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Regeneration Patterns in Canopy Gaps of Mixed-oak Forests of the Southern Appalachians: Influences of Topographic Position and Evergreen Understory

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ABSTRACT.—Canopy gaps in southern Appalachian mixed-oak forests were assessed for the effects of topographic, gap and stand variables on density of wood seedlings. Seedling density was significantly correlated with percent slope and positively with gap age (l-5 yr). Density varied substantially among topographic positions and increased with gap size. Species richness decreased over time and increased with gap size. Regeneration was dominated by *Acer rubrum* L. Other important species included *Quercus coccinea* Muench., *Q. rubra* L., *Q. velutina* Lamarck, *Liriodendron tulipifera* L. and *Cornus florida* L. Some known gap species increased in density with increasing gap size. Competitive inhibition effects of the evergreen understory (*Rhododendron maximum* L. and *Kalmia latifolia* L.) were also examined. Gaps containing over 50% cover of *R. maximum* had significantly lower densities than all other gaps, including gaps with >50% *K. latifolia* cover. Height distributions of major regenerating species were skewed away from small (< 1.5 cm) height classes. Species establishment was a function of gap area, gap age, topographic position and cover of *R. maximum*. In addition, species of varying degrees of tolerance of understory conditions are capable of establishment in small to medium size canopy openings in the absence of an evergreen shrub understory.

INTRODUCTION

The dynamics of most terrestrial ecosystems are a function of dominant disturbance regimes (White, 1979; Pickett and White, 198.5). The size, intensity and frequency of disturbance creates mosaics of patches (Runkle, 1981; Spies and Franklin, 1989) and, in the case of forests, these patches typically contain a narrow range of ages of regenerating tree species reflecting the initial period of colonization of the disturbed area (Skeen, 1976; White, 1979; Barden, 1981; Boring *et* al., 1981; Brokaw, 1985; Runkle, 1985; Foster, 1988; Lawton and Putz, 1988; Phillips and Shure, 1990). Many forests maintain high species diversity as a result of canopy gap regeneration processes (Grubb, 1977; Ricklefs, 1977; Denslow, 1980; Orians, 1982), which promote early and mid-successional tree species that would not otherwise be common in old-growth communities (Pickett, 1980; Runkle, 1981, 1985; Canham and Marks, 198.5). Although tree seedling establishment following large scale disturbances such as tornados (Peterson and Pickett, 1991) has been addressed, few studies have dealt with

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seedling release and/or estdblishrnent immediately following small-scale, low-intensity disturbance.

Establishment of seedlings of woody plants is often lirnitecl, depending upon gap size, to the first 1–5 yr following gap formation (Canham and Marks, 1985). The rate of seedling establishment is in part a function of the rate of biomass and leaf area recovery in the opening (Oliver, 1981) and the physical environment of the site (e.g., light, temperature, degree of site alteration), as well as the number and distribution of new microsites following the disturbance. Early establishment and rapid growth are critical for intolerant and intermediately tolerant understory species which require high light conditions for establishment and competitive growth rates.

Severe drought in the southern Appalachians can result in species-specific tree mortality patterns ('Fainter *et* al., 1984; Clinton *el al.*, 1993). This response is a function of the severity of' the drought and the condition of' the forest stand at the time of' the drought (Pickett and White, 1985; Waring, 1987). Ecosystem level responses, however, may be subtle with respect to release or mobilization of resources within the impact area (Wallace, I%%). Differences in disturbance intensity between drought and other random disturbances (*e.g.,* fire, severe wind, debris avalanches) will likely result in differences in subsequent recovery patterns. Because of the relative lack of forest floor disturbance when trees die standing, the distribution of new microsites would likely he different in kind and number compared to tree-fall openings where pits and mounds are usually present; hence, important selective influences due to disturbance type limit regeneration to species adapted to the environment associated with openings created when one or a few trees die standing.

