Forest Ecology and Management 257 (2009) 876–884

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Dynamics and determinants of *Quercus alba* seedling success following savanna encroachment and restoration

Lars A. Brudvig *, Heidi Asbjornsen

Department of Natural Resource Ecology and Management, 339 Science II Hall, Iowa State University, Ames, IA 50011-3221, United States

ARTICLE INFO

Article history:
Received 16 August 2008
Received in revised form 6 October 2008
Accepted 17 October 2008

Keywords:
Canopy thinning
Ecosystem stability
Microenvironment
Oak regeneration
Recruitment
White oak
Woody encroachment removal

ABSTRACT

The scattered tree layer that defines savannas is important for structuring the understory community and determining patterns of overstory recruitment. However, encroachment by woody plants has altered overstory tree densities and regeneration dynamics. We characterized seedling success of the savanna-forming species *Quercus alba* within Midwestern (USA) oak savannas that had been degraded by encroachment (control; $n = 4$) or experimentally restored by removal of encroaching woody vegetation (treatment; $n = 4$). In early 2004, 981 seedlings were transplanted along transects radiating from tree boles of overstory *Q. alba* trees to inter-canopy gaps and monitored for three growing seasons. Seedlings in restored sites had greater survival (>2×), height growth (by >50%), and basal diameter growth (by >20%). In general, seedling survival and growth parameters increased with distance from overstory trees and were greatest in inter-canopy gaps of restored sites. By the final growing season (2006), the seedling survival-by-distance from tree correlation was stronger in control ($r^2 = 0.25$) than treatment sites ($r^2 = 0.18$), due to relatively uniform (and greater) survival at all distances from trees in treatment sites. In 2006, growth parameters (seedling height, diameter, Δ height, Δ diameter, and # leaves) were significantly (and more strongly) positively correlated with distance from trees in treatment sites. However, seedling herbivory was also greater after treatment and increased with distance from overstory trees. To understand seedling/microenvironment relationships, we created logistic (survival) and linear regression models (Δ height, Δ basal diameter, # leaves in 2006). Control seedling models had consistently greater predictive power and included more variables, suggesting that savanna restoration may decouple seedlings from their microenvironments, potentially by decreasing competition for limiting resources. Encroachment of the savannas in this study is limiting regeneration of *Q. alba*, suggesting substantially altered regeneration dynamics from those under which these savannas originally formed. Initial responses from our test of restoration, however, were promising and mechanical encroachment removal may be a means to promote overstory regeneration of this species. Finally, the savannas in this study appear inherently unstable and a scattered canopy tree configuration is unlikely to persist without regular disturbance, even in the restoration sites. Repeated mechanical thinning treatments with selected retention of recruiting *Q. alba* individuals or reintroduction of understory fire or grazing animals may be potential mechanisms for promoting long-term persistence of savannas at these sites.

1. Introduction

Savannas occupy nearly one-third of the terrestrial globe, including >50 Mha in temperate regions of North America (McPherson, 1997; Scholes and Archer, 1997). Although represented by many different species, scattered or clustered overstory trees in low densities are a defining feature of all savannas (Scholes and Archer, 1997). Savanna trees are important for structuring understory plant communities through their modification of understory microclimate (including understory light and soil moisture levels), soil nutrients, and species composition (Scholes and Archer, 1997; Breshears, 2006). Through direct influences on microclimate and indirect effects on competing understory plants, savanna overstory trees also impact patterns of tree regeneration; however, impacts vary among savanna ecosystems. Due to variation in water availability, savanna trees may facilitate seedling survival below canopies in more xeric savanna ecosystems (e.g., Borchert et al., 1989; Hoffmann, 1996; Weltzin and McPherson, 1999) or limit recruitment to inter-canopy gaps by out-competing seedlings, as is often true in more mesic savannas

* Corresponding author. Present address: Department of Biology, Washington University, Campus Box 1137, One Brookings Drive, St. Louis, MO 63130-4899, United States. Tel.: +1 803 725 1758; fax: +1 803 725 0311.
E-mail address: brudvig@biology2.wustl.edu (L.A. Brudvig).

0378-1127/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2008.10.016

(e.g., Borchert et al., 1989; Rebertus and Burns, 1997; Holmgren et al., 2000). The effects of canopy trees on recruitment may result in savanna overstory densities that range from relatively stable (e.g., Weltzin and McPherson, 1999) to largely unstable, with a tendency toward canopy gap infilling (e.g., Archer, 1990).

One striking consequence of instability has been woody (e.g., brush) encroachment. Over the last century many savanna ecosystems have been encroached by woody species due to a combination of fire suppression, altered grazing regimes, and climate change (Archer et al., 1988; Abrams, 1992; Scholes and Archer, 1997; Bustamante et al., 2006). Encroachment has increased overstory tree density and canopy cover and has altered tree composition, since encroaching species are frequently different than the pre-encroachment overstory dominants (Archer, 1990; Abrams, 1992). Encroachment may disrupt understory resource and vegetation patterns (Breshears, 2006). Presumably, patterns of recruitment may also differ after encroachment; however, recruitment patterns in encroached savannas are not well understood. Furthermore, although removal of encroaching vegetation can restore at least some understory resource and vegetation dynamics (Brudvig and Asbjornsen, in press), it is not well known how encroachment removal impacts patterns of savanna tree recruitment. Understanding recruitment implications of encroachment and removal will be critical for restoring remnants.

