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Spatial distribution of gaps along three catenas in the moist forest of Taï National Park, Ivory Coast

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ABSTRACT. The spatial distribution of canopy gaps was analysed on three sites (total 71 ha) in the tropical moist forest of Taï National Park, Ivory Coast. Pattern analysis revealed a clustered distribution of gaps for two of the three sites. Catena dependent gap formation processes might explain local differences in the occurrence and distribution of gaps. Gap densities, sizes and percentage forest area in gap phase are higher on the upper and middle slope than on the crest or lower slope. As a consequence, regeneration of gap dependent tree species might be directed to the catena positions with the highest disturbance regime. The spatial distribution of gap dependent species can be clumped, not only due to the regeneration within gaps, but also due to the clustered nature of gap distribution on its own.

KEY WORDS: catena, forest dynamics, gap, Ivory Coast, Monte Carlo test, nearest neighbour, spatial distribution, tropical moist forest.

INTRODUCTION

Openings in the forest canopy are important for the regeneration of many rain forest tree species (Hallé *et al.* 1978, Hartshorn 1978, Pickett & White 1985, Whitmore 1984). Different species groups can be recognised with respect to their dependency on these gaps (Alexandre 1988, Denslow 1980, Hartshorn 1980, Oldeman & van Dijk 1991, Swaine & Whitmore 1988), and may be referred to as species guilds (Hubbell & Foster 1986). Information on gap density and the characteristics of gaps can indicate the possibilities for regeneration for different species and species groups. A high level of disturbance will result in many gaps or in large gaps, leading to a large percentage of the forest area under gap conditions. This would give rise to a relatively large share of species depending on gaps in the vegetation (Hartshorn 1980).

The mean gap density and other average gap features may be taken as characteristic of a whole forest area, but there is often much variation at different scales of observation, whether it is a spatial or a time scale which is regarded. One of the most extensive tropical data sets showing this aspect has been assembled for the rainforest of Los Tuxtlas, Mexico (Martínez-Ramos *et al.* 1988). Variability of gap disturbance was reported for 5 ha on a 5 m × 5 m plot basis, and for a time span of 70 years using bent-over palms (*Astrocaryum mexicanum*) as a dating device. Hubbell & Foster (1986) made a thorough census of canopy height for a 50 ha plot in Barro Colorado Island, Panama, focusing on spatial variability but not on temporal variability. Sanford *et al.* (1986) studied the sizes and spatial patterns of gaps in an area of nearly 100 ha in La Selva, Costa Rica, using aerial photographs.

Although it is known that disturbances may vary regionally, especially as a function of climate, and within a certain region as result of differences in topography, soil type, vegetation cover and other site variables (Runkle 1990, White 1979), relatively few studies have investigated the spatial distribution of gaps at this latter scale. Some studies on regional differences have been carried out, e.g. Brokaw (1982a) who studied differences between mature and secondary forest in Panama, Kapos *et al.* (1990) who studied gaps in relation to soil characteristics, and Jans *et al.* (1993) who studied gaps in relation to regional variability in climate and soil. This last study is one of the few gap studies carried out in African forests.

In this paper we focus on the spatial distribution of gaps in West African moist forest in Taï National Park, Ivory Coast. Special attention is paid to the influence of a catena with its accompanying change in forest structure and species composition upon the incidence of gaps. This study forms part of a larger study on vegetation gradients in the Taï forest (van Rompaey 1993). The following specific questions are addressed: (1) Are gaps randomly distributed? (2) If a non-random pattern is detected, what is the spatial scale? (3) Is gap occurrence related to position along the catena? (4) What could be the ecological consequences of the found spatial distribution of gaps for the regeneration of gap dependent tree species?

STUDY SITES

The study was conducted in Taï National Park in south-west Ivory Coast (5° 20′–6° 10′ N; 6° 50′–7° 25′ W) (Figure 1). The forest of Taï National Park is classified as a tropical lowland evergreen seasonal forest (Gaussen 1973) and is one of the largest blocks (4400 km^2) of primary forest remaining in West Africa. In 1982 UNESCO declared Taï National Park to be a World Heritage Site (Sayer *et al.* 1992).

The climate is tropical rainy (on the transition between Af and Aw, Köppen classification; Griffiths 1972) with an annual rainfall between 1700 and 2100 mm (ANAM 1987).

