Confirmation of Oak Recruitment Failure in Indiana Old-Growth Forest: 75 Years of Data

Preston R. Aldrich, George R. Parker, Jeanne Romero-Severson, and Charles H. Michler

Abstract: We report on a long-term study of changes in the diameter distribution of red and white oaks in old-growth forest of Indiana. We expand the scope of a prior 50-year demographic study of a 20.6-ha stand by (1) extending the census period, (2) comparing diameter distributions in the large stand with those of a smaller (2.3-ha) stand, and (3) examining small-diameter ingrowth of red oaks into both stands. Oaks displayed bell-shaped or even-aged diameter distributions in 1926, suggesting a history of disturbance from timber removal, grazing, and fire. These exogenous disturbances were suppressed starting in 1917 with acquisition of the property by Purdue University. Subsequent censuses indicated considerable ingrowth of nonoak stems into both stands. Oaks that were mid-sized in 1926 gradually moved through the size classes and were replaced by younger individuals in the small stand but not in the center of the large stand. The survey of red oak saplings confirmed this pattern, revealing numerous recruits in the small stand but virtually none in the large stand. These data support the view that oaks are failing to regenerate in part due to shade-intolerance and a waning disturbance regime in the large stand interior. FOR. SCI. 51(5):406–416.

Key Words: dbh, disturbance, edge effect, regeneration, size class, succession.

TREE DIAMETER DISTRIBUTIONS provide information on demographic processes. Even-aged populations typically exhibit the symmetry expected of a normal, bell-shaped distribution (Baker 1923, Mohler et al. 1978, Lorimer and Krug 1983) whereas all-aged populations commonly resemble a reverse-J shape, with numerous small stems and fewer large stems. The reverse-J distribution can be approximated using a negative exponential ($y = ae^{-bx}$) or negative power function ($y = ax^{-b}$), where y is the number of stems of size class x, a is the initial stocking rate, and b is the instantaneous rate of mortality (Schmelz and Lindsey 1965, Hett 1971, Hett and Loucks 1971, Johnson and Bell 1975, Lorimer 1980, Shimano 2000). The negative power function has the desirable property that the impact of the mortality rate (b) decreases with increasing size (x), whereas the exponential model assumes constant mortality.

Parameters a and b define the shape of the power function curve and may be useful in distinguishing tree regeneration strategies. Shimano (2000) proposed that tree species dependent on light gaps for regeneration should exhibit a mortality rate near $b = 2$ (i.e., $y = ax^{-2}$) in stands that are a mosaic of forest and gaps. The doubling of canopy size should reduce stem density four-fold due to space filling rules, not unlike the –3/2 power law (Yodah et al. 1963) that relates plant biomass to stem density through allometric scaling. In general, pioneering or shade-intolerant species should exhibit vigorous recruitment (large a) but also high mortality (b close to 2) as individuals compete for limited resources such as space and light within gaps. Conversely, shade-tolerant species should have low initial stocking rates (a) and low mortality rates (b) because they can persist under closed canopy and so are less spatially constrained.

Diameter-size distributions also can be used to evaluate the magnitude and timing of past disturbance events. In the exponential model, a low coefficient of determination (R^2) indicates that certain size classes are over- or underrepresented, as might arise from a disturbance event. Increases in R^2 over time suggest a return to a more balanced, all-aged diameter distribution. For example, Schmelz and Lindsey (1965) compared the size class distributions of nineteen hardwood stands that differed in disturbance intensity and timing. Cox Woods, Indiana, had experienced little human disturbance and fit the exponential model well ($R^2 = 0.96$) compared to a degraded woodlot ($R^2 = 0.66$), whereas Hoot Woods, a virgin Indiana forest recovering from windthrow, was intermediate ($R^2 = 0.90$). In the case of a large disturbance, one may be able to reconstruct the date of the event based on the size of the stems that form the deviation from the regression line in conjunction with information on growth rates (e.g., Johnson and Risser 1975).

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The diameter distribution of oak (*Quercus*) forests has gained attention because of evidence of recruitment failure (reviewed in Abrams 1992, 2003, Lorimer 1993). Possible causal factors are thought to include seed and seedling predation by rodents, deer, and livestock, which serve to limit the regenerative potential of tree species, and the suppression of disturbance regimes such as fire and timber harvest that had previously favored early- and mid-seral species like oaks by promoting an open canopy and subcanopy. Global climate change is another possible agent, but the relative importance of these several factors is yet to be resolved. Several lines of evidence suggest that Native Americans had a considerable effect on vegetation through the use of fire, and the results of extensive timber harvests in the 1800s by European settlers is well-documented (Delcourt and Delcourt 1985, Abrams 1992, Parker 1997, Abrams 2002, Dey 2002). However, widespread suppression of fires began in the 1930s–1950s (Pyne 1982, Pyne et al. 1996, Dey 2002), allowing the regeneration of shade-tolerant species that formed dense understory thickets of saplings, which rapidly filled canopy openings soon after formation (Abrams and Nowacki 1992).

Today, many Central Hardwood forests have canopies dominated by large oaks but understories dominated by shade-tolerant species such as maple (*Acer*) and beech (*Fagus*). The phenomenon has been described in remnant farm woodlots and in much less fragmented habitat such as the southern Appalachian Mountains (Lorimer 1993). These observations mostly have been made within the past fifty years. Our focus is to demonstrate the long-term nature of the pattern seen at so many other sites.

