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**Sapling richness and composition in canopy gaps of a southern
Appalachian mixed *Quercus* forest¹**

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HART, J. L. (Department of Geography, University of Alabama, Tuscaloosa, AL 35487), AND J. A. KUPFER (Department of Geography, University of South Carolina, Columbia, SC 29208). Sapling richness and composition in canopy gaps of a southern Appalachian mixed *Quercus* forest. *J. Torrey Bot. Soc.* 138: 207–219. 2011.—Canopy gaps create distinct microenvironments within the broader forest environment and provide a mechanism for regeneration and recruitment. In this study, we investigated patterns of sapling richness and composition in 40 canopy gaps in a secondary, mixed *Quercus* forest on the Cumberland Plateau in Tennessee. We found that sapling richness was high, with 34 species represented in canopy gaps. A species-gap area curve revealed that sapling richness increased steadily with gap sizes up to ca. 200 m², but then tended to level off. While minor components in the main forest canopy, *Acer saccharum*, *Fagus grandifolia*, and *Acer rubrum* were the most widespread and abundant species in gaps. Our analyses of floristic composition using ordination (NMS) and randomization techniques (MRPP) clarified the mechanisms responsible for structuring patterns of gap composition and species-environment relationships, including the effects of individual factors (gap formation mechanism, gap size, aspect, and soils) and their collective impacts. Snag-formed gaps were smaller in size and most common on southern exposures with stony loam soils. Gaps formed by uprooted trees were larger and most common on north-facing slopes with shallow, gravelly loam soils. Gap composition varied along these gradients. Saplings of current canopy dominant genera (*Quercus* and *Carya*) were largely restricted to small gaps on xeric sites, suggesting that gap-phase succession will result in a transition from a *Quercus*–*Carya* system to one with a much stronger *Acer*–*Fagus* component.

Key words: Appalachian forests, canopy gaps, Cumberland Plateau, disturbance, species composition, succession, Tennessee.

The dominant disturbance mechanisms in many forests in the Central Hardwood Region of the eastern US are highly localized events caused by the removal of one or a small cluster of canopy trees (Runkle 1985). Canopy gaps create distinct microenvironments within the broader forest matrix that are characterized by temporary increases in light and growing space and potential increases in the availability of water and nutrients. By providing regeneration and recruitment niches for species that would otherwise be absent from a closed canopy forest (Runkle 1982, Webster and Lorimer 2005), gap-scale disturbance processes

influence species richness and density of trees, promote uneven aged structures, modify the arrangement of biomass, and increase total forest heterogeneity by altering fine-scale biophysical conditions (Connell 1989, Frelich 2002).

Forest community responses to gap-scale disturbances are influenced by a range of gap characteristics such as size (Runkle and Yetter 1987), age (Brokaw 1985), formation frequency (Canham 1989), formation mechanism (Putz 1983, Clinton et al. 1993), distance from edge (Kupfer et al. 1997), topographic position (Clinton et al. 1994, Abe et al. 1995) and orientation (Poulson and Platt 1988) among others. In mesic, closed canopy forests light is commonly the most limiting resource (Oliver and Larson 1996) and gap characteristics are often important because of their direct influence on understory light regimes (Canham et al. 1990). While small canopy disturbances influence all forest strata, the biophysical changes caused by local canopy removal are often most evident in the regeneration layer (Brokaw and Busing 2000, Yamamoto 2000). Responses in this stratum are important

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because saplings represent the pool of species likely to recruit to larger size classes, so sapling composition in gaps is often an important determinant of future canopy composition in stands with disturbance regimes dominated by gap-scale processes (Wilder et al. 1999, Taylor and Lorimer 2003).

Understanding how sapling composition is influenced by canopy gap characteristics and environmental variables is important for successional projections. This information may be used by forest managers to mimic natural disturbance regimes, favor recruitment of certain species, or restore late-successional forest composition and structure through silvicultural operations (Seymour et al. 2002, Schumann et al. 2003, Keeton 2006). While some species are better adapted for gap regeneration than others, gap formation on a given site is stochastic and sapling composition in gaps may therefore be the product of chance and unexplained by biophysical characteristics of the gap environment (Brokaw and Busing 2000). The primary goal of this study was to document the variables that influence sapling richness and composition in canopy gaps of a mature hardwood forest on the Cumberland Plateau in north-central Tennessee. Surprisingly, few studies have analyzed the specific and collective factors that structure sapling composition in canopy gaps of secondary, mixed *Quercus* forests in this region. Our specific objectives were to: 1) document sapling richness and composition patterns within canopy gaps, 2) quantify what gap characteristic(s) or other biophysical variable(s) most strongly influence sapling composition in gap environments, and 3) discuss the implications of our findings toward the development of a mechanistic understanding of forest succession in the region.

Methods. **STUDY SITE.** Our study was conducted on the 1,505 ha Pogue Creek Natural Area (PCNA) located in Fentress County, TN (Fig. 1). Managed by the State of Tennessee's Department of Environment and Conservation, PCNA is a component of a contiguous network of state, federal, and private reserves in the region. The reserve is located on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman 1938). The underlying geology is primarily composed of Pennsylvanian sandstone, conglomerate, siltstone, shale, and

coal of the Crab Orchard and Crooked Forked Groups (Swingle et al. 1966). The region has irregular topography and is characterized by long ridges and valleys of varied widths with ridges capped by resistant sandstones and deeply incised stream networks (Fenneman 1938, Smalley 1986). A total of eight soil types exist in the PCNA. The canopy gaps sampled occurred across the three most prevalent types at middle slope positions: the Grimsley-Jefferson outrock complex, the Bouldin stony loam, and the Zenith gravelly loam (USDA 1995). While all three soil types are acidic they differ significantly in available water capacity and depth. Slope gradients ranged from 15–60% and the elevation of the studied gaps ranged from 260–490 m amsl.

