

Sapling strategies and gap partitioning in canopy gaps
of a successional forest in East Tennessee

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Abstract

Canopy gaps in a successional forest in East Tennessee were studied to determine the role of gaps in plant succession, sapling growth and mortality, and sapling colonization strategies. The possibility of niche partitioning within gaps was examined. Ten gaps (64-309 m², mean=186 m²) and four closed canopy plots (200 m² each) were surveyed by identifying and locating all trees, measuring terminal growth of saplings (n=933), and measuring diameter at breast height (D.B.H.) of trees > 3 m tall (n=504). The present canopy is dominated by oaks (*Quercus* spp.), pines (*Pinus* spp.), tulip tree (*Liriodendron tulipifera* L.), and beech (*Fagus grandifolia* Ehrh.), while dominant saplings are beech, red maple (*Acer rubrum* L.), and sugar maple (*A. saccharum* Marsh.). Sapling composition in gaps indicates that the current canopy will be replaced by a forest dominated by beech and maple. All three dominant sapling species showed significantly greater extensional growth in gaps ($p < .05$) than in closed forest. Red maple grew significantly less (mean annual growth=14.07 cm, $p < .05$) in gaps than did sugar maple (19.88 cm) or beech (16.52 cm), while sugar maple grew significantly less (5.13 cm, $p < .05$) than red maple (10.04 cm) or beech (9.49 cm) under closed canopy. Red maple and sugar maple may thus be exhibiting different gap strategies. Mortality of all trees in gaps over a 3 year period was 14.63%. Mortalities of potential canopy trees ranged from 6.59% for beech to 16.15% for red maple. All three major sapling species grew significantly more ($p < .05$) in the northern than southern end of gaps. Beech density was also significantly greater in the northern end of gaps ($p < .001$). No species showed greater growth or density in the southern end of gaps. The three dominant sapling species showed no significant growth differences between the center and edge of gaps.

Growth of individuals in gaps is highly variable, with microsite and genetic differences creating conditions that allow colonization by many species. Little evidence of niche partitioning within gaps was observed. Forest communities in East Tennessee may not have maintained a constant composition or disturbance regime for a long enough period of time for such fine niche partitioning to evolve.

Introduction

Although ecological studies of tree by tree replacement in light gaps within the temperate forests of North America are now fairly common (Barden 1981, Romme and Martin 1982, Runkle 1982, 1984, 1990, White et al. 1985, Yetter and Runkle 1986, Runkle and Yetter 1987, Canham 1988), only a few have been concerned with light gaps in second growth, mid-successional forests (March and Skeen 1976, Clebsch and Busing 1989) rather than in primary, old growth forests. It has been established that light gaps in old growth forests allow the dominant canopy trees to replace themselves over time (Barden 1979, 1980; Runkle 1981), as well as to aid in the canopy establishment of less shade tolerant species (Buckner and McCracken 1978, Barden 1981, Runkle 1982). It might be expected that gaps in second growth forests would additionally act as a mechanism through which succession could occur. Species richness is highest late in succession (Connell 1978, Clebsch and Busing 1989); gaps in successional forests may enhance species richness through the same mechanisms of gap partitioning found in old-growth forests. The idea that tree species might partition themselves along a gap size gradient has been discussed by Denslow (1980) for tropical climax forests, and verified in eastern deciduous old growth forests by Runkle (1984) and Canham (1988a). However, spatial partitioning within individual gaps has not been as extensively investigated (Barton 1984; Sipe and Bazzaz 1994, 1995), nor has niche partitioning of any kind in temperate second growth forests been studied.

The present investigation was undertaken to add to the available information on successional forest light gaps. Three aspects of gaps were investigated: 1) documentation of succession was established by comparing gap saplings to canopies, 2) sapling success and possible

sapling strategies for gap colonization were examined through comparison of gaps and closed canopy plots, and 3) the possibility of gap partitioning was investigated within individual gaps.

Materials and Methods

Site Description

All study plots were located in the Anderson County Wildlife Sanctuary in the Valley and Ridge physiographic province of East Tennessee (Fig. 1). Study sites were within a 42 ha area of second growth mid-successional forest between 250 and 358 m above mean sea level. This forest has been undisturbed since at least 1963; however, prior to 1963, some of the forest had been completely cleared for cultivation and cattle grazing, while most was selectively logged.

Gaps and closed canopy plots were chosen from four distinct habitats: the ridge top, the ecotonal mid-slope, the lower slope, and the mesophytic cove (Fig. 1). The ridge top was a xeric environment above 336 m, generally containing soil of the Armuchee-Muskingum complex (Moneymaker 1981). Slopes ranged widely from 0 to 15°, contributing to a relatively open forest composed primarily of chestnut oak (*Quercus prinus* L.) and Virginia pine (*Pinus virginiana* Mill.). Between the ridge top and the broad base of the ridge was the mid-slope, occupied by a narrow band of vegetation between 336 and 275 m elevation. The forests of this area were transitional between those of the lower slope and the ridge top, containing species characteristic of both. Slopes were in excess of 15° to the southwest. The lower slope below 275 m contained a mixture of oak species (including *Q. coccinea* Muenchh., *Q. rubra* L., *Q. velutina* Lam., *Q.*

