

Canopy accession strategies and climate responses for three *Carya* species common in the Eastern Deciduous Forest

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Abstract

Key message Maintenance of *Carya* in successional stands will require canopy disturbances larger than the gap-scale to increase understory light in conjunction with reduction in competition from shade-tolerant mesophytes.

Abstract A widespread compositional shift has been reported in *Quercus*–*Carya* forests throughout the eastern USA. *Quercus* and *Carya* are failing to regenerate and understories of these stands are increasingly dominated by shade-tolerant mesophytes. Important in this successional shift are the canopy accession strategies and climate sensitivities of the dominant and projected replacement species. The goals of our study were to document establishment and canopy accession strategies and examine the relationships between climate variables and radial growth for *Carya glabra*, *Carya ovata*, and *Carya alba*. The majority (75 %) of *Carya* individuals established in open canopy conditions. However, 40 % of our samples experienced suppression before canopy accession. Average age at canopy accession for trees that were suppressed prior to canopy recruitment was 49 years. *Carya* that established in closed canopy conditions were suppressed an average of 22 years and were 2.6 cm diameter at breast height (dbh) before they ascended to the canopy or experienced a

release episode. Gap origin-gap release trees were in open canopy conditions for an average of 18 years and were 6.5 cm dbh before experiencing a period of suppression. The three species exhibited similar responses to climate as they were generally sensitive to prior spring and current summer temperature, and prior winter and current summer precipitation, but radial growth trends were controlled more strongly by canopy position than climate. Maintenance of *Carya* in successional stands will require increases in understory light and reductions in competition from shade-tolerant mesophytes. Our results indicate that canopy disturbances larger than the gap-scale are needed for *Carya* establishment and canopy recruitment.

Keywords *Carya* (hickory) · Canopy accession · Climate · Disturbance · Stand development · Succession

Introduction

Carya species (hickory) are common and widespread throughout the Deciduous Forest Formation of eastern North America (Braun 1950; Monk et al. 1989). These species characterize many forest associations of this region and are best represented in the *Quercus* (oak)–*Carya* forest type that extends from eastern Massachusetts south to central Georgia, west to eastern Texas, and north to south-central Michigan (Kricher and Morrison 1998). *Carya* usually co-occur with *Quercus*, but are rarely dominant in these stands (Braun 1950; Nelson 1965; Monk et al. 1990; McCarthy 1994). *Carya* and *Quercus* share many silvical and life history characteristics (Watt et al. 1973; McCarthy 1994). For example, they are typically considered to be moderately tolerant of shade, slow growing, and long lived

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(Nelson 1965). Throughout the eastern USA and across a range of site types, a widespread successional shift has been documented in which *Carya* (and *Quercus*) are failing to regenerate (Sork 1983; McCarthy and Wistendahl 1988; McCarthy 1994; Hart and Grissino-Mayer 2008; Evans and Keen 2013). The small size classes in these *Quercus*–*Carya* stands are typically dominated by shade tolerant and mesophytic species (Nowacki and Abrams 2008). Thus, the *Quercus*–*Carya* forest type, which spans millions of hectares in the eastern USA, is projected to decline and be replaced by one with much stronger contributions from shade tolerant and mesophytic taxa such as *Acer saccharum* Marsh. (sugar maple), *Acer rubrum* L. (red maple), and *Fagus grandifolia* Ehrh. (American beech) among others (Lorimer 1984; Abrams 1992; Nowacki and Abrams 2008; McEwan et al. 2011).

Regeneration of *Carya* and *Quercus* is tied to canopy disturbance and subsequent increases in understory light levels (McCarthy and Wistendahl 1988; Lorimer 1993). Indeed, silviculture of these genera is largely focused on managing the light regime (Watt et al. 1973; Gottschalk 1983; Dey 2002). Understory stems of these mid-successional species must be released from midstory and overstory competition to ascend to the forest canopy (Crow 1988). Research has been conducted on the canopy accession patterns of co-occurring *Quercus* (Ruffner and Abrams 1998; Rentch et al. 2003; Hart et al. 2012a) and the most probable replacement species *A. saccharum* (Canham 1985), *A. rubrum* (Hart et al. 2012b), and *F. grandifolia* (Canham 1990). Although research has focused on *Carya* seedling establishment and growth response to sunlight (Sork 1983; Myster and McCarthy 1989; McCarthy 1994; Robison and McCarthy 1999), quantitative information on canopy accession strategies for *Carya* is lacking. The shade tolerance of *Carya* species, which is a strong control on succession, is somewhat debated and might vary regionally and at different stages of maturity (Baker 1949; Nelson 1965; Trimble 1975; Smalley 1991). Persistence in low quantity and poor quality light conditions, combined with the timing and extent of growth increases associated with canopy disturbances, strongly influence the ability of sub-canopy trees to recruit to co-dominant and dominant canopy positions (Kozlowski and Pallardy 1997; Naidu and DeLucia 1997). Knowledge of the canopy accession strategies of *Carya* may be used to develop silvicultural treatments designed to maintain these species in *Quercus*–*Carya* stands transitioning to support shade-tolerant mesophytes.

Also important in the future of the *Quercus*–*Carya* forest type is the response of these dominant taxa and the projected replacement species (i.e. *A. saccharum*, *A. rubrum*, and *F. grandifolia*) to climate change. Research has been conducted to document the influence of climate on

productivity of *Quercus* in the eastern USA and to predict how some of these species may respond to projected climate change (e.g. Speer et al. 2009; Goldblum 2010; LeBlanc and Terrell 2009; Copenheaver et al. 2011; White et al. 2011). To our knowledge no prior studies have documented the relationships between radial growth and climate for *Carya* species. Thus, we are unsure how sensitive the radial growth of common *Carya* species may be to climate, what climate variables, if any, influence radial growth rates, or how climate-growth relationships may vary within the genus. This information may be used to make predictions about the productivity of *Carya* under different climate change scenarios.

