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Scott R. Abella
University of Nevada, Las Vegas, scott.abella@unlv.edu

Neil W. MacDonald
Grand Valley State University

SPATIAL AND TEMPORAL PATTERNS OF EASTERN WHITE PINE REGENERATION IN A NORTHWESTERN OHIO OAK STAND

Scott R. Abella[1] and Neil W. MacDonald

Department of Biology, Grand Valley State University,
Allendale, Michigan 49401-9403

ABSTRACT

Eastern white pine (*Pinus strobus* L.) was often associated with oaks (*Quercus* spp.) on upland sites in presettlement forests of the upper Great Lakes region, but widespread logging and subsequent fires in the late 1800s converted these upland sites to fire-tolerant oak forests. Although white pine regeneration is occurring in these second-growth oak forests, white pine regeneration patterns in oak forests of the Great Lakes region are not well documented. We examined white pine regeneration in the southern Great Lakes region in an oak stand within the Oak Openings region of northwestern Ohio, where white pine plantations established in the 1940s have served as seed sources for white pine invasion of surrounding oak-dominated forests. White pine regeneration was aggregated in high-density clumps in the oak stand, with a mean white pine to white pine nearest-neighbor distance of 1.8 m. Eighty-one percent of invading white pine established during a 6-yr interval that corresponded with an extended period of below-average annual available water deficits (i.e., conditions were more moist than normal). No white pine recruitment has occurred in the oak stand in the last 15 yr since the 6-yr establishment interval, and we hypothesize that favorable white pine colonization sites in the oak stand were occupied during the initial invasion event. White pine regeneration in these oak forests may proceed in "leaps and bounds," with white pine expanding 100–300 m by clumped regeneration into new areas during unique regeneration events. White pine's present ability to reproduce successfully in northwestern Ohio appears related to reductions of historic fire frequencies.

INTRODUCTION

In presettlement forests of the upper Great Lakes region, eastern white pine (*Pinus strobus* L.) occurred in pure stands (Gevorkiantz & Zon 1930; Potzger 1946; Whitney 1987), in mixed stands with red pine (*P. resinosa* Aiton; Harvey 1922), in mixed northern hardwood stands (Nichols 1935; Brown & Curtis 1952), and in mixed *Quercus* stands (Waterman 1922; Maycock 1963; Kurczewski 2000). On dry upland sites, white pine commonly occurred with oaks (*Quercus* spp.) as an understory tree or as a canopy dominant (Kittredge & Chittenden 1929; Kenoyer 1933; Davis 1935). White pine distribution and regeneration success in these presettlement Great Lakes forests depended on substrate, disturbance regimes, climate, and interspecific competition (Whitney 1986).

Pure white pine and mixed white pine-red pine stands developed following catastrophic disturbances such as fire (Maissurow 1935; Hough & Forbes 1943), and white pine in these stands could be self-replacing through regeneration in

[1] Author for correspondence: Ecological Restoration Institute, College of Ecosystem Science, Northern Arizona University, Box 15018, Flagstaff, AZ 86011; sra8@dana.ucc.nau.edu

canopy gaps (Holla & Knowles 1988; Quinby 1991; Ziegler 1995). In mixed northern hardwood forests, white pine regeneration across the landscape was controlled by the distribution of large white pine seed trees and by competition with hardwoods (Palik & Pregitzer 1994; Saunders & Puettmann 1999). Following widespread logging and subsequent fires in the Great Lakes region in the late 1800s, white pine-oak forests on dry sites were converted to oak forests (Kittredge & Chittenden 1929). Although white pine regeneration is occurring in these second-growth oak forests (Elliott 1953; Host et al. 1987; Johnson 1992; Carleton et al. 1996), white pine regeneration patterns are not well documented in oak forests of the Great Lakes region.

