

Gap-scale disturbance processes in secondary hardwood stands on the Cumberland Plateau, Tennessee, USA

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Abstract Disturbance regimes in many temperate, old growth forests are characterized by gap-scale events. However, prior to a complex stage of development, canopy gaps may still serve as mechanisms for canopy tree replacement and stand structural changes associated with older forests. We investigated 40 canopy gaps in secondary hardwood stands on the Cumberland Plateau in Tennessee to analyze gap-scale disturbance processes in developing forests. Gap origin, age, land fraction, size, shape, orientation, and gap maker characteristics were documented to investigate gap formation mechanisms and physical gap attributes. We also quantified density and diversity within gaps, gap closure, and gap-phase replacement to examine the influence of localized disturbances on forest development. The majority of canopy gaps were single-treefall events caused by uprooted or snapped stems. The fraction of the forest in canopy gaps was within the range reported from old growth remnants throughout the

region. However, gap size was smaller in the developing stands, indicating that secondary forests contain a higher density of smaller gaps. The majority of canopy gaps were projected to close by lateral crown expansion rather than height growth of subcanopy individuals. However, canopy gaps still provided a means for understory trees to recruit to larger size classes. This process may allow over-topped trees to reach intermediate positions, and eventually the canopy, after future disturbance events. Over half of the trees located in true gaps with intermediate crown classifications were *Acer saccharum*, *A. rubrum*, or *Liriodendron tulipifera*. Because the gaps were relatively small and close by lateral branch growth of perimeter trees, the most shade-tolerant *A. saccharum* has the greatest probability of becoming dominant in the canopy under the current disturbance regime. Half of the gap maker trees removed from the canopy were *Quercus*; however, *Acer* species are the most probable replacement trees. These data indicate that canopy gaps are important drivers of forest change prior to a complex stage of development. Even in relatively young forests, gaps provide the mechanisms for stands to develop a complex structure, and may be used to explain patterns of shifting species composition in secondary forests of eastern North America.

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Introduction

All forest ecosystems are subject to natural disturbance events that shape species composition and stand structure. In many forest types, gap-scale disturbance processes are the dominant disturbance mechanisms. Thus, canopy gap characteristics and forest response have been studied in forests throughout eastern North America to elucidate patterns, and processes of gap-scale disturbances and forest vegetation dynamics. The overwhelming majority of canopy gap studies, however, have been conducted in old growth remnants (e.g., Lorimer 1980; Barden 1981; Runkle 1982; Cho and Boerner 1991; Runkle 2000). Throughout the Eastern Deciduous Forest Region, most forested land supports secondary stands (secondary referring to all non-primeval forests prior to a complex stage of development) composed of mixed hardwood species (Cowell 1998; Rebertus and Meier 2001). Few studies have analyzed gap-scale disturbances and forest response in secondary forests (but see Clebsch and Busing 1989; Dahir and Lorimer 1996; Wilder et al. 1999; Yamamoto and Nishimura 1999), and no such research has been conducted in mixed hardwood stands on the Cumberland Plateau.

Undoubtedly, forest disturbance dynamics differ between old growth remnants and mature secondary stands. Differences in disturbance characteristics are attributed to variations in species composition, biomass arrangement, and tree-age distribution. As forests mature, the distance between large individuals increases. Tree crowns separate into distinct categories, creating a more complex vertical structure, and species composition shifts to favor later-successional species (Goebel and Hix 1996; Oliver and Larson 1996; Goebel and Hix 1997). Forest response to disturbance events likely differs between old growth and secondary stands, because of differences in stand structure and species composition, and also because of the ages of the oldest trees, as older trees are less able to respond to increase in available resources resulting from disturbance events (Fritts 2001).

In old growth forests, the spacing between large individuals is greater than in secondary forests. Thus, when a canopy tree is removed from an old growth stand, the size of the canopy gap created should be larger than a comparable disturbance during earlier stages of forest development (Clebsch and Busing 1989; Spies et al. 1990; Tyrell and Crow 1994; Runkle

1998; Yamamoto and Nishimura 1999). Because canopy gaps are generally larger in old growth remnants, many of the gaps in these forests close by the height growth of subcanopy individuals rather than lateral crown expansion of perimeter trees (Runkle 1982). This gap-replacement process creates forests with complex age and size structures, and patchy species composition in the canopy (Lorimer 1980; Runkle 1982; Yetter and Runkle 1986; Runkle and Yetter 1987). Although canopy gaps in secondary forests are hypothesized to be smaller in size, they may still act as a mechanism for canopy tree replacement, and stand structural changes associated with older forests (Clebsch and Busing 1989; Wilder et al. 1999; Taylor and Lorimer 2003; Cole and Lorimer 2005).

The overarching goal of our study was to document the influence of localized, natural disturbance events on the development of secondary hardwood stands during the understory reinitiation stage of development. Our research was driven by four major questions. *Question 1*: What are the patterns and processes of canopy gap formation prior to a complex stage of forest development? We hypothesized that most canopy gaps would be created by uprooted stems, as windthrow has been widely reported from many old growth stands and visual observation of the forest revealed uprooted trees. *Question 2*: What percentage of the forest is occupied by canopy gaps and what are the shape, size, and age distributions for gaps in developing stands? We hypothesized that the land fraction of the forest in gaps would be within the range of variability reported from old growth stands, but the forest would contain a higher density of smaller gaps relative to older stands. *Question 3*: Do small canopy disturbances influence density and diversity patterns in secondary stands? We hypothesized that larger gaps would support a higher number of individuals as well as higher levels of diversity because they should contain more microsite heterogeneity, and the likelihood of documenting rare species should increase by sampling a larger spatial area. *Question 4*: How do the gaps close, and what effects do they have on composition and structure in developing stands? We hypothesized that most gaps would close by lateral crown expansion rather than height growth of subcanopy individuals and would cause the structure of the forest to move from a high density of small trees to a lower density of larger individuals, more typical of older stands.

Methods

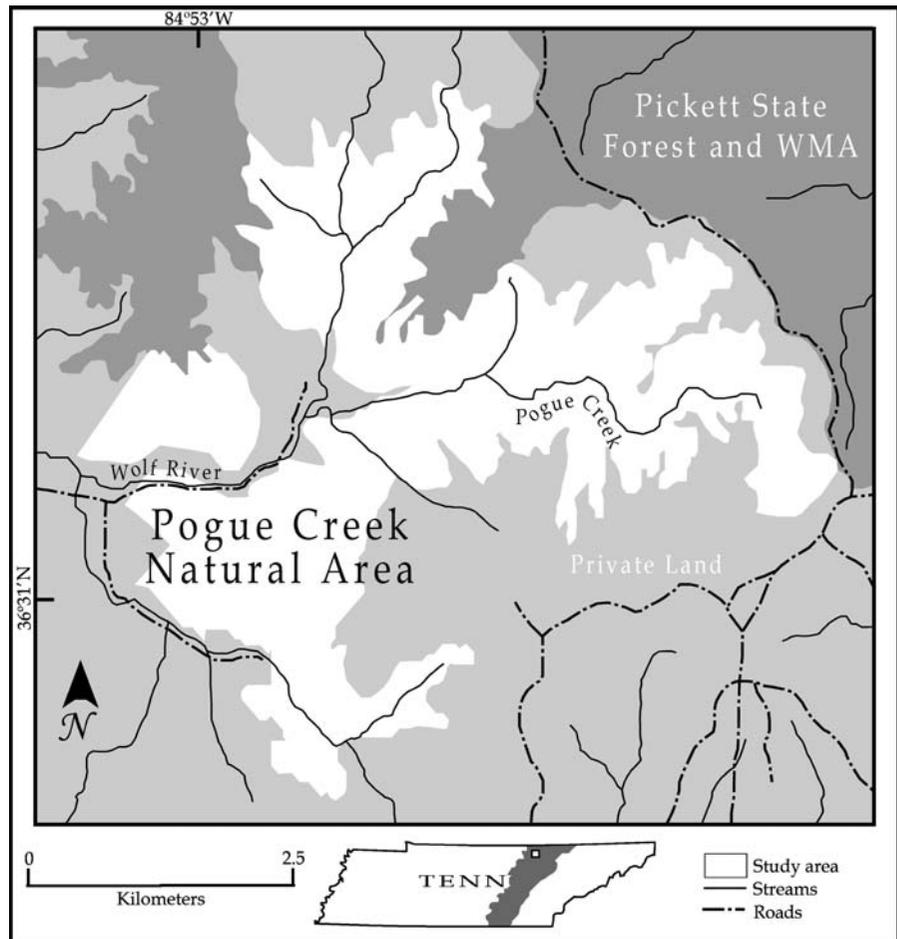
Study area

The 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 1,505 ha reserve managed by the State of Tennessee, Department of Environment and Conservation, Division of Natural Areas. The PCNA is located on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman 1938). The underlying geology consists of Pennsylvanian sandstone, conglomerate, siltstone, shale, and coal of the Crab Orchard and Crooked Forked Groups (Smalley 1986). The area has irregular topography (Fenneman 1938) characterized by long, narrow to moderately broad ridges and narrow to moderately broad valleys (Smalley 1986). Soils are

acidic, highly leached, and low in fertility (Francis and Loftus 1977; Smalley 1982; USDA 1995; Hart 2007). Depth to bedrock varies from 1 to 1.8 m and slope gradients range from 15% to 60%. The elevation of the study plots ranged from 260 to 490 m amsl.

