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Forest disturbance and natural regeneration in an African rainforest at Korup National Park, Cameroon

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This study investigated the effect of disturbance on the biodiversity of a tropical rainforest. Gap sizes, their distribution and the causal factors were evaluated in the 50 ha Korup Forest Dynamics Plot (KFDP). The regeneration of species was evaluated in the gaps of KFDP, Isangele roadside gaps and its adjoining closed forest. It was observed that gaps make up to 0.1% of the KFDP, and their distribution was clumped. The rocky and higher elevation had the highest number of gaps while the lowest part of the plot had the least. Out of the 303 gaps found in KFDP, 41.3% of these were as a result of tree snapping and the species *Oubanguia alata* was highly affected, while dead standing caused the least number of gaps (0.7%). Wind throw gaps had the largest sizes (143.88 m²) and the tree species *Protomegabaria stapfiana* was highly affected by this causal factor. Simpson diversity index of plant species at Isangele roadside was high (0.96) when compared to Isangele closed forest (0.92) and KFDP gaps (0.66) plots. Sørensen's similarity index of the Isangele road and closed forest was 0.88. Forest gaps may contribute to the maintenance of high species diversity which is significant in forest ecosystem management.

Key words: Causal factors, diversity index, gap sizes, closed forest, similarity index.

INTRODUCTION

The lowland tropical forests have the most diverse vegetation in the world. Many theories have been developed to explain the co-existence of such a large number of species with apparently similar regeneration requirements in the same area. The equilibrium theory stipulates that species dynamics are governed by deterministic processes dictated by species-specific attributes in relation to their surrounding environment (Norden et al., 2009). Non-equilibrium theorems point out that many species show large similarities in their life-histories and functioning. Chance processes such as sudden increase in light intensity on forest floor due to gap formation from natural or anthropogenic disturbances are largely responsible for species co-existence (Hubbell,

1999; Vandermeer et al., 2004; Martini et al., 2007). Niche partitioning contributes less, while chance events contribute more, to the maintaining of tree species richness via gap dynamics in tropical forests (Brokaw and Busing, 2000). Plant species recruitment after disturbance is the cornerstone to forest ecosystem dynamics and development.

Disturbances lead to the creation of forest gaps that cause changes in resource availability of the physical environment depending on its scale and severity (Martini et al., 2007). Natural disturbances such as wind throw, lightning, diseases, forest fires, individual tree fall and anthropogenic activities such as selective and non-selective logging, slash and burn agriculture, road construction, urbanization, etc create gaps for the re-colonization species (McCarthy, 2001; Martini et al., 2007).

Competitive lottery for gaps points out that species diversity is maintained at a high level when gaps are

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created and therefore open for reinvasion by different species (Begon et al., 1986). Gaps create major resource gradients for differential exploitation by the coexisting species, increase in light intensity, evaporation, temperature and decrease in humidity (McCarthy, 2001), thus creating a mosaic of regeneration phases of plants of different sizes and ages occurring simultaneously (Dalling et al., 1998; Denslow et al., 1998; McCarthy, 2001). Stomata conductance also shows a positive correlation with canopy openness (Vincent, 2001). Species differ in the way they react to this new microclimate and exploit it in different ways with respect to their growth and development-regeneration requirements forming different guilds (Hawthorne, 1993). Responses to the sudden removal of forest canopy are often rapid, as seeds and seedlings of shade intolerant woody plants take advantage of changed environmental conditions and regenerate. Suppressed seedlings and saplings as well as the branches of trees bordering the gap take advantage to grow faster in the gaps (Terborgh, 1992). Seeds may come from seeds of the neighbouring trees (seed rain) or from the soil seed bank.

The saplings of pioneer species are found only in gaps while those of primary species are found in gaps and in the understory of mature forest (Brokaw, 1985). Therefore, gap regenerative processes would only progress from the initial pioneer species mix if there is a ready seed source of mature phase species close by. The seeds of some shade intolerant tree species are short-lived and do not persist in the soil seed-bank. Therefore, seed of these species must come from a seed-source forest that exists close to the regenerating gap (McCarthy, 2001) otherwise the regeneration would stagnate at the pioneer stage. Seed fate depends on the mode of primary dispersal, the habitats on which the seeds land and the seed size (Forget et al., 1996; Norden et al., 2009). There is not much information on gap dynamics in tropical forest of west and central Africa. This present study was aimed at evaluating the spatial distribution of gaps, their causal factors, species regeneration, abundance and diversity at Korup Forest Dynamics Plot (KFDP), and Isangele road in Korup National Park (KNP), Cameroon.

