

Structural and compositional dynamics of a near-natural temperate deciduous forest in the central United States

Author(s): Robert C. Morrissey, Nathan T. King, John R. Seifert and Douglass F. Jacobs

Source: *The Journal of the Torrey Botanical Society*, Vol. 139, No. 4 (OCTOBER-DECEMBER 2012), pp. 379-390

Published by: Torrey Botanical Society

Stable URL: <http://www.jstor.org/stable/41811878>

Accessed: 21-12-2016 14:51 UTC

## REFERENCES

Linked references are available on JSTOR for this article:

[http://www.jstor.org/stable/41811878?seq=1&cid=pdf-reference#references\\_tab\\_contents](http://www.jstor.org/stable/41811878?seq=1&cid=pdf-reference#references_tab_contents)

You may need to log in to JSTOR to access the linked references.

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://about.jstor.org/terms>



*Torrey Botanical Society* is collaborating with JSTOR to digitize, preserve and extend access to *The Journal of the Torrey Botanical Society*

# Structural and compositional dynamics of a near-natural temperate deciduous forest in the central United States<sup>1</sup>

Robert C. Morrissey<sup>2</sup> and Nathan T. King

Department of Forestry and Natural Resources, Hardwood Tree Improvement and Regeneration Center, Purdue University, West Lafayette, IN 47907-2061

John R. Seifert

Indiana DNR Division of Forestry, 402 West Washington Street, Room W296, Indianapolis, IN 46204-2739

Douglass F. Jacobs

Department of Forestry and Natural Resources, Hardwood Tree Improvement and Regeneration Center, Purdue University, West Lafayette, IN 47907-2061

MORRISSEY, R. C. AND N. T. KING (Department of Forestry and Natural Resources, Hardwood Tree Improvement and Regeneration Center, Purdue University, West Lafayette, IN 47907-2061), J. R. SEIFERT (Indiana DNR Division of Forestry, 402 West Washington Street, Room W296, Indianapolis, IN 46204-2739), AND D. F. JACOBS (Department of Forestry and Natural Resources, Hardwood Tree Improvement and Regeneration Center, Purdue University, West Lafayette, IN 47907-2061). Structural and compositional dynamics of a near-natural temperate deciduous forest in the central United States. *J. Torrey Bot. Soc.* 139: 379–390. 2012.—Pioneer Mothers' Memorial Forest is a unique largely undisturbed, mixed mesophytic hardwood forest in south-central Indiana, USA. We report on 26 years of change in community composition and structure; plots were previously sampled in 1978 and 1989. In 2004, we re-measured trees  $\geq 5$  cm in diameter for 153 permanent plots, as well as downed woody debris, and standing dead trees. In 1978, density was 718 stems  $\text{ha}^{-1}$  and basal area 26.2  $\text{m}^2 \text{ha}^{-1}$ , but by 2004 density had decreased to 493 stems  $\text{ha}^{-1}$  with an increase in basal area to 31.4  $\text{m}^2 \text{ha}^{-1}$ . Large density decreases were attributed to *Acer saccharum*, *Sassafras albidum*, *Juniperus virginiana*, and *Cornus florida* mortality, while basal area increased largely because of *Liriodendron tulipifera* and *A. saccharum* growth. The stand exhibited a reverse-J diameter distribution, but density in the lower diameter classes,  $< 15$  cm, greatly decreased over time. The overstory (trees  $\geq 25$  cm) was dominated by *A. saccharum*, *L. tulipifera*, *Quercus* spp., and *Fagus grandifolia*. The understory was dominated by *A. saccharum*, which also accounted for  $> 60\%$  of the ingrowth over the observed period. Diversity exhibited a significant decline between 1978 and 1989 and a negative trend overall. Annual stand mortality averaged 2.2% since 1978, with a U-shaped distribution of high mortality rates in the smallest and largest diameter classes. Most plots (62%) experienced multiple canopy tree deaths, but were not sufficiently large to allow for the ingrowth of *Quercus* spp. Very few members of shade-intolerant species that dominated the canopy were able to attain canopy status, excepting *L. tulipifera* stems characterized by good growth rates (mean 7  $\text{mm yr}^{-1}$ ). Down woody debris and standing dead trees were moderately abundant in varying states of decay across all diameter classes. Without any major disturbance or understory disturbance, shade-intolerant species, notably *Quercus* and *Carya* spp., will likely be very limited in the stand, and the forest canopy will eventually be dominated by *A. saccharum* and *F. grandifolia*. This study highlights the importance of long-term studies of forest species composition and structure to understand forest ecosystem dynamics.

Key words: Central Hardwood Region, long-term monitoring, mixed mesophytic forest, near-natural.

Forests are no longer valued solely for their ability to produce timber, rather, it is widely recognized that forests foster and protect biodiversity, water resources, biogeochemical cycling, carbon sequestration, and aesthetics. Management plans are increasingly required to consider and protect these values, thus,

forest management and conservation efforts have increasingly focused on natural stand dynamics and structure as a means to enhance and preserve biodiversity and ensure sustainable ecosystem functioning (Attiwill 1994, Landres et al. 1999, Seymour et al. 2002). Attributes such as forest structure and composition are commonly used as indicators of 'naturalness', a term often used to describe the ecological value of a forest ecosystem (Angermeier 2000, Burton and Macdonald 2011, McRoberts et al. 2012). Forest reserves are invaluable to understanding natural processes relatively undisturbed by man to enhance management of non-reserve forests. Long-term

<sup>1</sup> This project was funded by the United States Forest Service Hoosier National Forest. We would also like to thank three anonymous reviewers for their comments and revisions.

<sup>2</sup> Author for correspondence. E-mail: rmorris@purdue.edu

Received for publication February 15, 2012, and in revised form August 1, 2012.

documentation of their changes in structure, composition, and function over time is essential to better understanding forest ecosystems.

The Central Hardwood Forest Region was widely deforested during the 19<sup>th</sup> and 20<sup>th</sup> centuries as expanded populations removed forest cover for agricultural use (Johnson et al. 2002, Ponder 2004). Indiana forests are largely secondary forests established around the turn of the 20<sup>th</sup> century. These forests have been extensively disturbed by extensive clearcut harvesting (Ponder 2004), livestock grazing (Den Uyl 1961), and human and natural fire regimes (Abrams 1992, Abrams and Nowacki 2008), all of which favor shade-intolerant species such as *Quercus* spp. and *Liriodendron tulipifera* L. It is estimated that < 1% of these forests escaped harvest or catastrophic disturbance and may be considered old-growth forests (Parker 1989). The rarity of old-growth forests in this region makes these sites a valuable resource for long-term observations to provide a baseline of information to evaluate anthropogenic and non-anthropogenic effects over time. They can also provide guidance in formulating new management approaches, such as emulating natural disturbance regimes (Franklin et al. 2002, Seymour et al. 2002) or managing for characteristics of late-successional forest habitats and functions (Keeton 2006, Bauhus et al. 2009).

