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

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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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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
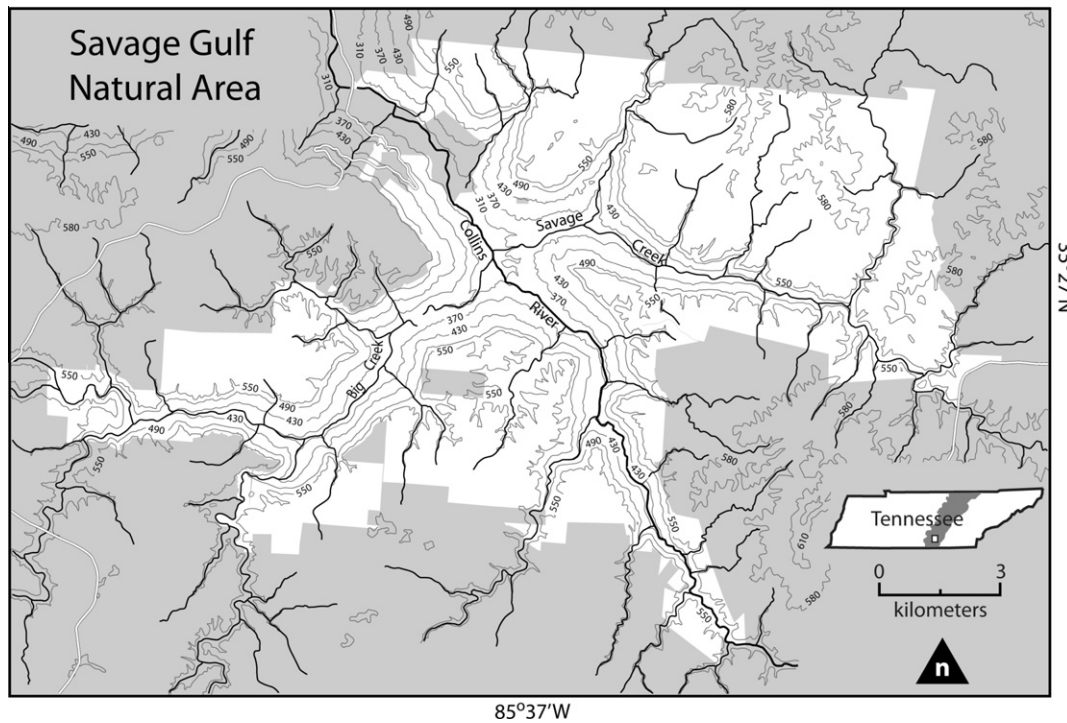
Fig. 1. Map of Savage Gulf Natural Area, Tennessee. Shaded portion on Tennessee inset map is the Cumberland Plateau physiographic section.
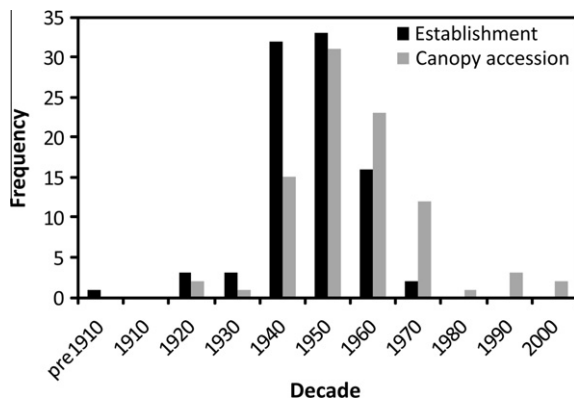

Fig. 2. Dates of establishment (innermost date at breast height) and canopy accession (initiation year of final canopy release) for 90 *Acer rubrum* trees in an old-growth *Quercus* forest on the Cumberland Plateau, Tennessee.

abundant species and together represented greater than 50% of all stems $\geqslant$ 5 cm dbh on the site. *Acer rubrum* was by far the most prolific species in the sapling layer (stems $\geqslant$ 1 m height, <5 cm dbh). Indeed, the canopy and understory strata were dissimilar indicating compositional instability (Hart et al., 2012). The oldest trees on the site established in the late-1600s, but *A. rubrum* was not abundant until a recruitment pulse began in the 1940s.

