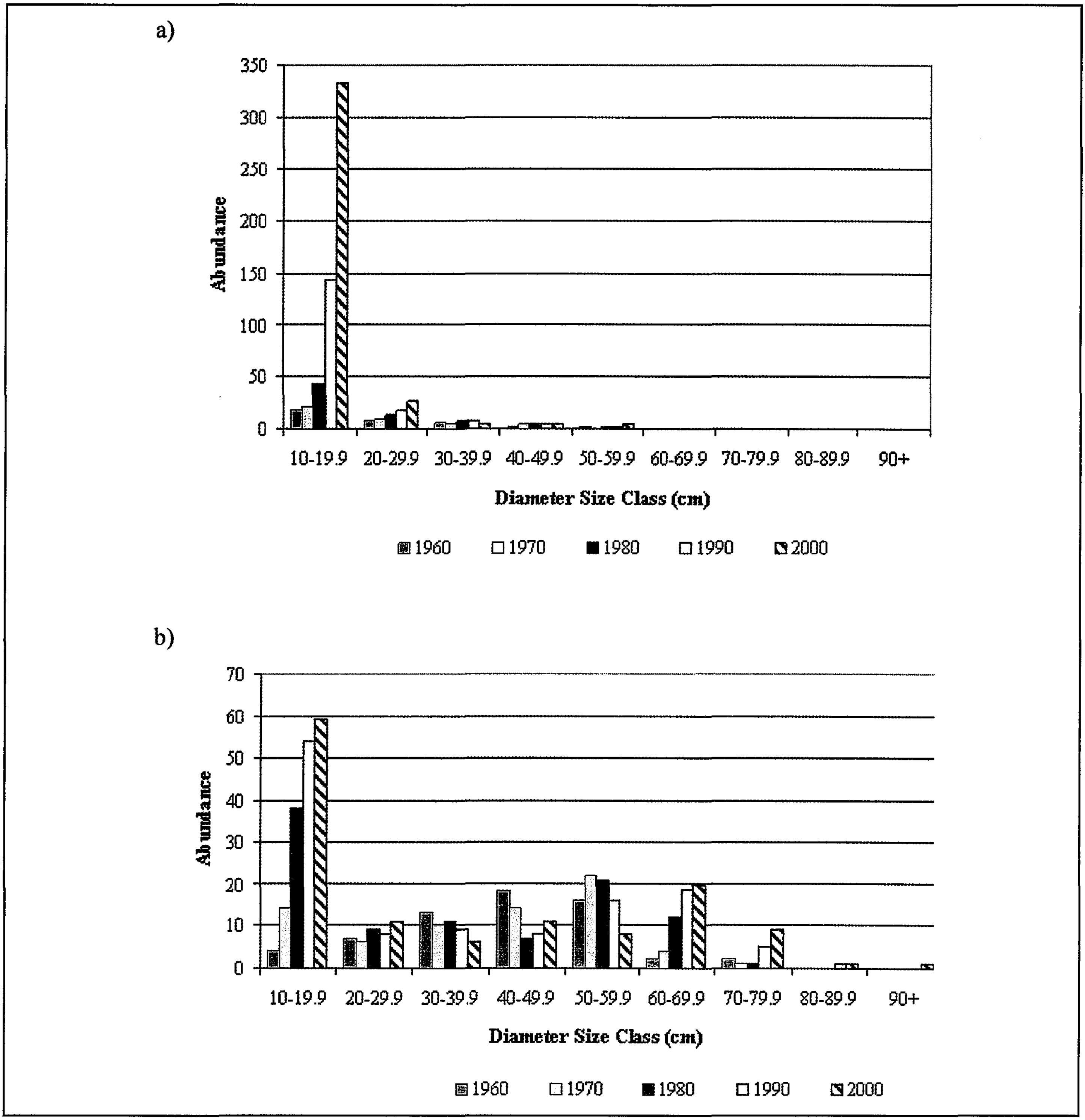

Figure 1. Diameter distribution by size class (cm dbh) of (a) sugar maple and of (b) tulip-poplar for all survey years.

