Effect of gap size and age on climber abundance and diversity in Budongo Forest Reserve, Uganda

Fred Babweteera*, Andrew Plumptre† and Joseph Obua‡

*Budongo Forest Project, PO Box 362 Masindi, Uganda, †Wildlife Conservation Society, NewYork 10460–1099, U.S.A., ‡Faculty of Forestry and Nature Conservation, Makerere University, PO Box 7062 Kampala, Uganda

Abstract

A study of the effects of gap size and age on climber abundance and diversity was carried out in Budongo Forest Reserve in Uganda. Data were collected from compartments N5, W21, B1 and B3. Stump records were used to locate and estimate the ages of 78 gaps. Sample plots 5×5 m were set up in the gaps to assess climber abundance and diversity.

Climbers were more abundant and diverse in gaps that were more than 400 m^2, 15 months old and had more than 25% canopy opening. *Momordica foetida* was the most abundant climber species occurring on stems, branches and crowns of seedlings and saplings. Therefore, in order to keep natural regeneration free from climber tangles and produce good quality timber, climber control should be a major activity in tropical high forest management.

Key words: abundance, Budongo, canopy, climbers, diversity, gap

Résumé

On a réalisé une étude des effets de la taille et de l'ancienneté des trouées sur l'abondance des plantes grimpantes dans la Réserve forestière de Budongo, en Ouganda. On a récolté des données dans les compartiments N5, W21, B1 et B3. On a utilisé le relevé des souches pour situer et estimer l'âge de 78 percées. On a créé des plots échantillons de 5/5 m dans les percées pour évaluer l'abondance et la diversité des plantes grimpantes.

Ces plantes sont plus abondantes et plus diverses dans les percées qui ont plus de 400 m^2, plus de 15 mois et ont plus de 25% d'ouverture de la canopée. *Momordica foetida* était l'espèce grimpante la plus abondante sur les jeunes pousses, les branches et les couronnes des jeunes plants et des jeunes arbres. C'est pourquoi, afin de préserver la régénération naturelle de l'enchevêtrement des plantes grimpantes et de produire du bois de bonne qualité, il faudrait consacrer au contrôle des plantes grimpantes une part majeure des activités de gestion des hautes forêts tropicales.

Introduction

One of the goals of Uganda's Forest Policy is to produce timber from sustainably managed natural forests. Forests are renewable resources and their regeneration is influenced by creation of gaps in the canopy. At the same time, the disruption of the forest structure by natural or human disturbance alters ecosystem processes and the microclimate of the forest floor, which in turn influences the natural regeneration and growth of climbers.

For a long time, the structure of Budongo Forest Reserve has been altered by mechanical logging, pitsawing and poisoning of selected trees with aboricides (Plumptre, 1996). High intensity logging has created gaps that have been covered by climbers (Plumptre, Reynolds & Bakuneeta, 1997). The climbers, which usually form tangles, suppress natural regeneration and delay forest recovery. Despite these problems, little is known about the relationship between gap size, gap age, climber abundance and diversity, and yet this information is essential for the management of natural

Correspondence: Fred Babweteera, PO Box 362, Masindi, Uganda. E-mail: bfp@swiftuganda.com

 Afr. J. Ecol., **38**, 230–237

forests for sustainable timber production and biodiversity conservation. Studies carried out in Budongo Forest Reserve have concentrated mainly on primate ecology and the effects of mechanical logging and aboricide treatment on the natural regeneration of timber species. This study has examined another important aspect of natural forest management, that is, the relationship between gap size and age and climber abundance and diversity. First, a brief overview of gaps, climber growth and natural forest regeneration is given, followed by a description of Budongo forest reserve. Methods used to collect the data and the results obtained are presented in the subsequent sections.

Gaps, climber growth and natural forest regeneration

The presence of gaps in the forest canopy is important because it initiates the forest growth cycle (Jans *et al.*, 1993). Gaps are vital for the regeneration of rainforest tree species and represent a unique microenvironment (Whitmore, 1996). Furthermore, light quantity varies with gap age and size, both of which influence natural regeneration.