Dendroecological analysis combined with forest inventory data indicated that the disturbance regime during stand development was characterized by gap-scale with several intermediate-scale events and that the frequency of stand-wide canopy disturbances declined since the early 1900s (Hart et al., 2012). Fire history for the site has not been reconstructed using biological archives, but we hypothesize that fire has not been a common disturbance on the site since the early 1900s. The State of Tennessee Bureau of Forestry was created in 1921 and the agency began a fire control program in 1922. In the 1940s, the State of Tennessee hired full-time firefighters and initiated a more concerted fire protection program. The landowner prior to State of Tennessee acquisition did not allow grazing or burning and actively suppressed fires (Samuel Werner, II, personal communication). Fire history reconstructions on the Appalachian Plateaus physiographic province are relatively sparse (Hart and Buchanan, in press). However, McEwan et al. (2007) documented a drastic reduction in fire frequency during the 1930s on the Cumberland and Alleghany sections of the province. Likewise, Hutchinson et al. (2008) noted a dramatically reduced incidence of fire in the 1930s which coincided with recruitment of *Acer* in second-growth forests on the Alleghany Plateau in southern Ohio. Similar patterns have been reported from adjacent provinces (Hart and Buchanan, in press).

2.2. Field and laboratory methods

Our field sampling was specifically focused within a *ca.* 600 ha, old-growth *Quercus* forest on the tablelands in the northeastern section of the SGNA. All *A. rubrum* series analyzed were collected on permanently established plots. Throughout the old-growth remnant, we established 87 0.04 ha fixed-radius plots arranged in a systematic grid pattern at 240 × 240 m spacing as part of a larger study examining broad-scale stand disturbance and development patterns (Hart et al., 2012). As part of our randomized sampling of tree-ring data, we collected one tree-core sample from 90 overstory *A. rubrum* individuals (i.e. trees with canopy dominant or co-dominant positions (Oliver and Larson, 1996)), which we used to analyze establishment patterns, suppression and release during canopy accession, and climate-growth relationships. We also collected a single tree-core sample from 30 *A. rubrum* trees in a suppressed canopy position (i.e. crown of the trees completely overtopped by dominant/co-dominant trees) on the plots to develop our criteria to delineate suppression and release periods.

In the laboratory, all tree-core samples were prepared and processed for dating using the methods outlined in Stokes and Smiley (1996). The cores were air-dried, glued to wooden mounts with

cells vertically aligned, and sanded with progressively finer abrasives to reveal the cellular structure of the wood (Orvis and Grissino-Mayer, 2002). Once processed, tree rings on all cores were dated using the methods established by Yamaguchi (1991). Once all rings were visually dated, we measured raw-ring width to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software for all overstory *A. rubrum* series. The measurement series from the 90 overstory trees were visually compared and statistically analyzed to ensure each growth ring was assigned to the proper calendar year of formation using the COFE-CHA computer software (Grissino-Mayer, 2001; Holmes, 1983). All segments that fell below the predetermined significance threshold ($r = 0.32$, $P > 0.01$) were flagged by the program. All flagged segments were re-inspected for possible dating errors and dating was adjusted if necessary. We were confident all tree rings on all *A. rubrum* series were dated to their exact calendar year of formation before proceeding to analyze growth trends. The last 3 yr of growth from the 30 suppressed *A. rubrum* series were measured to the nearest 0.001 mm as described above to determine average annual growth of suppressed trees.

A variety of methods are available to document suppression and release episodes in radial growth patterns (for a review see Rubino and McCarthy, 2004) though no technique has been standardized for *A. rubrum*. In this study we adopted a method developed by Canham (1985, 1990) to characterize patterns of suppression and release during canopy recruitment in *A. saccharum* and *F. grandifolia*. This method was appropriate for our study because it has been used by other researchers working with similar species (e.g. Poulson and Platt, 1996; Cao and Ohkubo, 1999). Additionally, the release dates are related directly to the quantified growth of suppressed trees on the site. The method uses a fixed radial-ring width value and a duration criterion to identify suppression periods. Differences in species growth rates and climate regimes dictate that the fixed value selected be adjusted for species- or site-specific characteristics (i.e. the value should be derived from individuals of the species growing at the study site). To develop our *A. rubrum*-specific and site-specific fixed radial growth threshold we followed the methods of Canham (1985, 1990) and used the mean radial growth value for the last 3 yr from 30 *A. rubrum* trees in a suppressed canopy position growing on the site and representing a range of ages and sizes between 5 and 20 cm dbh. Analysis was restricted to growth of the last 3 yr because beyond that period canopy disturbance history is unknown and growth during a release period could mistakenly be included. In addition, use of the last 3 yr excludes the juvenile growth period when productivity may be unrelated to growing conditions. We acknowledge that growing conditions during the 3 yr used to develop our fixed radial growth value may not have been representative of conditions that occurred throughout the lifespans of all *A. rubrum* analyzed in our study. However, light is the factor most influential on tree growth in closed canopy stands of the eastern US (Oliver and Larson, 1996) and canopy disturbance patterns that influence the light regime have remained relatively constant since the early 1900s (i.e. the period of stand history analyzed here (Hart et al., 2012)). As such, we assumed that radial growth of the 3 yr used to develop our threshold was largely representative of growth in the light-limited environment that existed throughout the lifespan of the sampled *A. rubrum* individuals. Mean annual width of the last three annual rings sampled from the 30 suppressed trees (90 rings) was 0.90 mm ± 0.08 (SE). Based on the mean radial growth of suppressed *A. rubrum* trees growing on the site, we selected 0.9 mm year^{-1} as our static value to denote suppression periods. This value was similar to that used in other studies to delineate periods of suppression and release in shade-tolerant species of the eastern US and Japan (Poulson and Platt, 1996; Cao and Ohkubo, 1999). We defined suppression as periods when radial growth was less than 0.9 mm year^{-1} for 4 yr during which growth never exceeded this threshold for more than three consecutive years (Canham, 1985, 1990; Poulson and Platt, 1996). Episodes when growth was above the fixed value for three or more consecutive years were defined as release events. The date of canopy accession was defined as the initiation year of the last release (Canham, 1985, 1990).