Some reports of tree-diameter size structure have provided extensive spatial replication over numerous stands (e.g., $N = 28$ stands, Lorimer and Krug 1983; $N = 48$, Lorimer 1980). Other studies have sacrificed spatial for temporal replication by reporting more than one census of the same stand or stands (e.g., $N = 10$ years, Schmelz and Lindsey 1965; $N = 10$, Abrell and Jackson 1977; $N = 11$, Weaver and Ashby 1971; $N = 23$, Christensen 1977; $N = 27$, McCune and Cottam 1985; $N = 35$, Boggess and Bailey 1964; $N = 50$, Whitney 1984). Still others have compared General Land Office surveys with extant forest (e.g., Fralish et al. 1991). Perhaps the longest running census of old-growth was established at the Harvard Forest in 1905 from which Foster (1988) reported 80 years of successional data, though a devastating 1938 hurricane essentially reset the successional status of this forest. One of the longest intervals free of a stand-initiating disturbance is 70 years for unthinned oak (*Quercus*)-mixed hardwood stands from Connecticut (Stephens and Ward 1992; Ward et al. 1999). The multispecies structure of these stands maintained a good fit to a negative exponential curve over the 70 years, but the oak diameter distribution did not (Ward et al. 1999; see also Johnson et al. 2002). Oaks began as a steep negative exponential but ingrowth dropped off by thirty years, after which there was only a basal rate of oak recruitment and the progression of the residual surge of even-aged oak recruits through the larger size classes.

Here, we report on a long-term study of an old-growth forest at the Davis–Purdue Research Forest (DPRF) in Indiana. Parker et al. (1985) conducted the first demographic review of changes in diameter distribution of all tree species over the course of 50 years. They examined stems $\geq$10 cm dbh in a large 20.6-ha stand and found considerable ingrowth of sugar maple (*Acer saccharum* Marsh.), which displayed a reverse-J–shaped size distribution by 1976. Oaks exhibited a bell-shaped diameter distribution in both 1926 and 1976 and were declining in numbers. We extend the demographic coverage of the center of the large stand and report previously unpublished diameter distribution data for this same time period for a nearby small (2.3-ha) stand that is mostly edge habitat. We address the following questions: (1) How do changes in red and white oak size structure compare with that of the other nonoak trees over this longer time period in the original large stand? (2) How do these patterns compare to those of the smaller stand? (3) Is there evidence of red oak recruitment in the small sapling size class ($1 \leq$ dbh ≤ 9.9 cm)? (4) Do the size structure data indicate a major disturbance event in the history of the stands, and if so, when did it (they) occur? (5) What are the management implications?

Materials and Methods

Study Site

The DPRF, located in Randolph County, Indiana (SE ¼ of Section 23, Township 21N, Range 12E), is one of the oldest and most studied tracts of remnant mature deciduous hardwood forest on the Tipton Till Plain, covering Illinois, Indiana, and Ohio (site descriptions in Parker and Leopold 1983; Parker et al. 1985). The forests reside in the Blufton Till Plain Section of the Central Till Plain Natural Region (Homoya et al. 1985), with four mesic soils present (Blount, Glynwood, Pewamo, and Saranac; see Spetich and Parker 1998). Two seasonal ponds (0.4–0.8 ha) accumulate in the largest stand in the spring, and smaller wet depressions are scattered throughout; Lindsey and Schmelz (1970) classified the site as lowland depressional forest. The smallest stand encompassed somewhat less edaphic heterogeneity, with less standing water during any given season.

We examined the largest (20.6 ha, compartment 1) and smallest (2.3 ha, compartment 4) of the four remnant forest stands at the DPRF, which are imbedded in an agricultural matrix established in the mid-1800s. Some of the large trees are quite old, such as bur oak (*Q. macrocarpa* Michx.) that have been aged at >350 years old (Parker et al. 1985), supporting the notion that the DPRF is at least in part a relict dating from the pre-European era (Beers 1960). Though documentation is scant, it is thought that disturbance from livestock grazing and selective timber harvest (and possibly fire) was present until purchase of the property by Purdue University in 1917. After acquisition, most exogenous disturbances were suppressed except for the removal of <50 dead and dying trees in the 1940s and 1950s (both stands) and in 1964 (small stand). A small surface fire occurred in 1972 in the western portion of the large stand. The small stand was composed mostly of edge habitat, in that no part was farther than ~75 m from an abrupt pasture–forest ecotone.

Species

In 1976, oaks had an importance value of 41.2% in the large stand canopy with 20.2% attributed to red oaks (*Quercus* section *Lobatae*) and 21.0% to white oaks (*Quercus* section *Quercus*; Parker and Leopold 1983). Three red oak species were present: northern red oak (*Quercus rubra* L.), Shumard oak (*Q. shumardii* Buckl.), and pin oak (*Q. palustris* Muench.). Red oaks can be difficult to identify to species and it is thought that interspecific hybridization is common (Jensen 1995). Hybrids among each pair of the species present at the DPRF have been described elsewhere (Laughlin 1963, 1964; Palmer and Steyermark 1935; Morsink and Pratt 1984), and an examination of the genetic composition of these species in the large stand using microsatellite markers (Aldrich et al. 2003a) revealed little interspecific differentiation. Therefore, we pooled the red oak species within each of the censuses and considered the overall demography of the red oak community. Likewise, we pooled the four members of the white oak group (section *Quercus*) including white oak (*Q. alba* L.), swamp white oak (*Q. bicolor* Willd.), bur oak (*Q. macrocarpa* Michx.), and chinkapin oak (*Q. muehlenbergii* Engelm.).