alba L., *Q. falcata* Michx., and *Q. stellata* Wang.), tulip tree (*Liriodendron tulipifera* L.), pine species (*P. virginiana* and *P. echinata* Mill.), beech (*Fagus grandifolia* Ehrh.), and red maple (*Acer rubrum* L.). Slopes ranged from 12 - 15° to the southwest; soil types were of the Armuchee-Muskingum complex and the Jefferson loam (Moneymaker 1981). The north facing cove was isolated between two ridges. Slopes were steep, from 20 to 35°, with soil types of the Jefferson loam and the Sequoia silt loam (Moneymaker 1981). The dominant canopy trees were beech and tulip tree.

Procedure

Ten gaps and four closed canopy plots were selected for study. Each habitat contained one closed canopy plot and two or three gaps. All the gaps used in this study, ranging in size from 64-309 m², were chosen arbitrarily; most of the gaps selected were openings in the forest canopy made by single treefalls. The sizes of the study gaps are not necessarily reflective of the range in gap sizes throughout the forest.

In 1992, a transect was established along the long axis of each gap. The long axis was defined to be the longest distance from one end of the canopy gap (defined as the area directly beneath the opening in the canopy, after Runkle 1984) to the other. Off of this axis, the gap was divided into 1 m² plots, each of which was given individual coordinates (Fig. 2). For closed canopy plots (measured in 1994), a grid of 1 m² plots extending 5 m on either side of a 20 m transect was established under the intact canopy. All woody stems over 1 m high were identified

to species (nomenclature follows Radford et al. 1968), tagged with a permanent number, and located within the 1 m² plot. Height and terminal growth of the leader stem of all saplings (defined as woody stems 1-3 m tall) were recorded. Terminal growth was measured from the base of one set of bud scale scars to the base of the next set on the leader and could generally be measured for the previous four years. Trees over 3 m high were classed as either sub-canopy or canopy and their D.B.H. (at 120 cm) recorded. Any other pertinent features within the plot (such as remains of the gap maker, stumps, large rocks, or depressions) were recorded. These features, along with the location of each tree, were recorded on a map, from which the area of each canopy gap was determined (Fig. 2).

In 1995, all gaps were resurveyed to determine the status of all trees. Eighteen trees could not be relocated due to lost tags; the remaining 1169 were tallied as dead or alive. In the case of dead trees, a cause of death was determined if possible.

Results

As indicated by the large compositional differences between the canopy and the sapling layers (Table 1), the forests of Lost Ridge can be classified as mid-successional. In particular, oak species comprise greater than 30% of the canopy of the ridge habitats, but never more than 7% of the sapling layer. Likewise, pine species compose 18.6% and 38.8% of the canopy of the mid- and lower-slope respectively, but are completely absent in the sapling layer. At the top of the ridge, Virginia pine composes 34.5% of the canopy, 37.5 % of the gap saplings, but 0% of the

saplings from the closed canopy plot.

Throughout Lost Ridge, more shade tolerant species dominate the sapling layer. In the lower slope, red maple and beech are abundant in both the sapling and canopy layers. Sugar maple (*Acer saccharum* Marsh.), black cherry (*Prunus serotina* Ehrh.), sweetgum (*Liquidambar styraciflua* L.), and blackgum (*Nyssa sylvatica* Marsh.) are absent from or minor components of the canopy, but occur in both gap and closed canopy sapling layers in moderate percentages (Table 1). The slope of the ridge presents a similar picture, but beech and red maple make up a larger fraction of the sapling layer while comprising a smaller fraction of the canopy. At the top of the ridge, beech saplings give way to more xeric species such as Virginia pine, pignut hickory (*Carya glabra* (Mill.) Sweet) and sassafras (*Sassafras albidum* (Nutt.) Nees). Red maple declines in the gap sapling layer but remains important under the closed canopy (43.2% of closed canopy saplings).

In the cove, oaks are a minor component of the canopy (9.1%) and pines are absent. Tulip tree makes up 40.9 % of the canopy stems but only 0.7% of the gap sapling stems. Beech, the other main canopy species (29.5%), is represented in the sapling layer, but not as abundantly as it is in the canopy. Red maple, pawpaw (*Asimina triloba* (L.) Dunal), and, to a lesser extent, sugar maple make up the other dominant gap sapling species (Table 1). Sugar maple is by far the most abundant sapling species under closed canopy (68.3%). Basswood (*Tilia americana* L.) is a minor component of both the canopy and the gap sapling layers, but is not found in the closed canopy plot.

There were significant differences in either abundance or growth, or both, in some sapling species under closed canopy and in gaps. Of the six species with over five individuals in the

closed canopy plots, pawpaw ($p < .001$) and beech ($p < .05$) had a higher density per unit land area in gaps than would be expected by chance (using a chi squared goodness of fit test); sugar maple ($p < .001$) had a higher density per unit land area in closed canopy plots. Sugar maple, beech, black cherry, and red maple showed significantly greater extensional growth over the same two year period in gaps than under the closed canopy (Table 2). Blackgum also grew more in gaps than under the closed canopy, but not significantly. Pawpaw grew significantly more under the closed canopy than in the gaps.

