Gap characteristics and regeneration in Bwindi Impenetrable National Park, Uganda

Dennis Babaasa[1]*, Gerald Eilu[2], Aventino Kasangaki[1], Robert Bitariho[1] and Alastair McNeilage[1]

[1]*Institute of Tropical Forest Conservation, PO Box 44, Kabale, Uganda and* [2]*Department of Forest Biology and Ecosystems Management, Makerere University, PO Box 7062, Kampala, Uganda*

Abstract

Before Bwindi Impenetrable forest, Uganda, became a national park in 1991, there was a high level of human activity in much of the forest, especially cutting of large trees for timber by pitsawyers. This created extensive gaps in this tropical Afromontane rain forest. We quantified and compared tree regeneration in three sites that were logged at different intensities. Gap sizes in Bwindi, even under fairly natural conditions are very large (mean = 4460.1 m^2). Logging further enlarged the gap sizes and had a negative impact on tree regeneration. The study shows the strong role of logging disturbance in promoting an alternative successional pathway, where the large gaps created by logging are in a low-canopy state dominated by a dense tangle of herbs, shrubs, and herbaceous or semi-woody climbers. We recommend periodic monitoring of gap size and tree regeneration in the gaps to ascertain the trend of recovery from past logging disturbance.

Key words: Bwindi impenetrable, gap dynamics, gap size, logging, succession, Uganda

Résumé

Avant que la forêt Impénétrable de Bwindi, en Ouganda, ne devienne un parc national en 1991, il y avait beaucoup d'activités humaines dans une grande partie de la forêt et particulièrement des coupes de gros arbres par des scieurs de long. Ceci a causé la présence de nombreux trous dans cette forêt tropicale afro-montagnarde. Nous avons quantifié et comparé la régénération des arbres sur trois sites qui ont été diversement exploités. La taille des trous à Bwindi, même dans des conditions relativement naturelles, est très grande (moyenne = 4.460,1 m^2). L'exploitation forestière a encore élargi ces trous et elle a eu un impact négatif sur la régénération des arbres. L'étude montre le rôle important joué par la perturbation causèe par l'exploitation, qui a entraîné un développement alternatif évolutif ; les grands trous créés par l'exploitation ont une canopée basse et sont dominés par un enchevêtrement d'herbes, de buissons et de plantes grimpantes herbacées ou semi-ligneuses. Nous recommandons la surveillance périodique de la taille des trous et de la régénération des arbres qui s'y déroule, pour évaluer la tendance à la récupération après la perturbation due à l'exploitation.

Introduction

Gap formation in the forest leads to rapid tree recruitment and redevelopment of the canopy (Brokaw, 1985a; Denslow, 1987). Gaps induce significant changes in the gap microclimate compared with the forest understorey (Denslow, 1987). As a result, the germination, establishment, growth, and reproduction of many gap plants are increased. Gaps maintain high pioneer tree density and diversity (Brokaw, 1985b; Lawton & Putz, 1988) as well as high liana species diversity (Schnitzer & Carson, 2001). However, gaps do not appear to maintain species diversity of non-pioneer, shade-tolerant trees (Uhl *et al.*, 1988; Hubbell *et al.*, 1999; Schnitzer & Carson, 2001). Patterns of plant growth and other ecological processes are thought to vary as a function of gap size, because gap size directly affects light levels and microclimates (Denslow & Hartshorn, 1994) and affect nutrient availability (Whitmore, 1996). Seedlings of mature forest tree species are released from the forest-floor seedling bank in small gaps to form the next growth cycle. In big gaps, these are replaced by or added to by pioneer species, germinated from seed after gap creation (Brokaw, 1985b).

**Correspondence:* Tel: 256 77 709753; Fax: 256 486 24122; E-mail: dbabaasa@hotmail.com

Gap closure rates are likely to vary with gap size. Small-tree and branch-fall gaps close primarily through lateral growth, whereas large gaps are closed by in-growth and upward growth of saplings (Denslow, 1987). An alternate successional pathway, whereby gap-phase regeneration in the large gaps is dominated by shrubs, lianas and large herbs and stalled in low-canopy state for many years before tree regeneration, is possible (Schnitzer, Dalling & Carson, 2000). Each of these pathways would have different successional trajectories that will favour the growth of a distinct suite of mature species and ultimately result in contrasting species composition.