Twenty-seven nonoak species also were present. These included boxelder (*Acer negundo* L.), silver maple (*A. saccharinum* L.), sugar maple (*A. saccharum* Marsh.), red maple (*A. rubrum* L.), Ohio buckeye (*Aesculus glabra* Willd.), American hornbeam (*Carpinus caroliniana* Walt.), bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch), pignut hickory (*C. glabra* (P. Mill.) Sweet), shagbark hickory (*C. ovata* (P. Mill.) K. Koch), hackberry (*Celtis occidentalis* L.), eastern redbud (*Cercis canadensis* L.), flowering dogwood (*Cornus florida* L.), hawthorn (*Crataegus* spp.), American beech (*Fagus grandifolia* (Ehrh.) Little), white ash (*Fraxinus americana* L.), black ash (*F. nigra* Marsh.), blue ash (*F. quadrangulata* Michx.), honey locust (*Gleditsia triacanthos* L.), black walnut (*Juglans nigra* L.), red mulberry (*Morus rubra* L.), ironwood (*Ostrya virginiana* (Mill.) K. Koch), American sycamore (*Platanus occidentalis* L.), eastern cottonwood (*Populus deltoides* Bartr. ex. Marsh.), black cherry (*Prunus serotina* Ehrh.), American basswood (*Tilia americana* L.), American elm (*Ulmus americana* L.), and red elm (*U. rubra* Muhl.).

Censuses

Prentice (1927) generated the first census of all stems ≥4 inches (≥10.2 cm) dbh for both the large 20.6-ha stand and the small 2.3-ha stand in 1926. Individuals were permanently marked with metal tags, identified to species, and mapped to quadrants. Later full-stand censuses of ingrowth (stems ≥10 cm) and mortality were conducted by Parker and colleagues in the large stand (1976, 1986, and 1992; see Spetich and Parker 1998) and the small stand (1987 and 1992, unpublished).

For the purpose of the present study, we considered recruitment in all 2.3 ha of the small stand and in a plot twice this size (4.6 ha) in the central portion of the large 20.6-ha stand to avoid edge effects. This central plot began at cell #528 (1992 grid) and covered 42 cells (420 m) extending westward and 11 cells (110 m) South. In addition to the above-mentioned surveys, we conducted a 2001 survey of red oak stems ≥2 m tall (roughly ≥1 cm dbh). This most recent survey extended the sampling of red oak stems ≥10 cm dbh initiated by Prentice and also provided information on ingrowth of red oaks into the small sapling class (1 cm ≤ dbh ≤ 9.9 cm).

Statistical Analyses

We conducted negative power function ($y = ax^{-b}$) regressions of stem frequency (stems ha^{-1}) versus dbh-class for the three stem classes (nonoaks, red oaks, and white oaks). First, we produced frequency distributions for each census using 20-cm dbh size intervals, beginning at 10 cm and including a final category ≥90 cm, using interval midpoints (20, 40, 60, 80, 100) for the regression. We then conducted the power regression using the program DataFit (ver. 8.0.32, Oakdale Engineering, Oakdale, PA), wherein the following biological interpretations apply: y is the number of stems per ha for a given size class x, a is the initial stocking or recruitment into the smallest size class, and b is the mortality rate (the slope of the data under a log-transformation).

We used the coefficient of determination (R^2) from the regression as an index of past disturbance. Low R^2 suggests a perturbation of stem densities in at least one of the size classes from expected values under the model.

We dated the disturbance event(s) using information on oak size structure in 1926 and observed growth rates. Red and white oaks displayed a bell-shaped distribution in both stands in 1926, with the peak dbh classes around 40–60 cm (Figures 1 and 2). Assuming that these peaks represent ingrowth following some major disturbance, we calculated the time required for these stems to reach this size using growth rate information. We estimated growth rates for the interval of the surveys (i.e., 1926 through 2001) using all trees of each species group appearing in at least two censuses.

Results

Nonoaks

Nonoak demography has remained similar in the large and small stands over the 66 years, judging from censuses of stems ≥10 cm dbh (Table 1, Figure 3). Recruitment or stocking (a) increased over time as did mortality (b) and the overall fit of the data to the model (R^2). The significance (t-test) of the regression parameters, particularly b, also increased with time. In addition to similarities in temporal trends, the absolute magnitudes of demographic parameters were quite similar among stands within each census period.