Regionally, climate is classified as humid mesothermal with moderately hot summers and short, mild to moderately cold winters (Thornthwaite 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). 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. The region has no distinct dry season.

PCNA occurs within the Cliff Section of the Mixed Mesophytic Forest Region as described by Braun (1950). Local topography and other factors related to soil water availability have a strong influence on forest composition (Hinkle 1989, Clatterbuck et al. 2006) and only the most sheltered sites are dominated by true mesophytic species. Regionally, forests are intermediate between mixed mesophytic and *Quercus-Carya* types (Hinkle et al. 1993). Hart and Grissino-Mayer (2008) documented species composition, stand structure, and disturbance history using dendroecological techniques for forest stands at PCNA. The canopy was dominated by *Quercus* and *Carya* species (*Quercus rubra* L., *Q. alba* L., *Q. prinus* L., *Carya ovata* (Mill.) K.Koch) while the subcanopy was dominated by *Acer* species and *Fagus grandifolia* Ehrh. (Table 1). The forest established in the late 1920s after the site was last harvested using the clear-cut method (Hart and Grissino-Mayer 2008). Based on field observations and analysis of 17 tree cross

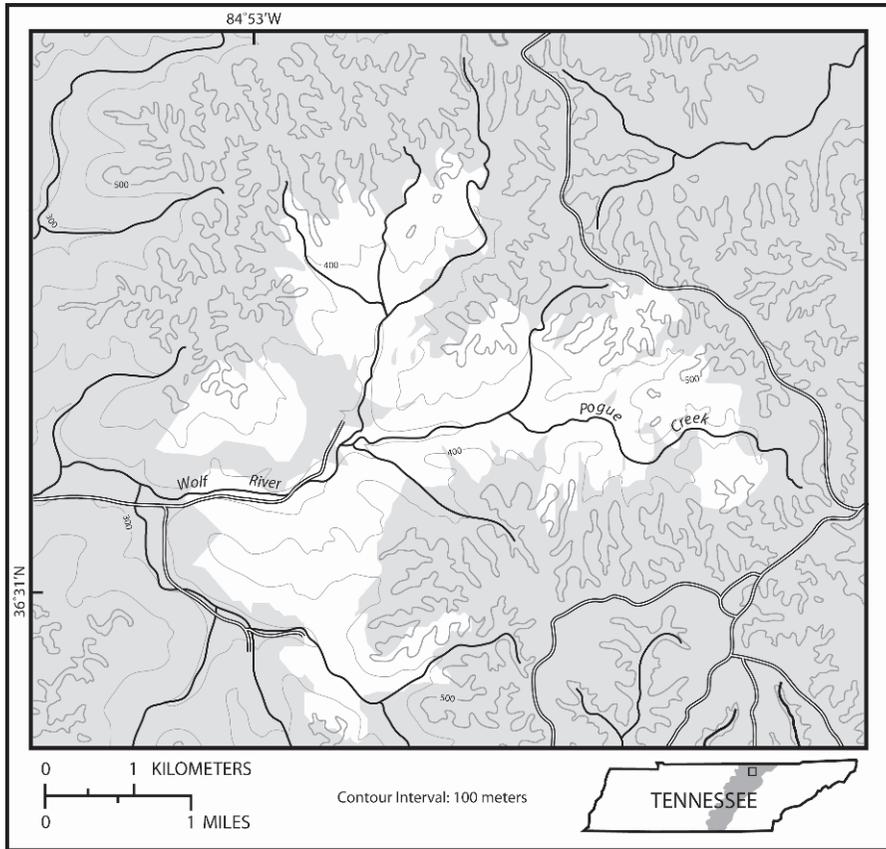


FIG. 1. Map of the Pogue Creek Natural Area in Fentress County, Tennessee. Shaded area on Tennessee inset map is the Cumberland Plateau physiographic section.

sections from a prior study, no signs of fire or other broad-scale disturbance events were evident since the anthropogenic disturbances of the 1920s (Hart et al. 2008a). Dendroecological analysis combined with stand composition and structure data indicated that the disturbance regime during stand development was characterized by gap-scale events that influenced fine-scale biophysical conditions (Hart and Grissino-Mayer 2008). *Odocoileus virginiana* Zimmerman hunting in Fentress and adjacent counties is a popular activity,

and many local land owners manage *O. virginiana* herds using Quality Deer Management or other programs. While we cannot discount the potential role that herbivory by *O. virginiana* may have had on vegetation patterns at PCNA, we did not see many *O. virginiana* or evidence of a dense population in the form of scat, rubs, scrapes, trails, or partially consumed vegetation.

STUDY DESIGN AND ANALYSES. To address our research questions we used sapling com-

Table 1. Crown class percentages by group for trees ≥ 5 cm dbh at the Pogue Creek Natural Area, Tennessee (Hart and Grissino-Mayer 2008). Canopy class categories were based on the amount and direction of intercepted light (Oliver and Larson 1996).

Group	Crown class			
	Overtopped	Intermediate	Codominant	Dominant
<i>Quercus</i>	1%	6%	33%	49%
<i>Carya</i>	12%	30%	42%	35%
<i>Acer-Fagus</i>	66%	43%	8%	10%
Others	22%	21%	18%	6%

position and biophysical attribute data for canopy gaps sampled on PCNA. Each of the 40 gaps sampled was located while walking line transects parallel to the slope contour from points randomly selected while in the field. All transects were classified as being located at lower-middle, middle, or upper-middle positions. We restricted our sampling to these 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. Canopy gaps were defined as environments where void space was visible 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. To document the full range of gap environments, gap size limits were not established. Gap area was quantified for expanded (area defined by the bases of canopy trees surrounding the void [Runkle 1981]) and observed (area unrestricted by canopy) gaps by measuring its length (largest distance from gap edge to gap edge) and width (largest distance perpendicular to length). To calculate area these measurements were fitted to the formula of an ellipse (Runkle 1982, Clinton et al. 1994).