Forest regeneration may vary locally as a result of human-induced disturbances, especially logging. Differences in gap characteristics between logged and unlogged forests lead to corresponding differences in microclimate, flora, fauna, frequencies of large herbivore incursions and plant succession (Kasenene, 1987). If damage from logging is great, these changes can result in suspended succession. Studies in a medium altitude tropical rain forest of Kibale National Park, Uganda, suggest four major factors responsible for the slow or possibly arrested post-logging tree regeneration (Kasenene, 1987; Struhsaker, Lwanga & Kasenene, 1996): (i) timber harvesting intensity; (ii) establishment and persistence of an aggressive shrub or herb layer; (iii) increased elephant use of logged areas compared with lightly logged and unlogged areas (as well as elephant use of forest gaps more than forest understorey of closed canopies), and large gaps more than small ones; and (iv) high seed predator rodent densities in the large gaps of logged areas. These factors need verification in other forest localities like Bwindi, where similar large-scale human disturbances have occurred.

Although in the last 30 years a lot of information on gap dynamics has been generated, few studies have compared the performance of saplings in gaps with those in forest understorey in logged sites (Struhsaker, 1997). In this paper, we analysed tree regeneration in a logged, tropical, Afromontane rain forest. The emphasis was on the extent to which sapling abundance and species composition varied with gap characteristics and logging intensity.

Materials and methods

Study area and logging history

Bwindi Impenetrable National Park, Uganda (latitude: 0°53′–1°8′S; longitude: 29°35′–29°50′E) is situated on the eastern edge of the Albertine Rift within an altitudinal range of 1160–2607 m. The topography is extremely rugged with numerous steep-sided hills and narrow valleys. The mean annual rainfall at Ruhija, situated at an elevation of 2350 m (Fig. 1), is 1440 mm. The vegetation is classified as a moist evergreen submontane and montane forest with a few deciduous trees at lower elevations and a small area of bamboo. Covering 331 km^2, it is the only large natural forest vegetation remaining as people have completely deforested most of the highlands of south western Uganda. The forest is important because it harbours nearly half the world's population of at least 700 critically endangered mountain gorillas (*Gorilla gorilla beringei*).

The forest was first protected by the Uganda Forest Department in 1932. In 1947, timber extraction by pitsawing was recommended as the best approach to harvest the valuable trees because of the steep and rugged terrain (Leggat & Osmarston, 1961). Pitsawing is the process of cutting timber trees and converting them to planks in the forest, involving at least two people operating a large manual saw. The log is rolled onto a frame over a pit for sawing; one person operates one end of the saw from within the pit below the log while the other operates the other end from the top. Pitsawing became the most prevalent human activity in the forest between 1947 and 1991. This activity altered the vegetation structure and composition of the forest considerably. About 10% of Bwindi remained intact, 61% was intensively pitsawn and 29% was selectively pitsawn (Fig. 1; Howard, 1991). Large forest gaps, characterized by a ground cover dominated by a dense tangle of herbs, shrubs and herbaceous or semi-woody climbers, are now common in much of the forest. The impact of such dense ground cover on gap-phase regeneration is unknown.

Volumes of hardwood timber removed from the forest are not known with certainty because there was widespread illegal logging in Bwindi (Butynski, 1984) for over 20 years until 1991, when the reserve was made a national park. Between 1961 and 1970, the recorded average was 710 m^3 per annum (Lockwood Consultants, 1974). Estimates for 1972–83 are about 940 m^3 or higher per year to about 4530 m^3 in 1983 alone (Butynski, 1984). Based on limited 1951 enumeration data, Lockwood Consultants (1974) estimated the average volume of commercial hardwoods of harvestable size (>50 cm d.b.h.) at just 45 m^3 ha^{-1}. The total sawn timber drain for 1983 was 140% more than the 1961 working plan recommendations.