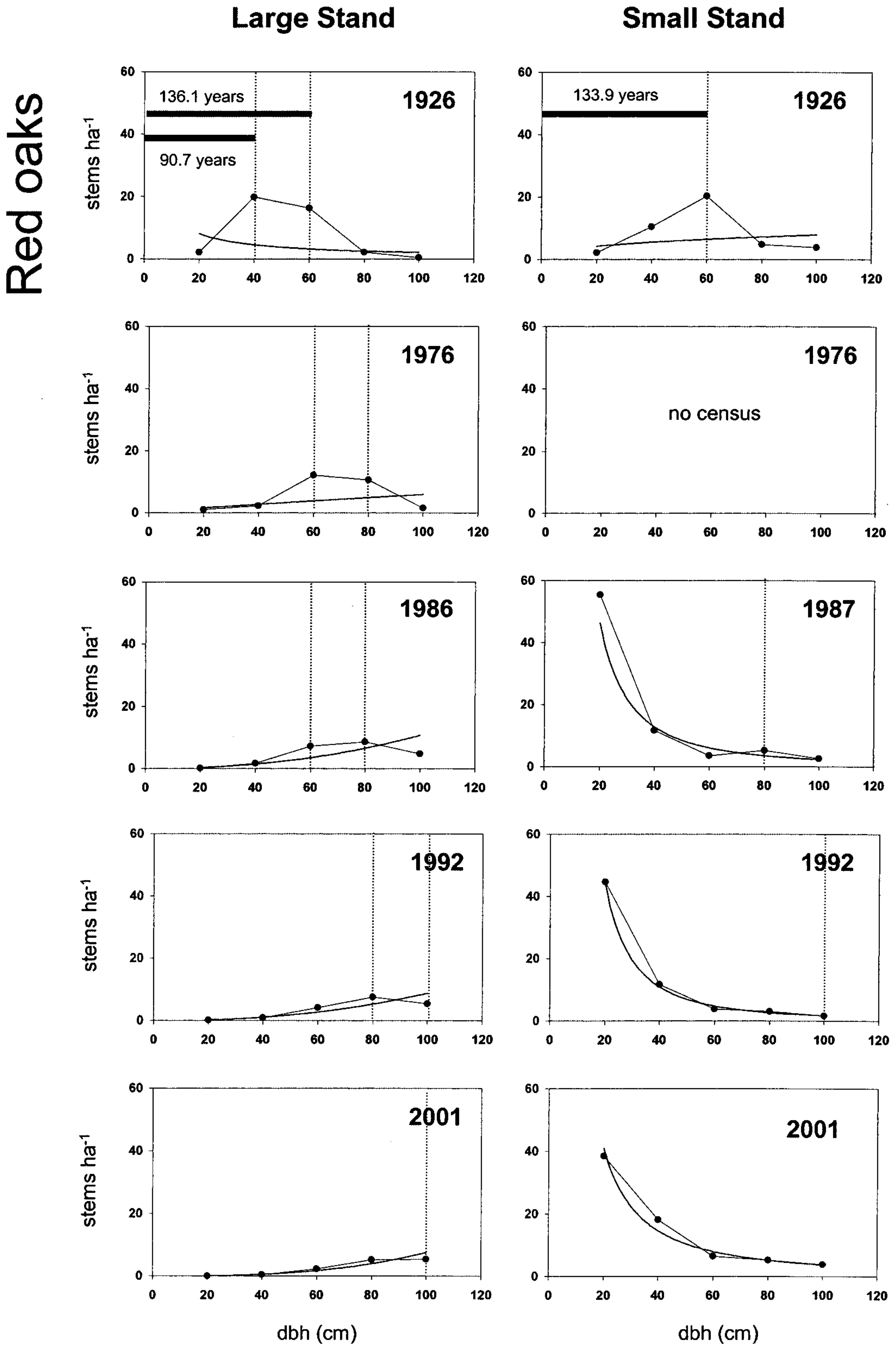

Figure 1. Diameter size distribution data spanning 75 years for red oak tree species (stems ≥10 cm dbh) in the large and small stands at the DPRF. Observed data points are the midpoints of 20-cm-wide diameter bins. The smoothed line is the power regression line fit to the observed data with parameters *a* and *b* and R^2 listed in Table 1. The vertical dotted lines mark recruitment peaks present in 1926 that moved through the size classes over time. The age of these cohorts is inferred from observed growth rates of the trees over the course of the study.

