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GAP REGENERATION IN SOME OLD-GROWTH FORESTS OF THE EASTERN UNITED STATES[1]

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Abstract. Tree replacement in gaps was studied in old-growth mesic forest stands in western Pennsylvania, Ohio, and the southern Appalachian Mountains. Predictions of future overstory composition, based on sapling composition in small gaps (average 200 m^2), were compared to current canopy composition. Both Markov analyses and simple average sapling composition of gaps support the hypothesis that regeneration in small gaps was sufficient to perpetuate the current canopy species composition of the stands studied. In some cases the saplings most likely to replace a dead canopy tree were of the same species. In other cases, especially low-diversity beech-sugar maple stands, each species seemed to enhance significantly the success of the other species.

Key words: Acer saccharum; *climax;* Fagus grandifolia; *gap phase disturbance; Great Smoky Mountains; Hueston Woods; Markov analysis; mixed mesophytic forest region; overstory-understory interactions; Tionesta; transition probabilities.*

INTRODUCTION

Forest succession or regeneration may be thought of as the sum of processes by which one canopy individual is replaced by another. In a succession the individuals tend to be of different species. In the regeneration of a 'climax' forest, the same species, at least on the average, are represented in roughly the same proportions after each regeneration cycle (i.e., after all canopy individuals present at one time have been replaced).

One approach to modeling this process is to construct a table of transition probabilities for each of the future states of the system based upon a knowledge of the present state. Such a table would give the probability of each potential canopy species occurring on a site after one generation, given the species of canopy tree presently on that site. If the transitions depend only on the present state of the forest, not on how it is reached, and if the transition probabilities are constant, the resulting matrix is a stationary Markov chain, which can be used to estimate the steady-state composition of the forest and to predict the response of the system to various types of perturbations (changes in initial species composition).

The stationary Markov chain approach has been used successfully by Stephens and Waggoner (1970) and Waggoner and Stephens (1970), from which the above statement was paraphrased. Their matrix of transition probabilities was based on several complete inventories of stems in four second-growth Connecticut forests over a period of 40 yr. During that time the probability that dominance in a given 0.01-ha plot would shift from one tree genus to another remained roughly constant for all pairs of major genera. Horn (1975*a*, *b*) constructed a transition matrix for a New Jersey mixed forest by recording the fraction of saplings of different species found under canopy trees of different species and assuming that all saplings had the same probability of replacing the canopy tree. Again, the match between predicted and actual canopy composition of his oldest, least disturbed stand was reasonably good. Botkin et al. (1972) and Shugart and West (1977) derived the transition probabilities from stochastic functions of species biology and the physical environment.

The present paper, which is part of a larger study on gap phase dynamics in unlogged mesic forests (Runkle 1979), examines likely transitions from one canopy species to another in windfall gaps. This examination has three main objectives: first, to compare several different methods of estimating transition probabilities to determine which is more generally successful at predicting the observed canopy composition; second, to determine whether disturbances created by individual treefalls are sufficient to perpetuate the current canopy species composition of the stands studied; and third, to examine the extent to which the species of tree creating a gap is related to the species composition of saplings in that gap.

STUDY AREAS

I sought study areas in which the predominant mode of forest regeneration is the formation and filling in of small gaps. Therefore, my basic criteria for choosing a suitable forest stand were that it be (a) without any obvious large-scale human or natural disturbances, as determined from historical records and the presence of very large individual trees, and (b) without evidence of extensive chestnut (*Castanea dentata*) mortality

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(which would greatly affect estimates of more normal rates of gap formation and more normal gap sizes). To decrease variability within and between samples, I also restricted myself to stands with reasonably homogeneous canopy species composition for an area of at least several hectares and with dominance by some combination of such mesic tree species as hemlock (*Tsuga canadensis*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), yellow birch (*Betula lutea*), yellow buckeye (*Aesculus octandra*), mountain silverbell (*Halesia carolina*), and white basswood (*Tilia heterophylla*), i.e., stands of the mixed mesophytic forest type and its segregates (Braun 1950). I avoided areas subject to recurring large-scale disturbances such as fire or hurricanes.

