

RADIAL GROWTH RESPONSES OF THREE CO-OCCURRING SPECIES TO
SMALL CANOPY DISTURBANCES IN A SECONDARY HARDWOOD
FOREST ON THE CUMBERLAND PLATEAU, TENNESSEE

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Abstract: We analyzed the radial growth patterns of *Liriodendron tulipifera*, *Acer rubrum*, and *Acer saccharum* growing in 39 canopy gaps in a mature secondary hardwood forest on the Cumberland Plateau in Tennessee to compare species-specific growth responses to small canopy disturbances. We tested for differences between mean radial growth increases during the year of release initiation (i.e., first year of discernible growth increase) over the year prior, mean percent growth increases during the year of release initiation over the year prior, mean release durations, and mean lag times between canopy gap formation and radial growth response. At each level of analysis (i.e., by species, canopy position, and gap position) only the radial growth increase during the year of release initiation over the year prior revealed significant differences. In each case where a systematic difference was noted, the growth increase of *L. tulipifera* was higher than one or both of the *Acer* species. However, field observation indicated accelerated growth of *L. tulipifera* is largely negated in the relatively small and short-lived gaps. Our findings provide information on the successional pathway of the forest, the physiological responses of these species to small canopy openings, and the applicability of these species to reconstruct canopy gap formation in secondary stands from tree-ring records. [Key words: *Acer rubrum*, *Acer saccharum*, canopy gap, dendroecology, *Liriodendron tulipifera*, Cumberland Plateau.]

INTRODUCTION

Disturbance events influence development and successional trajectories in all forest environments. In eastern North America, disturbance regimes of many hardwood forests in the complex stage of development (i.e., with old-growth structures) are characterized by gap-scale events that influence only neighboring trees and modify microenvironmental conditions (Lorimer, 1980; Barden, 1981; Runkle,

1982; Cho and Boerner, 1991; Runkle, 1991; Oliver and Larson, 1996; Runkle, 2000). During this late stage of development, regeneration is asynchronous and controlled by localized, low-magnitude disturbances that often involve the removal of only one or a few canopy individuals (Runkle and Yetter, 1987; Runkle, 1991). These small canopy disturbances promote multi-aged forests with patchy canopy dominance (Lorimer, 1980; Ross et al., 1982; Oliver and Larson, 1996). Most gap-scale disturbance studies have been focused in these older, complex stage stands. However, prior to a complex developmental stage, localized canopy disturbances may still influence species composition, stand structure, and successional pathways (Clebsch and Busing, 1989; Dahir and Lorimer, 1996; Wilder et al., 1999; Yamamoto and Nishimura, 1999; Hart and Grissino-Mayer, 2008). In mature secondary hardwood stands, gap-scale disturbances provide a mechanism for crown expansion and recruitment of sub-canopy trees to larger size classes. They may also allow for the establishment of new germinates (Rentch et al., 2003; Hart and Grissino-Mayer, 2009).

A widespread pattern of forest composition change has been reported from *Quercus* stands throughout the Central Hardwood Forest region. In *Quercus* forests, across a variety of site conditions *Acer saccharum* Marsh. and *Acer rubrum* L. have shown increased abundance in the understory (e.g., Lorimer, 1984; Abrams and Downs, 1990; Fralish et al., 1991; Abrams, 1992, 2003; McCarthy and Bailey, 1996; Ruffner and Abrams, 1998; Pierce et al., 2006; Hart et al., 2008; Nowacki and Abrams, 2008). An understory densely populated with *Acer* seedlings and saplings inhibits the regeneration of *Quercus* individuals (Lorimer, 1993; Lorimer et al., 1994) and many researchers have projected a composition shift from *Quercus* dominance to systems with stronger *Acer* components (e.g., Lorimer, 1984; McCarthy et al., 1987; Abrams, 1998; Hart and Grissino-Mayer, 2008; Nowacki and Abrams, 2008). In addition to this increase in *Acer* understory abundance, *Liriodendron tulipifera* L. commonly captures canopy gaps in mesic *Quercus* stands of the southern Appalachian Highlands (Loftis, 1990, 2004; Clinton et al., 1994; Hart et al., 2008).

In forests with dense *Acer* understories and/or those with *L. tulipifera* colonization in gap environments, gap-phase replacement processes do not favor the continued dominance of *Quercus* species. In such forests, competition in gap environments is largely between *A. saccharum*, *A. rubrum*, and *L. tulipifera* individuals as subcanopy trees that represent the pool of individuals that may be recruited to larger size classes or even the main forest canopy following gap formation. Thus, subcanopy composition is an important determinant of future canopy dominance in forests with gap-scale disturbance regimes (Runkle and Yetter, 1987; Webster and Lorimer, 2005). The growth response of these subcanopy individuals will ultimately determine which tree recruits to a larger size class or to the canopy. Gaps also allow trees with positions in the main canopy to extend their crowns laterally into the void space. This process provides a mechanism for trees to increase crown spread and photosynthetic potential (Runkle, 1981; Runkle and Yetter, 1987). Thus, the growth response of canopy trees to gaps is also important in stand development. Interestingly, no previous work has analyzed the radial growth responses of *A. saccharum*,

A. rubrum, and *L. tulipifera* to small canopy disturbance events in secondary forests where they commonly co-occur in gap environments.

