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## CANOPY CLOSURE RATE AND FOREST STRUCTURE

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**Abstract.** Natural disturbances produce openings in forest canopies. Gap opening and closure create a mosaic of regenerating phases in the forest, which are a source of environmental heterogeneity, contributing to the maintenance of community diversity. In this study we measured the rate of canopy closure using hemispherical photographs taken in the same points in August 1992, 1993, and 1994 at three temperate forests in Britain. We analyzed the change in percentage canopy openness in time and found that canopy closure occurred exponentially. These results were used to build a matrix model that incorporated canopy dynamics as a linear Markov-chain process of forest succession by classifying forest patches into types (according to percentage canopy openness) and calculating the probability of each patch type becoming the following patch type in one year's time. Standard matrix analysis allowed us to project forest structure (i.e., the proportion of patches of each type) at equilibrium, and to explore the effect of different disturbance rates on canopy dynamics. Simulations showed that higher disturbance rates result in a lower proportion of the forest under closed-canopy conditions, and that variation in disturbance rate has a dramatic effect on turnover rate. Forest dynamics studies could be based on a patch characterization system based on a quantitative scale of percentage canopy openness, which would make comparisons between forests possible.

**Key words:** canopy closure; forest regeneration cycle; hemispherical photography; matrix models; patch dynamics; secondary succession.

### INTRODUCTION

Forest canopy dynamics is the product of a permanent process of disturbances and regeneration. Although both processes are of equal importance, much more is known about gap formation than about canopy closure. Natural disturbances are a source of environmental heterogeneity and patch effects, which occur on a wide variety of spatial and temporal scales (Pickett and White 1985). In forest habitats, small disturbances, such as branch or tree falls, produce canopy openings; these eventually close due to the lateral extension of adjacent vegetation and the growth of new trees into the canopy (Runkle 1981, Runkle and Yetter 1987). This process results in a mosaic of regenerating phases represented by forest patches of various sizes and ages (Doyle 1981, Brokaw 1985, Martínez-Ramos et al. 1988). The disturbance/regrowth cycle involved in patch dynamics is of ecological interest in itself, but also because it is linked with many other ecological processes occurring at different spatial and temporal scales. Among other things, it provides a permanent source of environmental heterogeneity, which allows the coexistence of species with different life histories and ecological requirements, thus increasing commu-

nity diversity (Brokaw 1985, Pickett and White 1985, Runkle and Yetter 1987, Whitmore 1989, Alvarez-Buylla and García-Barrios 1991).

The rate at which new gaps are formed (i.e., the disturbance rate,  $k$ ) has often been reported in forest dynamics studies. It is defined as the proportion of the forest area that is affected by natural disturbances each year. Despite the differences in vegetation types and nature of disturbances involved, temperate forests show little variation in this parameter, with values of  $\approx 1\%$  (ranging from 0.5 to 2.0%; Runkle 1985, Runkle and Yetter 1987). Similar values have also been reported for tropical and subalpine forests (Brokaw 1985, Veblen et al. 1994, Battles et al. 1995). The study of forest disturbance rate is important not only because it determines forest structure, but also because turnover rates (i.e., the mean time between recurring gap formation at any one point in the forest, which is a function of  $k$ ) may act as an important selective force on certain life history traits among gap-colonizing species (Hartshorn 1978). Moreover, variations in the disturbance rate could alter the successional pattern and subsequent composition, diversity, and structure of the forest (Doyle 1981, Busing 1995). Some authors have explored this subject theoretically, describing the effect of a range of  $k$  values on forest canopy dynamics using models derived from generalized Lefkovich projection matrices (Horvitz and Schemske 1986, Alvarez-Buylla and García-Barrios 1991, Cipollini et al. 1993, 1994, Alvarez-Buylla 1994).

