Forest Ecology and Management 282 (2012) 124–132

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

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

Canopy accession strategies and climate-growth relationships in *Acer rubrum*

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ARTICLE INFO

Article history:
Received 24 April 2012
Received in revised form 19 June 2012
Accepted 21 June 2012
Available online 28 July 2012

Keywords:
Acer rubrum
Canopy accession
Canopy disturbance
Central Hardwood Forest
Quercus
Radial growth

ABSTRACT

A pervasive pattern of forest composition change is occurring throughout the Central Hardwood Forest of the eastern US. *Acer rubrum* has invaded the understory of *Quercus* stands across a variety of site types. The proliferation of *A. rubrum*, and that of other shade-tolerant mesophytes, inhibits the regeneration of *Quercus*. Without alterations in disturbance or climate regimes, composition in invaded stands is expected to shift towards *A. rubrum* dominance. Canopy accession strategies and climate-growth relationships of *A. rubrum* are critical factors in this successional shift. We quantified patterns of suppression and release during canopy accession, examined the relationships between climate variables and radial growth, and compared our findings for *A. rubrum* in an old-growth forest in Tennessee to other studies throughout the region to elucidate broad-scale patterns. The most common mode of *A. rubrum* canopy recruitment began with a tree originating in a gap followed by accession into the canopy without a period of suppression (61%). The remaining trees experienced a period of suppression before recruiting to the main canopy. A prominent establishment pulse occurred from the 1940s to the 1960s and 93% of trees that recruited to the canopy during this period established in gaps and were never suppressed. The mean age at canopy accession for individuals that experienced suppression was 24 yr. The transition from suppression to release phases in radial growth trends was abrupt. The mean interseries correlation and the average mean sensitivity of the *A. rubrum* tree-ring chronology were comparatively high for the region. *Acer rubrum* individuals were most productive during cool, wet springs preceded by wet autumns and warm winters. Our results indicate that *A. rubrum* will remain competitive in the coming decades without a change in current disturbance regimes and the *Quercus* component will be difficult for managers to maintain in similar stands of the Central Hardwood Forest.

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1. Introduction

An extensive pattern of forest composition change is occurring in *Quercus* stands throughout the Central Hardwood Forest of the eastern US. Shade-tolerant mesophytes, principally *Acer rubrum* L., have invaded the understory of many *Quercus* stands throughout the region (Abrams, 1998; Fei and Steiner, 2009). *Quercus* regeneration is inhibited in stands with a high density of shade-tolerant individuals in the understory because *Quercus* species are only moderately tolerant of shade (Lorimer et al., 1994). Based on the lack of *Quercus* regeneration and the severity of the *A. rubrum* proliferation, many researchers have concluded that the transition from *Quercus*-to-*Acer* is inevitable in many *Quercus* systems (e.g. Fei et al., 2011; McEwan et al., 2011; Nowacki and Abrams, 2008). Indeed, millions of hectares of *Quercus* stands in the Central Hardwood Forest are exhibiting this species-replacement pattern (Abrams, 2005). A key element in the projected successional shift, and one which is not well understood, is the canopy recruitment strategy of *A. rubrum*. The *A. rubrum* proliferation in many *Quercus* stands throughout the region initiated over a relatively uniform and narrow period (1920s–1950s). As such, *A. rubrum* stems in these forests are largely restricted to sub-canopy positions, but are projected to recruit to the canopy following the death of overstory trees.

Most trees in understory strata must be released from midstory and overstory competition to recruit to the main forest canopy (Runkle, 1981, 1989), and this is particularly true for *Quercus* species (Crow, 1988). The magnitude and timing of response to midstory and overstory removal is a strong determinant of canopy recruitment potential (Kozlowski and Pallardy, 1997; Naidu and DeLucia, 1997; Runkle, 1989). The positive response to increased growing space is often apparent in the radial growth rates of sub-canopy trees (Barden, 1983; Hart et al., 2010; Lorimer, 1985). Most *Quercus* stands of the eastern US have a high species

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0378-1127/$ - see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2012.06.033

richness, and a variety of ecological, life history, and resource allocation characteristics are represented. Some species, such as *Liriodendron tulipifera* L., are shade-intolerant and thus disturbance obligate (Orwig and Abrams, 1994). *Liriodendron tulipifera* exists in late-successional stands because of its ability to establish after local disturbance and quickly ascend to canopy height prior to canopy gap closure (Buckner and McCracken, 1978; Busing, 1994, 1995; Lorimer, 1980). In general, shade-intolerant species cannot endure suppression and typically must reach the canopy in one gap event. These species generally have higher annual growth rates relative to shade-tolerant species and are competitive in gap environments (Bazzaz, 1979; Canham, 1989; Hart et al., 2010). At the other end of the spectrum are shade-tolerant and disturbance facultative species, such as *Acer saccharum* Marsh. and *Fagus grandifolia* Ehrh., which can persist in the understory of a closed canopy for long periods while maintaining the ability to react to disturbance events (Canham, 1985, 1988, 1990; Tryon et al., 1992). Canham (1985, 1990) found that *A. saccharum* and *F. grandifolia* could persist in the understory for up to 213 and 172 yr, respectively, before ascending to the canopy.