Trees in the Taï National Park attain a height of 55 m, stem density is relatively high (mean density of 80 stems ha^{-1} for trees ⩾30 cm dbh; 14 stems ha^{-1} for trees ⩾70 cm dbh) and also basal area is high (17–30 m^2 ha^{-1}, trees ⩾30 cm dbh) in comparison with forests in other continents or even in Africa

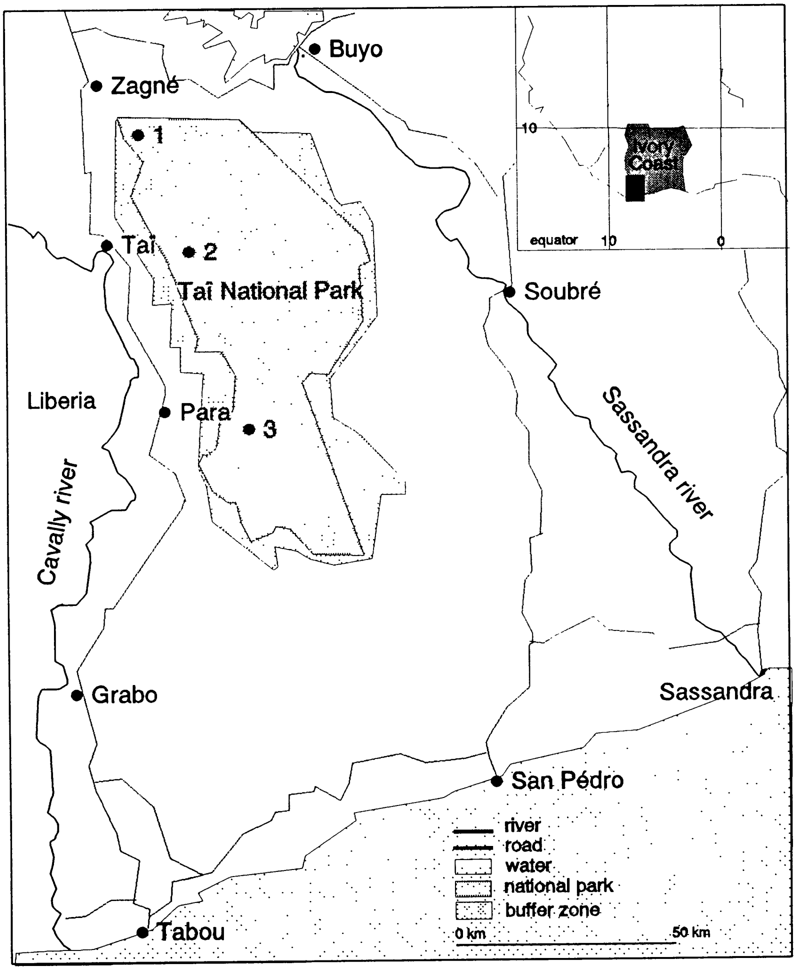

Figure 1. Map of Taï National Park (Ivory Coast) with the location of the three study sites indicated by black dots: Zagné (1), Taï (2) and Para (3).

(van Rompaey 1993). The forest has never been logged, but there is some evidence of human presence in the past (viz: potsherds and charcoal).

The main emergent tree species on the study sites are *Terminalia superba* (Combretaceae), *Erythrophleum ivorense* (Caesalpiniaceae), *Pycnanthus angolensis* (Myristicaceae), *Piptadeniastrum africanum* Hook (Mimosaceae), *Entandrophragma* spp. (Meliaceae) and *Sacoglottis gabonensis* (Humiriaceae). Other non-emergent tree species with high abundances are *Chidlowia sanguinea* (Caesalpiniaceae), *Corynanthe pachyceras* (Rubiaceae) and *Coula edulis* (Olacaceae). Nomenclature follows Hall & Swaine (1981). The species composition of the forest in the Park ranges from moist semi-deciduous to wet evergreen (*sensu* Hall & Swaine 1981).

Three sites were chosen, located within 75 km of each other (see Figure 1). They will be indicated by the names of the nearest villages: Zagné, Taï and

Para. These study sites are located within the study area of the research project of van Rompaey (1993) and are selected on the basis of their representativeness and their accessibility.