A single factor analysis of variance test was used to determine if there were significant differences in the average growth of saplings of different species in gaps. Only those species that had the potential to become canopy trees were tested (basswood, beech, black cherry, blackgum, pignut hickory, red maple, sugar maple, sweetgum, Virginia pine, and white ash (*Fraxinus americana* L.)). ANOVA indicated that there was a significant difference among the growth of species ($p < .001$); a Tukey-Kramer test (Kramer 1956) was used to make post-hoc comparisons between the species to determine where the differences lay. Table 3 summarizes these results.

A comparison of the growth and density of saplings in the northern and southern ends of the gap plots was made, excluding a 5 meter wide swath from the center of each gap. In general, both density and growth were higher in the northern ends of the gaps. The mean yearly growth over a five year period (1988-1992) of all species in the northern end of gap plots was 17.99 ± 12.64 ($n=825$); in the southern end of gap plots, the mean growth was 15.06 ± 13.60 ($n=448$) for the same five year period. This difference is highly significant ($p < .001$). However, only three species showed a significant difference in growth when compared individually (Table 4). Red maple, sugar maple, and beech all grew significantly more in the northern end of gaps

than in the southern end. An examination of mean growth of species within each subdivision of forest, rather than in the entire set of gap plots, showed that both red maple and sugar maple grew significantly more in the northern end than in the southern end of gaps within each forest subdivision in which they were found in sufficient numbers (> 10 individuals; > 5 individuals on both north and south sides, $p < .05$ in all cases). Beech grew significantly more ($p < .001$) in the northern than in the southern end of the cove gaps only. No species grew significantly more in the south than in the north in any of the forest subdivisions or in the entire set of gap plots.

Sapling density was also significantly greater in the northern end of gaps than would be expected by random chance (chi square goodness of fit test, $p < .001$). The total area within the northern end of gaps was 586.5 m^2 ; the total area within the southern end of gaps was 596.5 m^2 . Thus if saplings were distributed evenly and randomly throughout gaps, a ratio of .98 saplings in the north to 1 sapling in the south would be expected. However, the actual number of individuals of all species in the north was 225, while in the south it was 108. White ash, ironwood (*Carpinus caroliniana* Walter), beech, and tulip tree were all represented by significantly more individuals in the north than would be expected based on a random distribution (Table 5). Additionally, sugar maple, red maple, and sassafras displayed higher numbers in the north than in the south, although not significantly (Table 5). No species was found in significantly greater densities in the south than in the north.

Differences were also examined between growth and density of saplings in the centers of the gaps and at the gap edges. All saplings further than three meters from any canopy gap edge were categorized as being in the center of the gap; all other saplings were categorized as edge saplings. There was no significant difference between the overall growth of all sapling species in

the centers or along the edges of gaps. There were also few significant differences in the growth of single species (Table 6). Blackgum grew significantly more in the center of gaps than along the edges, while dogwood (*Cornus florida* L.) and pawpaw, two subcanopy species, grew significantly more along the edges of gaps. The three most abundant saplings that might potentially reach the canopy- beech, sugar maple, and red maple- showed no significant difference in growth in the center or along the edge of gaps.

Overall sapling density was significantly greater along the edge of canopy gaps than in the center (chi square goodness of fit test, $p < .001$). The expected densities of saplings in the center and edge were calculated in the same way as the expected densities in the north and south, based on the ratio of area of gaps in the center to area of gaps in the edge and assuming an even, random distribution. Beech, red maple, sassafras, pignut hickory, and oak spp. showed significantly greater densities in the edge than in the center. No species was significantly denser in the center than in the edge, which may be because the majority of debris from the gap event is concentrated in the center of the gap.

Out of 1169 trees, overall mortality in gaps between 1992 and 1995 was 14.63% ($n=171$). Sixty-one percent of all dead trees were either crushed by the fall of another tree after the initial gap event or died of injuries received from the fall of another tree. There was no correlation between gap location and mortality rate. Beech had the lowest mortality rate of any species containing more than 30 individuals; in addition, 81% of all dead beech trees were crushed or died of injuries subsequent to crushing, the highest percentage of any major tree species (Fig. 3). Dogwood had the highest mortality rate (23.64%) of any major species, followed by pawpaw (21.99%); red maple had the highest mortality rate of potential canopy species (16.15%, Fig. 3).