During the mid-1980s, a severe drought occurred in the southeastern U.S. (Swift *et al.,* 1989) which resulted in increased rates of mortality of over-story trees (Starkey *et* al., 1989; Stringer *et* al., 1989; Clinton *et al.,* 1993). This event influenced tree mortality from Arkansas to Virginia (Starkey PI *al.,* 1989). Clinton *et* al. (1993) characterized canopy openings in order to assess the relationships between gap formation and a significant drought period (1984–1988) at the Coweeta Hydrologic Laboratory, located in the southern Appalachians of western North Carolina.

Evergreen understory in the southern Appalachians, principally *Rhododendron* maximum I,. (rosebay rhododendron), is important in influencing canopy composition by limiting the regeneration success of potential canopy trees (Phillips and Murdy, 1985). McGee and Smith (3967) found that within *Rhododendron* thickets the forest canopy was older than the thickets themselves; none were younger, indicating that no recruitment to the overstory had taken place since the thicket established. This age structure is thought to be a result of mortality in the overstory due to the chestnut blight [*Cryphonectria parasitica* (Mm-r.) Barr; Anagnostakis and Hillman, 1992] during the 1930s and the consequent spread of *Rhododendron* (Woods and Shanks, 19.59). Several potential hypotheses (*e.g.,* allelopathy, litter depth and quality, light) could help explain this competitive exclusion phenomenon. The apparent low levels of light underneath *Rhododendron* is likely to be the primary inhibitor to seedling establishment and growth. For example, at the Coweeta Hydrologic Laboratory, incident photosynthetically active radiation (PAR; 400-700 nm) at the forest floor in rhododendron thickets is 14–34% of levels in the surrounding non-rhododendron forest where tight levels arc already ≈15% that of full sun.

The present study deals with variation in woody species richness and seedling density in newly formed small and medium sized drought-induced canopy gaps in mixed-oak forests of the southern Appalachians. Opening size is important with respect to changes in the light environment. Phillips and Shurr (1990) found that solar radiation was several times greater in large vs. small openings and observed increases in species richness across that same gradient. In this study, difference in opening size is used as a surrogate for shifts in the light resource. Our objectives were to examine the effects of canopy gap and stand characteristics on species assemblages and to characterize the effects of topographic position. We hypothesized that seedling presence within canopy gaps was a function of (1) the size of the opening, (2) the extent of evergreen understory, particularly *Rhododendron maximum* and *Kalmia latifolia* L. (mountain laurel), and (3) topographic position.

METHODS

Study site.—This study was conducted at the 1626-ha Coweeta Hydrologic Laboratory (Lat. 35°03′N, Long. 83°25′W; 675–1592 m elev.), located in the Blue Ridge physiographic province of the southern Appalachians near Franklin, North Carolina. The soils are primarily Ultisols (Typic and Humic Hapludults) and Inceptisols (Umbric and Typic Dystrochrepts and Typic Haplumbrepts; Velbel, 1988). Mean annual precipitation ranges from 178 cm at low elevations (670 m) to over 250 cm at high elevations (1600 m) with less than 5% falling as snow or ice. Precipitation is usually distributed evenly throughout the year. The duration of the drought event in this study was 5 yr (1984–1988) and peaked in 1986 when the rainfall deficit exceeded 30%. The return period for an event such as this was estimated to be 233 yr, based upon stream flow data (Swift *et* al., 1989). Mean annual temperature at Coweeta is approximately 13 C and ranges from −18 C in January to 24 C in July (Swift *et al.*, 1988).