The altitude of these study sites varies from 110 to 200 m above sea level. Topography ranges from flat to moderately steep (max. slope 25%). The Zagné and Taï sites are underlain by migmatite (a mixture of granite and gneiss), the Para site by sericite-schist (Papon 1973). The soil in the upper part of the catena contains large amounts of ironstone gravel, the fine earth fraction is clayey and loamy (van Herwaarden 1991). Soil characteristics in each site are strongly related to catena position, i.e. the relative location along the slope. Most of the soils on the slope and crest of the three sites have a red to brown colour, while soils on the valley bottom are mostly yellow-brown to white. Soils on crest and upper slope are mostly vertically drained while the soils on the middle and lower slope are superficially and laterally drained (Fritsch 1980). Soils on the valley bottom are very often waterlogged. On one part of each study site ironstone sheets are present on the highest crests; relics from a period in which very strongly weathered soils occurred over a large area (Ahn 1970, de Rouw *et al.* 1990). Although at each study site all catena positions were included, slopes and crests were better represented in the total study area than the other physiographic soil units.

METHODS

Gap location and size

In total 71 ha of forest (Zagné 25 ha, Taï 24 ha and Para 22 ha) were systematically searched for gaps, using the Brokaw (1982b) definition. Gaps smaller than 10 m^2 or with a regrowth higher than 2 m were disregarded. The exact location of the gap centre was positioned in an existing 100 m × 100 m grid system and the distance from the centre of the gap to the edge was measured in eight compass directions (0, 45, 90, 135, 180, 225, 270 and 315 degrees). By connecting gap edge points and adding the area of the eight triangles thus obtained the gap area was estimated, this giving an estimate of the vertically projected canopy opening. Gaps which fell partly outside the border lines of the study sites were only half included for the calculation of the gap density and the total gap area.

Gap age

The age of the gaps was estimated, and accordingly gaps were classified into two groups: gaps equal to- or younger than one year, and gaps older than one year. This was mainly based on the stage of decay of leaves and twigs, height of the regrowth of young vegetation, freshness of the snapping point, sprouting on the fallen trees, and the filling of the uprooting pit due to soil slippage.

Gap distribution pattern

With the measured locations of the gaps the spatial distribution was analysed. For each gap, the distance to its nearest neighbour was determined. For all gaps together, this gives a distribution function of nearest neighbour distances. This cumulative distribution function was compared with similar distribution functions, generated by random simulations. By means of a Monte Carlo test (Besag & Diggle 1977, Diggle 1983, Ripley 1981) the random or non-random nature of the gap distribution pattern could be detected, as well as the scale of possible clustering.

For each site 1000 simulations were performed, in which gaps were thrown in a pseudo random way; pseudo random, because the distance between the centres of two randomly scattered gaps was set at a minimum of 7 m. This was necessary, because in the calculations, gaps are regarded as points rather than surfaces. However, in the field, gap centres are at least as far apart as the sum of their radii. With a minimum gap size of 10 m^2 (and thus a minimum radius of 1.8 m) this is at least 3.5 m for two contiguous gaps. In practice, two gaps so close together were pooled in the field. Thus a minimum distance between two gap edges was necessary to regard them as separate entities. During data processing we have set this distance arbitrarily at 3.5 m. Consequently, for computer simulations gap centres were spaced at least 7 m apart. No edge corrections were made in this analysis, because in such Monte Carlo tests, the simulations undergo the same edge effects as the actual data set. For each computer simulation a cumulative distribution function of nearest neighbour distances was made. With the aid of 1000 simulations the 95% confidence interval was determined. For each successive point of the cumulative distribution function separately, the 1000 simulations were ranked. Every 26th and 975th simulation was plotted in a figure, thus providing a 95% confidence interval with which the actual observed values could be compared.

The average distance between gaps not only gives insight into the spatial distribution of gaps in relation to each other, but also in the likelihood that the occurrence of one gap will influence the formation of another. To assess the influence of already existing old gaps upon the formation of new ones, the distances between old gaps (>1 y) and the nearest newly formed young gaps ($\leqslant 1$ y) were calculated. To avoid the influence of plot border effects, only those old gaps were included, which were located at least as far from the border as the mean distance between two nearest neighbour gaps. If existing gaps enhance the formation of new ones, it is expected that the mean distance to the nearest young neighbour will be significantly smaller than the mean distance from a random point in the forest to the nearest young gap. To test this 100 points were thrown at random in each site, and the distance to the nearest young gap was calculated. The difference between the mean distance from old gaps to the nearest young gap, and from random points to the nearest young gap was tested using a Student's t-test. Prior to testing, data were square root transformed, in order to obtain a normal distribution. A Kolmogorov-Smirnov test was used to test whether there was a difference between the two distribution functions of nearest neighbour distances.

