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TREE ESTABLISHMENT DURING DRY SPELLS AT AN OAK SAVANNA IN MINNESOTA

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ABSTRACT

Recent research has challenged the long-standing hypothesis that forests in the Upper Midwest of the United States developed during wetter periods and retreated during dry periods. We explored this debate by examining patterns of tree establishment on an oak savanna in east-central Minnesota within the context of variable moisture availability and fire suppression. We used superposed epoch analyses (SEA) to evaluate the mean moisture conditions for a 21-year window surrounding tree establishment dates. Before effective fire suppression (1809–1939), 24 of 42 trees with pith dates (62%) grew to 30-cm height during dry years (Palmer Drought Severity Index < -1), *versus* only 5 of 42 (12%) that established in wet years (PDSI > 1). Significantly more trees established during dry periods (negative PDSI values) than would be expected with the proportion of wet-to-dry years ($\chi^2 = 10.738$, df $= 1$, p-value $= 0.001$). Twenty of the complete sample of 74 trees with pith dates (27%) established during drought in the 1930s. We hypothesize that dry conditions limited plant productivity, which in turn decreased competition between grasses and tree seedlings and reduced rates of accumulation of fine fuels, enabling seedlings to grow tall enough to resist subsequent fires. We recommend SEA as a methodological approach to compare historical climate conditions with the timing of regeneration success in other regions of forest expansion.

Keywords: oak savanna, drought, Palmer Drought Severity Index, tree establishment, bur oak, *Quercus macrocarpa*, northern pin oak, *Quercus ellipsoidalis*, green ash, *Fraxinus pennsylvanica*, Minnesota.

INTRODUCTION

Monitoring the past and current effects of climate change on vegetation is critical for developing predictive models of the future. The principal interactions between regional climate and local forest dynamics are particularly important at ecosystem boundaries where future change may be rapid (Allen and Breshears 1998). One such transition zone is the prairie–forest ecotone in southern Minnesota that was historically dominated by oak (*Quercus*) savannas (a mosaic of herbaceous and woody plants). Oak savannas covered *ca.* 12 million ha of the Midwest at the time of Euro-American settlement, but by 1985 high-quality remnants were cataloged on only about 0.02% of their original range (Nuzzo 1986). The structure of much of the remaining oak savanna has changed dramatically, with woody-plant abundance increasing substantially since the early- to mid-1900s, likely because of alterations in local fire regimes through fire suppression and grazing (Pierce 1954; Curtis 1959; Tester 1989; Faber-Langendoen and Davis 1995). It is unclear, however, what role other important factors such as climate, topography, soils, species composition, and disturbance have in effecting such changes.

The long-standing hypothesis for forest establishment at the prairie–forest border posits that cooler, moister conditions reduced the flammability of fuels and created more lakes that fragmented the land surface and served as natural fire breaks (Grimm 1983). The resulting lower fire frequencies allowed trees to establish along the prairie margin where they previously had been killed or stunted by fire. Recently, however, scientists have challenged the notion that forests