*Quercus* spp. are critical components of wildlife habitat, aesthetics, and culture of the region. They are economically valuable for use in numerous wood products, and are important to secondary and tertiary producers. In many eastern forests, *Quercus* spp. are important to local economies and ecosystems, but they are being replaced with mesophytic species (e.g., *Acer* spp. and *Fagus grandifolia* Ehrh.) in forests dominated by small-scale disturbances, particularly on mesic sites (Pallardy et al. 1988, Abrams and Downs 1990, Abrams 1992). Advance *Quercus* regeneration is critical to ensure its long-term presence in forests dominated by small-scale disturbances, although seeding and high height growth rates combined with overstory disturbance may also allow for canopy ascension (Larsen and Johnson 1998). Historically, understory disturbances such as fire (Abrams 1992, Abrams and Nowacki 2008) and livestock grazing (Den Uyl 1961) limited growth of many *Quercus* competitors, but the ability of *Quercus* species to resprout gives them an advantage by

building root mass until an overhead disturbance allowed for their release (Larsen and Johnson 1998). Since the early 20<sup>th</sup> century, aggressive fire suppression efforts and limited understory disturbance have favored the development of more shade-tolerant species.

Near-natural forests within the Central Hardwood Forest Region are rare, thus the few remaining areas provide a valuable baseline resource to understand dynamics of these forest ecosystems. We investigated natural stand dynamics over a 26-year period in a mixed mesophytic hardwood stand in south-central Indiana. In particular, we were interested in the following questions:

- 1) How did woody plant species diversity and composition change over time?
- 2) How did stand structure, including basal area, density, and associated importance values change over time?
- 3) Are there patterns in tree mortality, ingrowth, and canopy ascension that explain changes in stand structure and composition?
- 4) How do the remnant structures compare to old-growth forests within the region?

**Study Area.** Contained within Indiana's Hoosier National Forest, Pioneer Mothers Memorial Forest (38° 32.36' N, 86° 27.22' W) is comprised by 32.4 ha of mainly undisturbed, virgin, mixed mesophytic hardwood forest that the US Forest Service acquired in 1941. The stand's age and majestic trees were unique characteristics in the region, prompting the US Forest Service to preserve the stand for its scientific and aesthetic values and declare it a Research Natural Area in 1944. Since the time of acquisition, two previous in-depth inventories have been conducted within the stand, but findings have not been fully reported (Schlesinger et al. 1994).

The Pioneer Mothers Memorial Forest is in the Shawnee Hills natural region (Homoya et al. 1985), characterized by unglaciated rolling uplands. Average annual precipitation is 114 cm and uniform throughout the year with average yearly minimum and maximum temperatures of 4.8 and 18.6 °C, respectively (Wingard 1984). Soils are shallow with rock outcroppings present on upper slopes and karst topography is common in the area. Typic Paleudults (Crider series), Typic Hapludults (Caneyville and Gilpin series), and Ultic Hapludalfs (Wellston series) are the major soil

types present. The stand is characterized by a mixed mesophytic forest type with an average of > 6 large (> 80 cm diameter at breast height) dominant overstory trees ha<sup>-1</sup>. There has been no evidence of harvest of live trees on the site, and the only recorded disturbances to the area were in the form of a small 1940s *Pinus echinata* Mill. (shortleaf pine) planting (< 1 ha), an old grazing area (< 2 ha), and a tornado in 1897, which caused blow down in a 160 m path along the northern section of the property (Potzger et al. 1942).

**Methods.** The study was initiated in 1978 with 153 permanent plots established on a 50 × 50 m grid. Trees with a diameter at breast height (dbh) > 15 cm were sampled using a 0.1 ha circular plot, and trees 5–15 cm dbh were sampled within a 0.01 ha concentric circular plot. Species, dbh, azimuth, and distance from plot center were recorded for each tree within plots. This sampling protocol was used during the 1978 and 1989 sampling periods. In addition, tree ingrowth and mortality were recorded since the previous measurement period. While the majority of these plots were located within undisturbed forest, some plots were located in areas that had experienced more recent disturbance but they could not be identified with certainty. Species nomenclature follows USDA Natural Resources Conservation Service (2009).

Permanent plots were re-sampled again in 2004 using the same basic methods; however, several new measurements were included to identify other aspects of stand dynamics. Decay status of standing dead trees was recorded; they were classified as ‘Tight bark’, ‘Loose bark’, and ‘Decomposing’, which were considered reflective of time since death in relative terms. Volume of downed woody material and decay class (1–5), assigned based on McCarthy and Bailey (1994) were also recorded in 0.1 ha plots; class 1: bark intact, small branches present; class 2: loose bark or sloughing; class 3: little to no bark, not decomposing; class 4: no bark, some decomposition present; class 5: no bark, extensive decomposition and fragmentation. Pieces that exhibited more than one decay category were assigned to the most prominent decay class. Diameter of downed woody material longer than 10 cm was measured at mid-point with calipers. Volume was calculated using Huber’s formula:

$$[(M^2/2) * 3.14 * L]/10000 = \text{Volume}(\text{m}^3)$$

where,  $M$  is the diameter of the down material measured at the mid-point, and  $L$  is piece length (cm) (Husch et al. 2003).

**DATA ANALYSIS.** We used standard descriptors of density (trees ha<sup>-1</sup>), basal area (BA; m<sup>2</sup> ha<sup>-1</sup>), relative frequency, and importance value (IV; [relative density + relative BA + relative frequency]/3) for tree populations within each sample period. To evaluate changes in diversity over the sample period, we used species richness ( $S$ ), and the Shannon diversity ( $H'$ ) and Pielou’s evenness ( $J'$ ) indices based on BA. To estimate variance of the Shannon diversity index for each period we used a jackknife procedure (Zahl 1977) and compared samples between periods using a paired  $t$ -test.

For several analyses, we grouped species by their tolerance of shade according to Niinemets and Valladares (2006); species with an index value ≤ 3.5 were considered intermediate or intolerant of shade, were classified as intolerant, and all species with an index value ≥ 3.5 were classified as tolerant (Appendix A). Within shade tolerance groupings, we classified species by groups including *Liriodendron tulipifera*, *Quercus* spp. (red and white) groups, intolerant hardwoods, *Acer saccharum* Marsh., *Fagus grandifolia* Ehrh., and tolerant hardwoods; other species were included in total values but were not considered otherwise (see Appendix A for details). Diameters were grouped in 5 cm diameter classes to evaluate stand structure over time.

Average annual mortality by diameter class was based on the entire sample period from 1978 to 2004 and calculated as exponential decays (Runkle 1998). Ingrowth (trees ≥ 5 cm) was examined for the 1989 and 2004 samples by species group. Overstory (trees ≥ 25 cm) mortality and ingrowth was evaluated by species groups for the 1989 and 2004 samples to evaluate the change in species composition over time. We used a Monte Carlo simulation of the chi-square test to evaluate if distributions of species group ingrowth and canopy mortality were equal to the overstory proportions of species groups in each sample period. We simulated the sampling distribution of the chi-squared test statistic based on 5,000 replicates and calculated the  $P$ -value based on the number of simulations that produced a

Table 1. Shannon index of diversity ( $H'$ ) (Shannon and Weaver 1949) and Pielou's evenness index ( $J'$ ) (Pielou 1966) for trees  $\geq 5$  cm for three sample periods. Maximum diversity ( $H'_{\max}$ ) is the maximum level of diversity within a population based on observed species richness ( $S$ ) in a given population. Changes in diversity based on basal area differences of paired plots by sample period using a paired  $t$ -test; standard deviation (SD),  $t$ -value, and  $P$ -value have been provided for each comparison.

	1978	1989	2004	1978–2004
$H'$	2.57	2.49	2.45	
$H'_{\max}$	3.53	3.56	3.53	
$J'$	0.73	0.70	0.70	
$S$	34	35	34	
$\Delta H'$	-	-0.082	-0.038	-0.12
SD	-	0.142	0.135	0.213
$t$	-	4.43	1.31	3.79
$P$	-	<0.001	0.192	<0.001

chi-squared value more extreme than our sample chi-square statistic; tests were considered significant at  $\alpha \leq 0.05$ . Density of canopy recruitment (trees  $\geq 25$  cm) by species group and their average annual growth rates are also presented. Remnant structures of standing dead trees and down woody debris volumes by diameter class and decay status were considered for the 2004 sample. All analyses were conducted using the R programming language (R Development Core Team 2011).