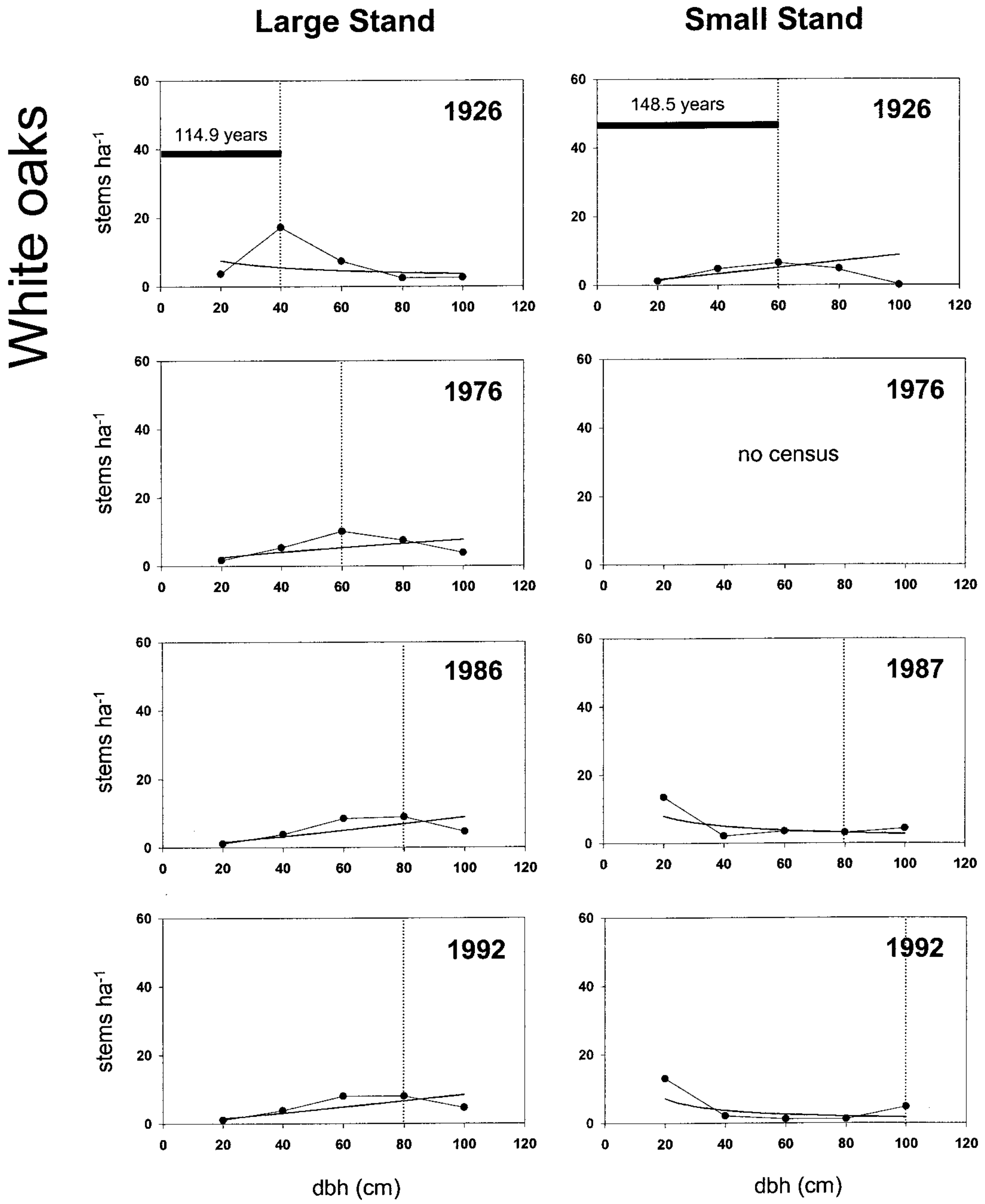

Figure 2. Diameter size distribution data spanning 66 years for white oak tree species (stems ≥10 cm dbh) in the large and small stands at the DPRF. See Figure 1 for descriptions.

Red Oaks

Red oaks displayed opposing demographic trends over 75 years in the large and small stands (Table 1, Figure 1).Though the fit of the data to the model increased with time in both stands, both ingrowth and mortality decreased in the large stand. The red oaks in the small stand, by contrast, displayed increasing ingrowth and mortality as was seen in the nonoak component of both stands.

The 2001 census of small sapling ingrowth of red oak stems (1 cm ≤ dbh ≤ 9.9 cm) revealed recruitment in the small stand but a complete absence of recruitment of this size into the large stand (not shown in Figure 1). We found 98 ingrowth stems in the 2.3 ha of the small stand (42.4 stems/ha) but we found no ingrowth of this size in the 4.6-ha plot at the center of the large stand.

White Oaks

White oaks displayed the same overall pattern as the red oaks, though magnitudes were not as extreme (Table 1, Figure 2). Ingrowth and mortality increased in the small stand but decreased in the large stand. The fit of the data to the model increased in both stands over time, though by 1992 R^2 was much lower in the large stand (0.424) compared to the small stand (0.806).

Table 1. Parameters of negative power function regressions [$y = ax^{-b}$] for diameter size distributions of nonoaks, red oaks, and white oaks in the large and small stand.

	Large Stand			Small Stand		
Species Group and Census Year	*a*	*b*	R^2	*a*	*b*	R^2
Nonoaks						
1926	2.637E + 3	1.291	0.754	915.159	1.112*	0.803
1976	1.025E + 7	3.548****	0.999	—	—	—
1986_L or 1987_S	1.629E + 7	3.668****	0.999	1.073E + 7*	3.316****	0.999
1992	9.493E + 6*	3.529****	0.999	3.186E + 6	3.008****	0.999
Red oaks						
1926	**15.509**	**0.162**	0.016	4.966	−0.130	0.013
1976	**0.895**	**−0.457**	0.118	—	—	—
1986_L or 1987_S	**0.132**	**−0.874**	0.515	3.924E + 4	2.191**	0.995
1992	**0.021**	**−1.262**	0.732	1.828E + 4**	2.008****	0.999
2001	**0.002**	**−1.779****	0.909	2.286E + 3	1.359***	0.982
White oaks						
1926	**17.876**	**0.251**	0.049	2.806	−0.054	0.003
1976	**1.437**	**−0.349**	0.187	—	—	—
1986_L or 1987_S	**0.535**	**−0.575**	0.398	619.453	1.294*	0.787
1992	**0.533**	**−0.564**	0.424	2.569E + 3	1.771*	0.806

NOTE: *y*, stem density (stems per ha); *x*, dbh (cm); *a*, stocking; *b*, mortality rate; R^2, coefficient of determination and disturbance index; —, no census; *, $P < 0.1$; **, $P < 0.05$; ***, $P < 0.01$; ****, $P < 0.001$. Numbers in bold denote demographic parameters whose values decreased over the time interval examined, values not in bold increased. Subscript L, large stand; subscript S, small stand.

NON-OAK SPECIES: *Acer negundo*, *A. saccharinum*, *A. saccharum*, *A. rubrum*, *Aesculus glabra*, *Carpinus caroliniana*, *Carya cordiformis*, *C. glabra*, *C. ovata*, *Celtis occidentalis*, *Cercis canadensis*, *Cornus florida*, *Crataegus* spp., *Fagus grandifolia*, *Fraxinus americana*, *F. nigra*, *F. quadrangulata*, *Gleditsia triacanthos*, *Juglans nigra*, *Morus rubra*, *Ostrya virginiana*, *Platanus occidentalis*, *Populus deltoides*, *Prunus serotina*, *Tilia americana*, *Ulmus americana*, and *U. rubra*.

RED OAK SPECIES: *Quercus palustris*, *Q. rubra*, and *Q. shumardii*.

WHITE OAK SPECIES: *Quercus alba*, *Q. bicolor*, *Q. macrocarpa*, and *Q. muehlenbergii*.

Historical Disturbance

We report growth rate estimates (Table 2) along with sample sizes (*N*) and the mean time span for each observation (e.g., 1986–1926 = 60 years). Growth rates of red oaks were nearly identical in the large (0.441 cm/yr) and small stands (0.448). White oaks grew more slowly (large stand, 0.348; small stand, 0.404). Based on these measures, the inferred dates of the disturbance(s) initiating the peak cohort of 1926 would have occurred anytime between 1778 and 1835.

Discussion

DPRF Stand Disturbance During the 19th Century

Three factors associated with European settlement during the 1800s can explain the 1926 bell-shaped size distributions: (1) timber harvests, (2) release of suppressed vegetation, and (3) removal of undergrowth through fire and grazing. Timber harvests in Indiana, and the Central Hardwoods in general, were extensive during European settlement (Parker 1997, Hicks 1998). Timber mill records (Steer 1948) document that oaks comprised 80% of Indiana timber production from 1869 to 1899, indicating that large oaks were present when Europeans arrived (Den Uyl 1954), and their removal would contribute to the rarity of large oaks by 1926 at the DPRF.

