



Bamboo for people, Mountain gorillas, and golden monkeys: Evaluating harvest and conservation trade-offs and synergies in the Virunga Volcanoes

Douglas Sheil^{a,b,c,*}, Mark Ducey^d, Fredrick Ssali^a, Joseph Mukasa Ngubwagye^a, Miriam van Heist^a, Pontious Ezuma^e

^a Institute of Tropical Forest Conservation, P.O. Box 44, Kabale, Uganda

^b Center for International Forestry Research, P.O. Box 0113, BOCBD, Bogor 16000, Indonesia

^c School of Environmental Science and Management, Southern Cross University, P.O. Box 157, Lismore, NSW 2480, Australia

^d Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH 03824, USA

^e Uganda Wildlife Authority, P.O. Box 3530, Kampala, Uganda

ARTICLE INFO

Article history:

Received 10 October 2011

Received in revised form 14 November 2011

Accepted 27 November 2011

Available online 30 December 2011

Keywords:

African mountain bamboo

Arundinaria/Sinarundinaria/Yushania alpina

Sustainable harvest

Community resource access

Clonal-growth

ABSTRACT

There are conflicting demands on bamboo (*Yushania alpina* (K. Schum.) Lin.) in Mgahinga Gorilla National Park (Virunga Volcanoes), Uganda. Local people lost legal access to bamboo when the park was gazetted in 1991 – but still request harvesting rights. Bamboo sprouts provide a key food for conservation significant Mountain gorillas (*Gorilla beringei beringei*) and African golden monkeys (*Cercopithecus mitis kandti*). We examined the impact of a localised harvest of mature bamboo on the production of new stems. We used a grid of 540 variable area plots to record and assess 9420 stems (including 1268 cut stems) and 1981 sprouts. Mean densities were 3.96 stems m⁻² and 0.68 sprouts m⁻². Densities and diameters were lower in areas with tree shade compared to those without. Densities of new stems were positively related to densities of older stems. Diameters of young stems were positively correlated with the diameters of older stems but younger stems were, in general, significantly larger. Cutting of mature stems had no detectable impact on either the density or diameter of subsequent new stems. Statistical power analysis adapted from pharmaceutical assessments indicates that a minor positive or negative impact remains possible (a positive effect appears more probable). We conclude that the bamboo is in a “building phase”, that densities and sizes of young stems are determined by the extent of the underground rhizome, and that this plot–scale relationship is not detectably influenced by harvesting older stems. Nonetheless, negative impacts may arise with repeated harvesting. Guidelines for any future harvest are suggested.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

We often assume trade-offs in forest resource management – but sometimes synergies may also be plausible. Good management requires such relationships to be better characterised. Uganda's Mgahinga Gorilla National Park (MGNP) is part of the Virunga trans-boundary protected area that includes parks in Rwanda and the Democratic Republic of Congo (DRC). This region harbours animals of global conservation concern including Mountain gorillas (*Gorilla beringei beringei*) and African golden monkeys (*Cercopithecus mitis kandti*) (Owiunji et al., 2005). These forest parks are under considerable pressure from surrounding human populations.

MGNP, like the rest of the Virunga, hosts extensive tracts of African mountain bamboo (*Yushania alpina* (K. Schum.) Lin.). Bamboo sprouts provide nutrition for primates, antelopes, buffaloes and elephants. For Mountain gorillas, bamboo sprouts are a preferred food and can contribute 90% of their diet in some periods (Weber, 1981; Elgart-Berry, 2004). Bamboo sprouts also provide a favoured food for African golden monkeys representing around 60% of their foraging (Aveling, 1984; Twinomugisha and Chapman, 2008).

Before MGNP became a protected area local people exploited the forest's wild bamboo: larger stems were used for construction, thin stems for bean stakes, old stems for fuel, and young stems for basketry (see also Bitariho and Mosango, 2005). All such use has been prohibited since 1992. People resent losing access to the Park's bamboo and illegal collection continues – often in conjunction with setting of snares and other harmful activities. It might improve relations with communities if authorities permitted controlled harvest.

Primate viewing has become a focus for Uganda's tourist industry and attracts considerable foreign exchange. For MGNP, gorilla

* Corresponding author at: Institute of Tropical Forest Conservation, P.O. Box 44, Kabale, Uganda.

E-mail addresses: DouglasSheil@itfc.org (D. Sheil), mjducey@cisunix.unh.edu (M. Ducey), ssali@itfc.org (F. Ssali), ngubwagyejose@yahoo.com (J.M. Ngubwagye), MiriamvanHeist@itfc.org (M.van Heist), pontious2010@gmail.com (P. Ezuma).

viewing fees brought in around 290,000 US Dollars (USD) in 2010 with a further 40,000 USD for the golden monkeys (UWA unpublished records). But these revenues could be higher if MGNP's gorillas were less inclined to regularly move across international borders where tourists cannot follow (i.e. around 1.5 Million USD). It has been suggested that these gorilla absences relate to a dearth of bamboo shoots in MGNP. Park staff state that bamboo sprouts have become scarcer in recent years. They suggest that without harvesting the bamboo is no longer stimulated to produce sprouts as it was in the past (UWA personal communication).

The park authorities asked the Institute of Tropical Forest Conservation to evaluate the impact of a trial harvest that they had supervised the year before. What, they wanted to establish, was the condition of this bamboo and what are the impacts of stem harvest on shoot production? Here we address these questions.

Previous studies of African mountain bamboo do not clarify the impact of harvesting mature stems (see Kigomo, 1988; Embaye, 2000). We consider three contrasting hypotheses concerning how the controlled harvest of mature bamboo impacts the production of bamboo sprout: (1) positive ("synergy"), (2) negative ("trade-off") and (3) none ("null").

Under our first hypothesis bamboo harvest offers a "win-win" synergy situation with people and animals benefitting. Compensation (and "overcompensation") in which loss of plant parts directly stimulates production is well established in herbivory studies and associated theory (Agrawal, 2000; Belsky, 1986; Belsky et al., 1993; McNaughton, 1983). Indeed such mechanisms have been implied by the observation that the harvest of sprouts can stimulate increased production in some (non-African) bamboo, e.g. *Otatea acuminata* in Mexico (Vazquez-Lopez et al., 2004, for a review see Kleinhenz and Midmore, 2001).

The second hypothesis implies a trade-off in which bamboo harvest has a negative influence such that the plants then produce fewer sprouts. Such harm could arise in many ways (Kleinhenz and Midmore, 2001); Wimbush (1945, cited in Kigomo, 1988) notes that clear-cutting depresses subsequent re-growth of *Y. alpina*. A decline of bamboo in the Echuya Forest Reserve, near to MGNP, has been ascribed to excessive harvesting (Banana and Tweheyo, 2001; Bitariho and McNeilage, 2008). These cases involve general harvesting in which young stems are collected – they do not clarify the impact of harvesting only older stems. This trade-off assumption is the primary justification of those who argue for complete protection of the bamboo in the name of conservation (e.g. Twino-mugisha and Chapman, 2008).