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Another major variable affecting canopy dynamics, the rate of gap closure, has rarely been studied (but see Runkle 1985, Cipollini et al. 1993). Many understory species depend on gap formation for the accomplishment of one or several phases of their life cycle, but as regeneration proceeds and gaps close, their demography may be strongly affected by the changing environmental conditions (Horvitz and Schemske 1986, Alvarez-Buylla and García-Barrios 1991, Cipollini et al. 1993, 1994, Valverde 1995). Thus, both gap formation and canopy closure rates have important consequences not only in terms of forest structure, but also because they impose times and rates on many other ecological processes within forest habitats (Brokaw 1982, Busing 1995).

In this study we investigated canopy closure rate in terms of the change in the light conditions over time with the aid of hemispherical photography. Based on our results of canopy closure, we then built a matrix model of canopy dynamics to project forest structure under different disturbance rates. The photographic technique has the advantage of being an instantaneous measurement that provides a quantification of the light conditions integrated over long periods of time (Mitchell and Whitmore 1993), and has also been used as a measure of gap size (Kennedy and Swaine 1992). However, to our knowledge, it has never been employed to measure canopy closure rate, although it provides a useful tool in the study of these and other related subjects regarding patch dynamics.

#### METHODS

**The study sites.**—Empirical data on canopy closure was collected at Dancers End Nature Reserve, in Buckinghamshire, UK (National Grid Reference SP902096), which is a *Fagus sylvatica* (beech) and *Fraxinus excelsior* (ash) forest on a chalky soil. It has traditionally been managed through coppice cycles of 5–10 yr, the coppiced species being mainly *Corylus avellana* (hazel) and *Crataegus monogyna* (hawthorn). The present study was part of a metapopulation study of *Primula vulgaris* in which the light conditions of several patches occupied by this herb species were being monitored (Valverde 1995, Valverde and Silvertown 1995). Thus, the sample points from which canopy closure rate was calculated were *P. vulgaris* patches in different light conditions, ranging from a gap to completely closed canopy. Six of these patches were studied at Dancers End forest.

Two additional forest patches (also bearing *P. vulgaris* populations) were considered too: one in Woburn Wood, a *Quercus robur* (oak) and *Castanea sativa* (chestnut) forest in Bedfordshire (NGR SP927325), and another one in Salcey Forest, a *Quercus robur* and *Fraxinus excelsior* forest in Northamptonshire (NGR SP814508).

**Hemispherical photography and light measurement.**—Hemispherical photographs were used to char-

TABLE 1. Mean percentage canopy openness (and standard deviations) obtained in eight forest patches in three consecutive years. All patches were on flat ground (i.e., with no slope); latitudes ranged from 51°48' (Dancers End) to 52°12' (Salcey Forest) N.

Patch	Canopy openness (%)			General description	n
	1992	1993	1994		
DE7	...†	13.21 (4.44)	11.16 (3.14)	large gap (≈450 m <sup>2</sup> )	7
DE2	12.01 (2.20)	9.12 (1.73)	7.31 (2.82)	large gap (≈400 m <sup>2</sup> )	8
DE5	5.95 (2.09)	4.88 (1.53)	3.16 (1.75)	small gap (≈100 m <sup>2</sup> )	7
WW	5.65 (2.92)	4.78 (3.13)	4.05 (2.48)	small gap (<100 m <sup>2</sup> )	15
SF	3.09 (1.28)	3.08 (1.73)	1.90 (1.00)	closing canopy	11
DE3	2.67 (1.36)	1.87 (0.88)	1.84 (0.60)	closing canopy	8
DE4	2.03 (0.71)	1.95 (0.58)	1.46 (0.72)	closed canopy	7
DE6	1.57 (0.79)	1.97 (0.81)	...	closed canopy	7

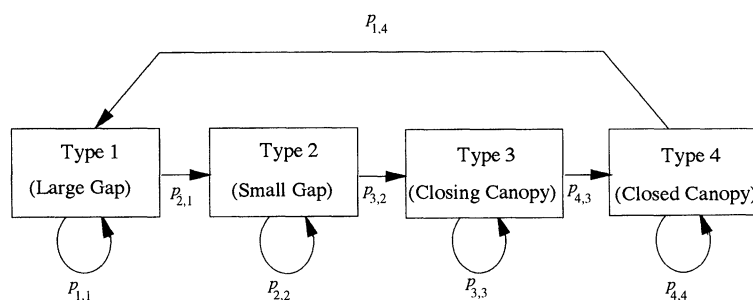
Note: Patches are listed in order of decreasing diffuse light (Dancers End, DE; Woburn Wood, WW; and Salcey Forest, SF); their general description corresponds to August 1992. Mean canopy openness was calculated from a varying number (n) of hemispherical photographs per patch.