Vegetation in the Coweeta Basin can be divided into four main forest types: northern hardwoods, cove hardwoods, oak-pine, and mixed-oak (formerly, oak-chestnut) (Swank and Crossley, 1988). The mixed-oak forest type is the most widely distributed forest type in the basin. *Quercus prinus* L. (chestnut oak) is the most widespread and important oak species and occurs most frequently at mid-elevations on slopes with mesic aspects. *Quercus rubra* L. (northern red oak) may dominate at higher elevations, whereas at lower elevations *Q. alba* L. (white oak) and *Q. velutina* Lam. (black oak) are important oak species. *Quercus coccinea* Muenchh. (scarlet oak) is found in both mesic and xeric mixed-oak forests as well as in the oak-pine forest type on drier slopes and ridges at lower and mid-elevations. The understory over much of the basin is dominated by the ericaceous shrubs *Rhododendron* maximum L. and *Kalmia latifolia* L. *Rhododendron* occurs on northern aspects and other mesic sites and is commonly found in dense thickets. *Kalmia* produces dense thickets as well but occurs primarily on xeric sites or occasionally in combination with *Rhododendron.*

Gap sampling.—In 1988 we systematically sampled canopy gaps located entirely or partially within nine permanent vegetation transects on midelevational slopes and ridges in mixed-oak forests. The transects are spaced at 200-m intervals along bearings of approximately N30°W and are 20 m wide. Within the transects are contiguous vegetation plots (20 × 40 m; 0.08 ha) that were initially established and inventoried in 1934 to provide baseline vegetation data for the Coweeta Basin (Day *et* al., 1988).

Canopy gaps were characterized based on the "expanded gap" definition (*i.e.*, the gap boundary was defined by the base of surrounding canopy trees) described in Runkle (1981). The sampling criteria used were: (1) the "gap maker(s)" must have been upper canopy trees at the time of gap formation and (2) gaps were less than 6-yr-old. Gap age was estimated by examining internode lengths of previously suppressed individuals within the opening. We assumed that distinct increases in internode length were coincident with gap formation. Gap age was determined by averaging the number of these substantially longer internodes on several individuals within the opening.

The vegetation in 28 gaps was inventoried. Regeneration (new seedlings and advanced regeneration) was inventoried in two 1-m-wide transects located along the two principal axes (longest and next longest perpendicular axis) with which gap area was calculated using the formula for an ellipse. Stems <2.5 cm diam breast height (dbh; 1.4 m above ground) were inventoried and identified to species. Height was measured to the nearest centimeter on all stems. No distinction was made between new seedlings and advance regeneration. Density values were determined as absolute (i.e., stems/m^2) as opposed to relative due to the presumed selective effect of gap area on species presence and abundance. All species nomenclature follows Radford *et al.* (1968).

Most gaps were at least roughly elliptical. Slope position, % slope, aspect, gap age, gap maker species, and percent evergreen understory cover were measured for each gap. Slope was measured in percentages with an Abney level. Two measures of slope taken on opposite sides of the gap makers were averaged. Aspect was measured to the nearest of 16 cardinal directions with a compass. It was converted to a relative moisture index, with SSW being the most xeric and NNE the most mesic (*see* Day and Monk, 1974).

Statistical analysis.—A folded form F statistic was used to test for homogeneous variances (SAS, 1987) with respect to species establishment patterns. When variances were equal, significant differences were evaluated with t-tests. When variances were not homogeneous, a t-test and Satterthwaite's approximation for computing degrees of freedom was used (SAS, 1987). These comparisons were made for age-classes, slope positions, and for single- vs. multiple-tree gaps. Analysis of variance (ANOVA) was used to test for differences among means. Duncan's Multiple Range Test (SAS, 1987) was used as a means separator where significant differences existed. The six species used for most of the comparisons had the highest density of all species in multiple tree gaps. All statistical comparisons were conducted at the $\alpha = 0.10$ significance level.

RESULTS

Species richness.—A total of 32 species was identified within gaps (Table 1). Species richness was highest for 2-yr-old gaps (24; $n = 8$), lower- and mid-slope positions (27; $n = 24$) and multiple-tree gaps (29; $n = 15$). In general, species richness decreased with increasing gap age and increased with gap size ($r = 0.72$; $P = 0.0001$). Gap size ranged from 60–630 m^2 with mean and median of 227 and 141 m^2, respectively.