For most all subcanopy trees to reach the main forest canopy they must be “released” from overstory competition by the removal of a canopy tree or a small cluster of trees (Runkle, 1981, 1989). Response to localized overstory removal is often evident in the growth rates and forms of trees and determines the competitive ability of the individual to occupy a dominant position in the canopy. *Liriodendron tulipifera*, *A. rubrum*, and *A. saccharum* have different ecological and life history characteristics, use different resource allocation strategies to reach the main forest canopy, and represent a gradient of shade-tolerance.

Liriodendron tulipifera is shade-intolerant and disturbance obligate (Orwig and Abrams, 1994). The species is known for rapid growth and occurs as an early successional and gap-phase forest component (Buckner and McCracken, 1978; Lorimer, 1980; Busing, 1994, 1995). *Liriodendron tulipifera* seeds will germinate under a closed canopy, but because the species is shade-intolerant, mortality will generally occur if a disturbance event does not open the canopy within the first few years following germination (Wallace and Dunn, 1980). *Acer rubrum* is classed as moderately shade-tolerant and can exist in the understory until canopy disturbances occur and the species is able to respond to increased resources (Wallace and Dunn, 1980; Abrams, 1998). *Acer saccharum* is a very shade-tolerant, late-successional species that can persist in the understory for extended periods while maintaining the ability to respond to disturbance events (Canham, 1985, 1988; Tryon et al., 1992).

Rapid growth rates are critical for shade-intolerant (*L. tulipifera*) and moderately intolerant (*A. rubrum*) species to remain forest components. Shade-intolerant species typically grow faster than those that are shade-tolerant (Canham, 1989), as photosynthetic rates are generally higher for sun-adapted species (Bazzaz, 1979). Based on the life history and resource allocation strategies of these three species, we hypothesized that *L. tulipifera* would have the greatest growth response to increased resources and that *A. saccharum* would have the most conservative response.

The overall goal of our study was to compare the growth responses of *L. tulipifera*, *A. rubrum*, and *A. saccharum* to small canopy openings in a mature hardwood forest. By quantifying the radial growth responses of these three species to small canopy openings, we can project which species is most likely to attain canopy dominance under the current disturbance regime. While height growth or lateral crown expansion determines which individual may fill a canopy void, we analyzed radial growth response because: (1) annual radial growth is directly related to the amount and duration of annual height growth (Kozlowski, 1971; Kariuki, 2002; Rentch et al., 2002, 2003); (2) sampling and analytical procedures for radial growth analyses are standardized (Fritts and Swetnam, 1989; Lorimer and Frelich, 1989; Nowacki and Abrams, 1997; Rubino and McCarthy, 2004); and (3) forest disturbance reconstructions are often developed from tree-ring data (Lorimer, 1985; Copenheaver et al., 2009). Specifically, we analyzed (1) radial growth increases during the year of release initiation (i.e., first year with a discernible growth increase) over the year prior; (2) percent growth increases during the year of

release initiation over the year prior; (3) duration of the releases; and (4) lag times between canopy gap formation and radial growth response. Data were analyzed at the species level and across species by canopy (i.e., vertical) and gap (i.e., horizontal) positions. We selected these four variables because we deemed these to be the most important determinants of probable gap capture that would be evident in radial growth patterns and because these measures are often included in dendroecological investigations. Our findings provide information on the successional pathway of the forest, information on the physiological responses of three commonly co-occurring species, and quantitative data on the applicability of these species to infer canopy disturbance history (specifically gap formation years) in secondary stands from tree-ring records.

METHODS

Study Site

This study was conducted in the Pogue Creek Natural Area (PCNA) located in Fentress County, Tennessee in the north-central portion of the state (Fig. 1). The PCNA is a 1505 ha nature reserve managed by the State of Tennessee, Department of Environment and Conservation, Division of Natural Areas. The study site is located on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman, 1938). The underlying geology consists primarily of Pennsylvanian sandstone, conglomerate, siltstone, shale, and coal of the Crab Orchard and Crooked Forked groups (Smalley, 1986). The Cumberland Plateau has irregular topography (Fenneman, 1938) characterized by long, narrow to moderately broad ridges and narrow to moderately broad valleys (Smalley, 1986). The soils of the study site are acidic, highly leached, and low in fertility (Francis and Loftus, 1977; Smalley, 1982; USDA, 1995; Hart, 2007). Depth to bedrock varies from 1.0–1.8 m and slope gradients range from 15–60%. The elevation of the study plots ranged from 260–490 m amsl.

Climate is classified as humid mesothermal with moderately hot summers and short, mild to moderately cold winters (Thorntwaite, 1948); however, local topography strongly influences microclimatic conditions. The average frost-free period is 160 days (from early May to late October) and the mean annual temperature is 13° C. The July average is 23° C and the January average is 2° C (USDA, 1995). Precipitation is evenly distributed throughout the year with no distinct dry season. Mean annual precipitation is 137 cm and mean annual snowfall is 50 cm (USDA, 1995). 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 region as described by Braun (1950). However, for this portion of the Cumberland Plateau, local topography strongly influences forest composition and true mesophytic species only dominate on protected sites such as coves. Regionally, forests are intermediate between mixed mesophytic and *Quercus–Carya* types (Hinkle, 1978, 1989; Hinkle et al., 1993). The forest of the PCNA was dominated by *Carya ovata* (P. Mill.) K. Koch, *Quercus rubra* L., *Quercus alba* L., and *Quercus montana*