We examined white pine regeneration in the southern Great Lakes region in Oak Openings Preserve within the Oak Openings region of northwestern Ohio. Presettlement vegetation in this region was dominated by black oak (*Quercus velutina* Lam.) and white oak (*Q. alba* L.) savannas and woodlands (Sears 1925). White pine did not occur in northwestern Ohio at the time of settlement (Moseley 1928), and the Oak Openings region is about 80 km south of the white pine's native range in southern Michigan. In the mid-1900s, however, white pine plantations were established throughout Oak Openings Preserve in a matrix of oak stands that had undergone succession from savanna or woodland to forest as a result of fire suppression (Abella et al. 2001). These white pine plantations have served as seed sources for white pine regeneration in surrounding oak-dominated forests. Since white pine did not occur in Oak Openings before it was planted in the mid-1900s, we had a unique opportunity to study white pine invasion patterns in an oak-dominated landscape. The objective of this study was to quantify the spatial and temporal patterns of white pine invasion of an oak stand to identify potential white pine regeneration patterns in oak-dominated forests of the Great Lakes region.

METHODS

The 1496-ha Oak Openings Preserve is in Lucas County, northwestern Ohio. We sampled a 5-ha oak-dominated stand (41°33′12′N, 83°50′8″W) in the preserve adjacent to a 0.8-ha white pine plantation. Soils in the oak stand are classified as mixed, mesic Aquic and Typic Udipsamments of the Ottokee and Oakville series (Stone et al. 1980). The oak stand originated about 1930, and the white pine plantation was created in 1947 with trees 3 m apart. In 2001, the plantation contained 43 m^2 ha^{-1} white pine basal area and had a white pine site index of 29 m at 50 yr. All white pine in the oak stand are understory trees and established from seed produced by parent white pine in the plantation once they reached reproductive age.

We sampled white pine regeneration in the oak stand using a stratified-random sampling design in March 2001 by dividing the oak stand into six 0.84-ha blocks and randomly locating one circular 0.1-ha (17.84 m radius) plot in each block. We determined in each plot the species and diameter at 1.4 m of all live trees greater than 1 cm diameter, and we aged white pine to the nearest year by counting branch whorls (Bormann 1965; Sharik et al. 1989; Palik & Pregitzer 1994). For each of the 167 white pine occurring in the 6 plots, we measured to the nearest cm the distance to the nearest white pine and the distance to the nearest codominant or dominant overstory oak (Avery & Burkhart 1983). Nearest neighbors that occurred outside of plots were measured to prevent artificially inflating nearest-neighbor distances for white pine near the outer edges of plots (Clark & Evans 1954; Cottam et al. 1957; Sinclair 1985). Nearest neighbors occurred outside of plots for 7 of 167 white pine measured in our study, and we did not use nearest-neighbor trees that occurred outside of plots in stand density calculations.

To assess the spatial pattern of white pine regeneration in the oak stand, we computed the Clark-Evans index (Clark & Evans 1954) using white pine nearest-neighbor distances for each white pine in the 6 plots. This index is calculated as the ratio of the actual mean nearest-neighbor distance for each individual to the mean nearest-neighbor distance expected if the population was distributed at random (Clark & Evans 1954). An index value of 0 indicates a spatial distribution of maximum aggregation of individuals, a value of 1 indicates a random distribution, and a value of 2.15 indicates a uniform distribution. We tested the significance of the departure from randomness with the standard variate of the normal curve (Clark & Evans 1954). There has been speculation that the Clark-Evans index is biased toward uniform distributions; however, the spatial distribution of white pine in our study was computed as significantly aggregated so we used the original Clark-Evans index (Sinclair 1985). To further assess white pine spatial patterns, we used a two-tailed paired *t*-test comparing white pine nearest-neighbor distances using data pooled for all plots (167 sampled white pine trees) to test the null hypothesis that the mean white pine to white pine distance did not differ from the mean white pine to overstory oak distance. Plot means were not used for this analysis because our objective was to evaluate stand-level spatial patterns, so we gave equal weight to each white pine sampled in the stand. We also used a chi-square test (degrees of freedom = 1) to test the null hypothesis that the proportion of white pine closest to other white pine and the proportion of white pine closest to an overstory oak were both 0.5.