† Ellipses indicate "not measured."

acterize the light environment and to evaluate the rate of change of canopy cover at each sample point in the forest. This technique involves the use of a hemispherical lens to photograph the forest canopy from below. Hemispherical photographs were taken at exactly the same points in each of the eight forest patches studied in August 1992, 1993, and 1994. These points were marked with plastic pipes sunk into the ground for relocation purposes. Seven to 15 photographs (depending on the variation in canopy cover) were taken at regular intervals along a transect incorporating the whole range of light conditions encountered in each patch. For example, in the case of well-defined canopy gaps (i.e., DE7, DE2, and DE5; see Table 1), the transect ran from the edge to the center of the gap in order to include the natural variability in the light conditions characteristic of these types of forest patches; the spacing between photographs along transects was consistent among different gaps. Transect length varied between 8 and 50 m, depending on the size of the patch and on the variation in the light conditions within it.

To take the photographs, the camera was placed 50 cm above the ground level (i.e., the height of the tripod) at each of the plastic pipes that served as markers. The lens was never obstructed by shrubs or other low vegetation; thus, the photographs captured the image corresponding to the shape of the canopy at its maximum height (which ranged from ≈ 7 to 20 m).

We used an Olympus Auto-fisheye lens (1:2.8, f = 8 mm) with a black and white, high-contrast film (ASA 50). The resulting hemispherical images were digitized

Matrix **P**

		Patch type at time $t$			
		1	2	3	4
Patch type at time $t+1$	1	$P_{1,1}$	0	0	$P_{1,4}$
	2	$P_{2,1}$	$P_{2,2}$	0	0
	3	0	$P_{3,2}$	$P_{3,3}$	0
	4	0	0	$P_{4,3}$	$P_{4,4}$

FIG. 1. Schematic model of forest canopy dynamics and corresponding matrix model. Each box represents a patch type, and the arrows indicate transitions between patch types over one time step, which correspond to matrix entries.

and then analyzed using the program Solarcalc 5.41 (Macintosh II), developed by Chazdon and Field (1987). This program can calculate a number of light variables derived from hemispherical photographs. We chose the percentage weighted canopy openness (which is a measure of diffuse light; Mitchell and Whitmore 1993) to characterize canopy conditions, as it is a direct measure of the percentage of open sky in the photograph and can also be used to describe gap size (Kennedy and Swaine 1992).

As hemispherical photographs were taken at the same points each year, we were able to detect changes in the level of canopy openness at each sample point from one year to the next; this information allowed us to calculate canopy closure rate (see *Results*). For these analyses each sample point was considered individually (i.e.,  $n = 60$  photographs/yr). However, with the aim of giving a general description of the light conditions in each patch, Table 1 shows the average percentage canopy openness per patch. Note that, in general, the variation in the light conditions within patches (which can be inferred from the standard deviations reported in the table) was larger in gaps than in closed canopy conditions, which resulted from the wide range of diffuse light values measured from the edge to the center of gaps.

**Canopy dynamics model.**—Based on our results of canopy closure, we built a generalized Lefkovich ma-

trix model, which incorporated canopy dynamics as a linear Markov-chain process of forest succession following disturbance (Horvitz and Schemske 1986, Alvarez-Buylla and García-Barrios 1991, Cipollini et al. 1993, 1994, Alvarez-Buylla 1994). We then used the model to explore the effect of different disturbance rates on forest structure.