**Results.** STAND SPECIES COMPOSITION AND STRUCTURE. A total of 35 woody species were identified among all three samples, but loss of the lone *Carya alba* (L.) Nutt. left 34 species in the 2004 sample (Table 1). Shannon index of diversity exhibited a significant pattern of

decline over time from 2.57 to 2.45 ( $P < 0.001$ ), and evenness also declined from 0.73 to 0.70 indicating species distribution had become less even. Diversity exhibited a significant decline between 1978 and 1989 ( $P < 0.001$ ), but no difference between the 1989 and 2004 period ( $P = 0.192$ ). Twelve species had densities  $\leq 1$  tree  $\text{ha}^{-1}$  in 2004 with no increase in IV since 1978, thus, potentially indicating a lack of successful regeneration of those species (data not shown). Species that increased in IV between 1978 and 2004 include *Acer saccharum*, *Fagus grandifolia*, *Quercus rubra* L., *Quercus velutina* Lam., and *Liriodendron tulipifera* (Table 2). Those that exhibited large IV declines over the same period; *Fraxinus Americana* L., *Carya ovata* (P. Mill.) K. Koch, *Sassafras albidum* (Nutt.) Nees, *Juniperus virginiana* L., *Cornus florida* L., and *Juglans nigra* L. all show large declines in density and/or relative frequency. *Acer saccharum*, *Liriodendron tulipifera*, and *Quercus* spp., and, to a lesser degree, *F. grandifolia*, consistently dominated the stand in terms of BA in all three measurement periods. Ubiquitous nature of *A. saccharum* is evident, as it occurred in more than 90% of all plots in all periods.

Size distribution is an important characteristic of understanding stand dynamics. Density diameter class distribution of all stems in the three time periods displayed a typical reverse-J-shaped curve indicative of a balanced uneven-aged stand or an even-aged stratified mixture (Fig. 1). While shade-tolerant species densities have maintained the reverse-J-structure over time, shade-intolerant species appear

Table 2. Density (trees  $\text{ha}^{-1}$ ), basal area ( $\text{m}^2 \text{ha}^{-1}$ ), relative frequency, and importance value of most important tree species. Only those species with importance value  $> 0.05$  in 2004 sample are shown.

Species	Density (trees $\text{ha}^{-1}$ )			Basal area ( $\text{m}^2 \text{ha}^{-1}$ )			Relative frequency			Importance value		
	1978	1989	2004	1978	1989	2004	1978	1989	2004	1978	1989	2004
<i>Acer saccharum</i>	288	273	238	6.3	6.9	8.1	0.92	0.93	0.95	0.52	0.55	0.56
<i>Liriodendron tulipifera</i>	49	43	40	3.7	4.8	6.3	0.65	0.65	0.67	0.29	0.30	0.32
<i>Fagus grandifolia</i>	37	37	42	3.3	2.6	2.4	0.54	0.56	0.59	0.24	0.24	0.25
<i>Fraxinus americana</i>	29	17	11	1.2	1.2	1.5	0.50	0.50	0.50	0.21	0.20	0.18
<i>Quercus rubra</i>	8	8	7	1.4	1.8	2.3	0.40	0.40	0.40	0.17	0.17	0.18
<i>Carya ovata</i>	16	11	10	1.1	1.1	1.2	0.40	0.40	0.40	0.17	0.15	0.15
<i>Quercus alba</i>	11	7	7	1.4	1.6	1.9	0.30	0.30	0.30	0.13	0.13	0.13
<i>Quercus velutina</i>	10	8	7	1.2	1.4	1.7	0.30	0.30	0.30	0.12	0.12	0.13
<i>Quercus muehlenbergii</i>	8	6	6	0.8	0.9	1.1	0.30	0.30	0.30	0.13	0.12	0.12
<i>Sassafras albidum</i>	40	19	14	0.7	0.6	0.6	0.40	0.30	0.30	0.15	0.13	0.12
<i>Juniperus virginiana</i>	61	53	31	1.1	1.2	1.1	0.30	0.20	0.20	0.14	0.12	0.11
<i>Cornus florida</i>	83	61	37	0.6	0.4	0.3	0.40	0.30	0.20	0.16	0.14	0.10
<i>Juglans nigra</i>	6	4	4	1.1	0.8	0.8	0.40	0.30	0.20	0.13	0.10	0.09
<i>Ulmus rubra</i>	7	6	9	0.3	0.2	0.3	0.20	0.16	0.19	0.07	0.06	0.07
Totals	718	593	493	26.2	27.2	31.4						