11 in 2000, and importance declined as well (Table 2). Flowering dogwood abundance in the forest survey plot increased from 1960 to a peak of 42 individuals in 1980. Since 1980, dogwoods decreased in abundance to three individuals in 2000. Flowering dogwood also reached its highest basal area in 1980, declining to a minimum in 2000, when importance was also minimal (Table 2). Redbud had its highest abundance in 1970 with 22 individuals, decreasing to seven individuals in 2000. Importance of redbud declined as well (Table 2). Hophornbeam increased in abundance from 1960 to its peak in 1980 with 43 individuals, declining to 27 in 2000. Importance of hophornbeam also declined slightly since 1980 (Table 2).

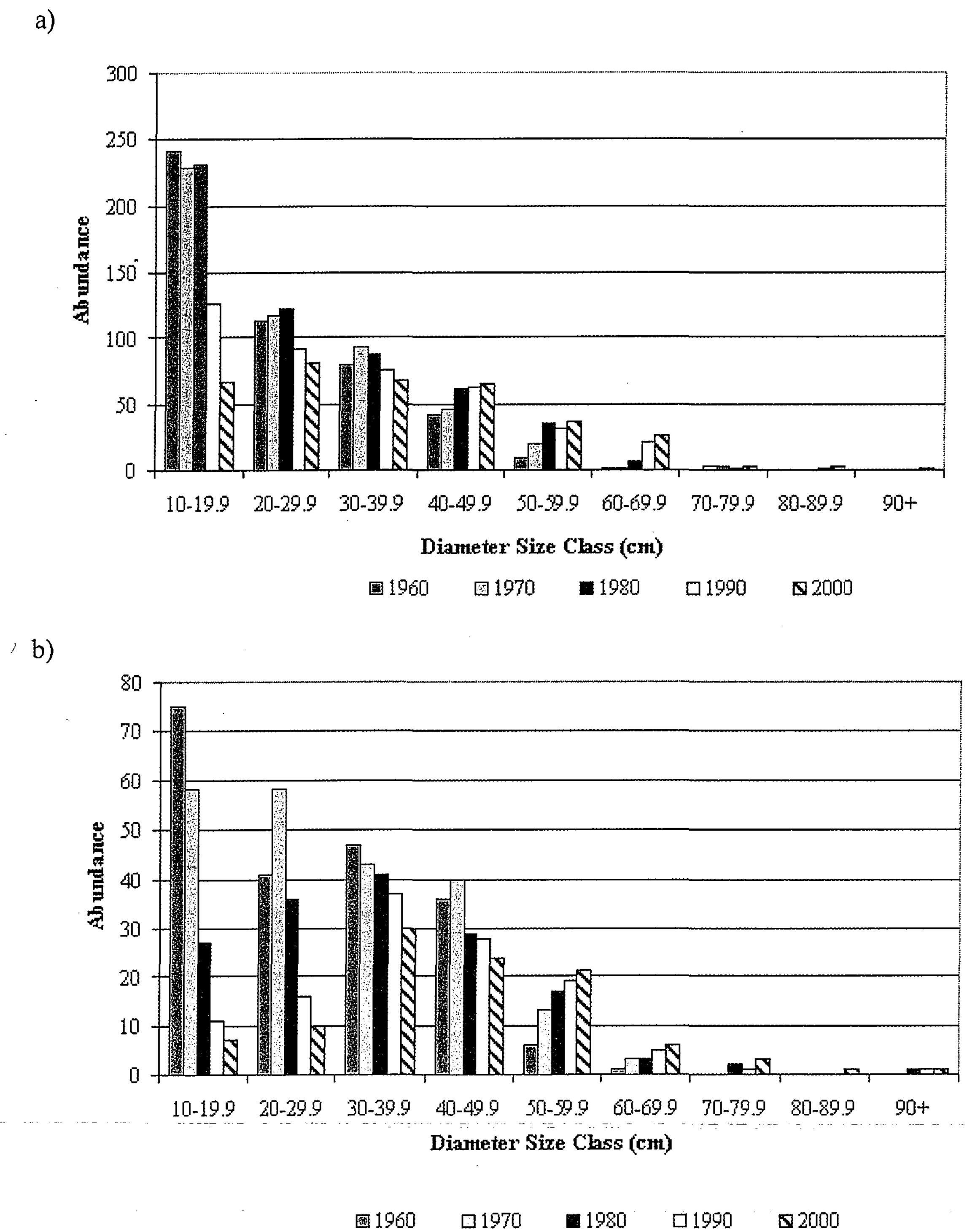

Figure 2. Diameter distribution by size class (cm dbh) of (a) white oak and of (b) black oak for all survey years.