To build the model, we subdivided the forest into four broad patch types, according to their level of canopy openness: large gaps, small gaps, closing canopy, and closed canopy patches (Fig. 1). The model assumes that each patch type may remain the same or become the next patch type in one time step as a result of canopy closure, and that type-1 patches (i.e., large gaps) may be created due to natural disturbances only in type-4 patches (completely closed-canopy conditions). We are aware that these disturbances may occur in any type of forest patch, as other authors have pointed out (Horvitz and Schemske 1986); however, for the sake of simplicity, the probability of large gaps being formed in other patch types was deemed negligible, as most of the forest is composed of type-4 patches.

The model is represented mathematically by matrix **P**, an  $n \times n$  matrix, where  $n$  is the number of patch types (Fig. 1). Each matrix entry,  $p_{ij}$ , represents the transition probability from a type- $j$  patch to a type- $i$  patch in one year's time. Let **f** <sub>$t$</sub>  be a vector representing the proportion of patches of each type at time  $t$  in the

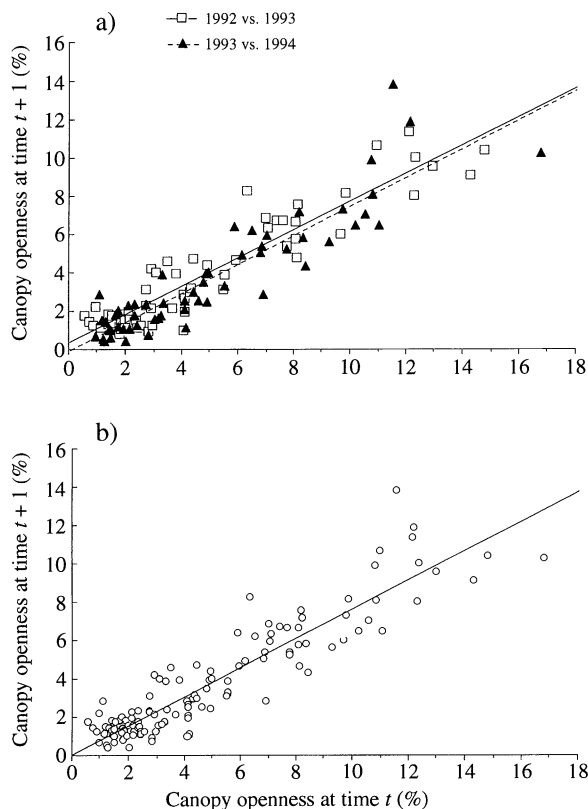


FIG. 2. Relationship between canopy openness at times  $t$  and  $t+1$  for (a) 1992 vs. 1993 and 1993 vs. 1994 separately, and for (b) the entire data set. See *Results* for details on the significance of the relationships and on the functions' coefficients.

forest. The structure of the forest after 1 yr can be described by the vector  $\mathbf{f}_{t+1}$ , where

$$\mathbf{f}_{t+1} = \mathbf{P} \times \mathbf{f}_t \quad (1)$$

The upper right matrix entry,  $p_{1,4}$ , represents the probability of gap formation in closed-canopy patches, i.e., the disturbance rate,  $k$ . Thus, the probability of closed-canopy patches remaining as such,  $p_{4,4}$ , is given by  $1 - k$ . Other matrix entries were calculated according to the rate of canopy closure (see *Results*). The right eigenvector of matrix  $\mathbf{P}$  associated with the dominant eigenvalue ( $\lambda = 1.000$ ) is proportional to the distribution of patch types in the forest at equilibrium, or the stable patch-type distribution.