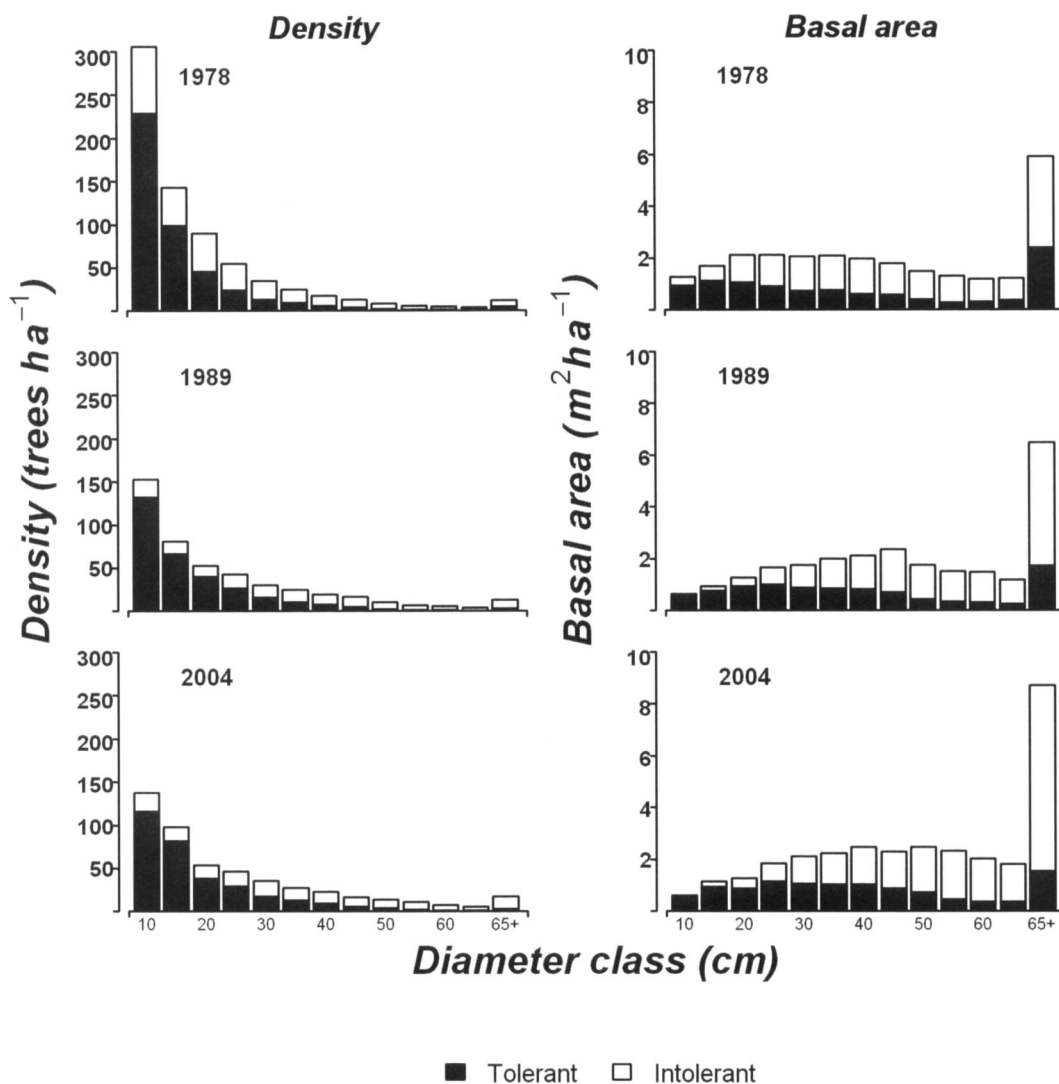


FIG. 1. Stand density (trees ha<sup>-1</sup>) and basal area (m<sup>2</sup> ha<sup>-1</sup>) diameter distribution averages classified by shade-tolerance for 1978, 1989, and 2004 samples. Values for dbh class represent upper limits of 5 cm diameter classes.

to be in transition from a reverse-J-structure to a more balanced structure across diameter classes. Tree distribution in terms of density and BA by diameter class and shade tolerance classification highlights the increasing relative prominence of shade-tolerant species in the smaller diameter classes over time (Fig. 1). In contrast, BA of shade-intolerant species of larger diameter classes is increasing proportionally over time, but decreasing in the smaller classes.

**MORTALITY AND RESIDUAL STRUCTURES.** Average annual mortality rate in the stand was 2.2% across all species from 1978 to 2004.

Annual mortality rates by diameter distribution showed a U-shaped distribution between 1978 and 2004 for both intolerant and tolerant species (Fig. 2). Intolerant species had high mortality rates, particularly in the smallest and largest diameter classes; in the 65+ cm diameter class, a large number of *Fagus grandifolia* trees accounted for the high rate of shade-tolerant deaths. Much of the mortality of intolerant species was related to *Sassafras albidum*, *Fraxinus americana*, *Juglans nigra*, and *Ulmus* spp., with almost 70% of those stems < 25 cm dbh (data not shown). *Liriodendron tulipifera*, *Carya* and *Quercus*

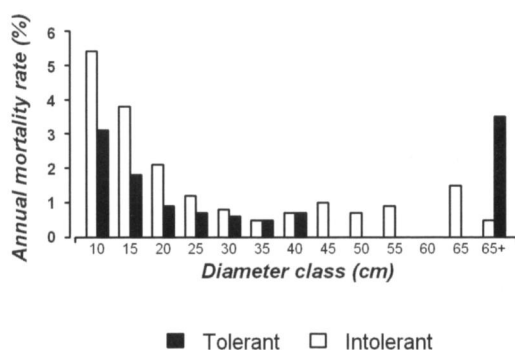


FIG. 2. Diameter class distribution of annual mortality rates classified by shade-tolerance. Values for dbh class represent upper limits of 5 cm diameter classes.

spp. groups, all had below average annual mortality rates, although more than 60% of members had dbh  $\geq 25$  cm. Despite the abundance of stems  $< 25$  cm dbh of *Acer saccharum*, annual mortality rates were well below average at 1.4%.

Mortality of canopy trees ( $\geq 25$  cm dbh) is an important mechanism in understanding stand dynamics. Of the 153 plots sampled, 131 experienced at least a single canopy tree mortality event between 1978 and 2004; of those, 63 plots had experienced the loss of a canopy tree upon re-sampling in both 1989 and 2004. Between 1978 and 2004, 24% of all plots lost a single canopy tree, but 62% of plots lost two or more canopy trees over that same period. Shade-intolerant stems accounted for the majority of canopy tree deaths, but in both 1978–1989 ( $\chi^2 = 0.493$ ;  $P = 1$ ) and 1989–2004 ( $\chi^2 = 0.281$ ;  $P = 1$ ) sample periods there were no differences in terms of expected

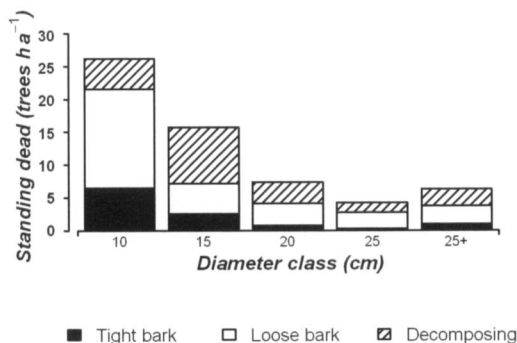


FIG. 3. Diameter class distribution of density (trees  $\text{ha}^{-1}$ ) of standing dead trees classified by state of decay in 2004 sample. Values for dbh class represent upper limits of 5 cm diameter classes.

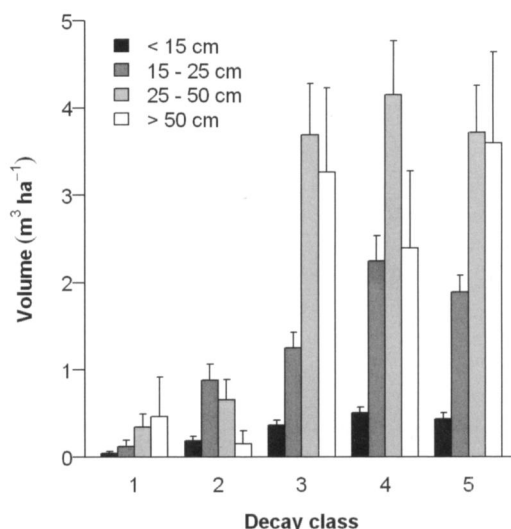


FIG. 4. Volume ( $\text{m}^3 \text{ha}^{-1}$ ) of downed woody debris classified by diameter at mid-point and state of decay in 2004 sample.

mortality by species group based on the existing overstory composition indicating no differences in mortality rates of overstory species groups. Of the approximately 23 canopy trees  $\text{ha}^{-1}$  that died over that period, most were blown over to decay on the forest floor. Approximately 6 (27%) canopy trees  $\text{ha}^{-1}$  remained standing after death (Fig. 3), with either the top still intact or blown off and sheared at a weak point along the stem, and at varying stages of decay. Understory ( $< 25$  cm) trees that died also contributed to residual structure with about 25% of trees between 5 and 25 cm dbh left standing after death, while stems  $> 10$  cm dbh appeared to remain standing longer in an advanced stage of decay. Not surprisingly, down woody debris  $< 15$  cm in size accumulated little volume, while pieces  $> 15$  cm were yielded far greater volumes, most of which was in more advanced states of decay, classes 3 to 5 (Fig. 4).