The third alternative is our null hypothesis in which bamboo harvest has neither a positive nor a negative effect on shoot production. This can also be seen as a strict version of the idea that permitting the harvest of older (senescent) stems will have no impact on the remaining plant.

2. Context and methods

2.1. African mountain bamboo

Y. alpina (K. Schum.) Lin. is the only high altitude bamboo species in Africa, but taxonomic revisions mean it has also been referred to as *Arundinaria alpina* K. Schum. and *Sinarundinaria alpina* (K. Schum.) C.S. Chao and Renvoize among other names (Chi-son and Renvoize, 1989, www.theplantlist.org accessed 10 November 2011). There is little beyond basic descriptive information concerning the biology of the African mountain bamboo (Kigomo, 1988; Embaye, 2000).

Bamboo plants establish from seed and spread vegetatively. For simplicity we refer to the aboveground ramets or culms as "stems", the incompletely expanded shoots as "sprouts" and the below-

ground stems as "rhizomes". *Y. alpina* stems can reach over 19 m in height and over 12 cm in diameter but typical stands are smaller and there is considerable variation between sites (Kigomo, 1988; Chi-son and Renvoize, 1989).

Like most bamboo species *Y. alpina* is monocarpic: flowering and seeding only once before dying. This occurs at 30–40 years of age and involves synchronous patches comprising one or more clones. In some species some rhizomes may persist after flowering (Miyazaki et al., 2009) – but evidence regarding *Y. alpina* is anecdotal (Wimbush, 1947 cited in Kigomo, 1988). Patches of flowering bamboo, comprising a few hectares each, were observed on the slopes of Mt. Sabinyo in MGNP in the early 1980s (Bitariho and McNeilage, 2008). Individual stems live for 10–15 years becoming gradually less green and leafy before they die and decay (Kigomo, 1988). A staged growth cycle has been described for each clone: this distinguishes a "building"-phase with increasing stem sizes from a subsequent more stable "mature"-phase (Agnew, 1985). Sprout production is believed to decline prior to flowering (see Huberman, 1959).

Some bamboo species appear adapted to disturbance (see Keeley and Bond, 1999; Gagnon and Platt, 2008). While not yet studied systematically, local accounts have led various observers to conclude that *Y. alpina* dominance is related to specific disturbance histories (Grimshaw, 1999).

2.2. Site

MGNP, located at the edge of the Western Rift Valley, is Uganda's smallest National Park (33.7 km²) (Fig. 1). Altitude ranges from 2227 m a.s.l. up the north facing slopes to the peaks of the three northernmost Virunga Volcanoes; i.e. Sabinyo (3645 m), Muhavura (4127 m) and Mgahinga (3474 m). Sabinyo likely dates to the early Pliocene while Muhavura and Mgahinga are considered late Pleistocene (Kampunzu et al., 1998).

Local soils are volcanic and possess low water storage capacity (Morrison and Hamilton, 1974). Rainfall follows a typical equatorial pattern with two rainy and two dry seasons. Annual rainfall at Ntebeko at 2350 m is about 1900 mm (ITFC and UWA unpublished data from 1995 to 2000).



Fig. 1. Location of the Mgahinga Gorilla National Park in SW Uganda (above), and location of the study (dark rectangle on the left) within the park (below). The three peaks on the southern border (West to East) are: Sabinyo, Mgahinga and Muhavura. The bold dotted line is the park boundary, 300 m contours in pale grey (increasing altitude from North to South), simple hatching is bamboo forest, and cross hatching is mixed bamboo and tree cover. The contour map and vegetation assessment were prepared in 1995 for a GIS database of the park, based on (Uganda) Department of Surveys and Mapping, topographic map series Y732 (1960–76), and a 1990 airphoto interpretation by M. van Heist.

Bamboo occurs between 2450 and 3000 m a.s.l. and dominates approximately 15.5 km² with 2–3 km² of that being localised areas where bamboo and tree cover are mixed (Fig. 1). Bamboo is scarce on Muhavura but is common on Mgahinga and Sabinyo possibly due to greater soil depth (Snowden, 1933).

Until this study there had been no legal harvest of bamboo since the park was established two decades previously. In 2009, park authorities designated an area of about 6 ha where local people could harvest mature and dead bamboo – these stems are referred to as “dry stems” due to their apparent lack of sap. About 30 people were allowed to enter four times a week for 2 months and remove one load. A ranger supervised the harvest for its 2-month period (May and June) but the edge of the collection area was not clearly marked on the ground and the collection area was imperfectly defined. Our assessment took place in October 2010: 15 months after the original harvest.

2.3. Plots

We predefined and located 540 recording points between 2500 and 2600 m a.s.l. as a systematic grid using a GPS (Garmin 60CSx with ± 3 –5 m accuracy). The area covered is 350 m by 875 m or 30.625 ha, and fully incorporates the trial harvest area. At each location we inserted a small stake in the ground and ran a measuring tape East–West horizontally. We moved a one-meter stick horizontally along the right hand side of the tape and recorded the first 20 fully expanded bamboo stems within that width. The distance to the center of the 20th stem was recorded as the length of the transect. Such variable area transects are more efficient than fixed area methods (Engeman and Sugihara, 1998; Parker, 1979; Sheil et al., 2003). We included cut stumps but omitted decayed stems (those soft enough to collapse when squeezed between finger and thumb). The plot was judged empty, and omitted from subsequent recording, when no bamboo stems were recorded within the first 5 m. We visually determined any tree shade – overhead, side, and none – within each plot.

Each stem was categorised: ‘young’ if green and shiny, ‘mature’ if duller matte green (often with algae/lichens), ‘dead’ if dry and lacking leaves but still firm (such categorisations have been widely used in bamboo studies, e.g. Franklin and Bowman, 2003). Cut stems were also recorded. ‘Broken stems’ were recorded if the break occurred below 2 m in height. We measured the diameter (midway between the first two nodes above the ground) of the first five stems in each plot using callipers.

Sprouts were recorded separately from the other 20 stems. We were concerned that sprouts may emerge or be removed during the study, creating a date dependent bias. Sprouts were recorded as intact or as ‘eaten’. We sometimes found sheaths and upper segments of eaten sprouts on the ground. We searched each plot for remnants of eaten sprouts, which often exuded a colourless liquid. In our analyses these were combined as ‘sprouts’.