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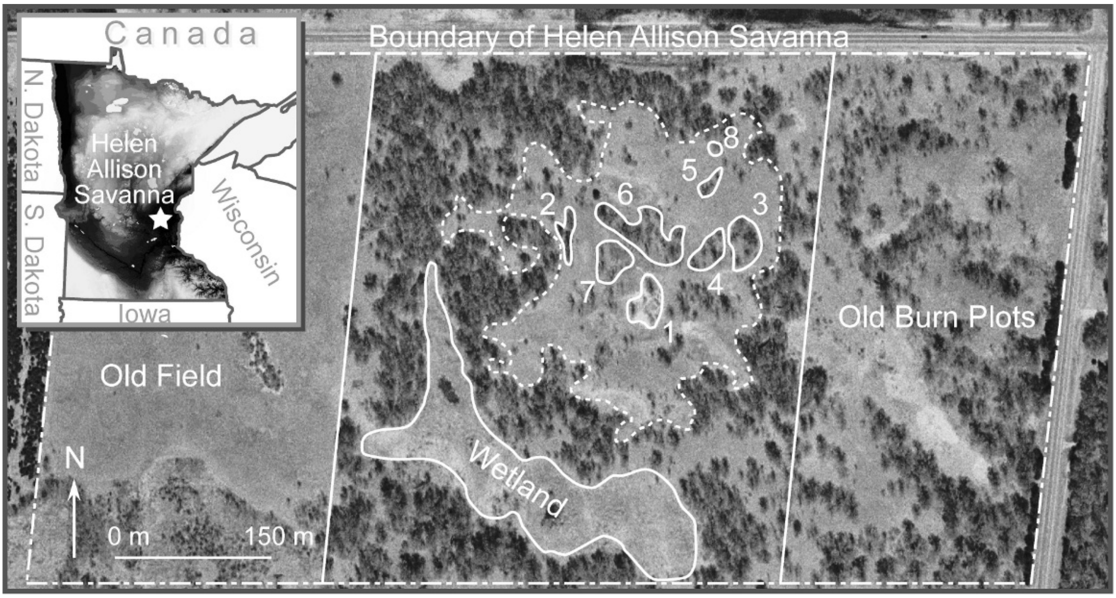

Figure 1. Aerial photo (2000) of 35-ha Helen Allison Savanna on the Anoka Sand Plain in east-central Minnesota. The study area is delimited by a dashed line, and individual tree clusters within the oak savanna are outlined and numbered.

developed during wetter periods and retreated during dry periods. Umbanhowar (2004, 675) surmised from charcoal and pollen records that deciduous forests expanded during drier rather than wetter periods, and concluded that "a better understanding is needed of … the relationship between precipitation and fire in grasslands *versus* forests … in order to understand past interactions of climate, fire and vegetation and to predict future change along the prairie–forest border and elsewhere." Paleoenvironmental analyses have indicated that lake levels fell and regional fire severity decreased as forests expanded into grassland and savanna during the past 800 year (B. Shuman, unpublished data). This climate–fire relationship is similar to the decrease in fire frequency during droughts in grasslands of the northern Great Plains (Clark *et al.* 2002). We undertook this case study to learn about the effects of climate and fire on tree establishment within an oak savanna at the western edge of its range (*cf.* Abrams 1992).

We tested the hypothesis that pulses of tree establishment (*i.e.* growth to coring height) coincided primarily with dry spells rather than wet spells by comparing annually-resolved tree-establishment dates with inter-annual climate variability at an oak savanna in east-central Minnesota. The higher resolution of this approach complements coarser-scale analyses of the ecological history of the oak savanna derived from lake sediments. Our specific objectives were to: (1) describe the relationship between annual to decadal moisture availability and tree establishment, (2) examine how fire suppression may have affected this relationship, (3) explore a novel application of Superposed Epoch Analysis to analyze climate–tree establishment relationships, and (4) provide a historical context for science-based stewardship (Noss 1985; Karnitz and Asbjornsen 2006).

METHODS

Study Area

Helen Allison Savanna (HAS) is a 35-ha preserve in east-central Minnesota (45°25′N, 93°10′W) owned by The Nature Conservancy (TNC) and managed by TNC and the Minnesota Department of Natural Resources as a Scientific and Natural Area (Figure 1). Oak savanna and oak woodland occupy 20 ha of the preserve (57%), while wetlands and old-field vegetation cover the remaining area. The site lies on the gently undulating Anoka Sand Plain. The Sartell fine sand of the oak savanna is excessively drained (Chamberlain 1977). The climate at HAS is continental, with hot, humid summers and cold winters.