All gaps were classed by gap origin as being caused by a snag (standing dead tree with intact crown), uprooted stem (root network uplifted), or snapped stem (bole broken below the crown) to determine the possible influence of gap formation on sapling richness and composition (Clinton et al. 1993). We recorded the number of overstory trees removed during gap formation as sapling response to single and multi-tree gaps may differ. Gap maker trees were classified to the lowest possible taxon to quantify possible relationships between trees in canopy and regeneration layers. We quantified the total basal area (m^2) removed by the loss of gap maker trees in each gap by measuring diameter at breast height (dbh, ca. 1.4 m above the surface or root collar for downed individuals) and length, as the amount of basal area lost is not necessarily related to the number of individuals that were removed from the canopy during gap formation. We also recorded the number of perimeter trees with dominant or codominant positions in the canopy surrounding each gap because these individuals represent the pool of trees that had the potential to close the

gaps by lateral crown expansion. All gaps were classified by the projected closure mechanism, either lateral crown expansion or sub-canopy height growth (Barden 1979, White et al. 1985). In the field we quantified percent slope, slope aspect, and elevation for each gap. Soil type for each gap was determined by locating the gap coordinate pairs on a georeferenced soil distribution map for the study area (USDA 1995).

We used dendroecological techniques to date the age of all gaps. Tree-core samples were collected from residual trees located in gap environments (mean of 19 residual tree samples per gap). We subjectively sampled trees that we deemed likely to exhibit positive growth changes associated with gap formation and avoided those which were obviously damaged during the fall of the gap maker(s). Radial growth patterns of residual trees were visually analyzed for releases (i.e., notable periods of increased growth). In addition, we collected cross sections from all gap makers that still had intact bark to document gap maker death dates. Tree rings on each cross section were measured to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software. The measurement series were visually compared to a reference *Quercus* chronology for the site developed by Hart and Grissino-Mayer (2008). We confirmed the graphical crossdating of all gap maker tree-ring series using the program COFECHA (Grissino-Mayer 2001). Once statistically confirmed, we assigned calendar years to all tree rings in each individual undated measurement series. We then used the release initiation dates and gap maker death dates to assign a single calendar year of formation to each canopy gap.

The sapling component of each gap was quantified by tallying all saplings (stems ≥ 1 m height, < 5 cm dbh) by species in the entire expanded gap area. For each gap we quantified species richness (total number of species) of the sapling layer and the total number of saplings gap^{-1} . Sapling species richness and density values were standardized (at value $\text{m}^{-2} \text{gap}^{-1}$). To document the relationship between sapling species richness and area we developed a sapling gap-area curve using the total number of species and expanded gap area. Sapling species composition was analyzed using relative frequency and density values.

To clarify the mechanisms responsible for structuring patterns of gap composition, we

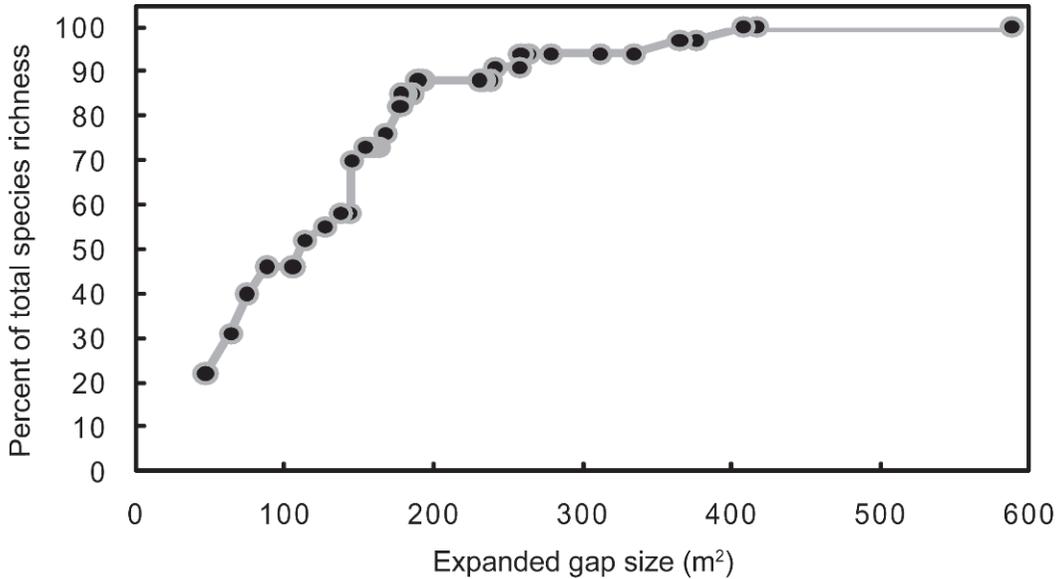


FIG. 2. Cumulative sapling (≥ 1 m height, < 5 cm dbh) species-gap area curve for 40 canopy gaps sampled at the Pogue Creek Natural Area in Tennessee. Gaps are shown in ascending size order. Total species richness of saplings in expanded gaps was 34.

used non-metric multidimensional scaling (NMS), a non-parametric ordination technique that seeks to determine the best position of n entities (in this case, plots) in a k -dimensional mathematical space based on a dissimilarity matrix (Legendre and Legendre 1998). The result of an NMS analysis is similar to that from other ordination techniques, but it entails fewer assumptions and is superior to parametric alternatives in many settings. Pairwise dissimilarities of species composition were calculated on the basis of sapling species abundance using the Bray-Curtis coefficient, which is robust with respect to ecological distance (Faith et al. 1987). Twelve species that occurred in only one or two gaps were dropped from the analysis.