Once suppression and release periods were identified, all *A. rubrum* canopy trees were placed into one of three establishment and accession strategy classes established by Rentch et al. (2003): gap origin, gap origin-gap release, or understory origin-gap release) to provide quantitative information on *A. rubrum* canopy recruitment. To characterize suppression and release during canopy recruitment we calculated the number of suppression and release periods prior to the final accession, understory residence time, diameter at the time of canopy accession, and age at the time of canopy accession. For trees that were suppressed for a period prior to canopy accession, we calculated the rate of change in radial growth immediately proceeding and subsequent to the canopy recruitment initiation date. As *A. rubrum* has been documented to quickly respond to canopy openings (Lorimer, 1980; Oliver and Stephens, 1977; Rentch et al., 1999; Tift and Fajvan, 1999), we analyzed the radial growth patterns 4 yr before and 4 yr after the release initiation date (Canham, 1985, 1990).

To analyze relationships between regional climate and radial growth, we developed tree-ring chronologies from all *A. rubrum* series that had interseries correlations of 0.5 or higher with the composite chronology created by the COFECHA program ($n = 42$). The interseries correlation is a Pearson correlation coefficient calculated for each tree-ring series against a composite chronology after the series being tested has been removed (Grissino-Mayer, 2001). This technique allowed us to build tree-ring chronologies using only individuals that exhibited common radial growth patterns. The ARSTAN program was used to remove disturbance- and age-related growth trends from the 42 selected *A. rubrum* series (Cook, 1985). To quantify climate-growth relationships, we calculated Pearson correlation coefficients for the Standard and Residual chronology types output by ARSTAN and monthly climate variables over a 16-month period (previous July to current October). The Standard and Residual ARSTAN chronologies were used to analyze the relationship with temperature and precipitation, respectively, as these chronologies best matched the frequency trends of the climate variables. Based on the subsample signal strength calculated in ARSTAN, the chronology sample depth became reliable for statistical analysis in 1947; thus, our climate-growth analyses spanned the period from 1947 to 2009. Climate variables included monthly mean, maximum, and minimum temperature and total precipitation. Data for monthly mean temperature and monthly total precipitation were used from Tennessee Climate Division 2 from the National Climate Data Center (NCDC, 2011). Monthly maximum and minimum temperature data were used from the parameter-elevation regressions on independent slopes model (PRISM) dataset (PRISM Climate Group, 2011). PRISM is a regression based model that uses interpolation of climate station data to create climate variable estimates given the surrounding topographic conditions (Daly et al., 1994, 2002). All statistical analyses were conducted in SAS v. 9.1.

3. Results

3.1. Establishment, suppression, and release

Of the 90 canopy *A. rubrum* trees analyzed in our study, the oldest established in 1878 and the youngest in 1970. The mean age of the samples was 58 yr ± 1. A prominent establishment pulse initi-

ated in the 1940s and continued through the 1960s (Fig. 2). Annual growth rates varied considerably from 0.08 to 8.16 mm yr^{-1} with a mean of 1.95 mm yr^{-1} ± 0.02 (Table 1). Patterns of growth rates varied among canopy accession strategies (Fig. 3). Mean growth during suppression periods was 0.72 mm yr^{-1} ± 0.00 and mean growth during release periods was 2.14 mm yr^{-1} ± 0.01, or 197% greater. *Acer rubrum* experienced periods of suppression for up to 62 yr and understory residence times prior to canopy accession of up to 71 yr.

Most (61%) of all *A. rubrum* canopy trees were of gap origin and reached the canopy without experiencing a suppression period (Figs. 3A and 4). The second most common strategy of canopy accession was understory establishment and gap release (24%). The least common recruitment strategy (14%) was gap establishment followed by suppression and eventual recruitment in a subsequent gap. The major pulse of *A. rubrum* establishment from the 1940s through the 1960s was largely of gap origin. In fact, 93% of *A. rubrum* that established during this 30-year period established in canopy gaps and never experienced a period of suppression before reaching a position in the forest canopy. The last gap origin *A. rubrum* individual established in 1970 (*n* = 2).