2.4. Analyses

Stem densities are estimated as $(n_{\text{stems}} - 1)/A$ in each plot, where n_{stems} is the number of stems used to define the sample (here 20) and A is the plot area (Parker, 1979; Sheil et al., 2003). For sprouts the variable area adjustment term is not required and density is simply n_{sprouts}/A , where n_{sprouts} is the count of sprouts. The per-plot density data are skewed but effectively normalised with a log transformation $\log_e(n_{\text{stems}} + 0.1)$. Statistical analyses were performed in MS-Excel, SPSS 9.0 and MATLAB. We explore the three relationships described above (i.e. positive, negative and null) – we also considered non-linear effects through the visual examination of residuals and chi-squared tests.

To examine whether overall distributions differed, we modelled the diameter distributions of the different categories of stems. We used Weibull distributions because of their flexibility using only two fitted parameters (Bailey and Dell, 1973). The need to fit separate models to each stem category was evaluated with a likelihood ratio test (Casella and Berger, 1990).

As commonly applied, statistical methods are often used to detect and quantify relationships. However, when such relationships are not detected they may exist nonetheless. These “false negative” cases refer to a situation known in statistics as a “type II error”, meaning failure to reject a null hypothesis when the alternative hypothesis is true. To quantify such a possibility requires an analysis of the ability of our tests given the data we have (power analyses). These power approaches are less commonly used in applied ecology so we offer a detailed summary of our approach. (Here we use “power” in a technical sense meaning the probability that our analysis will detect a true difference of a specified type given the data and procedures involved).

We assessed the power of our study to detect any influence of stem harvest (measured as cut stems) on density of young stems or sprouts. Null results (no relationship detected) are used to gauge the probability that any (undetected) underlying relationship could be larger or smaller than a given value. Our initial assessments examined scatter plots and residuals. The 95% confidence intervals for these relationships determine their uncertainty. This simple regression approach can, under some circumstances, underestimate uncertainties (Freckleton, 2002; Hoenig and Heisey, 2001). To provide a more rigorous evaluation we adopted a bio-equivalence approach developed for pharmaceutical assessments (Schuirmann, 1987). We ask whether the data can demonstrate that the effect of cutting, if any, is “small”. This requires an *a priori* operational definition of “small”. We defined this as one in which the expected difference between a plot with no cut stems, and one with the maximum observed density of cut stems, is less than 25%. We refit the regressions in a multiple regression framework, using the density of all old stems combined and of cut stems as predictor variables, and using the density of young stems, of sprouts, and of young stems and sprouts combined as response variables. All predictors and response variables were log-transformed (following the addition of 0.1 to avoid taking the logarithm of zero, as before). The resulting equations take the form:

$$\ln(\text{density} + 0.1) = \beta_0 + \beta_1 \ln(\text{density of old stems} + 0.1) + \beta_2 \ln(\text{density of cut stems} + 0.1)$$

To allow for any heteroscedasticity and non-normality in the relationships we used a nonparametric bootstrap with 10,000 repetitions to provide alternative, asymmetric confidence limits on the estimated parameters (Efron and Tibshirani, 1993). The value of β_2 provides our primary test of the hypothesis that presence of cut stems predicts changes in the abundance of sprouts or young stems. Using the bootstrap estimates of the slope, the data demonstrate a small effect at an $\alpha = 0.05$ significance level if the 0.05 and 0.95 quantiles of the bootstrapped values for β_2 fall within this interval (note that the quantiles are set at α and $1 - \alpha$, not $\alpha/2$ and $1 - \alpha/2$; (Schuirmann, 1987)).

3. Results

3.1. General characteristics: sample, stem counts, densities and sizes

The 540 sample points, and their principle characteristics, including empty plots, tree-cover, stem densities and sizes, were mapped (Fig. 2). Sixty-nine plots contained no bamboo – subsequent summary and analyses omit these empty plots unless otherwise stated (all density estimates can be adjusted by 0.872 if the

empty plots are included). The 471 plots with bamboo contain 8152 fully expanded uncut stems, 1268 cut stems and 1981 sprouts. The distribution of cut stems was patchy and not restricted to the intended harvest area.

Estimated stem densities, with 95% confidence intervals, are provided in Table 1. Density distributions were skewed with the maximum densities for all populations being many times higher than their means. The mean density for all stems combined was approximately 4 m^{-2} while about 0.9 m^{-2} were dead stems. The most common age class was “mature” averaging just over 1.6 m^{-2} , while young stems and sprouts were both present at around $0.6\text{--}0.7\text{ m}^{-2}$. All non-empty plots contained some mature stems but 48 and 86 had no young stems and no sprouts, respectively. Golden monkeys were actively feeding on sprouts in the research area during the study – though gorillas remained absent.

3.2. The effect of tree shade on bamboo stem density

Tree cover was associated with a significantly lower stem density, overall and for young stems and sprouts (Kruskal–Wallis test $\text{Chi}^2 = 46.9, 28.3$ and $13.0, p < 0.0005, 0.0005$ and 0.002 , respectively). The stem densities in unshaded areas were nearly twice those in locations with some overhead shade (Table 2). We detected no significant difference between locations with side-shade and no-shade.

Table 1

Total sample counts, estimated mean densities (m^{-2}) and 95% confidence intervals (CI), and maximum plot density, for the different stem categories based on 471 plots.

	Stems						
	Young	Mature	Dead	Cut	Broken	Total	Sprouts
N stems	1661	3954	2016	1268	521	9420	1981
Mean	0.661	1.636	0.885	0.523	0.255	3.960	0.679
Lower CI ^a	0.620	1.552	0.835	0.488	0.238	3.774	0.636
Upper CI	0.704	1.727	0.939	0.556	0.273	4.157	0.726
Maximum	8.30	9.60	10.27	7.56	6.73	25.68	6.04

^a Based on a log transformation.

3.3. Stem diameters

The mean stem diameter was just over 4 cm. The largest was 7.8 cm and the smallest 0.8 cm. Stem diameter data and their distributions are summarised in Table 3 and Fig. 3. Younger stems averaged larger diameters than older stems. Dead and especially broken stems were typically thinner than average. The difference in location of these five category populations was significant (Kruskal–Wallis test $\text{Chi}^2 = 328.8, \text{df} = 4, p < 0.0005$). All pair-wise comparisons in the sequence Young > Mature (>Dead > Broken) were significant (Mann Whitney U test). Cut stems were fractionally, but significantly, smaller in size than remaining mature stems (Mann Whitney U test = 34162, $p = 0.002$).