In the late 1800s, low intensity ground fires ignited by Native Americans, newly arriving European settlers, and lightning were common in southern Minnesota (Grimm 1984). Fewer fires burned at HAS from the 1920s through the 1930s, and then fires ceased to burn because of grazing and active fire suppression (Pierce 1954). In 1962, TNC reintroduced fire to parts of HAS; prescribed burns began in 1987 on the portion of the oak savanna that we studied.

Field Methods

We collected age-structure data from six randomly selected tree clusters and two subjectively chosen tree clusters based on tree size and species composition to obtain a representative sample of the tree species present on the savanna (Figure 1). Tree-cluster boundaries were defined by delineating all of the trees with overlapping canopies. We recorded the species and diameter at breast height (dbh) of all of the trees within each cluster. We then collected increment cores at 30 cm above ground level along two radii of each tree ≥ 5.0 cm dbh for a total of 138 trees. We also cut cross-sections from all dead saplings and a few live saplings within each cluster.

Laboratory Methods

All samples were dried, mounted, and sanded with progressively finer grit to obtain a highly polished surface for analysis. We visually cross-dated the cores and compared skeleton plots (Stokes and Smiley 1996) to ensure that the rings of each sample were absolutely dated. We used radial templates on core samples that lacked pith but provided sufficient ring curvature to estimate the number of missing rings to pith (Applequist 1958). Incomplete cores without sufficient curvature to estimate pith were excluded from further analyses.

We defined the date of establishment as the year that each tree attained coring height. Green ash (*Fraxinus pennsylvanica* Marsh.) can reach 30 cm in the first year of growth (Kennedy 1990). Bur oak (*Quercus macrocarpa* Michx.) can grow more slowly, especially if fire or herbivores suppress sapling growth. Most (11 out of 14) oak saplings harvested in 2007 for another study at HAS, however, grew from ground level to 30-cm height within two years (S. Margoles, unpublished data), and we did not add an age correction to coring height. We did not attempt to determine germination dates (Savage *et al.*, 1996) or history of post-fire resprouting, but rather we identified the climate conditions associated with tree establishment.

Data Analysis

We plotted tree pith dates against dbh and overlaid a 7-year moving average of June–July–August (JJA) values of the Palmer Drought Severity Index (PDSI) to examine the relationship between tree establishment and moisture availability. PDSI is a measure of relative moisture availability based on precipitation, soil moisture, and evapotranspiration (Palmer 1965). We used the tree-ring based JJA PDSI reconstruction (grid point 198, 45.0°N, 92.5°W, at the Minnesota–Wisconsin border about 70 km from HAS; Cook and Krusic 2004; Cook *et al.* 2004), and the instrumental record, which began in 1895 (National Climatic Data Center Minnesota Division 6; NCDC 2007). We compared the number of trees that established during dry periods (negative PDSI values) *versus* wet periods (positive PDSI values) relative to the number expected with the proportion of dry-to-wet years using a chi-square test (Legendre and Legendre 1998).

We conducted superposed epoch analyses (SEA; program EVENT Version 6.02P from the Dendrochronology Program Library; Holmes and Swetnam 1994) to evaluate the mean moisture conditions (PDSI) for a 21-year window surrounding the date when each tree grew to coring height. This span of ten years before and ten years after the trees reached 30-cm height was chosen to capture decadal-scale relationships between tree