Of 13 *A. rubrum* trees that reached the canopy with the gap origin-gap release strategy, only four had a release in radial growth between the initial establishment in a gap and the final canopy accession (one of these trees exhibited two releases between establishment and canopy recruitment). The mean period between the initial gap release and final canopy accession was 16 yr ± 4 for gap origin-gap release trees. The mean dbh at the time of accession for these trees was 8 cm ± 1 and the mean age at accession was 30 yr ± 4. The longest understory residence prior to canopy accession with this strategy was 60 yr (this individual was 15 cm dbh).

Of the 22 understory origin-gap release trees, 7 (32%) had multiple radial growth releases prior to canopy accession (two of these series had two release episodes prior to recruitment, the remainder had only one). The mean dbh for understory origin-gap release trees at the onset of canopy accession was 5 cm ± 1. For this strategy, the average age at canopy accession was 20 yr ± 4. The longest understory residence times prior to accession for this strategy were 71 and 70 yr. The dbh of understory origin-gap release trees at the time of accession was significantly less than that of gap origin-gap release trees (*P* < 0.05), but the understory residence times prior to canopy accession did not differ significantly.

Mean changes in radial growth during transition phases from suppression to release were rapid (Fig. 5). The transition from suppression to release was typically noted by a single year of drastically increased growth. Mean growth during the release onset year was on average 0.57 mm ± 0.08 greater than that of the year prior (the last year of suppression). Radial growth during release year one (first year after release onset) was greater than that of the release onset year (year zero). The average growth change from year zero to year one was 0.25 mm ± 0.07, and was significantly less (*P* < 0.01) than the average growth change of the prior year.

Table 1
Diameter growth rates, suppression durations, release durations, tree ages, and sizes for *Acer rubrum* trees sampled in an old-growth *Quercus* forest on the Cumberland Plateau tablelands in Tennessee.

Variable	Mean ± SE	Min	Max
Annual growth rate (mm)	1.95 ± 0.01	0.08	8.16
Annual growth during suppression (mm)	0.72 ± 0.00	0.11	2.22
Annual growth during release (mm)	2.14 ± 0.01	0.08	8.16
Duration of suppression episodes (yr)	12 ± 1	4	62
Duration of release episodes (yr)	39 ± 2	3	68
Age at accession (yr) [a]	24 ± 3	7	71
Size at accession (cm dbh) [a]	6 ± 1	2	20

[a] Gap origin-gap release and understory origin-gap release trees only.
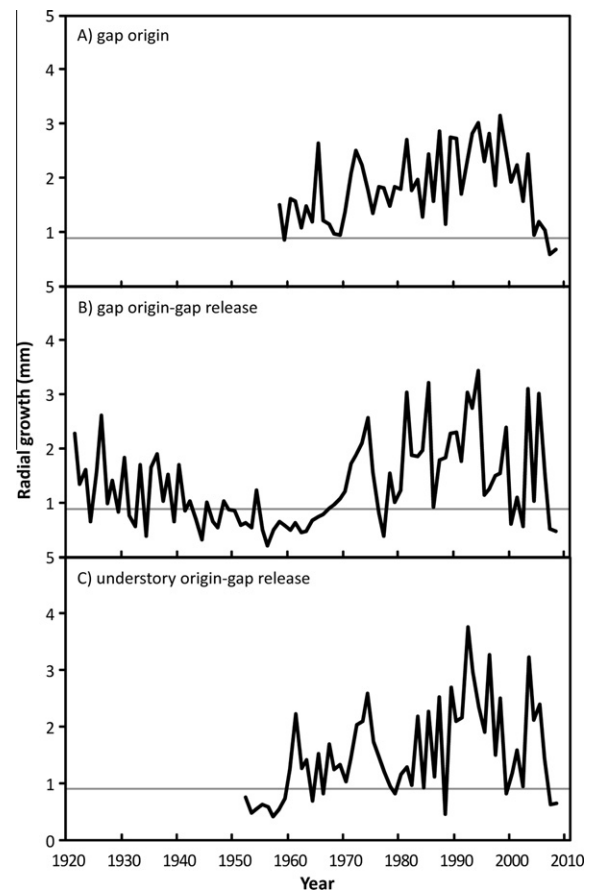
Fig. 3. Raw-ring width measurements for *Acer rubrum* individuals exhibiting three different canopy accession strategies in an old-growth *Quercus* forest on the Cumberland Plateau, Tennessee. The gray line indicates the threshold to delineate suppression from release used in our study (0.9 mm yr^{-1}).
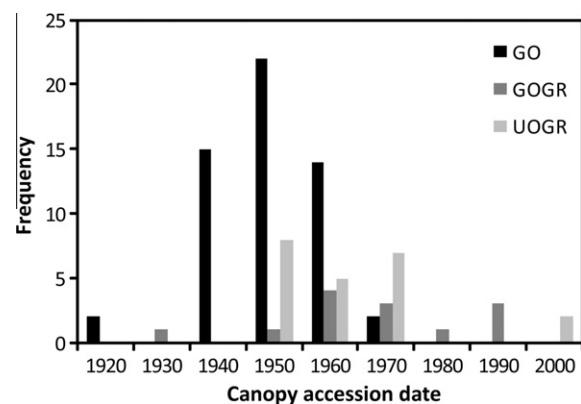
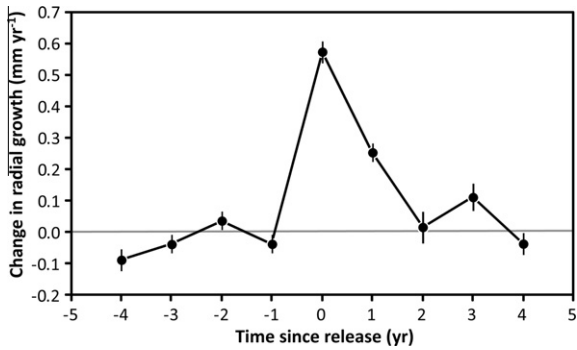