Discussion

Succession

Succession on Lost Ridge is favoring red maple, sugar maple, and beech at the expense of pines, tulip tree, and oaks (Table 1). The lack of recruitment of pines except at the top of the ridge is typical of secondary succession in the forests of the Valley and Ridge (Hinkle et al. 1993). At the top of the ridge, Virginia pine saplings are present in high numbers only in gaps (Table 1), indicating that Virginia pine may maintain itself at the top of the ridge through the colonization of gaps, much as tulip tree maintains itself in the more mesic forests of the Appalachians (Buckner and McCracken 1978, Busing 1995). Tulip tree, although dominant in the cove canopy, is not being recruited in the gaps studied. However, tulip tree utilizes a large gap ($>1000 \text{ m}^2$) colonization strategy (Barden 1981, Runkle 1984), and since the study gaps were all less than 309 m^2 , they may not be large enough for establishment by tulip trees. Nonetheless, this study indicates that tulip tree will not be as dominant a canopy tree in the cove in the future, since large sized gaps and other large scale disturbances are relatively infrequent in eastern deciduous forests (Barden 1981, Runkle 1985). Although Braun (1950) characterized the forests of this region as oak-chestnut, replacement of oaks by more shade tolerant species such as sugar maple and beech has been documented with some regularity in the last 35 years (Dix 1957, Shotola et al. 1992, Lorimer et al. 1994). Reasons for replacement are debated, but Lost Ridge appears to be following this trend.

Sapling Growth in Gaps and Closed Canopy Plots

Sipe and Bazzaz (1994, 1995) indicated that sugar maple showed little release growth in response to gaps in Harvard Woods, Massachusetts. On the other hand, Canham (1988a) found that sugar maple, although present in high densities under closed canopy, exhibited significant release growth in small gaps in the Adirondack Mountains, New York. Canham (1988a, 1989) suggested that sugar maple is an example of a species which is present in the understory but relies on gaps to increase growth and reach canopy height. The data of this study support Canham's hypothesis, as sugar maple was relatively more abundant under closed canopy than in gaps, but mean growth was approximately four times greater in the gap saplings than under the closed canopy (Table 2). Sugar maple had the greatest mean growth of any major sapling species (Table 3) and, in particular, was significantly greater than red maple.

Canham (1988a) indicated that beech also responds to low light level increases in small gaps. He noted that beech tends to respond less than sugar maple but grows more under closed canopy. In addition, Runkle (1984) found that beech is often present under a closed canopy as a few large saplings while sugar maple is present as abundant small saplings. Beech density in this study supports Runkle's finding in that beech is relatively more dense in gaps than would be expected based on a random distribution. On Lost Ridge, beech is growing more under closed canopy than is sugar maple, but less in gaps (Table 2). However, beech in this study doubled its average growth in gaps, a greater release growth response than was found by Canham (1988a).

The other dominant sapling species, red maple, is growing significantly less than beech or sugar maple (Table 3) within gaps, but its average growth in closed canopy plots is greater than beech and significantly greater than sugar maple. The data also tentatively indicate that upon

formation of a new gap, red maple has a height advantage over other saplings. It appears that red maple on Lost Ridge is capable of higher sustained growth under closed canopy but exhibits less of a response to gaps. Such a growth strategy might give red maple an advantage in very small gaps which remain open for only a few years. This strategy contrasts with that of sugar maple and may facilitate the coexistence of the two species.

Pawpaw, a subcanopy species commonly reproducing by sprouts (Lagrange and Tramer 1985), was the only sapling that grew significantly more under closed canopy than in gaps (Table 2). It also grew significantly more along the edge of gaps than in the center. However, pawpaw density was far greater in gaps than would be expected given a random distribution throughout the forest. Perhaps this subcanopy tree responds to gaps by increasing its clonal shoots rather than its growth. Field observations during this study indicate that pawpaw creates large clonal complexes within gaps, while in closed canopy plots it is represented by single individuals or small clumps of three to five clones.

Although growth differences within a single species between closed canopy plots and gaps were usually great enough to be statistically significant, differences in growth of different species within gaps were clouded by high variance within the sample (Tables 2 and 3). Individuals belonging to the same species exhibited an extremely high range of growth in gaps (Table 2). Apparently gaps provide an opportunity for, but not an assurance of, increased growth. Actual growth rates of individuals depend on both genetic potential and environmental microsite differences, such as variation in the amount of light reaching different areas of the gap (as demonstrated by Minckler et al. 1973).

A high degree of variability was also expressed in both density and diversity between gaps

and closed canopy plots. Because so many variables are involved in the formation of each gap, individual gaps represent highly unique microsites. Even within community groups, gaps may differ as much from each other as they do from their respective closed canopy plot or gaps in other community groups. Diversity within the Lost Ridge forest is likely increased by the high variability in both gap sites and individuals within the gaps. This variability allows numerous species to capitalize on gap events.

Within-Gap Partitioning

The differences in growth among red maple, sugar maple, and beech may represent between-gap partitioning based on gap size. Evidence of between-gap partitioning, in particular partitioning by size of gap, has been well documented in eastern North American deciduous forests (Minckler and Woerheide 1965; Barden 1981; Runkle 1982, 1984; and Canham 1988a, 1989). However, only ten gaps were surveyed in this study and conclusions based on comparisons of only these gaps must be tentative. Within-gap partitioning is another possible mode of gap partitioning (Barton 1984) which can be better documented in a study such as this. Theoretically, species may partition the gap site, even within relatively small gaps (Sipe and Bazzaz 1994, 1995). However, evidence for within-gap partitioning is scarce. Barton (1984) concluded that in neotropical forests of Costa Rica there was weak evidence to support the partitioning of large gaps by shade tolerant and pioneer species. Sipe and Bazzaz (1994, 1995) found photosynthetic differences between maple species, but little overall evidence of within-gap partitioning in small gaps ($<300 \text{ m}^2$) at Harvard Woods.