The goals of this project were to document establishment, canopy accession, and climate-growth relationships for *Carya glabra* (Mill.) Sweet (pignut hickory), *Carya ovata* (Mill.) K. Koch (shagbark hickory), and *Carya alba* (L.) Nutt (mockernut hickory) growing in association in a mixed hardwood forest on the Cumberland Plateau, Tennessee, USA. We selected these species because they are among the most common and widespread within the genus and they commonly co-occur in the same stands. Our study was conducted in a forest with a known developmental and disturbance history (Hart and Grissino-Mayer 2008), so we could examine establishment and canopy accession patterns within the context of stand initiation and stand-wide canopy disturbance events. Our specific objectives were to (1) document establishment and canopy accession strategies of *C. glabra*, *C. ovata*, and *C. alba* by quantifying patterns of suppression and release in radial growth and (2) examine the relationships between climate variables and radial growth of these three species. Our results provide information on the silvics and life history traits of these *Carya* species and may be used in part to inform management focused on the maintenance of the *Carya* component of the *Quercus*–*Carya* forest type.

Methods

Study area

The samples analyzed in our study were collected on the Pogue Creek Natural Area (PCNA), a 1,505-ha nature reserve, located in Fentress County, Tennessee, in the north-central portion of the state. The PCNA is located on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman 1938). The geology is composed primarily of Pennsylvanian sandstone, conglomerate, siltstone, shale, and coal of the Crab Orchard and Crooked Forked groups (Smalley 1986). The region has irregular topography characterized by long ridges capped by resistant sandstone and deeply incised

stream networks comprising valleys of varied widths (Fenneman 1938; Smalley 1986). Regionally, soils are acidic, highly leached, and low in fertility (Francis and Loftus 1977; Smalley 1982; USDA 1995). Depth to bedrock varies from 1.0 to 1.8 m and slope gradients range from 15 to 60 %. The elevation of our study location ranged from 260 to 490 m amsl.

The climate of this region is classified as humid mesothermal with moderately hot summers and short, mild to moderately cold winters (Thornthwaite 1948); however, the complex topography strongly influences local climate conditions. The average frost-free period is 160 days (from early May to late October) and the mean annual temperature is 13 °C. The average temperature in July is 23 °C and the January average temperature is 2 °C (USDA 1995). Mean annual precipitation is 137 cm and is distributed evenly throughout the year with no distinct dry season. Heavy rains that are often accompanied by moderate to severe thunderstorms and strong winds are common in late spring and summer (Smalley 1982).

The study site is located within the Cliff Section of the Mixed Mesophytic Forest as described by Braun (1950). However, local topography and other factors related to soil moisture availability have a major influence on forest composition (Hinkle 1989; Clatterbuck et al. 2006) such that true mixed mesophytic communities only occur on topographically protected sites and in riparian zones. Regionally, forests are intermediate between mixed mesophytic and *Quercus*–*Carya* types (Hinkle et al. 1993). Hart and Grissino-Mayer (2008) documented species composition, stand structure, and disturbance and developmental history for stands on the PCNA. They found the canopy was dominated by *Quercus* and *Carya* species and the understory was dominated by *A. saccharum*, *A. rubrum*, and *F. grandifolia*. The forest established in the late 1920s after the site was clear-cut and the disturbance regime during the development of these stands was characterized by localized, gap-scale events with one stand-wide canopy disturbance event in the early 1980s (Hart and Grissino-Mayer 2008).

Data collection and analysis

Our sample material was collected as part of a larger project aimed at documenting forest development and disturbance history and residual tree response (Hart and Grissino-Mayer 2008, 2009). Those studies included 60 inventory plots located at various mid-slope positions throughout the landscape. Increment cores were extracted from trees ≥ 5 cm diameter at breast height (dbh) on those plots, with cores taken parallel to slope contour to avoid reaction wood in radial growth trends (Scurfield 1973). For each tree sampled we documented species, dbh, and crown

class based on the amount and direction of intercepted light (Oliver and Larson 1996). All tree-core samples were prepared and processed for dating and analysis according to standard methods (Stokes and Smiley 1996). 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). From those original collections, we selected only those *Carya* series that included the pith and were extracted from trees not overtopped at the time of field sampling, yielding 121 tree-ring series (32 from *C. glabra*, 42 from *C. ovata*, and 47 from *C. alba*).

Tree rings on all series were dated using the list method (Yamaguchi 1991). When all growth rings were visually dated, we then measured total ring width to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software. To ensure each growth ring was assigned to the correct calendar year of formation, all series were visually compared and statistically analyzed using the COFECHA computer software (Holmes 1983; Grissino-Mayer 2001).

An array of methods have been used to identify suppression and release episodes in radial growth patterns (Rubino and McCarthy 2004; Fraver and White 2005; Copenheaver et al. 2009), each with strengths and weaknesses. No standard method has been used to document suppression and release growth phases in *Carya* species. For this study, we sought to separate suppressed growth phases caused by light limitation (i.e. crowns restricted from above) from release growth phases that would result from trees growing in high light conditions (i.e. crowns unrestricted from above). To this end we chose to use a modified version of the method developed by Canham (1985) and used subsequently in other studies to identify periods of suppression and release (e.g. Canham 1990; Poulson and Platt 1996; Cao and Ohkubo 1999; Hart et al. 2012b). This method uses a fixed radial-ring width value and a duration criterion to identify suppression episodes and reduces the confounding influence of climate on short-term radial growth patterns (Canham 1990). Unique species growth rates and spatial variability throughout the species' range require that the fixed ring-width value be species- and site-specific (i.e. the value should be derived from individuals of the same species growing at the study site; Ziaco et al. 2012). To develop our three species-specific fixed ring-width values, we calculated mean annual growth from all series of each species. We then defined suppression events as periods when raw-ring width was 25 % below the fixed threshold (i.e. the total mean annual increment for that species), for a minimum of 4 years during which growth never exceeded the fixed value for more than three consecutive years (Canham 1985, 1990; Poulson and Platt 1996; Hart

et al. 2012b). This method uses a 4-year window to ensure that low growth rates related to short-term climatic influences and growth reductions following masting events would not be included as suppressions (Canham 1985; 1990). Our annual increment thresholds were $0.98 \text{ mm year}^{-1}$ for *C. glabra*, $1.06 \text{ mm year}^{-1}$ for *C. ovata*, and $1.19 \text{ mm year}^{-1}$ for *C. alba*. Periods when growth was above the threshold for three or more consecutive years were defined as releases. The date of canopy accession was defined as the initiation year of the last release (Canham 1985, 1990).