## RESULTS

**Canopy closure rate.**—The rate of canopy closure was estimated by comparing the percentage canopy openness obtained in each sample point in consecutive years. The results of 60 photographs were compared between 1992 and 1993, and between 1993 and 1994. We obtained a strong positive correlation between percentage canopy openness at time  $t$  and at  $t+1$  for both periods (Fig. 2a): for 1992 vs. 1993,  $R^2 = 0.88$ ,  $P <$

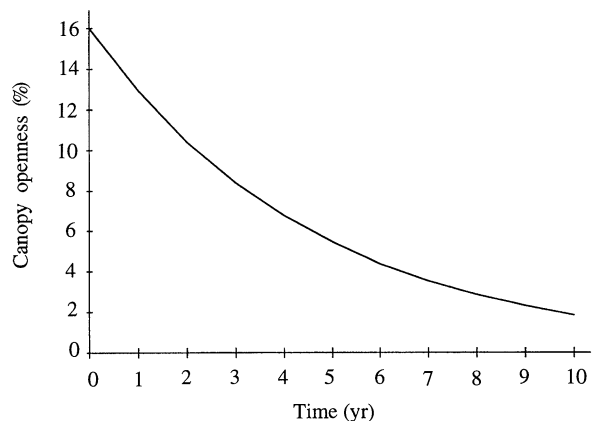


FIG. 3. Exponential change of diffuse light through time given by  $\alpha = \alpha_0 e^{ct}$ .

0.001,  $m = 0.67$ , and  $b = 0.53$ ; and for 1993 vs. 1994,  $R^2 = 0.86$ ,  $P < 0.001$ ,  $m = 0.80$ , and  $b = 0.18$  (where  $m$  and  $b$  are the slope and the y intercept, respectively). As data points were not totally independent from each other (i.e., they were grouped in particular forest patches), we corrected for the effect of patch by including the patch number as a nominal covariable in the analysis; the effect of the covariable was not significant ( $P = 0.55$  for 1992 vs. 1993, and  $P = 0.36$  for 1993 vs. 1994).

The slopes of the 1992 vs. 1993 and the 1993 vs. 1994 regression lines (Fig. 2a) were not significantly different ( $t = 0.361$ ,  $df = 10$ ,  $P > 0.9$ ). Thus, a single regression line was fitted to the entire data set (also including the effect of patch as a covariable) setting the y intercept at zero in order to account more realistically for the changes in canopy conditions (Fig. 2b). According to the latter, the relationship between canopy openness ( $\alpha$ ) in consecutive years is given by

$$\alpha_{t+1} = (0.79)\alpha_t \quad (2)$$

The linear relationship given by Eq. 2 implies that the change in the percentage canopy openness through time occurred exponentially (Fig. 3). This exponential function is described by the equation

$$\alpha = \alpha_0 e^{ct}, \quad (3a)$$

where  $t$  is time (in years),  $\alpha_0$  is percentage canopy openness at  $t = 0$ , and  $c$  is a constant given by  $\ln(0.79) = -0.23$ . This constant,  $c$ , represents the rate of change of canopy cover, defined here as the rate of canopy closure. Thus, the time required for a certain amount of canopy closure to occur can be calculated from Eq. 3a as:

$$t = \frac{\ln(\alpha/\alpha_0)}{c} \quad (3b)$$

**Patch-type evaluation and transition.**—In order to describe canopy dynamics as a Markov-chain process of forest succession following disturbance, we classi-

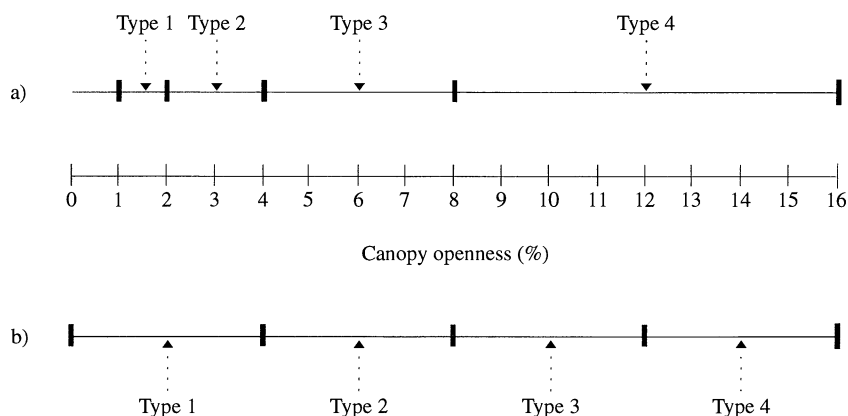


FIG. 4. Diagram showing the range of percentage canopy openness values defining the different patch types according to (a) the "geometric" and (b) the "uniform" patch-type classifications.