Climate is classified as humid mesothermal with moderately hot summers and short-mild to moderately cold winters (Thorntwaite 1948). 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). The area receives steady precipitation during the year with no distinct dry season. Mean annual precipitation is 137 cm and mean annual snowfall is 50 cm (USDA 1995). Late spring and summer are characterized by heavy rains that are often accompanied by moderate

Fig. 1 Map of the Pogue Creek Natural Area, Fentress County, Tennessee. Shaded portion of the Tennessee inset map is the Cumberland Plateau physiographic section



to severe thunderstorms and strong winds (Smalley 1982).

Braun (1950) classified the area as part of the Cliff Section of the Mixed Mesophytic Forest Region, but local topography influences forest composition and true mesophytic species only dominate on protected sites. Regionally, forests are intermediate between mixed mesophytic and *Quercus*–*Carya* types (Hinkle 1978; Hinkle 1989; Hinkle et al. 1993). Forest vegetation patterns of the PCNA were quantified by Hart and Grissino-Mayer (2008). The forest was dominated by *Carya ovata*, *Quercus rubra*, *Q. alba*, and *Q. montana*. The sparse sapling layer was dominated by *Acer saccharum*. The forest was established in the late 1920s after the cessation of local logging operations. From field observations and investigation of 17 tree cross sections from a previous study, no signs of fire or other large-scale disturbance events were evident since the anthropogenic disturbances of the 1920s (Hart 2007). *Castanea dentata* Marsh was a forest component prior to the arrival of *Cryphonectria parasitica* (Murrill) M.E. Barr (chestnut blight). The blight reached the Cumberland Plateau in the 1920s, and by the end of the 1930s, most *C. dentata* in the region were dead. Thus, the loss of the species roughly coincided with stand initiation.

Field sampling

Canopy gaps ($n = 40$) were located along transects throughout the reserve using the line intersect method (Runkle 1982; Runkle 1985; Veblen 1985; Runkle 1992). Gaps were defined as environments where a visible void space existed in the main forest canopy, leaf height of the tallest stems was less than three-fourths the height of the adjacent canopy, and gap makers were present. We did not use a minimum gap size threshold to document the full range of canopy gaps. Transects were established parallel to slope contour beginning at randomly selected points throughout the forest. All transects were located along mid-slope positions. We sampled at mid-slope positions, because the mid-slope forests of the reserve are indicative of slope forests of the greater Cumberland Plateau region and the majority of forested land in the reserve occurs along mid-slopes. Total transect length and transect length in expanded (boundary defined by the base of surrounding canopy trees (Runkle 1981)) and true (area unrestricted from

above) canopy gaps were documented by recording the number of paces across each. The fraction of land area in canopy gaps was calculated by dividing the transect distance in gaps by total transect length (Runkle 1985; Runkle 1992). At each gap, physical site characteristics, including percent slope, aspect, and elevation, were recorded. When walking transects through a forest, large gaps are more likely to be encountered than relatively small gaps, and sampling estimators have been created to correct for sampling bias (see De Vries 1974; Pickford and Hazard 1978). However, values obtained with the use of estimator equations and those obtained by simply dividing transect distance in gaps by total transect length are similar (Runkle 1985).

Gap area was determined for expanded and true gaps by, measuring length (largest distance from gap edge to gap edge) and width (largest distance perpendicular to the length). These measurements were fitted to the formula of an ellipse (Runkle 1985; Runkle 1992). Although gap shapes can be highly variable (Ferreira de Lima 2005), most gaps at the PCNA had elliptical shapes, which is common for forests of the southern Appalachian Highlands (Runkle 1982; Runkle 1992; Clinton et al. 1994). Thus, fitting the measurements to the formula of an ellipse was appropriate for this study.

Canopy gaps can be created by several different mechanisms that remove overstory trees. Biotic and abiotic forest conditions can be modified differently by canopy disturbances that are caused by different gap formation mechanisms. Differences between gap origins may also influence forest response. In order to analyze these patterns, gap formation mechanisms were classified into one of the three categories (snag, uprooted stem, or snapped stem) according to gap origin (Clinton et al. 1993). The number of trees involved in gap formation was also recorded to document the abundance of single-tree versus multi-tree events.

Gap maker trees were taxonomically classified to quantify any species-specific overstory mortality patterns and possible composition changes associated with small canopy disturbances. We measured gap maker diameter at breast height (dbh, ca. 1.4 m above the surface or root collar for downed individuals) and length. Basal area (m^2) was calculated for all gap makers that could be accurately measured and totaled by gap, to determine the amount of basal area lost per

disturbance event. This information may be used to document the amount of biomass naturally removed from a stand through gap-scale processes. Direction of gap maker fall relative to slope (i.e., down, across, or up slope) was also recorded and all gap makers were placed into one of four decay classes (1–4, with 4 being the most decayed) following criteria adapted from McCarthy and Bailey (1994).

In each gap, we recorded species, crown class, and diameter of all trees ≥ 5 cm dbh to characterize forest gap vegetation. Crown class categories (dominant, codominant, intermediate, and overtopped) were visually assessed based on the amount and direction of intercepted light (Oliver and Larson 1996). The location of each of these individuals was also recorded as being in either an expanded or true canopy gap. All saplings (woody stems ≥ 1 m height, < 5 cm dbh) in the expanded gap area were tallied by species to characterize gap regeneration patterns. The number of perimeter trees with dominant or codominant positions in the canopy was documented for each gap, to analyze the number of trees required to complete the canopy surrounding gaps, and the number of canopy individuals with the potential to close the void space through lateral crown expansion.

Tree core samples were collected to aid in the documentation of gap age. A minimum of nine trees were cored (mean = 18.6) per gap resulting in the collection of 742 cores. Tree core samples or cross sections were also collected from all gap makers that were not in an advanced state of decay (intact bark and no sapwood degradation), to aid with gap age determination and to document the seasonal timing of gap events, based on the amount of xylem produced during the last year of growth. Dating the seasonality of tree death and gap formation illustrates a new approach in dendroecology.

Data analyses

Tree core and cross section samples were prepared and processed for dating using the methods outlined in Stokes and Smiley (1996). The samples were air-dried, glued to wooden mounts, and sanded to reveal the cellular structure of the wood (Orvis and Grissino-Mayer 2002) before tree rings were dated with the aid of a stereo zoom microscope. All tree cores were visually analyzed for radial growth releases to document gap age. In order to document

gap maker death dates, tree rings were measured to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software for all sampled gap makers. The measurement series were visually compared to a reference *Quercus* chronology developed by Hart and Grissino-Mayer (2008) for the site. We confirmed the graphical crossdating of all gap maker tree-ring series using the computer software COFECHA, a quality-control program that uses segmented time series correlation analyses to confirm the placements of all tree rings (Holmes 1983; Grissino-Mayer 2001). In COFECHA, we tested consecutive 50-year segments (with 25-year overlaps) on each undated gap maker series to the reference *Quercus* chronology. Once statistically confirmed, we assigned calendar years to all tree rings in each individual undated measurement series. All gap ages were confirmed using gap maker decay classifications.

Canopy gaps can be caused by the removal of a single tree or a small cluster of trees. Because single-tree gaps may result from the death of a large canopy tree and multi-tree gaps may result from the deaths of relatively small trees, the amount of basal area lost between single- and multi-tree gaps was statistically analyzed using a two-tailed *t*-test. This information may be useful to analyze the quantity of basal area lost by small canopy disturbance events and applied to harvesting techniques that may mimic natural disturbance processes.

The rate of gap formation and closure may be balanced or may vary through time. Non-parametric correlation techniques were used to analyze the relationship between land fraction in gaps and gap age. Gaps may be caused by a variety of formation mechanisms that differ in the way overstory vegetation is removed, and the mechanism of canopy tree removal may influence gap size. In order to determine, if a relationship existed between gap size and gap origin, data were analyzed using a one-way ANOVA. A Tukey honestly significant difference (HSD) test was used to compare mean expanded and true gap sizes across origin categories to determine if gap size varied by gap formation mechanism.