Once suppression (growth in low light environments) and release (growth in high light environments) events were identified, each series was placed into one of three establishment and canopy accession strategy classes established by Rentch et al. (2003): gap origin, gap origin-gap release, or understory origin-gap release. These delineations allowed us to provide information on *Carya* canopy accession and to analyze differences across the three species tested. To characterize suppression and release events for each species, we calculated the number of suppression and release events, the duration of individual events, the diameter and age at the time of canopy accession, and the average growth during suppression and release episodes. Diameter at breast height at the time of canopy accession or release was estimated by doubling the length of the series from pith to the outermost ring and accounting for bark thickness. We used the species-specific bark thickness equations of Reinhardt et al. (1997). We visually and statistically tested the data for normality and variance homogeneity and subsequently tested for significant differences in these variables across the three species using ANOVA with Scheffe post hoc tests. Our sample size of 121 trees from 60 inventory plots did not allow us to run mixed-model ANOVAs with site as a random effect and we acknowledge this unknown source of potential variability.

To analyze relationships between regional climate and radial growth of the three *Carya* species, we developed species-specific chronologies of tree-ring growth from all 121 sampled individuals. The program ARSTAN was used to remove disturbance and age-related growth trends and to create the composite chronologies of radial growth (Cook 1985; Cook and Krusic 2011). We first applied a negative exponential curve to remove trends that were likely related to the decline in ring width associated with increasing tree size. If the negative exponential curve failed, a linear regression line was fit. Second, we used a cubic smoothing spline with a 50 % frequency response at wavelengths equal to 67 % of the individual series length. This double-detrending method was chosen because the first step removed the age-related growth trend that was present in a subsample of the tree-ring series and the second step

removed growth characteristics that were related to disturbance events (i.e. releases from suppression). For each individual, the raw ring-width series, the applied curves, and the resulting detrended series were plotted graphically and visually evaluated to ensure that the local mean of the data was followed by the curve fit and that variance ostensibly related to tree size and disturbance was removed. Following the detrending process, the individual tree-ring series were combined into species-specific chronologies using a bi-weight robust mean (Cook 1985). In all climate-growth analyses, the Standard chronology produced in ARSTAN was used (i.e. no autoregressive modeling was applied).

We compared interseries correlations and mean sensitivity values of the three *Carya* species using ANOVA with Scheffe post hoc testing. Interseries correlations are the Pearson correlation coefficients calculated for each tree-ring series against the composite chronology once the series being tested has been removed (Grissino-Mayer 2001). Mean sensitivity is a measure of the relative difference in the width of consecutive rings and is an indicator of climate sensitivity in the tree-ring record (Fritts 1976). We also calculated Pearson correlation coefficients between the three *Carya* tree-ring chronologies for the common period 1940–2005. This period was chosen to maximize sample depth of the three chronologies.

To quantify climate and radial growth relationships, we used the correlation analysis function in the program DENDROCLIM2002. The program uses bootstrapped confidence intervals to reduce potential error and yield more accurate results (Biondi 1997; Biondi and Waikul 2004). We calculated correlation coefficients for the Standard chronology types output by ARSTAN and monthly climate variables over a 20-month period (previous March to current October) from 1904 to 2005. Coefficients that equaled or exceeded the 95 % confidence level were identified by the program. Climate variables included monthly mean, maximum, and minimum temperature; total precipitation; and Palmer Drought Severity Index (PDSI). Data for monthly mean temperature, monthly total precipitation, and PDSI were derived from Tennessee Climate Division 2 from the National Climate Data Center (NCDC 2013). PDSI is used by the USA National Weather Service to monitor drought and wetness conditions and is commonly used in dendroclimatological studies in the eastern USA because it is a good measure of moisture conditions during the growing season. Monthly maximum and minimum temperature data were downloaded from the parameter-elevation regressions on independent slopes model (PRISM) dataset (PRISM Climate Group 2013). PRISM is a regression-based model that uses interpolation of station-derived climate data to estimate climate variables based on topography (Daly et al. 1994, 2002).

Results

Growth rates and canopy accession strategies

The average length of the entire tree-ring dataset was 81 year \pm 2 SE (Table 1). The mean tree-ring record length for *C. glabra* was 84 year \pm 4 SE, for *C. ovata* was 76 year \pm 3, and for *C. alba* was 82 year \pm 4 SE. The oldest individuals documented for each species were 177 years for *C. glabra*, 117 years for *C. ovata*, and 167 years for *C. alba*. Mean dbh at the time of data collection of the analyzed trees was 28.7 cm \pm 1.0 SE. The mean dbh of *C. glabra*, *C. ovata*, and *C. alba* samples was 27.4 cm \pm 2.1 SE, 29.0 cm \pm 1.7 SE, and 32.5 cm \pm 1.4 SE, respectively. Mean radial growth was 1.32 mm year⁻¹ \pm 0.10 (SE) for *C. glabra*, 1.41 mm year⁻¹ \pm 0.09 (SE) for *C. ovata*, and 1.59 mm year⁻¹ \pm 0.08 (SE) for *C. alba* and mean annual growth increment did not significantly differ ($P < 0.05$) across the three species. Annual growth rates varied widely with a maximum of 9.91 mm year⁻¹ found in a *C. glabra* and a minimum of 0.06 mm year⁻¹ from a separate *C. glabra* individual.

Of the 121 *Carya* samples, 40 % ascended to the canopy with the gap origin-gap release strategy, 35 % following the gap origin mode, and 25 % following the understory origin-gap release mode. The most common mode of establishment and canopy accession for *C. glabra* was gap origin-gap release followed by understory origin-gap release and gap origin without a suppression period (Fig. 1). In contrast, gap origin was the most common mode of canopy accession for *C. ovata* followed by gap origin-gap release and then understory origin-gap release. *Carya alba* exhibited little variability in canopy accession strategy. Results from a Chi square analysis indicated that no species was more likely than another to establish in a closed canopy versus open canopy setting.

Radial growth rates varied by canopy accession strategy (Fig. 2). Radial growth increment during suppression periods differed significantly for all three species and was greatest for *C. alba* and lowest for *C. glabra* (Table 1). Mean radial growth during release periods for *C. alba* was significantly greater than that for *C. glabra* and *C. ovata*. On average, radial increment during release phases was 192, 171, and 168 % greater than during suppression phases for *C. glabra*, *C. ovata*, and *C. alba*, respectively.