Sapling Survey

The 2000 forest sapling survey included 24 species and 2340 individuals (dbb ≥ 2.5 cm). Of the total individuals sampled, 62% (1460 individuals) fell within our sapling definition (2.5 to 10 cm dbh). Only data collected on canopy species are presented. Canopy species that were increasing in abundance and importance comprised the most saplings; however, tulip poplar had only two saplings while sugar maple had 939 (64% of all saplings sampled). The diameter distribution of sugar maple within the sapling plot was positively skewed (Table 3). Both elm species also consisted mostly of saplings. American elm had 106 saplings of 149

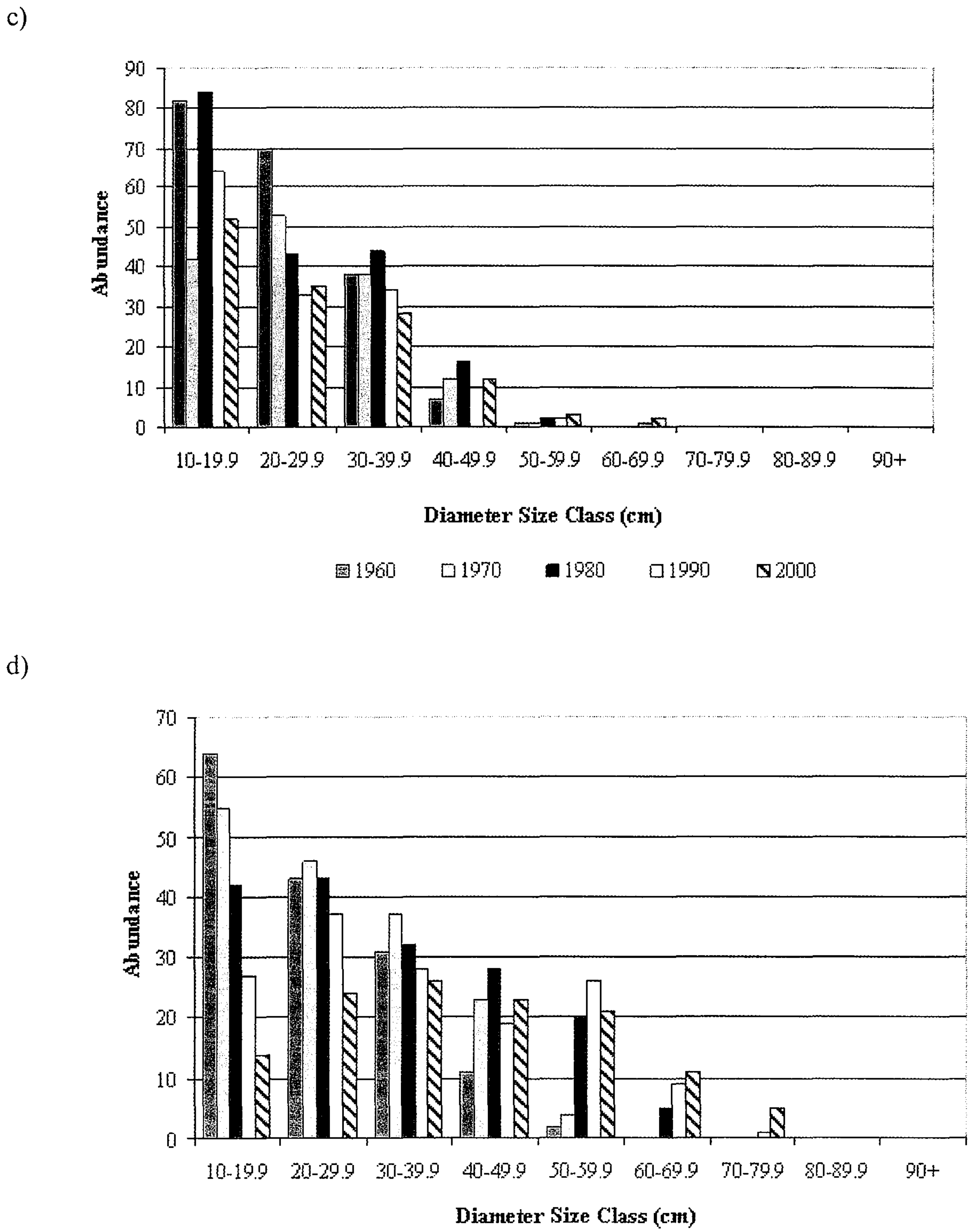

Figure 2 (continued). Diameter distribution by size class (cm dbh) of (c) pignut hickory and of (d) white ash for all survey years.