We found little evidence for within-gap partitioning of small gaps by potential canopy saplings. Although the data strongly support site differences within gaps (such as those between the northern and southern ends of gaps), no potential canopy species appears to be spatially partitioning these differences. Higher densities and growth rates in the northern end of gaps were probably the result of higher light levels (Minckler and Woerheide 1965, Canham 1988b), but no species displayed higher densities or growth in the southern end, as might be expected if species were partitioning the gap along a light gradient. Likewise, little evidence of gap partitioning along a light gradient was demonstrated by comparisons of the center and edge of gaps. Sub-canopy saplings of dogwood and pawpaw did show greater density and/or growth along the edge of gaps, but this tendency is probably part of the larger pattern of partitioning among subcanopy and canopy trees.

It is possible that trees recently extirpated by land use and other activities of man (such as *Castanea dentata* (Marshall) Borkh.) might have filled now vacant niches and thus given a clearer indication of gap partitioning. However, for partitioning within small gaps to occur, it would be expected that evolutionary pressures and disturbance regimes would have to remain constant for a relatively long period of time. It seems necessary that a regular pattern of small scale disturbances creating these gaps would have to follow periodic large scale disturbances over several successional periods with little environmental change in order for selection of particular traits and the development of gap partitioning in successional forests on such a fine scale. As recently as 9000 years ago, communities in this area were still reassembling following the end of the last ice age (Delcourt and Delcourt 1983). Evolutionary adaptations to gap exploitation may have developed while species of our current eastern deciduous forest were located in small isolated

refugia whose composition was much different than that of today (Tausch et al. 1993). Even relatively small scale climate changes during the Holocene have produced major impacts on eastern forests (Delcourt 1979), which have been in a period of flux for most of this time. Therefore, a constant selective pressure seems unlikely. In addition, recent short term environmental changes brought on by humans may have intensified this trend, creating new conditions and disturbances for which old adaptations are not suitable (Connell 1978, McAndrews 1988). Mortality rates within the Lost Ridge forest also seem to complicate an adaptive advantage for a well defined gap strategy. With 61% of all mortality in gaps due to random causes, the selective pressure placed on saplings to partition a gap spatially would be weakened.

The forest of Lost Ridge, like most of the eastern deciduous forests today, has been impacted by both human and climatically induced change. As a successional forest recovering from anthropogenic disturbance, it demonstrates forest processes that may be applicable to much of the eastern deciduous forest. Some evidence of between-gap partitioning is suggested by this study; additional studies are currently underway to examine the possibility. Lack of fine scale gap partitioning is probably reflective of both long and short term changes in the ecosystem. These changes prohibit the return of this forest to its pre-European condition.