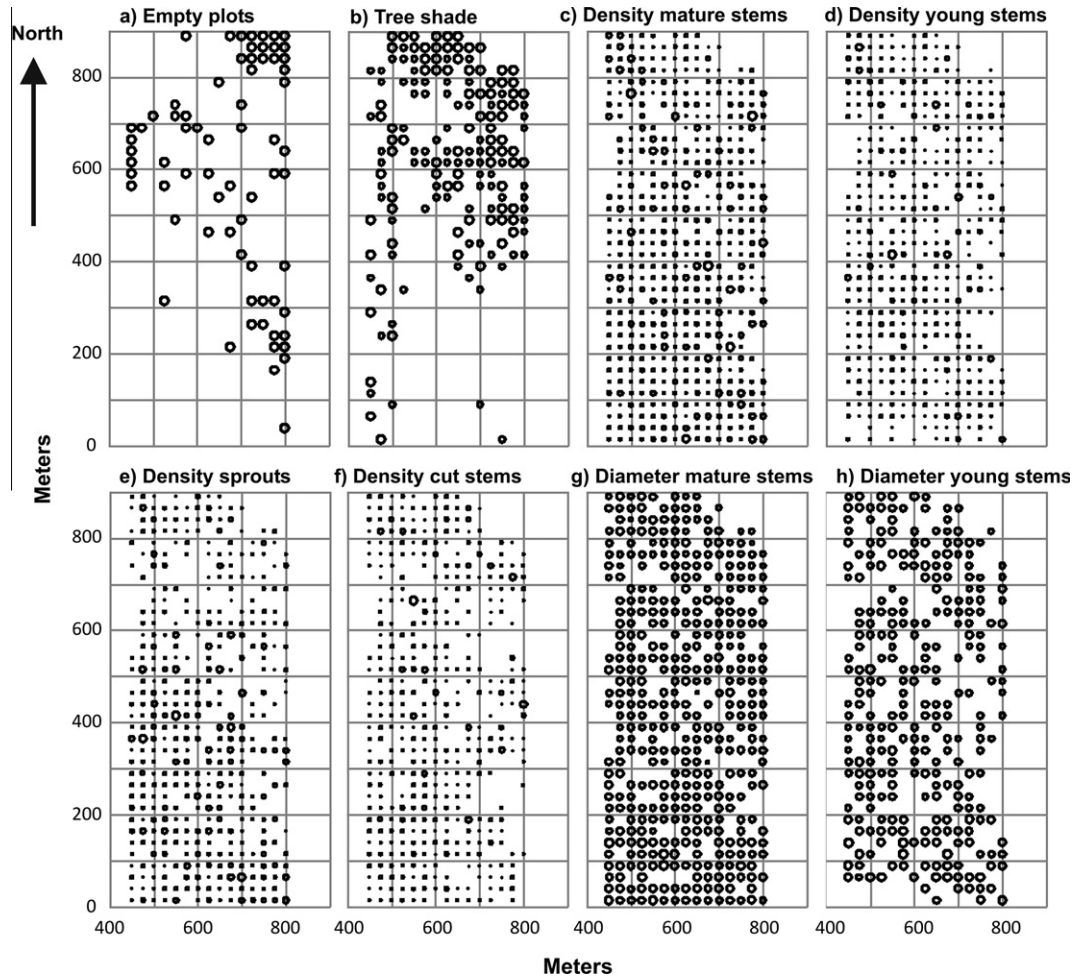


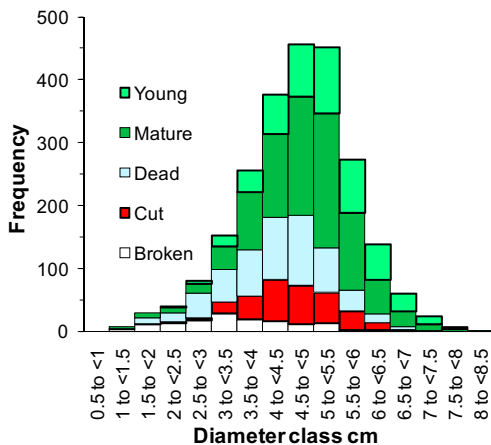
Fig. 2. Spatial arrangement of plot characteristics: (a) empty plots (b) tree shade: full (large symbols) and side tree shade (smaller symbols) (c) density of mature stems (d) density of young stems (e) density of sprouts (f) density of cut stems (g) mean diameter mature stems and (h) mean diameter of young stems. Note in (c–f) symbol areas are proportional to density (all use the same conversion) while in (g) and (h) symbol areas are proportional to diameter (same scale).

Table 2
Overall stem density (stems m⁻²) by tree presence with 95% confidence intervals (CI).

Tree cover	None	Side	Overhead
N plots	307	81	83
<i>All stems</i>			
Mean density m ⁻²	4.257	4.439	2.3936
Lower CI	3.888	3.725	2.001
Upper CI	4.626	5.152	2.786
<i>Young stems</i>			
Mean density m ⁻²	0.712	0.735	0.400
Lower CI	0.615	0.571	0.320
Upper CI	0.808	0.898	0.480
<i>Sprouts</i>			
Mean density m ⁻²	0.804	0.483	0.409
Lower CI	0.710	0.361	0.303
Upper CI	0.898	0.604	0.514

Table 3
Bamboo stem diameters (cm) by population categories and combined.

Population	N	Mean diameter	SD	Maximum	Minimum
Broken	137	3.11	1.17	6.4	0.9
Cut	283	4.18	0.84	6.6	1.1
Dead	527	3.81	1.03	6.4	0.8
Mature	911	4.41	0.99	7.8	0.8
Young	497	4.73	0.98	7.3	1.9
Combined	2355	4.237	1.076	7.8	0.8

**Fig. 3.** Diameter distributions of stems (each observation is one mean value from one plot for each population present). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The likelihood ratio test showed that separate Weibull distributions were required to model the five categories of stems ($D = 945.5$, $df = 8$, $p < 0.0001$). The distributions are shown in Fig. 4. Young stems had a relatively high shape parameter (5.43), indicating a sharply peaked distribution, while broken stems (shape parameter 2.83) had a broad but still unimodal distribution. Unsurprisingly none of the distributions had a “reverse J” shape (shape parameter ≤ 1 was outside the 95% confidence limits in all cases).

The diameter of mature stems was lower under tree shade than in non-tree sites (Kruskal Wallis test $\chi^2 = 53.58$, $p < 0.0005$). A similar, but less marked, relation was found for young stems (Kruskal Wallis test $\chi^2 = 16.1$, $p < 0.0005$).

Mean stem diameters by plots were correlated across age-classes implying a plant or location related influence. For example the diameter of mature and young stems was highly correlated (Kendall's tau-b [henceforth “tau”] = 0.414, $p = 10^{-6}$, $n = 233$). The rela-

tionship remained significant when sites with tree shade were excluded (tau = 0.358, $p = 10^{-6}$, $n = 142$).