individuals and slippery elm consisted of 77 saplings of 127 individuals, leading to a positively skewed diameter distribution (Table 3). Hackberry also had a positively skewed diameter distribution, with 84 saplings of a total 108 individuals. Canopy species that were decreasing accounted for only 1% of all saplings (2.5 to 10 cm dbh). There was only one sapling of red oak and no saplings of either white oak or black oak. The diameter distribution of all oak species within the sapling plot was negatively skewed (Table 3) because of low sapling numbers. Hickory species had a normal diameter distribution, while all other decreasing canopy species had a negatively skewed diameter distribution (Table 3). In the sapling plot, white ash

Table 2. Importance values for understory species for five sampling decades within the study plot. Importance values are the sum of relative frequency, relative density, and relative abundance for trees > 10 cm dbh. Species are ordered by their importance rank in 2000.

Species Name	1960	1970	1980	1990	2000
Ostrya virginiana	3.15	3.67	6.83	6.35	5.28
Sassafras albidum	3.15	3.67	6.83	6.35	5.28
Cercis canadensis	1.54	3	3.73	3.19	1.99
Cornus florida	2.61	3.06	7.21	6.79	0.71

had four saplings of 53 individuals and no green ash saplings were found. Black walnut had four saplings of 38 individuals in the sapling plot.

DISCUSSION

Canopy tree species increasing in abundance and importance at the Ross Biological Reserve over a 40-year period are generally shade-tolerant species of mesic conditions (Burns and Honkala 1990), most notably sugar maple. With a lack of disturbance, these species would be expected to increase in abundance and importance. In contrast, species intolerant of shade but tolerant of fire and more xeric conditions, mainly oaks and hickories, are generally declining with little regeneration of saplings. Understory species are also declining in abundance.

The overall trend of increasing abundance and importance of shade-tolerant species, especially sugar maple, is consistent with most midwestern hardwood forest experiencing little disturbance by fire (Lindsey 1962, Clapp and Ebinger 1988, Pallardy et al. 1988, Parker 1989, Cho and Boerner 1991, Shotola et al. 1992, Gilliam et al. 1995, Barton and Gleeson 1996, Abrams 1998, Jenkins and Parker 1998, and Spetich and Parker 1998). An apparent exception among increasing species, tulip poplar is shade-intolerant and does not compete well under heavy shade. However, tulip poplar can overcome competition from shade-tolerant species through its prolific seed production and rapid growth (Burns and Honkala 1990). These attributes help tulip poplar take advantage of gap openings and increase in abundance as well as importance. Elms and hackberry also consistently increased in abundance but have not increased greatly in basal area. The restriction of elms to the understory is most likely due to Dutch elm disease (*Ceratocystis ulmi*) (Parker 1989).

Table 3. Weibull probability density function c-parameter estimate, 95% confidence interval, and curve shape for all trees >2.5 cm dbh in the sapling study plot.

Species Name	*N*	*c*	95% *CI*	Curve Shape
Acer saccharum	1261	1.96	1.89-2.04	Positively skewed
Liriodendron tulipifera	61	4.75	3.80-5.94	Negatively skewed
Celtis occidentalis	108	2.18	1.90-2.50	Positively skewed
***Ulmus* spp.**	276	2.14	1.96-2.32	Positively skewed
Quercus spp.	186	11.89	10.36-13.64	Negatively skewed
Carya spp.	93	3.06	2.58-3.63	Normal
Juglans nigra	38	3.90	2.89-5.28	Negatively skewed
Fraxinus americana	53	5.46	4.27-6.98	Negatively skewed

Sapling data provide a better understanding of the future forest at the Ross Biological Reserve. Sugar maple has become prominent in the understory as well as becoming the second most important species in the canopy. Increases in sapling abundance of sugar maple are common throughout the midwestern United States hardwood region (Lindsey 1962, Johnson et al. 1973, Cho and Boerner 1991). Sugar maple will continue to increase in importance in the future due to great abundance of sugar maple saplings, unless some factor increases mortality of these saplings. Other shade-tolerant species such as elm and hackberry are also recruiting well. Size-class distributions of both sugar maple and tulip poplar in the forest plot also suggest that these species will continue to increase in abundance and importance at the Ross Biological Reserve.