Fig. 4. Frequency of canopy accession initiation years by decade across three accession strategies (GO: gap origin, GOGR: gap origin-gap release, UOGR: understory origin-gap release) for 90 *Acer rubrum* trees in an old-growth *Quercus* forest on the Cumberland Plateau, Tennessee.

The mean radial growth change during release year two (mean increase of 0.02 mm ± 0.10) was not significantly different (*P* = 0.06) than that of release year one.

3.2. Climate-growth relationships

The mean interseries correlation of the 42 *A. rubrum* series selected for the development of the climate chronology was statisti-

Fig. 5. Mean rates of change with standard errors in raw-ring width for the 4 yr prior and subsequent to the initiation of canopy accession for 35 *Acer rubrum* trees that were suppressed for a period prior to canopy accession in an old-growth *Quercus* forest in Tennessee.
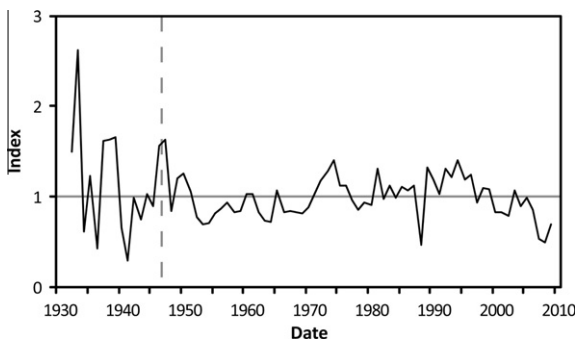

Fig. 7. Correlation analyses between the Residual tree-ring chronology and mean monthly precipitation. Month abbreviations preceded by 'p' indicate the previous year. Black bars indicate significance values of $P < 0.01$, gray bars indicate significance values of $P < 0.05$, and white bars indicate the relationships were not significant.

cally significant ($r = 0.63$, $P < 0.01$). None of the 90 tree-ring segments analyzed by the COFECHA program were flagged by the quality control program indicating that all were statistically significant with contemporary segments. Average mean sensitivity was 0.32. Mean length of *A. rubrum* series used in the climate chronology was 56 yr.

The tree-ring chronology extended 78 yr from 1932 to 2009 (Fig. 6). The tree-ring chronology used for climate-growth analyses extended from 1947 to 2009. Significant relationships were found between the tree-ring chronology and all climate variables. We documented significant positive relationships between the Residual chronology and mean precipitation of the previous October and current May and June (Fig. 7). We found significant positive relationships between the Standard chronology and mean temperature of the current January and negative relationships between the Standard chronology and current June mean temperature (Fig. 8). We documented significant positive relationships between the Standard chronology and minimum temperature for the previous October and the current January. Significant negative relationships were documented between temperature maxima during August of the prior year and June of the current year and the Standard chronology.
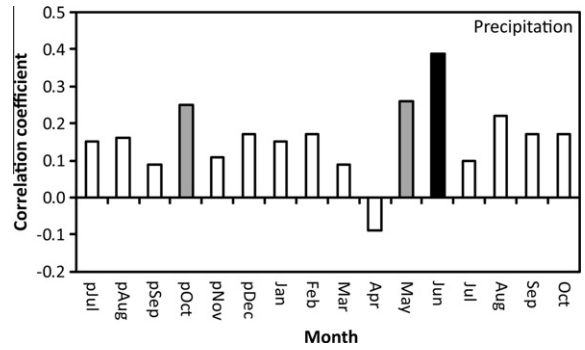
## 4. Discussion