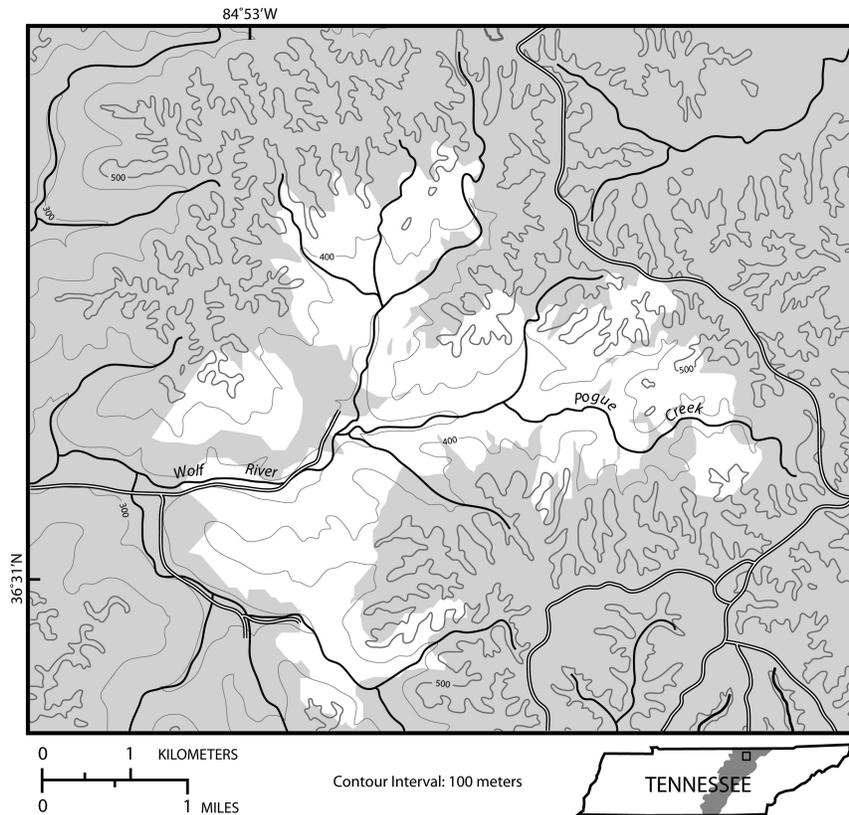


Fig. 1. Map of the Pogue Creek Natural Area in Fentress County, Tennessee. The nature reserve is the non-shaded area. Shaded portion of the Tennessee inset map is the Cumberland Plateau physiographic section.

Willd (Hart and Grissino-Mayer, 2008). The forest established in the late 1920s following the last logging event, which used the clear-cut method. Very few trees in the forest pre-date this harvesting event. Throughout the study site, *L. tulipifera*, *A. rubrum*, and *A. saccharum* had the highest density and dominance values of trees (≥ 5 cm dbh) in canopy gaps and were the most abundant species of the intermediate crown class in gap environments (Hart and Grissino-Mayer, 2009).

Methods

The 39 canopy gaps used in this study were located while walking transects through the reserve using the line intersect method (Runkle, 1982, 1985, 1992; Veblen, 1985). Gaps were defined as environments where a visible void space existed in the main forest canopy, terminal leaders of the tallest stems were less than three-fourths the height of the adjacent canopy, and gap-maker trees were present. No lower gap size limit was established so we could document the full range of

canopy gaps that occurred in the forest. All transects were established parallel to slope contour, beginning at randomly selected points throughout the reserve. The transects were located along mid-slope positions because the mid-slope stands of the PCNA are indicative of slope forests of the greater Cumberland Plateau region and the majority of forested land in the reserve occurs along slopes. Canopy gap characteristics (e.g., origin, shape, and size), tree density and diversity within gaps, gap closure mechanisms, and gap-phase replacement patterns were documented and analyzed by Hart and Grissino-Mayer (2009). The vast majority of gaps were caused by treefall (uprooted or snapped stems) rather than standing dead trees. Most gaps had elliptical shapes, and expanded gap (area defined by the base of the canopy trees that border the gap) size ranged from 47.10 m² to 587.91 m², with a mean of 214.26 m² ± 17.57 (SE). Mean gap age was 7 ± 0.7 years (SE; Hart and Grissino-Mayer, 2009).

We collected a total of 234 tree core samples from *A. saccharum*, *A. rubrum*, and *L. tulipifera* individuals growing within the 39 canopy gaps located throughout the PCNA. We subjectively sampled trees (defined as individuals ≥5 cm dbh) that we judged likely to exhibit positive growth changes associated with the canopy disturbance event and to represent a range of sizes and canopy and gap positions (Canham, 1988). We avoided trees with obvious signs of damage from the fall of the gap maker(s). All trees were cored parallel to slope contour to avoid the sampling of reaction wood in the radial growth patterns (Scurfield, 1973; Fritts, 2001; Grissino-Mayer, 2003). The core samples were all collected at breast height. We recorded the crown class based on the amount and direction of intercepted light as dominant, codominant, intermediate, or overtopped (Oliver and Larson, 1996) and the gap position as interior (i.e., unrestricted from above) or perimeter (i.e., restricted from above but within the expanded gap area; Runkle, 1981) for all individuals sampled.

In the laboratory, the core samples were allowed to air dry before they were glued to wooden core mounts. The samples were mounted with cells vertically aligned to provide a transverse view of the wood surface (Stokes and Smiley, 1996). The cores were then surfaced with progressively finer sanding paper following standard procedures to reveal the anatomical features of the wood before dating (Orvis and Grissino-Mayer, 2002).

