DEVELOPMENT, SUCCESSION, AND STAND DYNAMICS OF UPLAND OAK FORESTS IN THE WISCONSIN DRIFTLESS AREA: IMPLICATIONS FOR OAK REGENERATION AND MANAGEMENT

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Abstract.–Throughout the deciduous forests of the eastern United States, oak (*Quercus*) regeneration has declined in stands historically dominated by oak species. In the Wisconsin Driftless Area, the level of decline in oak regeneration is variable and influenced by stand structural development, historical disturbance regime, abiotic site characteristics, and historical land-use legacies. This research aims to elucidate the relative importance and site-specific nature of the factors influencing oak regeneration and identify interactions between drivers. To document stand succession, development, and factors influencing oak regeneration, we collected forest inventory and dendrochronological data from 11 sites distributed throughout the region. The stages of structural development identified across sites included pole, mature-sapling mosaic, mature, early-transition old-growth, and steady-state old-growth. Structural complexity was variable across the region but generally increased with advanced structural development. At all sites, oak regeneration was negligible, with significantly lower relative densities of oak species in the understory than in the overstory. Future analyses will use multivariate techniques to investigate the relationship between stand development, land-use history, disturbance history, abiotic conditions, and oak regeneration.

INTRODUCTION

Oak species (*Quercus* spp.) are a major component of forested ecosystems of the eastern United States, and the ecological, commercial, and societal importance of these oak forests represents a distinctive long-term legacy. However, throughout the Central Hardwood Forest region, a majority of oak species are failing to regenerate, and oak abundance is exhibiting a marked decline (Abrams 1992, Fei et al. 2011, Lorimer 1993). Coupled with this decline, shade-tolerant mesophytic species such as sugar maple (*Acer saccharum* Marsh.) and red maple (*Acer rubrum* L.) are increasing in abundance, particularly in the understory. This compositional shift has been documented across multiple site types and has led many researchers to predict a pervasive transition from oak-dominated systems to forests with overstories dominated by maple and other shade-tolerant taxa. Active fire suppression beginning in the early 20th century is the most often cited explanation for the oak replacement pattern. Additional drivers of the transition have been proposed and include alterations of canopy disturbance characteristics, changes in moisture regime, and the influence of differential historical land uses (Lorimer 1993, McEwan et al. 2011).

In the Driftless Area of southwestern Wisconsin, declines in the abundance of oak species regeneration have been documented throughout the past ca. 40 years (Hix and Lorimer 1991, Hix et al. 2005, Lorimer et al. 1994, Martin et al. 1992, Povak et al. 2008). The mosaic pattern of both the presettlement and modern vegetation represents the multitude of developmental

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pathways that have occurred in the region. These stand developmental pathways are dependent on factors that influence the initial stand composition and structure (e.g., previous land use, seed source availability, local and regional climate, microenvironmental abiotic conditions) as well as dynamic processes that operate throughout stand development (e.g., stand disturbance events, extreme weather events, silvicultural operations). While the decline in oak species regeneration has been documented throughout the Wisconsin Driftless Area (WDA), the degree of oak regeneration decline is variable and influenced by a given site's historical forest development, disturbance regime, moisture regime, and abiotic site characteristics. Here, we present results that quantify structural development, structural complexity, and the status of oak regeneration throughout the Wisconsin Driftless Area.

METHODS

To examine the development, succession, and stand dynamics of upland oak stands in the region, we collected forest inventory and dendrochronological data from 11 study sites distributed throughout the Driftless Area in southwestern Wisconsin (Fig. 1). The Wisconsin Driftless Area, located in the northern portion of the Central Hardwood Forest region, represents a unique physiographic province in the upper Great Lakes region because it was not glaciated during the last glacial maximum (Martin 1916). The disturbance regime in southwestern Wisconsin prior to widespread EuroAmerican settlement included frequent, low-intensity ground fires of lightning and Native American origin and wind events (Curtis 1959, Johnson 1976). However, the modern disturbance regime has changed considerably, caused most notably by the onset of active fire suppression in the early 20th century and the conversion of prairie and savanna landscapes to agriculture or closed-canopy forests (Curtis 1956, Rhemtulla et al. 2007). These changes in land use and land management have not only influenced the composition and structure of the WDA forested landscape, but have also affected the frequency and intensity of

Figure 1.—Map of Wisconsin showing the Wisconsin Driftless Area (shaded gray) and site locations (black dots).

the modern disturbance regime. Because oak species are only moderately tolerant of shade, the frequency and intensity of modern disturbances (whether caused by natural or anthropogenic means) have a large influence on the regeneration success of oak species in the WDA by removing portions of the canopy and increasing light levels in the forest understory.