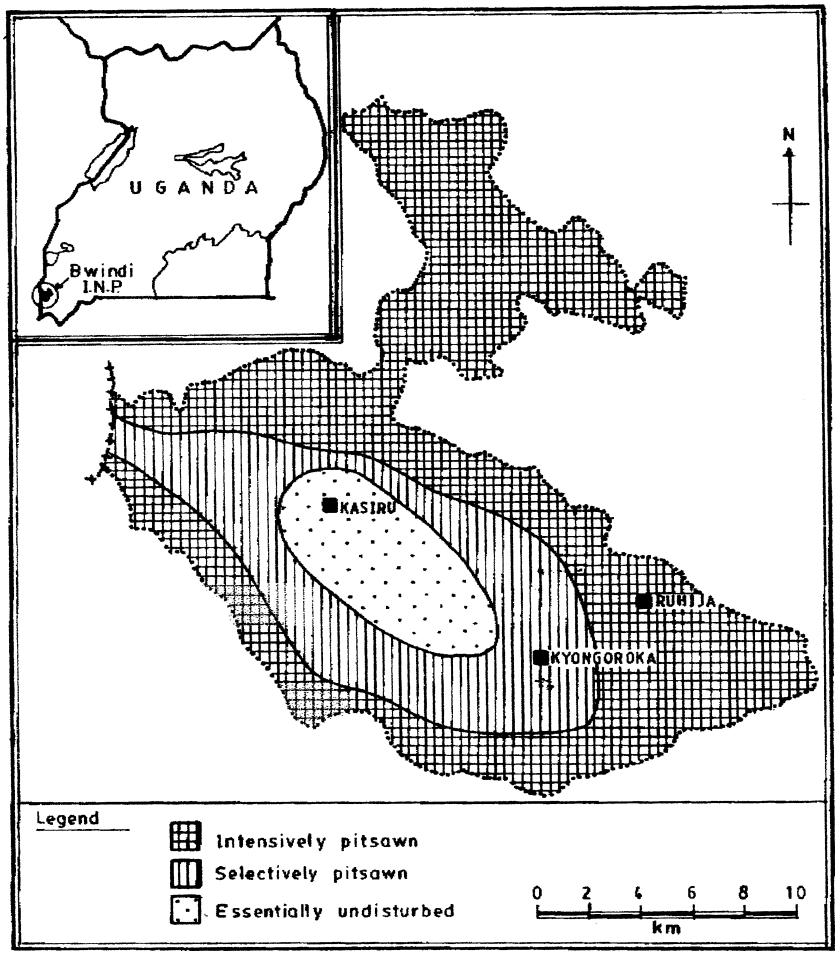

Fig 1 Pitsawing disturbance intensity in Bwindi Impenetrable National Park, Uganda. The study sites are also shown

Study sites

Three sample sites were selected on the basis of intensity of past timber harvesting as classified by Howard (1991), (Fig. 1):

1 Essentially undisturbed where there was very little pitsawing activity. Being far from forest edge and farther from public roads, these areas were relatively inaccessible and harvesting was limited to very high value timber trees, mainly *Podocarpus milanjianus* Rendle. Undisturbed forest was represented by Kasiru site (2170–2560 m).

2 Selectively pitsawn where 5–20% of trees exceeding 50 cm d.b.h. were exploited by pitsawyers. In these areas, timber harvesting was limited to removal of large trees of great timber importance mainly *P. milanjianus* and *Entandrophragma excelusum* (Dawe & Sprague) Sprague. Kyongoroka site (2040–2510 m) represented this type of forest.

3 Intensively pitsawn where more than 20% of trees exceeding 50 cm d.b.h. were exploited by pitsawyers. Being within about 6 km from the forest edge and public roads, the areas were easily accessible. These areas were represented by Ruhija site (2240–2450 m), with evidence of past pitsawing of a larger number of tree species including *Chrysophyllum* spp., *Zanthoxyllum gilletii* (De Wild.) Waterm., *Ficalhoa laurifolia* Hiern, *Podocarpus* spp., *Prunus africana* (Hook.f.) Kalkman, and *Symphonia globulifera* L.f.