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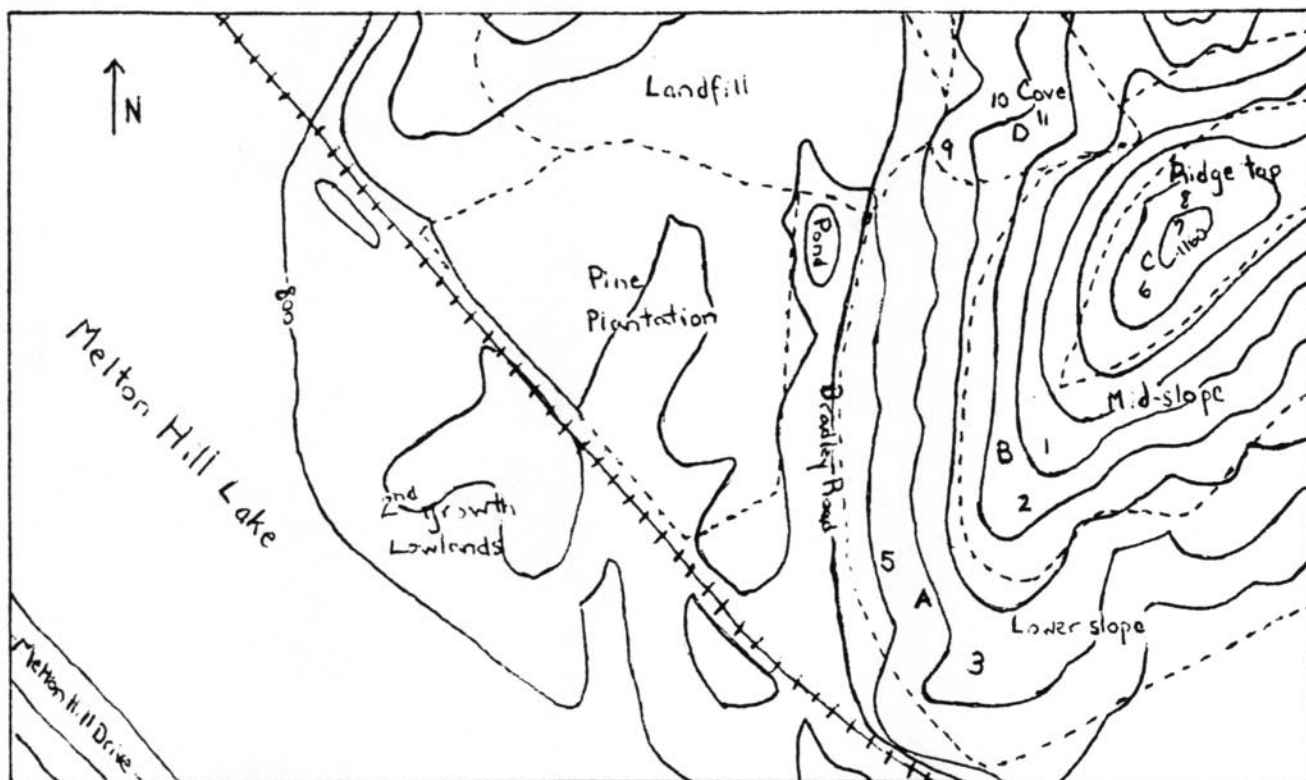
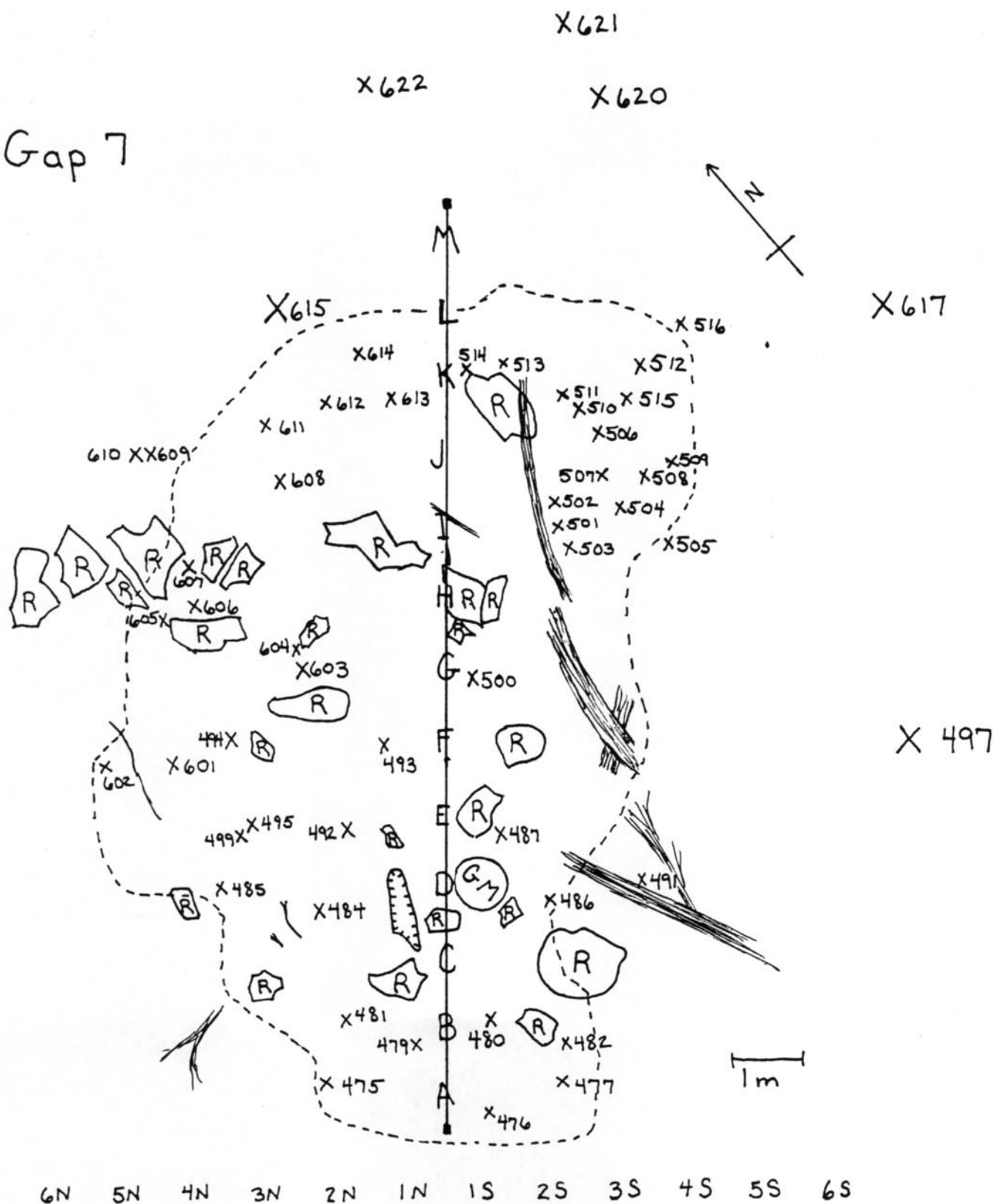


Figure 1. Map of Anderson County Wildlife Sanctuary with vegetation regions marked. Numbers signify location of study gaps; letters signify location of closed canopy plots. Contour interval = 40 feet.