Gaps created by timber harvesting are usually overrun by climbers which grow rapidly and hinder the process of natural regeneration. In addition, climbers can re-sprout easily after being disturbed by activities such as logging and occupy gaps in a short time (Fisher & Ewers, 1991).

Gaps are favourable sites for natural regeneration of forest trees, but they are often occupied by several climber species which form tangles and retard the regeneration process. Climber tangles have detrimental effects on trees in tropical forests. For instance, they grow rapidly in length and size and smother the host trees, thereby reducing tree growth rates (Putz, 1984). Moreover, trees with climber tangles often suffer higher mortality rates than trees that are climber tangle-free (Putz & Chai, 1987). In gaps created by natural tree fall and logging, climber tangles decrease the growth rates of regenerating trees and mechanically damage their hosts (Putz, 1991; Plumptre *et al.*, 1997). Forest recovery is also delayed and trees develop kinked stems due to climber infestation (Putz, 1980). Ultimately the quality and value of timber is reduced.

The effects of climber tangles are closely related to gap-size and age. According to Hegarty (1989), small gaps created by felling one or two trees are not likely to be overrun by climber tangles. Whitmore (1990) also reported that the removal of several trees by logging creates large gaps that are ideal for vigorous climber growth. Thus, there is a need to understand the influence of gap size, age and canopy openness on climber abundance, composition, diversity and natural regeneration. The need to provide such information prompted this study, which aimed to assess variations in climber composition, diversity and abundance with gap size and age in Budongo Forest Reserve. Such information is needed to develop appropriate natural forest management plans for sustainable timber production and biodiversity conservation. Moreover, the findings can be used in the tropical regions of the world for improving the management of natural forests where conservation is carried out alongside timber production. The study sought answers to the following questions: which climber species grow in gaps? What gap size and age favours the growth of climber tangles? Is climber abundance, composition and diversity influenced by gap size and age? What is the maximum gap size that should be created in a natural forest?

Description of Budongo Forest Reserve

Budongo forest reserve is a medium altitude moist semi-deciduous forest. It lies in Bugahya county in Hoima district, and in Buliisa, Bujenje and Buruli counties in Masindi district, in western Uganda. It is located between 1°35′–1°55′N and 31°18′–31°42′ E on the edge of the western rift valley in western Uganda (Howard, 1991). It covers an area of 825 km^2, making it Uganda's biggest forest reserve (Hamilton, 1984).

Budongo Forest Reserve was gazetted as a Central Forest Reserve in 1932. It has one of the longest continuous research records of any tropical high forest in Africa (Langoya & Long, 1997) with permanent sample plots dating back to the beginning of this century.

Budongo Forest is of exceptional biodiversity importance, ranking third in overall importance in the country (Howard, Davenport & Mathews, 1996). The reserve, which is a mixture of tropical high forest with a large population of mahoganies, woodlands and savanna grasslands thought to be capable of supporting forest, has about 465 species of trees and shrubs and about half of the forest reserve is dominated by *Celtis*, *Khaya* and *Cynometra*.

Table 1 Areas and logging history of compartments studied in Budongo Forest Reserve

		Logging dates and method	
Compartment	Area (ha)	Mechanical	Pitsawn
N5	568	1954	1995/96
W21	1116	1963/64	1995/97
B1	582	1935, 1982–86	1993/94*
B3	867	1939/40	1993/94*

*Illegal pitsawing; Source: Plumptre *et al.* (1997).

Materials and methods

The study was carried out from November 1996 to October 1997. Data were collected from 78 gaps located in compartments N5, W21, B1 and B3. Logging records of these compartments were obtained from Budongo Forest Office and used to identify and estimate gap ages. The size of the compartments and the logging history are given Table 1.