Acer rubrum is classed as shade-tolerant to moderately shade-tolerant (Walters and Yawney, 1990). *Acer rubrum* has relatively low rates of net photosynthesis and a low light compensation point (Abrams, 1998), which allow individuals to persist in the understory for long periods (Abrams, 1998; Wallace and Dunn, 1980). The mechanisms of *A. rubrum* establishment in the understory and recruitment to the overstory, however, remain largely unexplained. Prior studies have documented the dominance of *A. rubrum* in all vertical strata in the Central Hardwood Forest of the eastern US (Abrams, 1998; Nowacki and Abrams, 2008) and appear to support the *A. rubrum* dominance hypothesis first proposed by Lorimer (1984). Lorimer (1984) postulated that *A. rubrum* increased in abundance after European settlement when the disturbance regime changed from one of high frequency, high intensity events that favored *Quercus* to one of low frequency, low intensity events that favored *Acer*. Information on establishment and canopy accession strategies is required to both develop a mechanistic understanding of the canopy replacement process in *Quercus* systems that are transitioning to support a stronger *A. rubrum* component and to develop silvicultural prescriptions designed to inhibit the regeneration and canopy accession of *A. rubrum* and promote that of *Quercus* species.

A second key element in the *Quercus*-to-*Acer* compositional transition is the climate sensitivity of *A. rubrum*. The relationship between climate and secondary growth of this species has not been well documented, yet such information would assist in projecting *A. rubrum* productivity in the climate regime that is projected to occur throughout the Central Hardwood Forest in the coming decades. Although predictions vary across the region, temperatures are projected to increase and water is projected to become more limited during the growing season (Karl et al., 2009). Although projections are generally for increased temperatures and decreased water availability through the region, the establishment of *A. rubrum* in stands may result in a positive feedback mechanism whereby the sites become more "mesic" (Nowacki and Abrams, 2008). Despite the complications with projections introduced by this feedback loop, the species' sensitivity to climate and to what extent climate drives *A. rubrum* productivity is largely unknown. Projections on future forest composition have not fully considered how climate change will influence *A. rubrum* performance in successional stands as changing climate may dampen or amplify the widespread successional pattern apparent in the Central Hardwood Forest.

The major goal of this project was to identify strategies of establishment and canopy accession and climate-growth relationships for *A. rubrum*. By working in a forest where canopy disturbance for the past three centuries has been quantified (Hart et al., 2012), we were able to examine *A. rubrum* establishment and canopy accession in light of canopy disturbance events across the study site. Specifically, our objectives were to: (1) document establishment and canopy accession strategies of *A. rubrum* by quantifying patterns of suppression and release in radial growth, (2) examine the relationships between climate variables and radial growth, and (3) compare these trends for *A. rubrum* in an old-growth forest in Tennessee with a known canopy disturbance history (Hart et al., 2012) to other studies to deduce general patterns.

2. Materials and methods

2.1. Study area

The samples analyzed in our study were collected on the Savage Gulf Natural Area (SGNA) located in southeastern Tennessee (Fig. 1). The 6309 ha reserve is managed as a Natural Area by the Tennessee Department of Environment and Conservation. Land-uses in the reserve have been restricted to recreation and research since the property was transferred to the State of Tennessee in 1973. The SGNA occurs on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman, 1938). The Cumberland Plateau is the westernmost physiographic province of the Appalachian Highland realm. All study plots were located on the weakly dissected plateau landtype association of the true plateau subregion (Smalley, 1982). The true plateau subregion, which is widespread through the mid-Cumberland Plateau, has an undulating surface submaturely dissected by young valleys and incised bedrock streams locally disrupt the tableland surface (Fenneman, 1938; Smalley, 1982). The underlying geology consists largely of Pennsylvanian sandstone, conglomerate, siltstone, shale, and coal of the Crab Orchard and Crooked Forked Groups (Miller, 1974; Smalley, 1982). Regionally, soils are acidic, highly leached, and low in fertility (Francis and Loftus, 1977; Springer and Elder, 1980). The elevation of the study plots ranged from ca. 500–575 m amsl.

Regionally, the climate is classified as humid mesothermal (Thornthwaite, 1948) with long, moderately hot summers and short, mild winters. However, the complex topography strongly influences fine-scale climate conditions. The average frost-free period is ca. 200 days and the mean annual temperature is 14 °C. The July and January average temperatures are 24 °C and 3 °C, respectively (PRISM Climate Group, 2011). Precipitation is distributed relatively evenly throughout the year with no distinct dry season; however, short periods of water surplus or deficit are common. Mean annual precipitation is 145 cm (PRISM Climate Group, 2011). The region experiences more than 50 days annually with thunderstorms accompanied by intense rainfall and sometimes hail. These events are most common in late spring and summer. Snowfall is minimal and snow cover generally lasts no more than 3 days (Smalley, 1982).

This region was considered by Braun (1950) to be part of the Cliff Section of the Mixed Mesophytic Forest. However, vegetation of the Cumberland Plateau is intermediate between mixed mesophytic, mixed hardwood, and mixed *Pinus*–hardwood forest types (Hinkle, 1978, 1989; Smalley, 1982) and true mixed mesophytic communities only occur in coves or otherwise protected sites. Composition on the upland sites of the Cumberland Plateau is largely controlled by topographic characteristics, factors related to soil water availability, and past disturbance (Hinkle, 1978; Smalley, 1982). The forest studied on the SGNA was dominated by *Quercus alba* L., *A. rubrum*, *Pinus echinata* Mill., *Oxydendrum arboreum* (L.) DC., *Quercus coccinea* Muenchh., and *Quercus velutina* Lam. (Hart et al., 2012). *Acer rubrum* and *O. arboreum* were the most

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