MATERIALS AND METHODS

Korup National Park (KNP) is located 9° E and 5° N of the equator in the Bight of Biafra, in Mundemba, the South-West Region of Cameroon (Newbery et al., 1998). The Korup Forest Dynamics Plot (KFDP) has dimension of 1000 m (N-S axis) by 500 m (E-W axis), and is located 05° 03' 86" North and 08° 51' 17" East (Figure 1). The Korup forest has a minimum mean annual rainfall of 4027 mm to a maximum of 6368 mm. Soils tend to be skeletal, sandy near the surface and are very nutrient-poor because of the very high rainfall. The mean annual temperature is 30.6°C. Solar radiation varies little, ranging from 199 to 248 W/m² (Newbery et al., 1998). The topography of Korup National Park (KNP) is characterized by hills, at times very long high mountainous gradient (Thomas et al., 2003).

The Korup Forest Dynamics Plot (KFDP) was initiated in 1996, as part of the Centre for Tropical Forest Science (CTFS) network of 50 ha plots and it is located towards the southern end of KNP. It encompasses 1250 20 × 20 m quadrats (Thomas et al., 2003). Each 20 × 20 m quadrat was divided into four 10 × 10 m sub-quadrats which were further subdivided into four 5 × 5 m sub-quadrats, making sixteen 5 × 5 m sub-quadrats for each 20 × 20 m quadrat (Thomas et al., 2003).

To evaluate gap characteristics and estimate gap size, all 5 × 5 m quadrats of KFDK were revisited and all gaps mapped. Older gaps were mapped using height of vegetation growing in the gap as well as the presence of *Aframomum* sp. as a proxy for age. All gaps with vegetation height taller than 3 m were considered as old gaps while those lower than ≤ 3 were considered as new gaps. To estimate the size of gaps within KFDK, techniques of Vandermeer and Bongers (1996), Dickinson et al. (2001) and Pinzon et al. (2003) were modified into a simpler and unified method.

To estimate the gap sizes, shapes (triangles, rectangles and trapeziums) were mapped out by placing pegs at particular points, and their areas were calculated and summed. Gaps sizes were then classified following Brokaw (1982) as: small gap: < 100 m², medium gap: > 100 ≤ 400 m² and large gap: > 400 m². All tree species at KFDK have aluminium tags that have been stamped with tag numbers that are made up of a combination of the plot and tree number (Thomas et al., 2003). Within each gap, the causal factors were recorded and each species was identified using tag numbers and literature from KFDK census earlier carried out by Thomas et al. (2003).

To estimate the spatial distribution of gaps and the causal factors, KFDK was divided into three topographical ranges; the lower part which is flat and swampy, the slightly hilly middle part, and the upper part which is rocky and hilly. The number of gaps in each topographical category was used to evaluate the distribution of gaps in KFDK. All species that caused gaps were identified, and causal factors were recorded based on visual observation. The following causal factors were evaluated: snapping (SN), branch fall (BF), wind throw (WT), dead standing (DS) and others (OT) such as streams, collapsed rattans and lianas, and large rock outcrops (Figure 2). Multivariate analysis (principal component analysis) was used to evaluate the causal factors, to see which one had the greatest impact on gap size at KFDK, using Minitab 16 Professional (Minitab Inc., 2010).

Regeneration, diversity and relative abundance (RA), was evaluated by using 20 quadrats each of 5 × 5 m² were laid out in gaps at KFDK and Isangele road as well as at the Isangele understory/closed forest. All species present in each plot were identified and for those not identified voucher specimens were collected for identification at the Limbe Botanic Garden. Floristic comparisons were then carried out to evaluate diversity and similarity within and between forest gaps and under-storey. The Isangele roadside gaps were due to reconstruction of the road from Mundemba town to Isangele town.

