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Population structure and regeneration of multiple-use tree species in a semi-deciduous African tropical rainforest: Implications for primate conservation

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ABSTRACT

The conservation of threatened frugivorous primates (e.g. chimpanzees) and birds in the Albertine Rift Ecoregion rainforests requires the conservation of food tree species aided by an understanding of their natural regeneration and population trends. However, little is known of the population structure and regeneration patterns of a wide range of multiple-use tree species in many of these forests.

We examined the population structures and regeneration patterns of 15 tree species (including pioneer, non-pioneer and shade-bearers) that are both timber and primate food sources in Budongo Forest Reserve, NW Uganda, by constructing species population size-class distributions (SCDs), and calculating SCD slopes, seedling:juvenile and juvenile:adult ratios. The SCD slopes were used as indicators of population structure, while the slope values were used to summarise, in a single number, the shape of the SCD for a species.

Species composition between forest communities varied significantly, suggesting the influence of spatial environmental variations. Nine species had significant positive correlations between seedling and adult densities. Nine species, namely *Lasiodiscus mildbraedii*, *Celtis mildbraedii*, *Pouteria altissima*, *Chrysophyllum albidum*, *Cynometra alexandri*, *Diospyros abyssinica*, *Funtumia elastica*, *Chrysophyllum perpulchrum* and *Antiaris toxicaria* had highly negative SCD slopes spanning −2.47 to −1.1, and juvenile:adult ratios spanning from 5.34 to 1.62. Hence, clearly exhibiting 'inverse J' type curves, and suggesting a successful or healthy regeneration pattern. In contrast, both *Alstonia boonei* and *Cordia millenii* had weakly negative SCD slopes of −0.25, and juvenile:adult ratios <1; hence a pulsed or discontinuous regeneration pattern and low recruitment. The SCD slopes and juvenile:adult ratios varied between forest communities and historical management practices (HMPs). Most species recruit successfully and continuously over time, and hence have a more stable population structure. However, a discontinuous regeneration pattern for some, reflects unsustainable harvesting, that potentially eliminates seed sources for future generations. Hence, management of the Budongo Forest Reserve requires plans/practices that will enhance and facilitate the recruitment of both the vigorously and poorly regenerating species to ensure sustainable forest development. Preserving some fruiting trees in logged areas will benefit both long-term sustainable timber production and wildlife conservation, by providing food for frugivorous animals that will disperse the seeds.

1. Introduction

Tropical rainforests of Africa harbour unique biota, and their most distinctive feature is the abundance and diversity of large, ground living mammals, including species of primates and terrestrial herbivores (Primack and Corlett, 2005; Cordeiro et al., 2007). In sub-Saharan Africa, one of the regions of global importance as a centre of biodiversity and endemism is the Albertine Rift Ecoregion, which consists of several forests that harbour over nine primate species (Plumptre et al., 2007). Of these forests, Budongo Forest Reserve (BFR) in Uganda, is one of the most important for wildlife conservation as it has five diurnal primate species (Plumptre and Reynolds, 1994; Plumptre, 1996; Tweheyo, 2003), with probably the largest population of threatened chimpanzees (*Pan troglodytes*) in Uganda (Plumptre et al., 2007). The other diurnal primates are the black and white colobus monkeys (*Colobus guereza*), blue (*Cercopithecus mitis*), redtail monkey (*Cercopithecus ascanius*) and baboon (*Papio anubis*) (Plumptre and Reynolds, 1994). Hence, it is a flagship forest

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reserve for primate conservation. The long-term survival of these and other frugivorous primates in tropical rainforests requires implementation of management plans based on the conservation of food tree species (Tweheyo, 2003; Fashing, 2004). For example, the diet of chimpanzees of BFR, is dominated by fruits (e.g. Newton-Fisher, 1999) from woody plant species (e.g. Reynolds et al., 1998; Tweheyo and Lye, 2005). Therefore, maintaining viable populations of tree species which serve as food sources for chimpanzee and other primates is a crucial factor in primate conservation. However, in Uganda, like elsewhere in the tropics, conservation efforts are threatened by unsustainable exploitation for timber and medicine, and agricultural encroachment (Plumptre et al., 2003; Tweheyo and Lye, 2005; Fashing, 2004), that results in the loss of food trees for frugivorous primates and birds. Indeed, BFR faces ever increasing human utilisation and degradation (Mwavu and Witkowski, 2008a), that necessitates a strengthening of the ecological basis for its sustainable management (Guariguata, 2000). In many tropical forests both commercial and subsistence resource utilisation is increasingly using forest reserves (Whitmore and Sayer, 1992; Makana and Thomas, 2006; Mwavu and Witkowski, 2008a) and the future of the chimpanzees and other primates in these forests will depend on sustainable management of their habitats and food trees.

In this regard an understanding of the population structures and regeneration patterns of multiple-use tree species in BFR is important. However, tree regeneration studies in BFR have mainly focussed on African mahoganies (i.e. *Khaya anthotheca* (Welw.) C. DC. and *Entandrophragma* spp.), the key traditional timber species (e.g. Synnott, 1975; Mwima et al., 2001), as well as recruitment of tree species in permanent plots (Sheil, 1996). Hence, little is known of the seedling regeneration and population structure of a wide range of important multiple-use tree species which are harvested for subsistence and timber use, and at the same time form the major source of primate food. Yet, with the ever increasing human population coupled with increasing demand for wood products, the loss of woodlands in areas surrounding the Budongo Forest Reserve (Mwavu and Witkowski, 2008a), and diminishing stocks of African mahoganies, many tree species in this forest are increasingly being exploited for timber and other domestic needs. In addition, some of the timber species (e.g. *Antiaris toxicaria* (Pers.) Lesch., *Chrysophyllum* sp.) produce fruits that are eaten by primates and birds, while some primate and bird food trees (e.g. *Pouteria altissima* (A. Chiev) Aubrev. & Pellgr., *Celtis mildbraedii* Engl.) are also increasingly being used as timber, poles and fuel wood (Plumptre, 1995). Within these forest communities there are a variety of tree species that provide food for frugivorous primates (e.g. chimpanzees) and birds, including *Ficus* species, *C. mildbraedii*, *Cordia millenii* Bak., *Cynometra alexandri*, *Pseudospondias microcarpa* (A. Rich.) Engl. and a number of others (Reynolds et al., 1998; Tweheyo and Babweteera, 2007). Similarly, *A. toxicaria*, *Albizia gummifera*, *Albizia grandibracteata*, *C. millenii*, *Diospyros abyssinica*, *Funtumia elastica*, *P. altissima* have been reported to be food sources for colobus monkeys and mangabey in other Eastern African forests (Olupot, 1998; Fashing, 2004; Harris and Chapman, 2007).