Length and width of gaps were measured in the field. Ratios were calculated for length to width (L:W) of expanded and true gaps to document gap shape characteristics. This information is useful to understand the variation in the shape of gaps created

by the disturbance and has implications for forest response and microenvironmental changes within the gap environment.

For each gap, density and diversity (H') measures were calculated for saplings, trees, and total stems (all woody stems ≥ 1 m height) to document forest response to canopy disturbances. Gap size is believed to influence stem density and diversity. Correlation coefficients were calculated to determine if a relationship existed between gap size and density of individuals in gaps. Regression techniques were then used to model gap size and density relationships. In order to analyze the relationship between expanded gap area and diversity patterns, correlation coefficients were calculated for sapling, tree, and total stem diversity.

Canopy gaps can close by crown expansion of perimeter trees at canopy level or by the height growth of understory individuals. The likely closure mechanism, either by height growth or lateral crown expansion, of each gap was recorded in the field to document changes in forest structure following the removal of canopy trees. Probable gap successors, which are the individuals that will likely fill the canopy void, can often be determined in the field (Barden 1979; Barden 1980; White et al. 1985; Yamamoto and Nishimura 1999). The documentation of replacement trees is useful to project the future composition of the stand and to analyze the influence of canopy gaps on forest succession. In order to quantify recruitment following overstory removal, crown class distributions were constructed for all trees located in true gap environments for the 15 most dominant species with canopy potential. These measures may be used to document future canopy trees and recruitment patterns associated with gap-scale disturbance processes.

Results

Gap formation patterns and processes

Of the 40 gaps sampled, 8 (20%) were created by snags, 16 (40%) were created by uprooted stems, and 16 (40%) were created by snapped stems. Eventually, snag trees will fall, generally during mild to severe wind events, possibly causing further disturbance to the forest. It is possible that a gap created by a snag,

subsequently blown down, was classified incorrectly. However, measures were taken to avoid this issue, such as documenting the decay class of gap makers and noting the position of the gap maker relative to other downed logs. The number of gap maker trees involved with opening the canopy ranged from one to four. The majority (78%) of the canopy gaps involved the death of only one individual. Of the nine multi-tree gaps, six (66%) resulted from uprooted stems including the gap that consisted of the removal of four canopy individuals, while the three other multi-tree gaps resulted from snapped boles.

We identified 50 gap maker trees in the 40 canopy gaps studied. Most gap makers ($n = 36$, 72%) could be identified to the species level; however, 4 (8%) could only be identified to genus and 10 (20%) were too decayed to be taxonomically classified. Of the 36 gap makers that could be identified to species, 12 different species were represented. The most common species that caused canopy gap formation was *Quercus montana* ($n = 8$). At the genus level, 50% of all gap makers were *Quercus*.

Diameter was measured at ca. 1.4 m above the surface or root collar for 46 gap makers. Diameter measurements could not be collected for four gap makers that were in a state of advanced decay. Average gap maker diameter at breast height was $38.38 \text{ cm} \pm 11.6$ (SD). The minimum diameter of a gapmaker was 19.5 cm and the maximum was 70 cm. The gap maker with a diameter of 19.5 cm was involved in a multi-tree uprooting event that also included the death of an individual with a diameter of 28 cm. Average basal area lost per gap was $0.16 \text{ m}^2 \pm 0.10$ (SD). The minimum removed was 0.05 m^2 and the maximum was 0.52 m^2 . Multi-tree gaps (mean = $0.24 \text{ m}^2 \pm 0.13$ (SD)) resulted in a larger amount ($P < 0.01$) of basal area lost compared to single-tree events (mean = $0.14 \text{ m}^2 \pm 0.08$ (SD)).

Age was determined for all canopy gaps by the identification of radial growth releases, crossdating the gap makers to document death dates, field observation, and gap maker decay classification. Gap ages ranged from 1 to 17 years with a mean of 7 years. Multiple gaps occurred in 13 years. The highest frequency of gap events during any one year was five, which occurred during 3 years (1999, 2002, and 2003).

Gap seasonality was determined for 17 gaps by examining the amount of xylem produced during the

last year of growth. Other gapmakers were too decayed for this analysis. Of these 17 events, only one occurred during the dormant season. For the dormant season gap, the latewood portion of the last ring was complete and buds were still present on the tree. All other gap makers had partial rings, indicating that the gap events occurred during the growing season. Because the majority of these individuals had already completed the production of earlywood prior to death, we surmise that these events occurred in the middle or later part of the growing season.

Gap fraction and physical characteristics

Total transect length was 4.47 km, with 15% of the total length in expanded gaps and true gaps, and 6% in true canopy gaps only. When percentage values were standardized at the hectare level, 1,500 m²/ha were in expanded gaps and 600 m²/ha were in true gap environments. Total transect length in true canopy gaps was plotted by gap age to analyze patterns of gap formation and closure (Fig. 2). The largest amount of land area in true canopy gaps occurred in gaps that were 2 years of age and no gap area occurred in gaps aged 5, 6, 14, 15, or 16 years. A significant negative relationship existed, where older gaps occupied a smaller amount of land area relative to younger gaps.

Average expanded gap area was 213.34 m² ± 108.44 (SD). The maximum expanded gap area was 587.91 m² and the minimum was 47.10 m². Average true gap area when sampled was 42.78 m² ± 40.16 (SD), with a maximum of 157.84 m² and a minimum of 1.14 m². The size of expanded gaps created by uprooted stems was significantly larger than that of gaps created by snags (Fig. 3). No other size differences between gap origins were significant.

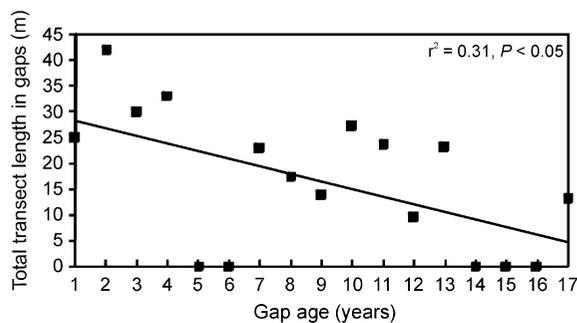


Fig. 2 Relationship between land fraction in true canopy gaps and gap age in the Pogue Creek Natural Area in Tennessee

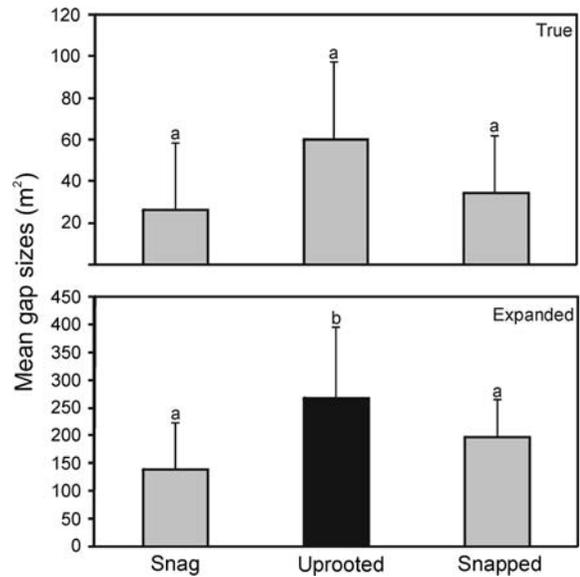


Fig. 3 Mean sizes of expanded and true canopy gaps by gap origin with standard deviations. Solid bar and different letter indicate a significant ($P < 0.05$) difference between gap origins as detected by ANOVA and Tukey’s post-hoc testing

The average L:W ratio of expanded gaps was 1.58:1, with a maximum of 3.60:1 and a minimum of 1.01:1. Thus, the average expanded gap was 58% longer than it was wide. Similar patterns were observed for true gap areas, for which the mean ratio was 2.58:1. The maximum length of true gaps was 475% the width. The minimum L:W patterns of expanded and true gaps revealed circular over ellipsoidal shapes.

Density and diversity within gaps

The mean number of canopy trees that bordered gaps was 6.38 ± 1.79 (SD). The maximum number of perimeter trees was 12, and minimum number of trees required to complete the canopy around a gap was 4. In general, larger canopy gaps were bordered by a higher number of canopy trees relative to smaller gaps.