Annual growth rings on all samples were visually inspected with the aid of a microscope for patterns of wide and narrow rings and other diagnostic characteristics that could be used to crossdate all series. Notable (e.g., unusually narrow or otherwise distinct) rings and sequences of rings were recorded to aid in crossdating (i.e., the list method of crossdating; Yamaguchi, 1991). Once crossdated, annual rings of each sample were assigned calendar years starting with the first ring beneath the bark and continuing backward until the innermost ring or pith was reached, carefully noting troublesome areas of the samples identified during the crossdating process. All tree rings were then measured to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software. All measurement series were statistically analyzed as an additional check to ensure all growth rings were assigned the proper year of formation using the computer program COFECHA (Holmes, 1983; Grissino-Mayer, 2001). The COFECHA program uses

segmented time series correlation analyses to determine the strength of association between 50-year segments lagged 25 years from each individual series against a master chronology created from the remaining series. 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.

Once we were confident all tree rings were assigned to their proper year of formation, we investigated the raw measurement files for periods of increased growth that could be attributed to a canopy disturbance event. All individuals were sampled in canopy gap environments; thus, we hypothesized most individuals would exhibit a period of increased growth. For each tree-ring series we noted single years or periods when growth increases were evident. In some tree-ring series, growth following the canopy disturbance did not show a notable change or revealed a decrease rather than an increase. These individuals were included in our analyses of the percent of individuals by species that exhibited release events, but were excluded from analyses focused on the actual release characteristics (e.g., percent growth change over the prior year). Individuals that did not exhibit positive growth changes in the radial growth record may have been injured by the canopy disturbance event. In our analyses, we did not use one of the standard release detection methods (e.g., 10-year running mean or median) because our goal was not to reconstruct forest disturbance history using these samples, but rather to isolate the gap formation year and to quantify radial growth changes in these species caused by the small canopy disturbance events. Our overarching purpose was to investigate how canopy disturbance processes actually influence radial growth patterns. Once discernible release events (defined as evident growth increases) were assigned to all series where increased growth was apparent, we compared release dates and durations with all other tree-ring series collected from the same gap. We used this corroborative evidence to assign a single formation year to all 39 canopy gaps (Runkle, 1982; Barden, 1983; Lorimer, 1985).

When all 39 gaps were assigned to a calendar year of formation and all release episodes were documented on all 234 tree-ring series, in which a notable positive growth change occurred, we calculated (1) the radial growth increase (mm) during the year of release initiation over the prior year, (2) the percent growth increase during the year of release initiation over the prior year, (3) the duration of the release, and (4) the lag from gap formation to tree release. We decided that calculations of the first year of notable increased growth over the year prior (both the raw and percent increases) and release duration and lag to response would be the best indicators of the actual physiological responses to small canopy gaps. Although these measures of the raw growth increases and the percentage growth changes are only calculated over a two-year period, we contend that these measures are best for quantifying the actual radial growth response of individuals to increased resources caused by canopy disturbance events. This short period allowed us to detect the formation year of small canopy openings and the influence of those openings on individual trees. In addition, while the growth changes were calculated over a two-year period, the growth releases were identified based on longer radial growth trends. The length of the growth increase was quantified separately. For statistical analyses, the duration of release values were only used for individuals that did not exhibit a

Table 1. Sample Depth, Mean (with standard error), Minimum and Maximum Series Length, and Radial Growth Values for the Three Studied Species

| Species | <i>n</i> | Series length (yrs) | | | Radial growth (mm) | | |
|--------------------------------|----------|---------------------|-----|-----|--------------------|------|-------|
| | | Mean \pm SE | Min | Max | Mean \pm SE | Min | Max |
| <i>Liriodendron tulipifera</i> | 47 | 31.74 \pm 2.51 | 10 | 70 | 2.13 \pm 0.04 | 0.09 | 11.86 |
| <i>Acer rubrum</i> | 72 | 52.24 \pm 2.09 | 18 | 129 | 1.17 \pm 0.02 | 0.05 | 7.78 |
| <i>Acer saccharum</i> | 114 | 46.07 \pm 1.48 | 16 | 96 | 1.13 \pm 0.01 | 0.09 | 10.83 |

release during the last year of record because we could not be certain that the releases were indeed finished. We used chi-square to determine if significant ($p < 0.05$) differences existed between the numbers of individuals sampled and the number that experienced a release by species. ANOVA with a Scheffe post-hoc test ($p < 0.05$) was used to analyze differences of the mean values for the four variables. Data were analyzed by species and then differentiated by crown position (canopy: dominant and codominant or subcanopy: intermediate and overtopped) and gap position (interior or perimeter) to determine the possible influence of these vertical and horizontal variables on the physiological responses of the three species. It is possible the measured growth changes were caused by climatic influences rather than increased resources associated with the canopy disturbances. However, we think this is unlikely because a *Quercus* tree-ring chronology constructed from the site showed very weak relationships to climate variables (Hart and Grissino-Mayer, 2008), the sampled series did not exhibit common growth patterns, general release synchrony existed in samples from the same gap, moisture is not generally limited in the forest (Smalley, 1982), and in closed canopied forests of the region, light is known to be the most commonly limiting factor (Oliver and Larson, 1996).