Gaps and catena position

We evaluated the influence of soil type and catena position on gap formation, by relating the incidence of gaps to the physiographic soil units. Detailed physiographic soil maps were available for the three sites (van Herwaarden 1991). Five physiographic units were distinguished (crest, upper slope, middle slope, lower slope, valley) differing in catena position, parent material, gravel content and drainage characteristics. Overlays with gap locations were compared with the soil maps. For each physiographic unit, the density of gaps per hectare, the mean gap area and percentage of the area in gap phase were calculated. Differences between the five physiographic units with regard to these mean gap characteristics were tested, using the non-parametric Kruskal-Wallis test.

RESULTS

Gap location, size and age

The three sites Zagné, Taï and Para have nearly the same mean gap density (2.1 gaps ha^{-1}) (Table 1), of which about 33% are younger than one year (Jans *et al.* 1993). The mean gap sizes for the three sites are similar. In Jans *et al.* (1993), more information on gap frequency, gap size and forest turnover time is given. Gap locations in relation to physiographic soil units are shown in Figure 2. From the figure it can be derived that for Zagné, gap occurrence is a local phenomenon. Some spots in the forest have been more prone to disturbances than others, whereas for Taï gap occurrence is more or less a random event.

Distribution pattern and scale of clumping

The results of the Monte Carlo tests (Figure 3) show a non-random pattern for the study sites Zagné, Para and Taï. The gap distribution pattern of Para is clearly clustered. Relatively many gaps have a shorter mutual distance than expected, indicated by the cumulative distribution function which runs close to the upper limit of the 95% confidence interval. The large amount of gaps with a mutual distance of 25–30 m is statistically significant. Zagné also shows a clustered distribution pattern, although the clustering is less intense. Intergap distances of 20–25 m are more frequent here than expected. The relatively low number of gaps with a mutual distance of 80–95 m also indicates a clustered pattern. For Taï, the Monte Carlo test also suggests a non-random distribution pattern, as one observed point lies outside the confidence envelope. However, most of the observed distribution function of Taï runs close to the central line of the confidence interval. The single, outlying gap is thus almost meaningless. Consequently, gaps in Taï can be regarded as being randomly distributed.

Table 1. Area of physiographic unit within the sample plots, mean gap density, mean gap size and percentage area in gap phase for different catena positions (crest, upper slope, middle slope, lower slope and valley bottom) for the sites Zagné (Z), Taï (T) and Para (P), and for the three sites combined (All). Only gaps larger than 10 m^2 are included.

	Area of physiographic unit (%)				Gap density (ha^{-1})				Mean gap size (m^2)				Area in gap phase (%)			
Catena position	Z	T	P	All	Z	T	P	All	Z	T	P	All	Z	T	P	All
Crest	16	9	5	10	1.5	1.9	0	1.4	25	40	—	31	0.4	0.7	0	0.42
Upper slope	30	57	23	37	3.0	1.9	2.2	2.3	44	40	25	39	1.3	0.8	0.5	0.88
Middle slope	49	20	64	44	2.0	2.3	2.3	2.2	44	66	40	46	0.8	1.5	0.9	0.99
Lower slope	2	10	6	6	0	1.3	0.7	0.9	—	27	23	26	0	0.3	0.2	0.19
Valley	3	5	1	3	0	3.2	3.6	2.2	—	34	28	33	0	1.1	1.0	0.74
All positions	100	100	100	100	2.1	2.0	2.1	2.1	42	44	36	41	0.87	0.87	0.75	0.84