The average number of saplings in expanded gaps was 54.48 ± 28.47 (SD) with a maximum of 144 and a minimum of 13 (Fig. 4). The mean number of trees in expanded gaps was 22.73 ± 7.99 (SD) with a maximum of 44 and minimum of 11 individuals. The average number of all stems ≥1 m height in expanded gaps was 74.20 ± 34.14 (SD). The highest number of stems in an expanded gap was 188 and the

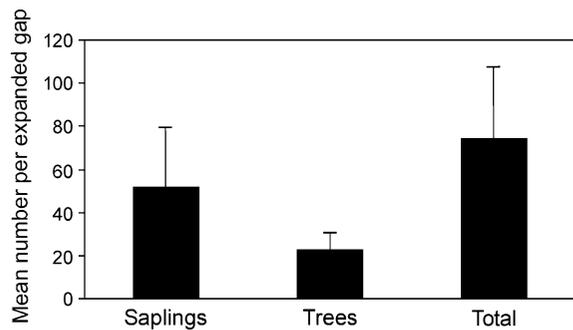


Fig. 4 Mean number of saplings (≥ 1 m height, < 5 cm dbh), trees (≥ 5 cm dbh), and total stems (all stems ≥ 1 m height) with standard deviations in expanded canopy gaps in the Pogue Creek Natural Area in Tennessee

lowest number of individuals was 28. The highest values for saplings and trees occurred in the same gap that was 10 years old and caused by the uprooting of four trees.

The sum of all saplings in all expanded gaps was calculated by species and standardized at the hectare level to document sapling establishment, and possible species recruitment in gap environments. The most abundant species in the sapling layer of expanded gaps was *Acer saccharum* followed by *Fagus grandifolia* and *Acer rubrum* (Table 1). Together these three species comprised almost 69% of all saplings in expanded gaps.

Acer saccharum represented 29.18% of all trees in true canopy gaps followed by *A. rubrum* and *Liriodendron tulipifera* (Table 2). Collectively, these three species represent over half of all trees in true canopy gaps. Dominance (based on basal area) was also calculated for all canopy gap trees. The most dominant species were *A. saccharum* and *A. rubrum* (Table 2). The *Acer* species were followed by a second tier of species that included *L. tulipifera* and *Carya ovata*. No other species represented more than 6% of the basal area. Species and diameter of all snags in true canopy gaps were also recorded. A total of 40 snags were documented and mean snag diameter at breast height was $10.89 \text{ cm} \pm 6.21$ (SD). Of the 40 snags within true gaps, 12 different species were represented with *A. rubrum*, *A. saccharum* and *Q. montana* being the most common ($n = 8$ for all species).

Expanded canopy gaps contained 34 different species in the sapling layer. Mean sapling diversity (H') was 1.43 ± 0.42 (SD) (Fig. 5). Maximum

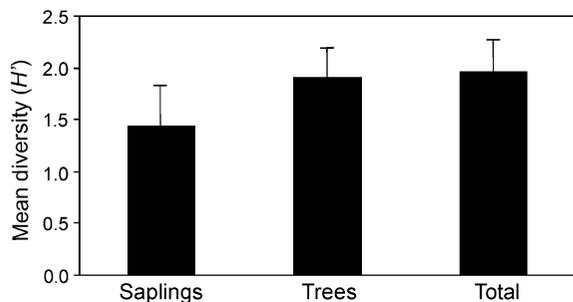
Table 1 Density of saplings (≥ 1 m height, < 5 cm dbh) in expanded canopy gaps in the Pogue Creek Natural Area in Tennessee

Species	Density/ha	Relative density
<i>Acer saccharum</i> Marsh.	863.63	35.70
<i>Fagus grandifolia</i> Ehrh.	474.70	19.62
<i>Acer rubrum</i> L.	327.83	13.55
<i>Asimina triloba</i> (L.) Dunal	168.03	6.95
<i>Magnolia acuminata</i> (L.) L.	158.63	6.56
<i>Fraxinus americana</i> L.	88.13	3.64
<i>Liriodendron tulipifera</i> L.	49.35	2.04
<i>Oxydendrum arboreum</i> (L.) DC.	48.18	1.99
<i>Cornus florida</i> L.	37.60	1.55
<i>Ulmus rubra</i> Muhl.	31.73	1.31
<i>Nyssa sylvatica</i> Marsh.	30.55	1.26
<i>Cercis canadensis</i> L.	29.38	1.21
<i>Tilia heterophylla</i> Vent.	12.93	0.53
<i>Aesculus flava</i> Ait.	11.75	0.49
<i>Carpinus caroliniana</i> Walt.	8.23	0.34
<i>Ilex opaca</i> Ait.	8.23	0.34
<i>Magnolia tripetala</i> L.	8.23	0.34
<i>Quercus montana</i> Willd.	8.23	0.34
<i>Carya ovata</i> (P. Mill.) K. Koch	5.88	0.24
<i>Ostrya virginiana</i> (P. Mill.) K. Koch	5.88	0.24
<i>Sassafras albidum</i> (Nutt.) Nees	5.88	0.24
<i>Ailanthus altissima</i> (Mill.) Swingle	4.70	0.19
<i>Betula lenta</i> L.	4.70	0.19
<i>Diospyros virginiana</i> L.	4.70	0.19
<i>Quercus alba</i> L.	4.70	0.19
<i>Ulmus alata</i> Michx.	3.53	0.15
<i>Amelanchier laevis</i> Weig.	2.35	0.10
<i>Carya tomentosa</i> (Poiret) Nutt.	2.35	0.10
<i>Quercus rubra</i> L.	2.35	0.10
<i>Ulmus americana</i> L.	2.35	0.10
<i>Hamamelis virginiana</i> L.	1.18	0.05
<i>Magnolia macrophylla</i> Michx.	1.18	0.05
<i>Morus rubra</i> L.	1.18	0.05
<i>Quercus velutina</i> Lam.	1.18	0.05
Total	2419.33	100.00

sapling layer diversity was 2.22 and the minimum was 0.78. Total species richness of the tree layer was 28. Average diversity of all trees in expanded gaps was 1.90 ± 0.35 (SD) with maximum and minimum values of 2.44 and 1.20, respectively. Mean total diversity of all stems ≥ 1 m height was 1.95 ± 0.36

Table 2 Density and dominance measures for all trees (stems ≥ 5 cm dbh) in true canopy gaps in the Pogue Creek Natural Area in Tennessee

Species	Density/ha	Relative density	Dominance (m ² /ha)	Relative dominance
<i>Acer saccharum</i>	807.30	29.18	0.59	24.34
<i>Acer rubrum</i>	391.95	14.16	0.32	13.15
<i>Liriodendron tulipifera</i>	251.55	9.09	0.23	9.37
<i>Carya ovata</i>	146.25	5.29	0.21	8.68
<i>Oxydendrum arboreum</i>	146.25	5.29	0.14	5.91
<i>Fagus grandifolia</i>	175.50	6.34	0.13	5.48
<i>Tilia heterophylla</i>	122.85	4.44	0.10	4.15
<i>Carya tomentosa</i>	81.90	2.96	0.09	3.58
<i>Carya glabra</i> (P. Mill.) Sweet	64.35	2.33	0.08	3.38
<i>Nyssa sylvatica</i>	99.45	3.59	0.08	3.25
<i>Fraxinus americana</i>	70.20	2.54	0.07	2.95
<i>Quercus alba</i>	5.85	0.21	0.07	2.85
<i>Cornus florida</i>	111.15	4.02	0.06	2.59
<i>Quercus montana</i>	40.95	1.48	0.05	1.94
<i>Magnolia acuminata</i>	52.65	1.90	0.03	1.44
<i>Quercus rubra</i>	23.40	0.85	0.03	1.40
<i>Ulmus rubra</i>	40.95	1.48	0.03	1.16
<i>Cercis canadensis</i>	35.10	1.27	0.02	0.89
<i>Carya cordiformis</i> (Wangenh.) K. Koch	17.55	0.63	0.02	0.67
<i>Ostrya virginiana</i>	23.40	0.85	0.02	0.66
<i>Diospyros virginiana</i>	11.70	0.42	0.01	0.51
<i>Sassafras albidum</i>	11.70	0.42	0.01	0.49
<i>Prunus serotina</i> Ehrh.	5.85	0.21	0.01	0.31
<i>Aesculus flava</i>	5.85	0.21	0.01	0.25
<i>Ulmus alata</i>	5.85	0.21	0.00	0.21
<i>Betula lenta</i>	5.85	0.21	0.00	0.17
<i>Magnolia tripetala</i>	5.85	0.21	0.00	0.13
<i>Ulmus americana</i>	5.85	0.21	0.00	0.10
Total	2767.05	100.00	2.41	100.00

**Fig. 5** Mean diversity for saplings (≥ 1 m height, < 5 cm dbh), trees (≥ 5 cm dbh), and total stems (all stems ≥ 1 m height) with standard deviations in expanded canopy gaps in the Pogue Creek Natural Area in Tennessee

(SD). The highest total diversity value was 2.46 and the lowest was 1.17. Interestingly, diversity patterns differed by category (i.e., sapling, tree, and total). For example, the gap with the lowest sapling diversity was not the same gap with the lowest tree diversity. However, the gap with the highest sapling and highest total woody stem diversity values was an exception.