fied forest patches into four broad types (Fig. 1). We used our canopy openness measurements to define quantitatively each of these patch types along the range of percentage canopy openness values obtained through the hemispherical photographs (i.e., from 0 to 16%). We applied two patch-type classification criteria: (1) a "geometric" one, in which the range of canopy openness defining each patch type was chosen along a geometric series (Fig. 4a) and (2) a "uniform" one, in which the range of canopy openness was equivalent for all patch types (Fig. 4b).

For each patch-type classification, the time required for a certain patch type to advance to the following type was approximated as the time required to go from the center of one patch-type category to the center of the next category. Thus, in the "geometric" patch-type classification, for instance, the time required for a typical type-1 patch (12% canopy openness) to become a typical type-2 patch (6% canopy openness) was 3 yr (see Eq. 3b), and full canopy closure would occur 9 yr after gap opening. The time required for different patch-type transitions in both patch-type classifications is given in Table 2.

**Canopy dynamics.**—Fig. 1 shows the matrix model of canopy dynamics,  $\mathbf{P}$ . Matrix entries represent transition probabilities between patch types in one year, and were calculated from the time required for each patch type to become the following patch type: if a type- $x$  patch takes  $n$  yr to become a type- $y$  patch, then, on average  $1/n$  of type- $x$  patches will become type- $y$  patches every year, whereas  $1 - (1/n)$  will remain in

the type- $x$  category. The canopy dynamics matrices calculated in this way for the two patch-type classifications are given in Table 3.

The probability of gap formation in closed-canopy patches (matrix entry  $p_{1,4}$ ) corresponds to the disturbance rate,  $k$ , i.e., the rate at which new gaps are formed. In this study, we considered several theoretical  $k$  values (ranging from 0.5 to 5%, covering the observed natural variation in this parameter) to obtain the dominant right eigenvector of matrix  $\mathbf{P}$ , which is proportional to the stable patch-type distribution. The results of these simulations are shown in Fig. 5. Forest structure at equilibrium is dominated by type-4 patches for both patch-type classifications. In the "geometric" classification, type-1, -2, and -3 patches showed the same relative frequency, regardless of the disturbance rate (Fig. 4a). However, in the "uniform" classification brighter patches showed lower frequency than relatively darker patches for all  $k$  values (Fig. 4b). This follows from the fact that, according to this classification, darker patches take longer to become the following patch type (Table 2).

The projected forest structure at equilibrium was

TABLE 3. Matrix models of canopy dynamics based on (a) the "geometric" patch-type classification and (b) the "uniform" patch-type classification.  $k$  = disturbance rate.

Patch type at time $t + 1$	Patch type at time $t$			
	1	2	3	4
a)				
1	0.7	0	0	$k$
2	0.3	0.7	0	0
3	0	0.3	0.7	0
4	0	0	0.3	$1 - k$
b)				
1	0.3	0	0	$k$
2	0.7	0.6	0	0
3	0	0.4	0.8	0
4	0	0	0.2	$1 - k$

Note: All columns sum to unity.

TABLE 2. Time (in years) required for different patch-type transitions in the two patch-type classifications used.

Patch-type transition	Patch-type classification	
	"Uniform"	"Geometric"
1 to 2	1.46	3.01
2 to 3	2.22	3.01
3 to 4	4.78	3.01