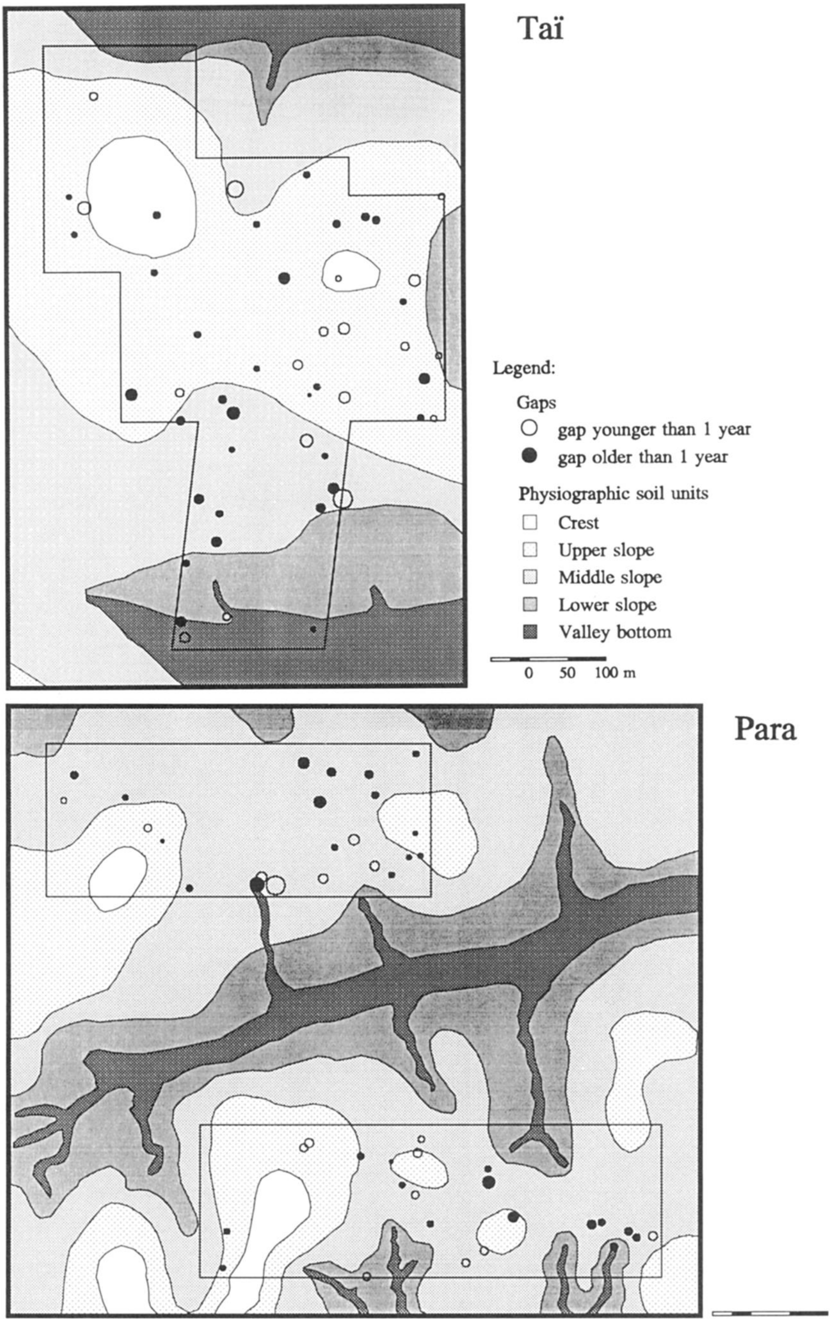

Figure 2. Maps of the three study sites showing the spatial distribution of the gaps on the physiographic soil units. The circles represent irregularly shaped gaps, drawn proportionally to the area of the gaps, but not to scale.