RESULTS

Species Level

Average age of the sampled trees varied by species and ranged from a mean of 31.74 ± 2.51 (SE) years for *L. tulipifera* to a mean of 52.25 ± 2.09 (SE) years for *A. rubrum* (Table 1). Mean radial growth was greatest for *L. tulipifera* and lowest for *A. saccharum*. Tree diameter ranged from 5 to 55 cm dbh; both of these individuals were *A. saccharum* (Fig. 2). Of the 234 trees analyzed, 193 exhibited discernible growth increases. While we did not use a predetermined growth change threshold, we note that only four of the 193 documented discernible growth responses exhibited a less than 10% increase over the prior year. Radial growth releases attributed to a known canopy disturbance were exhibited in over 80% of the individuals sampled from all species and no significant differences were noted. The relative number

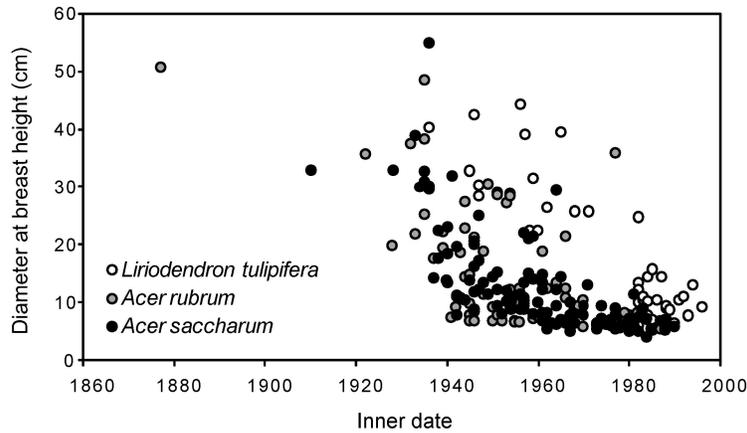


Fig. 2. Diameter-age relationships for trees sampled at the Pogue Creek Natural Area, Fentress County, Tennessee.

of tree-ring series from each species that released was actually quite consistent (82–86%).

The mean radial growth increase for *L. tulipifera* during the year of release initiation was 1.04 mm greater than growth of the prior year (Fig. 3). The growth increases of the *Acer* species were similar, with a mean increase of 0.77 mm for *A. rubrum* and 0.73 mm for *A. saccharum*. The mean growth during the year of release over the prior year was significantly greater for *L. tulipifera* compared to *A. saccharum*. The greatest growth increase occurred in a *L. tulipifera* individual and was 3.39 mm greater than the prior year. Only three individuals in the dataset increased growth more than 3.00 mm over the previous year (one *L. tulipifera* and two *A. saccharum* individuals). The percent growth increase during the year of release initiation over the prior year was consistent across all three species as mean percent increases ranged from 46.33% for *L. tulipifera* to 42.05% for *A. rubrum*. The maximum percent growth change was 88% and occurred in a *L. tulipifera*. The maximum growth changes for *A. rubrum* and *A. saccharum* were 86% and 80%, respectively.

Mean release durations for all three species were relatively short. The range of values documented within the three species was narrow, with *L. tulipifera* and *A. saccharum* both having mean release durations of 3.02 years and *A. rubrum* having a mean duration of 2.88 years. The longest sustained release episode was nine years. Releases of this duration were documented in three *A. rubrum* and two *A. saccharum* samples. Of note, all five releases of this length occurred in response to different canopy disturbance events. The minimum release duration was 1 year. In fact, 42% of all *L. tulipifera*, 42% of all *A. rubrum*, and 21% of all *A. saccharum* releases were sustained for just a single year. Samples with releases in the last year of record were excluded from these calculations. Mean lag time from the estimated year of canopy gap formation to the year of radial growth release was less than one year for all species. The longest duration between canopy gap formation and tree

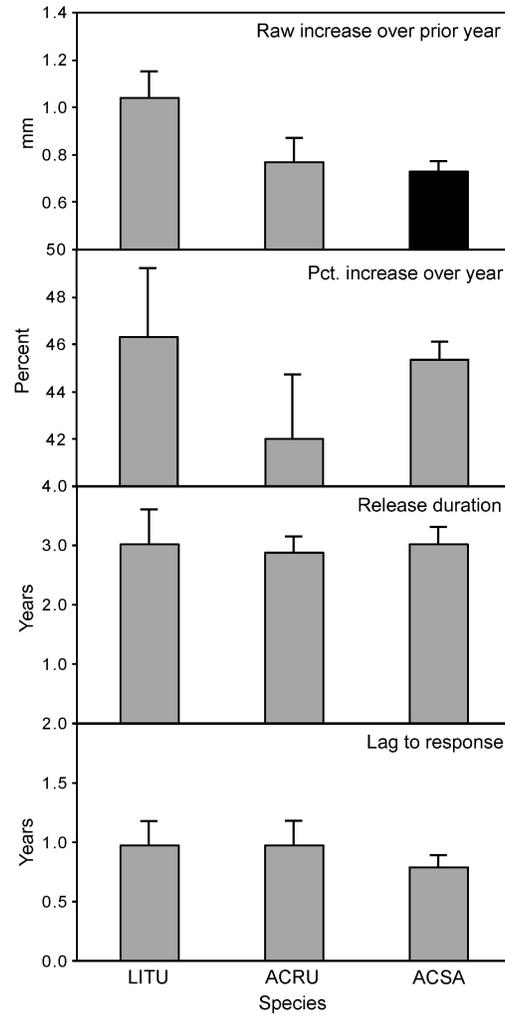


Fig. 3. Mean radial growth increase over the prior year, percent growth increase over the prior year, release duration, and lag from gap formation to tree response with standard errors by species. Solid bar represents significant differences ($p < 0.05$). Species abbreviations are the first two letters of the genus and first two letters of the specific epithet.

response was five years and was recorded in *L. tulipifera*. Neither of the *Acer* species had a single lag time of more than four years.