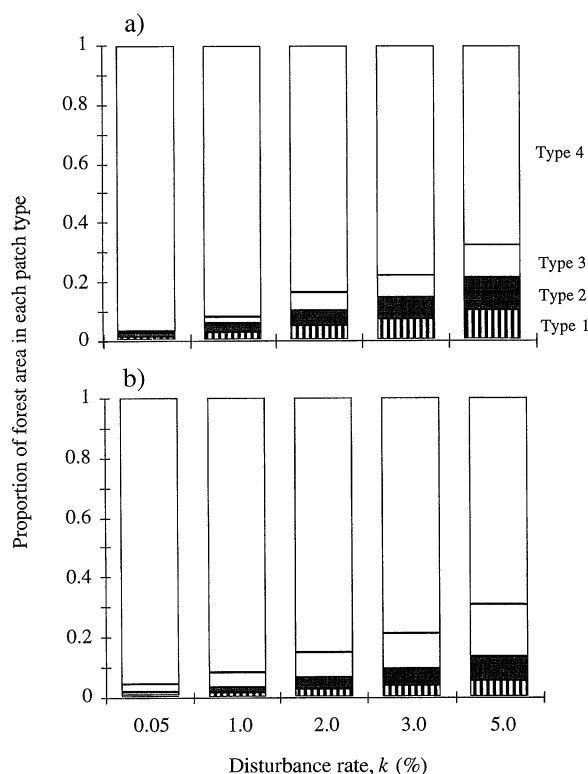


FIG. 5. Projected forest structure (i.e., stable patch-type distributions) for different disturbance rates ( $k$ ) for (a) the "geometric" and (b) the "uniform" patch-type classifications.

strongly affected by the disturbance rate but only slightly affected by the patch-type classification used (Fig. 5): the proportion of the forest area under closed-canopy conditions varied between 95.4 and 67.4% (with  $k = 0.5$  and 5%, respectively) in the "geometric" patch-type classification, and between 95.7 and 69.1% (with  $k = 0.5$  and 5%, respectively) in the "uniform" patch-type classification.

Disturbance rate had a dramatic effect on turnover rate (Fig. 6), which is the mean time between successive gap formations at any one point in the forest [calculated as:  $(1/p) \times i$ , where  $p$  = the proportion of the forest in new gaps, and  $i$  = the time interval during which type-1 patches remain as such]. Given the range of disturbance rate values tested, the turnover rate varied from 200 to 28 yr and it was practically the same for the two patch-type classifications tested (Fig. 6).

#### DISCUSSION

Our results indicate that canopy closure occurred at an exponential rate. This is in agreement with the suggestions made by other authors who have implied that structural changes are faster during the first stages of gap closure (Horvitz and Schemske 1986), and that regeneration in gaps occurs at a faster rate just after gap formation, becoming slower as the size of the gap

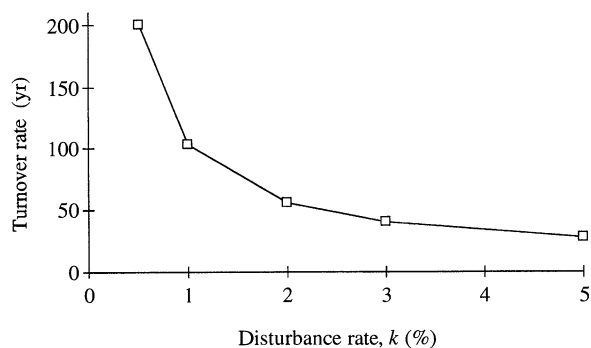


FIG. 6. Effect of disturbance rate ( $k$ ) on turnover rate (i.e., mean time between successive gap formations at any one point in the forest).

decreases (Brokaw 1985). The exponential canopy closure rate obtained implies that, in general, changes in percentage canopy openness were more noticeable at points with higher initial diffuse light than at points with relatively lower diffuse light (Fig. 2b). Correspondingly, our results also appear to suggest that changes in percentage canopy openness were more readily detectable near the center of gaps than close to the edges; however, the type and structure of our data set were not designed to address this particular question and our results should not be considered conclusive in this respect.