**INGROWTH.** The term ingrowth is used to describe trees that are sufficiently large ( $\geq 5$  cm dbh) to be sampled but were not present in the previous sample. Based on the overstory composition of the previous sample period, distribution of ingrowth by species group was significantly different in both 1989 ( $\chi^2 = 350.6$ ;  $P = 0.0002$ ) and 2004 ( $\chi^2 = 388.6$ ;  $P = 0.0002$ ). *Acer saccharum* dominated ingrowth of both sample periods, accounting for more than 60% of all ingrowth, much higher than

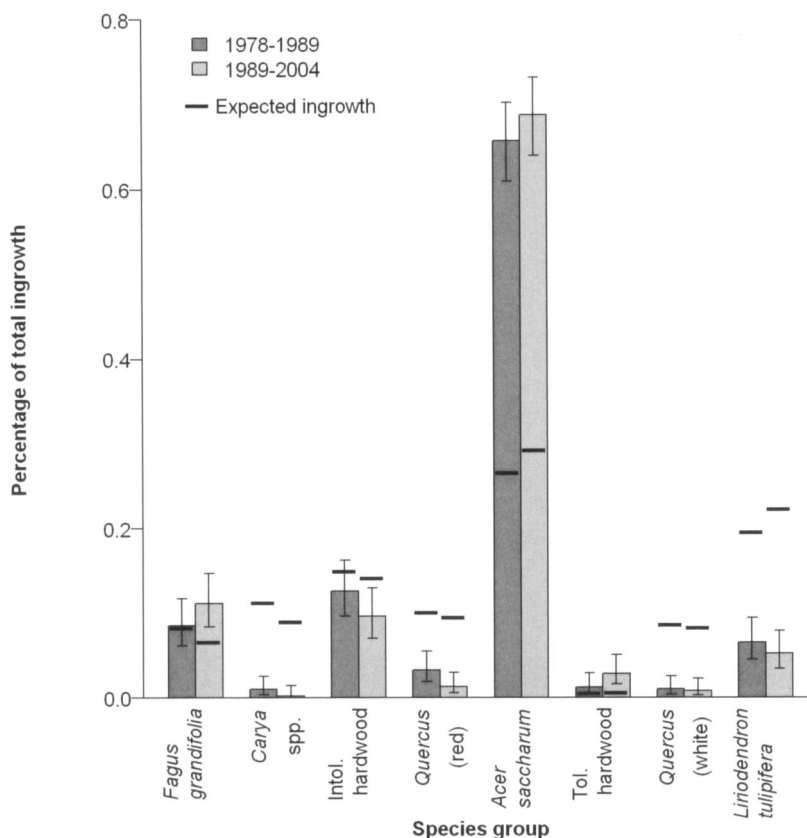


FIG. 5. Percentage of total ingrowth by species group for 1989 and 2004 inventories and 95% confidence intervals. Lines indicate expected ingrowth percentages for each species group and sample period based on percent species group composition of the overstory (trees  $\geq 25$  cm).

the expected estimates (Fig. 5). In contrast, *Liriodendron tulipifera*, *Carya* spp., and *Quercus* spp., groups that dominate the canopy accounted for less than 10% of ingrowth over the same period, much less than expected values. Although the intolerant hardwood group exhibited a relatively large number of ingrowth trees in each period, they are largely made up of *Ulmus* spp. and *Sassafras albidum*, species that exhibited high mortality rates. Ingrowth, however, is no guarantee of success. Recruitment of trees into the upper canopy (trees  $\geq 25$  cm dbh), a better indicator of competitiveness, was also dominated by *Acer saccharum* in terms of density in both periods despite low average annual dbh growth rates of 4 mm (Table 3). *Liriodendron tulipifera* showed mixed results in the two periods in terms of canopy recruitment, but annual dbh growth rates were among the highest. *Carya* and *Quercus* spp. groups had low canopy recruitment rates in both periods, although the

*Quercus* (red) group did exhibit comparable growth rates to *L. tulipifera*.

**Discussion.** Pioneer Mothers Memorial Forest exhibits many features characteristic of mesic Central Hardwood, old-growth forests. Although no samples were obtained to determine age, historical records indicate protection from harvest and abundance of very large commercial species signify many trees likely date back to the early 19th century and beyond. Diameter distribution, assumed to be at least partially reflective of the age diversity of the trees (Sano 1977, Tubbs 1977, Leak 1985), diverse canopy structure, abundance of canopy gaps, large downed logs and standing snags all characterize old-growth forests of the region (Parker 1986, Martin 1992, McCarthy 1995, Spetich et al. 1999). Long-term studies of forest composition and structure can provide invaluable insight into management efforts to promote and enhance biodiversity.



Table 3. Canopy recruitment (trees  $\geq 25$  cm dbh) by species group density (trees ha<sup>-1</sup>) and average annual dbh growth (mm yr<sup>-1</sup>) of trees during the 1978–1989 and 1989–2004 sample periods.

Species group	1978–1989		1989–2004	
	Density (trees ha <sup>-1</sup> )	Avg. annual growth (mm)	Density (trees ha <sup>-1</sup> )	Avg. annual growth (mm)
Tolerant				
<i>Acer saccharum</i>	8.8	4 $\pm$ 0.2	13.5	4 $\pm$ 0.2
<i>Fagus grandifolia</i>	1.0	4 $\pm$ 0.4	1.6	6 $\pm$ 1.1
Tolerant hardwood	0.3	10 $\pm$ 3.6	0.1	11 $\pm$ 7.3
Intolerant				
<i>Liriodendron tulipifera</i>	6.5	7 $\pm$ 0.3	3.7	7 $\pm$ 0.7
Intolerant hardwood	4.4	5 $\pm$ 0.5	4.4	4 $\pm$ 0.3
<i>Quercus</i> spp. (red)	0.9	7 $\pm$ 1.5	1.0	7 $\pm$ 1.3
<i>Quercus</i> spp. (white)	0.8	5 $\pm$ 2.2	0.7	5 $\pm$ 0.8
<i>Carya</i> spp.	0.5	2 $\pm$ 0.6	0.7	2 $\pm$ 0.5

STAND COMPOSITION. The *Liriodendron tulipifera* and *Quercus* spp. abundance in the overstory likely reflects past disturbance regimes, perhaps a single large disturbance event or a combination of disturbances, notably burning and small-scale canopy gaps (Abrams 1992, Abrams and Nowacki 2008), that perpetuate those species. Species composition corresponded closely to other previously studied old-growth forests (e.g., Parker et al. 1985, Shotola et al. 1992, Zaczek et al. 2002) with overstories similarly dominated by larger, shade-intolerant species, including *L. tulipifera* and *Quercus* spp., intermixed with more scattered large *Fagus grandifolia* and *Acer saccharum* (Table 2; Fig. 1). Increased importance of shade-tolerant species, notably *A. saccharum* and *F. grandifolia*, in the understory of a more diverse, predominantly shade-intolerant overstory was observed, and similar trends of increasing abundances of mesic species have been reported in numerous eastern old-growth forests (Schlesinger 1976, Parker et al. 1985, Abrams and Downs 1990, Shotola et al. 1992, Zaczek et al. 2002, Galbraith and Martin 2005). Despite observed decreases in absolute values of *A. saccharum*, this species increased in terms of relative density coinciding with a large increase in basal area (Table 2). Similarly, Zaczek et al. (2002) reported high mortality rates in *A. saccharum* accompanied by large increases in basal area and attributed changes to intense competition for light and resources in an overpopulated understory.