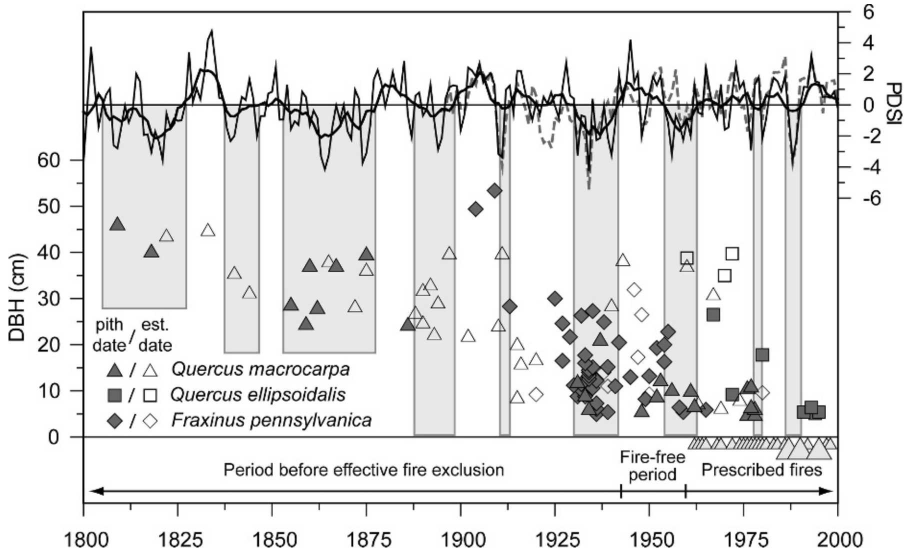

Figure 2. Tree diameter at breast height (dbh) and pith date; drought history; and fire periods at Helen Allison Savanna (HAS). Palmer Drought Severity Index (PDSI) shows relative moisture availability. Thin PDSI line indicates mean June–July–August (JJA) reconstructed values (Cook and Krusic 2004). Dashed line represents mean JJA instrumental PDSI from 1895 to 2000 (NCDC 2007). Heavy black PDSI line shows 7-year moving average (reconstructed values for 1800 to 1894; instrumental record from 1895 to 2000). Grey vertical boxes align with periods when 7-year average PDSI was negative, indicating below-average moisture availability. Small triangles at bottom right corner of figure represent prescribed fires conducted in burn units east of the study site; large triangles indicate fires that burned within the study area.

establishment and moisture availability. The establishment dates we used in the SEA were derived only from cores that contained pith. Each SEA set included analyses of the entire period (1809–2005), the era before total fire exclusion (1809–1939), and the period of altered fire regime (1940–2005). Bootstrapped confidence intervals for the SEA were calculated in program EVENT using 1,000 runs of a Monte Carlo simulation.

RESULTS

Bur oak and northern pin oak (*Quercus ellipsoidalis* E.J. Hill) trees dominated most of the clusters, while two clusters (one randomly selected and one subjectively selected) were composed almost entirely of green ash. Increment cores from 74 of the 138 trees (53%) sampled contained pith, with dates ranging from 1809 to 1995. We estimated establishment dates for 52 trees (38%) with ring curvature but no pith. We presented these estimated dates graphically, but we did not include these data in any calculations linking moisture availability to establishment success. Twelve trees (9%) had incomplete cores and were not included in any of our analyses.

Bur oak is the longest-lived species at HAS. The oldest bur oak we cored established in 1809, and 6 trees predated 1860. The oldest green ash tree established in 1905, but most green ash stems grew to coring height between 1925 and 1960. The youngest trees sampled were northern pin oak, with stems reaching coring height each decade from the 1960s to the 1990s.

We noticed striking patterns in the relationship between PDSI and establishment dates (Figure 2). Bur oak establishment aligned closely with most periods of extended drought (*i.e.* negative values of 7-year average PDSI highlighted by gray boxes in Figure 2). Most green ash grew to coring height in the 1930s during the Dust Bowl drought. Many of the northern pin oaks established during wetter spells after the prescribed fire program was established at HAS.