Crown Position

For canopy trees, no significant differences were noted among mean radial growth increases during the year of release initiation over the prior year between the three species (Fig. 4). However, the mean radial growth release of *L. tulipifera*

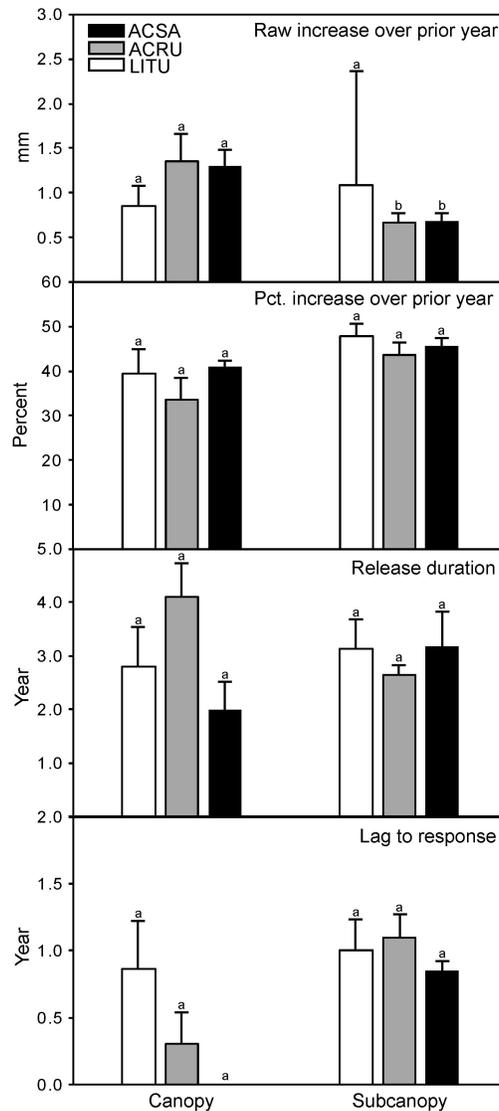


Fig. 4. Mean radial growth increase over the prior year, percent growth increase over the prior year, release duration, and lag from gap formation to tree response with standard errors by species and canopy position. Bars with different letters represent significant differences across species ($p < 0.05$). Canopy represents trees classed as dominant or co-dominant and subcanopy represents trees classed as intermediate or overtopped. Species abbreviations are the first two letters of the genus and first two letters of the specific epithet.

was greater than that of the *Acer* species for subcanopy individuals. In the subcanopy, the mean growth increase of *L. tulipifera* was 1.08 mm, while the mean increases of *A. rubrum* and *A. saccharum* were 0.66 mm and 0.70 mm, respectively. The mean percent growth increases were relatively uniform when the data

were divided by canopy position. Likewise, no significant differences were noted in the mean release durations in the canopy or subcanopy classes. The greatest range of values occurred between *Acer* species in the canopy, as *A. rubrum* had a mean release duration of 4.1 years while *A. saccharum* had a mean release duration of just 2.0 years. The greatest mean lag to response was 1.1 years and was observed in subcanopy *A. rubrum*. Interestingly, mean lag to response times exhibited a greater range for canopy versus subcanopy for *A. rubrum* and *A. saccharum*, while mean times for *L. tulipifera* were similar across both canopy positions. Also of note, *A. saccharum* in the canopy had a mean response time of zero years.

Gap Position

The mean radial growth increases of *L. tulipifera* were significantly greater than the *Acer* species for interior trees (Fig. 5). For trees located in gap interiors, the mean radial growth increase of the release initiation year was 1.12 mm for *L. tulipifera*, while the mean increases of *A. rubrum* and *A. saccharum* were 0.63 mm and 0.70 mm, respectively. No significant differences were noted between the mean radial growth releases of trees growing at gap perimeter locations. The longest mean release length occurred in interior *A. saccharum* (3.4 years), while the shortest mean release length occurred in perimeter *A. saccharum* (2.1 years). The smallest range of mean release duration values was documented in interior and perimeter *A. rubrum*. Like the results for canopy position, mean release durations for *L. tulipifera* were similar across both gap position classes. The longest mean lag to response was 1.2 years and was observed in perimeter *L. tulipifera*, while the shortest mean lag time was 0.6 and was documented for perimeter *A. rubrum*.

DISCUSSION

Although sample sizes varied, over 80% of all sampled individuals of each species exhibited a marked increase in radial growth that could be attributed to a canopy disturbance. These data indicate that all three species are sensitive to small canopy disturbance events. We found it interesting that approximately the same percentage of individuals of the shade-intolerant and noted gap-phase *L. tulipifera* released as individuals of the shade-tolerant and late successional *A. saccharum*. The percentage of trees that showed a notable increase in radial growth may be attributed to the age of the stand, as it is hypothesized that young trees are more likely to take advantage of increased resources, compared to older trees (Fritts, 2001). An anomalously old tree occurred in our sample—a 129-year old *A. rubrum* that did not show a notable increase in radial growth following the canopy disturbance event. Although the single “old” tree in our sample did not release, some studies have found older trees to be responsive to canopy disturbance events (e.g., Orwig and Abrams, 1994; McEwan and McCarthy, 2008).