The compartments have mixed-exploited forest (Plumptre *et al.*, 1997). The common species found are *Alstonia boonei, Celtis* spp., *Chrysophyllum albidum, Funtumia elastica, Ficus* spp., and *Trichilia* spp.

Determination of gap size, age and canopy openness

Sample plots 5×5 m were set up in the gaps at intervals of 5 m, starting from the gap edge and across the widest section of the gap (Hawthorne, 1993). Distances from the centre of the gap to the edges were measured in eight compass directions, namely 0, 45, 90, 135, 180, 225, 270 and 315° and a sketch map of the gap was drawn. The compass points on the edge of the gap were joined on the map and eight triangles were formed. The areas of the triangles were computed to obtain gap size (Jans *et al.*, 1993). Gap sizes were categorized as small (40–400 m^2), medium (401–800 m^2), and large (> 801 m^2). Canopy openness was determined using a spherical densiometer and canopy height estimated with a Suunto clinometer.

Assessment of climber abundance

The sample plots were subdivided into 1×1 m quadrants to assess the abundance of climbers. A quadrant was considered to be covered by climbers if two-thirds of its area had climber tangles. Climber abundance was recorded as the percentage of the plot having climber tangles.

Climber diversity and infestation of natural regeneration

Climbers that were present on saplings, poles, small trees (d.b.h. of 10–19.9 cm), medium sized trees (d.b.h. of 20–29.9 cm) and large trees (d.b.h. of > 30 cm) were identified, counted and scored as follows: no climbers (0), climbers present on stem (1), branches (2), and crown (3) (Plumptre *et al.*, 1997).

Data analysis

Data were analysed using SPSS computer software. Partial and bivariate correlations (Sokal & Rohlf, 1969) and multiple regression analysis (Snedecor & Cochran, 1967) were used to show the association between gap size, gap age, canopy openness, and climber abundance, composition and diversity.

Chi-squared tests were used to show the relationships between timber tree species cut and gap size; timber tree species cut and number of platforms constructed; and number of platforms and gap size. Shannon's diversity index was used to determine the diversity of climbers in gaps (Magurran, 1988). It is represented as $H' = -\Sigma\, p_i \log_e p_i$ where H' is the diversity index of climbers and p_i is the proportional abundance of the *i*th climber species (also represented as n_i/N). The minus sign is included in the formula in order to give a positive value. Polynomial curves were used to show variation in climber abundance and diversity with gap size, age and canopy openness.

Results and discussion

Gap size, age and canopy openness

Gap sizes ranged from 86 to 1845 m^2 and the ages ranged from 6 to 25 months (Table 2). Forty per cent of the gaps were small (40–400 m^2), 38% were medium size (401–800 m^2) and 22% were large (> 801 m^2). A chi-squared test ($\chi^2 = 18.1$, d.f. = [76,2], $P \leq 0.001$) showed that gap size was significantly associated with timber tree species cut. Wide gaps were created whenever mahogany trees with large diameters and wide crowns,

Table 2 Age and sizes of gaps studied in Budongo forest reserve

Age (months)	Gap size			
	Small	Medium	Large	%
6	1	3	2	8
7–12	7	6	2	19
13–18	18	12	2	41
19–24	5	6	3	18
25	0	3	8	14
%	39.8	38.4	21.8	100

for example *Khaya anthotheca* and *Entandrophragma* spp., were cut whilst smaller gaps were created when nonmahogany species such as *Maesopsis eminii* and *Cordia mellenii* were cut.

It was noted that pitsawers constructed two or more sawing platforms in each gap whenever a mahogany tree was felled. Gap size was further increased through clearing of undergrowth to create room for constructing the platforms. A chi-squared test showed that there was a significant association between the timber tree species cut and the number of platforms constructed ($\chi^2 = 14.1$, d.f. = [76,2], $P \leq 0.05$) and the number of platforms and gap size ($\chi^2 = 13.7$, d.f. = [76,2], $P \leq 0.05$). Sixty-seven per cent of the timber species felled were mahoganies and 85% of the gaps where they were cut had more than two platforms.