Dominant gap species.—*Acer rubrum* L. (red maple) was the most frequent species (Table I), had the highest density for gap ages 1 to 4 (Fig. 1) and was the most dense in single- and multiple-tree gaps (Table 1). The oak species were generally well-represented; however, *Quercus alba* L. (white oak) accounted for only 3% of total density and occurred in only one-third of all gaps.

Most woody stems (70%) were ≤ 20 cm tall and 95% were ≤ 1 m tall (Fig. 2). For *Acer rubrum,* 60% of the stems were $\leq$ IO cm. *Cornus florida* was also skewed away from smaller height classes but showed a more even distribution among height classes, as indicated by the lowest values for Kurtosis (7.14) and skewness (1.97) in its distribution, than did the other shade-tolerant species (Fig. 2). *Liriodendron tulipifera,* a very shade-intolerant species, was less represented in all height classes but showed a small peak around 10 cm (Fig. 2), likely a response to canopy removal. Although no estimates of seedling ages were made, the height distribution of the species in Figure 2 suggests that most of the regeneration was relatively recent and was likely the result of canopy removal.

Topographic effects.—Species used in this comparison (Table 2) had the highest densities in multiple-tree gaps, with the exception of a common deciduous shrub [*Symplocos tinctoria* (L.) L'Her] (Table 2). Ridges had significantly ($P = 0.0006$) greater total density than mid- or lower slopes, which were not significantly different from one another. Among slope positions, *Acer rubrum* occurred at a significantly ($P = 0.005$) higher density on ridges and

TABLE 1.—Canopy gap regeneration in **rank** order by frequency (n = 28). Included are density (stems/m^2) for single- (n = 12) and multiple-tree (n = 16) gaps

	All gaps	Single-tree	Multi-tree
Species	Freq (%)	Density	Density
Acer rubrum	0.86	0.60	0.43
Quercus rubra	0.64	0.12	0.22
Q. velutina	0.61	0.14	0.10
Q. prinus	0.57	0.12	0.17
Castanea dentata	0.53	0.10	0.07
Nyssa sylvatica	0.50	0.07	0.09
Q. coccinea	0.46	0.18	0.24
Carya spp.	0.46	0.09	0.10
Betula lenta	0.43	0.08	0.10
Pyrularia pubera	0.39	0.23	0.11
Q. alba	0.39	0	0.08
Cornus florida	0.36	0.25	0.33
Sassafras albidum	0.32	0.18	0.15
Liriodendron tulipifera	0.29	0.09	0.24
Magnolia fraseri	0.29	0.04	0.04
Acer pennsylvanicum	0.21	0.06	0.06
A. saccharum	0.21	0.05	0.02
Hamamelis virginiana	0.21	0.16	0.08
Kalmia latifolia	0.18	0.09	0.03
Tsuga canadensis	0.18	0.08	0.04
Castanea pumila	0.14	0.08	0.06
Fagus grandifolia	0.11	0	0.03
Prunus serotina	0.11	0.03	0.04
Rhododendron maximum	0.07	0	0.09
Symplocos tinctoria	0.07	0	0.26
Oxydendron arboreum	0.07	0.03	0.02
Fraxinus americana	0.07	0.04	0.04
Betula lutea	0.04	0.07	0
Pinus strobus	0.04	0	0.03
Tilia americana	0.04	0	0.11
Robinia pseudoacacia	0.04	0.06	0
Totals		3.04	3.36

Liriodendron tulipifera L. (yellow poplar) occurred with the lowest density on mid- and lower slopes (Table 2). *Liriodendron tulipifera* had significantly (P = 0.0001) higher density in gaps on ridge positions, as did *Quercus velutina* (black oak) (P = 0.002). Total density for all species was inversely related to percent slope (r = -0.38, P = 0.05; n = 28).