Across the 11 study sites, we established 34 circular plots 0.04-ha in size and recorded the species, diameter at breast height (d.b.h.), and crown class for all trees (stems ≥10 cm d.b.h. and ≥1.37 m height) and saplings (stems ≤10 cm d.b.h. and ≥1.37 m height). All plots were located within stands that the Wisconsin Department of Natural Resources classified as being dominated by oak or central hardwood species and that established prior to 1940. To analyze stand age structure, disturbance history, and climate-growth relationships, we collected one increment core sample from all stems ≥10 cm d.b.h. within each plot. After the tree-ring samples were processed in the laboratory, tree-ring widths were measured to the nearest 0.001 mm and the measurement series were statistically compared to ensure accurate crossdating. Sampled stands were multi-aged, so the stage of structural development was determined using the median age of canopy trees and a modified version of the decision tree developed by Lorimer and Halpin (2014). We constructed diameter distributions with 5 cm size-class intervals and determined the general trend of each distribution by fitting polynomial functions to the semilogarithmic-transformed diameter distributions using all possible combinations of d.b.h., d.b.h.^{2}, and d.b.h.^{3}. The best-fitting model was selected from significant models ($p < 0.05$) based on the highest adjusted r^2 and the lowest root mean square error. Distribution shape was determined by examining the model variables that were present and the sign of the model coefficients. We calculated several indices that quantify structural diversity: standard deviation$_{dbh}$, the coefficient of variation$_{dbh}$, the Gini coefficient$_{dbh}$, and the Shannon diversity index (H'_{dbh}). Indices of oak species regeneration and maple species regeneration were calculated for each site as the difference between the relative density of understory stems and the relative density of overstory stems.

RESULTS

In the Wisconsin Driftless Area, site-level density values of all saplings and trees (i.e., all stems ≥1.37 m height) ranged between 919 and 2,058 stems/ha and site-level basal area values ranged between 20.5 and 47.1 m^2/ha (Table 1). Across the region as a whole, forest canopies were dominated by oak species (Table 2), while the sapling layer was dominated by more mesic species including sugar maple and red maple (Table 3). This pattern of a predicted compositional shift was further evidenced by negative regeneration indices for oak and positive regeneration indices for maple throughout the region (Table 4). The oldest documented oak tree established at breast height in 1825 while the youngest sampled oak tree established at breast height in 1992. Across the 11 sites, stages of stand structural development varied, with stands in the pole, mature-sapling mosaic, mature, early-transition old-growth, and steady-state old-growth stages represented. The progression of structural stages mirrored the progression of increasing density of large trees (≥45 cm d.b.h.) (Table 1). Four diameter distribution shapes were identified across the region: concave, increasing-*q*, negative exponential, and rotated sigmoid (Fig. 2). Two sites did not yield significant regression models. The standard deviation$_{dbh}$, coefficient of variation$_{dbh}$, Gini coefficient$_{dbh}$, and Shannon diversity index (H'_{dbh}) all generally increased with increasing structural development (Table 5).

Table 1.—Site characteristics for 11 upland oak sites within the Wisconsin Driftless Area. Sites are arranged in ascending order by the density of trees ≥45 cm d.b.h. Unless otherwise noted, values were calculated from all sampled saplings (stems ≤10 cm d.b.h. and ≥1.37 m height) and trees (stems ≥10 cm d.b.h.).