In many of the remnant woodlots of the region, selective cuts and subsequent burning left cull and small stems of hardwood species (Den Uyl 1954), especially the fire-tolerant oaks. Canopy removal released understory stems from competition and shade suppression, and these cohorts of small oak stems eventually would grow to dominate many of the forested areas in the Central Hardwoods (Hicks 1998, Dey 2002). The abundant mid-sized (40–60-cm dbh) individuals of 1926 at the DPRF may be an example of this wave of oak recruitment.

Several factors would have convened to deplete the smallest (<40 cm dbh) understory stems from the DPRF by 1926. Some mortality would have occurred during timber removal while others simply grew out of the smaller size classes. In conjunction with fire, intensive livestock grazing associated with agriculture also regulated ingrowth and survivorship in the understory. Burning had become common in Indiana woodlands during European settlement and as much as 85% of the farm woods in the agricultural counties of Indiana were used for livestock grazing (Den Uyl 1954). Burr N. Prentice described the 1926 DPRF understory as open and parklike, as forests appear when they have experienced long-term burning (Lorimer 1993) and grazing (Den Uyl et al. 1938).

Dating the DPRF Disturbance Event(s)

Our growth rate estimates for the oaks were comparable to those reported elsewhere. Growth of red oaks (large patch, 0.441 cm/yr; small patch, 0.448) and white oaks (0.348 and 0.404, respectively) fell within the range of values summarized by Johnson et al. (2002) for a variety of initial tree diameters (red oaks: *Q. rubra*, 0.414–0.737 cm/yr) (white oaks: *Q. alba*, 0.284–0.452;

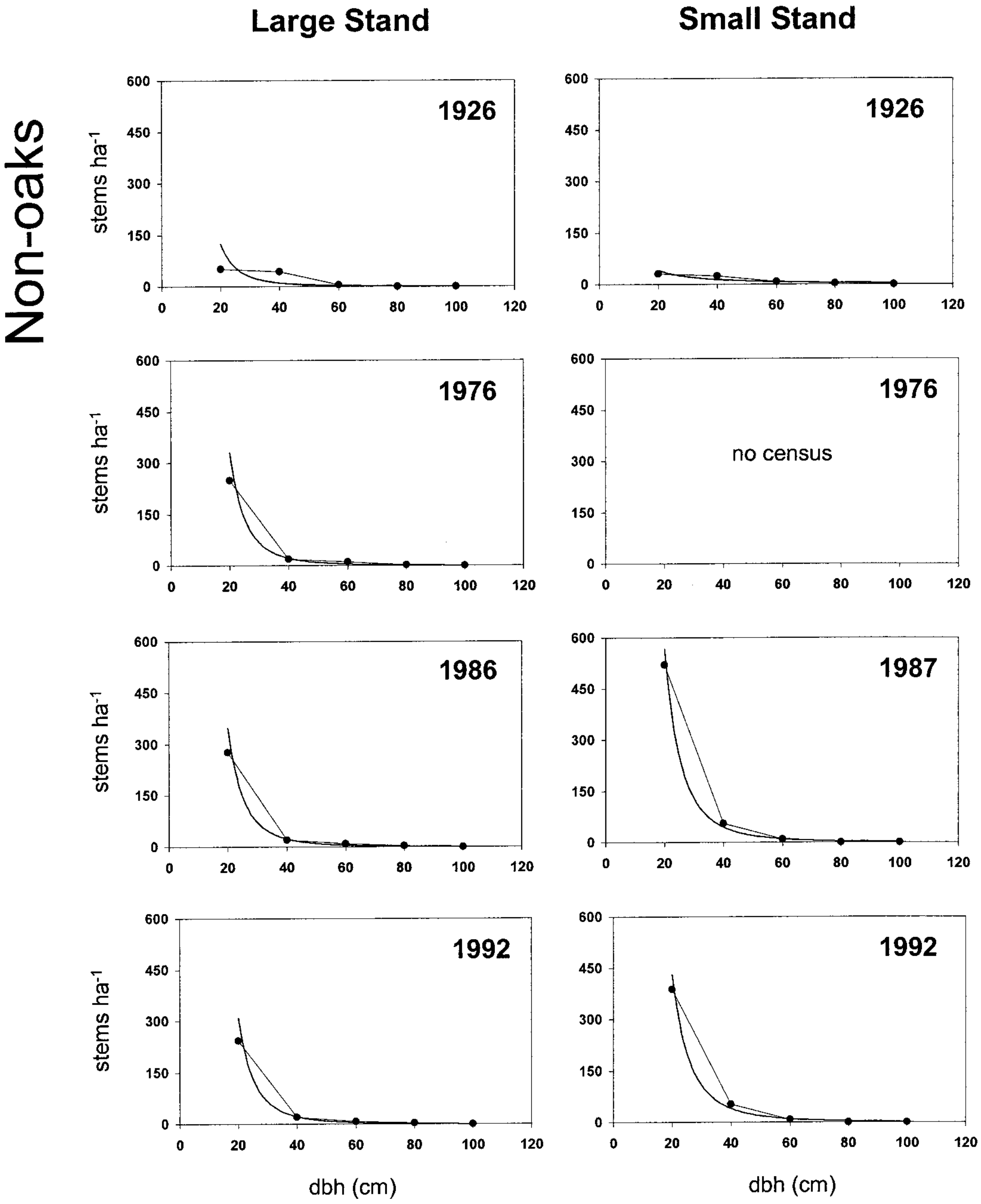

Figure 3. Diameter size distribution data spanning 66 years for nonoak tree species (stems ≥10 cm dbh) in the large and small stands at the DPRF. Observed data points are the midpoints of 20-cm-wide diameter bins. The smoothed line is the power regression line fit to the observed data with parameters *a* and *b* and R^2 listed in Table 1.