The average age at canopy accession for trees that were suppressed prior to canopy recruitment (i.e. gap origin-gap release and understory origin-gap release) was 49 year \pm 3 SE. This value varied from a low of 46 year \pm 6 SE for *C. ovata* to a maximum of 51 year \pm 5 SE for *C. alba*. We found no significant differences ($P < 0.05$) in age at canopy accession across species. Likewise, dbh at the time of

Table 1 Various attributes used to assess growth patterns of co-occurring *C. glabra*, *C. ovata*, and *C. alba* trees sampled in a mixed hardwood forest on the Cumberland Plateau in Tennessee

	<i>Carya glabra</i>	<i>Carya ovata</i>	<i>Carya alba</i>
Series length (years)	84.40 \pm 4.43a	75.60 \pm 2.62a	82.30 \pm 3.50a
Average growth (mm year ⁻¹)	1.32 \pm 0.10a	1.41 \pm 0.09a	1.59 \pm 0.08a
Suppression growth (mm year ⁻¹)	0.63 \pm 0.01a	0.69 \pm 0.01b	0.74 \pm 0.01c
Release growth (mm year ⁻¹)	1.84 \pm 0.02a	1.87 \pm 0.018a	1.98 \pm 0.02b
Rate of change (mm year ⁻¹)	0.81 \pm 0.14a	0.54 \pm 0.08a	0.57 \pm 0.07a
Release duration (years)	25.76 \pm 2.93a	27.54 \pm 2.92a	30.03 \pm 2.74a
Suppression duration (years)	23.56 \pm 2.49a	22.29 \pm 2.04a	17.47 \pm 1.57a
Age at accession (years)	48.16 \pm 6.75a	46.38 \pm 5.69a	51.41 \pm 5.37a
Diameter at accession (cm)	11.14 \pm 1.59a	11.16 \pm 1.49a	12.56 \pm 1.25a

Means with rows followed by the same letter are not significant ($P < 0.05$)

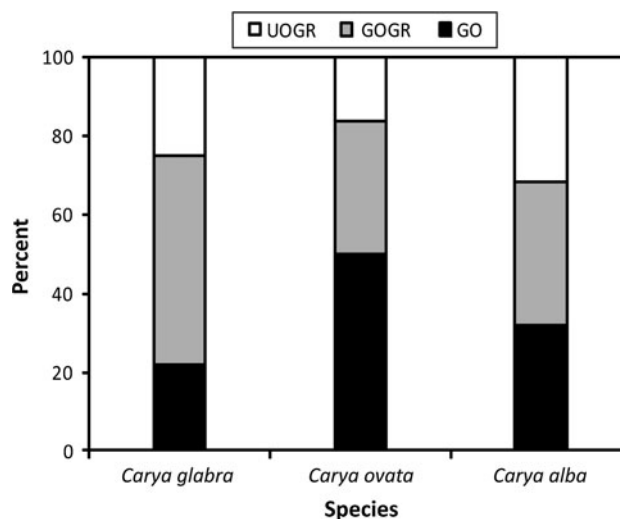


Fig. 1 Canopy accession strategy class percentages for *Carya glabra*, *Carya ovata*, and *Carya alba*. Canopy accession strategy classes are UOGR understory origin-gap release, GOGR gap origin-gap release, GO gap origin

canopy accession for gap origin-gap release and understory origin-gap release trees exhibited little variability with means of 11.1 cm \pm 1.6 SE, 11.2 \pm 1.5 SE, and 12.6 \pm 1.3 SE for *C. glabra*, *C. ovata*, and *C. alba*, respectively, and did not differ significantly across species.

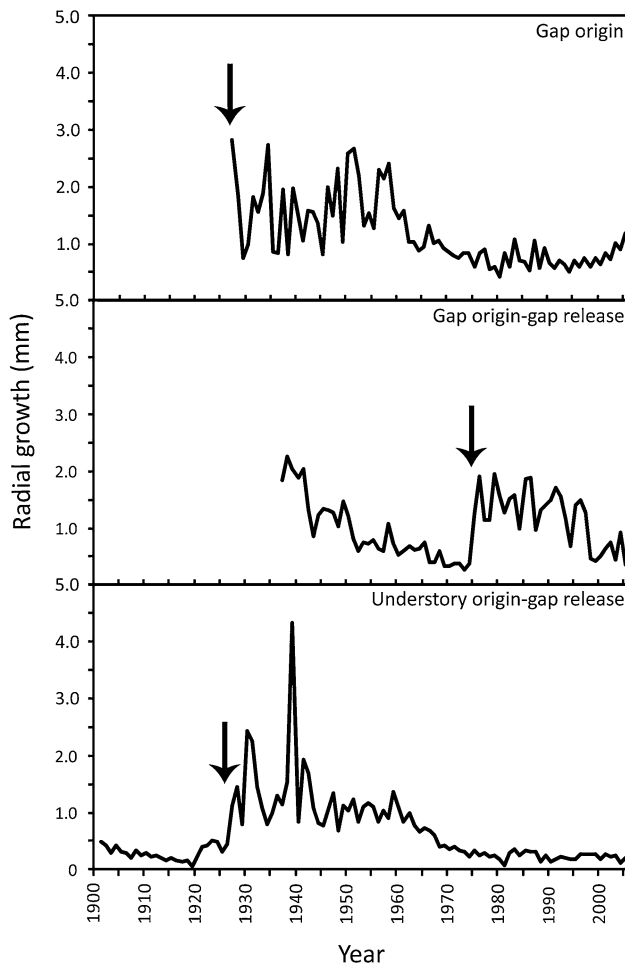


Fig. 2 Selected growth patterns meant to represent the three canopy accession strategies exhibited by *Carya glabra*, *Carya ovata*, and *Carya alba* individuals in a mixed hardwood forest on the Cumberland Plateau, Tennessee. Arrows indicate year of canopy accession

Most (62 %) of understory origin-gap release trees recruited to the canopy with only one suppression period. The remaining understory origin-gap release trees (38 %) experienced two ($n = 16$) or three ($n = 2$) suppression periods before canopy accession. Understory origin-gap release trees were suppressed at establishment an average of $21.5 \text{ year} \pm 2.7 \text{ SE}$ prior to canopy accession or a period of release that did not result in canopy recruitment. The average length of suppression for these trees was $24.3 \text{ year} \pm 4.7 \text{ SE}$ for *C. glabra*, $19.1 \text{ year} \pm 4.9 \text{ SE}$ for *C. ovata*, and $21.2 \text{ year} \pm 5.0 \text{ SE}$ for *C. alba*. The longest understory residence time prior to canopy accession or release was 58 years for a *C. alba*. The average dbh for understory origin-gap release trees at the time of accession or release was $2.6 \text{ cm} \pm 0.3 \text{ SE}$. The largest such tree was a *C. alba* at 6.7 cm dbh.