Some stands within each of the following areas were sampled: Great Smoky Mountains National Park of North Carolina and Tennessee; Joyce Kilmer Wilderness Area of western North Carolina; Walker Cove Research Natural Area near Asheville, North Carolina; Hueston Woods State Park near Oxford, Ohio; and Tionesta Scenic and Natural Areas in northwestern Pennsylvania. Although in general the stands studied seemed to fit the criteria concerning disturbance history and species composition listed above, large disturbances may have occurred in some stands. In the area now included in the Great Smoky Mountains National Park, logging and settlements had occupied large areas. Although areas totally logged were easy to avoid, some selective cutting may have occurred within some of areas studied. Also, although no large fires or hurricanes have been recorded within the types of stands studied, occasional tornadoes destroying several hectares of forest have been noted and so may have affected my stands sometime in the past. In Joyce Kilmer small tornadoes appear periodically (C. Lorimer, *personal communication,* Runkle 1979) and probably are important in influencing canopy composition. However, gaps created by single trees also are important. My sample included gaps created by single trees, and by as many as nine canopy trees, and therefore should cover most of the range of gap sizes which normally occur. In northwestern Pennsylvania as a whole, large-scale disturbances have occurred frequently enough to have generated stands of white pine (*Pinus strobus*), such as occur at Heart's Content and Cook's Forest (Lutz 1930, Morey 1936*a, b*). Although mature white pine has not been recorded at Tionesta, windstorms in 1808 and 1870 damaged two large areas within the Tionesta Scenic and Research Natural Areas, causing increases in relatively shade-intolerant hardwood species (Bjorkbom and Larson 1977). The areas I studied were not affected greatly by those two windstorms, however. Thus the region as a whole probably has been strongly influenced by both large- and small-scale disturbances. Another influence in Tionesta is heavy browsing by deer, which can seriously affect the regeneration of many hardwoods (Jordan 1967, Marquis 1974, 1975, Bjorkbom and Larson 1977). Hueston Woods has remained relatively undisturbed since its original purchase in 1797. However, selective logging for desirable species probably occurred, and the undergrowth in some places has received heavy trampling.

To meet the objectives of this paper I needed to analyze samples with a reasonably homogenous species composition but with enough gaps examined to reduce errors due to small sample size. The analyses to be described were repeated for the following six areas. The first study area, the southern Appalachians as a whole, included all sites from the Great Smoky Mountains, Joyce Kilmer, and Walker Cove. In order to reduce within-sample variability, within the southern Appalachians I repeated the analyses for Roaring Fork, a midelevation cove with much hemlock, Albright Grove and Kalanu Prong, midelevation coves with substantially less hemlock, and Walker Cove, a high elevation cove with no canopy hemlock or silverbell. Hueston Woods and Tionesta were analyzed separately. The number of gaps sampled and canopy species composition for each study area are given in Table 1.

METHODS

Beginning at randomly chosen points, transects were walked along compass lines parallel to the long axis of each suitable study area. At random places along these transects the point-centered quarter method (Cottam and Curtis 1956) was used to record the canopy vegetation: the first point fell 0–25 paces from the beginning of the transect and subsequent points 25–75 paces (approximately 17–50 m) apart. At each point were measured distances to and diameters of nearest trees $\geq$25 cm dbh in each quarter; trees of $\geq$25 cm dbh usually have reached the canopy and can create gaps.

A gap is defined to include the ground area under a canopy opening extending to the bases of canopy trees surrounding the canopy opening. This definition was adopted for two reasons. First, it includes areas directly and indirectly affected by the canopy opening: the effects of light, especially, may be offset from the gap center. Second, at least some of the forestry literature (e.g., Tryon and Trimble 1969) defines opening the same way I define gap, although a precise definition of 'opening' often is not given. For the purposes of this study gaps are taken to become indistinguishable from the background overstory when regeneration within the gap has reached a height of 10–20 m.

The area A for each gap intersected by the transects was estimated by fitting gap length L (largest distance from gap edge to gap edge) and width W (largest distance perpendicular to the length) to the formula for an ellipse (most gaps are shaped at least roughly like an ellipse; $A = \pi LW/4$). The regeneration within the gap was recorded as the number and species of woody

TABLE 1. Relative densities (%) of trees ≥25 cm dbh. "Other" includes species in the canopy not represented in a particular sample by at least one gapmaker; it may include a species listed below if that species is represented in only some study areas by at least one gapmaker. Study areas are as follows: SA = Southern Appalachians, AK = Albright Grove and Kalanu Prong, RF = Roaring Fork, WC = Walker's Cove, TA = Tionesta, HW = Hueston Woods; see text for details. Sample sizes are given as the number of trees selected using the point-centered quarter method and as the number of gaps intersected by transects and used in the analysis.

	Study areas					
Species	SA	AK	RF	WC	TA	HW
Acer rubrum	1	. . .	. . .	. . .	7	. . .
A. saccharum	16	14	12	34	5	39
Aesculus octandra	8	8	1	20	. . .	. . .
Betula lutea and *B. lenta*	4	6	1	. . .	6	. . .
Fagus grandifolia	18	19	15	22	58	41
Fraxinus americana	2	2	. . .	4	. . .	. . .
Halesia carolina	17	20	23	. . .	. . .	. . .
Liriodendron tulipifera	1	. . .	1	. . .	. . .	. . .
Magnolia fraseri	<1	1	. . .	. . .	. . .	. . .
Tilia heterophylla	7	7	. . .	11	. . .	. . .
Tsuga canadensis	23	20	41	. . .	20	. . .
Other	3	3	6	9	4	20
Number of trees	1498	471	264	295	828	408
Number of gaps	256	80	38	34	75	36

stems ≥1 m high and the dbh and species of woody stems ≥2 m high. All individuals ≥1 m high within gaps will be referred to as saplings. The species of the tree(s) creating the gap ('gapmakers') also was noted; only rarely was it difficult to determine the species.