Gap size also increased where pitsawers cut several smaller trees (10–40 cm d.b.h.) for constructing the platforms. A multiple regression analysis ($R^2_{adj} = 0.93$, $P \leq 0.001$) showed that there was a significant association between gap size and the number of these trees. A regression equation $Y = 34.18\,x + 23.5$ was generated and used to estimate gap size (Y) (m^2) where the number of smaller trees (x) cut was known.

It is clear from literature that the degree of canopy openness usually depends upon gap size and canopy height. In this study a partial correlation analysis showed that there was a strong association between gap size and canopy openness ($r = 0.75$, $P \leq 0.001$). This finding is consistent with Danslow's (1987) observation that gaps with short canopy heights often have more open canopies. A stepwise multiple regression analysis showed that there was a significant relationship between gap size (x) and canopy height (c) ($R^2_{adj} = 0.48$, $P \leq 0.001$). Both variables were used to estimate canopy opening (Y) using the regression equation $Y = 0.03 \times -1.07\,c + 40.8$.

Climber abundance

There was a relationship between climber abundance (expressed as a percentage of climber cover) and gap size (Fig. 1), gap age (Fig. 2) and canopy openness (Fig. 3).

Figures 1–3 show that climber abundance increased with gap size, age and canopy openness. Consequently,

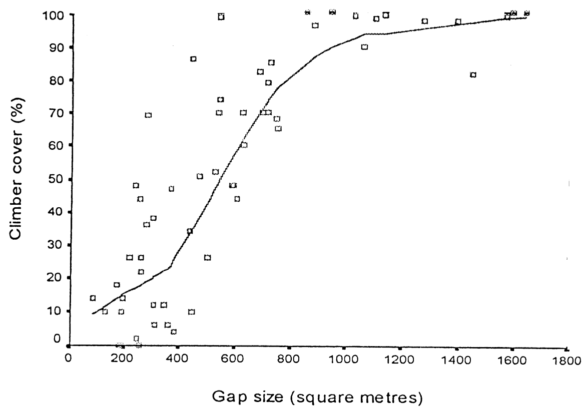

Fig 1 Relationship between gap size and climber abundance.

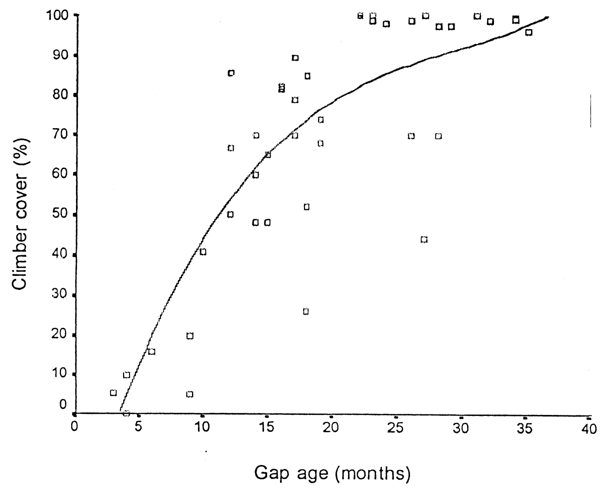

Fig 2 Relationship between gap age with climber abundance.

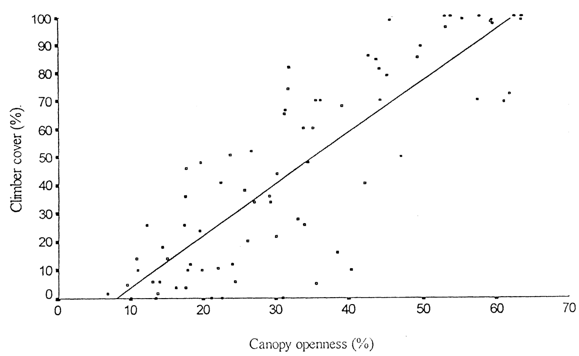

Fig 3 Relationship between canopy openness and climber abundance.

the hypothesis that there is no significant variation in the abundance of climbers with gap sizes and age was rejected. Furthermore, a partial correlation analysis showed that there was a relationship between gap size and climber abundance ($r = 0.6$, $P \leq 0.001$) and gap age and climber abundance ($r = 0.5$, $P \leq 0.001$). At the same time, there was a significant relationship between gap age and size and climber abundance ($R^2_{adj} = 0.58$, $P \leq 0.001$).