Data collection

Between November 1999 and April 2000, 200 m wide transects of varying length were established in each of the three study sites of differing timber harvesting intensity; 6 km transects for each of Kasiru and Kyongoroka and 5 km for Ruhija (Fig. 1). All large gaps (canopy openings of at least 650 m^2) encountered along transects were recorded. A gap was delimited by visual estimation of gap edges based on the distribution of light-demanding herb/climber species such as *Mimulopsis*, *Pteridium*, *Rubus*, *Momordica* and *Sericostachys*. The centre of a gap was located at the intersection of the largest length from one gap edge to the opposite gap edge and largest width perpendicular to the length. At the centre of each gap, the slope angle was measured using a clinometer and altitude was measured using an altimeter. Gap areas were estimated by measuring the distances from the centre of the gap to the points on the edge along eight compass directions (0, 45, 90, 135, 180, 225, 270 and 315 degrees) using a range finder. Gap edge points were connected and by adding up the area of the eight right-angled triangles thus obtained, gap area was calculated (Jans *et al.*, 1993). Saplings were identified and counted in a 10 × 10 m plot established at the centre of each gap. Within the same 10 × 10 m plot, herb and semi-woody climber infestation in the gap was scored on an ordinal scale as follows: if a species was present as a single stand it was given a score of 3; if two species were dominant, each was given a score of 2; if three species were dominant, each would be given a score of 1; if a species already encountered in other gaps was not present, it was scored 0. This scoring method was adopted, instead of the widely used density or percentage of ground cover method for estimating herb or climber infestation, because the gaps in Bwindi were so large and the ground cover was uniformly dense. Saplings in the forest understorey adjacent to each gap were identified and counted in a 10 × 10 m plot set up at 10–12 m from the gap edge. The plot was located in a direction determined by taking a random compass bearing between 0 and 360 degrees. Saplings included all those young trees >1.5 cm height to <10 cm d.b.h. at 1.3 m above the ground. The study was conducted approximately 10 years after pit-sawing was banned in Bwindi but it was not possible to ascertain the ages of the individual gaps studied. Taxonomic nomenclature followed the Flora of Tropical East Africa (Polhill, 1952-onwards). We analysed all data using SYSTAT (Release 8.0) and considered the results to be statistically significant at $P \leq 0.05$.

Results

Gap density and size

We counted more gaps per unit area in the intensively and selectively pitsawn sites than in the essentially undisturbed site (Table 1). Similarly, there were more gaps per unit area in the intensively pitsawn site than in the selectively pitsawn site. Values for the fraction of forest area covered by the gaps ranged from 7.8 to 25.6% for the essentially undisturbed site and selectively pitsawn site, respectively. In terms of size, gaps in the selectively and intensively pitsawn sites were larger than those in the essentially undisturbed site (Table 2).

Of the total area of gaps, the very large gaps (>20,000 m^2) contributed 28% in the essentially undisturbed site, 30% in the selectively pitsawn site and 16% in the intensively pitsawn site, although they comprised only 5, 12 and 3%, respectively, of the total number of gaps sampled (Fig. 2). The essentially undisturbed site had a roughly negative exponential or 'reverse-J' gap size-class frequency distribution that is typical of montane forests under natural disturbance regimes (Arriaga, 1988; Lawton & Putz, 1988).

Table 1 Gap characteristics of the three study sites under different timber harvesting intensities in Bwindi Impenetrable National Park, Uganda

Characteristic	Essentially undisturbed site	Selectively pitsawn site	Intensively pitsawn site	Three sites together
Transect area (ha)	120	120	100	340
Number of gaps per site	21	30	30	81
Number of gaps (ha^{-1})	0.18	0.25	0.30	0.24
Gap area as percentage of total area inventoried	7.8	25.6	21.1	18
Mean gap size (m^2)	4460.1	10229.7	7045.2	7554.4
Range gap size (m^2)	855.1–26512.7	870.6–44434.2	656.9–36751.7	656.9–44434.2

Table 2 Results of a one-way ANOVA testing for differences in gap and forest understorey variables between sites under different timber harvesting intensities in Bwindi Impenetrable National Park, Uganda

Variable	*F*-value	Level of significance[a]	Tukey's test[b]
Gap size	8.83	**	2 > 1, 3 > 1
Slope angle	8.47	*	1, 3 > 2
Number of sapling stems in gaps	4.44	*	1 > 2, 3
Number of sapling species in gaps	8.498	**	1 > 2, 1 > 3
Number of sapling stems in forest understorey	3.07	n.s.	1, 2, 3
Number of sapling species in forest understorey	0.45	n.s.	1, 2, 3
Number of sapling stems in gaps of similar size	13.18	**	1 > 2, 2 > 3
Number of sapling species in gaps of similar size	9.41	**	1 > 2, 1 > 3

[a] Significant at $*P < 0.05$, $**P < 0.01$; n.s. = not significant at $P = 0.05$.

[b] 1 = essentially undisturbed; 2 = selectively pitsawn; 3 = intensively pitsawn.