For each study area only species represented by at least one gapmaker are used in the analysis of gapmakers and saplings. Eliminating rarer species can cause some important events to be missed, e.g., the invasion into a stand of a species not yet well established in the canopy. However, rare species were not included for two reasons. First, in the computation of transition probabilities given below it is helpful for each species to be represented as a gapmaker at least once. Second, it reduces the problem of species (trees or shrubs) which are common as seedlings or as understory individuals but which rarely reach the canopy. A size distribution heavily skewed to small individuals can indicate either high mortality (e.g., white ash, *Fraxinus americana*, in many stands), a relatively small maximum height limit (e.g., Juneberry, *Amelanchier arborea*, or ironwood, *Ostrya virginiana*), or a population about to increase in importance. For the stands studied the first two possibilities seem more important; eliminating rare species in other stands where the third possibility is more likely (e.g., in the case of hardwoods invading a first generation pine plantation) could produce an erroneous interpretation, however.

For each gap I computed three measures of importance for each species: relative density (fraction of stems ≥1 m high in the gap), relative dominance (fraction of total basal area in the gap), and the average of these two values.

The probability of transition from canopy species i to canopy species j was assumed equal to the relative importance of species j in gaps created by species i. Therefore, the expected importance of species j in the next generation is

$$N_j(t + 1) = \sum_i N_i(t)P_{ij}$$

where $N_j(t)$ is the relative importance of species j in the canopy in generation t and P_{ij} is the transition probability that species j will replace species i. The measures of sapling importance used are fairly crude since they assume that the future growth and survival rates of each sapling of a given size are identical, without regard to species or environmental differences (e.g., between large and small gaps). This is clearly a first-order approximation but it has the merit of being easy to apply to a fairly wide range of species and location.

The equilibrium species composition of trees ≥25 cm dbh was predicted in two ways using the composition of saplings in gaps. First, starting with the relative frequencies of different species among the recorded gapmakers in a given study area, the transition probabilities were used to estimate the relative frequencies of each species in the canopy for the next generation. Then, given the canopy composition in the second generation, the same transition probabilities were used to estimate the canopy composition of the third generation. The process was repeated until the canopy compositions of two consecutive generations were nearly identical. I used the final values for canopy composition obtained by this iterative procedure as one prediction of equilibrium canopy composition. The whole iterative procedure, from relative frequencies of gapmaker species to expected canopy composition at equilibrium, was repeated three times, once for each measure of sapling importance. A second prediction of canopy species composition at equilibrium was obtained by averaging the relative importance values of each sapling species for all gaps. Again three different sets of predicted values were obtained, one for each measure of sapling importance.

Horn (1975*b*) suggested weighting the predicted canopy importance value for each species by that species' potential longevity. However, I did not follow this suggestion, for three reasons. First, the key value here is not maximum species longevity but average time spent in the canopy, the difference between average age of death and average age at time of entry into the canopy. Values for average time spent in the canopy are poorly known and apt to be highly site specific, especially in rugged topography, where growth rates may vary greatly from site to site. Second, using maximum longevity values assumes that all species spend the same fraction of their lifespans in the canopy. However, species with relatively long maximum longevities (e.g., beech, hemlock, and sugar maple) probably spend relatively less of their lifespan as canopy individuals. Third, despite the above problems, adjusting for maximum longevities may be beneficial when the species studied vary greatly in that parameter; however, the stands studied were dominated by several tolerant species whose lifespans probably are similar.

Three estimates of canopy composition (based on trees $\geq$25 cm dbh) were obtained from the point-centered quarter data: relative density; the average of relative density and relative dominance; and the Wisconsin importance value (relative dentisy + relative dominance + relative frequency) expressed as a percentage. However, these measures produced similar results and so only those results based on relative density will be used here.

Comparisons between observed and expected canopy composition were made using percentage similarity (Whittaker 1975) and the correlation coefficient r with tests of its significance (Snedecor and Cochran 1967). The significance of interactions among canopy and sapling species was tested by an analysis of variance. For each of the 18 combinations of six study areas and three measures of sapling importance (relative density, relative dominance, and their average) the following model for sapling importance value (IV) was used:

$$IV_{ijk} = M + A_i + B_j + C_{ij} + E_{ijk},$$

where M is a scale parameter, A_i is the main effect of canopy species i, B_j is the main effect of sapling species j, C_{ij} is the interaction between canopy species i and sapling species j, and E_{ijk} is the error term for the kth replicate (gap) with canopy species i and sapling species j. Where interactions were found to be significant, a secondary analysis of variance was conducted for each sapling species to determine for which sapling species importance values showed significant overall variations among canopy species. Where significant overall variation was found, differences between particular pairs of species were tested for significance using Tukey's w-procedure (Steel and Torrie 1960), as modified by Spjøtvoll and Stoline (1973) for unequal sample sizes.

RESULTS AND DISCUSSION

Relationships between observed and predicted canopy composition

The study areas were dominated by various combinations of canopy species (Table 1). At least 91% of canopy trees were of species represented by at least one gapmaker for all study areas except Hueston Woods, where such species made up 80% of the canopy individuals (Table 1). Mean gap size (extending to the bases of trees surrounding the gap) was about 200 m^2 although it ranged from 28 m^2 to 2009 m^2.