Canopy openness also influenced climber abundance (Fig. 3). As noted by Putz (1985), wide open canopies tend to allow plenty of light into gaps which then supports the growth of climbers. A stepwise multiple regression analysis showed that there was a significant relationship between gap age, size and canopy openness ($R^2_{adj} = 0.77$, $P \leq 0.001$).

As noted earlier, climbers proliferate in high light environments. Consequently, factors that increase light intensities in gaps, such as gap size and canopy openness favour the growth and abundance of climbers (Putz, 1985; Castellanos, 1991). This study has shown that *Momordica foetida* was the most abundant climber species growing in gaps. Two-thirds of the gaps that had 50% climber cover had *M. foetida.* tangles. According to Putz (1984), climbers are more abundant in newly created gaps (less than 3 years old) because such gaps receive full sunlight and climbers grow extremely long and cover vast areas rapidly. Data presented here also show that the age of gaps studied in Budongo Forest reserve varied from 3 to 36 months. Generally, factors such as gap orientation (Poulson & Platt, 1989) and soil fertility (Putz, 1985) also influence climber abundance. The effects of these environmental factors on climber abundance need to be examined in a future study.

Climber diversity and infestation of natural regeneration

Fourteen climber species were identified in the gaps (number of saplings infested are given in brackets) viz: *Adenia gummiferra* (30), *Cissus oliveri* (7) *Cissus patiolata* (20), *Congronema latifolium* (13), *Desmodium intotuene* (6), *Desmodium repandum* (15), *Dioscorea lecardii* (14), *Dioscorea sansibarensis* (24), *Diplocyclos palmatus* (9), *Iodes africana* (14), *Momordica charantia* (18), *Momordica foetidia* (364), *Pyrecantha sylvestris* (90) and *Solanum* spp. (80). There was a negative correlation between climber infestation and gap size, age and canopy openness (Table 3) suggesting that there were fewer climbers in smaller, younger and less open gaps. On the other hand there were positive correlations between climber infestation and gap size, age and canopy openness. *Momordica foetida*, family Cucurbitaceae, covered crowns of 80% of the seedlings and saplings (Table 4). Analysis of variance shows that the number of climbers did not significantly vary on the stems, branches and crowns of seedlings and saplings (Table 5). *Momordica foetida* was the most common climber found in gaps and on most saplings. More than 40% of the saplings infested with climbers had *Momordica foetida* (Table 3), and 22% of these were found on the branches. *Pyrecantha sylvestris* was the second most abundant climber species found mainly on the stems. *Dioscorea lecardii, Congronema latifolium, Cissus oliveri and Desmodium*

Table 3 Correlation between climber infestation and gap size, age and canopy openness. Values are Spearman's correlation coefficient (r)

	Climber infestation (score)			
Gap parameter	0	1	2	3
Size	-0.50^b	0.0	0.0	0.56^b
Age	-0.19^a	0.0	0.0	0.52^b
Canopy openness	-0.51^b	-0.23^b	0.0	0.52^b

Values followed by same letters are statistically significant at $P \leq 0.01^a$ and $P \leq 0.001^b$.