Q. bicolor, 0.356; *Q. macrocarpa*, 0.330; *Q. muehlenbergii*, 0.208–0.277).

A primary disturbance event seems to have occurred at the DPRF in the early 1800s. According to the 1926 size

Table 2. Estimation of growth rates and time since primary disturbance event based on oak diameter size distributions in 1926 at the DPRF

Group and Stand	N (stems)	Mean time (yrs)	Growth Rate (cm/yr)	Peak size class in 1926 (cm)	Minimum age of peak (yrs)	Earliest date of disturbance (yrs)
Red oaks						
Large	85	63.7	0.441	40–60	90.7–136.1	1835–1790
Small	25	66.9	0.448	60	133.9	1792
White oaks						
Large	130	62.8	0.348	40	114.9	1811
Small	58	31.0	0.404	60	148.5	1778

structure data and growth rate estimates, the 40–60-cm dbh cohorts were between 90.7 and 148.5 years old in 1926, placing their date of establishment at 1778–1835. It was only three years later in 1838 that the land patent for the DPRF property was transferred from the federal government to private ownership (Bureau of Land Management, General Land Office Records). This coincided with the settlement of most of Indiana, which occurred from 1810–1870, though the majority of timber extraction occurred between 1870 and 1910 after the heaviest wave of European settlement (Latta 1938, Den Uyl 1954).

There are several reasons to expect that the last primary disturbance event at the DPRF occurred more recently than 1835. (1) The 40–60-cm stems of 1926 may have existed as suppressed individuals at the time of disturbance, so their ages would over-estimate the disturbance date. (2) Growth rates probably increased following the disturbance due to release from shade-suppression, leading to over-estimation of the time required to enter the 40–60-cm dbh size class. Note that post-1926 growth rates for oaks were greater in the small stand with more edge habitat compared to the large stand. (3) Mortality of small stems (<30 cm dbh) would have truncated a reverse-J-shaped oak distribution contributing to the formation of a bell-shaped distribution by 1926. Mortality from heavy grazing and fire could have occurred as recently as the early 1900s, before purchase by Purdue University in 1917.

Patterns of 20th Century Oak Regeneration at the DPRF

Parker et al. (1985) first reported recruitment failure for oaks in the large stand at the DPRF, and we corroborate these findings over a longer time frame. Ward and Parker (1989) found fewer than 4.3 stems/ha of red and white oaks within the 2.0–9.9-cm dbh class in the large stand from a single survey of 4.0 ha in 1986. Twenty-five years later, we have found virtually no red oak stems 1.0–9.9 cm dbh in 4.6 ha of the large stand. This rate of attrition is about as expected given the findings of Ward and Stephens (1994) that between 67–90% of intermediate and suppressed *Q. rubra* died over a thirty-year period. Though we noted that acorns were produced in abundance, only about 10–20 seedlings (generally <20 cm tall) were observed in the central plot of the large stand over the course of the study (P.R. Aldrich, Forest Service, personal observation, 2001), suggesting very low survivorship from the acorn to small sapling stage.

Vigorous oak regeneration in the small stand at the DPRF provides an interesting contrast. Though both stands began in 1926 with bell-shaped diameter distributions, the size-class distributions of both stands fit the model well by the final censuses. However, this end state was achieved through different paths described by the parameters *a* and *b*. In the large stand, the excess of mid-sized stems in 1926 can be seen growing into the larger size classes in later censuses (see vertical dotted lines, Figure 2), though gradually diminishing in numbers (low mortality rate). New recruits generally did not replace these larger individuals (low stocking rate) and the size-class distribution eventually fit the exponential model through attrition. In the small stand, the excess of mid-sized stems also can be seen moving into the larger size-classes. However, new recruits more than replaced the larger stems (high stocking rate) despite the high mortality rate, and the size-class distribution acquired a reverse-J shape. With respect to Shimano's (2000) interpretation of the demographic parameters, the oaks displayed the pioneer recruitment strategy in the small stand but that of a late-seral species in the center of the large stand, albeit less successfully.

Possible Causes of 20th Century Oak Regeneration Failure at the DPRF

Competition

The census data we have presented focus on the tree species, and so our strongest test of the various hypotheses presented to explain oak reproductive failure lies in exploring the observed demographic patterns in light of known life history attributes of these species, chief of which here is shade-tolerance. In a study of the large DPRF stand, Aldrich et al. (2003b) showed that the populations of shade-tolerant tree species increased in stem density and became more aggregated between 1926 and 1986, whereas shade-intolerants (including oaks) declined in numbers and lost their clumpy spatial structure, likely the result of attrition without replacement. Ward and Parker (1989) found that light gaps have become small and infrequent in the large stand, and have not afforded oak saplings sufficient time to enter the canopy before gap closure. As first noted by Parker et al. (1985), a dense subcanopy layer of the shade-tolerant sugar maple has accrued in the large stand, likely suppressing oak regeneration and out-competing oaks in the race to occupy the occasional canopy opening. Our present analysis of the central plot in the large stand shows an increase in sugar maple from 1.3% of total stems in 1926 to 24.8% by 1992. This contrasts with a decline in sugar maple in the small stand over the same interval from 0.7 to 0.3%. Oak regeneration rebounded in the small stand probably due in part to edge effects, because ambient light levels throughout the stand would be greater due to both lateral penetrance of light from nearby edges and higher canopy disturbance rates (Pursell and Parker 1988).