4.1. Establishment, suppression, and release

The majority of *A. rubrum* trees in the canopy were gap-opportunists during establishment and ascended into the canopy with-

Fig. 6. Composite ring-width index generated from 42 *Acer rubrum* individuals sampled in an old-growth *Quercus* forest in Tennessee. Mean growth was standardized to 1.0. The dashed vertical line indicates the point at which the chronology becomes reliable for statistical analysis based on the subsample signal strength output generated by the program ARSTAN.
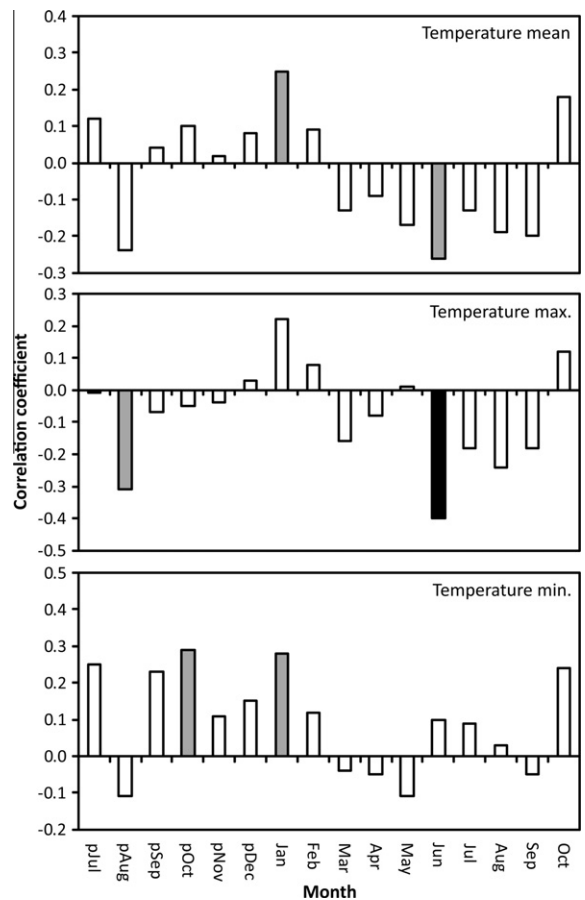
Fig. 8. Correlation analysis between the Standard tree-ring chronology and mean monthly temperature, the Standard chronology and maximum monthly temperature, and the Standard chronology and minimum monthly temperature. Month abbreviations preceded by 'p' indicate the previous year. Black bars indicate significance values of $P < 0.01$ and gray bars indicate significance values of $P < 0.05$.

out a period of suppression. This finding was somewhat surprising given evidence and widespread theories that *A. rubrum* is a shade-tolerant species that dominates the understory for long-periods in the absence of disturbances. Hart et al. (2012) reconstructed canopy disturbance history for the study site using dendroecological techniques and did not document any stand-wide disturbances or an anomalously high frequency of local canopy disturbances during this period of *A. rubrum* establishment.

We stress that the preponderance of gap origin *A. rubrum* does not necessarily indicate that gap frequency was unusually high or otherwise above the background level, but rather that *A. rubrum* were in position to establish in and capture the gaps that did form. Also, we hypothesize that the establishment pulse lasting three decades was unrelated to short-term local or regional-scale climate conditions. We speculate that the relatively high frequency of *A. rubrum* trees originating in a gap may be attributed to the sudden shift in the disturbance regime from high-frequency intense disturbances of the late 1800s and early 1900s to low-frequency low intensity disturbances of the mid 1900s. Prior to the onset of *A. rubrum* recruitment in the 1940s few individuals occurred on the site whereas, the species is now abundant in the understory and actually represents over 26% of all stems on the site ⩾5 cm dbh (Hart et al., 2012). The increased density of *A. rubrum* in the stand may influence the recruitment mode that will be most successful. During the recruitment pulse of the mid-1900s, most trees originated in gaps and ascended to the canopy without experiencing suppression. With a dense understory, we hypothesize that it will be rare for *A. rubrum* trees to reach the canopy without experiencing at least one suppression period. Thus, we speculate that the strategy used for canopy accession will shift (or has already) from gap origin to understory origin-gap release and perhaps to a lesser extent gap origin-gap release.