Table 4 Number of climbers found on different parts of seedlings and saplings growing in gaps in Budongo forest reserve

Climber species	Stem	Branch	Crown
Adenia gummifera	22	5	3
Cissus oliversi	4	3	0
Cissus patiolata	2	13	15
Congronema latifolium	6	7	0
Desmodium intotuene	2	4	0
Desmodium repandum	8	5	2
Dioscorea lecardii	8	6	0
Dioscorea sansibarensis	8	10	6
Diplocylclos palmatus	2	4	3
Iodes africana	7	5	2
Momordica charantia	6	6	6
Momordica foetida	35	44	267
Pyrecantha sylvestris	73	15	2
Solanum spp.	30	35	5

intotuene were found on the stems and branches only. The effect of climber infestation has been discussed by Plumptre *et al.* (1997) who noted that climbers that cover the entire crown tend to retard the growth of seedlings and saplings. The presence of climbers on different parts of the host plants is attributed to climber physiology and development, and climber–host interactions (Jaffe & Galston, 1968; Putz, 1984; Kelly, 1985; Hegarty, 1989, 1991). Therefore climber control should be a major activity in natural forest management.

There were negative and weak correlations between climber diversity and gap size ($r = -0.35$, $P \leq 0.01$), age ($r = -0.46$, $P \leq 0.01$), and canopy openness ($r = 0.47$, $P \leq 0.01$). Figure 4 shows that climber diversity was highest in gaps of about 400 m^2 and Figs 5 and 6

Table 5 One way ANOVA of climbers covering stems, branches and crowns of seedlings and saplings

ANOVA result	Stem	Branch	Crown
F	3.32	1.47	1.99
P	0.132	0.033	0.142
Mean	15.21	11.57	22.21
SE	5.26	3.21	18.85
Standard deviation	19.69	12.45	70.56

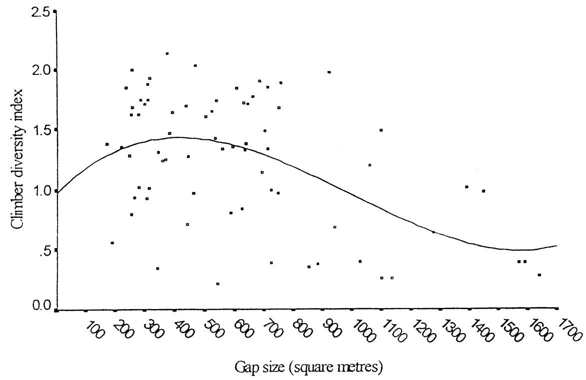

Fig 4 Variation in climber diversity with gap size.

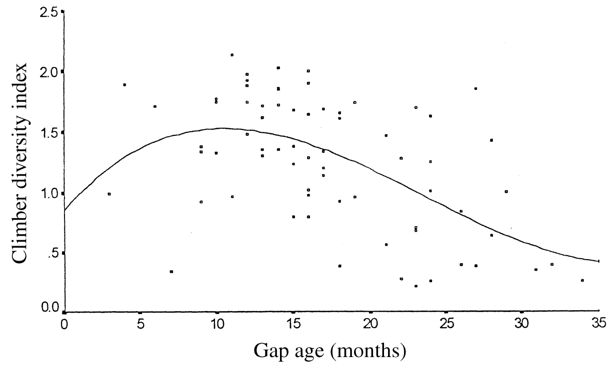

Fig 5 Variation in climber diversity with gap age.

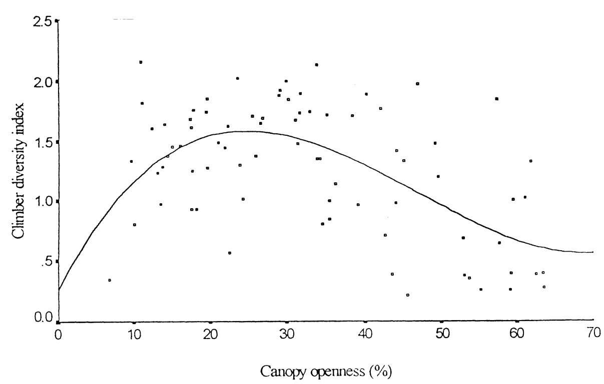

Fig 6 Variation in climber diversity with canopy openness.

show that there were variations in climber diversity with gap age and canopy openness.