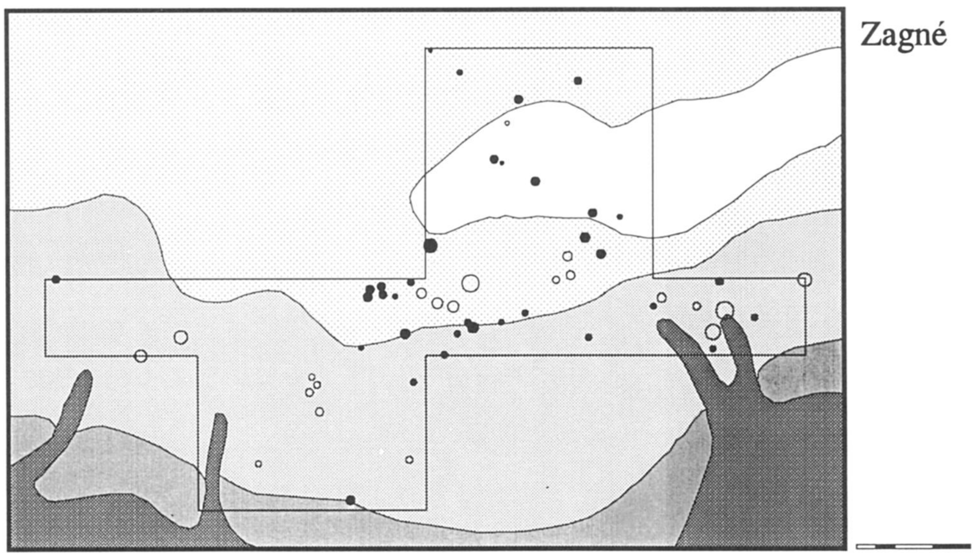

Figure 2. Continued.

For all three sites the most common distance between gaps is between 20 and 40 m (Figure 4). One has to bear in mind that this is the distance between subsequent gap centres, and that the gap edges are even closer to each other. Young gaps are on average not significantly closer to old gaps (61 m for back-transformed data) than to arbitrary random points in the forest (62 m) (Student's *t*-test, $T = 0.24$, $P > 0.05$). In addition, the distribution functions of nearest neighbour distances were not different either (Kolmogorov-Smirnov Two-sample test, $P > 0.05$).

Gaps and catena position

The mean number of gaps per hectare and the percentage area in gap phase are remarkably similar for the three sites. Within sites however, differences do occur (Table 1). It is clear that the gaps are not evenly distributed over the catena. All three sites show the same tendency, i.e. the disturbance influences are higher on the upper- and middle slope than on the crest and lower slope. The valley bottom is quite variable in this respect, partly due to the small area sampled. There was no statistically significant effect of catena position upon any one of the disturbance parameters.

However, if the valley bottom is excluded from further analysis, another picture emerges. Gap densities are significantly higher on the upper- and middle slope, than on the crest and lower slope (Kruskal-Wallis test, $Chi^2 = 8.56$, $P < 0.05$). Mean gap sizes are also larger here (39–46 m^2) than on the crest (31 m^2) or lower slope (26 m^2), but this is not significant (Kruskal-Wallis test, $Chi^2 = 2.29$, $P > 0.10$). Finally, the interaction between catena dependent gap density and gap size results in a percentage of forest area in gap phase which