Establishment pulses coincided with dry rather than wet periods (*i.e.* more symbols in Figure 1 fall within the gray boxes than outside of them) before fire exclusion. Significantly more

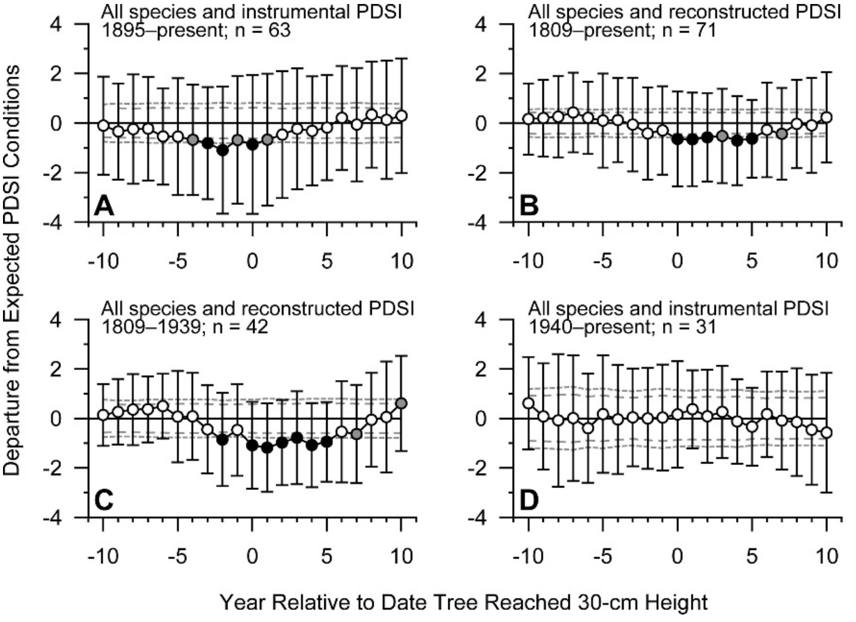

Figure 3. Superposed epoch analyses. Circles indicate departure of actual mean JJA PDSI surrounding pith dates from expected PDSI based on a Monte-Carlo simulation of 1,000 runs. Horizontal zero line charts average moisture availability; negative numbers are drier and positive number are wetter than average conditions. Dashed lines indicate boot-strapped confidence intervals of 95% (long dashes) and 99% (short dashes). Gray circles surpass 95% confidence limit; black circles surpass 99% confidence limit; white circles indicate the relationship is not significant. Error bars show ±1 SD of actual PDSI values. 3A and 3B used instrumental and reconstructed PDSI, respectively. 3C shows the period before fire exclusion, and 3D depicts the time of altered fire regime.

trees established during dry years (negative PDSI values) than would be expected with the proportion of wet (positive PDSI values) to dry years ($\chi^2 = 10.738$, df = 1, p-value = 0.001). Between 1809 and 2005, the proportion of dry years with PDSI < -1 (32%, n = 64) to wet years with PDSI > 1 (30%, n = 59) was relatively even based on reconstructed PDSI for 1809–1894 and instrumental PDSI for 1895–2005. During this same period, 50% of 74 trees grew to 30-cm height during the dry years, whereas only 30% of the trees reached that height in the wet years. The association of tree establishments with dry years was strongest from 1809 to 1939, when 62% of our sample (26 of 42 trees) grew to 30 cm during dry years, *versus* 12% (5 of 42 trees) that established in wet years. Twenty-seven percent of the complete sample of 74 trees, including most green ash, reached coring height during the drought of the 1930s.

Our superposed epoch analyses identified different relationships between moisture availability and tree establishment over different periods (Figure 3). All statistically significant relationships between tree establishment and moisture conditions (filled circles in Figure 3) within ±9 year of establishment coincided with drier than expected conditions based on the Monte Carlo simulations. Climate was significantly drier than normal ($p \leq 0.05$) for at least four years before and one year after seedlings reached 30-cm height for all trees with pith dates after 1895 (Figure 3A). When we considered those trees with pith dates between 1809 and 2005, significantly dry conditions were associated with the year of establishment and for at least five years after establishment (Figure 3B). Before the onset of fire exclusion (1809–1939), eight of the ten years surrounding tree establishments were significantly dry (Figure 3C). The relationships between moisture availability and tree establishment in the period of altered fire regime (1940–2005) were not significant within our 21-yr window of analysis (Figure 3D).