Despite the ability of *A. rubrum* to persist in the understory for long periods, accession into the canopy does largely appear to be dependent on relatively small gap-scale disturbances that will favor this species over *Quercus* (Hibbs, 1982; Lorimer, 1984). Although our study does not demonstrate a causal relationship between canopy disturbance regime changes and *A. rubrum* proliferation, our results support the *A. rubrum* dominance hypothesis proposed by Lorimer (1984). The last stand-wide canopy disturbance in this old-growth forest occurred in 1903 (Hart et al., 2012). In the three centuries prior, the return interval for stand-wide events was ca. 42 yr. *Acer rubrum* has been establishing and recruiting into the canopy since the 1920s during a period without stand-wide canopy disturbances and with active fire suppression. The contemporary disturbance regime in this forest is characterized by localized and asynchronous gap-scale events (Hart et al., 2012). Indeed, recent research indicated a decline in the frequency of large gap-scale disturbances over the past ca. 300 yr throughout the eastern US (Buchanan and Hart, 2012). Because *A. rubrum* was able to establish under both high-light (gap origin) and low-light (understory origin) conditions, and then wait for a canopy disturbance event to recruit into the overstory, the species will likely maintain dominance in this community over the long-term.

The canopy trees we sampled that did not establish in a gap, had a mean understory residence time of 24 yr prior to canopy accession. However, some trees experienced a short radial growth release prior to canopy accession such that the mean duration of all suppression periods was just 12 yr. This value is slightly lower than that documented for *A. saccharum* and *F. grandifolia* by Canham (1985, 1990). We note however, that *A. rubrum* individuals had understory residence times of 71 and 70 yr prior to canopy accession (these trees were 18 and 20 cm dbh, respectively). Mean dbh for gap origin-gap release trees at time of canopy accession (8.1 cm dbh) was greater than that of understory origin-gap release trees (4.7 cm dbh). This finding is likely a function of increased growth rates of trees that established in gap environments relative to those that established in the understory.

Using the same dendroecological methods, Canham (1985, 1990) found increased growth during the year of release initiation over the year prior to be 0.3 to 0.4 mm for *A. saccharum* and *F. grandifolia*, respectively. Here we found annual growth at recruitment initiation was almost 0.6 mm greater than the year prior. In addition, *A. rubrum* had shorter individual suppression periods and

shorter total understory residence time prior to canopy accession compared to *A. saccharum*. The mean raw and percentage growth increase from suppression to release growth phases was similar between our study and that of Barden (1983). The transition from suppression to release was typically noted by only a single year of drastic change in radial growth. Indeed, the mean annual ring-width during release periods was 197% greater than the mean annual ring-width during suppression periods. Canham (1985, 1990) found similar patterns with *A. saccharum* and *F. grandifolia*. Thus, the gap response for these mesophytes is, in this regard, similar. These findings indicated that productivity is abruptly rather than gradually altered by increased resources and illustrate the phenotypic plasticity that makes *A. rubrum* competitive in high light environments.

4.2. Climate-growth relationships

Acer rubrum individuals across our study site were most productive during cool, wet springs preceded by wet autumns and warm winters. Moisture availability during autumn supports the production and storage of carbohydrates and, when coupled with abundant moisture during the subsequent growing season, results in increased productivity. October is typically the driest month of the year for the study site and is when leaf fall occurs, thus moisture availability during this month has a significant positive influence on growth of the following year. We suspect carbohydrate storage from the prior growing season is especially important for *A. rubrum* based on its flowering phenology (i.e. early spring flowering, Walters and Yawney, 1990). The documented mean and maximum temperature signals likely corresponded to water stress via the influence of temperature on evapotranspiration rates. A warm January may lead to early bud break which would increase frost damage probability and thus tree productivity. The relationship between temperature minima of the prior autumn was likely related to the length of the growing season and potential frost damage. In this region, leaf fall and the first frost is typically in mid-October. Warm autumn temperatures may extend the growing season, but low autumn temperatures that occur before senescence may result in tree damage that may reduce productivity the following year.

Many climate models project an increase in drought frequency in the southeastern US in the coming decades (Seager et al., 2009). We suggest that a decrease in available moisture during the autumn and spring seasons would have a negative impact on *A. rubrum*. Likewise increased mean and maximum temperatures during spring and summer seasons may reduce *A. rubrum* productivity. However, higher winter temperatures and higher minimum temperatures during autumn may offset these negative effects. Warmer autumn temperatures may lengthen the growing season, but Norby et al. (2003) observed that leaf retention in autumn may increase the risk of frost damage and have negative consequences on *A. rubrum* productivity. With regard to moisture changes, *A. rubrum* has small guard cells and is more effective at controlling stomata relative to co-occurring species (Abrams and Kubiske, 1990). Thus, *A. rubrum* has the ability to exist across a variety of site moisture regime classes (Abrams, 1998).