Gap age and area effects.—Gap age was significantly and positively correlated with overall density (r = 0.37; P = 0.05). For all oak species combined, 5yr-old gaps had significantly higher density than l-yr-old gaps (P = 0.06). For individual species, *Cornus florida* I,. (P = 0.0004) and *Liriodendron tulipifera* (P = 0.006) bad significantly higher densities in 5-yr-old gaps. *Acer rubrum* had significantly higher densities than all other species in l-yr-old gaps (P = 0.04). *Quercus rubra* and *Q. velutina* were significantly lower in density in gap age 5 (P = 0.06) among six important gap species (Fig. 1).

For all gaps, density was positively correlated with gap size (r = 0.45; P = 0.02). Fur-

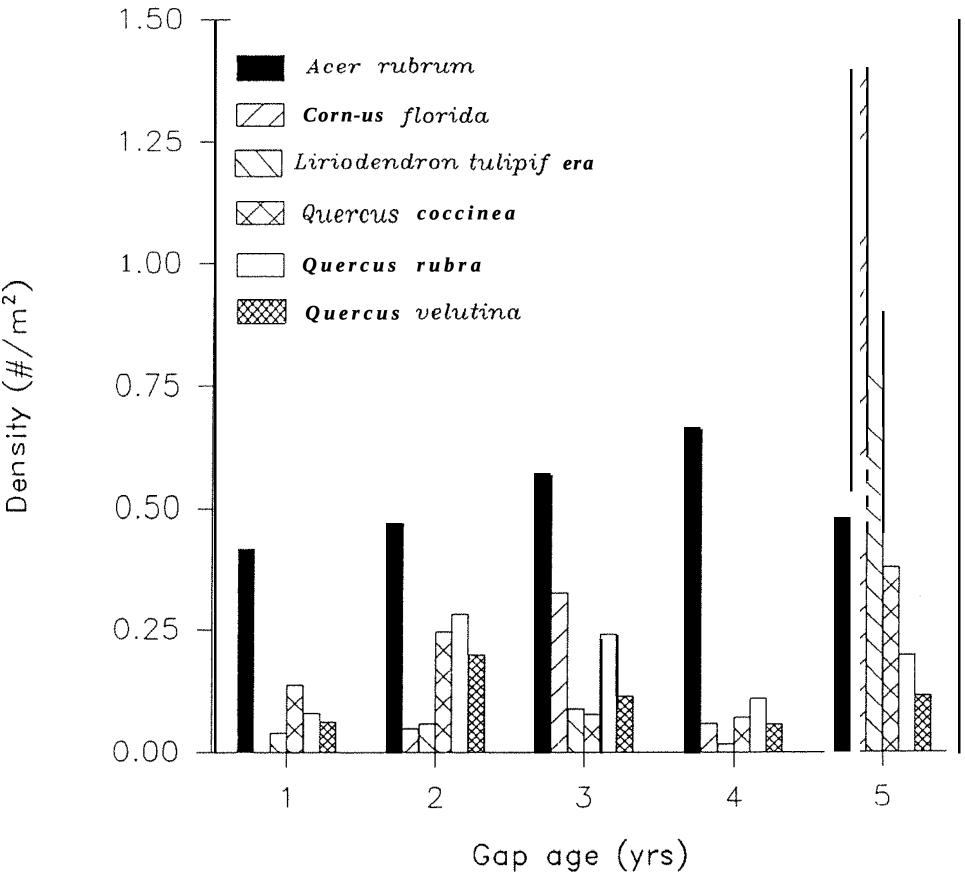

FIG. 1.—Mean woody seedling density (stems/m^2) by gap age for six dominant gap species

thermore, since most gaps formed after the drought were single-tree snags, gap types were combined into single- and multiple-tree gaps to compare area effects from a pre- and post-drought perspective (Table 1). The average area for single- and multiple-tree gaps in this study was 168 and 333 m^2, respectively.