Despite ingrowth of intolerant hardwoods group (Fig. 5), largely *Sassafras albidum* and *Ulmus* spp., and their modest success in reaching the overstory (Table 3), their overall

mortality rates likely precluded them from attaining permanent positions in the canopy against the high ingrowth, canopy recruitment, and low mortality rates of larger *Acer saccharum*. Understory *Liriodendron tulipifera*, despite its low ingrowth numbers, < 3 trees ha<sup>-1</sup>, had low mortality rates and appeared sufficiently opportunistic to achieve some overstory canopy positions through high annual growth rates before canopy closure (Table 3). The low numbers of other shade-intolerant species, notably *Quercus* and *Carya* spp., indicate that they are at a disadvantage compared to *L. tulipifera*, which may be related to growth habits. *Quercus* spp. tend to invest resources into root growth rather than shoots when young (Johnson et al. 2002), and *Carya* spp. is typically a slow grower (Burns and Honkala 1990), but *L. tulipifera* exhibits rapid growth when conditions are favorable. Species tolerant of shade (e.g., *Acer saccharum*, *Fagus grandifolia*) were able to persist in the understory and reach overstory positions as smaller gaps were created, while fast-growing species, such as *L. tulipifera*, appeared able to establish in larger gaps and reach overstory positions before canopy closure, as Runkle (1998) observed in old-growth forests of North Carolina, USA. Regeneration and subsequent canopy recruitment of *Quercus* spp. historically relied on disturbance regimes that favored *Quercus* life history strategies, e.g., fire or grazing, and selected against their competitors (Larsen and Johnson 1998). Large declines in density of *Cornus florida* were observed between 1979 and 2004, and has been reported in other eastern old-growth forests (Zaczek et al. 2002, Galbraith and Martin 2005). This may be attributed to

shaded understory conditions, herbivory, or the fungus (*Discula destructive* Replin) that causes dogwood anthracnose.

In a previous study of Pioneer Mothers Memorial Forest, Schlesinger et al. (1994) used a subset of plots to evaluate changes in diversity between 1941 and 1989; they determined that the 37 years prior to permanent plot establishment, 1978, tree species diversity was increasing slightly, but, similar to our findings, they determined a statistically significant decline between 1978 and 1989. They decided because the rate of decrease from 1978 to 1989 was no greater than the rate of increase prior to 1978 the change was not biologically significant. Although our findings indicated no significant decline in diversity between 1989 and 2004, the overall trend of declining tree diversity over the 26 yr period may pose reason for concern and highlights the value of these long-term monitoring plots in near-natural forests.

**STAND STRUCTURE.** Despite a decrease in density over the course of almost three decades, total basal area increased from 26.2 m<sup>2</sup> ha<sup>-1</sup> in 1979 to 31.4 m<sup>2</sup> ha<sup>-1</sup> in 2004, due largely to increases in canopy trees of *Acer saccharum* and *Liriodendron tulipifera*, and, to a lesser degree, *Quercus* spp. (Table 2). Held and Winstead (1975) proposed that climax mesophytic forests exhibit basal areas of 25 to 32 m<sup>2</sup> ha<sup>-1</sup> (trees > 10 cm dbh), and despite large fluctuations in density on the site, basal area was within that range during the study period. Basal area increases and values are comparable to other reported values of eastern old-growth forests (Miceli et al. 1977, Schlesinger 1989, Shotola et al. 1992). The stand exhibited a reverse-J age distribution driven by small-scale natural disturbances and differential shade tolerance of species. In 1978, intolerant species made up a larger portion of the understory (Fig. 1), but, because of high mortality rates of intolerant species in diameter classes < 15 cm dbh (Fig. 2), by 2004, density of intolerants was more balanced across diameter classes, while basal area of overstory intolerants continued to increase (Fig. 1).

Death of overstory trees creates a shifting mosaic of patches that vary in size, composition, structure, shape, and successional stage (Runkle 1998, Franklin et al. 2002). The diversity of gaps was evident in terms of the number of overstory trees that died in individual plots during the sample period to

create new gaps, however, the low number of *Liriodendron tulipifera* and *Quercus* spp. in the understory indicated the gaps are not sufficiently large to allow for successful regeneration and self-replacement of these species. Smaller gap events scattered over long time periods release growing space more slowly, thus, favoring shade-tolerant species. Dendroecological studies of five eastern old-growth stands by Rentch et al. (2003) determined that overstory *Quercus* spp. endured understory residence times from 38 to 89 years prior to gap releases that allowed canopy recruitment and suggested that the level of understory shade was considerably less prior to 1900. Runkle (1998) observed that *L. tulipifera* regeneration was present in only 20% of gaps and responded to gap size and had higher relative densities in gaps that had experienced multiple tree fall events in both periods, while *Acer saccharum* showed no relationship to gap size or age but was present in 87% of gaps. Runkle (1998) proposed that gaps in those forests had served only to advance species already present in the understory. McCarthy et al. (2001) determined that a similar pattern observed in an old-growth mixed mesophytic forest in 1970 was present 30 years later, further highlighting the importance of overstory to understory relations.

Standing dead trees and downed wood are important elements of old-growth structure and function (Bauhaus et al. 2009). The diameter distribution of standing dead trees exhibited a reverse-J distribution, similar to live trees, with almost 60 snags ha<sup>-1</sup>, most of which were understory trees (Fig. 3). When trees ≥ 10 cm dbh were considered, snag density was 33.7 snags ha<sup>-1</sup>, which was similar to the mean number of snags Spetich et al. (1999) observed across 12 upland hardwood sites in the Central Hardwood Region, which included this study site. The ratio of live to dead standing trees observed, 0.095 for trees ≥ 10 cm dbh, was consistent with the reported mean of Spetich et al. (1999), 0.10, and 0.09 reported by Shifley et al. (1997). Downed woody debris averaged 30.4 m<sup>3</sup> ha<sup>-1</sup> (Fig. 4), which was lower than would be expected given it is a mesic site. It was within the range from all 12 sites reported by Spetich et al. (1999), but was low compared to the reported mean of 60 m<sup>3</sup> ha<sup>-1</sup>. Shifley et al. (1997) observed a mean of 36 m<sup>3</sup> ha<sup>-1</sup> across five old-growth sites in Missouri, which are more xeric sites in contrast to our study area.

Historically, eastern forests with frequent fire or other (e.g., grazing) understory disturbance regimes presumably had fewer structural elements, such as standing dead trees < 25 cm dbh, and lower inputs of downed woody debris and leaf litter because of frequent disturbance in forests that reduced shade-tolerant understory vegetation. Management efforts to restore historic disturbance regimes and stand structure based on observations of modern old-growth forests and their functional roles may be misleading without further evidence to explore historic forest structure. Caution is prudent when considering current management goals to recreate similar observed forest structures in forests that have had limited understory disturbances and include abundant small standing dead trees and downed woody debris, which presumably are far more abundant today because of the ingrowth and high mortality observed in smaller diameter classes. Modified understory structure and composition also have other implications that influence dynamics and function of old-growth forests; for example, differing composition and higher quantities of leaf litter may create an environment for seeds that favors survival of certain species (Spetich et al. 1997) or altered nutrient dynamics (Rodgers et al. 2008, Gómez-Aparicio and Canham 2008); mast availability and consumption by wildlife (McShea 2000, Schnurr et al. 2002, McShea et al. 2007); or altered neotropical bird habitat (Diaz et al. 2005, Barg et al. 2006, Bakermans and Rodewald 2009).

**Conclusion.** This study has reported a trend of declining diversity over 26 years. This near-natural forest appears to be in a late stage of succession with increasing importance of shade-tolerant species, notably *Acer saccharum*, and a concurrent decline of shade-intolerant *Quercus* and *Carya* spp. Their seeming inability to regenerate given current disturbance regimes is a trend that has been observed in several other eastern old-growth studies (Parker et al. 1985, Abrams and Downs 1990, Shotola et al. 1992, Zaczek et al. 2002). Given the current structure and composition of Pioneer Mothers Memorial Forest, without any major disturbance or understory disturbances to reduce competition, *Quercus* and *Carya* spp. will likely have limited roles in this stand, with a continued transition to a forest dominated by

*A. saccharum* and *Fagus grandifolia*. Replicating conditions under which these species historically regenerated is unlikely in modern natural areas protected from anthropogenic disturbance, however, unique natural areas such as these still have much to teach us about the past, as well as the future. Permanent plots allow for observation of successional changes against the background of not only protection, but also climate change, gypsy moth (*Lymantria dispar* L.), emerald ash borer (*Agrius planipennis* Fairmaire), and other invasive species, which can be used to help guide management and protection efforts.