We describe the population structure and seedling regeneration patterns of 15 selected multiple-use woody species and their variation in community composition across the forest, with a view to improve the understanding of their regeneration ecology in BFR. We explored the following questions: (1) How is species (seedlings and adults) composition related to forest community types (FCTs; Mwavu et al., 2008) and historical management practices (HMPs)? (2) What is the regeneration status (i.e. healthy or hampered) of these species at the (i) total forest, (ii) FCT, and (iii) HMPs level? Hence, the number of seedlings (stem diameters <2.0 cm), juveniles (2.0–10.0 cm) and adult trees (DBH > 10.0 cm), was quantified using 32, 0.5 ha plots. To answer question 2, the population structure (stem size-class distributions; SCDs) of the selected 15 multiple-use woody species that have been documented by Plumptre (1995) and Tweheyo and Babweteera (2007) as being both timber and primate food sources was examined. In the absence of long-term data, forest dynamics (e.g. changes in species composition and regeneration) are most often inferred from a single survey and the analysis of static forest inventory data by constructing species population size-class distributions (SCDs; e.g. Poorter et al., 1996; Sano, 1997; Lykke, 1998; West et al., 2000; Obiri et al., 2002; McLaren et al., 2005). Some of these studies have described SCDs of trees and used them as indicators of species composition change and rejuvenation. Characterisation of SCD serves as a means of projecting population trend, and to some extent past trends (Harper, 1977), and its interpretation has been useful in assessing the state of populations for a variety of management purposes (e.g. Luoga et al., 2002; Obiri et al., 2002; Wilson and Witkowski, 2003; Botha et al., 2004; McLaren et al., 2005). Furthermore, SCDs give good indication of the impact of disturbance and of successional trends in savannas and dry tropical forest systems (Lykke, 1998).

2. Materials and methods

2.1. Study area

The Budongo Forest Reserve is an equatorial semi-deciduous rainforest, situated between 1°37′–2°03′N and 31°22′–31°45′E, with an average altitude of 1050 m. It is a mid-altitude semi-deciduous moist tropical rainforest, since several of the dominant trees (including representatives of the genera *Celtis*, *Maesopsis* and *Ficus*) are at least briefly deciduous (Eggeling, 1947; Langdale-Brown et al., 1964), except for the widely spread shade-tolerant *C. alexandri* (Sheil, 1996). The canopy trees are generally high and emergent stems occasionally reach over 60 m (Sheil, 1996). Monthly average rainfall is 139 ± 67 mm and a relatively constant minimum temperature with a monthly average of 20.9 ± 0.9 °C. It is the largest forest reserve in Uganda, covering about 825 km^2, 53% of which is continuous tropical forest, the remaining area comprising grasslands (Howard, 1991).

Most of the forest's compartments have been treated with arboricides and today some 77% of the forest has been logged at least once, except for a few that from the onset have been managed as nature reserves. Consequently, the forest composition has been altered into a mosaic of forest types. Recently, using abundance data for stem diameter >2.0 cm four forest types namely; *P. microcarpa* Swamp Forest, *F. elastica*–*P. altissima* Forest, *Lasiodiscus mildbraedii*–*K. anthotheca* Forest and *C. alexandri*–*Rinorea ilicifolia* Forest were identified (Mwavu et al., 2008).

2.2. Methods

2.2.1. Sampling procedure and data collection

Within the forest we identified areas that have been subjected to (1) logging and arboricide treatment, (2) logging alone, and (3) those without logging or arboricide treatment (nature reserve)—representing the major historical management practices in this forest. This also helped to capture the different forest community types of BFR as classified by Mwavu et al. (2008). The selection of areas of different HMPs was aided by the presence of well marked management compartments within the forest, whose management practices history is documented (e.g. MNR, 1997). In each HMP at least two topographic gradient transects were established, each providing at least three topographic positions (lower slope (swamp/riparian), mid-slope, upper-slope, and flat/ridge-top). Plots of 100 m × 50 m (0.5 ha) separated by at least 150 m were laid for each available topographic position. Each 0.5 ha plot was further divided into five 20 m × 50 m contiguous sub-plots, which were systematically searched for seedlings. As defined for this study, a seedling is a woody plant individual of stem diameter $<$2.0 cm and height $\leq$1 m. Stem diameter was measured using a diameter tape at breast height (1.3 m), unless there were irregularities at this height or trees were shorter. For individuals with buttresses or other stem irregularities at breast height, DBH was measured above the buttresses. Each 20 m × 50 m plot was also systematically searched for seedlings. A total of 32, 0.5 ha plots; 6 in the nature reserve, 19 in logged and arboricide treated, and 7 in logged only were sampled. The number of plots per HMP corresponds to the size of the area in the forest.

2.3. Data analysis

2.3.1. Variation in species composition

Variations in species composition for seedlings and $>$2.0 cm individuals among forest communities and HMPs for the studied species, were tested employing ANOSIM (ANalysis Of SIMilarity), a randomization permutation test in CAP 3.1 (Seaby et al., 2006). The test statistic (R_{ANOSIM}) values generated by CAP 3.1 are a relative measure of separation of *a priori* defined groups. A zero (0) indicates that there is no difference among groups, while a one (1) indicates that all samples within groups are more similar to one another than any of the samples from other groups. A randomization process is used to find the probability of gaining particular values of R_{ANOSIM} by chance. The association/relationship between seedling and adult ($>$2.0 cm stem diameter) densities for the 15 species at the 0.5 ha level was also tested using Spearman rank-order correlation (Dytham, 2003).

2.3.2. Population structure of the 15 multiple-use woody species

The inventory data for each of the 15 species (Table 1) was tallied into stem diameter size classes as follows: 1, 2–5, 6–10, 11–15, 16–20, 21–25, 26–30, ... 56–60, 61–70, 71–80 cm, etc. This classification was used to balance the samples across size classes, because the number of individuals declines with increasing stem diameter size (Condit et al., 1998; Lykke, 1998). To display the species population size-class distributions (SCDs) the number of individuals ($N + 1$ natural log transformed) for each stem diameter size class were plotted against the mid-point of the respective size class. The SCDs were further analysed using the method proposed by Condit et al. (1998) and Lykke (1998). For each species a least-squares linear regression was performed with the size-class mid-point as the independent variable and the mean number of individuals in that class (N_i) as the dependent variable. To derive N_i the number of individuals in each size class is divided by the width of the class (Lykke, 1998). The size classes are a linear increment of the dbh and were not transformed, however, in order to derive straight-line plots of the size-class distributions, the N_i for each size class was transformed by $\ln(N_i + 1)$ because some classes had zero individuals (Lykke, 1998; Obiri et al., 2002; McLaren et al., 2005). The slopes of the regressions are referred to as SCD slopes, and were used as indicators of population structure (Lykke, 1998; Obiri et al., 2002; McLaren et al., 2005). The slope values were used to summarise, in a single number, the shape of the SCD for a species. For each species the SCDs slopes were calculated at the (i) total forest, (ii) forest community, and (iii) HMP levels.