Gap 7



- (R) rock
- X tagged tree
- (GM) gap maker (standing dead)
- canopy edge
- long axis of gap

Figure 2. Reproduction of the final map of Gap 7. Following this grid system, tree 486 would have a coordinate of 2SD.

Table 1. Species compositions showing successional changes. Percentages are based on total canopy, gap sapling, and closed canopy sapling stems.

Species	Ridge top			Mid-slope			Lower slope			Cove		
	% canopy stems	% gap sapling stems	%closed canopy sapling stems	% canopy stems	% gap sapling stems	%closed canopy sapling stems	% canopy stems	% gap sapling stems	%closed canopy sapling stems	% canopy stems	% gap sapling stems	%closed canopy sapling stems
	500m ² n=29	300m ² n=120	200m ² n=37	477m ² n=29	277m ² n=120	200m ² n=37	816m ² n=29	616m ² n=120	200m ² n=37	841m ² n=29	641m ² n=120	200m ² n=37
<i>Acer rubrum</i>	0.0	4.2	43.2	12.9	29.1	66.7	16.3	17.8	13.3	2.3	32.2	0.0
<i>Acer saccharum</i>	0.0	3.3	0.0	0.0	1.8	0.0	0.0	16.8	6.7	4.5	9.2	68.3
<i>Asimina triloba</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	24.5	11.0
<i>Carpinus caroliniana</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	6.7	0.0	2.7	1.2
<i>Carya glabra</i>	3.4	12.5	2.7	6.5	5.5	0.0	0.0	0.0	0.0	2.3	0.3	0.0
<i>Cercis canadensis</i>	0.0	0.8	0.0	0.0	3.8	0.0	0.0	0.0	0.0	0.0	1.4	3.7
<i>Cornus florida</i>	0.0	2.5	5.4	0.0	0.0	0.0	0.0	2.0	0.0	0.0	5.2	0.0
<i>Fagus grandifolia</i>	0.0	0.0	5.4	0.0	29.1	33.3	16.3	25.7	20.0	29.5	10.2	8.5
<i>Fraxinus americana</i>	0.0	2.5	0.0	0.0	0.0	0.0	0.0	2.0	0.0	4.5	2.8	3.7
<i>Juniperus virginiana</i>	0.0	0.0	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Liquidambar styraciflua</i>	0.0	0.0	0.0	0.0	0.0	0.0	2.3	9.9	6.7	0.0	0.6	0.0
<i>Liriodendron tulipifera</i>	0.0	0.0	0.0	0.0	0.0	0.0	9.3	0.0	0.0	40.9	0.7	0.0
<i>Nyssa sylvatica</i>	0.0	1.7	16.2	3.2	18.2	0.0	4.7	6.9	26.7	0.0	0.1	0.0
<i>Pinus echinata</i>	0.0	0.0	0.0	6.5	0.0	0.0	9.3	0.0	0.0	0.0	0.0	0.0
<i>Pinus virginiana</i>	34.5	37.5	0.0	32.3	0.0	0.0	9.3	0.0	0.0	0.0	0.0	0.0
<i>Prunus serotina</i>	3.4	8.3	5.4	0.0	5.5	0.0	0.0	13.9	20.0	0.0	1.0	0.0
<i>Quercus coccinea</i>	0.0	0.0	0.0	3.0	1.9	0.0	14.0	0.0	0.0	0.0	0.0	0.0
<i>Quercus montana</i>	44.8	3.3	2.7	29.0	0.0	0.0	0.0	0.0	0.0	6.8	0.0	0.0
<i>Quercus falcata</i>	3.4	0.0	0.0	3.2	0.0	0.0	4.7	0.0	0.0	0.0	0.0	0.0
<i>Quercus velutina</i>	10.3	3.3	0.0	3.2	0.0	0.0	9.3	0.0	0.0	0.0	0.1	0.0
<i>Quercus rubra</i>	0.0	0.8	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0
<i>Sassafras albidum</i>	0.0	16.7	10.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Tilia americana</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.8	5.7	0.0
Other*	0.2	2.6	8.1	0.2	1.5	0.0	2.2	2.0	0.1	2.3	3.3	3.6
Totals	100.0	100.0	99.9	100.0	100.0	100.0	100.0	100.0	100.0	99.9	100.0	100.0

* less than 3% in any category

Table 2. Comparison of sapling growth between gaps and closed canopy plots.