Slope angle and gap size

Generally, lower slope angles were recorded in the selectively pitsawn site than either the intensively pitsawn site or essentially undisturbed site (Table 2). There was no significant relationship between gap size and slope angle in the gaps of the three sites ($F_{1,79} = 1.45$, $P > 0.05$). This was also true within individual sites: intensively pitsawn site ($F_{1,28} = 2.9$, $P > 0.05$); selectively pitsawn site ($F_{1,19} = 2.21$, $P > 0.05$); and, essentially undisturbed site ($F_{1,19} = 0.24$, $P > 0.05$). These results suggest that gap size is not a function of slope steepness characteristic of Bwindi terrain.

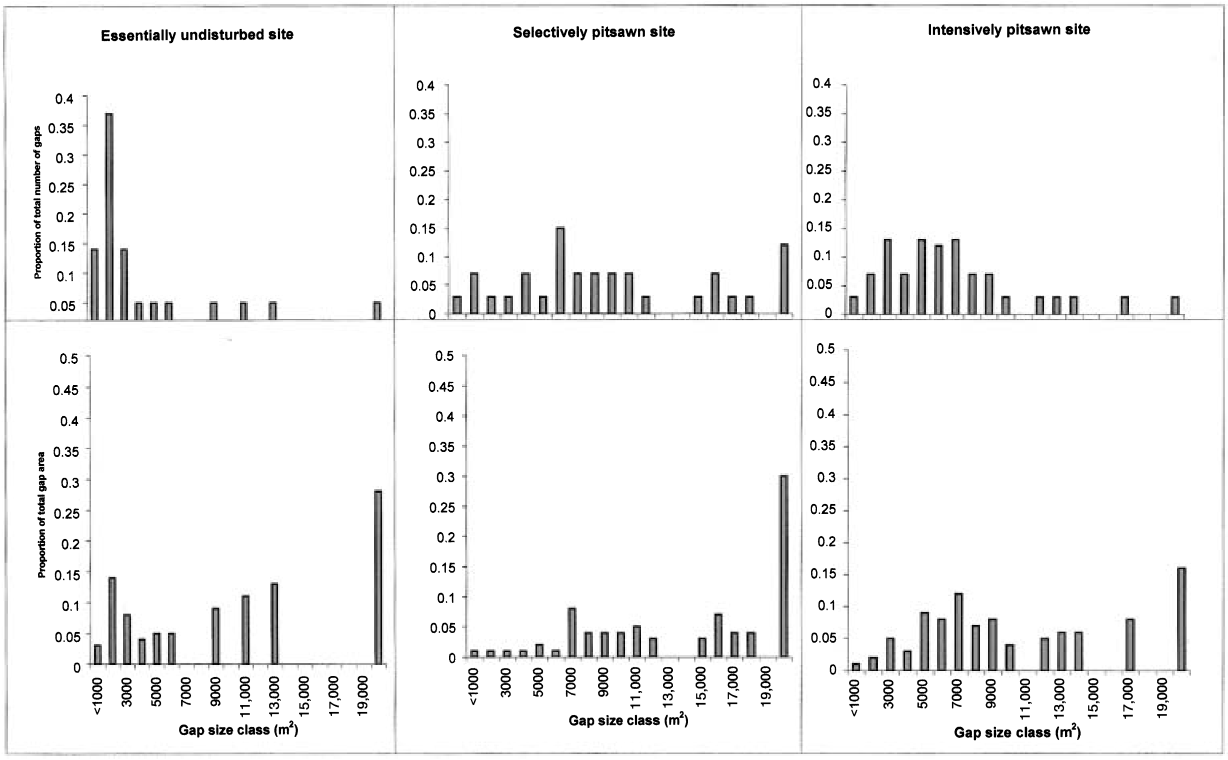

Fig 2 The distribution of the areas of gaps in sites of different timber harvesting intensity in Bwindi Impenetrable National Park, Uganda, as proportions of the total number of gaps and as proportions of the total gap area

Saplings, pitsawing intensity and gap size

Species richness and number of stems of saplings were significantly lower in gaps of intensively and selectively pitsawn sites than in gaps of the essentially undisturbed site (Table 2). This inverse relationship between disturbance intensity and species richness and stem numbers did not hold for forest understorey sites.