The increased dominance of *A. ruburm* may result in changes to the biophysical environment. Nowacki and Abrams (2008) coined the term "mesophication" to describe the positive feedback mechanism between establishment of shade-tolerant and mesophytic taxa in *Quercus* forests that modify understory light levels and soil characteristics thereby promoting relatively moist, cool microenvironmental conditions. *Acer rubrum* individuals typically have denser canopies than *Quercus*, which is hypothesized to reduce understory temperature and increase understory relative humidity (Alexander and Arthur, 2010). *Acer rubrum* leaves and woody mate-

rial decompose faster than *Quercus* leaf and woody litter (Abrams, 1990; Carreiro et al., 2000; MacMillan, 1988) and an increase in this relatively fast decaying organic matter is expected to increase infiltration capacity of the soil, increase soil moisture holding capacity, and modify soil nutrient pools thereby creating more mesic site conditions.

The ecological effects of *A. rubrum* proliferation are still largely speculative as empirical tests are lacking. However, Alexander and Arthur (2010) examined seasonal variations of precipitation throughfall and stemflow quantity and quality and assessed net nitrogen mineralization rates in underlying soils of *A. rubrum*, *Quercus prinus* L. and *Q. coccinea* on the Cumberland Plateau. They found the dense canopies of *A. rubrum* intercepted precipitation and directed the flow of water down the smooth stems toward the base of the tree where the roots were concentrated (Alexander and Arthur, 2010). This spatial redistribution of water and nutrients may be especially important during periods of water deficit. Thus, the ecosystem consequences of increased *A. rubrum* dominance may dampen the negative impacts of a warmer, drier climate regime via mesophication processes (Nowacki and Abrams, 2008).

5. Management implications

The increasing abundance and dominance of *A. rubrum* in *Quercus* stands has drawn increased attention over the past decade (Abrams, 2005). The results of our study provide information on the mechanisms controlling the proliferation of *A. rubrum* in the understory and its canopy accession strategies that may help inform management decisions. *Acer rubrum* can invade a forest and persist in the understory for extended periods until overhead canopy disturbance provides conditions for accession or recruitment to a larger size class. On many *Quercus* sites throughout the Central Hardwood Forest, *A. rubrum* appears to have invaded the understory regardless of canopy disturbance patterns. Indeed, on our study site, Hart et al. (2012) did not find relationships between the timing of *A. rubrum* proliferation and canopy disturbance. However, radial growth analysis indicated that the major establishment and recruitment pulse of the mid-1900s was largely gap-mediated. Thus, managers of sites not currently invaded by *A. rubrum* should closely monitor gap environments that are created by natural disturbance events or harvest entries. Spot treatments using herbicides of *A. rubrum* in gap understories may be necessary for managers wishing to maintain *Quercus*.

Our results also illustrated the opportunistic nature of *A. rubrum* in response to canopy disturbance. Although *A. rubrum* trees can remain suppressed in the understory for decades (in our study up to 71 yr) they maintain their ability to respond positively to changes in the light regime caused by local overstory and/or midstory removal. These findings highlight the need to pre-treat invaded *Quercus* sites prior to harvesting operations for managers that want to maintain *Quercus*. Indeed, harvesting operations on sites proliferated by *A. rubrum* may actually accelerate canopy recruitment of the species (Abrams and Downs, 1990; Abrams and Scott, 1989). We suggest a pre-harvest treatment to mechanically remove or chemically deaden *A. rubrum* stems. Prescribed burning is being proposed across the region as a method to eradicate or reduce *Acer* abundance in the understory (Abrams, 2005; Spetich et al., 2011); however, repeated dormant-season burning in undisturbed stands has not reduced the amount of *A. rubrum* because of its ability to sprout (Alexander et al., 2008; Green et al., 2010). Prescribed burning may be most efficient when combined with canopy disturbance (Hutchinson et al., 2012). Burning in canopy gaps or creating gaps on recently burned sites may be most effective if advanced *Quercus* regeneration is present at the time of the burn, and may be most effective after *Acer* leaf out in early spring (Brose and Van Lear, 1998)

Although we found *A. rubrum* to be sensitive to precipitation and temperature variables, it is unclear to what extent the productivity or survival of the species on this site and others will be modified by changes in the climate regime. In particular, the species' ability to modify the microclimatic conditions of the stands in which it exists confounds the predictive capacity of current climate-growth relationships. Thus, managers should not take the approach that this mesophyte will not be able to attain or maintain dominance in a warmer and drier climate. Furthermore, biophysical changes created by *A. rubrum* dominance may dampen the negative effects of a less favorable climate regime on productivity of the species. This process combined with the generalist character of *A. rubrum* (Abrams, 1998) lead us to speculate that it will remain competitive across many site types of the Central Hardwood Forest in the coming decades.

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