The interpretation of the SCD slopes was based on the types of SCDs described in Everard et al. (1994). Slopes are usually negative, since larger size classes have fewer individuals, and indicate recruitment. Flat distributions with a slope of zero indicate equal numbers of regenerating trees and mature individuals. Positive slopes are sometimes referred to as unimodal since they are typically characterised by relatively many canopy individuals but no regeneration. SCDs were further analysed following the method of West et al. (2000). A ratio of small stems ($<$10 cm DBH; juveniles) to large stems ($>$10 cm DBH; adults) was calculated for each species at the (i) total forest, (ii) forest community, and (iii) HMP level. Species which are successfully recruiting are expected to have small:large stem ratios of $>$1. While ratios of $\ll$1 would indicate species with low recruitment and hence low representation in juvenile classes.

3. Results

3.1. Variation in the composition and distribution of the 15 multiple-use species

Seedling species composition varied significantly between forest communities (Global $R_{\text{ANOSIM}} = 0.43$, $p < 0.001$), with five of the six pair-wise comparisons being significantly different (exception was *L. mildbraedii*–*K. anthotheca* and *C. alexandri*–*R. ilicifolia* forests; $R_{\text{ANOSIM}} = 0.05$, $p = 0.3$). Similarly, species composition for DBH $>$ 2.0 cm individuals varied significantly between forest communities (Global $R_{\text{ANOSIM}} = 0.55$, $p < 0.001$), with five of the six pair-wise comparisons being significantly different

Table 1

Spearman rank-order correlations between seedling and adult densities of 15 multiple-use woody species studied in Budongo Forest Reserve, NW Uganda. Species guilds following Hawthorne (1995, 1996)[a] are also included.

Species	Species guild[a]	Spearman rank-order correlation statistic		
		R	$t\,(N-2)$	p
Albizia glaberrima (SchumACH. & Thonn.) Benth.	Pioneer	0.47*	2.93	0.006
Albizia grandibracteata Taub	Non-pioneer	0.66*	4.85	<0.001
Albizia zygia (D.C.) Macbr.	Non-pioneer	0.54*	3.49	0.001
Alstonia boonei De Wild	Pioneer	−0.2	−1.12	0.271
Antiaris toxicaria (Pers.) Lesch.	Non-pioneer	0.09	0.52	0.61
Celtis mildbraedii Engl.	Shade-bearer	0.41*	2.52	0.003
Chrysophyllum albidum G. Don	Shade-bearer	0.27	1.54	0.133
Chrysophyllum perpulchrum Hutch. & Dalz	Shade-bearer	0.67*	4.95	<0.001
Cordia millenii Bak.	Pioneer	0.28	1.57	0.127
Cynometra alexandri C.H. Wright	Shade-bearer	0.64*	4.61	<0.001
Diospyros abyssinica (Hiern) F. White	Pioneer	0.24	1.35	0.187
Funtumia elastica (Preuss) Stapf	Non-pioneer	0.34	1.99	0.055
Lasiodiscus mildbraedii Engl.	Shade-bearer	0.7*	5.39	<0.001
Pouteria altissima (A. Chiev.) Aubrev. & Pellgr.	Non-pioneer	0.49*	3.05	0.004
Raphia farinifera (Gaertn.) Hylander	–	0.83*	8.14	<0.001

[a] *Source*: Sheil et al. (2000).

* Statistically significant correlations.

Table 2

The 15 multiple-use woody species, indicating family, total number of seedling individuals (<2.0 cm) and their frequency (number of plots in which they were recorded out of 32), number of juveniles (2.0–10.0 cm DBH), adults (>10 cm DBH) and total plants; seedling:juveniles ratio, juveniles:adults ratio; size-class distributions (SCDs) parameters, stem sprouting following damage, and use. The species are arranged according to decreasing SCD slopes.

Species	Family	Seedling			Total number of.		Ratios		SCDs			Stem sprouting[a]	Use[b]
		Number	Freq.	Juveniles	Adults	Plants	Seedling:juveniles	Juveniles:adults	Slope	t	r^2 (%)		
Lasiodiscus mildbraedii	Rhamnaceae	14,961	28	3742	701	19,404	4.00	5.34	−2.47	16	97	Yes	S, PF
Celtis mildbraedii	Ulmaceae	1,621	29	1852	613	4,086	0.88	3.02	−1.69	22.21	96	Yes	T, S, PF
Pouteria altissima	Sapotaceae	299	22	255	91	655	1.17	2.80	−1.41	20.2	97	Yes	T, PF
Chrysophyllum albidum	Sapotaceae	825	32	120	54	999	6.88	2.22	−1.37	10.45	89	Yes	T, S, PF
Cynometra alexandri	Fabaceae	12,623	29	628	387	13,638	20.1	1.62	−1.35	12.4	86	Yes	S, PF
Diospyros abyssinica	Ebenaceae	303	16	93	30	426	3.26	3.1	−1.32	13.8	95	Yes	S
Funtumia elastica	Apocynaceae	285	28	1243	605	2,133	0.23	2.05	−1.29	6.35	83	Yes	S, PF
Chrysophyllum perpulchrum	Sapotaceae	192	23	121	34	347	1.59	3.56	−1.11	12.42	91	Yes	T, S
Antiaris toxicaria	Moraceae	155	26	182	90	427	0.85	2.02	−1.1	16.55	94	Yes	T, S, PF
Raphia farinifera	Palmae	528	3	0	19	547	528/0	0	−1.07	3	50	No	S, PF
Albizia zygia	Fabaceae	312	20	12	31	355	26	0.39	−1.06	4.18	66	Yes	T
Albizia glaberrima	Fabaceae	883	26	18	30	931	49.06	0.6	−1.01	5.26	63	Yes	T, S
Albizia grandibracteata	Fabaceae	71	2	15	7	93	4.73	2.14	−0.99	6.14	82	Yes	T, S
Alstonia boonei	Apocynaceae	1	1	20	64	85	0.05	0.31	−0.25	4.55	48	Yes	T
Cordia millenii	Boraginaceae	2	1	18	26	46	0.11	0.69	−0.25	6.47	72	No	T, PF

Source: T, timber; S, subsistence use; PF, primate food (leaves, fruits or wood).

[a] Mwavu and Witkowski (2008b).

[b] Plumptre (1995), MNR (1997), Tweheyo and Babweteera (2007).

Table 3

Juvenile:adult ratios and SCDs parameters (i.e. slope, t, and r^2 values) for the 15 multiple-use tree species across forest community types in Budongo Forest Reserve. The SCDs parameters are calculated based on the combined (including seedling, juveniles and adults) data for each species.