Comparisons of observed and expected canopy composition based on percentage similarity (Table 2) and the correlation coefficients (not shown) were similar and complementary. Use of the correlation coefficient allows calculation of the probability that $r \neq 0$, i.e., that the two sets of values for canopy composition do not occur randomly with respect to each other. However, the significance level depends upon the number of species present; e.g., a perfect negative correlation will result if only two species are present and they are ranked in a different order by two different techniques, no matter how close in actual value. For that reason percentage similarity provides a clearer way of comparing predictions from different study areas. Also, significance levels for r are influenced more strongly by rare species than are the values of percentage similarity. Although a statistical test of significance for percentage similarity is not available, Bray and Curtis (1957) suggested that replicate samples of the same forest community probably would have values of $\approx$80–85%. To obtain another estimate of the sampling distribution for percentage similarity values I computed all 36 possible values for the eight stands in the southern Appalachians for which I had measured canopy composition (Runkle 1979). For these stands percentage similarity (mean ± SD) was 69.1 ± 16.0%, with a range of 25–80%.

Using a value of $\approx$85% for percentage similarity it can be seen that the match between observed and expected canopy composition is quite good, regardless of the exact prediction method used. The best fit for each technique is shown in Fig. 1. Because the match between observed and predicted canopy composition is fairly good for the mesic stands studied, a disturbance regime dominated by small gaps seems sufficient to account for the present canopy composition; i.e., the existence of occasional large-scale disturbances is not a necessary component of the regeneration cycle for these stands. For the Tionesta wilder-

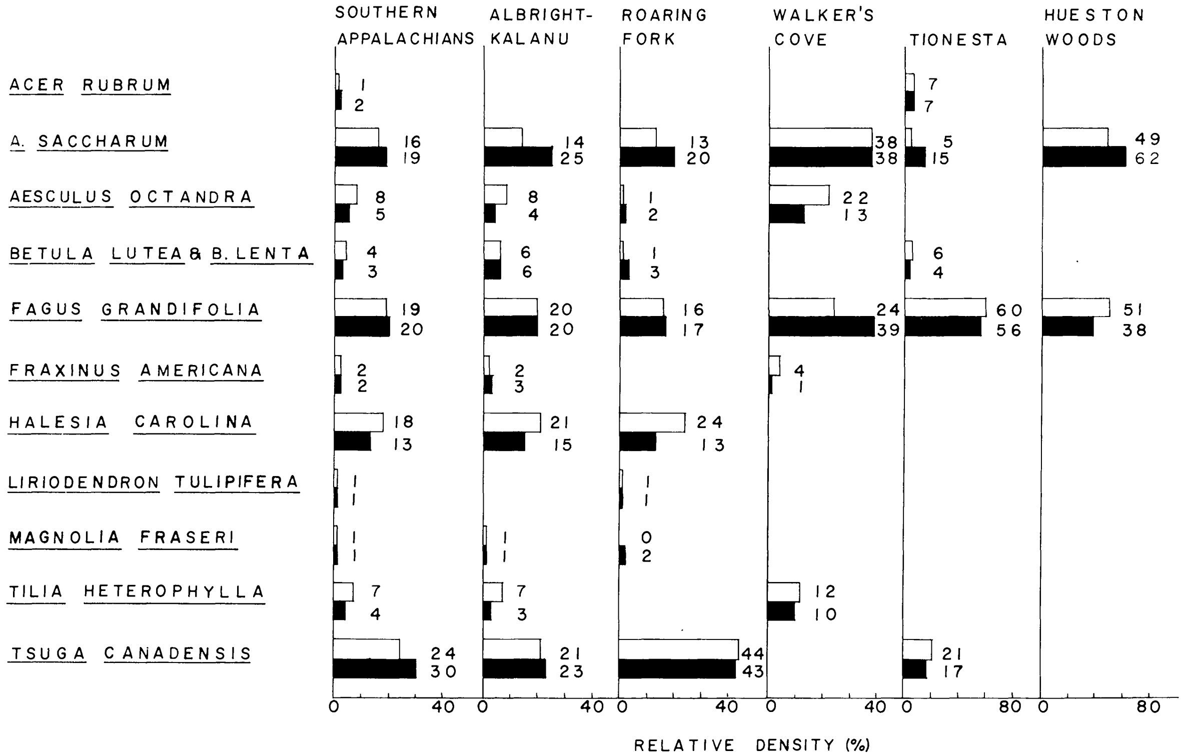

FIG. 1. Observed (open bars) and predicted (shaded bars) relative densities (%) of trees ≥25 cm dbh of species which were represented by at least one gapmaker. Observed values are from the point-centered quarter method. Predicted values are best fits from Table 2; in case of ties values for average sapling composition are used. Note the difference in abscissa scale for the right two study areas.

ness areas this result suggests that heavy deer browsing (Bjorkbom and Larson 1977) should have little immediate impact on canopy composition, largely because beech, the dominant species, is relatively unpalatable (Bjorkbom and Larson 1979).