3.4. Size versus density

Despite the fact that size and density of mature stems were both negatively correlated with tree shade across plots, no correlation was detected between mature stem density and stem diameter among the plots (tau = 0.006, $p = 0.867$, $n = 407$). Similarly no correlation between the per-plot mean-diameter and density of young stems was detected (tau = -0.024, $p = 0.56$, $n = 278$). The density of sprouts (but not of young stems) was positively correlated with the mean diameter of mature stems (tau = 0.153, $p = 0.0000061$, $n = 407$). We also detected a small positive correlation between mature stem size and the local density of cut stems (tau = 0.103, $p = 0.0025$, $n = 407$, suggesting that harvesters target areas with larger stems).

3.5. Harvest intensity versus abundance of younger stems and sprouts

We use a series of complementary analyses. Our initial null hypothesis was that stem cutting has no impact on the density of (a) young stems or (b) sprouts. We made a regression of log-transformed densities of all older stems combined (including mature, dead, broken and cut stems) against those of (a) young stems and (b) sprouts. We then evaluated the residuals against the densities of cut stems. If cutting encourages sprouts we expect to detect a positive relationship, if it has a deleterious effect we expect a negative relationship. These analyses are presented in Fig. 5. The residual plots show no significant trends. Specifically, the log_e transformed density of sprouts had a marked positive relationship against log_e transformed density of older stems: $p = 5.41 \times 10^{-19}$ with a 95% confidence that the gradient lies between 0.385 and 0.589. Log_e transformed density of young stems also had a positive relationship against log_e transformed density of older stems: $p = 5.75 \times 10^{-29}$ with a 95% confidence that the gradient lies between 0.466 and 0.6478. The 95% confidence intervals of the gradient of the relationship of the residuals of these two relationships versus the density of cut-stems both encompasses zero (between -0.153 and 0.090 for sprouts and -0.039 and 0.162 for young stems). Thus the null hypothesis, harvest has no effect, is accepted in both cases.

A second linear analysis considered ratios. Our null hypothesis was that the per-plot-ratio of cut to other stems has no impact on the ratio of (a) young stems or (b) sprouts. We ask how the number of young stems and the number of sprouts varies against the number of cut stems in each plot. Fig. 6 shows the exploratory scatter of these data – these analyses with untransformed data also help us to gauge our ability to detect any effect. The confidence intervals around the gradient of the trend lines indicate that to remain undetected any effect would have to contribute less than $\pm 10\%$ of total variation in sprout and young stem production. Rank correlation tests of these relationships indicated no strong relationships (Kendall's τ -b rank correlation, $p > 0.05$ for all pairs).

To address the possibility of non-linear relationships we summarised the per plot numbers of young stems and sprouts against eight categories based on the number of cut stems (0–6 and more than 7) and tested the null hypothesis that the proportion of young stems or sprouts will not vary. The null expectation was accepted ($\chi^2 = 2.013$ and 4.384, $p = 0.83$ and 0.33 for young stems and sprouts, respectively).

3.6. Assessing the probabilities of type II error

With our previous analyses, accounting for local stem densities, having failed to exclude the null hypothesis (cutting has no effect

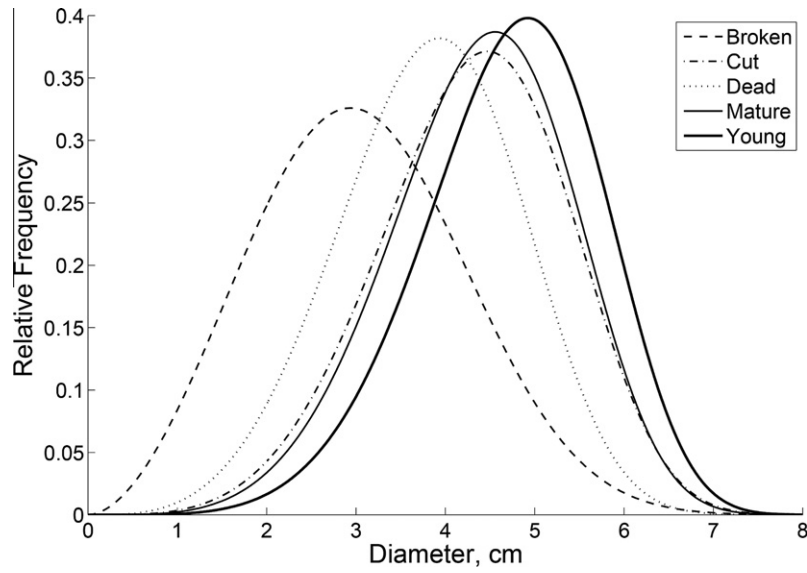


Fig. 4. The distinct Weibull distributions for each stem category.