Site	Plot n	Density	Basal area	Density of trees ≥45 cm d.b.h.	Basal area of trees ≥45 cm d.b.h.	Quadratic mean d.b.h.[a]	Developmental stage[b]
		stems/ha	*m^2/ha*	*stems/ha*	*m^2/ha*	*cm*	
New Glarus	2	1,675.0	20.5	12.5	4.2	18.7	P
Dunville	1	1,875.0	23.1	25.0	5.2	24.9	MSM
Perrot	4	993.8	23.5	25.0	5.8	24.0	MSM
Nelson Dewey	1	1,200.0	21.4	50.0	11.8	23.9	MSM
Dell Creek	2	1,337.5	38.9	50.0	12.9	25.0	M
Mirror Lake	4	9,18.75	31.1	50.0	9.5	26.4	M
Blue Mound	3	2,058.3	37.1	50.0	9.2	28.8	M
Borst Valley	3	1,341.7	33.8	66.7	16.0	25.7	M
Devils Lake	4	1,512.5	44.4	81.3	17.7	29.0	M
Kickapoo Valley	7	1,796.4	47.1	82.3	25.3	31.0	OG-ET
Wyalusing	2	950.0	43.3	100.0	21.7	29.1	OG-SS

[a] Includes all stems ≥8 cm d.b.h.
[b] P = pole; MSM = mature-sapling mosaic; M = mature; OG-ET = early transition old-growth; OG-SS = steady-state old-growth.

Table 2.—Density, relative density, dominance, relative dominance, and importance value (average of relative density and relative dominance) for all trees (stems ≥10 cm d.b.h.) sampled on upland oak stands in the Wisconsin Driftless Area, sorted by importance value

Species	Density	Relative density	Dominance	Relative dominance	Importance value
	stems/ha		*m^2/ha*		
Quercus rubra L.	95.31	18.77	14.90	42.12	30.44
Quercus alba L.	75.00	14.77	6.84	19.34	17.06
Acer rubrum L.	92.19	18.15	2.19	6.19	12.17
Acer saccharum Marshall	64.06	12.62	2.47	6.97	9.79
Tilia americana L.	27.34	5.38	2.53	7.14	6.26
Ostrya virginiana (Mill.) K. Koch	37.50	7.38	0.51	1.45	4.42
Pinus strobus L.	17.97	3.54	1.45	4.11	3.82
Carya cordiformis (Wangenh.) K. Koch	16.41	3.23	0.75	2.11	2.67
Quercus velutina Lam.	9.38	1.85	1.11	3.15	2.50
Ulmus rubra Muhl.	16.41	3.23	0.59	1.66	2.44
Fraxinus americana L.	14.06	2.77	0.70	1.98	2.37
Juglans nigra L.	15.63	3.08	0.44	1.25	2.16
Carya ovata (Mill.) K. Koch	9.38	1.85	0.32	0.91	1.38
Quercus bicolor Willd.	3.91	0.77	0.06	0.17	0.47
Prunus serotina Ehrh.	3.13	0.62	0.05	0.15	0.38
Acer negundo L.	2.34	0.46	0.11	0.30	0.38
Pinus resinosa Aiton	1.56	0.31	0.11	0.30	0.31
Quercus macrocarpa Michx.	0.78	0.15	0.16	0.46	0.31
Betula papyrifera Marshall	2.34	0.46	0.04	0.13	0.29
Celtis occidentalis L.	1.56	0.31	0.01	0.04	0.17
Robinia pseudoacacia L.	0.78	0.15	0.02	0.06	0.11
Prunus pensylvanica L. f.	0.78	0.15	0.01	0.03	0.09
Total	507.81	100.00	35.38	100.00	100.00

Table 3.—Density, relative density, dominance, relative dominance, and importance value (average of relative density and relative dominance) for all saplings (stems ≤10 cm d.b.h. and ≥1.37 m height) sampled on upland oak stands in the Wisconsin Driftless Area, sorted by importance value