We determined the optimal number of NMS axes by fitting the data using 1-, 2-, 3-, and 4-dimensional solutions and plotting the Kruskal stress function, which measures the correspondence between the ordination and the original data, vs. the number of dimensions in an NMS scree plot. The starting configuration of the final NMS was derived from an initial run using 50 iterations. Corresponding species scores were generated by weighted averaging and simultaneously plotted in NMS space. Species-environment relationships were clarified by calculating Pearson correlation coefficients between the NMS axis values and

continuous environmental variables and between species composition and categorical variables using a multi-response permutation procedure (McCune and Grace 2002). All ordinations and MRPP analyses were conducted using PC-ORD v. 5.0 (McCune and Mefford 2006).

Results. Most of the sampled canopy gaps were caused by uprooted (40%) or snapped (40%) stems, and the majority of gaps (75%) were formed by the death of a single canopy tree. Gap ages ranged from 1 to 17 years (two gaps were 17 years old) with a mean of 7 ± 0.7 years (SE). The mean expanded area of the gaps was 213.34 ± 17.15 m² (SE) with a range of 47 to 588 m². Gaps were well represented across the full range of gap sizes. Of the 39 gaps with known soil types, 61% occurred on Zenith gravelly loams, 26% occurred on Bouldin stony loams, and 13% occurred on the Grimsley-Jefferson outrock complex.

We recorded 34 sapling species from the 40 canopy gaps. Sapling species richness increased with increasing gap size until gaps reached ca. 200 m² (Fig. 2). At this size, 88% of the 34 total species had been recorded in a gap. Only four new species were found in gaps between 190–408 m², and sapling species richness did not increase in gaps larger than 408 m². Mean sapling species density was

Table 2. Size, sapling species richness, and sapling density data for canopy gaps sampled at the Pogue Creek Natural Area, Tennessee.

	Gap size (m ²)	Sapling density	
		Species (m ⁻² gap ⁻¹)	Individuals (m ⁻² gap ⁻¹)
Minimum	47.10	0.01	0.10
Median	158.18	0.04	0.23
Maximum	587.91	0.15	0.62
Mean (± SE)	213.34 (± 17.15)	0.05 (± 0.00)	0.27 (± 0.02)

0.05 m⁻² gap⁻¹, with minimum and maximum values of 0.01 and 0.15 m⁻² gap⁻¹, respectively. Thus, on average a new sapling species was encountered every 20 m² (Table 2). Mean sapling density was 0.27 m⁻² gap⁻¹ or a within-gap spacing of 3.7 m² individual⁻¹. The majority of species were relatively rare as just eight species comprised > 90% of all saplings, and 22 species individually represented less than 1% of all saplings. Eight species occurred in only a single gap.

The optimal NMS solution for gap composition had three axes and a moderately low stress (12.5), suggesting an adequate representation of sites in ordination space. NMS Axis 1 and Axis 3 captured 34.6% and 31.0% of the variation in the original species matrix, respectively. Placement of plots along these axes indicated that their composition was strongly related to the gap's aspect and area, and to a lesser degree, the number of gap-making individuals and the basal area lost during the gap-making event (Table 3). Gap composition was also significantly related to the mechanism of gap creation (MRPP: $A = 0.020$, $T = -1.78$, $P = 0.05$), with composition in gaps created by uprooting events differing from that in gaps created by snag forming events ($A = 0.029$, $T = -1.91$, $P = 0.049$) or stem snapping ($A = 0.016$, $T = -1.70$, $P = 0.063$). This influence was noticeable in the location of most gaps created by uprooting events at higher NMS Axis 3 values vs. those with

remaining snags or formed by snapping at low- to moderate values (Fig. 3A). The association of gaps formed by uprooting with larger gap areas at higher NMS Axis 3 values supports our finding that gaps created by uprooting (mean expanded and observed gap areas of 266 m² and 60 m²; mean gap age = 7.8 yrs) were larger than those formed by standing snags (150 m² and 30 m²; 6.8 yrs) or snapping (197 m² and 34 m²; 5.7 yrs).

NMS Axis 2 captured 21.0% of the variation in the original species matrix and clearly demonstrated the role that soils played in shaping gap successional trajectories (Fig. 3B). Results of the corresponding MRPP analysis were highly significant (MRPP: $A = 0.082$, $T = -6.984$, $P < 0.00001$) and indicated that gap composition on Bouldin stony loams differed significantly from that on Zenith gravelly loams ($A = 0.090$, $T = -10.294$, $P < 0.00001$) and the Grimsley-Jefferson outrock complex ($A = 0.081$, $T = -3.523$, $P = 0.003$). NMS Axis 2 was also linked, albeit more weakly, to variables more strongly associated with Axis 1 or 3: transformed aspect, basal area lost and the number of gap forming trees (Table 3). Nonetheless, Axis 2 was orthogonal to both Axis 1 and 3 ($r^2 < 0.015$), implying that the secondary effects of these variables on gap composition were unique and related to interactive effects with soil properties.

Individual species responses to environmental factors, and their collective contributions to

Table 3. Significant relationships between non-metric multidimensional scaling (NMS) axis values and environmental variables for regeneration in gaps at the Pogue Creek Natural Area, Tennessee. Values shown are Pearson correlation coefficients.