One way ANOVA at 95% CI with Tukey's multiple comparisons was computed to test if there were significant differences in the size of gaps caused by the different causal factors of gaps in KFDK, using Minitab 16 Professional (Minitab Inc., 2010). Simpson's diversity index (Begon et al., 1986) was used to evaluate the diversity of species in gaps and in the closed forest. Sørensen similarity index was used to assess similarity between the Isangele road gaps, Isangele road closed forest and the KFDK plots (Chao et al., 2006).

Simpson's diversity index

$$D = 1 - \sum(P_i)^2$$

Where D = Simpson's index

Where P_i = Proportion of species i in the community.

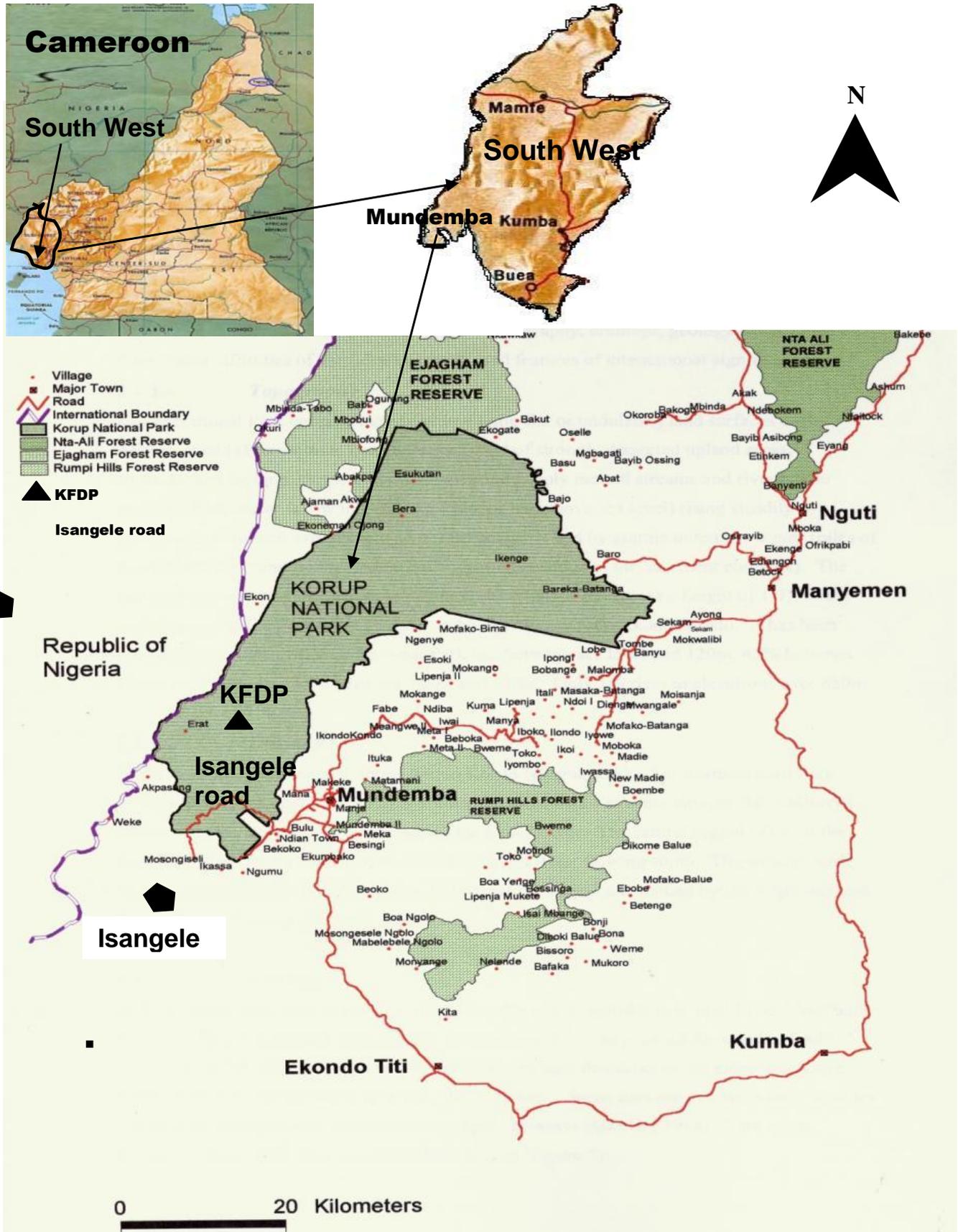


Figure 1. Location of KNP and KFDP in the South West Province, Cameroon (Thomas et al., 2003).