Species	Density	Relative density	Dominance	Relative dominance	Importance value
	stems/ha		*m^2/ha*		
Acer rubrum L.	256.25	26.28	0.64	36.28	31.28
Acer saccharum Marshall	241.41	24.76	0.34	19.60	22.18
Ostrya virginiana (Mill.) K. Koch	146.88	15.06	0.31	17.56	16.31
Ulmus rubra Muhl.	57.03	5.85	0.11	6.53	6.19
Fraxinus americana L.	44.53	4.57	0.05	2.76	3.66
Prunus serotina Ehrh.	39.84	4.09	0.03	1.98	3.03
Quercus alba L.	18.75	1.92	0.05	2.66	2.29
Tilia americana L.	16.41	1.68	0.04	2.27	1.98
Carya cordiformis (Wangenh.) K. Koch	17.97	1.84	0.03	1.82	1.83
Carya ovata (Mill.) K. Koch	12.50	1.28	0.03	1.92	1.60
Zanthoxylum americanum Mill.	28.13	2.88	0.01	0.32	1.60
Celtis occidentalis L.	21.09	2.16	0.02	0.92	1.54
Prunus pensylvanica L. f.	17.97	1.84	0.02	0.92	1.38
Juglans nigra L.	5.47	0.56	0.02	1.02	0.79
Pinus strobus L.	7.81	0.80	0.01	0.66	0.73
Hamamelis virginiana L.	10.16	1.04	0.00	0.24	0.64
Carpinus caroliniana Walter	10.16	1.04	0.00	0.21	0.63
Acer negundo L.	4.69	0.48	0.01	0.64	0.56
Crataegus spp.	4.69	0.48	0.01	0.61	0.54
Euonymus atropurpureus Jacq.	7.81	0.80	0.00	0.07	0.44
Quercus rubra L.	1.56	0.16	0.01	0.51	0.33
Rhamnus cathartica L.	1.56	0.16	0.00	0.27	0.21
Quercus bicolor Willd.	0.78	0.08	0.00	0.25	0.16
Cornus alternifolia L. f.	0.78	0.08	0.00	0.00	0.04
Salix purpurea L.	0.78	0.08	0.00	0.00	0.04
Total	975.00	100.00	1.76	100.00	100.00

Table 4.—Regeneration indices for all species with sapling or tree importance values ≥1, sorted in ascending order by index value

Species	Index value
Quercus rubra L.	-18.61
Quercus alba L.	-12.85
Tilia americana L.	-3.70
Pinus strobus L.	-2.74
Juglans nigra L.	-2.52
Quercus velutina Lam.	-1.85
Carya cordiformis (Wangenh.) K. Koch	-1.39
Carya ovata (Mill.) K. Koch	-0.56
Prunus pensylvanica L. f.	1.69
Fraxinus americana L.	1.80
Celtis occidentalis L.	1.86
Ulmus rubra Muhl.	2.62
Zanthoxylum americanum Mill.	2.88
Prunus serotina Ehrh.	3.47
Ostrya virginiana (Mill.) K. Koch	7.68
Acer rubrum L.	8.13
Acer saccharum Marshall	12.14

Table 5.—Indices quantifying diameter diversity of all stems ≥3 cm diameter at breast height (d.b.h.) for 11 upland oak sites within the Wisconsin Driftless Area. Sites are arranged in ascending order by the density of trees ≥45 cm d.b.h.

Site	Developmental stage[a]	Standard deviation	Coefficient of variation	Gini coefficient[b]	Shannon diversity index[c]	Average *q*-factor (± SE)[d]
New Glarus	P	9.0	0.7	0.3	1.6	1.1 (± 0.6)
Dunville	MSM	12.6	0.9	0.4	1.7	1.4 (± 0.4)
Perrot	MSM	12.1	0.8	0.4	1.8	1.2 (± 0.3)
Nelson Dewey	MSM	12.4	1.1	0.4	1.4	0.9 (± 0.4)
Dell Creek	M	12.8	0.8	0.4	1.9	1.1 (± 0.3)
Mirror Lake	M	13.8	0.7	0.4	2.1	1.5 (± 0.3)
Blue Mound	M	13.9	0.9	0.5	1.7	1.7 (± 0.4)
Borst Valley	M	14.1	0.9	0.4	1.9	1.4 (± 0.4)
Devils Lake	M	14.8	1.0	0.5	1.6	1.6 (± 0.4)
Kickapoo Valley	OG-ET	16.2	1.1	0.5	1.7	1.4 (± 0.3)
Wyalusing	OG-SS	15.7	0.9	0.4	2.0	1.5 (± 0.5)

[a]P = pole; MSM = mature-sapling mosaic; M = mature; OG-ET = early transition old-growth; OG-SS = steady-state old-growth.