White oak, black walnut, and white ash have continued to increase in basal area throughout the study due to growth of existing individuals, not because of recruitment of new individuals. Other species that are declining overall have maintained a fairly constant basal area or have decreased since their year of peak abundance. The importance values of oak, hickory, ash, and walnut species at the Ross Reserve were at their peaks early in this study. By 1970, six of the nine species had reached their peak importance, only to decline since. The overall trend for oak, hickory, ash, and black walnut has been a declining importance with reduced disturbance. Bitternut hickory, white ash, and black walnut are classified as being shade-intolerant (Burns and Honkala 1990), while pignut hickory, shagbark hickory, and all three oak species are classified as intermediate in shade tolerance. These species do not, however, regenerate well under competition or heavy shade. The lack of disturbance for 55 years and competition from shade-tolerant species, mainly sugar maple, may explain the decreasing importance of these species at the Ross Biological Reserve.

Recruitment of oak, hickory, ash, and walnut species was minimal, with few individuals less than 10 cm dbh for all of these species combined. Size-class distributions of these species also demonstrate a lack of recruitment and continued growth of larger individuals. This suggests that these species may continue to be a main component in the forest in the near future, but that in the long term, abundance and importance are likely to decline. A similar trend has been observed in these species throughout the Midwest in hardwood forests that lack disturbance (Clapp and Ebinger 1988, Pallardy et al. 1988, Gilliam et al. 1995, Barton and Gleeson 1996, Jenkings and Parker 1998, and Spetich and Parker 1998).

Declines in abundance and importance of understory species (especially sassafras, flowering dogwood, and redbud) were similar, although most drastic in flowering dogwood. In a separate study over a larger area, flowering dogwood has declined by more than 50% since 1980, and this decline has been particularly acute in mesic areas where maple recruitment is strongest (Pierce et al., unpubl. data). These understory species are generally shade-intolerant (Burns and Honkala 1990), and the lack of disturbance recently at the Ross Reserve, leading to an increase in sugar maple, likely explains their decline. Maple species reduce light availability because their oval shape casts denser shade and their leaves unfold a month earlier than oak species, thus increasing the period of shading on understory species (Reisch et al. 1975). The rapid increase of sugar maple in the last two decades likely explains the dramatic concurrent decrease of most understory species. Hophornbeam, however, had increased in abundance and importance until 1980, and has since remained fairly stable. Hophornbeam is classified as shade-tolerant (Burns and Honkala 1990) and is common in the understory of beech and maple forests.

If the successional trend documented at the Ross Biological Reserve continues, the important mast producing oak and hickory species will continue to decline as well as the important soft mast producing understory species of flowering dogwood and sassafras. These declines will likely affect wildlife populations, as the mast they produce is an important food source for both birds and mammals (Weeks 1989). Continued research is needed to determine if the surge of sugar maple will continue or if local disturbances, such as canopy gaps, will allow the maintenance of a diverse canopy and understory. If a goal of forest management of areas like the Ross Biological Reserve is the maintenance of plant and animal diversity, then clearly this goal is a moving target in that species composition is likely to be dynamic. Successional change and invasion of exotic species over decades, along with changes such as those documented here that could take centuries to stabilize, mean that understanding forest dynamics is essential for realistic protection of biological diversity.

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LITERATURE CITED

Abrams, M.D. 1998. The red maple paradox. Bioscience 48:355-364.

Barton, A.M., and S.K. Gleeson. 1996. Ecophysiology of seedlings of oaks and red maple across a topographic gradient in eastern Kentucky. Forest Science 42:335-342.

Begon, M., J.L. Harper, and C.R. Townsend. 1990. Ecology: Individuals, Populations and Communities. 2nd ed. Blackwell Scientific, Boston, Mass.