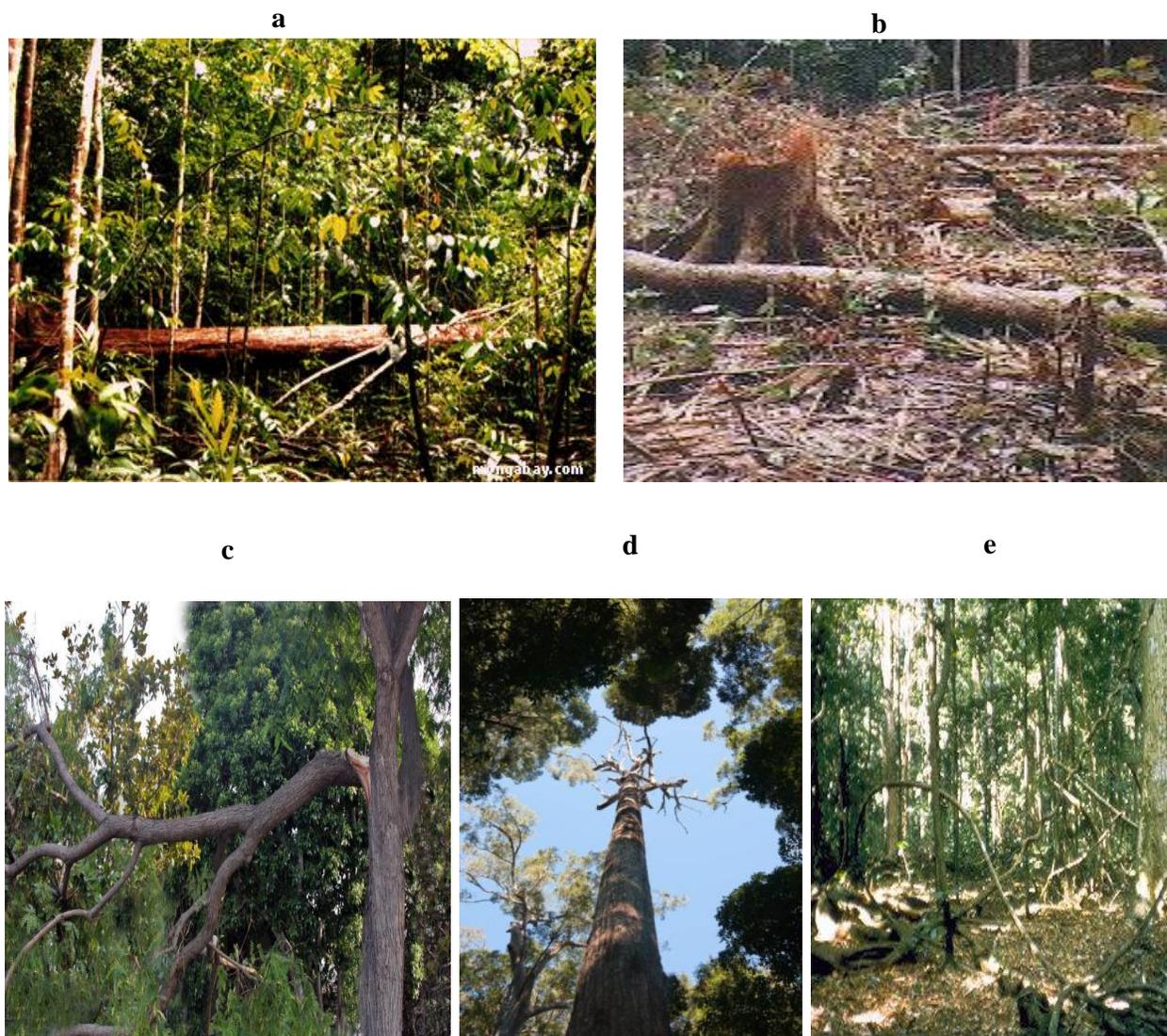


Figure 2. Some of the apparent results of some causal factors in KDFP: (a) Wind throw; (b) snapping; (c) branch fall; (d) Dead standing; (e) collapsed lianas.