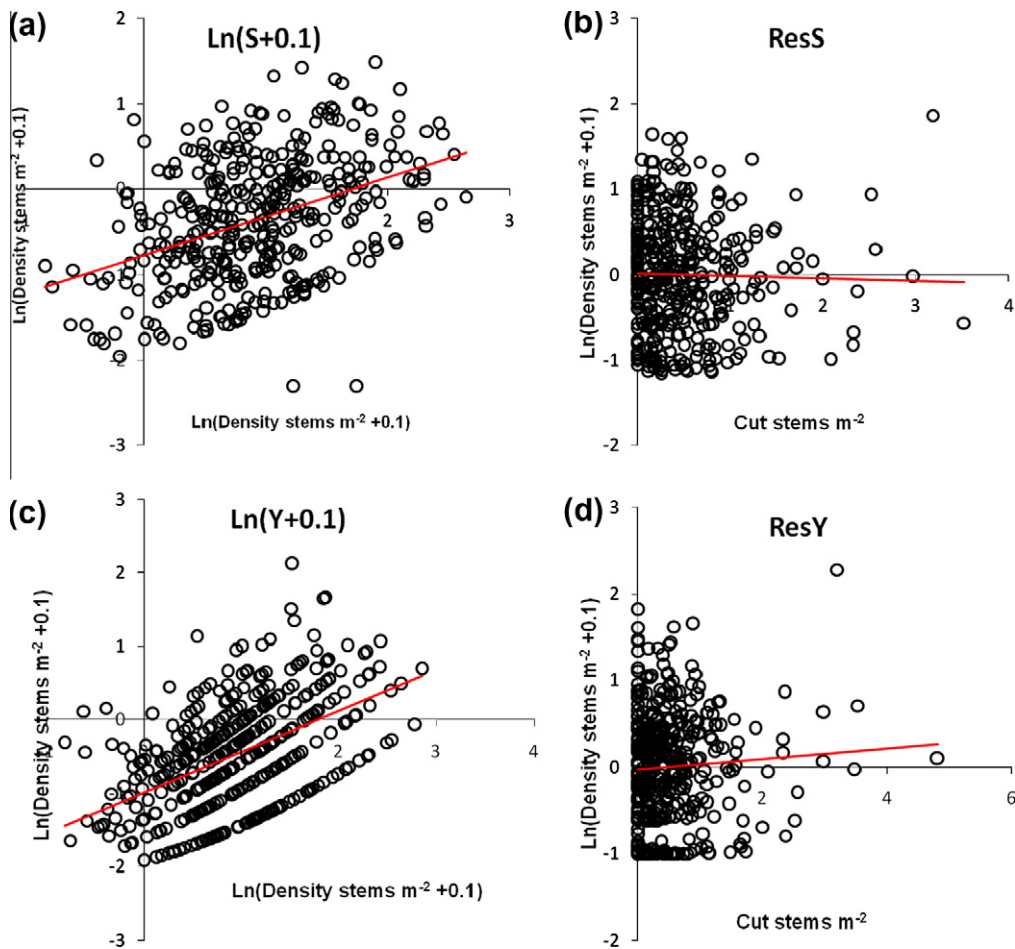


Fig. 5. Regressions of log-transformed (a) sprout density and (c) young stem density against log-transformed density of all older stems and the relationship of the residuals from these relationships for (b) sprouts and (d) young stems against density of cut stems.

on the production of younger stems) we applied a more formal power analysis to assess how large any such effect might be and remain undetected in the regression analyses. We adapted an ap-

proach used in pharmaceutical research (see Section 2 for an introduction). We defined a “small effect” as one in which the expected difference between a plot with no cut stems, and one with the

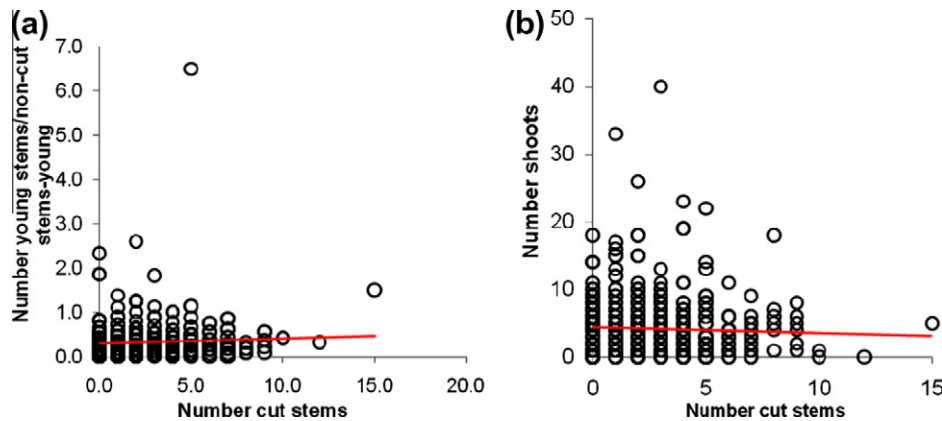


Fig. 6. (a) Number of young stems as a proportion of non-cut older stems (mature, dead and broken) and (b) number of sprouts against the number of cut stems. Note that many of these points include multiple observations. The lines represent regression fitted trend-lines. The trend-line for (a) is not significant (slope = 0.012, $p = 0.155$ and with 95% confidence, it lies between -0.005 and 0.029) and (b) is negative but not significant (slope = -0.092 , $p = 0.324$ with 95% confidence the relationship lies between -0.276 and 0.091).

Table 4

Results of bootstrapped “small effect” test.

Predicted variable	Estimates (95% confidence limits)			Equivalence test for β_2			
	β_0	β_1	β_2	Lower quantile	Result	Upper quantile	Result
Young stems	-0.8019 (-1.0035, 0.1068)	0.2569 (0.1068, 0.4067)	0.1182 (0.0069, 0.2311)	0.0262	Passed	0.2109	Failed
Sprouts	-0.8678 (-1.0920, -0.6439)	0.1657 (-0.0049, 0.3291)	-0.0098 (-0.1334, 0.1117)	-0.1122	Failed	0.0902	Failed
Young stems and sprouts combined	-0.1709 (-0.3523, 0.0176)	0.2909 (0.1469, 0.4343)	0.0597 (-0.0423, 0.1662)	-0.0266	Passed	0.1500	Failed

maximum observed density of cut stems, is less than 25% in either direction (see Section 2). Using the observed transformed densities, this translates into a range for β_2 between -0.0541 and 0.0541 .

The regression results are shown in Table 4. These confirm a positive relationship between plot level densities of young and older stems. The regressions failed the equivalence tests indicating the data are insufficient to prove that effects are small. However, for both young stems and for young stems and sprouts combined, the difference is due solely to the possibility of a large positive relationship with cutting; a large negative impact is ruled out by these data. For sprouts, the data are insufficient to entirely rule out either a large positive or negative impact, due to the high variability in sprout abundances.

3.7. Cutting intensity versus diameter of stems

There was no detectable rank relationship between the density of cut stems and the diameter of young stems either for all plots ($\tau = 0.082$, $p = 0.062$, $n = 278$), or for only plots without tree shade ($\tau = 0.071$, $p = 0.189$, $n = 179$). Nor was there any significant correlation between the density of cut stems and the local (i.e. per plot) difference in diameter between young and mature stems ($\tau = -0.04$, $p = 0.376$, $n = 233$).

4. Discussion

4.1. The state of the bamboo

Local densities of bamboo in the long protected study site (over 39000 ha^{-1}) were three or four times those reported elsewhere in regularly harvested stands of African mountain bamboo (e.g.

9,000–13,000, Bitariho and McNeilage, 2008; Embaye et al., 2005; Kigomo, 1988). Despite the park authority’s concerns about few sprouts the densities we observed were high (e.g. several times those reported from the neighbouring Echuya Forest Reserve, Bitariho and McNeilage, 2008). These high sprout densities occurred even in areas lacking stem-harvesting. Younger stems had larger diameters than older stems indicating that the plants are still in a building phase (*sensu* Agnew, 1985).

Densities of younger stems were positively related with local bamboo stem density. This was expected since stems already present indicate the scale of the underlying rhizome which determines the likelihood of new sprouts. In addition, tree cover had a negative association with bamboo density and thus on the generation of new sprouts. Tree shade was associated also with smaller stem diameters (as previously indicated by Bitariho and Mosango, 2005). Since tree shade appears to have a negative effect local clearing of all competing vegetation, including other bamboo, might similarly reduce competition and stimulate sprout production (though this is not clearly observed in the harvesting data). Further study is needed to clarify the degree to which shade and root densities of trees, bamboo and other plants influence bamboo sprout production, growth and survival.