Gaps of nearly similar size were compared for species richness and number of stems of saplings between sites of different timber harvesting intensity. Gaps within the essentially undisturbed site were taken as a reference and five gaps within a range of ±250 m^2 area from each of the other two sites selected. There was no significant difference in size of the gaps selected ($F_{2,12} = 0.012$, $P > 0.05$). More species and stems of saplings occurred in the essentially undisturbed site than in selectively and intensively pitsawn sites (Table 2). In other words, if gap size was held constant, more regeneration of more tree species occurred in gaps of lightly pitsawn forest than heavily pitsawn forest. Because of the limited number of gaps of nearly similar size in a randomly harvested natural forest, the pattern described here should be interpreted with caution.

The results of model II regression analysis (reduced major axis method) showed a strong negative relationship between the number of sapling species and gap size for the pooled data of the three sites ($F_{1,79} = 4.88$, $P < 0.05$) but this did not hold for the number of sapling stems ($F_{1,79} = 0.29$, $P > 0.05$). This implies that regeneration of tree species is gap size-specific, with large gaps having few species of young trees, although gap size appears to have no effect on sapling stem abundance. When each site is considered separately, there is no relationship between number of sapling species and gap size: essentially undisturbed ($F_{1,19} = 1.49$, $P > 0.05$); selectively pitsawn ($F_{1,28} = 1.38$, $P > 0.05$); intensively pitsawn ($F_{1,28} = 0.29$, $P > 0.05$). This was also true for the number of sapling stems in gaps and gap sizes: essentially undisturbed ($F_{1,19} = 0.09$, $P > 0.05$); selectively pitsawn ($F_{1,28} = 1.74$, $P > 0.05$); intensively pitsawn ($F_{1,28} = 0.37$, $P > 0.05$). The essentially undisturbed site had the smallest gaps and the highest sapling species diversity in gaps. The two pitsawn sites had larger gaps and lower sapling richness in gaps. When the three sites are pooled, this site difference drove a negative relationship between gap size and sapling diversity.

Saplings in gaps and forest understorey

In the essentially undisturbed site, there were no differences between gaps and forest understorey in the number of sapling species (Paired sample *t*-test: $t = -1.95$, d.f. = 20, $P > 0.05$) and number of sapling stems (Paired sample *t*-test: $t = -0.24$, d.f. = 20, $P > 0.05$). However, in the two heavily pitsawn sites, sapling stem and species numbers were significantly lower in the gaps than the forest understorey (Paired sample *t*-test; selectively pitsawn site: sapling species $t = -5.36$, d.f. = 29, $P < 0.01$; sapling stems $t = -3.30$, d.f. = 29, $P < 0.01$; intensively pitsawn site: sapling species $t = -5.43$, d.f. = 29, $P < 0.01$; sapling stems $t = -2.95$, d.f. = 29, $P < 0.01$).

Gaps in the essentially undisturbed site had saplings of shade-tolerant species – *Chrysophyllum* spp., *Ocotea usambarensis* Engl., *Olea hochstetteri* Bak. and *S. globulifera*. However, these sapling species were not observed in gaps greater than 2000 m^2. The most common and abundant sapling species in the gaps of the three sites were *Macaranga kilimascharia* Pax. and *Neoboutonia macrocalyx* Pax. All the sapling species found in the gaps occurred in the forest understorey.

Environmental parameters and saplings in the gaps

Analysis of the effects of gap environmental factors (altitude, gap size, slope angle, and herbaceous and semi-woody climbers – *Sericostachys scandens* Gilg and Lopr., *Pteridium aquilinum* (L.) Kuhn, *Mimulopsis solmsii* Schweinf., *Rubus steudneri* Schweinf. and *Momordica foetida* Schumach.) on sapling performance using stepwise multiple regression procedure with backward interactive elimination showed that the dense ground cover of *P. aquilinum* and *R. steudneri*, and gap size had a negative impact on gap sapling species richness ($R^2_{adj} = 0.067$, $P = 0.04$), while low sapling stem abundance in the gaps was caused by a dense tangle of *S. scandens*, *M. solmsii* and *P. aquilinum* ($R^2_{adj} = 0.08$, $P = 0.03$). *S. scandens* and *P. aquilinum* were each found either as single-species stands or mixed with other herbs or climbers in half the number of gaps studied in the three sites together.