We integrated climatic factors that may affect white pine seed output and seedling survival by estimating available water deficits (potential evapotranspiration – actual evapotranspiration) on a monthly basis for the period 1955–1994 using the Thornthwaite water balance equation (Mather 1978). Moisture availability in upper soil layers is most likely to affect white pine seedling establishment (Smith 1940; Shirley 1945; Thomas & Wein 1985), so we based available water holding capacity on the upper 50 cm of soil. For the water balance calculations, we obtained monthly precipitation and mean monthly temperature data measured at the Toledo Express Airport in Lucas County, Ohio, 5 km from our study site, from the National Climatic Data Center Summary of the Day database (Earthinfo, Inc., Boulder, CO).

RESULTS

White pine occurred as an understory tree beneath an overstory dominated by several oak species (Table 1, Fig. 1). In addition to white pine, white oak and red maple (*Acer rubrum* L.) were abundant in the understory. The Clark-Evans index was < 1 and indicated that the spatial distribution of invading white pine was significantly clumped in the oak stand, and the mean white pine to white pine distance was less than the mean white pine to overstory oak distance (Table 2). Of 167 white pine sampled, 72% occurred closer to other white pine than to an

TABLE 1. Mean stand variables for live trees > 1 cm diameter for a northwestern Ohio oak stand. SD = Standard Deviation; the "other" category includes *Acer rubrum*, *Sassafras albidum*, and *Prunus serotina*.

Variable	Species			Other
	Quercus alba	*Quercus velutina*	*Pinus strobus*	
Density (trees ha^{-1})	223	280	278	262
SD	87	64	229	209
Basal area (m^2 ha^{-1})	5.5	18.4	0.9	1.0
SD	2.8	3.6	1.0	0.4
Diameter (cm)	15.7	28.5	4.4	6.6
SD	4.7	2.0	2.6	2.0

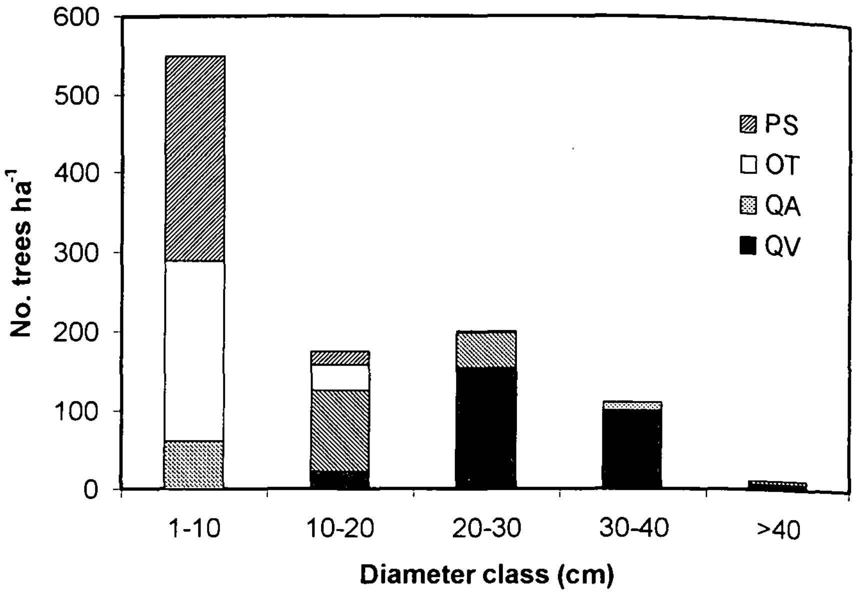

FIGURE 1. Diameter distribution for a northwestern Ohio oak stand. PS = *Pinus strobus*, OT = other (includes *Acer rubrum*, *Sassafras albidum*, and *Prunus serotina*) , QA = *Quercus alba*, and QV = *Quercus velutina*.

overstory oak; this proportion differed significantly from 0.5 (Table 2). Mean age of invading white pine in the oak stand at the time of sampling in 2001 was 20.5 yr (standard error = 0.2). White pine invasion of the oak stand began in 1974 when the parent white pine in the plantation were age 27 yr, and 81% of the invading white pine established in the oak stand between 1977 and 1982 (Fig. 2). This establishment interval corresponded with an extended period of below average annual available water deficits (Fig. 3).