Boerner, R.E.J. 1991. Vegetation of Drew Woods an old-growth remnant in western Ohio and issues of preservation. Natural Areas Journal 11:48-54.

Bormann, F.H., and G.E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. American Scientist 67:660-669.

Burns, R.M, and B.H. Honkala (eds.). 1990. Silvics of North America, Vol. 2, Hardwoods. Agriculture Handbook 654, U.S. Forest Service, Washington, D.C.

Cho, D.S., and R.E.J. Boerner. 1991. Canopy disturbance patterns and regeneration of *Quercus* species in two Ohio old-growth forests. Vegetatio 93:9-18.

Clapp, L.A., and J.E. Ebinger. 1988. Vegetation survey of Rock Branch Nature Preserve, Clark County, Illinois. Transactions of the Illinois Academy of Science 81:9-18.

Delanglade, R.A. 1961. The vegetation and flora of the Ross Biological Reserve. M.S. thesis, Purdue University, West Lafayette, Ind.

Delcourt, H.R., and P.A. Delcourt. 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. Conservation Biology 11:1010-1014.

Gilliam, F.S., N.L. Turrill, and M.B. Adams. 1995. Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forest. Ecological Applications 5:947-955.

Goebel, P.C., and D.M. Hix. 1996. Development of mixed-oak forests in southeastern Ohio: a comparison of second-growth and old-growth forests. Forest Ecology and Management 84:1-21.

Harrod, J., P.S. White, and M.E. Harmon. 1998. Changes in xeric forests in western Great Smoky Mountains National Park, 1936-1995. Castanea 63:346-360.

Jenkins, M.A., and G.R. Parker. 1998. Composition and diversity of woody vegetation in silvicultural openings of southern Indiana forests. Forest Ecology and Management 109:57-74.

Johnson, H.S., J.S. Berkebile, and G.R. Parker. 1973. An ecological inventory of Bryan Nature Preserve. Proceedings of the Indiana Academy of Science 83:167-172.

Krebs, C.J. 1994. Ecology: the Experimental Analysis of Distribution and Abundance. HarperCollins College Publishers, New York.

Lindsey, A.A. 1962. Analysis of an original forest of the lower Wabash floodplain and upland. Proceedings of the Indiana Academy of Science 72:282-287.

McGee, C.E. 1996. Loss of *Quercus* spp. Dominance in an undisturbed old-growth forest. Journal of the Elisha Mitchell Scientific Society 102:380-389.

Pallardy, S.G., T.A. Nigh, and H.E. Garrett. 1988. Changes in forest composition in central Missouri: 1968-1982. American Midland Naturalist 120:380-389.

Parker, G.R. 1989. Old-growth forests of the Central Hardwood Region. Natural Areas Journal 9:5-11.

Reisch, K.W., P.C. Kozel, and G.A.Weinstein (eds.). 1975. Woody ornamentals for the Midwest (deciduous). Kendall/Hunt, Dubuque, Iowa.

Schlesinger, R.C. 1976. Hard maples increasing in an upland hardwood stand. Proceedings of the Central Hardwood Forest Conference 1:177-185.

Shifley, S.R., and E. Lentz. 1985. Quick estimation of the three-parameter Weibull to describe tree size distributions. Forest Ecology and Management 13:195-203.

Shotola, S.J., G.T. Weaver, P.A. Robertson, and W.C. Ashby. 1992. Sugar maple invasion of an old-growth oak-hickory forest in southwestern Illinois. American Midland Naturalist 127:125-138.

Spetich, M.A., and G.R. Parker. 1998. Distribution of Biomass in an Indiana old-growth forest from 1926-1992. American Midland Naturalist 139:90-107.

Thoman, D.R., L.J. Bain, and C.E. Antle. 1969. Inferences on the parameters of the Weibull distribution. Technometrics 11:445-460.

Von Culin, H.J. 1973. Two decades of vegetational and floristic change in the Ross Biological Reserve, Tippecanoe County, Indiana. Ph.D. diss., Purdue University, West Lafayette, Ind.

Ward, J.S., and G.R. Parker. 1989. Spatial dispersion of woody regeneration in an old-growth forest. Ecology 70:1279-1285.

Weeks, H.P, Jr. 1989. Mast importance, production, and management. Central Hardwood Notes, U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn.