Gap Phase Dynamics of a Mature Indiana Forest

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Introduction

The classic view of forest succession has been subjected to increasing scrutiny in recent years with research focusing on the spatial and temporal dynamics of forests. Forested ecosystems are characterized by change and equilibrium is rarely if ever achieved (13,14). In recent years research has focused on disturbance, both internal and external to the ecosystem, and its role in determining species distributions within forest communities (1,5,15). The effects of such large scale exogenous disturbances as wildfire, flooding, and clearcutting on forest compositional change have been well documented for many regions in the country, but only recently has attention shifted toward endogenous perturbations such as single and/or multiple canopy tree falls resulting from senescence and death or minor, localized wind forces.

The fall of a dominant or codominant canopy individual, for whatever reason, creates a gap in an otherwise closed canopy which increases solar radiation to the forest floor. Increased light levels favor the release and subsequent growth of previously suppressed, shade tolerant individuals and may provide conditions favorable for colonization by new individuals of early to mid-seral species. Thus, these dynamic gap replacement processes may be the key to understanding species abundance and distributions within forested ecosystems (10,12,16).

The long-term dynamics of the Eastern Deciduous Forest are not well understood, and this is especially true of the Central Hardwoods Region which includes the till plain region of central Indiana, Ohio, and Illinois. Most stands are dominated by various *Quercus* species in the canopy while understories are comprised largely of *Acer saccharum, Fagus grandifolia* and *Ulmus* species (2,3,4,7,11). The purpose of this study is to attempt to relate canopy gap replacement processes to this apparent compositional change by determining species composition and diameter class distributions within canopy light gaps.

Study Area

The Davis-Purdue Research Forest (Figure 1) is located in Randolph County in east-central Indiana (Section 23, T21N, R12E). This old-growth forest, dominated by *Quercus* species, is registered as a National Natural Landmark by the National Park Service and has been recommended for State Nature Preserve status by the Indiana Department of Natural Resources, Division of Nature Preserves. It is one of the largest (20.6 ha) remaining old-growth deciduous forests on the Tipton Till Plain and has not been significantly disturbed since 1917 when it was donated to Purdue University by the Davis family. Some removal of dead or dying trees did occur during the middle part of this century, and grazing by domestic livestock probably occurred prior to 1917. Specific details on the history, topography and soils of this stand are given elsewhere (6,7).

Methods

In 1926, Professor Burr N. Prentice of Purdue's Department of Forestry divided the Davis-Purdue Research Forest into fifty-five quadrats (most an acre in size) and mapped all stems which were greater than 4 in (10.2 cm) dbh (diameter at breast height

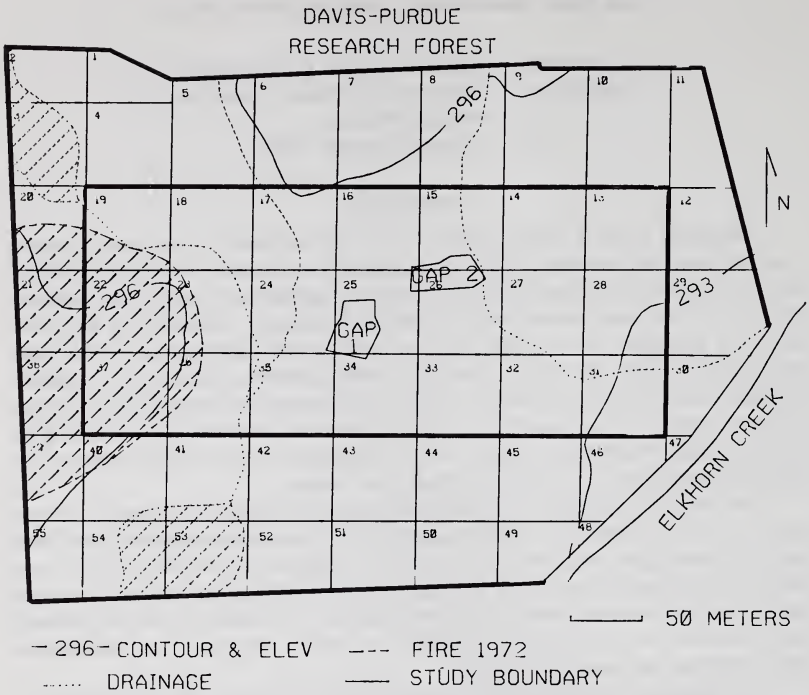

FIGURE 1. Computer map of Davis-Purdue Research Forest showing the location of Gaps 1 and 2.

= 1.37 m aboveground) within each quadrat. Each tree was numbered, measured for diameter and height, described in detail by species, and tagged (8). In 1976 forty-six of the original quadrat corners were relocated, and the remaining twenty five were approximated with a staff compass and 100 ft tape. Within the central 21 quadrats (8.5 ha) all stems greater than or equal to 10 cm dbh were measured for diameter by species and mapped to the nearest meter. Trees were then classified as ingrowth, survivors, or mortality based on a comparison of map location in 1926 vs. 1976 and the presence of a 1926 tag. Ingrowth were those individuals not tagged in 1926 but at least 10 cm dbh in 1976 (6,7).

During the summer of 1985 two canopy gaps were located in the central 8.5 ha of the Davis-Purdue Research Forest (Figure 1). Canopy gaps were defined as openings in the canopy created by the fall of a dominant or codominant individual or canopy openings created by crown breakup of dead dominant or codominant individuals which were still standing (snags). The boundary of the canopy gap was defined to be the boles of the surrounding perimeter trees whose crowns formed the outer perimeter of the light gap. Thus, the entire canopy gap area was defined to be the area of the light gap opening in the canopy plus the expanded gap area to the boles of surrounding perimeter trees (9).

Within the gap, all individual stems which were greater than or equal to 0.5 cm at dbh were measured for diameter and tallied by species. Selected individuals of the surrounding perimeter trees were cored with an increment borer for annual ring analysis

in the laboratory. In order to determine the date of gap formation, and thus gap age, annual rings were analyzed with the aid of a Henson Incremental Measuring Machine to determine differential release in annual ring growth as a response to increased light levels.

Results and Discussion

Gap 1 is located on a well drained, mesic upland site with a north to south orientation and a total area of 0.0942 ha (Figure 2). This gap was formed by the death of

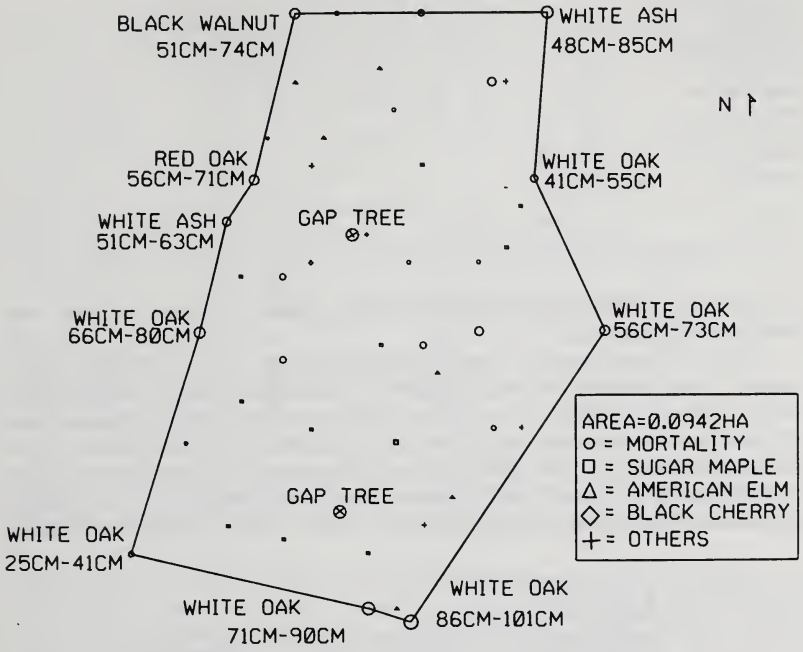

FIGURE 2. Computer illustration of Gap 1 showing: perimeter trees with 1926 dbh-1976 dbh, gapmaker trees, and the mapped location of all stems 10 cm dbh or greater.

two *Quercus alba* individuals, still standing at the time of sampling. Gap perimeter trees, 70 percent of which are *Quercus* species, are shown with their 1926 and 1976 diameters. The location of all subcanopy individuals, 10 cm dbh or greater, which were alive at the time of sampling or had died since 1926 are also given in Figure 2. Living stems are well distributed over the gap area.

Acer saccharum is dominant across all occupied diameter classes in Gap 1 with a relative density of 48% for stems 10 cm dbh or greater and 64% for stems 0.5 cm dbh to 9.9 cm dbh (Table 1). This species also occupies the largest diameter class for all stems found within the gap. *Ulmus americana* occupies a secondary position in this gap, being confined to the mid to lower diameter classes with a relative density of 26% in the 10 cm dbh or greater classes and only 4% for stems 0.5 cm dbh to 9.9 cm dbh. Ten other tree species, two subcanopy tree species and one shrub were sampled in this gap. Most of the individuals found growing within the gap boundary

TABLE 1. Number of Stems/HA by species and diameter class for Gap 1.