Gap closure rate depends, among other things, on the characteristics of the gap, such as its size and shape. Runkle (1985) pointed out that small gaps usually close through the lateral extension of branches of bordering canopy trees, which occurs at a rate that ranges from 4 to 26 cm per year. In agreement with these results, Cipollini et al. (1993) obtained tree lateral extension rates of 17–18 cm/yr. The closure of large gaps, though, depends mainly upon the growth of new trees into the canopy (Runkle 1981). Our results regarding canopy closure rate are not directly comparable with previous estimates, as we measured the change in percentage canopy openness rather than the rate of expansion or growth of bordering trees. However, our estimate of the time required for full canopy closure after gap formation ( $\approx 9$  yr) appears reasonable compared to the results for both tropical and temperate forests reported by other authors: Runkle (1981) stated that the maximum time needed for a gap to close is given by the time required by saplings to reach a 10–20 m height, combined with the effect of the lateral extension of adjacent trees; according to this, gaps must take between 10 and 40 yr to close. Additionally, Horvitz and Schemske (1986) estimated that full canopy closure would occur 10 yr after gap formation, whereas Cipollini et al. (1993) reported an estimate of 8 yr. Thus, our results, based on empirical data on canopy closure, are in agreement with previous estimates. How realistic these estimates are will ultimately depend, among other

TABLE 4. General results of the canopy dynamics model with four and eight patch types and with different disturbance rates ( $k$ ) values. The "geometric" patch-type classification was used (see Fig. 4).

Model result	Number of patch types in the model			
	4		8	
	$k = 0.5\%$	$k = 5\%$	$k = 0.5\%$	$k = 5\%$
Proportion of the forest area in closed canopy conditions	0.95	0.67	0.89	0.46
Turnover rate (yr)	200	28	200.5	19.7

things, on the size and type of disturbance and on the species involved in the regeneration.

It could be argued that our results underestimate the actual time required for a newly created gap to develop into a closed-canopy patch. Thus, we also considered a model with twice the number of patch types, which delayed the formation of closed-canopy patches to  $\approx 18$  yr. The results showed that, when  $k = 0.5\%$ , the turnover rate was the same regardless of the number of patch types considered, and the proportion of the forest area in closed-canopy conditions decreased slightly when the number of patch types in the model was doubled (Table 4). When  $k = 5\%$ , both the turnover rate and the projected proportion of the forest in closed canopy conditions decreased when the model was run with eight patch types. However, our general results agree with those obtained by Horvitz and Schemske (1986) in that the disturbance rate had a more dramatic effect on forest structure and turnover rate than did the number of patch types in the model. Regarding the two patch-type classifications considered, our results showed that they had practically no effect on turnover rate and only a small effect on the projected forest structure at equilibrium (Fig. 5).

Turnover rates of natural forests have been reported as typically between 200 and 50 yr for disturbance rates of 0.5–2% (Runkle 1985). The turnover rates we obtained for comparable  $k$  values were within this range. Thus, most of our results are in general agreement with previous analyses, which strongly suggests that our canopy closure measurements, on which the canopy dynamics model is based, are reliable and accurate. Note that, unlike other canopy dynamics models (Horvitz and Schemske 1986, Cipollini et al. 1993), our model did not use an age-based patch-type classification; instead, patches were classified according to stages along the canopy regeneration cycle. Stage-based models that classify forest patches according to both size and age of disturbance have been used before (Alvarez-Buylla and García-Barrios 1991, Alvarez-Buylla 1994). Here, we suggest that the use of more objective variables (such as percentage canopy openness) for the classification of forest patches would certainly aid in the construction and interpretation of this kind of patch dynamics models.

Several studies have stressed the importance of gap

size, in particular, as a key factor affecting both canopy dynamics and the dynamics of gap-dependent species, and thus, forest structure and composition (Dirzo et al. 1992, Busing 1995). However, gaps have been defined according to varying criteria, which has led some authors to doubt the validity of comparisons of gap and turnover times between studies (Vandermeer et al. 1994, Vandermeer and Bongers 1996). Light measurements derived from hemispherical photography are reliable estimates that may be used as a description of gap size (Kennedy and Swaine 1992). Here, we have shown that they are useful also in the derivation of some canopy dynamics variables. Future forest dynamics studies could use a patch characterization system based on a quantitative scale of percentage canopy openness, which, if widely adopted, would make comparisons between forests possible.

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