Variable	NMS Axis 1	NMS Axis 2	NMS Axis 3
Transformed slope aspect (BEERS)	0.41***	0.36**	0.38**
Number of gap-creating trees (GAPRE)	-0.34**	-0.30*	0.09
Basal area of gap-creating trees (BALOST)	-0.19	-0.32*	0.29
Expanded gap area (EXAREA)	-0.07	-0.15	0.70****
Observed gap area (OBAREA)	-0.23	-0.14	0.52****

Significance: * 0.10 > P > 0.05; ** 0.05 > P > 0.01; *** 0.01 > P > 0.001; **** P < 0.001

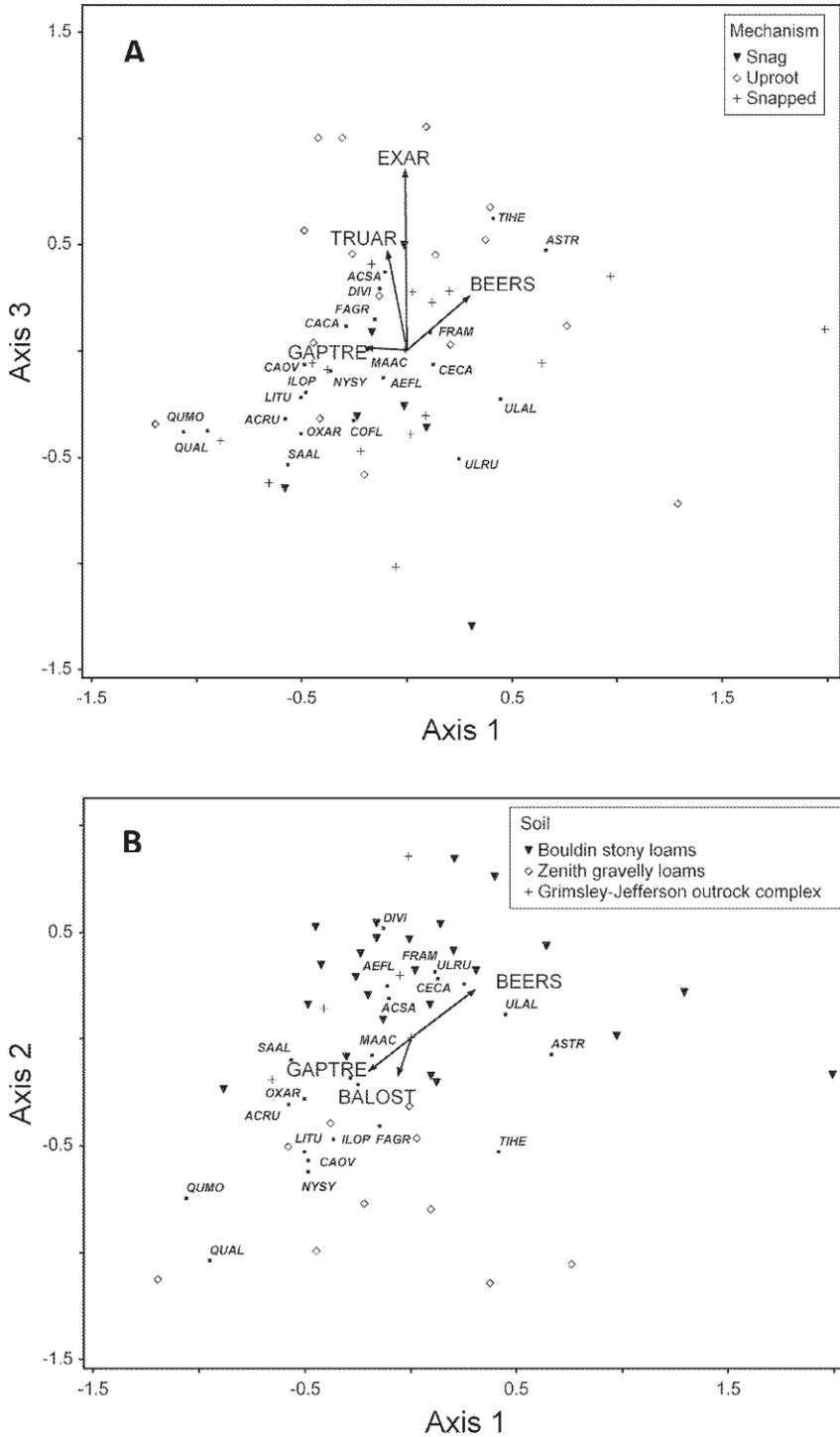


FIG. 3. Non-metric multidimensional scaling ordination of sapling composition in 39 canopy gaps, Pogue Creek Natural Area, Tennessee. BALOST: basal area removed by the disturbance based on gap maker size; GAPTRE: genus of gap maker; BEERS: transformed slope aspect; EXAR: expanded gap area; TRUAR: observed gap area.

Table 4. Relative frequency (% of gaps in which the species occurred), density (stems ha⁻¹), and relative density of saplings (≥ 1 m height, < 5 cm dbh) in expanded canopy gaps at the Pogue Creek Natural Area, Tennessee.