Significant positive relationships were found for the number of saplings ($r = 0.54$, $P = 0.0003$), trees ($r = 0.73$, $P < 0.0001$), and total stems ($r = 0.62$, $P < 0.0001$) (Fig. 6). However, the largest gap did not contain the highest number of stems, which

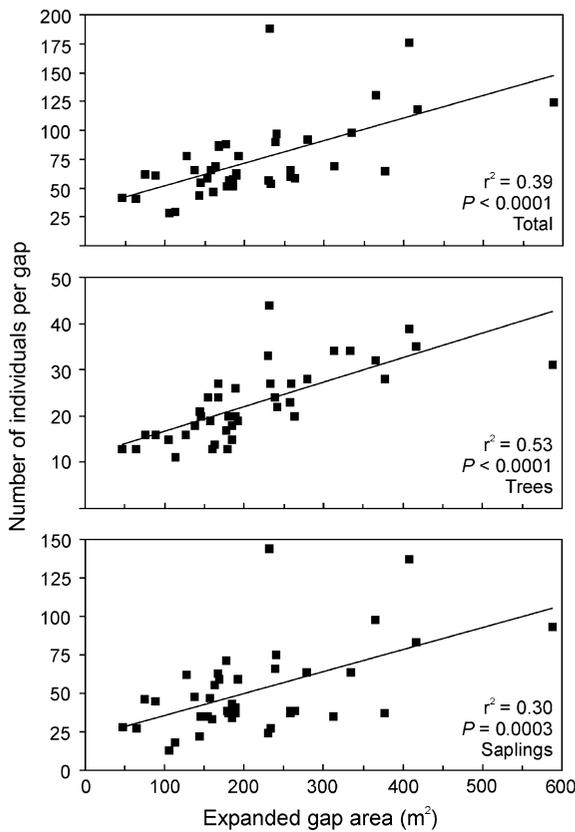


Fig. 6 Relationships between the number of saplings (≥ 1 m height, < 5 cm dbh), trees (≥ 5 cm dbh), and total stems (all stems ≥ 1 m height) and expanded gap area in the Pogue Creek Natural Area in Tennessee

occurred in a gap of an intermediate size class (188 individuals/231.97 m²). A weak negative relationship existed between sapling diversity and gap size ($r = -0.33$, $P = 0.04$) (Fig. 7). A similar pattern was also observed for total stem diversity ($r = -0.39$, $P = 0.01$). Tree diversity showed no relationship to expanded gap size. Shannon diversity (H') is a dimensionless index such that gap size would not bias the diversity measure.

Gap closure and recruitment

Of the 40 gaps studied, 10 were projected to close by height growth of understory individuals and the remaining 30 gaps were projected to close by lateral branch growth of canopy trees surrounding the voids. Mean expanded area of gaps likely to close via the height growth of understory trees was $285.13 \text{ m}^2 \pm 137.58$ (SD), which was ca. 34% greater than the mean

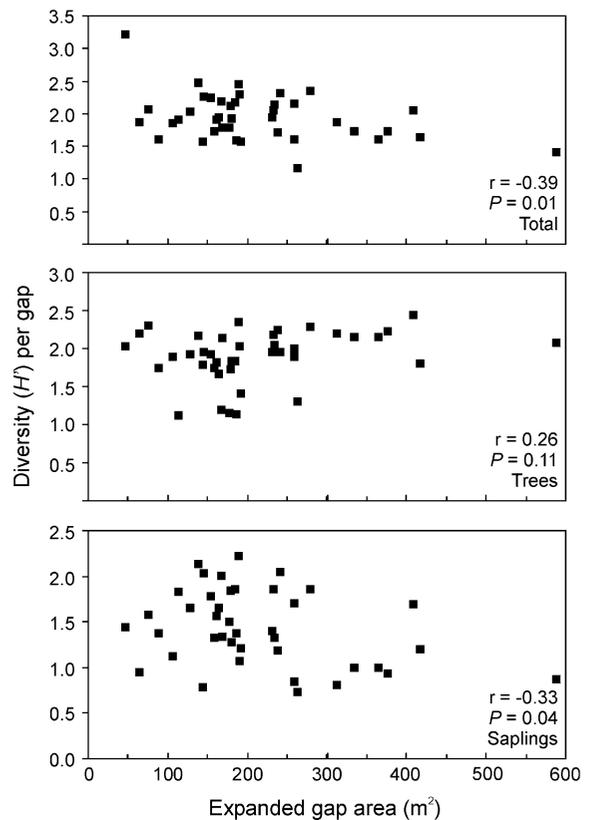


Fig. 7 Relationships between diversity values for saplings (≥ 1 m height, < 5 cm dbh), trees (≥ 5 cm dbh), and total stems (all stems ≥ 1 m height) and expanded gap area in the Pogue Creek Natural Area in Tennessee

expanded area for all 40 gaps (213.34 m²). The gap with the largest expanded area (587.91 m²) was projected to close by understory height growth. However, a relatively small gap (153.59 m²) was also projected to close by height growth of a subcanopy individual.

Of the 10 successor trees documented, five species were represented (*A. saccharum*, *A. rubrum*, *C. ovata*, *Q. montana*, and *Quercus alba*). *Acer rubrum* was the most common gap successor ($n = 3$) followed by *A. saccharum* ($n = 2$), *C. ovata* ($n = 2$), *Q. montana* ($n = 2$), and *Q. alba* ($n = 1$). *Acer saccharum* represented 28.7% of trees with intermediate positions of all 15 selected species within true gap environments (Table 3). *Acer saccharum* was followed by *A. rubrum* (13.45%) and *L. tulipifera* (13.45%), a noted gap-phase species. Collectively, these three species represented 55.6% of the intermediate trees from the 15 selected species. A similar

Table 3 Crown class distributions for all trees (stems ≥ 5 cm dbh) in 40 true canopy gaps in the Pogue Creek Natural Area in Tennessee

Species	Overtopped		Intermediate	
	Density	Relative density	Density	Relative density
<i>Acer saccharum</i>	72	36.36	64	28.70
<i>Acer rubrum</i>	37	18.69	30	13.45
<i>Liriodendron tulipifera</i>	13	6.57	30	13.45
<i>Carya ovata</i>	4	2.02	21	9.42
<i>Tilia heterophylla</i>	11	5.56	10	4.48
<i>Oxydendrum arboreum</i>	16	8.08	9	4.04
<i>Fraxinus americana</i>	3	1.52	9	4.04
<i>Carya glabra</i>	1	0.51	9	4.04
<i>Fagus grandifolia</i>	21	10.61	8	3.59
<i>Carya tomentosa</i>	5	2.53	8	3.59
<i>Quercus alba</i>	1	0.51	8	3.59
<i>Quercus montana</i>	1	0.51	6	2.69
<i>Nyssa sylvatica</i>	12	6.06	5	2.24
<i>Quercus rubra</i>	0	0.00	4	1.79
<i>Carya cordiformis</i>	1	0.51	2	0.90
Total	198	100.00	223	100.00

pattern was observed for overtopped positions, with *A. saccharum* being the most abundant (36.36%) followed by *A. rubrum* (18.69%) and *F. grandifolia* (10.61%).

Discussion

Gap formation patterns and processes

The majority (80%) of the gaps documented originated from uprooted or snapped stems. Other studies have also found these mechanisms to be the most common means of gap formation in the southern Appalachians (Barden 1979; Barden 1981; Romme and Martin 1982; Runkle 1982). However, Clinton et al. (1993) found snag gaps to be more prevalent following drought in secondary forests of the Appalachian Highlands in North Carolina. Based on the means by which canopy trees were removed, we speculate that wind is the dominant disturbance agent in the forest as strong winds have the potential to uproot trees and snap boles. Wind also has the potential to alter forest composition and structure by

blowing down snag trees. Standing dead trees are often removed by mild to severe wind events, but the potential for snags to be blown down varies by site conditions (Jans et al. 1993). Further, snags that eventually fall likely alter the forest differently than gaps that are caused rapidly (Franklin et al. 1987; Krasny and Whitmore 1992; Clinton et al. 1994). The eventual fall of a snag may cause additional forest disturbance, possibly with a greater magnitude than the initial event. Also, the bole and branches of standing dead trees may block sunlight from reaching the understory, thereby, facilitating gap closure by perimeter trees rather than subcanopy individuals.