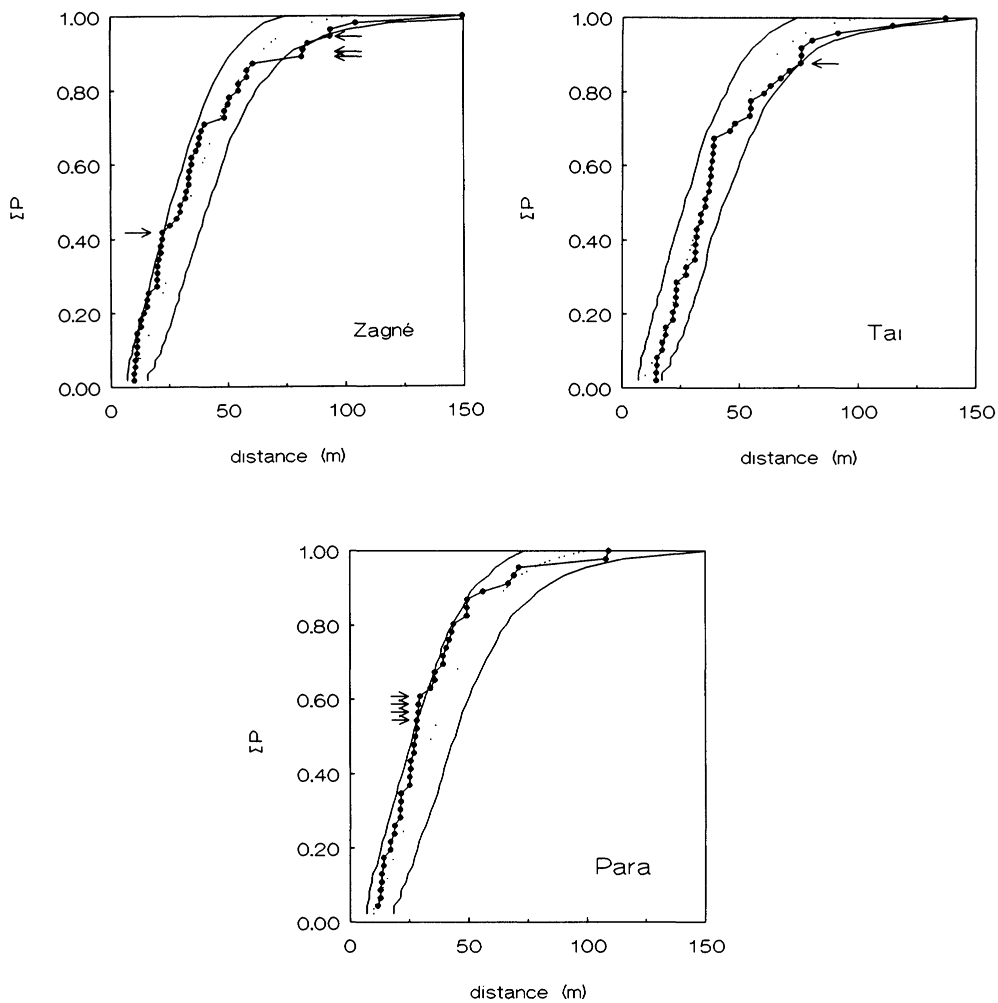

Figure 3. Observed and simulated cumulative distribution functions (ΣP) for the nearest neighbour distances of gaps. Black dots show the actual found cumulative distribution function, dotted lines the estimated cumulative distribution function, and solid lines show their 95% confidence envelope (based on 1000 random simulations per site). Arrows indicate significant values. The study sites Zagné, Taï and Para are shown respectively.

is significantly higher on the upper and middle slope positions than on the crest and lower slope (Kruskal-Wallis test, $Chi^2 = 8.22$, $P < 0.05$).

DISCUSSION

Distribution pattern

Average gap densities are remarkably constant when large tracts of forests are considered. Not only at a local scale, for one particular site, but even at a

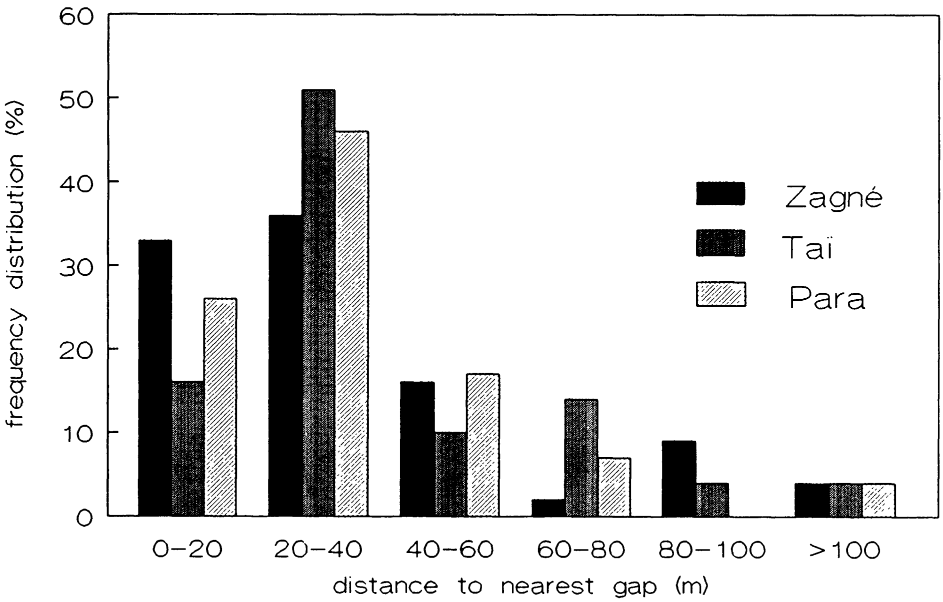

Figure 4. Relative frequency distribution (%) of nearest neighbour distances for gaps for the sites Zagné, Taï and Para.

regional scale for different forest zones along a climatic gradient (Jans *et al.* 1993). However, spatial analysis reveals that the occurrence of gaps is not a random event, but a determined process, in which some places are more likely to have gaps than other places. A clumped distribution pattern was shown for two of the three sites.