Species	*Pseudospondias microcarpa* Swamp				*Funtumia elastica–Pouteria altissima*				*Lasiodiscus mildbraedii–Khaya anthotheca*				*Cynometra alexandri–Rinorea ilicifolia*			
	Juvenile:adult ratio	SCDs			Juvenile:adult ratio	SCDs			Juvenile:adult ratio	SCDs			Juvenile:adult ratio	SCDs		
		Slope	t	r^2 (%)		Slope	t	r^2 (%)		Slope	t	r^2 (%)		Slope	t	r^2 (%)
Albizia glaberrima	0.56	−0.75	4.48	55.61	0/4	−0.66	3.62	44.96	1.00	−0.66	4.72	58.21	0.25	−1.08	4.17	52.05
Albizia grandibracteata	1.00	−5.79	2.11	21.77	2.33	−3.53	8.91	83.24	–	–	–	–	3.50	−0.93	4.85	59.55
Albizia zygia	0.50	−1.23	4.50	55.83	0.54	−0.74	4.90	59.98	0.14	−1.65	4.14	51.70	0.33	−1.44	4.70	57.97
Alstonia boonei	0.50	−2.38	1.69	0.15	0.25	−4.68	4.30	53.66	0.25	−0.83	1.07	6.67	0	−9.92	1.88	18.15
Antiaris toxicaria	2.60	−1.43	7.24	76.63	1.67	−1.17	16.69	94.57	1.90	−1.00	14.15	92.60	16/0	−1.06	5.78	67.58
Celtis mildbraedii	7.78	−1.07	10.03	86.29	4.09	−1.03	10.71	87.75	2.95	−0.62	14.45	92.88	2.67	−0.65	12.89	91.21
Chrysophyllum albidum	1.63	−0.95	6.05	69.57	3.62	−0.83	7.65	78.55	1.80	−0.75	8.07	80.28	1.88	−0.88	5.60	66.23
Chrysophyllum perpulchrum	8.50	−1.19	6.64	73.38	2.00	−1.01	7.16	76.22	3.50	−0.98	11.48	89.18	–	–	–	–
Cordia millenii	0.33	−1.78	0.46	1.29	0.20	−3.19	3.66	45.58	0.89	−1.61	1.96	19.30	–	–	–	–
Cynometra alexandri	2.66	−0.65	6.98	75.27	4.79	−0.77	8.32	81.21	3.19	−0.51	7.94	79.76	0.38	−0.59	5.43	64.78
Diospyros abyssinica	0/5	−1.49	3.96	49.44	6.00	−1.15	7.85	79.37	3.75	−1.15	7.52	77.95	2.85	−0.83	7.72	78.84
Funtumia elastica	2.49	−1.01	12.22	90.32	3.28	−0.70	15.56	93.80	1.61	−0.64	9.37	84.60	2.15	−1.27	10.48	87.29
Lasiodiscus mildbraedii	8.49	−0.55	12.39	90.56	42.00	−0.74	7.61	78.36	5.66	−0.46	18.13	95.36	3.31	−0.51	16.45	94.42
Pouteria altissima	1.67	−1.46	6.52	72.67	3.07	−0.79	14.50	92.93	3.09	−1.00	12.47	90.68	0	−1.18	3.72	46.42
Raphia farinifera	59.95	−0.59	3.91	48.82	–	–	–	–		–	–	–	–	–	–	–

(exception was *P. microcarpa* Swamp and *C. alexandri*–*R. ilicifolia* forests; $R_{\mathrm{ANOSIM}} = 0.07$, $p = 0.18$). For the HMP level, there was no significant difference in seedling or >2.0 cm species composition. A significant positive correlation (Spearman rank-order) was found between seedling and adult densities ($r_s = 0.54$, $p = 0.001$) for the combined species data. While, species-specific analyses at the 0.5 ha scale showed positive significant correlations between seedling and adult densities for only nine species (Table 1).

Seedlings for 10 species were each recorded in more than 20 (62.5%) sampling plots, with *Chrysophyllum albidum*, *C. mildbraedii*, *C. alexandri*, *F. elastica*, and *L. mildbraedii* being the most frequent. *C. alexandri* (14,961 individuals) and *L. mildbraedii* (12,623 individuals) were the most abundant and widely distributed, with occurrences in 29 and 28, of the 32 sampling plots, respectively (Table 2). Thus, they were represented in all four forest communities (Table 3). In contrast, *Alstonia boonei* and *C. millenii*, were the rarest species, with only 1 and 2 individuals each recorded, respectively. On the other hand, *Raphia farinifera* was restricted to the *P. microcarpa* Swamp forest community. The 15 multiple-use woody species (Table 2) represented 9 families, each with 1–4 species.

3.2. Population structure

Apart from *F. elastica*, *A. toxicaria*, *C. millenii*, and *A. boonei*, the other 11 species had higher numbers of seedlings than juveniles (individuals 2.0–10.0 cm DBH) (Table 2, Fig. 1). No juveniles were recorded for *R. farinifera*. Considering stems with DBH > 50 cm, *C. alexandri* had the highest number (189 individuals), while *R. farinifera*, *A. grandibracteata*, *Albizia glaberrima*, and *L. mildbraedii* had none. Generally, for each species, stem abundances declined with increasing stem diameter size as shown by the negative SCD slopes (Tables 2 and 3). The higher number of seedlings relative to juveniles for nine species (Table 1) indicates that they have a better regeneration potential.

At the total forest level, the SCD slopes ranged from −2.47 (for *L. mildbraedii*) to −0.25 (*A. boonei*) indicating high numbers of individuals in the lowest diameter classes and a gradual decline in