Evergreen understory effects.—Mean stem density in *Rhododendron* gaps was approximately 0.5 stems/m^2. No significant differences in total (all species) density were found among gaps containing *Rhododendron*. However, when compared to gaps containing *Kalmia* (1.6 stems/m^2) and gaps with no appreciable evergreen understory cover (2.1 stems/m'), total density was significantly lower in *Rhododendron* gaps ($F = 5.16$; $P = 0.01$). Tree seedling density within *Kalmia* gaps was not significantly different from gaps containing no evergreen understory.

DISCUSSION

Canopy gap regeneration was dominated by seedlings and advanced regeneration of *Acer rubrum*. This intermediately shade-tolerant species (Hallow and Harrar, 1969) is ubiquitous with respect to microsite requirements; hence, it is able to colonize within a variety of

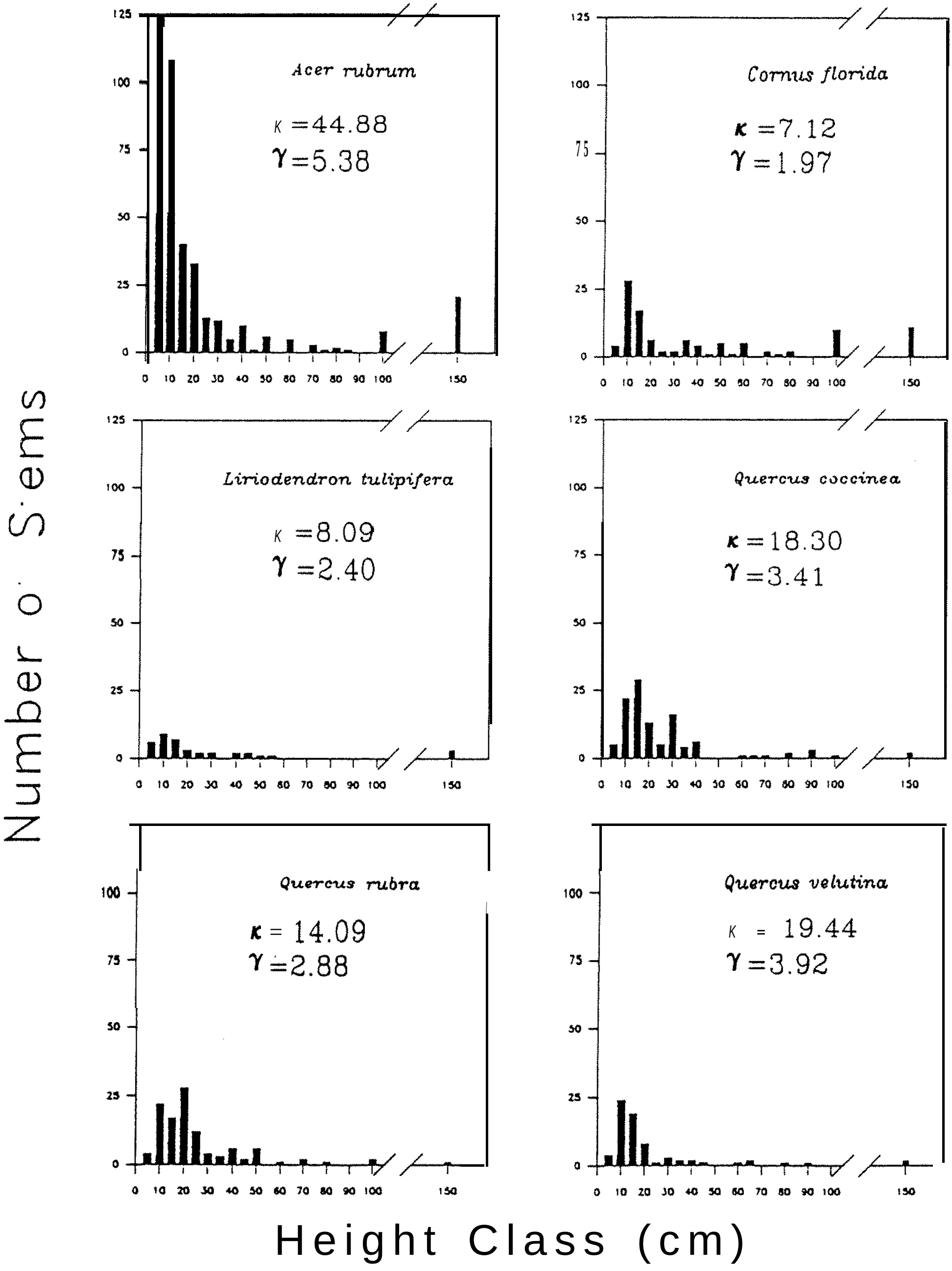

FIG. 2.—Height distribution of six dominant gap species for all gaps combined. Values on the X-axis represent the upper limit of 5-cm height classes. The value beyond the break is a general height class for all stems >1 m in height and <2.5 cm dbh. Estimates of Kurtosis (K) and skewness (y) are given for each distribution (Computing Resource Center, 1992)

TABLE 2.—Means and standard errors for density (stems/m^2) on three slope positions for six important southern Appalachian species which occurred with the highest density in single- and multiple-tree gaps

	Slope position					
	Ridge		Mid		Lower	
Species	Mean	SE	Mean	SE	Mean	SE
Acer rubrum	0.88^{a1}	0.126	0.45^{a2}	0.120	0.38^{a2}	0.138
Liriodendron	0.90^{a1}	—	0.07^{b2}	0.029	0.04^{b2}	0.022
Quercus coccinea	0.41^{ab1}	0.178	0.15^{b2}	0.038	0.17^{ab2}	0.049
Q. velutina	0.29^{ab1}	0.12	0.08^{b2}	0.015	0.08^{b2}	0.019
Q. rubra	0.18^{b1}	0.06	0.22^{ab1}	0.071	0.15^{ab1}	0.045
Cornus florida	0.63^{ab1}	0.397	0.19^{ab1}	0.137	0.13^{ab1}	0.075

Note: Significant differences were evaluated at the $P = 0.10$ level (Duncans Multiple Range Test). Density values with the same superscript are not statistically different among species (a,b) and among slop? positions (1,2)