Establishment dates of the three species at the PCNA differed. Most of the *A. rubrum* and *A. saccharum* trees we sampled had established prior to 1960, and many had experienced multiple releases during their growth and development (Fig. 6). In contrast, most of the *L. tulipifera* we sampled had established in the

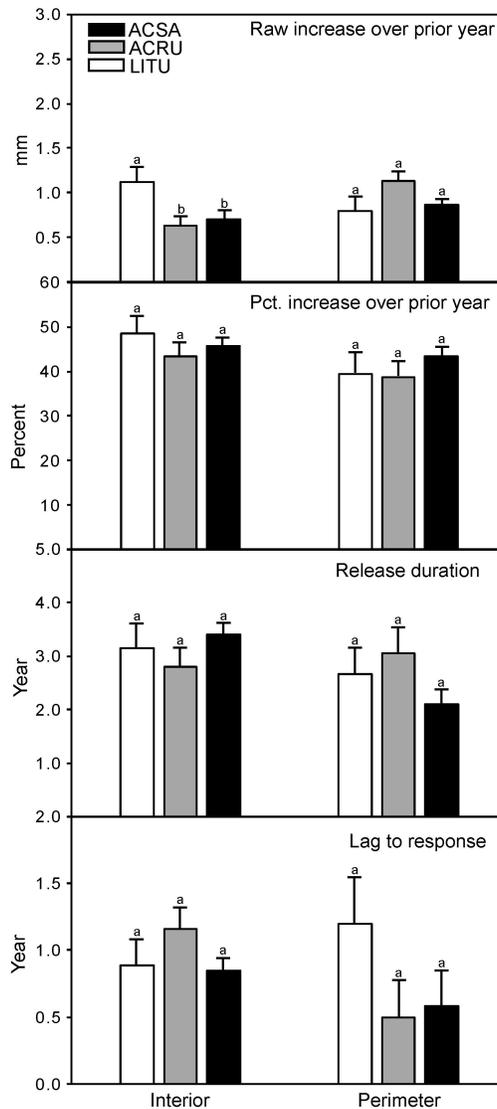


Fig. 5. Mean radial growth increase over the prior year, percent growth increase over the prior year, release duration, and lag from gap formation to tree response with standard errors by species and gap position. Bars with different letters represent significant differences across species ($p < 0.05$). Interior represents trees in the true gap unrestricted from above and perimeter represents trees along the gap perimeter. Species abbreviations are the first two letters of the genus and first two letters of the specific epithet.

mid-1970s. This pattern would be expected of these species based on what is known about their ecology and life history, especially their shade tolerance. It is possible that tree age influenced the growth responses documented, but the trees sampled are representative of the study site and broader landscape.

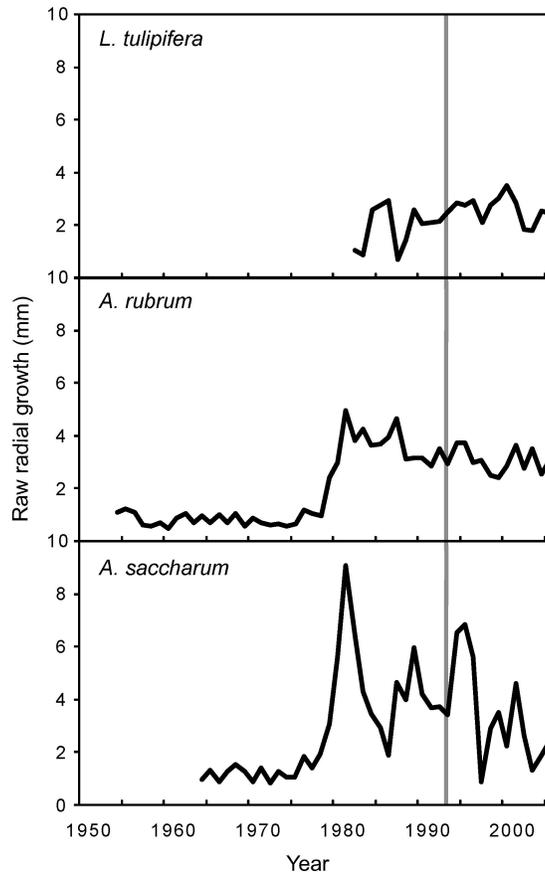


Fig. 6. Raw-ring width measurements for three individuals sampled in the same canopy gap at the Pogue Creek Natural Area. The grey line indicates the year of canopy gap formation.

Gap size may also have influenced the radial growth patterns documented. In our study, mean expanded gap area was 214 m². Although a large range of gap sizes was documented, in general, all gaps in the secondary hardwood forest were relatively small, especially when compared to canopy gaps in complex stage or old-growth stands. Gap size has been shown to influence radial growth of understory individuals (Tryon et al., 1982), but quantity and quality of insolation are highly variable in the gap environment during the course of the growing season (Canham, 1988). As such, gap size does not necessarily have a strong influence on the physiological response of trees in gaps (Canham, 1988, 1989). Also, increased radial growth caused by gaps has been documented in individuals 30 m away from the edge of the canopy void (Tryon et al., 1992).

The radial growth rates recorded in our study were lower than those documented by Barden (1983) for the same three species in canopy gaps of an old-growth cove forest in the Great Smoky Mountains National Park (GSMNP). Although average

[Author: Tryon et al., 1982 or 1992, as in references list?]

growth for the *Acer* species prior to gap formation (data were not available for *L. tulipifera* prior to gap formation in Barden, 1983) were similar between the sites, radial growth post-canopy disturbance was greater in GSMNP. This difference may be attributed to growing conditions in the different forest types and/or regions, or may be related to structure of old-growth versus secondary stands (e.g., canopy cover and vertical structure).