### Literature Cited

- ABRAMS, M. D. 1992. Fire and the development of oak forests. *BioScience* 42: 346–353.
- ABRAMS, M. D. AND J. A. DOWNS. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. *Can. J. For. Res.* 20: 1864–1870.
- ABRAMS, M. D. AND G. J. NOWACKI. 2008. Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. *Holocene* 18: 1123–1137.
- ANGERMEIER, P. L. 2000. The natural imperative for biological conservation. *Cons. Biol.* 14: 373–381.
- ATTIWILL, P. M. 1994. The disturbance of forest ecosystems - the ecological basis for conservative management. *Forest Ecol. Manag.* 63: 247–300.
- BAKERMANS, M. H. AND A. D. RODEWALD. 2009. Think globally, manage locally: The importance of steady-state forest features for a declining songbird. *Forest Ecol. Manag.* 258: 224–232.
- BARG, J. J., D. M. AIAMA, J. JONES, AND R. J. ROBERTSON. 2006. Within-territory habitat use and microhabitat selection by male Cerulean Warblers (*Dendroica cerulea*). *The Auk*. 123: 795–806.
- BAUHUS, J., K. PUETTMANN, AND C. MESSIER. 2009. Silviculture for old-growth attributes. *Forest Ecol. Manag.* 258: 525–537.
- BURNS, R. M. AND B. M. HONKOLA, tech. cords. 1990. *Silvics of North America: Volume 2: Hardwoods*. USDA For. Serv. Agric. Handb. 654. Washington, DC.
- BURTON, P. J. AND S. E. MACDONALD. 2011. The restorative imperative: Challenges, objectives and approaches to restoring naturalness in forests. *Silva Fenn.* 45: 843–863.
- DEN UYL, D. 1961. Natural tree reproduction in mixed hardwood stands. *Purdue Univ. Agric. Exp. Stn. Res. Bull.* 728. 19 p.
- DÍAZ, I. A., J. J. ARMESTO, S. REID, K. SIEVING, AND M. F. WILLSON. 2005. Linking forest structure and composition: avian diversity in successional forests of Chiloé Island, Chile. *Biol. Cons.* 123: 91–101.
- FRANKLIN, J. F., T. A. SPIES, R. VAN PELT, A. CAREY, D. THORNBURGH, D. R. BERG, D. LINDENMAYER, M. HARMON, W. S. KEETON, D. C. SHAW, K. BIBLE, AND J. CHEN. 2002. Disturbances

- and the structural development of natural forest ecosystems with some implications for silviculture. *Forest Ecol. Manag.* 155: 399–423.
- GALBRAITH, S. L. AND W. H. MARTIN. 2005. Three decades of overstory and species change in a mixed mesophytic forest in eastern Kentucky. *Castanea* 70: 115–128.
- GÓMEZ-APARICIO, L. AND C. D. CANHAM. 2008. Neighborhood models of the effects of invasive tree species on ecosystem processes. *Ecol. Monogr.* 78: 69–86.
- HELD, M. E. AND J. E. WINSTEAD. 1975. Basal area and climax status in mesic forest systems. *Ann. Bot.* 39: 1147–1148.
- HOMOYA, M. A., D. B. ABRELL, J. D. ALDRICH, AND T. W. POST. 1985. The natural regions of Indiana. *Proc. IN Acad. Sci.* 94: 245–268.
- HUSCH, B., T. W. BEERS, AND J. A. KERSHAW, JR. 2003. *Forest mensuration*. John Wiley & Sons, Inc., Hoboken, NJ. 456 p.
- JOHNSON, P. S., S. R. SHIFLEY, AND R. ROGERS. 2002. *The ecology and silviculture of oaks*. CABI Publishing, New York, NY. 503 p.
- KEETON, W. S. 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *Forest Ecol. Manag.* 235: 129–142.
- LANDRES, P. B., P. MORGAN, AND F. J. SWANSON. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* 9: 1179–1188.
- LARSEN, D. R. AND P. S. JOHNSON. 1998. Linking the ecology of natural oak regeneration to silviculture. *Forest Ecol. Manag.* 106: 1–7.
- LEAK, W. B. 1985. Relationships of tree age to diameter in old-growth northern hardwoods and spruce-fir. *Res. Note NE-329*. Broomall, PA: U.S. Dept. of Ag., USFS, Northeastern For. Exper. Stn. 4 p.
- MARTIN, W. H. 1992. Characteristics of old-growth mixed mesophytic forests. *Nat. Area. J.* 12: 127–135.
- MCCARTHY, B. C. 1995. Eastern old-growth forests. *Ohio Woodland J.* 2: 8–10.
- MCCARTHY, B. C. AND R. R. BAILEY. 1994. Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. *Can. J. For. Res.* 24: 1317–1329.
- MCCARTHY, B. C., C. J. SMALL, AND D. L. RUBINO. 2001. Composition, structure, and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. *Forest Ecol. Manag.* 140: 193–213.
- MCROBERTS, R. E., S. WINTER, G. CHIRICI, AND E. LAPPOINT. 2012. Assessing forest naturalness. *For. Sci.* 58: 294–309.
- MCSHEA, W. J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. *Ecol.* 81: 228–238.
- MCSHEA, W. J., W. M. HEALY, P. DEVERS, T. FEARER, F. H. KOCH, D. STAUFFER, AND J. WALDON. 2007. Forestry matters: decline of oaks will impact wildlife in hardwood forests. *J. Wildl. Manag.* 71: 1717–1728.
- MICELI, J. C., G. L. ROLFE, D. R. PELZ, AND J. M. EDGINGTON. 1977. *Brownfield Woods*, Illinois: woody vegetation and changes since 1960. *Am. Midl. Nat.* 98: 469–475.
- NIINEMETS, U. AND F. VALLADARES. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecol. Monogr.* 76: 521–547.
- PALLARDY, S. G., T. A. NIGH, AND H. E. GARRETT. 1988. Changes in forest composition in Central Missouri: 1968–1982. *Am. Midl. Nat.* 120: 380–390.
- PARKER, G. R. 1989. Old-growth forests of the central hardwood region. *Nat. Area. J.* 9: 5–11.
- PARKER, G. R., D. J. LEOPOLD, AND J. K. EICHENBERGER. 1985. Tree dynamics in an old-growth, deciduous forest. *Forest Ecol. Manag.* 11: 31–57.
- PIELOU, E. C. 1966. The measurement of diversity of different types of biological collection. *J. Theor. Biol.* 13: 131–144.
- PONDER, F., JR. 2004. Ecological regions and soil conditions in the Hoosier-Shawnee ecological assessment area, p. 9–22. *In* F. R. Thompson, III [ed.], *The Hoosier-Shawnee Ecological Assessment*. USDA For. Serv. Gen. Tech. Rep. NC-244.
- POTZGER, J. E., R. C. FRIESNER, AND C. O. KELLER. 1942. *Phytosociology of the Cox Woods: A remnant of the forest primeval in Orange County, Indiana*. Butler University Botanical Studies 5: 190–221.
- R DEVELOPMENT CORE TEAM. 2011. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- RENTCH, J. S., M. A. FAJVAN, AND R. R. HICKS. 2003. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region. *Forest Ecol. Manag.* 184: 285–297.
- RODGERS, V. L., B. E. WOLFE, L. K. WERDEN, AND A. C. FINZI. 2008. The invasive species *Alliaria petiolata* (garlic mustard) increases soil nutrient availability in northern hardwood-conifer forests. *Oecologia* 157: 459–471.
- RUNKLE, J. R. 1998. Changes in southern Appalachian canopy tree gaps sampled thrice. *Ecology* 79: 1768–1780.
- SANO, J. 1997. Age and size distribution in a long-term forest dynamics. *Forest Ecol. Manag.* 92: 39–44.
- SCHLESINGER, R. C. 1976. Hard maples increasing in an upland hardwood stand, p. 177–186. *In* J. S. Fralish, G. T. Weaver, and R. C. Schlesinger [eds.], *Proceedings of the Central Hardwood Forest Conference*. Southern Illinois University, Carbondale, IL.
- SCHLESINGER, R. C. 1989. Dynamics of the sugar maple component of a white oak-yellow poplar community. p. 262–266. *In* G. Rink and C. A. Budelsky [eds.], *Proceedings, 7th Central Hardwood Conference*, USDA For. Serv. Gen. Tech. Report NC-132, St. Paul, MN.
- SCHLESINGER, R. C., D. T. FUNK, P. L. ROTH, AND C. C. MYERS. 1994. Assessing changes in biological diversity over time. *Nat. Area. J.* 14: 235–240.
- SCHNURR, J. L., R. S. OSTFELD, AND C. D. CANHAM. 2002. Direct and indirect effects of masting on