Spatial scale

The scale at which clumping takes place can give insight into which underlying gap forming processes bring about the found spatial distribution. Several causes can be put forward for the aggregation of gaps: (1) one gap can influence the formation of another by altering the canopy roughness, resulting in an increased turbulence in the surroundings, (2) local gusts of wind can result in the simultaneous fall of several nearby trees, (3) soil factors, topography or physiography may affect the rooting of the trees, and the species composition and structure of the forest. As a result size and occurrence of gaps may be affected.

Our data (in Zagné and Para more intergap distances in the range of 20–30 m than expected on basis of Monte Carlo simulations; Figure 3) suggest that direct gap to gap influences might have played a role. The nearest neighbour method showed that in one fifth of the cases gaps are within 20 m of each other. However, this hypothesis is not confirmed by the average distance between existing old gaps and newly formed young ones, which is not significantly smaller than the distance from an arbitrary point in the forest to a young gap. An alternative hypothesis might be that many small intergap distances in Zagné and Para are due to local gusts of wind. In that case, absence of these local gusts in Taï during the last years, may have resulted in a random gap distribution here. Lawton & Putz (1988) found for a cloud forest in Costa Rica an aggregation of gaps at a patch size of 0.1 ha, with more gaps within 20 m of a gap than expected. Treefall groups often occurred downwind from existing gaps. Hubbell & Foster (1986) showed that the fall of canopy trees is more likely to take place if adjacent places in the canopy were opened already. In spite of this, gaps were randomly distributed on their site on Barro Colorado Island, Panama.

Over and above the influence of individual gaps upon each other, and on a larger scale, catena dependent gap formation processes may form an overriding factor for the occurrence and distribution of gaps. Gap sizes are a little larger on the upper and middle slope, and mean gap density and percentage area in gap phase are significantly larger here than on the crest or lower slope. An explanation may be the influence of soil characteristics upon the structure of the forest. Shallow, hardened ironstone sheet layers at the crests in Taï and Para result in an impeded drainage, which may influence the rootability of the soil. Consequently, the forest at the crest has an irregular structure, consisting of many, small, low stature trees (Vooren 1985). When a tree falls, affected gap sizes are small, often not exceeding our lower limit of 10 m^2. The well-developed vertically drained soils of the slopes on the contrary, form a good substrate for trees. Total biomass and height of the trees are higher here than on the ironstone crests or the lower slope (Vooren 1985, van Rompaey 1993). Consequently, treefall results in larger-sized gaps and a larger area in gap phase. In a study in the same forest, Bonnis (1980) found more gaps on the higher slope than on the crest and the valley bottom. He related this to the topography and wind exposure. Winds should be more effective on the top of the catena than down in the valley bottom. Moreover, trees were larger on the higher slope and thus the size of treefall gaps too. In the lowland wet tropical forest of La Selva, Costa Rica, differences in number of gaps and in gap areas were found between plateau, steep slopes, rolling slopes and swamps (Hartshorn 1978). Swamps were more dynamic than other environments, most probably as a result of a poorly drained, less stable soil.

What are the consequences for regeneration?

There is much direct and indirect evidence that gaps may influence the spatial distribution of trees. The aggregation of trees is often linked to the regeneration of light demanding trees in gaps (Armesto *et al.* 1986, Forman & Hahn 1980). Newbery *et al.* (1986) found that the scale of pattern for tree distribution matched the size of windthrow gaps. We suggest that spatial aggregation of trees is not only the result of an enhanced regeneration of trees in gaps, but could also be the result of the clustered character of gap distribution on its own.

Some parts of the forest are more prone to disturbances than others. In that case, it is likely that early successional regeneration is directed towards those places where gaps are larger and more frequent than in other places. We found that the higher slope positions were more dynamic than crests or lower slopes. If this pattern in gap occurrence does not alter over time, this might be reflected in the distribution of light demanding tree species. Unfortunately, no data were available to test this hypothesis. Hubbell & Foster (1986) had such data at their disposal, and indeed they were able to show that the average disturbance regime was reflected in the tree species composition of the forest. The proportion of heliophilous trees was positively correlated with the canopy openness of the forest.

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