4.2. The impacts of harvest and statistical uncertainties

Our analyses failed to detect any relationship between local (plot scale) stem cutting and the presence of new stems. At first glance this failure to find statistical support for either a positive or negative relationship – hypotheses 1 and 2 – concludes that our third (null) hypothesis is preferred. Our power analyses revisit this conclusion by gauging our ability to detect such (non-null) patterns depending on their magnitudes. Examination of regression residuals, and our

more sophisticated bootstrap analyses, offer somewhat contrasting implications. The 95% confidence intervals of the residuals from the simple (log-transformed) regression suggest that any relationship lies between +9% and –15% for sprouts and between +16% and –4% for young stems. The more conservative bootstrap analyses suggest markedly greater uncertainty so that a 25% relationship cannot be excluded with 95% confidence for either the upper or lower relationship for sprouts and cannot be excluded for any positive relationship for young stems (though an equally marked negative relationship is ruled out). This result does not imply that such marked deviations are likely – only that they cannot be rigorously excluded.

All the analyses for the young stems support the specific conclusion that *if* there is a negative impact it is very unlikely to account for more than a 25% change in density; while *if* there is a positive impact a 25% change, though unlikely, cannot be entirely ruled out. Fortunately, while this suggests a less clear conclusion than we might like, we can conclude that if there is an impact it is likely to be minor and that synergy is more likely than a trade-off.

It is important to underline our results apply to only one harvest event, 15 months previously, in one location. Though we believe our results are helpful this was not a carefully designed study with randomised treatments, control areas, and before-and-after monitoring. Hidden biases or confounding factors are possible. The data suggest no relevant treatment biases aside from a marginal tendency for areas with large-diameter stems to be subject to increased harvest intensities. Might we have missed stems, cut-stems or sprouts? We consider this a concern only for sprouts: as some may have come up after the survey or have been already eaten by animals before our study and remained undetected. We cannot gauge the effect of such possible omissions but they will not influence analyses of young stems. We note that the harvesting was not restricted to the area intended: cut stems were found more widely. It is possible that some cut stems reflect illegal harvest. While this raises some uncertainties it can be considered “noise” in the data and does not undermine our conclusions that recent cutting has had a limited impact on the growth of new stems. Longer term impacts deserve particular consideration.

4.3. The longer-term impact of bamboo harvest

Repeated harvest may increase exposure and susceptibility to pathogens. It may also impact nutrient dynamics and competition with other vegetation. We know little about bamboo health but can briefly consider nutrients and competition.

Repeated bamboo removal implies significant nutrient losses from the overall plant–soil system with impacts on subsequent nutrient availability (Embaye et al., 2005). Studies with other bamboo species indicate that production can be nutrient limited – and growth can be stimulated by fertiliser (Li et al., 1998; Kleinhenz and Midmore, 2001). Phosphorus and potassium additions have been highlighted as necessary to maintain bamboo harvests in Ethiopia (Embaye et al., 2005). Given the relatively base rich volcanic soils of MGNP such interventions may not be urgent but may ultimately deserve consideration.

Harvest will influence how bamboo interacts with other vegetation. Much of the lower area of MGNP is recovering from past encroachment (Lejju, 2004) and both tree- and bamboo-cover are expanding into previously open areas. The longer-term balance between bamboo and other vegetation is uncertain. If, as many suggest, bamboo benefits from certain types of disturbance events (Grimshaw, 1999) – the recurrence of such events may be influential. It is very likely such events have been heavily determined by human presence over the last millennia and strict protection without interventions may not favour extensive bamboo forests in the long-term.

4.4. Recommendations

We find no immediate reasons to prevent the controlled harvesting of dry bamboo from MGNP: we detected no severe impacts on plant productivity. Nonetheless we advise caution. Here we offer a few suggestions and recommendations to minimise risks.

- Any stem harvesting requires careful management, supervision and monitoring.
- Harvesting must avoid sprouting seasons to avoid disturbance of sprouts and feeding animals.
- Areas where harvesting is to be allowed must be clearly marked and enforceable.
- Harvested areas ought to be rotated with at least 4–5 years between harvests.
- Replicated control plots should be included as part of the monitoring.
- Young stem densities and diameters should be recorded across each stand.
- Maintaining long term production may require artificial fertilisation (due to repeated nutrient export with harvesting).
- In the longer-term it may be necessary to clarify if there are any areas where maintaining bamboo, and favouring it over tree cover is, or should be, an explicit management objective.

5. Conclusions

None of our analyses detect any statistically significant short term impacts of cutting old bamboo on the density or diameter of subsequent plant growth. There is no evidence that cutting stimulates or inhibits production of new sprouts – if such influences exist they are small relative to overall variation. We conclude that controlled harvest should not cause an immediate threat to primate food availability and may improve community-park relationships and associated conservation outcomes.

Our conclusions apply to the short-term impacts of a one-time harvest of old bamboo stems. Repeated harvesting will impact nutrient availability and vegetation dynamics and may influence pathogen dynamics and exposure – thus longer-term effects may emerge over time. If stem harvesting is allowed it requires careful regulation and monitoring. We suggest a rotational system in which clearly marked areas are harvested only every few years and replicated zero-harvest control plots are included as part of a monitoring system.

Acknowledgements

ITFC received funding from the John D and Catherine T. MacArthur Foundation and USAID via WCS which enabled them to support this work. D.S. and M.v.H. are supported part time by WCS. We thank UWA staff at MGNP: Bakebwa Ismael, Uwhoreye Allen, Adrama Francis and Halera George, for their help in collecting data. Robert Bitariho provided helpful guidance and references. We thank the reviewers for their comments and suggestions. D.S., M.v.H. and P.E. designed the study and trained the field teams, F.S. and J.M.N. supervised the data collection, D.S. and M.D. analysed the data, and D.S. wrote the paper with contributions from all authors.

References

- Agnew, A.D.Q., 1985. Cyclic sequences in plant communities of the Aberdare Mountains, Kenya. *East African Natural History Society* 75, 1–12.
- Agrawal, A.A., 2000. Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. *Trends in Plant Science* 5 (7), 309–313.
- Aveling, C., 1984. Notes on the golden monkey, *Cercopithecus-mitis-kandti*, of the Virunga Volcanos, Rwanda. *African Journal of Ecology* 22, 63–64.