The percentage of single-tree gaps (78% of gaps sampled) was within the range of what has been reported from old growth forests of the eastern USA (Runkle 1990). Of the multi-tree disturbance events, most were caused by uprooted stems. Windthrow gaps have the potential to cause more site modification than gaps caused by other mechanisms, because as the root network is lifted, microtopography (pits and mounds) and soil characteristics are also modified (Clinton et al. 1994; Beckage et al. 2000).

Average diameter of gap maker trees was 38.38 cm at breast height and the average diameter of canopy trees (dominant and codominant crown classes) that surrounded gaps was 38.83 cm \pm 6.04 (SD). This result is contrary to what has been reported for old growth forests of the southern Appalachians, where gap makers were significantly larger than border trees (Runkle 1998). This pattern may be related to the age of the forest. In second growth forests, canopy trees are within a narrower diameter range as their age (and diameter) structure is not complex. Thus, in mature second growth forests, size does not indicate that one individual is more likely to be removed from the canopy than another. Also, the smallest gap maker was just 19.5 cm dbh, but was a component of a multi-tree gap with another individual of 28 cm. Although both of these individuals were below the average size for gap makers, the removal was enough to open the canopy and modify the forest.

Of the 17 disturbance events with known seasonality, one occurred during the growing season. Most growing season deaths occurred after the formation of earlywood cells but before the completion of latewood cells. We interpret the amount of xylem produced during the last year of growth to indicate

that the majority of the canopy disturbance events occurred during the middle or later part of the growing season. The timing of death combined with the primary origins of formation (uprooted and snapped stems) indicated that strong winds associated with frontal and convection storms may be the major agents that disrupt the forest. Severe wind events in the region are associated with thunderstorms that occur ca. 55 days per year, usually during late-spring and summer (Smalley 1982). Documenting the season of gap formation is important because the time of year a gap forms may influence the ability of residual trees to exploit the additional resources (Runkle 1989). Gaps that form during the growing season may expose shade-developed leaves to changes in environmental conditions. When light levels increase, expanding leaves and leaves produced in the new environment may acclimate to high-light conditions. Fully shade-developed leaves are not able to change their anatomy to acclimate to modifications in the light regime. Thus, fully shade-developed leaves may undergo a period of photoinhibition after gap events (Kozlowski 1957; Naidu and DeLucia 1997). Plastic species that periodically flush throughout the growing season may be best suited to take advantage of the increased resources of the gap environment (Kozlowski and Pallardy 1997). Gap seasonality may be especially important in secondary forests, where gaps are generally small and relatively short-lived.

Gap fraction and physical characteristics

The fraction of land area in expanded gaps and true gaps is within the range of what has been reported elsewhere in the Eastern Deciduous Forest Region (Runkle 1982; Beckage et al. 2000). Based on gap fraction and mean gap size, we conclude that the secondary forest supported a higher number of gaps compared to older stands throughout the region. Thus, we propose that during the understory reinitiation stage of development, forests support a higher density of smaller gaps, but similar total land area in gap environments compared to stands in a complex developmental stage. The fraction of land area in gaps was highest for younger gaps and generally decreased with increased gap age. This pattern was expected because older gaps have had a longer time to be filled. No gaps were documented over 17 years

of age. From this, we propose that most gaps in the forest are filled within 20 years of formation, but many are likely filled within shorter periods. Hart and Grissino-Mayer (2008) statistically analyzed radial growth releases attributed to canopy disturbances in *Quercus* individuals from the PCNA and found mean release durations of only 4 years. Thus, we speculate that most gaps are short-lived in these secondary hardwood stands, and that the increase in available resources is generally not sustained for more than 4 years.

In general, L:W patterns were similar for expanded and true gaps as both had ellipsoidal shapes. The shape of the disturbed canopy area is largely a function of the mechanism of tree death and architecture of the gap maker. Circular gap shapes resulted from canopy disturbances related to snags rather than uprooted or snapped stems. Trees that remained standing after their death did not fall, and remove vegetation in a linear pattern starting at the base of the tree as is normal for treefall disturbances. The majority (55%) of the gaps were oriented downslope from the base of the tree, while 40% were oriented across slope and 5% of the trees fell up slope. Thus, most canopy disturbances resulted in ellipsoidal shaped gaps that were oriented perpendicular to slope contours. The shape, size, slope, orientation, height of surrounding forest, residual plants, and post-treefall debris of canopy gaps, as well as latitudinal position, are important in determining the microenvironmental conditions of the disturbed area (Poulson and Platt 1989; Runkle 1989). These physical gap characteristics may be useful if forest management plans have a goal of mimicking natural disturbance processes.

Density and diversity within gaps

Significant positive relationships were documented between expanded gap size and the number of saplings, trees, and total stems. Although, this result may seem expected, a significant positive relationship between gap size and stem number does not always occur (Runkle 1982). Larger gaps may be the result of high intensity events with few residual trees, may be characterized by abiotic conditions (e.g., full sunlight and high temperatures) not conducive to the growth of forest interior species, and may support increased herbivory. Interestingly, in our study, the

largest gap did not support the highest number of stems, which occurred in an intermediate size gap. The density measures analyzed were for expanded gap areas. Individuals in the entire area of an expanded gap do not benefit from increased resources such as light. Because the true gap area gets smaller with time since the disturbance, gap age may play an important role in the number of individuals that inhabit a gap site (Runkle 1982; Clinton et al. 1994). Also, the number of individuals within the gap should decrease through self-thinning processes as they compete to reach the canopy.

We hypothesized that larger gaps would support higher diversity values. By containing more surface area, larger gaps have the potential to contain more site heterogeneity and microsites that may favor certain species over others. However, only weak relationships existed between diversity and gap size and two of the relationships (saplings and total stems) were negative. Perhaps, gap size is not as important to diversity as the physical site characteristics of the gap or the biotic assemblage of the gap prior to formation. It is also possible that the gaps sampled in this study (and those in other secondary forests of similar age) were not large enough for the pattern to manifest. Although canopy gaps should increase biological diversity, this pattern does not necessarily occur at the gap-level, but at the stand-level, where a collection of different sized and aged canopy gaps across a variety of sites may support species that are otherwise absent or sparse under the closed forest canopy.

Gap closure, recruitment, and succession

No clear species-specific patterns were observed with gap successors, indicating that the location of an individual within the gap and its vertical crown position prior to the disturbance may be the most important factors that determine how the gap is closed, and by what species. As further evidence of this point, radial-growth response of understory individuals has been shown to be related to position within a canopy gap (Tryon et al. 1992).

Species composition of gaps is a good predictor of future forest composition (Runkle and Yetter 1987). Three species (*A. saccharum*, *F. grandifolia*, and *A. rubrum*) represented 69% of all saplings in expanded gaps. Because saplings represent the pool

of individuals that may be recruited to larger size classes following disturbance events, we hypothesize that *Acer* species and *F. grandifolia* will become more abundant in intermediate, and eventually, canopy positions under the current disturbance regime. There is a greater likelihood that individuals of these species will be able to exploit current and future gap events, because they are so abundant in the sapling layer.

We projected that the majority of the canopy gaps would close by lateral crown expansion rather than height growth of understory individuals. However, even gaps that close by lateral branch growth still provide a means for understory trees to recruit to larger size classes. This process may allow over-topped trees to reach intermediate positions, and eventually, the canopy following future disturbance events. Trees already in intermediate positions may expand their crowns to become dominant or codominant in the canopy. Over half of all trees located in true gaps with intermediate crown classifications were *A. saccharum*, *A. rubrum*, or *L. tulipifera*.

Acer species and *L. tulipifera* have the greatest potential to recruit in gaps based on density, dominance, and crown class measures. It is interesting that species with such different life history characteristics were well represented in canopy gaps, and employ different strategies to reach canopy level. *Acer saccharum* is very shade-tolerant and has the ability to persist in the understory of a closed canopy while maintaining the ability to rapidly respond to increased light (Canham 1988; Tryon et al. 1992). *Acer rubrum* is classed as moderately shade-tolerant and can exist in the understory of a relatively closed canopy until the formation of gaps when the species has also been shown to quickly respond to increased resources (Wallace and Dunn 1980). In general, the life history characteristics of the *Acer* species may be classed as conservative. Both *A. saccharum* and *A. rubrum* can establish in at least relatively shaded conditions and wait for the formation of small canopy gaps to recruit to larger size classes and higher canopy positions. In contrast to the *Acer* species, *L. tulipifera* is disturbance obligate. The species is shade-intolerant and cannot exist under a closed forest canopy. However, *L. tulipifera* is capable of quickly responding to increased resources when they become available and is a common component in forests with disturbance regimes that consist of small

localized events (Buckner and McCracken 1978; Wallace and Dunn 1980; Orwig and Abrams 1994; Busing 1995; Lafon 2004).