The agreement between overstory and understory species composition is not, perhaps, surprising for these mesic stands largely dominated by tolerant species. However, because of the growing evidence that large-scale disturbances such as fires and massive windthrows are widespread (e.g., Heinselman 1973, Rowe and Scotter 1973, Spurr and Barnes 1973, Wright and Heinselman 1973, Henry and Swan 1974, Sprugel 1976, Lorimer 1977, Connell 1978, Garwood 1979) it is necessary to reaffirm the importance of small-scale disturbances in forests where they are most likely to be the primary source of forest turnover (Wright 1974).

TABLE 2. Percentage similarity between observed (point-centered quarter method) relative densities of trees ≥25 cm dbh and composition predicted from relative importance of saplings in gaps. Three measures of sapling importance were used: relative density in gaps, relative dominance in gaps, and the average of relative density and relative dominance. Predictions were made in two ways: by using a Markov analysis, and by averaging sapling composition under species. Study area symbols are explained in Table 1.

	Markov analysis by canopy species			Overall average sapling composition		
Study area	Relative density	Relative dominance	Average	Relative density	Relative dominance	Average
SA	80	78	87	80	80	87
AK	84	66	76	86	66	80
RF	62	76	88	65	79	88
WC	82	75	83	82	78	85
TA	75	89	84	75	89	85
HW	75	87	84	66	75	72

TABLE 3. Predicted canopy densities for three important species, using two different importance values, as a percent of all gapmaker species. Study area symbols are explained in Table 1.

Study area	*Acer saccharum*		*Fagus grandifolia*		*Tsuga canadensis*	
	Relative density	Relative dominance	Relative density	Relative dominance	Relative density	Relative dominance
SA	28	11	23	18	17	41
AK	25	6	19	11	23	52
RF	33	9	24	11	18	62
WC	47	29	33	46	...	...
TA	7	15	84	56	6	17
HW	83	74	17	26	...	...

The conclusion that the canopy compositions of the different areas are in equilibrium is based upon the assumption that the sapling species composition now will determine the canopy species composition later. However, another possible assumption is that the sapling composition now is determined by the present canopy species, with the rain of recruits into the understory roughly proportional to the importance of each species in the canopy. Both assumptions may be true, resulting in an equilibrium forest composition (sapling composition determines canopy composition which determines sapling composition and so on). On the other hand, differential growth and mortality among sapling species could result in a change in the species composition of the canopy. However, although some such changes did occur, in general the dominant species were important in gaps of all ages studied (through age 28 yr), implying that this possibility is unlikely to be very important (Runkle 1979).

For all study areas except Hueston Woods a better or equivalent fit was obtained with overall average sapling composition than with results from a Markovian analysis based on the species of former canopy tree in each gap. That is, in general, canopy individuals did not influence the species of their successors on a scale sufficient to affect strongly the future overall canopy composition. Despite this result, some relationships between particular pairs of canopy and sapling species were significant, as discussed below. However, apparently these differences were insufficient to counter errors introduced due to some gapmaker species being represented by few replicates (gaps).

In general a better fit between observed and predicted canopy composition was obtained by averaging relative density and relative dominance than by using either alone as a measure of sapling importance. The actual canopy densities of some species are predicted better using relative sapling density, and the actual canopy densities of other species are predicted better using relative sapling dominance. Table 3 summarizes results for sugar maple, beech, and hemlock. Sugar maple is usually present in a young gap as many small individuals capable of moderate growth rates. Because they are small an importance value based solely on basal area tends to underestimate their importance; because they are so numerous a value based only on density tends to overestimate it. The only exception occurs in Tionesta, where high deer population levels probably prevent sugar maple from becoming very dense in a gap (Jordan 1967, Marquis 1974, 1975, Bjorkbom and Larson 1977). On the other hand, hemlock is usually present as a few large individuals with very slow average growth rates (Frothingham 1915). Therefore importance values based partly on density underestimate it and, due to the slow growth rates, values based solely on basal area overestimate it. Beech varies from site to site. Generally relative density results in the higher estimate of its importance; in Walker's Cove, however, the reverse is true. Fig. 1 shows the extent to which all species are under- or overestimated by the predictions of equilibrium canopy density which most closely match observed canopy composition.

Sapling-canopy species interactions

The analysis of variance shows that the strength of sapling-canopy species interactions varies from study area to study area (Table 4). "Interaction" here is used in its statistical sense to mean variation in the relative importance of a sapling species in gaps created by different canopy species. Why some sapling species do better or worse in different gaps is a question not addressed here. In comparing the importance of sapling-canopy species interactions among different study areas it is useful to distinguish between the magnitude of interaction effects (*F* values) and their significance level (which depends upon sample size). In most cases the interactions between canopy species and sapling species were highly significant ($P \leq .01$); Roaring Fork and Walker's Cove were exceptions. In comparing the magnitude of the interaction effects Hueston Woods is singled out as showing especially strong relationships. Next strongest were interactions from the southern Appalachians as a whole. Tionesta and the Albright Grove and Kalanu Prong sites showed intermediate values.