DISCUSSION

Moister conditions could result in fewer fires, allowing trees to grow up in prairies and oak savannas (*sensu* Grimm 1983). We observed a different pattern of tree establishment, however, particularly for bur oak that established during *dry* spells throughout the 1800s. More trees grew to 30 cm during the Dust Bowl drought of the 1930s than in any other decade in the past century. Most of the green ash stems established during the dry 1930s, even though the species typically is associated with wetlands rather than sandy, droughty uplands (Kennedy 1990). These results support the idea that forests were able to invade the prairie during dry periods (Umbanhower 2004). Native American burning, grazing, and agriculture likely influenced vegetation dynamics too (*e.g.* Batek *et al.* 1999; Black *et al.* 2006), but our goal was to identify the climate–tree establishment relationship. A future study could reconstruct the fire history of this oak savanna to provide further context for our results.

Fire regimes of oak savannas in the Midwest historically included frequent, low-severity fires (*e.g.* Cutter and Guyette 1994; Wolf 2004), and are in many ways similar to the fuel-limited fire regimes of some ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests of the American Southwest (Dieterich 1983; Baisan and Swetnam 1990; Swetnam and Baisan 1996). Conditions at an annual scale in these western systems are commonly conducive to burning, and the probability of a fire is heavily influenced by the abundance and connectivity of fuels (Martin 1982). Oscillations between wet and dry conditions are therefore key drivers of fire events, as fuels develop and then dry out (Swetnam and Betancourt 1990; Swetnam and Betancourt 1998). Dry conditions for several years after a fire would reduce plant productivity or even lead to grass mortality and bare soils, thereby slowing the accumulation of fine fuels that are required to carry a surface fire. We reconcile the apparent contradiction of successful tree establishment during dry rather than wet periods, with the following explanation: Dry conditions on the droughty soils may have limited the productivity of grasses and other herbaceous species, thinning the ground cover and creating openings for oaks to grow. Dry conditions during and after tree establishment may have slowed fuel accumulation rates (*cf.* Sala *et al.* 1988), reduced the probability of fires, and enabled seedlings and saplings to grow enough that they could survive the next fire (*cf.* Scholes and Archer 1997).

Additional evidence supporting this explanation is offered by the differences in climate–tree establishment relationships identified through SEA before and after the onset of fire exclusion at HAS. Climate influenced the timing of fire events before European settlement in many different ecosystems (*e.g.* Clark 1990; Swetnam and Betancourt 1990; Johnson and Larsen 1991; Swetnam 1993; Veblen *et al.* 2000; Taylor and Beaty 2005; Guyette *et al.* 2006). The arrival of Euro-American settlers and the onset of fire suppression, however, have masked the climate–fire relationship in some Midwestern ecosystems (*e.g.* Stambaugh and Guyette 2006), and have effectively eliminated wildfires in many others (Abrams 1992, 2006). In some prairies, a lack of fire weakens the relationship between precipitation and plant productivity as the buildup of litter and organic material change the microsite nutrient availability and hydrology (Briggs and Knapp 1995). The disruption of the fire regime at HAS by 1940 may have weakened the influence of climate on tree establishment by changing the effects of climate on plant productivity and eliminating the previous climate–fire relationship.

We have begun to answer timely questions about the interacting role of climate and fire in shaping vegetation patterns. Our tree-ring analyses illustrate a potential mechanism behind the patterns in forest establishment observed through the coarser-scale lake sediment analyses of Umbanhowar (2004) and Shuman (unpublished data). We also used SEA to examine climate–tree establishment relationships in a novel way that can be applied at additional sites to test the relationships that we identified. Our research, coupled with forthcoming dendroecological analyses of fire history at this and other savanna remnants, illuminates how climate and fire interact to influence vegetation development. Without such data, one cannot fully understand past or present ecology, or predict vegetation responses to restoration efforts and to future climate change (Swetnam *et al.* 1999; Kipfmueller and Swetnam 2001).

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