As noted earlier, climbers proliferate in areas with high light intensities. Therefore, the low climber diversity that was observed in the small gaps could be attributed to the low light intensities that were received. On this basis, climber diversity would be expected to increase with gap size. In contrast, this study has shown that gaps that are more than 400 m^2 have low climber diversity. This is probably because climber species such as *Momordica foetida* that grow rapidly and cover vast areas tend to out-compete other climbers and reduce their diversity. Climber diversity was found to be low in gaps where *Momordica foetida* was dominant and the forest highly disturbed. There was a correlation between forest disturbance and species diversity, a subject that has already been discussed by several authors (e.g. Connell, 1978; Carl, 1986; Plumptre *et al.*, 1997). They noted that plant diversity is often high in highly disturbed natural forests. This observation compares well with the data presented here because it was found that climber diversity was high in gaps that were more than 10 months old (Fig. 5) and created in the highly disturbed parts of the forest. Variation in climber diversity may therefore be linked to level of forest disturbance, gap age, canopy openness and time taken by climbers to colonize and establish in gaps. On this basis, older gaps will most probably have higher climber diversity. Canopy openness also influenced climber diversity because it was found that climber diversity was highest in gaps with more than 25% canopy opening (Fig. 6). The obvious explanation here is that large gaps with low canopy cover tend to allow in high light intensities that support the growth of climbers.

Conclusions and recommendations

Based on the above findings, the following conclusions can be drawn.

1 The number of trees cut and damaged during pitsawing and the number of sawing platforms constructed contributed to the creation of large gaps. Controlled timber harvesting and pitsawing would help to minimize the problems of climber infestation and suppression of natural regeneration.

2 Climber abundance, composition and diversity increased with gap size, age and canopy openness. Climbers were abundant in gaps that were more than 15 months old, larger than 400 m^2 in size and more than 25% canopy opening. Four hundred square metres therefore appears to be the optimum gap size that pitsawers should be advised to open up in the forest if climber infestation is to be kept low.

3 *Momordica foetida* was the most common and abundant climber species in gaps in Budongo forest reserve and were found covering the stems, branches and crowns of seedlings and saplings. Forest management interventions aimed at improving the quality and quantity of timber production should focus on climber control in order to reduce the infestation of seedlings and saplings.

4 Construction of several sawing platforms in the forest tends to create wide gaps. As a result, pitsawers should be advised to construct only one platform per gap. In addition, they should use small diameter trees and poles to construct the platforms. The same trees and poles should be re-used to construct subsequent platforms.

5 There is a need to investigate the recruitment, growth and survival of seedlings in gaps in order to determine the minimum gap size and age at which climbers have the highest impact on natural regeneration and whether or not such impacts are largely due to reduction of light levels and physical strangling of the host plant.

Acknowledgements

The research leading to this paper was carried out as part of the first author's MSc study. Many thanks to the Budongo Forest Project (BFP) for financing the field work. Thanks also to the anonymous reviewers for their valuable comments on the previous version of the manuscript.

References

Carl, F.J. (1986) Local effects of tropical deforestation. In: *Conservation Biology: the Science of Scarcity and Diversity* (ed. E. S. Michael). Sinauer Inc. Publishers, Sunderland, Massachusetts.

Castellanos, A.E. (1991) Photosynthesis and gas exchange in vines. In: *Biology of Vines* (Eds F. E. Putz and H. A. Mooney). Cambridge University Press, Cambridge.

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310.

DANSLOW, J.S. (1987) Tropical rainforest gaps and tree species diversity. *Ann. Rev. Ecol. Syst* **18**, 431–451.

FISHER, B.J. & EWERS, W.F. (1991) Structural responses to stem injury in vines. In: *Biology of Vines* (Eds F. E. PUTZ and H. A. MOONEY). Cambridge University Press, Cambridge.

HAMILTON, A. (1984) *Deforestation in Uganda.* Oxford University Press, Nairobi.