Although overall sapling-canopy interactions may

TABLE 4. Significance of sapling-canopy species interactions based on an analysis of variance and a list of sapling species whose importance values show significant ($P \leq .05$) overall variation under different canopy species. Study area symbols are explained in Table 1. * = $.01 < P < .05$, ** = $P \leq .01$. Average = (Relative density + Relative dominance) ÷ 2. Table 2 was used to select best importance value.

Study area	Best importance value	Sapling × canopy F value	Number of observations	Significant sapling species
SA	Average	3.56**	3586	*Acer rubrum, Acer saccharum, Aesculus octandra, Fagus grandifolia, Magnolia fraseri, Tilia heterophylla, Tsuga canadensis*
AK	Relative density	1.90**	1221	*Acer saccharum*
RF	Average	0.71	408	. . .
WC	Average	1.64	230	. . .
TA	Relative dominance	2.71**	415	*Tsuga canadensis*
HW	Relative dominance	10.37**	66	*Acer saccharum, Fagus grandifolia*

be highly significant for a given area, examining sapling species individually may result in no significant variations in importance under different canopy species (i.e., even if the probability of several events occurring together by chance alone is very low, the probability of any one event occurring by chance may be fairly high). Thus, although overall sapling-canopy interactions were highly ($P \leq .01$) significant for the Albright Grove and Kalanu Prong sites, only sugar maple showed significant ($P \leq .05$) variations in sapling importance under different canopy species. Even for sugar maple, average values under no two canopy species were found to be significantly different from each other using Tukey's procedure. Similarly, in Tionesta only hemlock showed significant ($P \leq .05$) variations, with no two mean values being significantly different. Most of the significant interactions between specific pairs of species occurred in Hueston Woods and the southern Appalachians as a whole.

Results from Hueston Woods, Tionesta, and the southern Appalachians as a whole support and help clarify some of the tentative conclusions of a growing literature on sapling-canopy interactions in species-poor stands. Hueston Woods was dominated in both the understory and overstory by beech and sugar maple (Table 1). However, the relative proportions of the two species varied greatly in the two size classes: in the canopy the relative densities of sugar maple, and beech are 49% and 51%; among saplings in gaps overall the relative densities are 83% and 17%. Similar differences have been noted by several authors, who generally predict that sugar maple should increase in relative importance over time, citing such factors as regional decreases in both fire frequency and deer browsing over the last few decades as reasons for the shift (see general review by Vankat et al. 1975).

The idea of the present steady state between beech and sugar maple being achieved through sapling-canopy interactions has recently been explored by several researchers. Woods (1979) and Fox (1977) found that sugar maple seems favored under beech and beech under sugar maple, a situation Woods (1979) has termed 'reciprocal replacement.' Fox (1977), studying Warren Woods, a beech-sugar maple stand in southwest Michigan similar to Hueston Woods, examined possible reciprocal replacement in 47 gaps using two indices: total sapling density, and species of the largest saplings within each gap, giving ties to beech, which grows faster than sugar maple in these size classes (Laufersweiler 1955, Fox 1977: however, these sources do not indicate the environmental conditions, e.g., gap vs. nongap, in which the measurements were

TABLE 5. Transition probabilities for selected pairs of species, compared only to each other.

Sapling species	Transition probabilities under species No. 1	Transition probabilities under species No. 2	Equilibrium relative densities
A. Warren Woods: total density (Fox 1977)			
1. Sugar maple	.63	.77	.68
2. Beech	.37	.23	.32
B. Warren Woods: largest individual (Fox 1977)			
1. Sugar maple	.36	.77	.55
2. Beech	.64	.23	.45
C. Hueston Woods: relative dominance			
1. Sugar maple	.50	.80	.62
2. Beech	.50	.20	.38
D. Hueston Woods: relative density			
1. Sugar maple	.69	.86	.74
2. Beech	.31	.14	.26
E. Tionesta: relative dominance			
1. Hemlock	.22	.22	.22
2. Beech	.78	.78	.78

TABLE 6. Transition probabilities for the Southern Appalachians as a whole. Values with the same letter for the same sapling species are significantly different ($P \leq .05$) by Tukey's procedure. Significance values: ** = $P \leq .01$. Symbol + is used for values >0 but <.005.