TABLE 2. Summary of spatial patterns of regenerating white pine in a northwestern Ohio oak stand.

Variable	Value	Test statistic	Probability
Clark-Evans index	0.6	$z = 9.9$	< 0.0001
Nearest-neighbor distances		$t = 5.75$	< 0.0001
White pine to white pine distance (m)[1]	1.8 ± 0.1		
White pine to overstory oak distance (m)[1]	2.7 ± 0.1		
Frequency of proximity		$\chi^2 = 33.7$	< 0.0001
No. white pine closer to other white pine	121		
No. white pine closer to an overstory oak	46		

[1] Mean ± standard error.

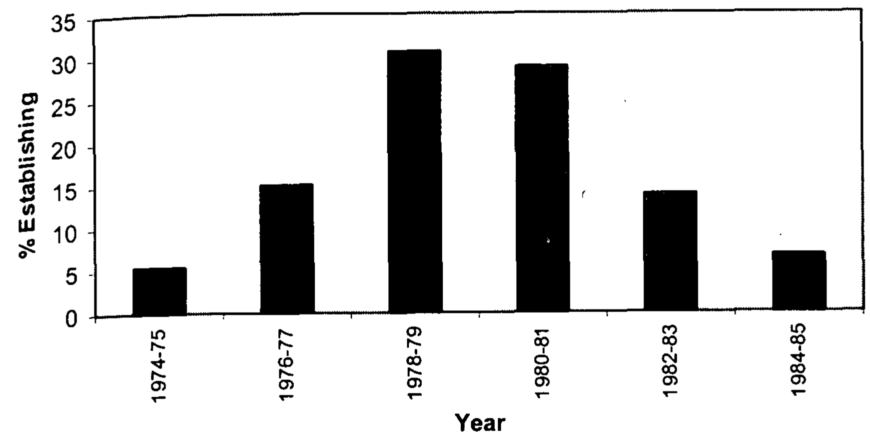

FIGURE 2. Percent of the total white pine sampled (n = 167) establishing in a northwestern Ohio oak stand by 2-yr classes. No white pine established in the oak stand before 1974 or after 1985.

DISCUSSION

Aggregation of white pine regeneration in high-density clumps suggests certain areas in the oak stand were optimal for white pine establishment, although these areas have no known history of disturbance. These optimal zones for white pine regeneration may result from favorable light conditions, favorable seedbeds free from understory competition, or optimal seedbed moisture conditions (Cornett et al. 1998). Peterson and Squiers (1995a, b) also found that white pine regenerated in clumps in a bigtooth aspen (*Populus grandidentata* Michx.) forest in northern Michigan, and these clumps were distributed away from overstory aspen. Hibbs (1982) hypothesized that white pine saplings may reach the overstory in dense hardwood stands of New England through group reproduction where a clump of white pine saplings serves as a buffer from hardwood compe-

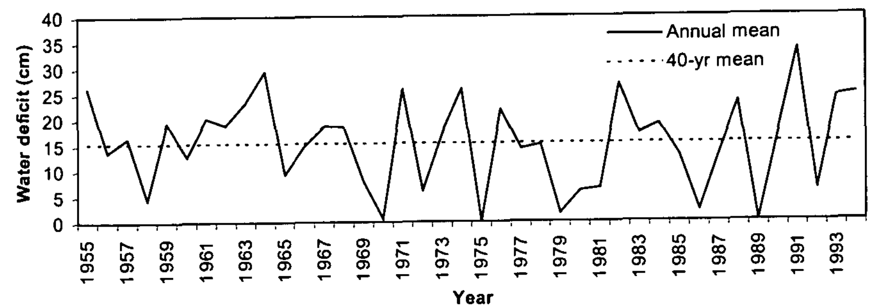

FIGURE 3. Forty-year records of annual available water deficits in the Oak Openings region of northwestern Ohio.

tition around a central white pine. White pine regeneration was also aggregated in pure white pine stands in Ontario (Quinby 1991) and New England (Yeaton 1978). These studies combined with our results suggest that white pine commonly regenerate in clumps in a variety of forest types including oak-dominated forests of the Great Lakes region.