opening sizes and under-story conditions (Wallace and Dunn, 1980; Boring *et* al., 1981). The recent increase in the rate of gap formation in the Coweeta Basin (Clinton *et al.*, 1993) may have contributed to the dominance of this species in the seedling and sapling size class.

Our study supports findings by other investigators where species of varying tolerance to shade were found in small canopy openings (Barden, 1981; Canham, 1988). This may be due to the relatively low leaf area in these mixed-oak scdnds at the mid- and upper-slope positions where two-thirds of the gaps in this study occurred (*e.g.*, 5% light transmittance for high leaf area stands vs. 15% for mid-slope and ridge sites at Coweeta). However, although not statistically significant, the density of some known gap species, such as *Liriodendron tulipifera*, *Cornus florida*, and *Quercus rubra* L. (northern red oak), increased, possibly due to the effect of presumed increased light levels with increasing gap size. By comparison, woody seedling density under average conditions of canopy cover is 1.5 stems/m^2 in permanent plots at Coweeta, which includes some areas affected by the loss of canopy cover. Other studies of tree replacement in small canopy gaps in the southern Appalachians suggest that less shade-tolerant species can be maintained by colonizing canopy openings (Barden, 1979, 1980) and, therefore, are important in tree replacement processes. The advantage, however, with respect to site occupation and eventual dominance is with species which rely upon advance sapling regeneration. Their presence in the opening at the time of gap formation suggests that they would be the likely successors to dead canopy trees (Canham, 1988). All species in Figure 2 show some ability to persist in the understory in the absence of disturbance as indicated by the number of stems in the larger height classes. These larger stems were more than likely present at the time of gap formation.