The mean duration of the first release (i.e. the period from establishment to initiation of a suppression episode) for gap origin-gap release individuals was $17.6 \text{ year} \pm 1.8$

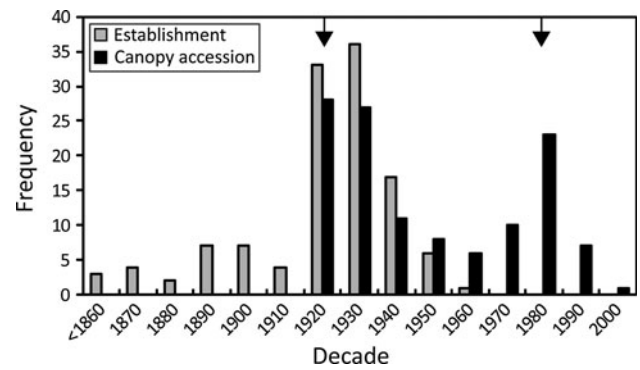


Fig. 3 Dates of establishment (innermost date at breast height) and canopy accession (initiation year of final canopy release) for 121 *Carya glabra*, *Carya ovata*, and *Carya alba* trees in a mixed hardwood forest on the Cumberland Plateau, Tennessee. Arrows indicate stand-wide disturbances

SE. The longest such release episode was 51 years and was documented in a *C. glabra*. The mean dbh for gap origin-gap release trees at the time of the first suppression period was $6.5 \text{ cm} \pm 0.8 \text{ SE}$. The dbh values at this time averaged $6.9 \text{ cm} \pm 1.7 \text{ SE}$ for *C. glabra*, $4.4 \text{ cm} \pm 0.8 \text{ SE}$ for *C. ovata*, and $7.8 \text{ cm} \pm 1.2 \text{ SE}$ for *C. alba*. The largest gap origin-gap release tree was also the tree that was the oldest at the time of the first suppression (26.0 cm dbh at 51 year).

Although we found no significant differences in the length of release and suppression periods exhibited by each species, the average growth during these phases differed significantly (Table 1). Increases in radial growth at the onset of a release (i.e. growth change from the year of canopy accession to the year prior) were not significantly different across the three species. Mean radial growth increase at this transition was $0.81 \text{ mm year}^{-1} \pm 0.14 \text{ SE}$ for *C. glabra*, $0.54 \text{ mm year}^{-1} \pm 0.08 \text{ SE}$ for *C. ovata*, and $0.57 \text{ mm year}^{-1} \pm 0.07 \text{ SE}$ for *C. alba*. The maximum percent growth change we documented was an increase of 182 % over the year prior (an increase of 2.92 mm) exhibited in a *C. alba* individual.

Establishment of the sampled *Carya* trees began in the 1840s and was low, but continuous, through the 1910s (Fig. 3). An establishment pulse began in the 1920s and continued through the 1930s and early 1940s. This establishment pulse coincided with a stand initiating disturbance (i.e. a clear-cut harvest) in the 1920s. Establishment of *Carya* individuals included in our study last occurred in the 1960s. Canopy accession events exhibited two pulses: one in the 1920s that coincided with the clearing of the forest and one in the 1980s that coincided with a stand-wide canopy disturbance event. We did not observe any species-specific trends in the timing of establishment or canopy accession.

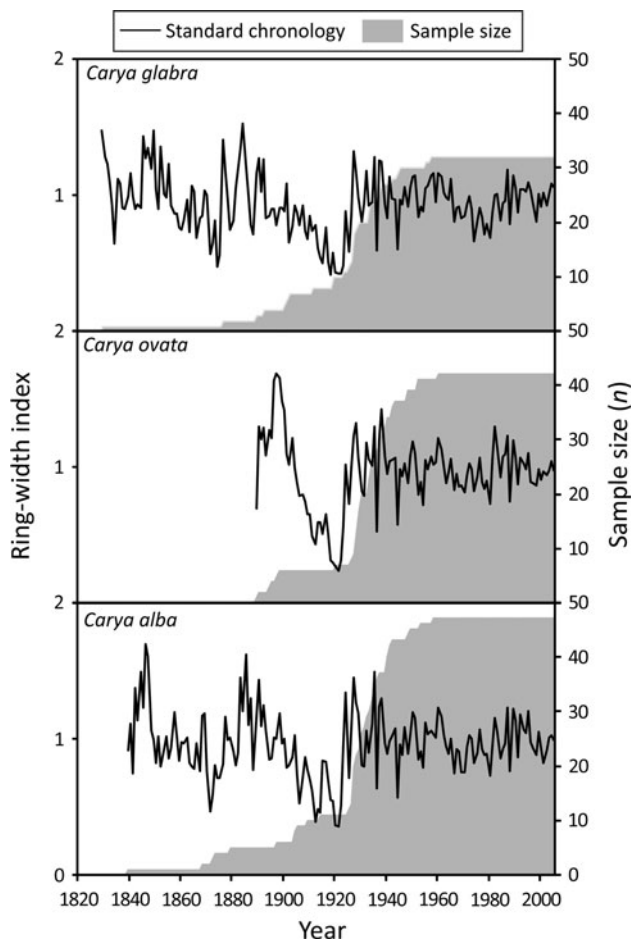


Fig. 4 Standardized ring-width index generated from 32 *Carya glabra*, 42 *Carya ovata*, and 47 *Carya alba* individuals sampled in a mixed hardwood forest on the Cumberland Plateau in Tennessee. Mean growth was standardized to 1.0

Climate–growth relationships

The mean interseries correlation (i.e. the average of the Pearson correlation coefficients for each series against the composite chronology for that species) for *C. glabra*, *C. ovata*, and *C. alba* was 0.38 ± 0.04 SE, 0.45 ± 0.03 SE, and 0.52 ± 0.03 SE, respectively. Interseries correlation values between *C. glabra* and *C. alba* were significantly different ($P < 0.05$). Likewise, mean sensitivity (i.e. year-to-year variability in radial growth) between these two species was also significantly different. Average mean sensitivity was 0.29, 0.28, and 0.26 for *C. glabra*, *C. ovata*, and *C. alba*, respectively.