Shade-intolerant species, such as *L. tulipifera*, must reach the canopy in one gap event, because once the gap closes, they will not be able to survive under the canopy (Hibbs 1982; Runkle and Yetter 1987; Cole and Lorimer 2005; Webster and Lorimer 2005). Thus, in forests with a disturbance regime characterized by small localized events, there are few opportunities for shade-intolerant species to exist (Runkle 1998). Shade-tolerant species are more likely to be present in a gap when they form; thus, they are generally more likely to recruit or reach the canopy in small gaps (Henry and Swan 1974; Dahir and Lorimer 1996; McClure et al. 2000; Taylor and Lorimer 2003). Gaps of a larger size, however, may allow time for germinants to establish and recruit. Because of its rapid growth, *L. tulipifera* can reach the canopy in gaps of ca. 400 m² and larger (Busing 1994; Busing 1995). Although gaps of that size were documented in this study, we do not think *L. tulipifera* will reach the canopy at any of the gap sites before closure. The majority of the gaps documented will close by lateral branch growth before understory individuals can reach the canopy. Although individuals are recruited to larger size classes and higher vertical positions in these gaps, it will take multiple disturbance events for most subcanopy individuals to reach the main canopy level. Because it will generally take multiple events for individuals to be recruited to the canopy, shade-tolerant *A. saccharum* and moderately-tolerant *A. rubrum* are the species most likely to attain canopy dominance under the current disturbance regime. Interestingly, half of the canopy gaps were caused by the removal of a *Quercus* individual, but *Acer* species represented a large proportion of trees likely to either reach the canopy or recruit to larger size classes. These data indicate a likely shift in composition if gap processes continue to remove *Quercus* from the canopy and provide the means for *Acer* recruitment.

Conclusions

Canopy gaps obviously have an important influence on forest composition and structure. However, little

information is available on natural gap-scale disturbances in secondary hardwood forests. By analyzing gap formation mechanisms, physical gap characteristics, and forest response to canopy gaps, we can gain a better understanding of the role of gap-scale disturbance processes in the development of hardwood forests. This study showed that disturbances that involved the death of a single tree or a small cluster of trees were common events throughout secondary stands on the Cumberland Plateau in Tennessee. The fraction of the forest in canopy gaps was within the range reported from old growth remnants throughout the region. However, gap size was smaller in the developing stands indicating that secondary forests contain a higher density of smaller gaps. These localized disturbances modified biomass arrangement and tree-age distribution patterns as they allowed for crown expansion of canopy trees, recruitment of understory individuals, and in some instances, establishment of new germinants. Thus, canopy gaps provide the mechanism for forests to develop a complex size and age structure indicative of older stands. Gap-scale processes may also be used to help explain shifting species composition that has been widely reported throughout the Central Hardwood Forest Region of the eastern US. Half of the canopy gaps documented in this study were caused by the removal of a *Quercus* individual, but *A. saccharum*, *A. rubrum*, and *L. tulipifera* were the most likely species to capture canopy gaps. The gaps documented favored the very shade-tolerant *A. saccharum* because most gaps were small, and multiple overstory removal events would be required for trees to reach the main canopy level. In conclusion, this study demonstrated that natural disturbance processes have significant influences on forest development and successional patterns. Thus, small-scale disturbance events must be considered when developing long-term forest management plans.

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References

- Barden LS (1979) Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the southern Appalachians, Tennessee. *Oecologia* 44:141–142. doi:[10.1007/BF00346412](https://doi.org/10.1007/BF00346412)
- Barden LS (1980) Tree replacement in a cove hardwood forest of the southern Appalachians. *Oikos* 35:16–19. doi:[10.2307/3544722](https://doi.org/10.2307/3544722)
- Barden LS (1981) Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. *Oikos* 37:205–209. doi:[10.2307/3544466](https://doi.org/10.2307/3544466)
- Beckage B, Clark JS, Clinton BD et al (2000) A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. *Can J For Res* 30:1617–1631. doi:[10.1139/cjfr-30-10-1617](https://doi.org/10.1139/cjfr-30-10-1617)
- Braun EL (1950) Eastern deciduous forests of North America. Blakiston, Philadelphia
- Buckner E, McCracken W (1978) Yellow-poplar: a component of climax forests? *J For* 76:421–423
- Busing RT (1994) Canopy cover and tree regeneration in old-growth cove forests of the Appalachian Mountains. *Veg- etatio* 115:19–27
- Busing RT (1995) Disturbance and the population dynamics of *Liriodendron tulipifera*: simulations with a spatial model of forest succession. *J Ecol* 83:45–53. doi:[10.2307/2261149](https://doi.org/10.2307/2261149)
- Canham CD (1988) Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69:786–795. doi:[10.2307/1941027](https://doi.org/10.2307/1941027)
- Cho D, Boerner REJ (1991) Canopy disturbance patterns and regeneration of *Quercus* species in two old-growth forests. *Veg- etatio* 93:9–18
- Clebsch EEC, Busing RT (1989) Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. *Ecology* 70:728–735. doi:[10.2307/1940223](https://doi.org/10.2307/1940223)
- Clinton BD, Boring LR, Swank WT (1993) Canopy gap characteristics and drought influence in oak forests of the Coweeta Basin. *Ecology* 74:1551–1558. doi:[10.2307/1940082](https://doi.org/10.2307/1940082)
- Clinton BD, Boring LR, Swank WT (1994) Regeneration patterns in canopy gaps of mixed-oak forests of the southern Appalachians: influence of topographic position and evergreen understory. *Am Midl Nat* 132:308–319. doi:[10.2307/2426587](https://doi.org/10.2307/2426587)
- Cole WG, Lorimer CG (2005) Probabilities of small-gap capture by sugar maple saplings based on height and crown growth data from felled trees. *Can J For Res* 35:643–655. doi:[10.1139/x04-210](https://doi.org/10.1139/x04-210)
- Cowell CM (1998) Historical change in vegetation and disturbance on the Georgia Piedmont. *Am Midl Nat* 140:78–89. doi:[10.1674/0003-0031\(1998\)140\[0078:HCIVAD\]2.0.CO;2](https://doi.org/10.1674/0003-0031(1998)140[0078:HCIVAD]2.0.CO;2)
- Dahir SE, Lorimer CG (1996) Variation in canopy gap formation among developmental stages of northern hardwood stands. *Can J For Res* 26:1875–1892. doi:[10.1139/x26-212](https://doi.org/10.1139/x26-212)
- De Vries PG (1974) Multi-stage line intersect sampling. *For Sci* 20:129–133
- Fenneman NM (1938) *Physiography of Eastern United States*. McGraw-Hill Book Company, New York
- Ferreira de Lima RA (2005) Gap size measurement: the proposal of a new field method. *For Ecol Manag* 214:413–419. doi:[10.1016/j.foreco.2005.04.011](https://doi.org/10.1016/j.foreco.2005.04.011)
- Francis JK, Loftus JS (1977) Chemical and physical properties of the Cumberland Plateau and Highland Rim forest soils. USDA, Forest Service, Research Paper SO-138
- Franklin JF, Shugart HH, Harmon ME (1987) Tree death as an ecosystem process. *Bioscience* 37:550–556. doi:[10.2307/1310665](https://doi.org/10.2307/1310665)
- Fritts HC (2001) *Tree rings and climate*. Blackburn Press, Caldwell, New Jersey
- Goebel PC, Hix DM (1996) Development of mixed-oak forests in southeastern Ohio: a comparison of second and old-growth forests. *For Ecol Manag* 84:1–21. doi:[10.1016/0378-1127\(96\)03772-3](https://doi.org/10.1016/0378-1127(96)03772-3)
- Goebel PC, Hix DM (1997) Changes in the composition and structure of mixed-oak, second-growth forest ecosystems during the understory reinitiation stage of stand development. *Ecoscience* 4:327–339
- Grissino-Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree Ring Res* 57:205–221
- Hart JL (2007) A multi-scale analysis of disturbance dynamics in hardwood forest communities on the Cumberland Plateau, USA. Dissertation, University of Tennessee, Knoxville
- Hart JL, Grissino-Mayer HD (2008) Vegetation patterns and dendroecology of a mixed hardwood forest on the Cumberland Plateau: implications for stand development. *For Ecol Manag* 255:1960–1975
- Henry JD, Swan JMA (1974) Reconstructing forest history from live and dead plant material—an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55:772–783. doi:[10.2307/1934413](https://doi.org/10.2307/1934413)
- Hibbs DE (1982) Gap dynamics in a hemlock-hardwood forest. *Can J For Res* 12:522–527. doi:[10.1139/x82-081](https://doi.org/10.1139/x82-081)
- Hinkle CR (1978) The relationship of forest communities and selected species to edaphic and topographic factors on the Cumberland Plateau of Tennessee. Dissertation, University of Tennessee, Knoxville
- Hinkle CR (1989) Forest communities of the Cumberland Plateau of Tennessee. *J Tenn Acad Sci* 64:123–129
- Hinkle CR, McComb WC, Safely JM Jr, Schmalzer PA (1993) Mixed mesophytic forests. In: Martin WH, Boyce SG, Echemnach AC (eds) *Biodiversity of the Southeastern United States: upland terrestrial communities*. Wiley, New York, pp 203–253
- Holmes RL (1983) Computer assisted quality control in tree-ring dating and measurement. *Tree Ring Bull* 43:69–78
- Jans L, Porter L, van Rompaey RSAR et al (1993) Gaps and forest zones in tropical moist forest in Ivory Coast. *Biotropica* 25:258–269. doi:[10.2307/2388784](https://doi.org/10.2307/2388784)
- Kozłowski TT (1957) Effect of continuous high light intensity on photosynthesis of forest tree seedlings. *For Sci* 3:220–224
- Kozłowski TT, Pallardy SG (1997) *Physiology of woody plants*, 2nd edn. Academic Press, San Diego
- Krasny ME, Whitmore MC (1992) Gradual and sudden forest canopy gaps in Allegheny northern hardwood forests. *Can J For Res* 22:139–143. doi:[10.1139/x92-019](https://doi.org/10.1139/x92-019)
- Lafon CW (2004) Stand dynamics of a yellow-poplar (*Liriodendron tulipifera* L.) forest in the Appalachian