Sørensen similarity index

$$C_s = 2C/(a + b)$$

Where C_s = Sørensen similarity index; $C = ab$ = Number of species present in sample A and sample B (joint occurrence); a = number of species present in sample A and not sample B; b = number of species present in sample B and not sample A

RESULTS

Gap characteristics

There were 95 species in 34 families that regenerated in KDFP gaps and these gaps were caused either by wind thrown, snapped, or dead standing or lost their branches,

leading to the creation of gaps (Table 1). *Oubanguia alata* had the highest frequency of gaps by snapping (16) and branch fall (10) while *Protomegabaria stapfiana* caused the highest frequency of wind throw (23) (Table 1). The tree species most affected by causal factor was *P. stapfiana*. There were 303 gaps recorded in KDFP and the highest number of gaps (41.3%) was initiated by snapping trees while dead standing trees initiated the least (0.7%) (Table 2). About 14.5% of the total gaps were caused by other factors such as collapsed lianas, streams, or large rocky outcrops. Wind throw caused the widest gaps with mean gap size of 143.88 m² and the least gap size was 75 m² which was caused by dead standing trees. Principal component analysis also showed that wind throw gave highest mean gap size (Table 2).

Gaps make up about 0.1% of the 50 ha KDFP forest

Table 1. Frequency (F) and relative abundance (RA) of some gap initiators in KFDP according to APG-2 (2003) (Ten of the most significant species out of 93 species are listed below).

Tree species	Family	Snapping		Wind throw		Branch fall		Dead standing	
		F	% RA	F	% RA	F	% RA	F	% RA
<i>Oubanguia alata</i> Bak. F.	Scytopetalaceae	16	12.80	3	3.57	10	20.83	1	50.00
<i>Protomegabaria stapfiana</i> (Beille) Hutch	Euphorbiaceae	8	6.40	23	27.38	3	6.25	1	50.00
<i>Dichostema glaucascens</i> Gürke	Euphorbiaceae	5	4.00	6	7.14	0	0.00	0	0.00
<i>Hymenostegia afzelii</i> (Oliv.) Harms	Leguminosae	3	2.40	2	2.38	1	2.08	0	0.00
<i>Homalium longistylum</i> Mast	Flacourtiaceae	3	2.40	2	2.38	0	0.00	0	0.00
<i>Diospyros gabunensis</i> Gürke	Ebenaceae	3	2.40	1	1.19	0	0.00	0	0.00
<i>Klaineanthus gaboniana</i> Pierre ex prain	Euphorbiaceae	3	2.40	1	1.19	0	0.00	0	0.00
<i>Strombosia</i> sp.	Olacaceae	3	2.40	0	0.00	1	2.08	0	0.00
<i>Garcinia conrauana</i> Engl.	Gittiferae	3	2.40	0	0.00	0	0.00	0	0.00
<i>Scottellia klaineana</i> Pierre	Floacourtiaceae	3	2.40	0	0.00	0	0.00	0	0.00
<i>Cola acuminata</i> Engl	Sterculiaceae	2	1.60	2	2.38	0	0.00	0	0.00
<i>Cola lateritia</i> K. Schum	Sterculiaceae	2	1.60	2	2.38	0	0.00	0	0.00

Table 2. Number of gaps caused by each causal factor and their mean gap sizes and their Eigen values.

Causal factor	Number of gap	% gap	Mean gap size	Principal component proportion	Eigen value
Wind throw	84	27.7	143.88 ^a	0.39	1.94
Snapping	125	41.3	131.25 ^{ab}	0.21	1.04
Branch fall	48	15.8	123.48 ^{ab}	0.19	0.96
Dead standing	2	0.7	75.00 ^b	0.06	0.33
Others	44	14.5	92.59 ^{ab}	0.15	0.74

HSD 0.05. Means with the same letter within the column are not significantly different.

cover. Medium gaps were more frequent (53%) while very large gaps were scarce (1.65%) (Figure 3).