The *C. glabra* tree-ring record was the oldest and extended to 1829 (Fig. 4). The *C. alba* record began in 1839 and the *C. ovata* record extended to 1889. All three tree-ring chronologies were significantly positively correlated throughout the period analyzed (1940–2005; $P < 0.0001$; Table 2). They all showed a gradual decline in

Table 2 Pearson correlation coefficients between the species-specific tree-ring chronologies for the period 1940–2005

	<i>Carya glabra</i>	<i>Carya ovata</i>	<i>Carya alba</i>
<i>Carya glabra</i>	–	$r = 0.78$	$r = 0.84$
<i>Carya ovata</i>	$r = 0.78$	–	$r = 0.90$
<i>Carya alba</i>	$r = 0.84$	$r = 0.90$	–

All values are significant at $P < 0.0001$

growth beginning in the late 1800s that hit a nadir in ca. 1920. In the 1920s all three chronologies exhibited marked increases in growth rates. All chronologies also exhibited punctuated periods of low growth in the 1930s and 1940s, a general decline beginning in the 1960s, and increased growth rates in the early 1980s.

We found statistically significant relationships among the three chronologies and the regional climate variables (Fig. 5). Based on the number of significant relationships, *C. alba* was the most sensitive to climatic variables. *Carya glabra* exhibited significant negative correlations with prior March mean, maximum, and minimum temperature and significant negative correlations with mean and maximum temperature of the current June. *Carya glabra* revealed significant positive relationships with mean precipitation of the prior August and current June. This species exhibited a significant negative correlation between prior May PDSI and a positive correlation with prior December PDSI. We found significant negative relationships between radial growth of *C. ovata* and mean and maximum temperature of the prior March and current summer. In addition, *C. ovata* exhibited significant positive correlations with mean precipitation of the current June and PDSI of the prior December. Our analyses revealed significant negative relationships between radial growth of *C. alba* and mean, maximum, and minimum temperature of the prior March and current summer and a positive relationship between the minimum temperature of the prior July. In addition, we noted significant positive correlations between radial growth of *C. alba* and mean precipitation of the prior August and current May and June and PDSI of the prior December and current January.

Discussion

Growth rates and canopy accession strategies

Radial growth rates provide quantitative information on life history characteristics (Bazzaz 1979; Brokaw 1985; Canham 1989) and forest developmental history (Henry and Swan 1974; Lorimer 1985; Abrams et al. 1995; Fraver and White 2005). Radial growth of *C. alba* during

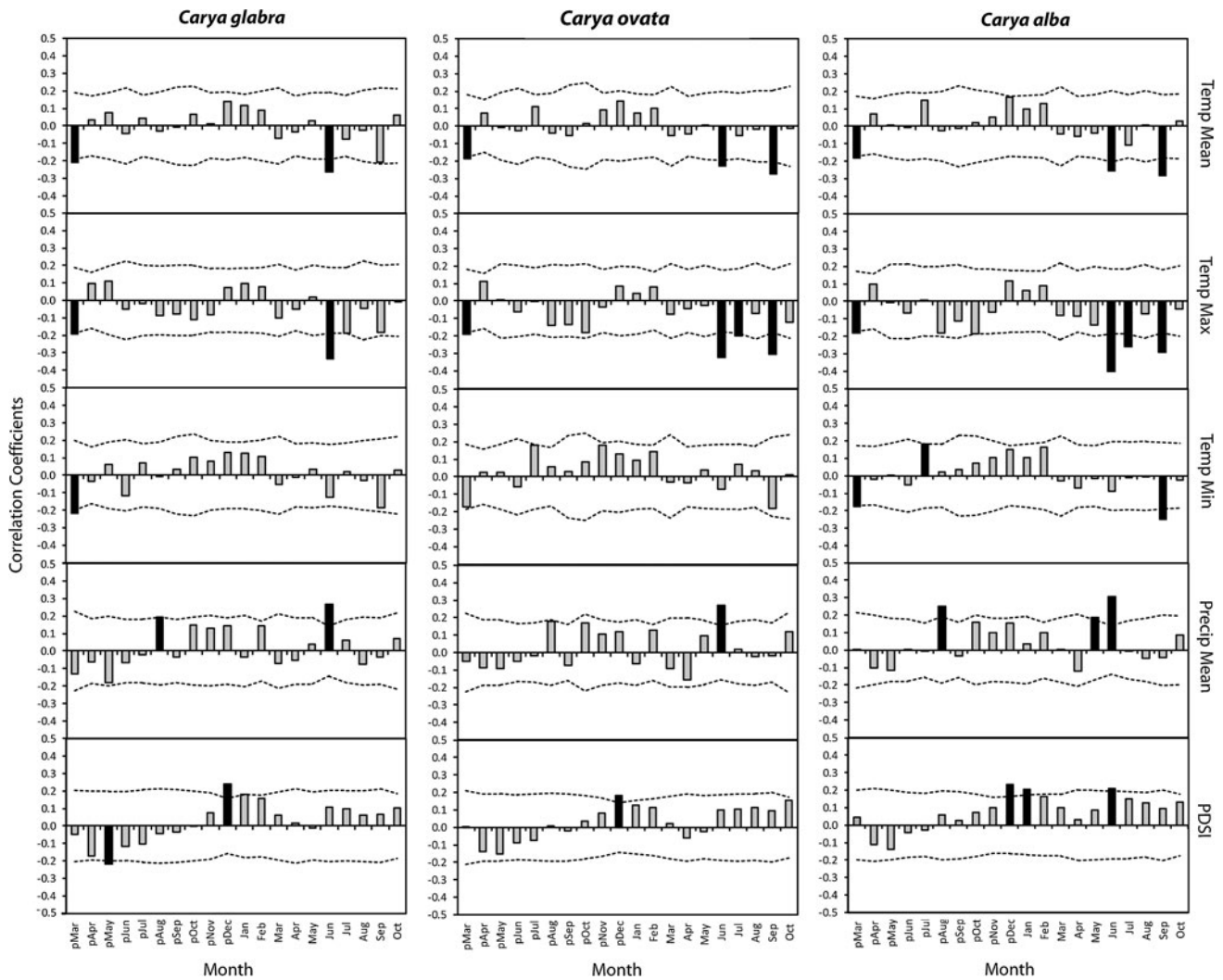


Fig. 5 Correlation analysis between the Standard tree-ring chronologies and mean monthly temperature, maximum monthly temperature, minimum monthly temperature, mean monthly precipitation, and PDSI from previous March (pMar) to current October (Oct) for the