- rodent populations and tree seed survival. *Oikos*. 96: 402–410.
- SEYMOUR, R. S., A. S. WHITE, AND P. H. DE MAYNADIER. 2002. Natural disturbance regimes in northeastern North America: evaluating silvicultural systems using natural scales and frequencies. *Forest Ecol. Manag.* 155: 357–367.
- SHANNON, C. E. AND W. WEAVER. 1949. The mathematical theory of communications. University of Illinois Press, Urbana, IL. 125 p.
- SHIFLEY, S. R., B. L. BROOKSHIRE, D. R. LARSEN, AND L. A. HERBECK. 1997. Snags and down wood in Missouri old-growth and mature second-growth forests. *North. J. Appl. For.* 14: 165–172.
- 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. *Am. Midl. Nat.* 127: 125–138.
- SPETICH, M. A., S. R. SHIFLEY, AND G. R. PARKER. 1999. Regional distribution and dynamics of coarse woody debris in Midwestern old-growth forests. *For. Sci.* 45: 302–313.
- SPETICH, M. A., S. R. SHIFLEY, G. R. PARKER, AND F. PONDER. 1997. Ground cover in old-growth forests of the central hardwood region, p. 152–160. *In* S. G. Pallardy, R. A. Cecich, H. E. Garrett, and P. S. Johnson [eds.], *Proceedings, 11th Central Hardwoods Conference*, USDA For. Serv. Gen. Tech. Report NC-188, St. Paul, MN.
- TUBBS, C. H. 1977. Age and structure of a Northern Hardwood Selection Forest, 1929–1976. *J. For.* 75: 22–24.
- USDA NATURAL RESOURCES CONSERVATION SERVICE. Retrieved June 18, 2009 from The PLANTS database, version 3.5. <<http://plants.usda.gov>>
- WINGARD, R. C. 1984. Soil survey of Orange County, Indiana. U.S.D.A. Soil Conservation Service, Washington, D.C. 124 p.
- ZACZEK, J. J., J. W. GRONINGER, AND J. W. VAN SAMBEEK. 2002. Stand dynamics in an old-growth hardwood forest in Southern Illinois, USA. *Nat. Area. J.* 22: 211–219.
- ZAHL, S. 1977. Jackknifing an index of diversity. *Ecology* 58: 907–913.

#### Appendix A

Shade tolerance of observed species at Pioneer Mother's Research Natural Area, USFS Hoosier National Forest, IN. Adapted from Ülo Niinemets and Fernando Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs* 76: 521–547.

Scientific name	Shade tolerance index value	Shade tolerance classification	Species group
<i>Juniperus virginiana</i> L.	1.28	Intolerant	NA
<i>Gleditsia triacanthos</i> L.	1.61	Intolerant	Intol hardwood
<i>Sassafras albidum</i> (Nutt.) Nees.	1.68	Intolerant	Intol hardwood
<i>Pinus echinata</i> P. Mill.	1.86	Intolerant	NA
<i>Juglans nigra</i> L.	1.93	Intolerant	Intol hardwood
<i>Pinus virginiana</i> P. Mill.	1.99	Intolerant	NA
<i>Carya cordiformis</i> (Wangenh.) K. Koch.	2.07	Intolerant	Hickory
<i>Liriodendron tulipifera</i> L.	2.07	Intolerant	Yellow-poplar
<i>Carya alba</i> (L.) Nutt. ex Ell.	2.20	Intolerant	Hickory
<i>Quercus muehlenbergii</i> Engelm.	2.22	Intolerant	White oak
<i>Morus rubra</i> L.	2.34	Intolerant	NA
<i>Fraxinus americana</i> L.	2.46	Intolerant	Intol hardwood
<i>Prunus serotina</i> Ehrh.	2.46	Intolerant	Intol hardwood
<i>Gymnocladus dioica</i> (L.) K. Koch.	2.50	Intolerant	Intol hardwood
<i>Carya glabra</i> (P. Mill.) Sweet.	2.69	Intolerant	Hickory
<i>Quercus velutina</i> Lam.	2.72	Intolerant	Red oak
<i>Quercus rubra</i> L.	2.75	Intolerant	Red oak
<i>Quercus alba</i> L.	2.85	Intolerant	White oak
<i>Platanus occidentalis</i> L.	2.86	Intolerant	Intol hardwood
<i>Cercis canadensis</i> L.	3.00	Intolerant	NA
<i>Ulmus americana</i> L.	3.14	Intolerant	Intol hardwood
<i>Celtis occidentalis</i> L.	3.17	Intolerant	Intol hardwood
<i>Ulmus rubra</i> Muhl.	3.31	Intolerant	Intol hardwood
<i>Carya ovalis</i> (Wangenh.) Sarg.	3.40	Intolerant	Hickory
<i>Carya ovata</i> (P. Mill.) K. Koch.	3.40	Intolerant	Hickory
<i>Acer rubrum</i> L.	3.44	Intolerant	Tol hardwood
<i>Nyssa sylvatica</i> Marsh.	3.47	Intolerant	Tol hardwood
<i>Tilia americana</i> L.	3.98	Tolerant	Tol hardwood
<i>Diospyros virginiana</i> L.	4.21	Tolerant	Tol hardwood
<i>Amelanchier arborea</i> (Michx. f.) Fern.	4.33	Tolerant	NA
<i>Carpinus caroliniana</i> Walt.	4.58	Tolerant	NA
<i>Ostrya virginiana</i> (P. Mill.) K. Koch.	4.58	Tolerant	NA
<i>Fagus grandifolia</i> Ehrh.	4.75	Tolerant	American beech
<i>Acer saccharum</i> Marsh.	4.76	Tolerant	Sugar maple
<i>Cornus florida</i> L.	4.87	Tolerant	NA