Midwestern oak savannas historically occupied 10–13 Mha as an ecotone between North American prairie grasslands to the west and deciduous forests to the east (Nuzzo, 1986). A scattered oak overstory and a continuous herbaceous understory are maintained by frequent understory fires; however, Midwestern oak savannas have largely been either converted to agriculture or degraded by woody encroachment resulting from fire suppression during the past 150 years (Nuzzo, 1986). Less than 1% remains intact and non-encroached, making Midwestern oak savannas a priority for conservation and restoration (Nuzzo, 1986). Due to fluctuations in climate and ensuing expansion and contraction of North American prairies, the precise range of Midwestern oak savannas has varied in size and position during that last 10,000 years (Clark et al., 2001). Thus, Midwestern oak savannas are interesting for studying recruitment dynamics, as they naturally exhibit range expansion (favorable recruitment periods) and contraction (non-favorable recruitment periods).

In this paper, we investigate spatial seedling dynamics within a large-scale Midwestern (USA) *Quercus alba* (white oak) savanna restoration experiment. We transplanted *Q. alba* seedlings into oak savannas with a prominent *Q. alba* overstory component that had been degraded by woody encroachment and into oak savannas that had been restored by mechanically removing woody encroachment. We then monitored seedlings for three growing seasons to address the following research questions: (1) what are the effects of restoration on seedling success (defined by survival and growth parameters)? (2) Does success vary along gradients from overstory *Q. alba* tree boles to inter-canopy gaps and is this influenced by restoration? (3) How does microenvironment at the level of the individual seedling influence seedling success and how are these relationships influenced by restoration? By answering these questions, we elucidate impacts of encroachment and restoration on savanna overstory recruitment patterns and stability.

2. Materials and methods

2.1. Site description

We conducted this study within a large-scale oak savanna restoration experiment, initiated in 2002 (Brudvig and Asbjornsen, 2007). Sites ($n = 8$) ranged in size from 1.5 to 3.3 ha and were located along the western shore of Saylorville Lake, a flood control reservoir near Des Moines, IA, USA (41°76′N, 93°82′W). These sites historically supported oak savannas with low densities of *Q. macrocarpa* (bur oak) and *Q. alba* overstory trees (Asbjornsen et al., 2005) and although never plowed, were grazed by cattle for ~100 years until purchase by the U.S. Army Corps of Engineers between 1965 and 1975 (Karnitz and Asbjornsen, 2006). Following purchase, sites were unmanaged and subsequently encroached by fire sensitive, shade tolerant tree species over the next several decades (e.g., *Ostrya virginiana*, *Fraxinus americana*, *Ulmus americana*; Karnitz and Asbjornsen, 2006), which filled inter-canopy gaps and resulted in overstory canopy closure (Brudvig and Asbjornsen, 2007). Soils were a mosaic of the Hayden (Glossic Hapludalf; developed under oak/hickory forest) and Lester series (Mollic Hapludalf; developed under oak savanna; United States Department of Agriculture, 2008). Des Moines' annual averages are 10 °C, 882 mm of precipitation, and 133 frost-free days (National Oceanic and Atmospheric Administration, 2008).

To remove woody encroachment, two sites received the restoration treatment during winter 2002–2003, whereby all non-*Quercus* woody vegetation >1.5 m tall and ranging in diameter from <1 to >50 cm was cut with chain saws and burned in off-site slash piles. Cut stumps were not treated with herbicides. Two additional sites received the restoration treatment in winter 2003–2004 and the remaining four sites were kept as unmanipulated controls. Two years were necessary to conduct the restoration treatment because it took approximately two months to treat each site and treatments were only conducted during winter, when the soil was frozen and disturbance was minimized.

Past work at these sites has quantified changes to the overstory and understory communities and structure. Encroachment removal reduced canopy cover from 84–89% to 8–52%, basal area from 14–37 m^2/ha to 2–27 m^2/ha, and significantly altered overstory composition in favor of *Quercus* species (Brudvig and Asbjornsen, 2007). In control sites, canopy cover (84–92%) and basal area (16–27 m^2/ha) were unchanged during this time period (Brudvig and Asbjornsen, 2007). Following removal, canopy cover values fell within the published range for Midwestern oak savannas (Packard, 1993). By three years after treatment, understory cover had increased to over 80% and species richness had increased to 14–21 species/m^2 in treatment sites, compared to understory cover <20% and richness of 8–11 species/m^2 in control sites (Brudvig, in press; Brudvig and Asbjornsen, 2007).

2.2. Data collection

In early April 2004, we randomly selected 10 open-grown *Q. alba* overstory trees (canopy radius >6 m) from level uplands at each of the eight sites. For each tree, we established two randomly oriented transects, starting at the tree bole and extending 1.5× the distance to the canopy edge (see Brudvig and Asbjornsen, 2005 for details on canopy measurements). Along each transect, we transplanted one *Q. alba* seedling every 2 m, starting 0.5 m from the tree bole. This resulted in 5–6 seedlings/transect. For each tree, we also transplanted three seedlings at 3× the distance to the canopy edge, oriented in an equilateral triangle with sides 2 m long (hereafter 'gap seedlings'), in the same direction as one of the sampling transects. This resulted in a total of 981 transplanted seedlings (hereafter, 'full data set'). Seedlings were 2-0 bare root-stock and of central Iowa genotype, obtained from the Iowa Department of Natural Resources state forest nursery (Ames, IA). For each seedling, we collected the following data in July 2004–2006: basal diameter at the root collar, height (ground to tip of the highest live stem), number of leaves (2005 and 2006 only) and