- Bailey, R.L., Dell, T.R., 1973. Quantifying diameter distributions with the Weibull function. *Forest Science* 19, 97–104.
- Banana, A.Y., Tweheyo, M., 2001. The ecological changes of Echuya afro-montane bamboo forest, Uganda. *African Journal of Ecology* 39, 366–373.
- Belsky, A.J., 1986. Does herbivory benefit plants? A review of the evidence. *American Naturalist* 127, 870–892.
- Belsky, A.J., Carson, W.P., Jensen, C.L., Fox, G.A., 1993. Overcompensation by plants: herbivore optimization or red herring? *Evolutionary Ecology* 1993 (7), 109–121.
- Bitariho, R., McNeilage, A., 2008. Population structure of montane bamboo and causes of its decline in Echuya Central Forest Reserve, South West Uganda. *African Journal of Ecology* 46, 325–332.
- Bitariho, R., Mosango, M., 2005. Abundance, distribution, utilisation and conservation of *Sinarundinaria alpina* in Bwindi and Mgahinga Forest National Parks, South West Uganda. *Ethnobotany Research Applications* 3, 191–200.
- Casella, G., Berger, R.L., 1990. *Statistical Inference*. Wadsworth and Brooks/Cole, Pacific Grove, CA, USA.
- Chi-son, C., Renvoize, S.A., 1989. A revision of the species described under *Arundinaria Gramineae* in Southeast Asia and Africa. *Kew Bulletin* 44, 349–367.
- Efron, B., Tibshirani, R.J., 1993. *An Introduction to the Bootstrap*. Chapman, Hall, New York, USA.
- Elgart-Berry, A., 2004. Fracture toughness of Mountain gorilla *Gorilla gorilla beringei* food plants. *American Journal of Primatology* 62, 275–285.
- Embaye, K., 2000. The indigenous bamboo forests of Ethiopia: an overview. *Ambio* 29, 518–521.
- Embaye, K., Weih, M., Ledin, S., Christersson, L., 2005. Biomass and nutrient distribution in a highland bamboo forest in southwest Ethiopia: implications for management. *Forest Ecology and Management* 204, 159–169.
- Engeman, R.M., Sugihara, R.T., 1998. Optimization of variable area transect sampling using Monte Carlo simulation. *Ecology* 79, 1425–1434.
- Franklin, D.C., Bowman, D., 2003. Bamboo, fire and flood: regeneration of *Bambusa arnhemica* Bambuseae: Poaceae after mass-flowering and die-off at contrasting sites in monsoonal northern Australia. *Australian Journal of Botany* 51, 529–542.
- Freckleton, R.P., 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *Journal of Animal Ecology* 71, 542–545.
- Gagnon, P.R., Platt, W.J., 2008. Multiple disturbances accelerate clonal growth in a potentially monodominant bamboo. *Ecology* 89, 612–618.
- Grimshaw, J.M., 1999. The Afro-montane bamboo, *Yushania alpina*, on Kilimanjaro. *Journal of East African Natural History* 88, 79–83.
- Hoenig, J.M., Heisey, D.M., 2001. The abuse of power: the pervasive fallacy of power calculations for data analysis. *American Statistician* 55, 19–24.
- Huberman, M.A., 1959. Bamboo silviculture. *Unasylva*, 13, online: <www.fao.org>.
- Kampunzu, A.B., Bonhomme, M.G., Kanika, M., 1998. Geochronology of volcanic rocks and evolution of the Cenozoic Western Branch of the East African Rift System. *Journal of African Earth Sciences* 26, 441–461.
- Keeley, J.E., Bond, W.J., 1999. Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. *American Naturalist* 154, 383–391.
- Kigomo, B.N., 1988. *Distribution, Cultivation and Research Status of Bamboo in Eastern Africa*. Kenya Forestry Research Institute, Nairobi, Kenya.
- Kleinhenz, V., Midmore, D.J., 2001. Aspects of bamboo agronomy. *Advances in Agronomy* 74, 99–153.
- Lejju, J.B., 2004. Ecological recovery of an afro-montane forest in south-western Uganda. *African Journal of Ecology* 42, 64–69.
- Li, R., Werger, M.J.A., Daring, H.J., Zhong, Z.C., 1998. Carbon and nutrient dynamics in relation to growth rhythm in the giant bamboo *Phyllostachys pubescens*. *Plant and Soil* 201, 113–123.
- McNaughton, S.J., 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40, 329–336.
- Miyazaki, Y., Ohnishi, N., Takafumi, H., Hiura, T., 2009. Genets of dwarf bamboo do not die after one flowering event: evidence from genetic structure and flowering pattern. *Journal of Plant Research* 122, 523–528.
- Morrison, M.E.S., Hamilton, A.C., 1974. Vegetation, climate in the Uplands of South-Western Uganda during the later pleistocene period: II. Forest clearance, other vegetational changes in the Rukiga Highlands during the past 8000 years. *Journal of Ecology* 62, 1–31.
- Owiunji, I., Nkuutu, D., Kujirakwinja, D., Liengola, I., Plumptre, A., Nsanzurwimo, A., Fawcett, K., Gray, M., McNeilage, A., 2005. The Biodiversity of the Virunga Volcanoes. Edited by WCS with DFGFI, ICCN, ORTPN, UWA, IGCP, Kampala.
- Parker, K.R., 1979. Density estimation by variable area transect. *Journal of Wildlife Management* 43, 484–492.
- Schuurmann, D.J., 1987. A comparison of the two one-sided tests procedure and the power approach for assessing the equivalence of bioavailability. *Journal of Pharmacokinetics and Biopharmaceutics* 15, 657–680.
- Sheil, D., Ducey, M.J., Sidiyasa, K., Samsodin, I., 2003. A new type of sample unit for the efficient assessment of diverse tree communities in complex forest landscapes. *Journal of Tropical Forest Science* 15, 117–135.
- Snowden, J.D., 1933. A study in altitudinal zonation in South Kigezi and on Mounts Muhavura and Mgahinga, Uganda. *Journal of Ecology* 21, 7–27.
- Twinomugisha, D., Chapman, C.A., 2008. Golden monkey ranging in relation to spatial and temporal variation in food availability. *African Journal of Ecology* 46, 585–593.
- Vazquez-Lopez, J.M., Vibrans, H., Garcia-Moya, E., Valdez-Hernandez, J.J., Romero-Manzanares, A., Cuevas-Guzman, R., 2004. Effects of harvesting on the structure of a neotropical woody bamboo *Otatea*: Guadalupe populations. *Interciencia* 29, 207–211.
- Weber, A.W., 1981. Conservation of the Virunga Gorillas: a Socio-Economic perspective on habitat and wildlife preservation in Rwanda. MSc, University of Wisconsin.
- Wimbush, S.H., 1945. The African alpine bamboo. *Empire Forestry Journal* 24 (1), 23–39.
- Wimbush, S.H., 1947. The African alpine bamboo. *East African Forestry Journal* 13, 56–60.