Species	Gaps				Closed Canopy				p-value
	mean growth (cm)	standard deviation	range (cm)	n	mean growth (cm)	standard deviation	range (cm)	n	
<i>Acer rubrum</i> *	14.10	12.19	56.2	132	10.04	6.61	21.8	30	0.007
<i>Acer saccharum</i> *	19.28	14.54	69.2	165	5.13	4.53	26.9	106	<0.001
<i>Asimina triloba</i> **	6.36	4.94	18.1	71	10.48	5.47	20.5	18	<0.001
<i>Fagus grandifolia</i> *	16.52	10.23	42.4	231	9.49	6.60	21.5	22	< 0.001
<i>Nyssa sylvatica</i> *	12.69	9.47	35.0	36	11.16	7.60	23.7	10	0.32
<i>Prunus serotina</i> *	13.77	8.13	43.8	67	6.84	2.39	6.0	5	<0.001

*growth in 1991 and 1992 **growth in 1994 and 1995

Table 3. Analysis of variance of growth of major sapling species which could potentially reach canopy height

ANOVA, single factor, summary

Groups	Count	Sum	Average	Variance	Tukey-Kramer
<i>Acer saccharum</i>	336	6680.7	19.88	221.06	a*
<i>Liquidambar styraciflua</i>	57	1096.2	19.23	322.69	a,b
<i>Tilia amercana</i>	147	2660	18.10	218.80	a,b
<i>Fagus grandifolia</i>	478	8330.8	17.43	109.16	a,b
<i>Fraxinus americana</i>	98	1663.2	16.97	121.26	a,b,c
<i>Nyssa sylvatica</i>	98	1478	15.08	135.16	b,c
<i>Pinus virginiana</i>	130	1939	14.92	77.84	b,c
<i>Carya glabra</i>	72	1048	14.56	145.97	b,c
<i>Prunus serotina</i>	138	1945.8	14.10	98.99	b,c
<i>Acer rubrum</i>	292	4108.6	14.07	146.72	c

* species sharing a common letter are not significantly different at the .05 level

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	8262.097	9	918.011	6.06991	1.9E-08	1.88497
Within Groups	277676.1	1836	151.24			
Total	285938.2	1845				

Table 4. Comparison of yearly mean leader growth in the northern and southern ends of gaps over a five year period (1988-1992) for major sapling species

Species	North			South			p=
	mean growth (cm)	s.d.	n	mean growth (cm)	s.d.	n	
<i>Acer rubrum</i>	17.90	14.36	103	8.27	8.22	71	<.001
<i>Acer saccharum</i>	20.39	14.71	119	15.70	13.12	81	0.01
<i>Cornus florida</i>	15.29	10.07	84	16.10	8.22	24	0.36
<i>Fagus grandifolia</i>	18.54	10.16	166	15.84	11.77	75	0.04
<i>Nyssa sylvatica</i>	15.19	14.64	27	15.74	9.79	23	0.44
<i>Pinus virginiana</i>	14.67	8.94	30	15.15	9.24	29	0.43
<i>Prunus serotina</i>	14.57	9.92	38	13.14	7.24	47	0.23
<i>Tilia americana</i>	16.56	8.51	26	19.48	22.96	20	0.3

Table 5. Densities of major sapling species in the northern and southern ends of gaps, p-value indicates the likelihood that these densities reflect an even, random distribution

Species	Individuals in north	Individuals in south	Total Individuals	p=
<i>Acer rubrum</i>	28	16	44	0.06
<i>Acer saccharum</i>	31	19	50	0.08
<i>Carpinus caroliniana</i>	14	2	16	0.002
<i>Carya glabra</i>	5	4	9	0.7
<i>Cercis canadensis</i>	2	3	5	0.7
<i>Cornus florida</i>	22	6	28	0.002
<i>Fagus grandifolia</i>	42	18	60	0.001
<i>Fraxinus americana</i>	13	0	13	0.0003
<i>Liquidambar styraciflua</i>	4	2	6	0.4
<i>Liriodendron tulipifera</i>	5	0	5	0.02
<i>Nyssa sylvatica</i>	6	5	11	0.7
<i>Pinus virginiana</i>	10	9	19	0.8
<i>Prunus serotina</i>	9	11	20	0.7
<i>Sassafras albidum</i>	9	3	12	0.08
<i>Tilia americana</i>	7	5	12	0.5

Table 6. Comparison of yearly mean leader growth in the center and edge of gaps over a five year period (1988-1992) for major sapling species

Species	Center			Edge			p=
	mean growth (cm)	s.d.	n	mean growth (cm)	s.d.	n	
<i>Acer rubrum</i>	15.90	11.96	45	13.68	12.14	248	0.13
<i>Acer saccharum</i>	19.92	15.16	104	19.70	14.82	234	0.45
<i>Asimina triloba</i>	6.49	5.99	60	9.25	8.13	205	0.002
<i>Cornus florida</i>	12.29	11.43	47	16.81	11.02	114	0.01
<i>Fagus grandifolia</i>	18.24	11.45	84	17.26	10.23	394	0.22
<i>Fraxinus americana</i>	17.41	9.95	29	16.78	11.49	69	0.40
<i>Nyssa sylvatica</i>	19.70	11.18	22	13.75	11.48	76	0.02
<i>Pinus virginiana</i>	15.32	9.56	22	14.89	8.73	107	0.42
<i>Prunus serotina</i>	13.70	8.17	34	14.23	10.50	104	0.38
<i>Tilia americana</i>	18.18	9.88	41	18.06	16.34	106	0.48
all species	15.92	12.11	567	16.08	12.64	2123	0.4

Figure 3. Mortality rates of *Acer rubrum*, *A. saccharum*, and *Fagus grandifolia* in gaps over a three year period, 1992-1995