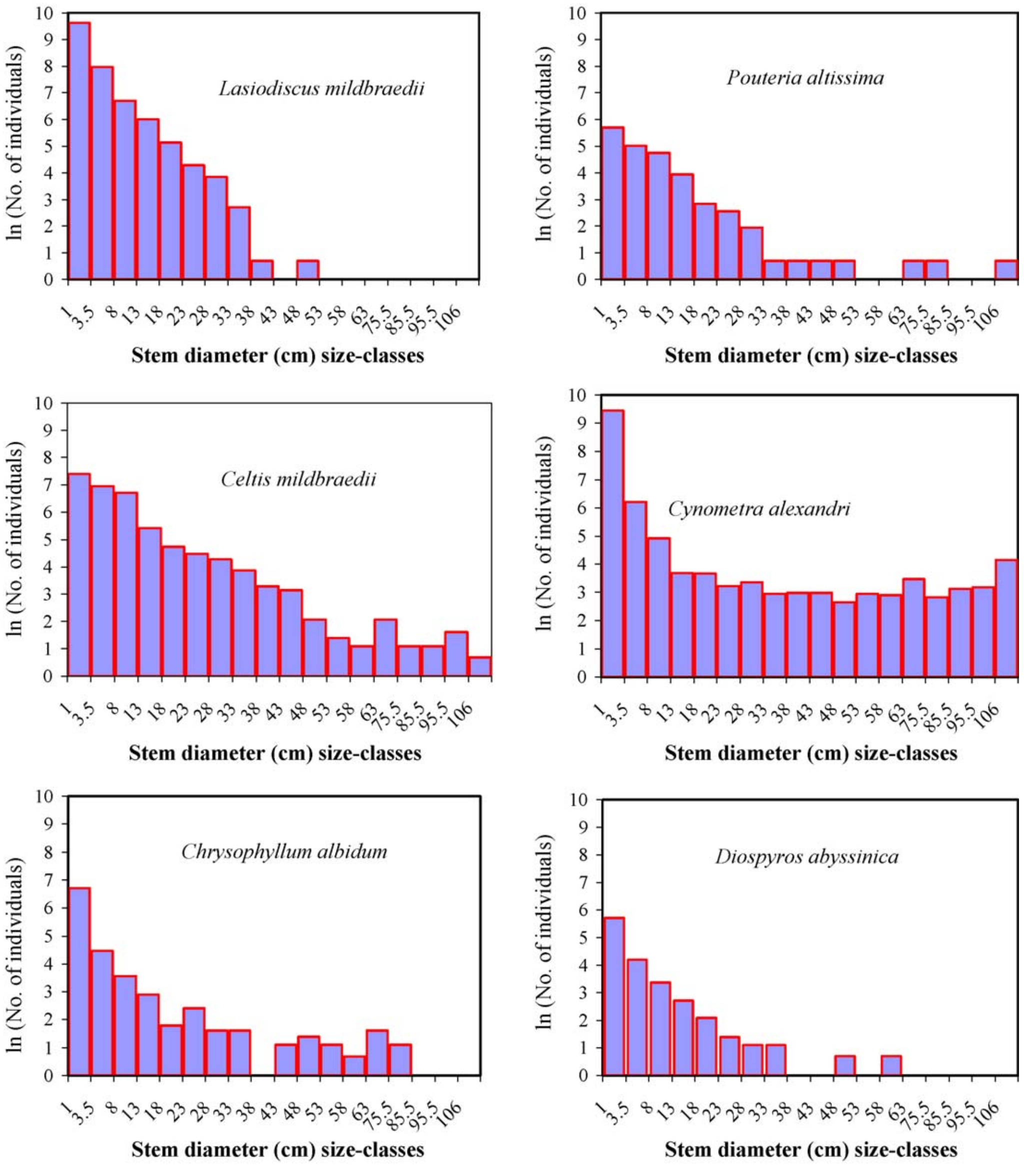

Fig. 1. Stem size-class distributions exhibited by 15 selected multiple-use woody species in Budongo Forest Reserve, Uganda, arranged according to SCD slope values. Mid-points of the classes are plotted. For *Celtis mildbraedii*, *Pouteria altissima*, *Cynometra alexandri*, *Antiaris toxicaria* and *Alstonia boonei* all individuals >100 cm DBH have been grouped together for graphing.

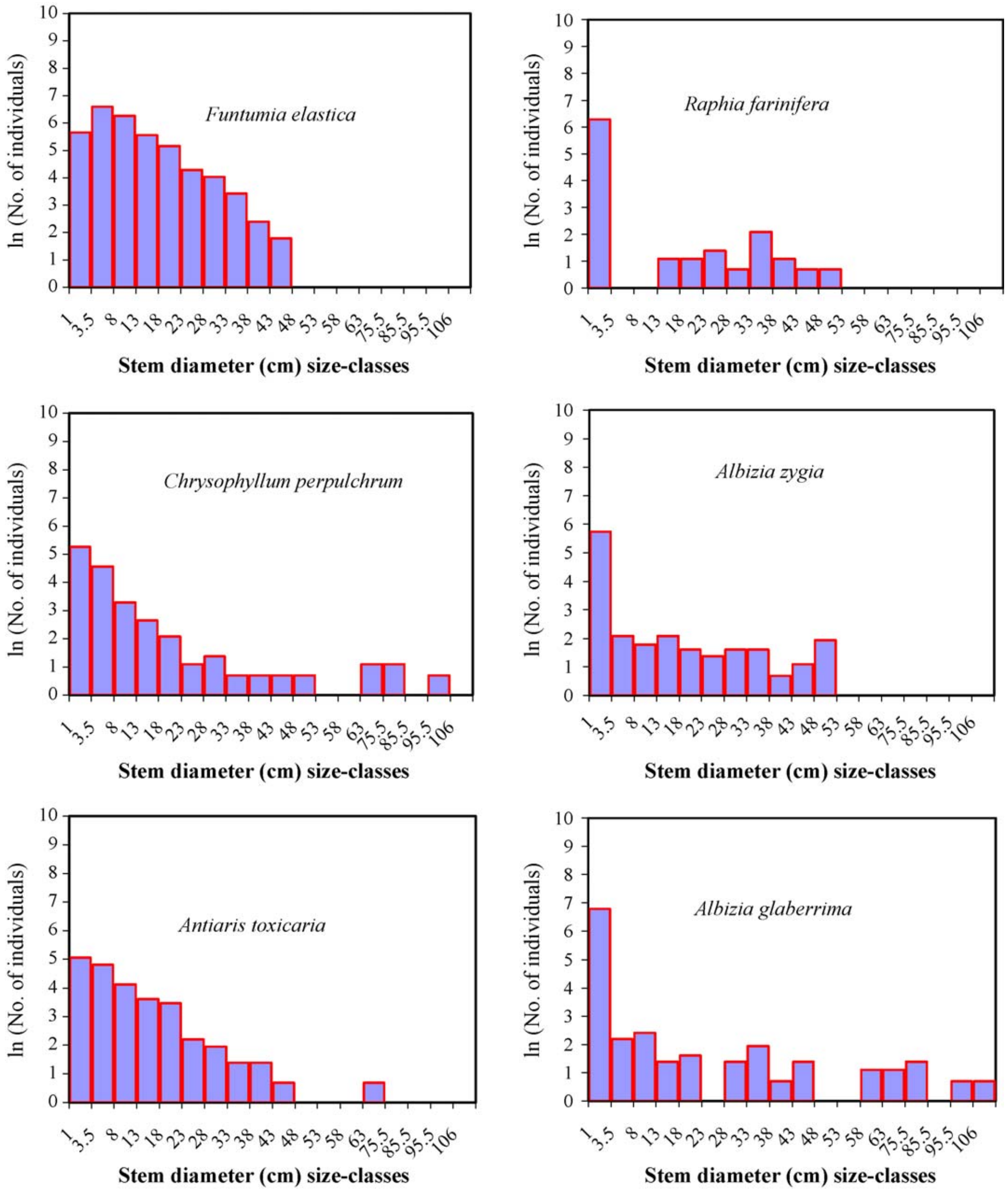

Fig. 1. (*Continued*).