The distribution of gaps varied significantly with the topography. The number of gaps was highest at higher rocky elevation (121); the middle altitude had 101 and 81 gaps at the lower altitude. The spatial distribution of gaps in KFDP increased from lower elevation towards the high elevation where it was clumped (Figure 4).

Regeneration of species in the gaps of KFDP and Isangele roadside and Isangele closed forest showed that *Lecomtedoxa klaineana* had the highest relative abundance in the Isangele road understorey (16.63%) and in the Isangele roadside gap (15.12%) (Table 3). In KFDP gaps, *O. alata* had the highest relative abundance (57.08%) and *Aframomum* species were found regenerating only in gaps. The highest number of individuals was found in KFDP gaps (420) and the lowest at Isangele roadside gaps (340) (Table 4). The highest number of species was noted in Isangele closed forest (87) while the lowest was in KFDP gaps (72). However, the species diversity was highest in Isangele roadside gaps with Simpson's diversity index of 0.96 and lowest species diversity was in KFDP gaps (0.66).

The highest Sørensen's similarity index was between

the Isangele roadside gaps and closed forest plots (0.88), while the lowest was between the Isangele closed forest plots and KFDP gaps (0.56) (Table 5).

DISCUSSION

The probability for a gap to be created in a particular area in KFDP was low as it represents a very small percentage of the forest stand. Out of the 303 gaps in KFDP, the majority were medium size gaps while large gaps were very rare. This is in line with Thomas et al. (2003) who observed in KFDP that gaps tend to be small, resulting from the fall of one or a few trees. The distribution of gaps in KFDP at higher elevation was clumped because of many large out-crop of boulders which hinders germination and establishment of the seedlings on the forest floor. Also, the marshy topography of the middle part of KFDP increases the chances for trees to be uprooted especially during the rainy season because the waterlogged soil offers little resistance to the prevailing wind and storms (Terborgh, 1992; Deb and Sundriyal, 2007).

Most of the gaps in KFDP were initiated by snapping

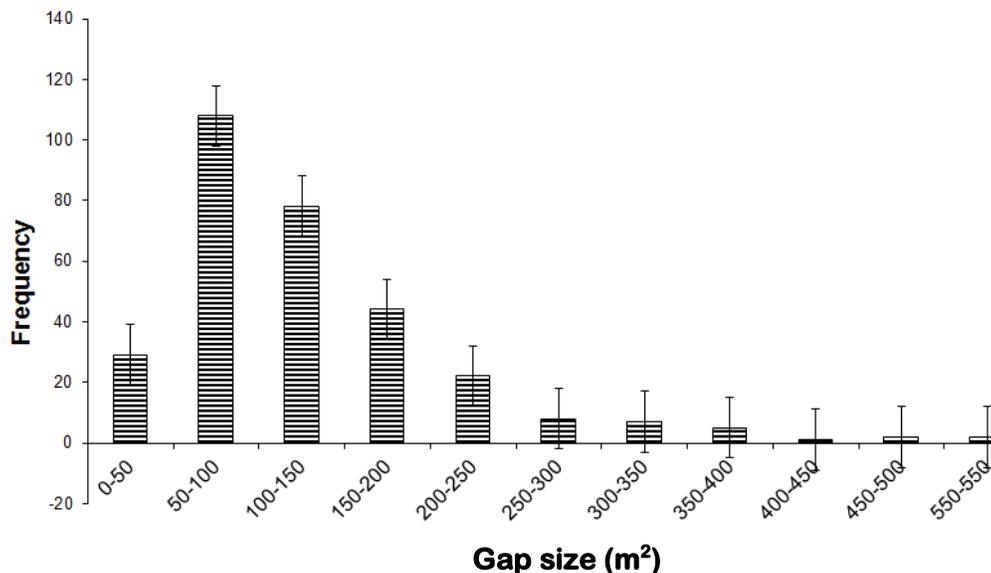


Figure 3. Comparison of the different of gap sizes in KFD.