	Diameter Class (CM, Lower Limit)										
SPECIES	0.5	2.5	5.0	7.5	10.0	12.5	15.0	17.5	20.0	22.5	25.0>
Acer saccharum	1218	461	102	31	61	41			10		10
Aesculus glabra	450	31									
Fagus grandifolia	20					10					
Prunus serotina					20				10		
Tilia americana									10		
Fraxinus americana	51										
Carya cordiformis			10	10							
Carya glabra	10										
Celtis occidentails			10								
Acer negundo	10										
Ulmus americana	82	41	20	41	41	20					
Ulmus rubra	31										
Carpinus caroliniana	82		20		10						
Ostrya virginiana	31	20				10					
Lonicera sep.	20										
TOTALS	1923	553	162	82	132	81			30		10

are normally classified as late seral, shade tolerant species. No *Quercus* species were found growing in the gap.

Gap 2 is located partly in a moist depressional area with a small drainage way running through one corner of the gap (Figure 3). This gap has an east to west orientation with a total area of 0.0909 ha. Two *Quercus rubra* individuals and one *Quercus bicolor* individual are the gapmakers on this site, and all three of these individuals are down as a result of windfall. Eighty percent of the gap perimeter trees are *Quercus* species with *Quercus rubra* making up 40%; *Quercus macrocarpa* making up 30%, and *Quercus muehlenbergii* making up the remaining 10%. Figure 3 shows no apparent clumping

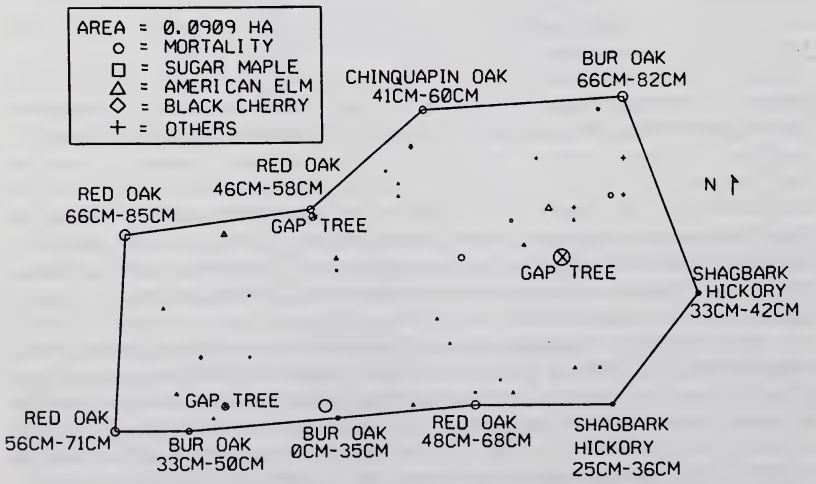

FIGURE 3. Computer illustration of Gap 2 showing: perimeter trees with 1926 dbh-1976 dbh, gapmaker trees, and the mapped location of all stems 10 cm dbh or greater.

pattern for individuals 10 cm dbh or larger growing within the gap boundary although there is a conspicuous absence of *Acer saccharum* in the eastern section of the gap. *Ulmus americana* appears to be randomly distributed throughout the gap.

Ulmus americana is dominant on this site across the middle to upper diameter classes with no individuals found occupying the 0.5 cm and 2.5 cm diameter classes (Table 2). This is reflected by the reduction in relative density for this species from

TABLE 2. Number of Stems/HA by species and diameter class for Gap 2.

	Diameter Class (CM, Lower Limit)										
SPECIES	0.5	2.5	5.0	7.5	10.0	12.5	15.0	17.5	20.0	22.5	25.0>
Acer saccharum	319	286	55	33	33						
Aesculus glabra	33	11		22	33						
Fagus grandifolia					11						
Fraxinus americana	11			11	11						
Carya cordiforms	22		11								
Fraxinus nigra	33	11									
Carya ovata		22									
Quercus muehlenbergil	11	11									
Prunus serotina								22			
Celtis occidentalis		22									
Acer negundo	33	44		11	11						
Ulmus americana			33	22	77	44	33		22		11
Ulmus rubra	33	22			11						
Carpinus caroliniana	11	44			11		11				
Asimina triloba	231										
Crataegus spp.	11				11						
Cornus racemosa	44										
Lindera benzoin	572	22									
TOTALS	1364	495	99	99	209	44	44	22	22		11

57% for the 10 cm dbh or greater diameter classes down to 3% for the 0.5 cm dbh to 9.9 cm dbh classes. In contrast to Gap 1, *Acer saccharum* on this site is confined to the middle and lower diameter classes with a relative density in the 10 cm dbh or larger diameter classes of only 7% while comprising 33% of the 0.5 cm dbh to 9.9 cm dbh diameter classes. Only two small diameter individuals of *Quercus muehlenbergii* were found in this gap. There is an increase in species richness, from 15 species occupying Gap 1 to a total of 18 species occupying Gap 2, with an associated increase in the relative abundance of moist site shrubby species.