Species	Relative frequency	Stems ha ⁻¹	Relative density
<i>Acer saccharum</i> Marsh.	100.00	863.63	35.70
<i>Fagus grandifolia</i> Ehrh.	92.50	474.70	19.62
<i>Acer rubrum</i> L.	75.00	327.83	13.55
<i>Asimina triloba</i> (L.) Dunal	35.00	168.03	6.95
<i>Magnolia acuminata</i> (L.) L.	85.00	158.63	6.56
<i>Fraxinus americana</i> L.	50.00	88.13	3.64
<i>Liriodendron tulipifera</i> L.	30.00	49.35	2.04
<i>Oxydendrum arboreum</i> (L.) DC.	40.00	48.18	1.99
<i>Cornus florida</i> L.	40.00	37.60	1.55
<i>Ulmus rubra</i> Muhl.	22.50	31.73	1.31
<i>Nyssa sylvatica</i> Marsh.	25.00	30.55	1.26
<i>Cercis canadensis</i> L.	40.00	29.38	1.21
<i>Tilia heterophylla</i> Vent.	15.00	12.93	0.53
<i>Aesculus flava</i> Ait.	22.50	11.75	0.49
<i>Ilex opaca</i> Aiton	12.50	8.23	0.34
<i>Carpinus caroliniana</i> Walt.	10.00	8.23	0.34
<i>Quercus prinus</i> L.	5.00	8.23	0.34
<i>Magnolia tripetala</i> (L.) L.	2.50	8.23	0.34
<i>Carya ovata</i> (P. Mill.) K. Koch	10.00	5.88	0.24
<i>Sassafras albidum</i> (Nutt.) Nees	7.50	5.88	0.24
<i>Ostrya virginiana</i> (P. Mill.) K. Koch	5.00	5.88	0.24
<i>Diospyros virginiana</i> L.	10.00	4.70	0.19
<i>Ailanthus altissima</i> (Mill.) Swingle	5.00	4.70	0.19
<i>Quercus alba</i> L.	5.00	4.70	0.19
<i>Betula lenta</i> L.	2.50	4.70	0.19
<i>Ulmus alata</i> Michx.	7.50	3.53	0.15
<i>Carya alba</i> (L.) Nutt.	5.00	2.35	0.10
<i>Ulmus americana</i> L.	5.00	2.35	0.10
<i>Amelanchier laevis</i> Wiegand	2.50	2.35	0.10
<i>Quercus rubra</i> L.	2.50	2.35	0.10
<i>Hamamelis virginiana</i> L.	2.50	1.18	0.05
<i>Magnolia macrophylla</i> Michx.	2.50	1.18	0.05
<i>Morus rubra</i> L.	2.50	1.18	0.05
<i>Quercus velutina</i> Lam.	2.50	1.18	0.05
Total		2419.33	100.00

gap community composition, were manifested in their locations within ordination space and their abundance across gradients of gap area and slope aspect. Perhaps most notable was the absence or relative scarcity of the major overstory species in the area, *Carya ovata*, *Quercus rubra*, *Q. alba*, and *Q. prinus* (Table 4). When present, these species were restricted almost exclusively to gaps on south-facing slopes on stony loam soils (Fig. 3). Instead, regeneration was dominated by *Acer saccharum* Marshall and *Fagus grandifolia*, which occurred in 100% and 92.5% of the gaps, respectively, and together accounted for more than 50% of all saplings (Table 4). The relative density of these species was fairly insensitive to gap area, increasing slightly but non-significantly ($0.20 < P < 0.10$) across the range of gap sizes examined in this study (Fig. 4). The relative importance of *F. grand-*

ifolia vs. *A. saccharum* was dictated mainly by aspect and soils, with: 1) *F. grandifolia* having greater mean abundance on south-facing slopes (mean: 35 vs. 10 saplings per gap), and 2) *A. saccharum* dominating northwest- and northeast-facing slopes, particularly on Zenith gravelly loam soils (Fig. 3).

Acer rubrum occurred in at least 75% of the gaps and had the third highest relative density (Table 4). It was particularly prevalent on south and northwest-facing slopes. The next most abundant species were *Asimina triloba* (L.) Dunal and *Magnolia acuminata* (L.) L., but neither represented 7% of all saplings. *Fraxinus americana* L., *Oxydendrum arboreum* (L.) DC., *Cornus florida* L., and *Cercis canadensis* L. represented a second tier of frequently encountered species, each occurring in at least 40% of the gaps sampled. Distributions of these species were likewise structured

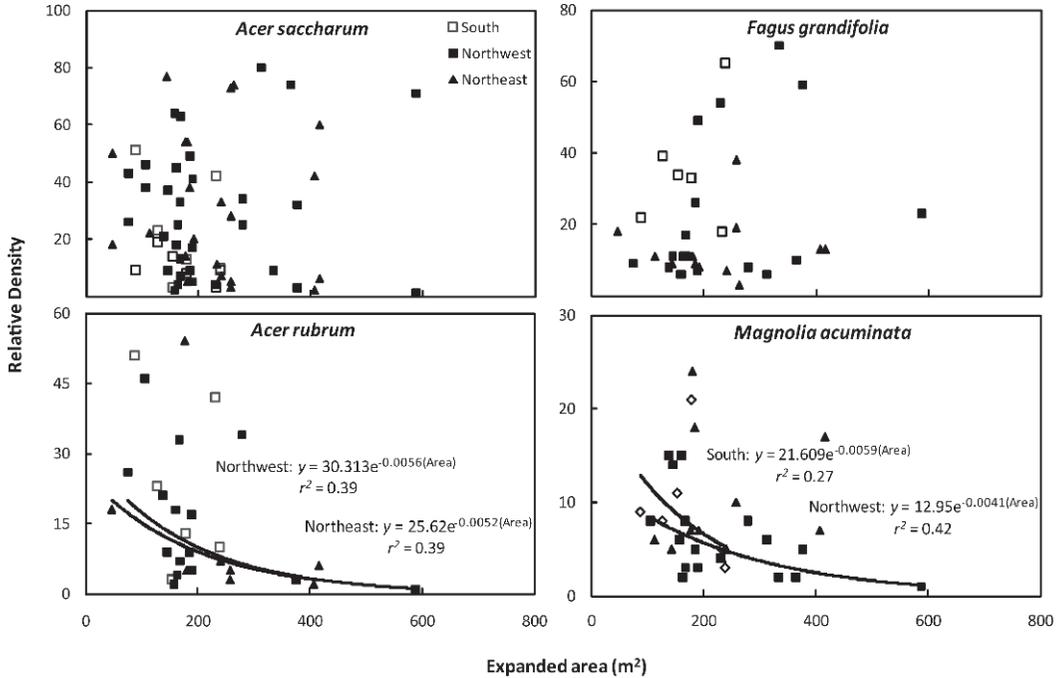


FIG. 4. Relationship between sapling relative density and expanded gap area for four common species in 39 canopy gaps, Pogue Creek Natural Area, Tennessee. Trend lines are shown when the two variables exhibited a significant relationship ($P < 0.05$). Note that y-scale varies.