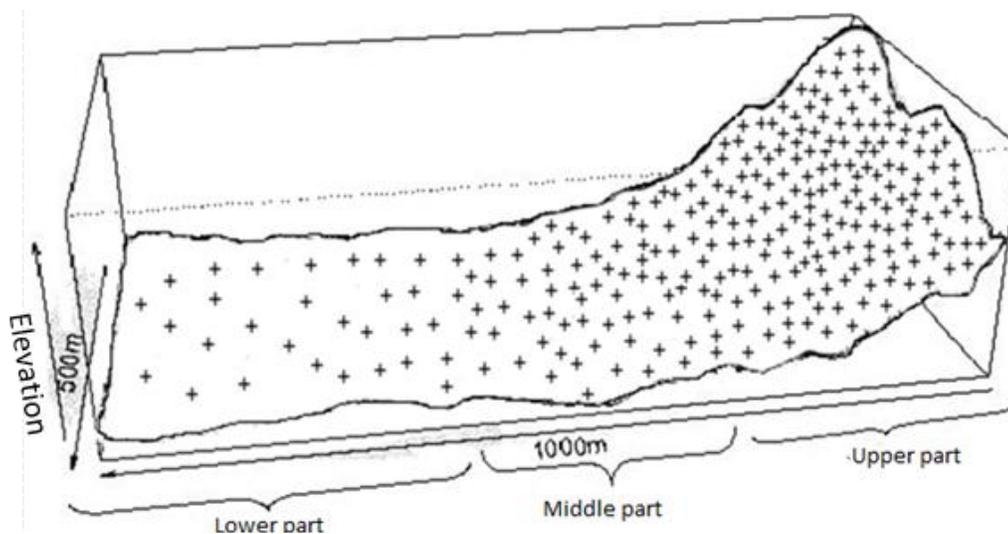


Figure 4. Spatial distribution of gaps in the different topographical positions of KFD.

trees. More trees snap during the rainy season because of heavy water load at the tree crown and large trees are more vulnerable due to larger crown size and higher epiphyte load. Some trees crowns are also asymmetrical, and more likely to fall towards the heavy side (Rentch, 2011). Vandermeer and Bongers (1996) and Arriaga (2000) found that snapping trees caused 62% of gaps in the Nouragues forest in French Guiana and 37.6% in the Tamaulipas forest in Mexico respectively.

The mean gap size caused by wind throw was highest, which is in line with that obtained by McCarthy (2001) who reported that wind throw creates larger and more

complex or heterogeneous gaps. Wind throw caused the highest domino effect because, though it caused a lesser number of gaps than snapping, the mean gap size of wind throw gaps was higher than that of snapping. This might be due to the fact that, when a whole tree falls, it would occupy more space on the forest floor than when its branches or part of the stem falls.

It was observed that most of the branches of a single tree might be attached to other trees and when this tree falls, it creates a bigger gap as it pulls the other branches and trees along with it. *O. alata* caused the highest number of gaps by snapping and also the highest number

Table 3. Frequency (F) and relative abundance (RA) of species recruitment in sampled plots at KFDP and Isangele road plots (ten of the most significant species out of 161 species are list below).

Species	Family	Isangele road understorey		Isangele roadside gap		KFDP gap	
		F	% RA	F	% RA	F	% RA
<i>Lecomtodoxa klaineana</i> (Pierre ex Engl.) Dubard	Sapindaceae	70	16.75	52	15.25	8	1.89
<i>Phyllobotryon spathulatum</i> müll. Arg.	Flacourtiaceae	62	14.83	15	4.40	3	0.71
<i>Scytopetalum klaineanum</i> Pierre ex Engl.	Scytopetalaceae	48	11.48	6	1.76	0	0.00
<i>Rinorea ilicifolia</i> (Boivin ex Tul.) Grey-Wilson	Violaceae	38	9.09	6	1.76	0	0.00
<i>Rinorea leiophylla</i> M. Brandt	Violaceae	10	2.39	12	3.52	0	0.00
<i>Strombosiopsis tetrandra</i> Engl.	Olacaceae	10	2.39	6	1.76	2	0.47
<i>Rinorea</i> sp.	Violaceae	10	2.39	6	1.76	0	0.00
<i>Microberlinia bisulcarta</i> A. Chev.	Leguminosae	8	1.91	9	2.64	0	0.00
<i>Drypetes</i> sp.	Euphorbiaceae	8	1.91	3	0.88	0	0.00
<i>Gambeya</i> sp.	Sapotaceae	8	1.91	3	0.88	0	0.00
<i>Pleiocarpa bicarpellata</i> Stapf	Apocynaceae	8	1.91	3	0.88	0	0.00

Table 4. Mean Simpson's diversity index at KFDP gaps, Isangele roadside gaps and Isangele closed forest.