Evergreen understory effects.—Canopy gaps with dense *Kalmia* under-stories were significantly higher in tree seedling density than gaps containing dense *Rhododendron* understories. The overstory canopy in some areas occupied by *Kalmia* is generally lower in leaf area (Wallace, 1988). This is due primarily to reductions in overstory density following southern pine beetle infestation (Smith, 1991) on sites where scattered individual pines had coexisted with xeric-site hardwoods. McGinty (1972) estimated average leaf surface areas for *Kalmia* and *Rhododendron* co be 621 m^2/ha and 1516 m^2/ha, respectively, which are likely to be substantial underestimates for sites where these species occur in dense clumps. Nevertheless, these estimates indicate that *Kalmia* leaf surface area is sufficiently less than *Rhododendron* so as to allow enough light to reach the forest floor, even in dense clumps, for successful germination of species of varying understory tolerance in the absence of canopy gaps. Therefore, much of the regeneration in *Kalmia* gaps is probably in the "advance" form.

Phillips and Murdy (1985) found that total tree regeneration was lower in plots containing heavy *Rhododendron* cover compared to plots containing little or no *Rhododendron* and that the magnitude of the difference increased with time. Monk *et al.* (1985) found that dense stands of *Rhododendron* may interfere with tree establishment. Several hypotheses exist which could explain this phenomenon (*e.g.*, low light, competition for water and nutrients, allelopathy, litter quality). Furthermore, *Rhododendron* may account for as much as 32% of the total standing crop of leaf biomass in some forests. The apparent limitations to tree seedling regeneration patterns within canopy gaps occupied by *Rhododendron* has significant ecological implications. Since the chestnut blight (Keever, 1953), *Rhododendron* has increased in importance (Phillips and Murdy, 1985). Given the influence by *Rhododendron* on regeneration, it seems apparent that *Rhododendron* is important in determining patterns of tree replacement where disturbance intensity is relatively low.

Influence of drought on tree replacement.—Rates of gap formation more than doubled in the 2 yr following the 1986 drought compared with the 3 previous yr that gap formation was predominantly caused by standing-dead-snags (Clinton *et* al., 1993), unlike old-growth cove forests which are dominated by fallen-tree gap types (Barden, 1979, 1981; Romme and Martin, 1982; Runkle, 1982; White *et al.,* 1985). Given this event and the drought history reported in the past (Hursh and Haasis, 1930; Tainter *et al.,* 1984), we hypothesized that cyclically recurring drought-induced mortality, which results in standing-dead-snags, is a major disturbance regime in this region. In contrast to windthrows, standing-dead-snag gaps result in a minimum of forest floor and soil disturbance. Typically, the forest floor remains intact, acting as a physical barrier to initial establishment, particularly for small seeded plants (Marquis, 1965; Putz, 1983). The absence of bare soil in gaps formed by standing-dead-snags greatly reduces the chance of establishment by species that require mineral soil for seed germination. In addition, older saplings and advance regeneration of understory-tolerant species present at the time of gap formation incur less damage under snags vs. fallen trees (White *et al.,* 1985).

Many shade-intermediate species (*i.e., Quercus rubra, Acer rubrum*) were present in our gap plots. The physiological plasticity (Wallace, 1988) of some species allows for a quick response to the changes in light and other resources in and around small canopy openings; this gives them a distinct advantage over species which are less tolerant to shade. The advantage with respect to tree replacement is with individuals in stages of advance regeneration; their eventual occupation of the upper canopy is a function of the probability of subsequent openings at that location (Lorimer *et al.,* 1988; Runkle, 1990).

Periodic episodes of extreme drought are important in tree replacement and related ecosystem processes by creating mosaics of patch sizes and disturbance intensities of relatively narrow ranges peculiar to such events. The intensity of disturbance events which result in standing-dead-snags in the presence of *Rhododendron* is low enough so as to minimally interfere with competitive exclusion influences exerted by this species. This study suggests that, in the southern Appalachians, the combined importance of this type of low intensity disturbance and the presence of *Rhododendron* maximum in determining spatial patterns of age classes and stand structure is underestimated.

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