on the basis of their individual responses to variations in gap area, aspect, gap-forming mechanism, and soil type; however, nearly all species declined in relative density in larger gaps (e.g. *A. rubrum*, *M. acuminata*, Fig. 4).

Discussion. Sapling species richness at PCNA was high, even when compared to other productive hardwood sites of the southern Appalachians. For example, richness was ca. 6% greater than that documented by Clinton et al. (1994) at Coweeta Hydrologic Laboratory in western North Carolina. Gap sapling richness was also much higher than the sapling richness under the closed forest canopy for the same study area ($S = 34$ in gaps and 5 in non-gaps), as reported by Hart and Grissino-Mayer (2008). This discrepancy between gap and non-gap sapling richness may be explained by several processes. Gap micro-environments may contain saplings of all tree species on the site regardless of shade tolerance or life history characteristics or gaps may support an increased abundance of shade intolerant species that would be nonexistent or very rare in shaded conditions (Busing and White 1997). We speculate that many of the

shade tolerant species occurred in the gap environment prior to gap formation and that the shade intolerant species established in response to the disturbance event. In addition, sampling of the sapling layer was more intensive in the present study compared to Hart and Grissino-Mayer (2008). Thus, sampling techniques may partially explain this pattern.

Species richness increased only minimally after gaps reached a size of ca. 200 m². The 200 m² threshold is interesting as it approximates or is slightly less than the mean canopy gap size reported in other mesic hardwood forests in the region (Runkle 1981, Clinton et al. 1994, Wilder et al. 1999). Indeed, this area is less than the mean expanded size of the gaps we observed in this secondary, mixed *Quercus* forest. However, when viewed by formation mechanism, only gaps created by uprooted trees had mean sizes above this threshold. This finding suggests that most gaps formed by uprooting were larger than the relevé, while those formed by other mechanisms were typically smaller than the minimal area, as established by the species gap-area curve, required to capture most inhabitant species

of the sapling layer. Increasing gap area beyond 200 m² (to the largest gap of 588 m²) only yielded four additional species (*Magnolia tripetala* (L.) L., *Magnolia macrophylla* Michx., *Ailanthus altissima* (Mill.) Swingle, and *Morus rubra* L.). *Morus rubra* and the *Magnolia* species are shade tolerant and occur at low densities throughout the forest. As such, the canopy gaps likely had little bearing on their presence. In contrast, *A. altissima* (the only alien species noted in our study) is shade intolerant and its presence in the forest interior is entirely dependent on local canopy disturbances. This species occurred in only two gaps and none smaller than 365 m².

The NMS results provide insights into the factors structuring gap composition, including the effects of individual factors (gap formation mechanism, gap size, aspect, and soils) and their collective impacts. For example, composition of gaps created by uprooting events differed significantly from that in gaps created by snags or snapped stems. This pattern may simply be attributed to the physical alteration of the gap environment by the uprooting process. Intra-gap heterogeneity caused by uprooting canopy trees has been shown to be an important determinant of species composition in gaps (Putz 1983, Yamamoto 2000). However, gap formation is coupled with other factors. Soils and aspect influence the gap formation mechanism and the gap formation mechanism in turn influences gap size. We found that snag-formed gaps were most common on south-facing slopes with stony loam soils. At this latitude, south-facing slopes receive high insolation inputs and have high temperatures and evapotranspiration rates compared to other aspects. The stony loam soils of these relatively xeric sites are classed as having low available water capacities. Therefore, we speculate these sites are water limited and trees that occur on them are more susceptible to water stress induced mortality or other killing agents such as soil fungi that damage root systems of stressed trees (e.g., *Armillaria mellea* Vahl ex Fr.). Moisture stress has been shown to result in snag-formed gaps in southern Appalachian hardwood forests (Clinton et al. 1993, Clinton et al. 1994), and snag density has been shown to be higher on xeric vs. mesic sites in the region (McComb and Muller 1983). These snag-gaps are small relative to gaps formed by other mechanisms (Hart and Grissino-Mayer 2009).

In contrast, gaps formed by uprooted canopy trees were most common on north-facing slopes with gravelly loam soils. North-facing slopes at this latitude receive lower insolation inputs and tend to have lower temperatures and evapotranspiration rates compared to southern exposures. The gravelly loam soils are characterized by high available water capacities. On these more mesic sites, we speculate that canopy tree death associated with moisture stress would be uncommon and that snag-formed gaps would thus be relatively rare. However, these soils are quite shallow, with depth to bedrock typically ranging from ca. 100–150 cm. In mesic forests of the southern Appalachians, wind-induced mortality is the predominant gap formation mechanism (Barden 1979, Runkle 1981, 1982), and uprooting is common in shallow soils because trees are not firmly anchored (Schaeztl et al. 1989). The uprooting of gap makers results in relatively large gaps as a larger portion of the stand is disturbed by the uplift of the root network and fall of the tree crown compared to trees that die and remain upright (Hart and Grissino-Mayer 2009).