suppression and release periods was significantly greater than that of *C. glabra*. Increased growth rates may provide a competitive advantage of *C. alba* over *C. glabra*. However, although annual radial growth is directly related to the amount and duration of annual height growth (Kozłowski 1971; Kariuki 2002; Rentch et al. 2002, 2003), differences of an annual radial growth increment of 0.11 mm during suppression periods and 0.14 mm during release periods are negligible. The average annual radial growth rate for co-occurring *Quercus* on the study site was 2.09 mm year⁻¹ (Hart and Grissino-Mayer 2008). Most *Carya* and *Quercus* individuals established at the time of stand initiation (Hart and Grissino-Mayer 2008) and the greater growth rate of *Quercus* may largely explain why the genus more frequently occupied dominant positions in the canopy than *Carya* (40 canopy dominant *Quercus* ha⁻¹

period 1904–2005. Month abbreviations preceded by ‘p’ indicate the previous year. Dashed lines indicate 95 % confidence intervals and black bars indicate statistically significant months

versus 30 canopy dominant *Carya* ha⁻¹; Hart and Grissino-Mayer 2008). The slower growth rate of *Carya* may have allowed these individuals to be overtopped by competing *Quercus*, thus, providing an explanation for why many of the *Carya* trees established in open canopy conditions at stand initiation, but became overtopped prior to canopy recruitment (Graney 1990).

The majority (75 %) of *Carya* individuals established in open canopy conditions where light was not limited. However, 40 % of the *Carya* samples experienced a period of suppression before canopy accession (i.e. they were gap origin-gap release) and this was the most common mode of canopy recruitment for *C. glabra* (53 % of the samples) and *C. alba* (36 %). In contrast, 49 % of *C. ovata* were able to reach the canopy without experiencing a suppression period as gap origin was the most common mode of canopy

accession for this species. Differences in radial growth and tree age do not appear to explain this pattern as *C. ovata* radial growth was not significantly greater than the other *Carya* species and the trees did not establish earlier than the other species. Perhaps this pattern is attributed to tree height growth or crown characteristics (e.g. crown area, shape, live crown ratio), which were not analyzed in our study. In the studied forest, the basal area contribution of *C. ovata* was relatively high ($5.3 \text{ m}^2 \text{ ha}^{-1}$; Hart and Grisino-Mayer 2008). The dominance of *C. ovata* over the other *Carya* species may be attributed to the fact that disproportionately more *C. ovata* were able to reach the canopy without a period of suppression.

Carya individuals that established in closed canopy conditions (i.e. understory origin-gap release trees) were suppressed an average of 22 years before they either ascended to the canopy or experienced a short release episode. These trees had a mean dbh of only 2.6 cm at the time they either recruited to the canopy or experienced a release. Gap origin-gap release trees were in open canopy conditions for an average of 18 years before experiencing a period of suppression. At the onset of this suppression period these trees were on average 6.5 cm dbh. Thus, after approximately 20 years of growth, trees that grew in open canopy conditions were on average 150 % larger than trees that grew in closed canopy conditions.

Our findings indicate that these common *Carya* species can establish in low light or high light environments and still reach positions in the main forest canopy. On average, *Carya* individuals that established in closed canopy (i.e. light limited) environments survived for 20 years in those conditions prior to canopy accession or release. We documented an understory origin-gap release *C. alba* that survived in low light conditions 58 years, was released for 3 years and was then suppressed another 8 years before ascending to the canopy. Based on our findings, we hypothesize that *Carya* are relatively tolerant of shade early in life and can withstand overtopped conditions, but if they are not released within ca. 20 years mortality rates will increase. Monk (1981) found seedlings that were up to 21 years of age in *Quercus-Carya* stand in Georgia, USA, but none that were older. Myster and McCarthy (1989) and McCarthy (1994) found light limitation did not influence mortality rates of *C. alba* seedlings during the first few years of growth. The unresponsiveness of young seedlings to light was attributed to the large seed size of *Carya* (McCarthy 1994). In addition, *Carya* allocate a disproportionate amount of resources to below-ground biomass, which may in part allow them to withstand periods of stress such that may be caused by low light conditions or drought (Latham 1992; Robison and McCarthy 1999). Nixon et al. (1983) stated that suppressed *Carya* stems should be released before age 20 years or they may fail to respond positively.

In contrast, 40 % of the *Carya* trees we analyzed established and grew in high light conditions for ca. 20 years and during this time reached ca. 7 cm dbh then withstood relatively long periods of low light conditions (i.e. suppression). The mean time between initiation of suppression and canopy accession for these trees was 31 years. Notably, we documented a gap origin-gap release *C. glabra* that did not recruit to the canopy until 172 years of age. The ability of these species to withstand low light conditions seems dependent upon their size. Although *Carya* are typically considered to be intermediate in shade tolerance, tolerance may vary by species, size, and geographic location (Baker 1949; Nelson 1965; Trimble 1975; Smalley 1991; Kneeshaw et al. 2006; Niinemets and Valldares 2006). Our results support the conclusions of other researchers that *Carya* life history appears to be characterized by slow and persistent growth in light-limited environments with periods of more rapid growth and recruitment to larger size classes dependent upon increased insolation caused by overhead canopy disturbance (Monk 1981; Sork 1983; Robison and McCarthy 1999).