Plot	Number of species	Number of individual	Simpson's diversity index
Isangele roadside gap	75	340	0.96
Isangele closed forest	87	414	0.92
KFDP gap	72	420	0.66

Table 5. Sørensen similarity indices between the KFDP gaps, Isangele roadside gaps and Isangele closed forest plots.

Plot	Isangele roadside	Isangele close forest	KFDP (gap)
Isangele roadside	-		
Isangele close forest	0.88	-	
KFDP (gap)	0.62	0.56	-

of gaps by branch fall. Their stems are not hard enough to sustain their large crown, increasing their probability to snap especially during the rainy season when winds and storms are prevalent (Thomas et al., 2003).

P. stapfiana initiated the highest number of gaps by wind throw. Their crowns are asymmetrical, increasing the tendency to be uprooted especially during the raining season in the direction of the larger branches in the crown.

Simpson's diversity index was low in gaps of KFDP than the closed forest which is contrary to observations of Begon et al. (1986) for lowland tropical rainforests. However, the result collaborates with the findings of Deb and Sundriyal (2007) in their study at the Namdapha National Park in India. The reason for the differences might be due to the type of tree species surrounding the gaps since it had the highest number of individuals when compared with the Isangele closed forest.

The high species diversity in gaps of Isangele roadside compared to Isangele closed forest was also reported by Begon et al. (1986) for lowland tropical rainforest. This signifies higher regeneration of species in gaps than in the forest understorey in tropical rainforests. This is in conformity with the observations of Schnitzer and Carson (2001) and McCarthy (2001) who reported that diversity is higher in gaps because different microclimates allow for an overall sustained increase in plant establishment and growth due to resource partitioning. It conforms to the theory of competitive lottery for gaps where species diversity is maintained at a high level when gaps are created and therefore open for reinvasion by different species (Begon et al., 1986). This demonstrates the importance of chanced processes in the maintenance of species diversity in tropical rainforests (Brokaw and Busing, 2000), acquiescent to the non-equilibrium theorem. *O. alata* regenerate only when

gaps are created in tropical rainforest, as indicated by its high relative abundance in KFDP gaps, and the absence of its saplings in the forest understorey (Brokaw, 1985). This enhances the role of adaptation of species to different regeneration sites in tropical tree communities, as gaps are widely recognised for their role in reproduction, growth, establishment and survival of rainforest trees (Denslow, 1987).

Afromomum species are gap colonizers and can be used as a proxy for the age of gaps with respect to their abundance. More *Afromomum* clumps were found in the KFDP gaps, indicating they were older than the Isangele roadside gaps. The high species similarity between the Isangele closed forest and Isangele roadside plots than between Isangele closed forest and KFDP or Isangele roadside and KFDP may be as a result that most of the seedlings and saplings which were regenerating at the Isangele road side originated from species in the Isangele closed forest or from the soil seed bank which contains mostly seeds from species in the closed forest (Forget et al., 1996; McCarthy, 2001; Norden et al., 2009). This is also emphasized by the high relative abundance of *L. klaineana* in the Isangele understorey and in the Isangele roadside gaps.

Conclusion

Forest gaps contribute to the maintenance of high biodiversity in tropical rainforests because of their high heterogeneity. Tropical rainforests are more diverse as they are more finely graded in their light requirements and growth rates. However, species such as *O. alata* can only regenerate when there is sudden increase in irradiation due to gaps formation, noting the influence of the non-equilibrium theorem in the dynamics of tropical rainforests. The stochastic availability of gaps, and limited recruitment of juveniles, means that gaps are filled mostly by chance occupants rather than by best adapted species.

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