Sapling species	Canopy species										
	Acer rubrum	*Acer saccharum*	*Aesculus octandra*	*Betula lutea*	*Fagus grandifolia*	*Fraxinus americana*	*Halesia carolina*	*Liriodendron tulipifera*	*Magnolia fraseri*	*Tilia heterophylla*	*Tsuga canadensis*
*Acer rubrum***	.01	+	.01	.03	.01	.02	.02	0	.03	.01	.03
*Acer saccharum***	.09	.26	$.35^{a}$	.14	.18	.21	.21	.23	$.10^{a}$	.27	.14
*Aesculus octandra***	.08	.09	$.23^{a-e}$	$.04^{a}$	$.04^{b}$	.10	$.05^{c}$	.02	$+^{d}$	.11	$.03^{e}$
Betula lutea	0	.02	.03	.05	.02	.01	.03	.04	.03	.03	.04
*Fagus grandifolia***	.17	.22	.16	.17	$.29^{a,b}$	.19	$.14^{a}$	0	.19	.19	$.16^{b}$
Fraxinus americana	.04	.02	0	.02	.01	0	.02	.01	.01	.01	.02
Halesia carolina	.04	.08	.05	.17	.12	.21	.13	.15	.11	.11	.15
Liriodendron tulipifera	0	+	+	.01	.01	0	+	0	+	+	.01
*Magnolia fraseri***	0	$+^{a}$	0^{b}	$+^{c}$	$0^{d,i}$	0^{e}	$.01^{f}$	0	$.06^{a-h}$	$+^{g}$	$.02^{h,i}$
*Tilia heterophylla***	.06	$.08^{e}$	.04	$.01^{a}$	$.03^{b}$	$.01^{c}$	.03	.08	.05	$.12^{a-d}$	$.02^{d,e}$
*Tsuga canadensis***	.50	.23	.12	.36	.28	.26	.34	.46	.41	.15	.36
Number of gapmakers	3	33	10	11	79	7	59	1	11	26	86

made). Transition matrices for beech and sugar maple saplings and canopy individuals are given in Table 5 for this study and that of Fox (1977).

Assuming approximately equal generation times these probabilities can be converted into equilibrium relative values. Let M and B be the equilibrium values for sugar maple and beech respectively. Then for Warren Woods using total density (Table 5, A):

$$M = (\text{Probability of maple replacing maple}) \times M + (\text{Probability of maple replacing beech}) \times B$$

$$M = .63M + .77B$$

$$M = 2.08B.$$

Letting $M + B = 100$ results in equilibrium values for sugar maple and beech of 68% and 32%. Similarly, for Warren Woods based on the largest sapling within the gap (Table 5, B):

$$M = .36M + .77B$$

whence equilibrium values are 55% and 45%.

These values may be compared with the canopy proportions 9% and 91% (Cain 1935, based on relative density of trees ≥25 cm dbh). Thus reciprocal replacement, particularly when based on the relative size of saplings, was useful in explaining part, but not all, of the discrepancy between canopy and sapling relative composition.

Similarly, Vankat et al. (1975) examined differences in composition between gaps and closed forest in Hueston Woods for canopy, subcanopy (individuals >2 m high), and smaller size classes. The effects of gaps were most pronounced for the subcanopy class. Relative Wisconsin importance values for sugar maple and beech were 39% and 61% for canopy individuals, 75% and 25% for subcanopy individuals under a closed canopy, and 51% and 49% for subcanopy individuals in gaps.

My results agree with the above studies in finding (a) that beech does better in gaps created by sugar maple and vice versa, and (b) that both species should persist at equilibrium though sugar maple should increase in relative canopy density. Although the conclusion that beech should decrease in relative canopy density is still tentative it is supported by the finding that in my sample, beech makes up 76% of the gapmaking individuals but only 52% of living trees ≥25 cm dbh.

The Tionesta region also has been examined previously; Fox (1977) found a reciprocal replacement scheme to exist between beech and hemlock. Converting my data into a transition table of just beech and hemlock (i.e., making each column section sum to 1.00), no sign of reciprocal replacement was detected (Table 5, E). The explanation for this discrepancy may arise from Fox's (1977) observation that large areas are dominated by beech and lack any hemlock reproduction. The reciprocal replacement phenomenon should be clear only near hemlock patches, where Fox (1977) conducted his studies. Because I did not record which beech-caused gaps occurred near hemlock, our results are not strictly comparable.

In Tionesta, beech had a relative dominance of .770 in gaps created by sugar maple vs. .536 in gaps created by beech and .562 in gaps overall, i.e., it seems to be favored under sugar maple but not appreciably harmed under itself. Sugar maple, on the other hand, had a relative importance of .199 in gaps created by beech vs. .085 in gaps created by sugar maple and .151 overall. Thus sugar maple seems to be favored under beech but also inhibited under itself. None of these relationships was significant, however, so the nature of the interaction between the two species remains unsettled.

Other studies in species-poor stands also have tended to find evidence for reciprocal replacement. Forcier

(1975) looked at associations among seedlings, saplings, and canopy individuals of beech, sugar maple, and yellow birch in central New Hamshire, and suggested that yellow birch tends to be replaced by sugar maple which tends to be replaced by beech, which tends to replace itself via root suckers until some disturbance occurs, at which time yellow birch gets established and the cycle begins again. Schaeffer and Moreau (1958) summarized much European work on alternation of species. Beech (*Fagus sylvatica*), fir (*Abies*), and spruce (*Picea*) regenerate better under each other than under themselves. Historical records have shown the same woodlot to alternate several times between two dominant species. In addition to Warren Woods and Tionesta, Fox (1977) examined several other communities dominated by two species. In most cases he found saplings of each species to be more common under canopy individuals of the other species than under their own species.