Clumps of regenerating white pine occurred in the oak stand as far as 200–300 m away from the parent white pine in the plantation. These distances are further than those reported by Palik & Pregitzer (1994), who found that little or no white pine regeneration occurred greater than 100–140 m from large white pine seed trees in an aspen forest in northern Michigan. White pine seed is primarily wind dispersed (Burns & Honkala 1990), and the greater dispersal distances we recorded likely result from the open vertical structure of the oak stand that facilitated white pine seed dispersal. Small mammals can also disperse white pine seeds by caching (Burns & Honkala 1990), but it is unlikely that seed caches were the primary dispersal mechanism for white pine seed in the oak stand because most seed caches are eaten in a given year (Smith 1940; Abbott & Quink 1970; Cornett et al. 1998). The distance seeds traveled in the oak stand from the parent trees in the plantation and the large number of white pine establishing during a narrow time frame are consistent with wind dispersal of seed for white pine colonization of this oak stand.

White pine began establishing in the oak stand when the parent white pine in the plantation were age 27 yr, and 81% of white pine regeneration in the oak stand occurred during a 6-yr period. Our results are similar to those of Sharik et al. (1989) in hardwood forests of lower Michigan, who found that residual white pine following catastrophic fire were age 26–37 yr when the first post-fire white pine seedlings originated. White pine invasion of the oak stand in our study corresponded with a 5-yr period of below average available water deficits, indicating that moisture stress was low during white pine seedling establishment. The onset of seed production by plantation white pine, corresponding with a climatic period favorable for white pine seedling survival, created optimal conditions for white pine regeneration during their establishment interval in the oak stand (Burns and Honkala 1990).

Aggregation of white pine regeneration, the narrow time span of invasion, and the lack of subsequent recruitment suggest that white pine invasion of the oak stand was a discrete event. This invasion event was facilitated by initial seed produced by the parent white pine in the plantation, favorable white pine regeneration sites available in the oak stand, and favorable climatic conditions for white pine seedling survival. Lack of subsequent white pine recruitment in the oak stand since 1985 is probably not due to a lack of seed because good white pine seed years generally occur every 3–5 yr (Burns & Honkala, 1990). Climatic conditions characterized by low available water deficits, similar to those during the initial invasion event, also have occurred since 1985 but did not correspond with further white pine regeneration in the oak stand.

Our results suggest that most of the favorable white pine colonization sites in the oak stand were occupied during the initial invasion event, and intraspecific competition with established white pine clumps occupying favorable regeneration sites in the oak stand has inhibited subsequent recruitment. Several established white pine in the oak stand, however, are currently growing greater than 0.5–1 m yr^{-1} and will eventually reach the overstory (Hibbs 1982). These white pine are nearing reproductive age with a mean age of 20.5 yr and will begin to produce seed that may initiate white pine invasion of other adjacent oak stands. White pine regeneration in these oak forests may proceed in "leaps and bounds," with white pine expanding 100–300 m by clumped regeneration into new areas during unique regeneration events following the onset of seed production by maturing trees.

Although white pine did not occur in the Oak Openings region at the time of settlement, its present ability to reproduce successfully in northwestern Ohio appears to be related to human alteration of historic disturbance regimes. Moseley (1928) noted that the complete absence of conifers in the Oak Openings region was "peculiar," and the sandy soils of Oak Openings are similar to those in lower Michigan where white pine was abundant in presettlement forests (Waterman 1922; McCool & Veatch 1924; Veatch 1928). Before settlement, oak savanna and woodlands in the Oak Openings region burned frequently and intensely (Bourne 1820), and small white pine cannot survive frequent fire (Kittredge & Chittenden 1929; Burns & Honkala 1990). Following logging in Michigan in the late 1800s, for example, intense fires scorched upland areas formerly dominated by white pine, eliminating regenerating pine and favoring fire-tolerant oaks (Beal 1888, 1902; Kittredge & Chittenden 1929). Similar burning regimes occurred historically in the Oak Openings region (Bourne 1820; Moseley 1928), and white pine's present ability to reproduce successfully in northwestern Ohio likely results from human suppression of the presettlement fire regimes that white pine could not have survived.

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