In southern Appalachian hardwood forests, gaps formed by uprooting typically have elliptical shapes that extend from the former canopy tree base to the resting place of the fallen crown (Runkle 1982, Clinton et al. 1994), while snag-formed gaps have circular shapes (Hart and Grissino-Mayer 2009). Sapling composition in these larger and more mesic gaps was thus markedly different from composition in smaller gaps on xeric sites. Gaps formed by stem snapping are somewhat more difficult to explain as it is possible the gaps first formed as snags that subsequently snapped. Indeed, standing dead trees are often removed by mild to severe wind events. This process complicates formation-specific descriptions because the category likely represents a combination of gaps that formed directly by stem snapping and those that first formed as snags. Snags that are eventually snapped likely create distinct microenvironmental conditions and forest response may differ between these gaps and those that are formed rapidly (Krasny and Whitmore 1992, Clinton et al. 1994).

Quercus and *Carya* saplings were almost exclusively restricted to small and xeric gaps. While *Acer saccharum* and *Fagus grandifolia* were the most abundant sapling species, they

were relatively sparse in snag-formed gaps on stony loam soils, especially *A. saccharum*. Variation exists at the species level, but *Quercus* and *Carya* are considered only moderately tolerant of shade. An understory densely stocked with shade tolerant species inhibits *Quercus* and *Carya* reproduction (Lorimer et al. 1994). Thus, the presence of the species in small, xeric gaps may be explained by the scarcity of shade tolerant competition, favorable physical site conditions, or some combination of both factors.

Acer saccharum, *Fagus grandifolia*, and *Acer rubrum* saplings were by far the most abundant species in the regeneration layer of canopy gaps. However, these species were only minor components in the main forest canopy. The collective density of canopy dominant and codominant *A. saccharum*, *A. rubrum*, and *F. grandifolia* for the study site was 17 trees ha⁻¹ (Hart and Grissino-Mayer 2008). Based on this pattern, we suggest that through gap-phase succession the forest will transition from a *Quercus-Carya* type typical of the Central Hardwood Region to a system with a much stronger *Acer-Fagus* component more typical of the Northern Hardwood Region. Interestingly, the probable gap closure mechanisms (sub-canopy height growth or lateral crown expansion) and probable gap successors were quantified for these 40 gaps by Hart and Grissino-Mayer (2009). Only 25% of the sampled gaps were projected to close by sub-canopy height growth. *Acer rubrum* and *A. saccharum* were projected to fill three and two gaps, respectively. None of the sampled gaps were projected to close by the height growth of a *F. grandifolia*. The gaps in this secondary forest were relatively small and short lived (Hart and Grissino-Mayer 2009). Based on the size of the gaps, we propose that multiple canopy disturbance episodes are needed for sub-canopy trees to recruit to the main forest canopy. Thus, the more shade tolerant species (such as *A. saccharum*, *A. rubrum*, and *F. grandifolia*) are most likely attain canopy dominance under this disturbance regime.

As the forest matures, the spacing between canopy individuals and the crown spread of each canopy tree should increase. The removal of a canopy tree would then result in a relatively large gap (Clebsch and Busing 1989, Oliver and Larson 1996). In these larger gaps, the probability of gap capture by a sub-

canopy tree should increase (Hart et al. 2010). While the relatively small and short-lived gaps at the site have not typically been filled by sub-canopy trees they have still provided a mechanism for trees to recruit to larger size classes (Hart and Grissino-Mayer 2008, 2009).

This successional pattern has been reported throughout the Central Hardwood Forest Region and has led many researchers to project a widespread and inevitable transition from *Quercus*-dominated systems to those dominated by *Acer* and other mesic taxa (Nowacki and Abrams 2008). Anthropogenic cessation of low intensity surface fires has been the most often cited explanation for this phenomenon. However, alternative hypotheses including changes in growing season climate, land-use modifications, facilitative processes, decline of *Castanea dentata* (Marsh.) Borkh., and changes in wildlife population densities have also been proposed (Lorimer 1993, Abrams 2005, Hart et al. 2008b, McEwan et al. 2011). On some sites, the successional shift can likely be attributed to a single causal factor, but throughout the region these mechanisms may have operated in a synergistic manner and included positive feedbacks (Nowacki and Abrams 2008, McEwan et al. 2011). In attempts to maintain the *Quercus* components to these forests, resource managers have experimented with a variety of silvicultural treatments including group selection harvesting. In the group selection system, much attention is focused on the size of the openings created. The created gaps must be sufficiently large to recruit mid-tolerant *Quercus* species, but not too large to support faster growing shade intolerant species. Our results demonstrate that managing for opening size alone is insufficient as regeneration is dictated by a range of more complex and interacting factors. Additionally, abundant advanced regeneration by shade tolerant species and the relative scarcity of established *Quercus* individuals in the regeneration layer further complicate group selection management.

Conclusions. Species richness of the regeneration layer of canopy gaps in the secondary, mixed *Quercus* forest was relatively high, with sapling richness increasing sharply to a size of ca. 200 m². While the mean size of canopy gaps in the forest exceeded the minimal area to accurately characterize the sapling assemblage, gaps formed by snags and snapped stems were

typically less than this threshold size. It is well established that forest community composition is shaped by the physical environment and species-specific responses to disturbance events. From a theoretical perspective, the effects of individual disturbance events are often viewed as being superimposed over the influences of the physical setting. The effects of disturbance and the physical environment are not discrete and independent drivers of forest conditions; rather these factors interact to drive community patterns. While forest community response to a disturbance event is indeed constrained by the physical environment, the disturbance regime itself may also be largely influenced by the setting. In this study, we found gap formation mechanism, soils, aspect, and gap size to strongly influence sapling composition in canopy gaps. However, we noted that the collective influence of these variables was more important than any individual factor alone.

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