Discussion

Gap sizes in Bwindi, even under relatively natural conditions, are very large. For example, the mean gap size in the essentially undisturbed site was four times the mean gap size for a heavily logged compartment of a medium altitude tropical forest of Kibale, Uganda (Kasenene, 1987). This large gap phenomenon in Bwindi may be due to frequent treefalls on the gap edges due to the steep slopes (Denslow & Hartshorn, 1994) and the susceptibility of unstable soils (Leggat & Osmaston, 1961) to landslides in the canopy openings during periods of heavy rainfall. This is supported by an earlier study (Eilu, Obua & Pomeroy, 2004) that reports presence of many variable-aged fallen trees and evidence of landslide disturbances, which occur irregularly in Bwindi.

Gaps in Bwindi vary dramatically in their characteristics that largely reflect the management history of the forest. Gap sizes in the two heavily pitsawn sites were significantly larger and covered a significantly larger proportion of forest area than the essentially undisturbed site. We attribute this difference in gap sizes and the area of forest they cover to the harvesting intensity of valuable timber tree species. Windthrow or snapping of surviving trees could also increase in gaps created by logging (Skorupa & Kasenene, 1984; Kasenene & Murphy, 1991). Repeated postlogging human-induced fires, which are common during the long periods of drought in the highly disturbed areas, also contribute to large gap formation on the ridges of Bwindi.

The limited number of sapling species and stems in gaps of the two heavily pitsawn sites relative to the adjacent forest understorey and gaps in the essentially undisturbed site is attributed to the larger and more abundant gaps neighbouring each other in the heavily pitsawn sites, which influence regeneration through an edge effect between the gaps (Struhsaker, 1997). A neighbourhood gap effect in Bwindi is suggested by data showing that when gap size is held constant, the number of species and stems of young trees decrease as pitsawing intensity increased. Edge effect promoted rapid growth of existing and newly established herbs, shrubs or climbers. Once a dense shrub or herb layer is established, succession becomes slow or arrested. This seems to be the case for Bwindi where *P. aquilinum* and *R. steudneri* in the big gaps are affecting sapling species regeneration and *S. scandens*, *M. solmsii* and *P. aquilinum* are lowering sapling growth and survival in the gaps. The effect is in the form of competition for light, space, water, and nutrients and perhaps allelopathy (Struhsaker, 1997). Ground vegetative cover in the gaps can also affect tree regeneration indirectly by providing habitat and food for herbivores that feed on seeds and young trees (Kasenene, 1987; Struhsaker *et al.*, 1996).

Elephant activity in large gaps has been identified as one of the main factors contributing to the retardation of forest succession in heavily logged sites (Struhsaker *et al.*, 1996). During this study, it was observed, that elephants excavate and feed on the rhizomes of *P. aquilinum*, thereby creating 'elephant gardens' in the gaps. This elephant activity may have a positive feedback in the large gaps of Bwindi because although they are trampled or fed on, dense herb or climber communities in the gaps persist or even increase (Watts, 1987; Plumptre, 1993), thus preventing tree regeneration. A study of habitat selection by elephants in Bwindi showed their preference for heavily logged areas (Babaasa, 2000).

The lack of significant differences in sapling species richness and stem abundance in the gaps and forest understorey of the essentially undisturbed site corroborate with findings of Uhl *et al.* (1988) and Hubbell *et al.* (1999) which show that in undisturbed mature tropical rain forests, gaps do not affect sapling community composition, species richness, or relative species abundance. Uhl *et al.* (1988) noted that gaps remained dominated by shade-tolerant tree species that were present as advance regeneration before gap formation. However, Hubbell *et al.* (1999) suggested that the intermediate gap disturbance regime in an old-growth tropical forest did not control variation in local tree diversity of both pioneers and shade tolerants, as indicated by the high degree of constancy of relative species richness during gap-phase regeneration despite large changes in stem density during gap regeneration. Thinning and noncatastrophic mortality reduce both the tree density and species diversity in areas of low gap frequency (Denslow, 1995).

We conclude that gap sizes in Bwindi, even under fairly natural conditions, are very large. Logging activity increased gap sizes and had a negative impact on local abundance and species richness of tree regeneration in this Afromontane forest. The regeneration of tree species in Bwindi is gap size-specific, with large gaps having few species of young trees, although gap size had no effect on sapling stem abundance. This study demonstrates the strong role of human-induced disturbance in precipitating an alternate successional pathway where the large gaps created by logging, are in a low-canopy state of a dense tangle of herbaceous and semi-woody climbers. We recommend periodic monitoring (perhaps once every 10 years) of gap size and vegetation composition to ascertain the course of regeneration and understand the processes that influence the rate of the process in Afromontane forests.

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