Carya establishment on the site was low, but continuous, since the mid-1800s. The forest was cleared with a regeneration harvest in the early 1920s. Certainly large, marketable *Carya* stems were cut leaving residual *Carya* stems that were small or low quality. In fact, in 1920 the mean dbh of our *Carya* samples that established prior to the harvest event was $4.0 \text{ cm} \pm 0.7 \text{ SE}$ with a minimum of 0.03 cm and a maximum of 15.4 cm. All *Carya* stems in our collection that established prior to 1920 were of understory origin and none had recruited to the canopy. A major establishment pulse began following the stand initiating disturbance of the 1920s. *Carya* stems up to ca. 20 cm dbh will readily stump sprout (Graney 1990; Smalley 1990; Smith 1990), but we do not know the importance of stump sprouting during this establishment pulse. However, while in the field we did not often observe *Carya* that were visibly of stump sprout origin. This pulse lasted for three decades and none of the *Carya* samples we analyzed established after the 1960s. Canopy accession exhibited two peaks, one coincident with the stand initiating disturbance of the 1920s and one coincident with a stand-wide disturbance event in the 1980s. We do not know the cause of the stand-wide disturbance in the 1980s, but speculate that it was related to strong winds. Notably, the stand-wide event of the 1980s did not result in establishment of *Carya* that were included in our study.

Based on a lack of regeneration by canopy *Quercus* and *Carya* and the density of shade-tolerant mesophytes in the forest understories, many researchers have concluded that a shift from the *Quercus-Carya* forest type to one with a much stronger *Acer-Fagus* component is inevitable without active forest management (e.g. Nowacki and Abrams

2008; Fei et al. 2011; McEwan et al. 2011). Managers that desire to maintain the *Carya* component to these stands will need to increase light in the understory and reduce competition from the shade-tolerant mesophytes. Our results indicate that *Carya* can establish in low light conditions and still recruit to canopy positions, but the more common mode of *Carya* accession appears to be establishment in high light environments and either accession to the canopy before closure or accession to the canopy after subsequent overhead disturbance. The natural canopy disturbance rate of stands in the Eastern Deciduous Forest Formation is 1–2 % year⁻¹ (Runkle 1985; Runkle 1991). This rate of canopy disturbance is not sufficient for establishment and canopy recruitment of *Carya* (McCarthy and Wistendahl 1988). Maintenance of these species requires disturbances larger than the gap-scale (Robison and McCarthy 1999). We found stand initiating disturbances resulted in high rates of *Carya* establishment and canopy accession. Many *Carya* stems that were suppressed before reaching canopy positions ascended to the canopy following a stand-wide disturbance at stand age 60 years (Hart and Grissino-Mayer 2008). Stand-wide disturbances may result in accession of sub-canopy *Carya*, but are likely not sufficient for establishment of *Carya* stems. Thus, we suggest managers that wish to maintain a canopy *Carya* component create stand-wide canopy disturbances that fall within the range of intermediate-scale events (Oliver and Larson 1996). Removing too much of the canopy may actually result in a lack of response by *Carya* and may cause increased competition from shade-intolerant species (Nixon et al. 1983; Schweitzer and Dey 2011). Some evidence indicates that these relatively large canopy disturbances may have been more common historically and a reduction in the frequency of these events may in part explain the decline in the dominance of mid-successional *Carya* and *Quercus* species (Ellsworth and McComb 2003; Stueve et al. 2011; Buchanan and Hart 2012). On sites with abundant shade-tolerant mesophytes in the understory, release treatments should be timed in conjunction with competition reduction measures such as fire and herbicide application (Schweitzer and Dey 2011; Hutchinson et al. 2012; Brose et al. 2013).

Climate–growth relationships

The mean interseries correlation of the *C. alba* chronology ($r = 0.52$, $P < 0.01$) was relatively high for the region. The mean interseries correlation for the *C. ovata* chronology ($r = 0.45$, $P < 0.01$) was similar to what Hart and Grissino-Mayer (2008) documented for a mixed *Quercus* species chronology ($r = 0.44$, $P < 0.01$) developed from trees growing at the study site. *Carya glabra* exhibited the lowest mean interseries correlation ($r = 0.38$, $P < 0.01$)

and the highest mean sensitivity (0.29). This pattern may be attributed to the adaptability or phenotypic plasticity of the species. We note that our series were not whitened, so part of the interseries correlation may be linked to the autocorrelative structure of the series (e.g. red noise in the climate series that was transferred to radial growth trends). *Carya glabra* exhibited the greatest rate of change from suppressed to released growth phases. As these changes in radial growth patterns occurred asynchronously across *C. glabra* individuals, we suggest the ability and the degree of response to growing conditions resulted in lower agreement in radial growth trends across *C. glabra* trees and greater annual variability in radial increment.

Radial growth rates of all three species exhibited similar relationships with climate variables as all species were sensitive to prior spring and current summer temperature and prior winter and current summer precipitation. Interestingly, Speer et al. (2009) and White et al. (2011) found June temperature and June and prior August precipitation had the strongest relationships with radial growth of *Quercus* species in the southern Appalachian region. The temperature signal we documented likely corresponded to water stress by the influence of temperature on evapotranspiration rates. Moisture availability during the growing season supports the production and storage of carbohydrates and, when coupled with abundant moisture during the subsequent growing season, results in increased productivity. *Carya ovata*, which is the species most likely to dominate on moist sites (Braun 1950; Graney 1990), was the least sensitive to water stress. With the exception of *C. ovata* being somewhat less responsive to precipitation, all three species were responsive to the same climatic conditions. They were most productive when the summer season was cool and wet. None of the species exhibited exceptionally strong relationships between radial growth and climate variables and we suggest canopy position is a strong control on annual growth rates and dampens the climate signal in radial growth trends.

Most climate models project a continued increase in warming through the twenty-first century and a decrease in summer precipitation for the eastern USA (US Global Climate Change Research Program 2009). We suggest that a decrease in available moisture during the summer and autumn seasons would have a negative impact on *Carya* productivity and could possibly result in mortality (Stringer et al. 1989; Clinton et al. 1993; Richards and Hart 2011). Likewise, we hypothesize increases in summer temperature would also negatively impact *Carya* productivity. Interestingly, the climate variables to which *Carya* (and *Quercus*) appear to be most sensitive (summer temperature and precipitation) are those projected to change most dramatically during this century (US Global Climate Change Research Program 2009). The influence of unfavorable

climate conditions may exacerbate the regeneration failure of *Carya* and if drought-induced mortality results in localized canopy disturbances, rather than stand-wide events, such climate-related disturbances may accelerate the compositional shift from *Quercus–Carya* to *Acer–Fagus*.

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Conflict of interest The authors declare that they have no conflict of interest.

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