the middle and larger diameter classes. The ratios of juvenile:adult stems (2.0–10.0 cm DBH /> 10 cm DBH) ranged from 0.0 (for *R. farinifera*) to 5.34 (for *L. mildbraedii*; Table 2). There were three major patterns of stem diameter size-class distributions (Fig. 1). The first group comprises nine species: *L. mildbraedii*, *C. mildbraedii*, *P. altissima*, *C. albidum*, *C. alexandri*, *D. abyssinica*, *F. elastica*, *Chrysophyllum perpulchrum*, and *A. toxicaria* (Fig. 1), with SCD slope values ranging from −2.47 to −1.1, and juvenile:adult ratios ranging from 5.34 to 1.62. They showed high numbers of individuals in the lowest diameter classes, mainly seedlings, and a gradual decline in the middle and larger diameter classes, and exhibited a clearly 'inverse J' curve. This shows a continuous representation of individuals in all diameter classes, suggesting a healthy regeneration pattern. The second group, consisting of *R. farinifera*, *Albizia zygia*, *A. glaberrima* and *A. grandibracteata* exhibited a nearly 'inverse J' curve size-class distribution. Although for *R. farinifera* the juvenile/adult ratio was $\gg 1$, it was not represented in the sapling class. The strong peak in the seedling size class followed by an absence of juveniles for *R. farinifera* indicates that its regeneration is hampered. The third group comprised *A. boonei* and *C. millenii* with weakly negative SCD slopes of −0.25 for both, and juvenile:adult ratios of 0.31 and 0.69 respectively, indicating low recruitment. They are also characterised by stem size-class distribution curves that deviate from the classic 'inverse J' and show evidence of pulsed or sporadic regeneration patterns because of under-representation in the seedling and medium size classes (Fig. 1).

At the forest community level, SCDs slopes for the 15 species varied from −9.9 to 0 (Table 3). The zero (0) SCD slopes were for *C. millenii*, *C. perpulchrum*, and *R. farinifera* all in the *C. alexandri–R. ilicifolia* forest community. *R. farinifera* had zero SCD slopes and zero juvenile:adult ratios in all but the *P. microcarpa* Swamp forest.

Of the 15 species, 9 had juvenile:adult ratios of less than 0.4 (with six having zero values) in at least one forest community type. Thus, except for the five species (*F. elastica*, *C. mildbraedii*, *L. mildbraedii*, *C. alexandri* and *C. albidum*) with juvenile:adult ratio >1 across all forest communities, the rest had poor recruitment of juveniles to adult trees. Only two species (*R. farinifera* and *F.*

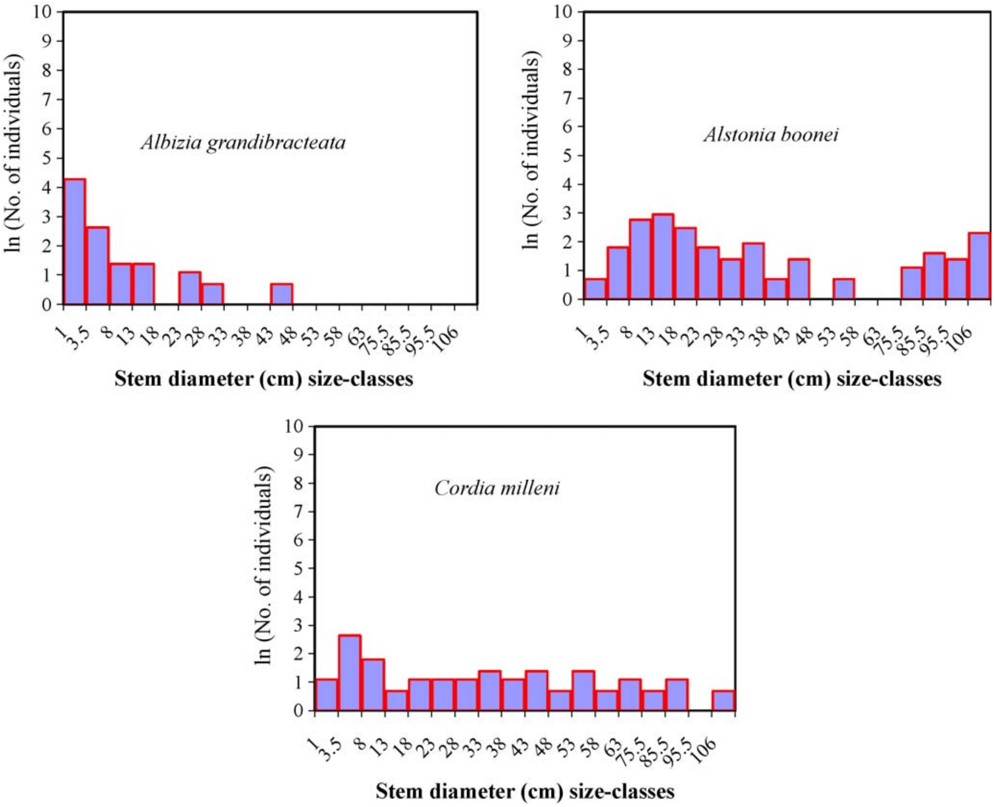

Fig. 1. (*Continued*).

elastica) had the highest juvenile:adult ratios in their representative forest communities (Table 3). For all species with a ≫1 juvenile:adult ratio across all forest communities, it was lower in the *C. alexandri–R. ilicifolia* forest compared to the other communities. The juvenile:adult ratio for *C. alexandri* was also lowest in the *C. alexandri–R. ilicifolia* forest, and highest in *F. elastica–P. altissima* forest community. Thus, the dominance of *C. alexandri* adults in an area is likely to negatively affect the seedling regeneration of many woody species, itself included.

At the HMP level, different species had highly negative SCD slopes in each management practice; nature reserve (*A. glaberrima* = −2.09), logged and arboricide treated (*A. grandibracteata* = −5.48), and logged only (*A. boonei* = −9.43; Table 4). The highest number of species with a juvenile:adult ratio >1 was for the logged and arboricide treated (9), followed by logged only (8) and the nature reserve (7 species; Table 4). For the logged and arboricide treated, of the six species with a juvenile:adult ratio >1, only 1 had a zero value. The nature reserve and the logged only areas each had three species with a juvenile:adult ratio of zero. Generally, the logged and arboricide treated areas have better regeneration for most tree species.

4. Discussion

4.1. Variation in species composition and distribution

Species composition varied significantly among the forest communities but not HMPs. Thus, the variation in species seedling

Table 4

Juvenile:adult ratios and SCDs parameters (i.e. slope, t, and r^2 values) for the 15 multiple-use tree species across HMP types in Budongo Forest Reserve. The SCDs parameters are calculated based on the combined (including seedling, juveniles and adults) data for each species.