In contrast to these studies on species-poor stands, many more possible interactions among species exist within the southern Appalachians as a whole (Table 6). Interpretation of sapling-canopy species interactions is complicated because the several study areas lumped together differ somewhat in species composition, soils, and geology. Statistically, the effect of lumping sites is to increase the sums of squares or total variation in the model. However, total degrees of freedom also increase so the mean squares used in testing significance of results are similar. Obtaining a large sample size from one forest type would have been preferable, but the surviving unlogged remnants of the mixed mesophytic forest are small, so some lumping is necessary. Environmental differences among study areas need to be considered in interpreting the results, however.

Seven of the 11 species represented by at least one gapmaker in the southern Appalachians show significant variations in sapling relative importance under different canopy species. This high fraction of significant results is due both to the large sample size and to the relatively high magnitude of the variation (Table 4). Most pairs of values which are significantly different involve one species doing better under itself than under other species. In three of the four cases: beech, Fraser's magnolia (*Magnolia fraseri*), and white basswood, the species showing significant self-replacement relies to a great extent upon vegetative reproduction. The results for yellow buckeye confound two levels of association. On one scale, silverbell, Fraser's magnolia, and hemlock were entirely absent from the samples at Walker's Cove, where buckeye reached its maximum importance (Table 1). Although hemlock was found nearby, the relative scarcity of buckeye under these three species may be due to factors other than microsite considerations. The low importance of buckeye under yellow birch (which was present in Walker's Cove but relatively scarce and not represented by a gapmaker) may occur for similar reasons. However, buckeye's relative scarcity under beech cannot be so explained and may well represent significantly different microsite preferences. Also, the relatively large buckeye fruits probably do not disperse much beyond the parent tree. Microsite preferences also may be involved in two other significantly different pairs of values: basswood did better under sugar maple than under hemlock, and sugar maple did better under buckeye than under Fraser's magnolia. No tendencies toward recpirocal replacement were found, however. Beech and sugar maple each did better under their own species than under the other, as did hemlock.

The least diverse community studied, then, Hueston Woods, was found by several methods (Tables 2, 4) to possess the strongest relationships among species. Relationships in the most diverse community, the southern Appalachians taken as a whole, also were strong (though not as strong as at Hueston Woods) but stressed self-replacement, for which vegetative reproduction, limited dispersal, and specific site preferences are probably more important than site modification by the canopy individual. Several reasons for this general result may be hypothesized. When only a few species occur, each can have an increased effect on a localized area, with many neighboring canopy trees likely to be of the same species as the gapmaker, and with the effects of leaf decomposition, root secretions, etc. being less diluted by other species. For example, Stone (1977) found that only 5% of the leaves of marked trees remained on their estimated rooting area, implying that a great deal of horizontal mixing of effects occurs. Increasing the number of species also increases the average distance from a canopy tree of one species to a gap created by another. Therefore the regeneration in many gaps will be dominated by the same species as the gapmaker, even though a second species may be favored where both are present. The result is selection against forming strong relationships with another species and toward being fairly successful under many species.

The extent of interspecific relations may have been underestimated in the analysis. The nature and extent of the relationships may vary with topographic position, soil, and other variables, such that species A may be favored under species B in coves but under C on slopes. Lumping data from several topographic positions would obscure this sort of relationship. Lumping data from many areas, as was done for the southern Appalachians as a whole, also can be misleading if a species is excluded from a large group of gaps (e.g., silverbell from Walker's Cove) for reasons not related to replacement probabilities. However, such topographic and distributional complexities are common natural occurrences and thus factors of importance in the evolution of loose or tight relationships between species pairs.

CONCLUSIONS

As a way of predicting equilibrium community composition a Markov approach should be used with caution. No one way of computing transition probabilities seems to work for all species in all communities. Density, basal area, or an average of the two each seems particularly effective in different situations, although in general for the communities studied the average seems best. The size and direction of deviations from the predicted equilibrium can be useful in understanding individual species, however. Also, despite all the analysis demonstrating a reciprocal relationship between beech and sugar maple in Warren Woods, because they lacked a predictive model, previous workers could not state whether the observed interactions were sufficient to account for the observed canopy composition or whether the canopy composition actually was in a state of flux.

The close agreement in general between observed canopy composition and that predicted from sapling composition in gaps, whether or not a Markov procedure was used, helps substantiate the impression that in these moist protected sites the primary forces of forest regeneration are small disturbances, on the order of single tree gaps, rather than the large-scale catastrophes which are important in many other places. This conclusion is based to some extent upon circular reasoning: a close fit of predicted to observed values is used both to validate the technique and to substantiate the hypothesis that the community is in a steady state. However, the worst fit of any technique had a percentage similarity value of 62 with most values 75% or greater. Relative to a value of 80–95% for the same stand sampled twice and 69% for average values between stands in my sample, these values are fairly high. The correlation coefficients were generally highly significant ($P \leq .01$) also. The agreement among results based on different techniques serves to strengthen the conclusions reached above.

In many cases the species of tree creating a gap seemed to influence the species composition of its likely successors (saplings within the gap). However, for the most part these relationships consisted of significant tendencies toward self-replacement, for which many factors may be responsible. Only in the most species-poor stand, dominated by beech and sugar maple, was there a marked tendency for saplings of each species to do significantly better in gaps created by individuals of the other species than in gaps created by individuals of their own species.

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