At each level of analysis (i.e., by species, canopy position, and gap position), only the raw radial growth increase during the year of release initiation over the year prior revealed systematic differences. In each case in which a systematic difference was noted, the growth increase of *L. tulipifera* was significantly higher than that of one or both of the *Acer* species. The radial growth response of *L. tulipifera* compared to that of *A. rubrum* and *A. saccharum* is not necessarily surprising, as the species is known for its rapid growth and ability to colonize and recruit in canopy gaps (Buckner and McCracken, 1978; Runkle, 1981; Orwig and Abrams, 1994; Busing, 1995). Although the species only significantly differed in the radial growth increase during the year of gap initiation over the prior year, this is likely the most important variable, as radial growth is related to height growth (Kariuki, 2002; Rentch et al., 2002, 2003) and no significant differences were noted between mean release durations or mean lags to response. Although height growth is the primary factor that determines the gap-capture ability of subcanopy individuals (Hibbs, 1982; Runkle and Yetter, 1987; Webster and Lorimer, 2005), the timing and duration of the response is also important (Runkle, 1989; Kozlowski and Pallardy, 1997; Naidu and DeLucia, 1997; Hart and Grissino-Mayer, 2009). For example, if one species responds significantly faster than another or if the response is sustained longer, it may be at a competitive advantage regardless of the actual increase in height growth by competitors (Runkle, 1989; Naidu and DeLucia, 1997). Of course, the actual range of height growth between competitors may negate any advantage gained by the timing and duration of the physiological response. Our dendroecological results alone would indicate that *L. tulipifera* has the greatest probability of capturing these small canopy gaps. However, probable gap closure (i.e., by subcanopy height growth or lateral crown expansion) and probable gap successors were documented for these 39 gaps by Hart and Grissino-Mayer (2009). Only 10 of the gaps were projected to close by subcanopy height growth, and *A. rubrum* and *A. saccharum* were projected to capture three and two gaps, respectively. No gaps in the study were projected to close by the height growth of a *L. tulipifera* individual. Thus, we propose that the increase in *L. tulipifera* growth relative to the *Acer* species is negated by gap size and gap duration in this forest. These gaps were relatively small and short lived (Hart and Grissino-Mayer, 2009). Thus, multiple canopy disturbance events are likely needed for subcanopy trees to reach the main canopy level. This disturbance regime favors the more shade tolerant *Acer* species.

As the forest ages, the spacing between canopy trees will increase and thus, gap size caused by the removal of a canopy individual should also increase (Clebsch and Busing, 1989; Spies et al., 1990; Tyrell and Crow, 1994; Runkle, 1998; Yamamoto and Nishimura, 1999). As gap size increases, the likelihood of closure by lateral crown expansion should decrease and gap capture by subcanopy individuals should become more common. In larger gaps that must close by subcanopy

height growth, *L. tulipifera* may have a competitive advantage because of its greater increase in growth relative to the *Acer* species. The size threshold for gap capture by *L. tulipifera* has been hypothesized to be 400 m² (Busing, 1994, 1995); however, in the southeastern U.S., the species has been shown to reach the canopy in smaller gaps (Hart et al., 2008).

One unknown element in the structural development of this forest is the relationship between disturbance dynamics and the increased dominance of the *Acer* species. In the PCNA, as in many other forests throughout the Central Hardwood region, *Acer* species are projected to increase in dominance with the loss of over-story *Quercus* (Hart and Grissino-Mayer, 2008). Canopy gaps likely play an important role in this process. If *A. rubrum* and *A. saccharum* are able to reach the canopy in these smaller gaps, the time required for the stand to reach a structural stage where canopy gaps would become too large to be filled by lateral crown expansion may be delayed. As *Quercus* individuals are removed from the canopy, the *Acer* species may fill those voids and continue to recruit to larger size classes. Thus, the more liberal growth of *L. tulipifera* may continue to be negated as gap size may remain relatively small. It is possible to imagine a situation where gaps sufficiently large so that they must be filled by subcanopy height growth would occur in a system where *Acer* is or is among the most dominant taxa.

Our results also have implications for disturbance history reconstructions using these species. Standard dendroecological techniques exist to reconstruct stand history (for a review see Rubino and McCarthy, 2004 or Copenheaver et al., 2009). In many such techniques, release events are determined by analyzing changes in raw radial growth relative to a pre-determined criterion using a percent growth change equation (Lorimer, 1985; Lorimer and Frelich, 1989; Nowacki and Abrams, 1997; Frelich, 2002). Commonly, a release is identified when raw-ring width for a year exceeds a pre-determined percentage (e.g., 25%) of the mean or median of an established prior and subsequent period (e.g., the mean of the 10 years prior and 10 years subsequent) and the increase in growth is sustained for a minimum number of years (Lorimer and Frelich, 1989; Nowacki and Abrams, 1997; Rubino and McCarthy, 2004). Our results indicate *L. tulipifera*, *A. rubrum*, and *A. saccharum* are useful for reconstructing disturbance history in secondary stands using such techniques, as over 80% of these individuals growing in and around gap environments recorded the disturbance in their annual growth patterns. The percent growth change of the release year ranged from 42% to 46% over the prior year and the releases were sustained for ca. three years. In order to reconstruct disturbance history from tree-ring records, the actual growth response of the selected species to canopy disturbance events should be quantified (Fraver and White, 2005). We suggest using values reported here as starting points to establish standard release detection criteria when using these species in similar settings, as we documented tree response to known canopy disturbance events. Of note, some of the marked increases in radial growth were actually less than the mean of the 10 years prior, which may indicate that a window of 10 years (which is a common length used) is too long when reconstructing the formation of relatively small canopy gaps such as those documented here in a secondary hardwood forest prior to a complex stage of

development. We suggest that the minimum release duration threshold be three years when using these species in similar settings.

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