- Mountains, Virginia, USA. *Dendrochronologia* 22:43–52. doi:[10.1016/j.dendro.2004.09.002](https://doi.org/10.1016/j.dendro.2004.09.002)
- Lorimer CG (1980) Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 61:1169–1184. doi:[10.2307/1936836](https://doi.org/10.2307/1936836)
- McCarthy BC, Bailey DR (1994) Distribution and abundance of coarse woody debris in a managed forest landscape. *Can J For Res* 24:1317–1329
- McClure JW, Lee TD, Leak WB (2000) Gap capture in northern hardwoods: patterns of establishment and height growth in four species. *For Ecol Manag* 127:181–189. doi:[10.1016/S0378-1127\(99\)00129-2](https://doi.org/10.1016/S0378-1127(99)00129-2)
- Naidu SL, DeLucia EH (1997) Acclimation of shade-developed leaves on saplings exposed to late-season canopy gaps. *Tree Physiol* 17:367–376
- Oliver CD, Larson BC (1996) *Forest stand dynamics*, update edition. Wiley, New York
- Orvis KH, Grissino-Mayer HD (2002) Standardizing the reporting of abrasive papers used to surface tree-ring samples. *Tree Ring Res* 58:47–50
- Orwig DA, Abrams MD (1994) Contrasting radial growth and canopy recruitment patterns in *Liriodendron tulipifera* and *Nyssa sylvatica*: a gap-obligate versus gap-facultative tree species. *Can J For Res* 24:2141–2149. doi:[10.1139/x94-276](https://doi.org/10.1139/x94-276)
- Pickford SG, Hazard JW (1978) Simulation studies on line intersect sampling of forest residue. *For Sci* 24:469–483
- Poulson TL, Platt WJ (1989) Gap light regimes influence canopy tree diversity. *Ecology* 70:553–555. doi:[10.2307/1940202](https://doi.org/10.2307/1940202)
- Rebertus AJ, Meier AJ (2001) Blowdown dynamics in oak-hickory forests of the Missouri Ozarks. *J Torrey Bot Soc* 128:362–369. doi:[10.2307/3088668](https://doi.org/10.2307/3088668)
- Romme WH, Martin WH (1982) Natural disturbance by tree-falls in old-growth mixed mesophytic forest: Lilley Cornett Woods, Kentucky. In: Muller RN (ed) *In: Proceedings of the central hardwood forest conference*. University of Kentucky, Lexington, pp 367–383
- Runkle JR (1981) Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62:1041–1051. doi:[10.2307/1937003](https://doi.org/10.2307/1937003)
- Runkle JR (1982) Patterns of disturbance in some old-growth mesic forests of the eastern United States. *Ecology* 63:1533–1546. doi:[10.2307/1938878](https://doi.org/10.2307/1938878)
- Runkle JR (1985) Comparison of methods for determining fraction of land area in treefall gaps. *For Sci* 31:15–19
- Runkle JR (1989) Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. *Ecology* 70:546–547. doi:[10.2307/1940199](https://doi.org/10.2307/1940199)
- Runkle JR (1990) Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. *Can J For Res* 20:632–641. doi:[10.1139/x90-085](https://doi.org/10.1139/x90-085)
- Runkle JR (1992) Guidelines and sample protocol for sampling forest gaps. USDA, Forest Service, Pacific Northwest Research Station, GTR 283, Portland
- Runkle JR (1998) Changes in southern Appalachian canopy tree gaps sampled thrice. *Ecology* 79:1768–1780
- Runkle JR (2000) Canopy tree turnover in old-growth mesic forests of eastern North America. *Ecology* 81:554–576
- Runkle JR, Yetter TC (1987) Treefalls revisited: gap dynamics in the southern Appalachians. *Ecology* 68:417–424. doi:[10.2307/1939273](https://doi.org/10.2307/1939273)
- Smalley GW (1982) Classification and evaluation of forest sites on the mid-Cumberland Plateau. USDA, Forest Service, Southern Research Experiment Station, GTR SO-38, New Orleans, Louisiana
- Smalley GW (1986) Classification and evaluation of forest sites on the northern Cumberland Plateau. USDA, Forest Service, Southern Research Experiment Station, GTR SO-60, New Orleans, Louisiana
- Spies TA, Franklin JF, Klopsch M (1990) Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can J For Res* 20:649–658. doi:[10.1139/x90-087](https://doi.org/10.1139/x90-087)
- Stokes MA, Smiley TL (1996) *An introduction to tree-ring dating*. University of Arizona Press, Tucson
- Taylor SO, Lorimer CG (2003) Loss of oak dominance in dry-mesic deciduous forests predicted by gap capture methods. *Plant Ecol* 167:71–88. doi:[10.1023/A:1023975026261](https://doi.org/10.1023/A:1023975026261)
- Thornthwaite CW (1948) An approach toward rational classification of climate. *Geogr Rev* 38:55–94. doi:[10.2307/210739](https://doi.org/10.2307/210739)
- Tryon EH, Lanasa M, Townsend EC (1992) Radial growth response of understory sugar maple (*Acer saccharum*) surrounding openings. *For Ecol Manag* 55:249–257. doi:[10.1016/0378-1127\(92\)90104-H](https://doi.org/10.1016/0378-1127(92)90104-H)
- Tyrell LE, Crow TR (1994) Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology* 75:370–386. doi:[10.2307/1939541](https://doi.org/10.2307/1939541)
- USDA (1995) Soil survey of Fentress and Pickett Counties. USDA, Soil Conservation Service, Tennessee
- Veblen TT (1985) Forest development in tree-fall gaps in the temperate rain forest of Chile. *Natl Geogr Res* 1:162–183
- Wallace LL, Dunn EL (1980) Comparative photosynthesis of three gap phase successional tree species. *Oecologia* 45:331–340. doi:[10.1007/BF00540201](https://doi.org/10.1007/BF00540201)
- Webster CR, Lorimer CG (2005) Minimum opening sizes for canopy recruitment of midtolerant tree species: a retrospective approach. *Ecol Appl* 15:1245–1262. doi:[10.1890/04-0763](https://doi.org/10.1890/04-0763)
- White PS, MacKenzie MD, Busing RT (1985) Natural disturbance and gap-phase dynamics in southern Appalachian spruce-fir forests. *Can J For Res* 15:233–240. doi:[10.1139/x85-041](https://doi.org/10.1139/x85-041)
- Wilder CM, Holtzclaw FW Jr, Clebsch EEC (1999) Succession, sapling density and growth in canopy gaps along a topographic gradient in a second growth east Tennessee forest. *Am Midl Nat* 142:201–212. doi:[10.1674/0003-0031\(1999\)142\[0201:SSDAGI\]2.0.CO;2](https://doi.org/10.1674/0003-0031(1999)142[0201:SSDAGI]2.0.CO;2)
- Yamamoto S, Nishimura N (1999) Canopy gap formation and replacement pattern of major tree species among development stages of beech (*Fagus crenata*) stands, Japan. *Plant Ecol* 140:167–176. doi:[10.1023/A:1009713002039](https://doi.org/10.1023/A:1009713002039)
- Yetter TC, Runkle JR (1986) Height growth rates of canopy gap tree species in southern Appalachian gaps. *Castanea* 51:157–167