HAWTHORNE, W.D. (1993) *Forest Regeneration After Logging.* Findings of a study in the Bia South Game Production Reserve Ghana. ODA Forestry Series no. 3, Natural Resources Institute, UK.

HEGARTY, E. (1989) The climbers- Lianes and vines. In: *Tropical Rain Forest Ecosystems: Biogeographical and Ecological Studies. Ecosystems of the World 14 B* (Eds LEITH, H. and WERGER, M. J. A.). Elsevier, Amsterdam.

HEGARTY, E.E. (1991). Vine–host interactions. In: *Biology of Vines* (Eds F. E. PUTZ and H. A. MOONEY). Cambridge University Press, Cambridge.

HOWARD, P.C. (1991) *Nature Conservation in Uganda's Tropical Forest Reserves.* IUCN Gland, Switzerland and Cambridge, UK.

HOWARD, P.C., DAVENPORT, T. & MATHEWS, R. (1996) *Budongo Forest Reserve Biodiversity Report.* Forest Department, Kampala.

JAFFE, M.J. & GALSTON, A.W. (1968) The physiology of tendrils. *Annu. Rev. Plant Physiol.* **19**, 417–434.

JANS, L., POORTER, L., VAN ROMPAEY, R.S.A.R. & BONGERS, F. (1993) Gaps and forest zones in tropical moist forest in Ivory coast. *Biotropica* **25**, 258–269.

KELLY, D.L. (1985) Epiphytes and climber of a Jamaican rainforest: vertical distribution, life forms and life histories. *J. Biogeogr.* **12**, 223–241.

LANGOYA, C.D. & LONG, C. (1997) Local communities and ecotourism development in Budongo Forest Reserve. *Rural Dev Network Paper* **22e**, 1–13.

MAGURRAN, A.E. (1988). *Ecological Diversity and its Measurement.* Cambridge University Press, Cambridge.

PLUMPTRE, A.J. (1996). Changes following sixty years of selective timber harvesting in the Budongo Forest reserve, Uganda. *For. Ecol. Management* **89**, 101–113.

PLUMPTRE, A.J., REYNOLDS, V. & BAKUNEETA, C. (1997) *The Effects of Selective Logging in Monodominant Tropical Forests on Biodiversity.* Final report of ODA project number R6057. Budongo Forest Project, Institute of Biological Anthropology, Oxford, U.K.

POULSON, T.L. & PLATT, W.J. (1989) Gap light regimes influence canopy tree diversity. *Ecology* **70**, 553–555.

PUTZ, F.E. (1980) Liana vs Trees. *Biotropica* **12**, 224–225.

PUTZ, F.E. (1984) The natural history of Lianas on Barro Colorado Island, Panama. *Ecology* **65**, 1713–1724.

PUTZ, F.E. (1985) Woody vines and forest management in Malaysia. *Commonw. For. Rev.* **64** (4), 359–365.

PUTZ, F.E. (1991) Silvicultural effects of lianas. In: *Biology of Vines* (Eds F. E. PUTZ AND H. A. Mooney). Cambridge University Press, Cambridge.

PUTZ, F.E. & CHAI, P. (1987) Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *J. Ecol.* **75**, 523–531.

SNEDECOR, G.W. & COCHRAN, W.G. (1967) *Statistical Methods*, 6th edn. Iowa State University Press, Iowa.

SOKAL, R.R. & ROHLF, F.J. (1969) *Biometry: the Principles and Practice of Statistics in Biological Research.* W.H. Freeman, San Francisco.

WHITMORE, T.C. (1990) *An Introduction to Tropical Rainforests.* Oxford University Press, New York.

WHITMORE, T.C. (1996) A review of some aspects of tropical rainforest seedling Ecology with suggestions for further inquiry. In: *Ecology of Tropical Forest Tree Seedlings* (Eds M. D. SWAINE). UNESCO/Parthenon, Paris.

(Manuscript accepted 23 October 1999)