Species	Nature reserve				Logged and arboricide treated				Logged only			
	Juvenile: adult ratio	SCDs			Juvenile: adult ratio	SCDs			Juvenile: adult ratio	SCDs		
		Slope	t	r^2 (%)		Slope	t	r^2 (%)		Slope	t	r^2 (%)
Albizia glaberrima	3/0	−2.09	5.13	62.19	0.58	−0.62	4.91	60.11	0.20	−0.81	4.01	50.18
Albizia grandibracteata	–	–	–	–	0.67	−5.48	2.09	21.41	3.50	−0.99	5.93	68.70
Albizia zygia	–	–	–	–	0.36	−0.74	5.16	62.46	0.50	−1.50	5.37	64.34
Alstonia boonei	0.07	0.09	0.05	0.01	0.33	−1.68	3.03	36.52	2/0	−9.43	2.36	25.78
Antiaris toxicaria	7.33	−1.23	6.95	75.11	1.71	−0.91	17.14	94.83	7.50	−1.01	5.66	66.68
Celtis mildbraedii	1.81	−0.74	11.08	88.48	4.92	−0.62	12.91	91.24	2.57	−0.84	14.38	92.82
Chrysophyllum albidum	2.00	−0.96	6.75	74.00	2.32	−0.72	9.38	84.61	2.29	−0.89	5.79	67.72
Chrysophyllum perpulchrum	4.75	−1.04	7.24	76.59	3.04	−0.90	11.47	89.15	–	–	–	–
Cordia millenii	0.33	−0.43	0.13	0.11	0.74	−2.90	6.65	73.43	–	–	–	–
Cynometra alexandri	0.82	−0.59	6.51	72.67	6.01	−0.50	8.34	81.31	0.42	−0.58	5.24	63.22
Diospyros abyssinica	1.80	−1.14	5.67	66.77	3.92	−1.09	10.47	87.27	2.85	−0.83	7.72	78.84
Funtumia elastica	0.93	−1.34	15.23	93.55	2.05	−0.58	10.26	86.80	6.85	−9.30	12.00	90.00
Lasiodiscus mildbraedii	2.11	−0.53	15.75	93.94	16.54	−0.46	13.90	92.35	3.26	−0.51	16.33	94.34
Pouteria altissima	4.20	−1.64	9.09	83.79	2.84	−0.75	23.91	93.75	2.43	−1.32	7.42	77.48
Raphia farinifera	0	−1.13	3.72	46.42	0/19	−0.59	3.91	48.83	–	–	–	–

and adult distributions can be attributed to spatial environmental variation rather than by chance only. Therefore, management interventions to maintain habitats for chimpanzee and other frugivorous primate conservation will have to consider capturing the various forest communities of Budongo Forest Reserve, because some of the primate food tree species (e.g. *P. microcarpa* and *R. farinifera*) are restricted to particular forest community types (Mwavu et al., 2008).

At the total forest level, 9 of the 15 species had highly negative SCD slopes, exhibiting near-perfect 'inverse J' curves (Fig. 1). Of these species, *A. toxicaria* was similarly reported to have had better regeneration in Kakamega forest where it is harvested for timber (Fashing et al., 2004). Hence, despite being targeted for timber and subsistence use, these species appear to be resilient to these disturbances and exhibit a healthy regeneration pattern. Additionally, these species resprout following stem damage in this forest (Mwavu and Witkowski, 2008b). The classic 'inverse J' curve is expected for populations that recruit fairly regularly over time (e.g. Oliver and Larson, 1990), and hence have a stable size-class structure (Silvertown, 1982). This is the case for 13 of the 15 species analysed, as they had small stem:large stem ratios $\gg$1; ratios expected of species that are successfully recruiting (West et al., 2000). Given that *C. mildbraedii* and *C. alexandri* are not currently greatly targeted for timber harvesting and are shade-bearers, their rather truncated size-class distributions need not necessarily be of concern at present in terms of population persistence. Thus, the death of an adult tree will at some point be replaced by one or more individuals growing up from the smaller size classes. On the other hand, species-specific SCD slopes and regeneration patterns varied among forest communities and HMPs, being good in some and poor in others. Plant community patterns may indirectly influence intrinsic population processes (e.g. stand-level regeneration patterns) because of the accompanying variation in forest canopy structure that influences both light availability and its spatial distribution (Bradshaw and Spies, 1992; Brown and Parker, 1994). In BFR, the forest communities differ in their seasonal light availability in the understory as a result of the variation in leaf area index (Mwavu et al., 2008). Moreover, light availability is a major environmental factor limiting growth and survival of many forest species (e.g. Whitmore, 1996) and its distribution may affect stand-level regeneration patterns of woody species (e.g. Clark et al., 1999; Nicotra et al., 1999). Hence, for shade intolerant pioneer species their regeneration will be hampered in areas dominated by canopy trees and of high leaf area index.

Generally, the higher number of juveniles compared to seedlings in *A. toxicaria*, *F. elastica*, *C. mildbraedii*, *C. millenii* and *A. boonei* (Table 2) may be attributed to differences in species guilds, phenologies and their responses to seasonal soil moisture variation. For chimpanzee food tree species, the number of species fruiting correlates positively with rainfall, and is higher during the rainy than the dry season (Tweheyo and Babweteera, 2007). Fruit production for woody species in BFR varies from year to year, with some trees not fruiting in some years; and none of the 15 species studied fruits throughout the year (Plumptre, 1995; Tweheyo and Babweteera, 2007). So after periods of low fruit production it is more likely to find low numbers of seedlings within the forest community, a situation that may further be exacerbated by seedling mortality.

At the total forest level seven species showed seedling/sapling ratios of >2.0, suggesting that some species in BFR experience high seedling mortality as a result of the dry season that is followed by loss of leaves for most species leading to increased light availability, temperatures and moisture stress at the ground. However, shade, competition for resources among seedlings, insect herbivory and disease (Augspurger, 1984; Teketay, 1997) may be other factors responsible for low recruitment to juveniles. Seedling recruitment processes (i.e. growth, survival and establishment) vary with species, light intensity and other habitat characteristics (Clark, 1990; Bazzaz, 1991; Teketay, 1996). The low numbers of seedlings for a particular species may also depend on whether it has a sufficient seed bank. Seed bank and seed rain have been emphasized as important potential sources of new individuals and species recruitment in a seasonal semi-deciduous forest in south-eastern Brazil (Grombone-Guaratini and Rodrigues, 2002).