The increase in the relative abundance of moist site shrubby species in Gap 2 (i.e. *Asimina triloba* 11% and *Lindera benzoin* 29%) probably preempts space which would otherwise be occupied by *Ulmus americana*. We might expect therefore that if these shrubby species were removed from this site there would be an associated increase in the relative abundance of *Ulmus americana* in the lower diameter classes. Although *Ulmus americana* occupies a dominant position on this site, it is not expected that any individuals of this species would mature to reach canopy status. Past studies in this forest have shown that Dutch elm disease and elm yellows (phloem necrosis) attack this species before individuals can reach canopy status, and only early reproductive maturity and shade tolerance allow *Ulmus americana* to persist as an important component though restricted to the smaller diameter classes (6).

Determining gap age, based on analysis of increment cores taken from selected gap perimeter trees, proved to be very difficult. Eight cores were analyzed in order

to determine differential increase in diameter growth as a result of increased light levels on the crowns of gap perimeter trees. For Gap 1, increment cores taken from four individuals of *Quercus alba* were analyzed along with a core from a *Fraxinus americana* individual. Increment cores from three individuals of *Quercus rubra* were anlayzed for Gap 2. In no case was a sharp increase in growth of annual rings discernable, although in several cases small gradual increases in annual ring growth were detected. This is probably attributable to the general lack of vigor of these large diameter perimeter individuals which is reflected in their inability to respond to crown release. Based on the detected small increases in annual increment, Gap 1 was aged at approximately 5 years, and Gap 2 was aged at approximately 12 years in the east section and approximately 1 to 2 years in the west section. This estimate for the west section correlates with the general lack of decay in the two *Quercus rubra* windfall individuals. Based on the above results, future age determination for canopy gaps will be accomplished by coring larger diameter individuals growing within the gap and sectioning individuals in the gap to determine release dates. This method would also provide the necessary data to determine whether stems occupying the gap are previously suppressed individuals or opportunists which colonized the opening after gap formation.

Conclusion

An earlier study in the Davis-Purdue Research Forest has shown that despite its old-growth appearance, this forest has undergone major structural and compositional change since 1926. For individuals 10 cm dbh and larger, early and mid-seral species are gradually being replaced by the more shade tolerant, late seral and climax species (7).

Although the sample size is small, the present study on gap replacement processes in the Davis-Purdue Research Forest supports this earlier conclusion with data on species replacement patterns within two canopy gaps. While 70% of the dominant perimeter individuals surrounding Gap 1 are *Quercus* species, no *Quercus* species individuals were found growing within the canopy gap. *Acer saccharum* accounts for 64% of stems less than 10 cm dbh, 48% of stems 10 cm dbh or larger, and the largest diameter individual in the gap. Although preliminary at best, we might expect *Acer saccharum* to maintain dominance in this opening and attain canopy status.

Of the 10 dominant individuals surrounding Gap 2, 80% are *Quercus* species while only two small diameter *Quercus muehlenbergii* individuals were found growing within the gap. On this moist site, preemption of space by shrubby species dominates the smaller diameter classes. *Ulmus americana* accounts for 57% of all stems 10 cm dbh or larger while *Acer saccharum* comprises 33% of all stems less than 10 cm in diameter. Although dominant on this site, it is doubtful whether *Ulmus americana* individuals will ever reach canopy status due to disease. This species should, however, maintain itself on this site and remain an important component, possibly excluding other species from reaching canopy status. *Acer saccharum* will probably dominate the better drained western section of this gap and perhaps reach canopy status.

The findings of this study support the hypothesis of a shift in species dominance in this forest. While the canopy of this old-growth forest is made up mostly of mid-tolerant *Quercus* species dominants, the composition of the replacement individuals is mostly shade tolerant *Acer saccharum* with *Ulmus americana* remaining an important understory component. As single tree and group selection cuts closely emulate single and multiple treefall canopy gaps, it is doubtful whether these silvicultural methods actually favor *Quercus* species reproduction. Most likely, as shown in this study, late seral, shade tolerant species like *Acer saccharum* are favored by these methods.

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