Differences in the demographic responses of red and white oaks could arise from several factors. White oaks generally are less tolerant of shade than red oaks, and the light entering the center of the small stand laterally through the edge may have been insufficient to illicit the same demographic response in white as in red oaks. Also, peak reproduction generally occurs sometime between 25 and 50 years of age in red oaks but between 50 and 150 years in white oaks (Burns and Honkala 1990, FEIS 2004 [Final Environmental Impact Statement, Fire Effects Information System. U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Res. Stn., Fire Sciences Lab. Available: http://www.fs.fed.us/database/feis]), which could produce a time lag in the demographic response of white oak populations to changes in their environment.

Site Differences

Old-growth stands on mesic sites typically maintain oaks as only a minor component in part because of the lowered frequency and intensity of fires (Frelich and Reich 2002). Oaks are more tolerant of fire but less tolerant of shade compared to many other Central Hardwood tree species (FEIS 2004). Active fire suppression after 1917 combined with mesic soils in the large DPRF stand promoted the establishment of dense subcanopy and canopy strata, favoring the regeneration of shade-tolerant species and selecting against oaks. Because fire was suppressed in both the large and small stands, though, fire regime cannot explain the observed site differences in oak regeneration. The soil moisture of the small stand appeared most similar to the better drained soils of the large stand, which could reflect differences in the water table and drainage patterns or simply a drying effect from winds penetrating the nearby edges of the small stand. Yet, oak species preferring dry or well-drained soils (e.g., *Q. macrocarpa*, *Q. rubra*) were present in the large stand along with those that readily tolerate wet soils (e.g., *Q. bicolor*, *Q. palustris*), and still regeneration was failing there.

Animal Effects

Animals have likely played a significant role in the development of the DPRF stands, though evidence is incomplete. Spetich and Parker (1998) concluded that cessation of grazing by farm livestock was a primary factor contributing to the heavy net ingrowth of stems between the 1926 and later censuses, and the spatial patterns of tree regeneration support this conclusion (Aldrich et al. 2003b). There is no information on subsequent deer grazing pressures at the DPRF. White-tail deer (*Odocoileus virginianus*) often favor oaks for browse in hardwood forests (Frelich and Lorimer 1985, Strole and Anderson 1992), though typically maples are taken as well. Weevil (*Curculio* spp.) damage to acorns was heavy (P.R. Aldrich, Forest Service, personal observation, 2001), though we did not quantify its effect. Forest rodents can differ in their response to fragmentation (Nupp and Swihart 2000, 2001) and effectiveness as dispersal agents (Steele and Smallwood 2002). For example, North American red squirrels (*Tamiasciurus hudsonicus*) tend to larder hoard (depositing many acorns per few sites) in Indiana, whereas gray squirrels (*Sciurus carolinensis*) scatter hoard (few acorns per numerous sites). The method of larder hoarding is much less effective at fostering oak regeneration and so the invasiveness of red squirrels into highly fragmented landscapes may be exacerbating the oak regeneration problem (Goheen and Swihart 2003). Clearly, more research on plant–animal interactions is warranted.

Management Implications

The diameter distribution data indicate that the DPRF was a disturbed forest during European settlement in the early to mid-1800s. Beers (1960) described the DPRF as a prime example of "undisturbed old-growth" characteristic of central Indiana. This is an apt characterization for the 20th century phase of DPRF stand history, and the forest does contain many large old trees that antedate settlement of this part of Indiana, but it belies the complex history of disturbance that seems to have played an important role in the development of this and other Central Hardwood forests. In fact, many of the red oak stands that we see today may be the first, and only, generation of closed-canopy oak forest on sites that otherwise have supported open oak savannahs or closed-canopy forests with a minor oak component (Lorimer 1993, Frelich and Reich 2002).

Retention of a strong oak component in Central Hardwood old-growth forests may be difficult under low-disturbance regimes when the natural successional trajectory fostered by site characteristics favors other species. Xeric sites that do not support closed-canopy forests might retain a stable oak component without exogenous disturbances like periodic fires, and indeed many oaks are increasingly limited to such upland sites (Abrams 2003). By contrast, rich mesic soils such as those at the DPRF promote the growth of many shade-tolerant tree species able to persist beneath closed canopy, and oaks may not fare as well under such circumstances. Greater intervention may be required on these mesic sites on which oaks are less competitive, provided that it is determined desirable to maintain oak dominance over that of more shade-tolerant species, for aesthetic, historical, or economic reasons or to provide mast for wildlife, for example.

Our study provides clear evidence that the oak regeneration problem is a long-term phenomenon, though we also have shown that an adjacent stand can follow an opposing developmental trajectory. Because our study is descriptive and lacks spatial replication, we are constrained in our ability to ascribe causation to these differences but our findings underscore the importance of research in four areas: (1) Landscape-level research. To what extent is the regenerative failure of oaks in the large DPRF stand counter-balanced by gains in other stands? (2) The role of animals. There is an association between shade-tolerance and the regenerative success of tree species at the DPRF (this study, Aldrich et al. 2003b). What is the role of animal seed vectors and seed and seedling herbivores/predators in the oak regeneration problem? (3) Climate change. Some models predict a decline of sugar maple with increasing CO_2 concentrations (Lovett and Mitchell 2004, and references therein). Will increases in the abundance of warmer, drier sites counterbalance the current oak regeneration failure? (4) Silvicultural treatments. What methods of canopy and/or understory removal by cutting or fire will promote oak regeneration without eroding biodiversity in the associated tree and animal communities? It is clear from our study that simply protecting the large DPRF stand from disturbance has not preserved its character and composition, because the forest had developed at least in part in response to disturbance regimes that later were suppressed.

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