The under-representation or a complete absence of individuals in some diameter size classes, particularly the middle size classes for some of the pioneer and non-pioneer species (e.g. *A. zygia*, *A. grandibracteata*, *A. glaberrima*, *R. farinifera*, *C. millenii* and *A. boonei*), indicates discontinuous regeneration (Poorter et al., 1996). Except for *R. farinifera* these trees are commonly harvested illegally and legally for timber. Logging for timber by local people also seems to affect the SCDs of *C. millenii* and *A. boonei*. Heavy exploitation of small stems for building purposes has similarly been blamed for poor recruitment of some tree species in Kakamega forests (Fashing et al., 2004). The lack of individuals in the sapling class for *R. farinifera* and the under-representation of *C. millenii* and *A. boonei* in the seedling size class (Fig. 1) is marked enough to raise questions concerning their long-term population persistence. Few seedling and sapling individuals make it unlikely that species populations can be maintained at the present level, because for a species to maintain a relatively constant population more individuals are required in the smaller diameter size classes than in the larger ones (Lykke, 1998). The size-class distributions exhibited by *R. farinifera*, *A. boonei* and *C. millenii* may reflect populations where regeneration has been temporarily interrupted through excessive harvesting of fruits or seeds, direct physical damage to seedlings, or lack of pollinators or dispersal agents (Peters, 1994). Moreover, *A. boonei* and *C. millenii* are pioneer species and under a closed canopy like in most parts of BFR they are more likely to have poor regeneration patterns. The poor regeneration of *A. boonei* in BFR compares with findings from Ituri forests where it was found to have poor seedling regeneration in all forest types (Makana and Thomas, 2006). In BFR, a number of *R. farinifera* seedlings are uprooted and the germinated seed remnants eaten probably by rodents (Mwavu, pers. obs.), while mature stems had been reportedly cut down by tobacco farmers to harvest leaves and leaf stalks. The cutting of mature *R. farinifera* plants effectively removes most of the seed sources for subsequent seed crops, the only source of natural regeneration for this species since it does not resprout from damaged stems (Mwavu and Witkowski, 2008b). It also has a low population density and restricted habitat preferences. On the other hand, the destruction of *R. farinifera* seedlings by baboons (Eilu, pers. comm.) has also been observed to reduce the number of potential sapling recruits. Similarly, in the Arabuko-Sokoke forest in Kenya, baboons and squirrels are seed predators, while monkeys are seed dispersers of *Afzelia quanzensis* (Gathua, 2000).

Although, for *R. farinifera* the small stem:large stem ratio and the SCD slope show a recruiting species, the lack of individuals in the sapling class suggests that it could be eliminated from the area if there is continued harvesting of the mature stems. A similar fate could face *C. millenii*, which is illegally cut for canoes making (Sheil, 1996), potentially removing its seed source. Therefore, the presence of species with a hampered regeneration pattern suggests the need to develop and implement forest management activities in order to reverse their declining population trend and facilitate a healthy regeneration pattern. This should also apply for those species presently exhibiting a healthy regeneration pattern. Hence, ensuring a continued availability of food sources for both frugivorous primates and birds; thereby contributing to the ability of frugivorous primate and bird species to persist in the forest. The maintenance of adequate regeneration of food trees for both frugivorous primates in BFR will go a long way in alleviating crop raiding from primates in the adjoining villages; an already significant source of people–forest conflict (Hill, 2000; Tweheyo et al., 2005). Moreover, food supply regulates chimpanzee and colobus monkey movements in tropical forests (Conklin and Wrangham, 1994; Reynolds et al., 1998, Harris and Chapman, 2007). Furthermore, forest plant composition determines the range of the feeding possibilities available to the primates, and is a major factor determining the abundance and distribution of forest dwelling primates (e.g. colobus monkeys and chimpanzees; Chapman et al., 2002; Fashing and Gathua, 2004; Reynolds, 2005).

The high number of stems in the ≥50 cm diameter class for *C. alexandri* compared to the other studied species may be attributed to human harvesting preferences and species-specific growth habits. *C. alexandri* is known to grow very large stems, but these are not harvested for timber, whereas the other species except *R. farinifera*, *L. mildbraedii* and *F. elastica* are harvested both legally and illegally. The impact of harvesting woody species for poles and timber, although minimal at present for a number of species (Mwavu and Witkowski, 2008b), may increase in future and impact on their regeneration pattern. According to the BFR Forest Management Plan (1997–2007), the recommended minimum felling DBH for most timber species is 50 cm, which is in fact even lower than for previous management plans. So, whereas some of the timber species may be currently exhibiting a healthy regeneration pattern, the continued harvesting of trees of DBH ≥ 50 cm for timber as recommended in the management plan, may in the long run adversely affect their population structure and regeneration. For most timber tree species in BFR, fruit production is highest at DBH ≥ 50 cm, and the density of seedlings rises exponentially with an increase in the number of trees over 50 cm DBH (Plumptre, 1995). Yet, there are no deliberate management efforts to ensure that mature trees that are potential seed sources are left, even in areas where legal timber harvesting takes place.

Leaving behind standing mature trees in logged areas would be of great importance to both timber and wildlife conservation as the fruit trees will provide food for frugivore primates and birds which will, consequently, disperse the seeds. However, the trees left behind should be of sufficient population size, and the members of the population should not be far apart, because plant population-size and spacing are important factors in the determination of the reproductive output of many tropical tree species (Ghazoul, 2005). Small populations are likely to be less attractive or less apparent to pollinators than large populations (e.g. Jennersten and Nilsson, 1993; Ägren, 1996) leading to both a decline in pollinator visits and poor pollen quality (Silander, 1978; Ghazoul, 2005). Also, some primates (e.g. black and white colobus monkeys) that eat fruit at least seasonally have relatively small home ranges and energetic constraints on their movements due to their unusual digestive anatomy, and thus would need the important tree species to not be far apart. Increased spacing among flowering conspecifics, through harvesting or habitat fragmentation, may reduce seed set through lower pollinator visitation or pollen quality. If this occurs, then the BFR woody plant community will be greatly affected since the seedling bank is presently its major mode of regeneration. Consequently, this is most likely to have a major influence on the socioecology of the animals that depend on them (Fashing and Gathua, 2004).

4.1.1. Conclusions and recommendations

This study showed that most of the selected multiple-use tree species had a classic 'inverse J' curve population structure and small stem:large stem ratios ≫1, which is expected of populations that recruit successfully and continuously over time, and hence have a more stable size structure. However, some species were under-represented or completely lacked individuals in some size classes (particularly seedlings and juveniles), indicating a discontinuous regeneration pattern, reflecting populations where regeneration has been temporarily interrupted through excessive harvesting of fruits or seeds, direct physical damage to seedlings, or lack of pollinators or dispersal agents. Some tree species (e.g. *C. millenii*, *Maesopsis eminii*, etc.) are unsustainably harvested for timber and non-timber products (e.g. *R. farinifera* and *Calamus deerratus* Mann & Wendl.), potentially eliminating seed sources for future generations. The presence of species with poor regeneration suggests the need for the BFR management to develop and implement forest management plans/activities that will enhance and facilitate both vigorous and poorly regenerating species, to ensure sustainable forest development. For example, leaving behind standing mature fruiting trees in logged areas would be of great importance to both timber and wild animal conservation as the fruit trees will provide food for both frugivorous primates and birds, which will, consequently, disperse the seeds. These, however, should be of sufficient population size, and the members of the population should not be too far apart, to facilitate their reproductive output. As more species are added onto the timber species list, studies are also required on seed banks, temporal patterns of seed rain, seedling survival and recruitment, as this information is important for conservation and management planning for these species.

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