[b]Values range from 0 to 1, with 0 corresponding to sites with perfect size equality and 1 representing maximum size inequality.

[c]Values range from 0 to ln(number of diameter classes), with 0 corresponding to all trees being in the same diameter class and maximum values representing an even distribution of trees within diameter classes.

[d]Calculated from 5-cm diameter classes beginning with the 5 cm class.

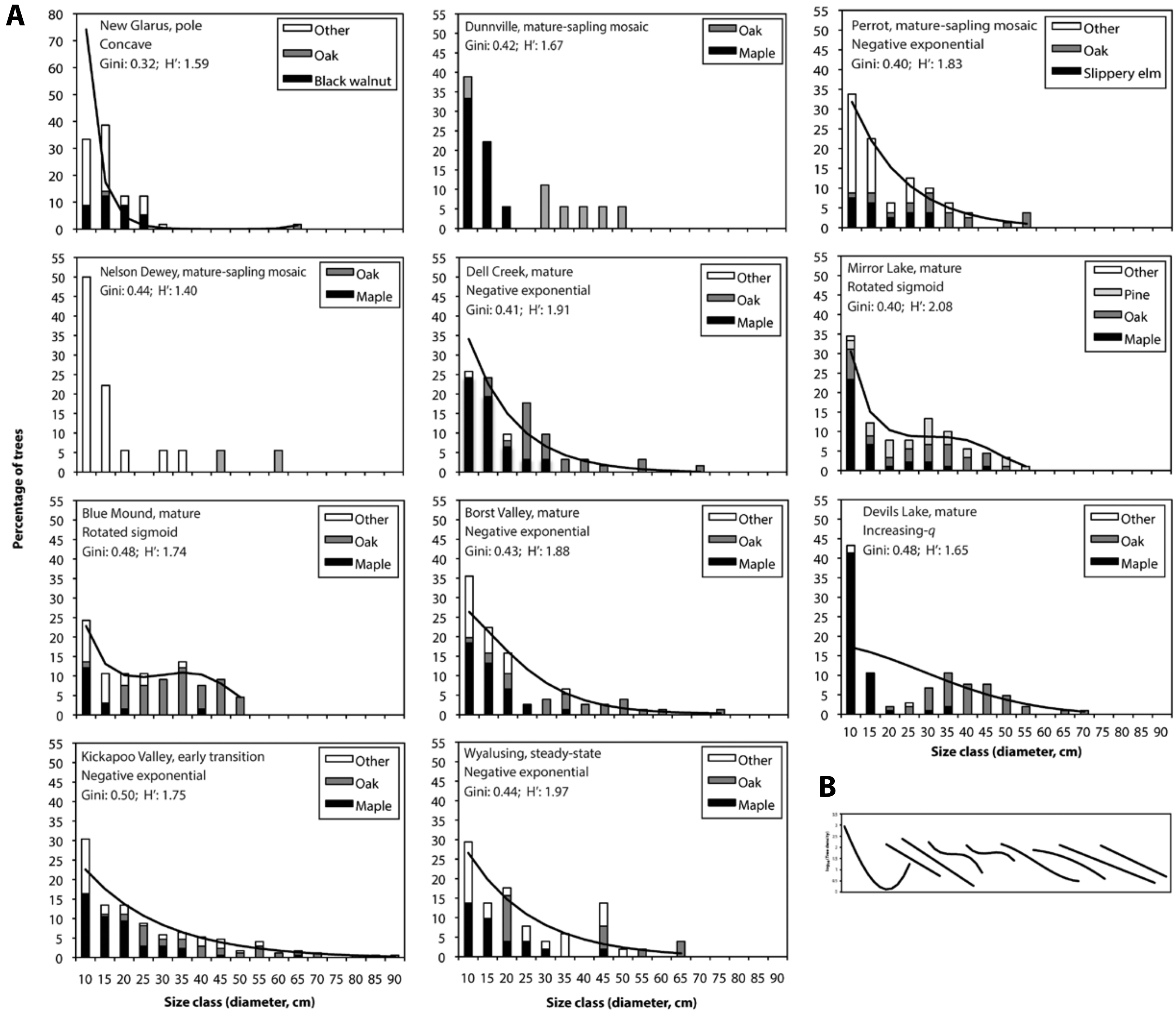

Figure 2.—(A) Size-class distributions (based on relative frequency) for all tree species in the 11 upland oak sites in the Wisconsin Driftless Area. Sites are arranged in ascending order by the density of trees ≥45 cm d.b.h. and regression curves are superimposed on the diameter distributions. (B) Change in the shape of the regression curves for all sites from pole (left) to steady state (right) ordered by density of trees >45 cm d.b.h.

CONCLUSIONS AND FUTURE ANALYSES

The results of this study indicate that the upland oak forest stands of the Wisconsin Driftless Area are transitioning from oak dominance to dominance by more shade-tolerant species such as sugar maple and red maple. Stands throughout the region are in different stages of structural development, and structural diversity generally increased with advancing structural development. Future research will use historical land survey analyses and dendrochronological methods to investigate the influence of historical land-use legacies, disturbance history, and extreme weather events on the composition, structure, and function of the upland oak stands.

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LITERATURE CITED

Abrams, M.D. 1992. **Fire and the development of oak forests.** BioScience. 42: 346-353.

Curtis, J.T. 1956. **The modification of mid-latitude grasslands and forests by man.** In: Thomas, W.L., Jr., ed. Man's role in changing the face of the earth. Chicago, IL: University of Chicago Press: 721-736.

Curtis, J.T. 1959. **The vegetation of Wisconsin: an ordination of plant communities.** Madison, WI: The University of Wisconsin Press.

Fei, S.; Kong, N.; Steiner, K.C.; Moser, W.K.; Steiner, E.B. 2011. **Change in oak abundance in the eastern United States from 1980 to 2008.** Forest Ecology and Management. 262: 1370-1377.

Hix, D.M.; Lorimer, C.G. 1991. **Early stand development on former oak sites in southwestern Wisconsin.** Forest Ecology and Management. 42: 169-193.

Hix, D.M.; Lorimer, C.G.; Guries, R.P.; Kotar, J. 2005. **A guide for classifying and managing forest sites in the Kickapoo River Watershed of southwestern Wisconsin.** College of Agricultural and Life Sciences Research Report. Madison, WI: University of Wisconsin-Madison. 68 p.

Johnson, P.S. 1976. **Modal development of regeneration in clearcut red oak stands in the Driftless Area.** Proceedings of the 1st central hardwood forest conference. Carbondale, IL: University of Southern Illinois: 455-475.

Lorimer, C.G. 1993. **Causes of oak regeneration problems**. In: Loftis, D.L., McGee, C.E., eds. Oak regeneration: serious problems, practical recommendations. Gen. Tech. Rep. SE-84. Asheville, NC: U.S. Forest Service, Southeastern Forest Experiment Station: 14-39.

Lorimer, C.G.; Chapman, J.W.; Lambert, W.D. 1994. **Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands.** Journal of Ecology. 82: 227-237.

Lorimer, C.G.; Halpin, C.R. 2014. **Classification and dynamics of developmental stages in late successional temperate forests.** Forest Ecology and Management. 334: 344-357.

Martin, J.; McGill, D.; Phibbs, A. 1992. **Red oak regeneration in southwest Wisconsin.** Forest Research Note 279. Madison, WI: University of Wisconsin-Madison.

Martin, L. 1916. **The physical geography of Wisconsin.** Wisconsin Geological and Natural History Survey, Bull. No. 36, Educational Series No. 4. Madison, WI.

McEwan, R.W.; Dyer, J.M.; Pederson, N. 2011. **Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America.** Ecography 34: 234-256.

Povak, N.A.; Lorimer, C.G.; Guries, R.P. 2008. **Altering successional trends in oak forests: 19 year experimental results of low- and moderate-intensity silvicultural treatments.** Canadian Journal of Forest Research. 38: 2880-2895.

Rhemtulla, J.M.; Mladenoff, D.J.; Clayton, M.K. 2007. **Regional land-cover conversion in the U.S. upper Midwest: magnitude of change and limited recovery in Wisconsin (1850–1935–1993).** Landscape Ecology. 22: 57-5.