Forest succession in Kibale National Park, Uganda: implications for forest restoration and management

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Abstract

Forest succession was studied in four plots in former grasslands at the Ngogo study area in Kibale National Park, Uganda. The plots were located in areas that had been protected from fire for 0.58, 25, 9 and ≈30 years for plots 1, 2, 3 and 4, respectively. Species richness reflected the length of time that the plot had been protected from fire; it was highest in plot 4 and lowest in plot 1. Species density, stem density and basal area were all highest in plot 4 and lowest in plot 1. The species densities of plots 2 and 3 were not different. Similarly, plots 2 and 4 did not differ with regard to stem density or basal area. Animal seed dispersers played a vital role in the colonization of grasslands by forest tree species.

Key words: tropical, forest, succession, disturbance

Résumé

On a étudié la succession forestière dans quatre plots d'anciennes prairies dans la zone de recherche de Ngogo, dans le Parc National de Kibale, en Ouganda. Ces plots étaient situés dans des endroits qui avaient été protégés du feu pendant 0, 58, 25, 9 et ± 30 ans pour les plots 1, 2, 3 et 4 respectivement. La richesse en espèces reflétait la durée pendant laquelle le plot avait été protégé du feu ; elle était maximale dans le plot 4 et minimale dans le plot 1. La densité des espèces n'était pas différente dans les plots 2 et 3. De même, les plots 2 et 4 ne différaient pas en ce qui concernait la densité des pousses ou la surface basale. Les animaux qui dispersent les semences ont joué un rôle vital dans la colonisation des prairies par les espèces d'arbres de forêts.

Introduction

Tropical rain forests (TRFs) cover only about 15% of the earth's surface but harbour about 50% of the world's species (Struhsaker, 1987; MacKinnon, 1997) and thus play a crucial role in biodiversity conservation. Forests also contribute to the maintenance of soil fertility, prevention of soil erosion, floods and landslides, and the provision of reliable water supplies (Hamilton, 1984; Struhsaker, 1987). Equally vital, although not fully understood, is their role in regulating regional and global climate (Hamilton, 1984; Struhsaker, 1987). Evapotranspiration from tropical rain forests contributes only 2–3% of the global water cycle (Bruenig, 1996), but can be extremely important regionally. For example, it contributes 48% of the rainfall in Amazonia (Salati, Vose & Lovejoy, 1986; Shukla, Nobre & Sellers, 1990).

Tropical rain forests are also important with regard to global warming, a serious environmental problem. Reducing emissions of carbon dioxide and other greenhouse gasses is the best way to address the problem, but political and economic factors make major reductions unlikely in the near future.

Extensive tree cover, especially in TRFs, can reduce the annual net addition of carbon to the atmosphere by carbon-fixing (Bruenig, 1996). In fact, plants grow faster in atmospheres rich in carbon dioxide (Bolin, 1977). However, Bruenig (1996) cautions that carbon fixation by trees cannot continue indefinitely, because no more net carbon fixation occurs after 10 to 20 years of growth. Thus, new planting is necessary. However, Schulze, Wirth & Heinmann (2000) contend that old-growth forests continue to remove carbon dioxide, even when they are fully mature.

Planting or conservation of trees for carbon sequestration may happen mostly in the developing countries, with the industrially developed nations acting as financiers

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(Kuper, 1996; Oates, 1999). Unfortunately, we have little information on the basic biology of tropical trees (Hubbell & Foster, 1992; Condit, Hubbell & Foster, 1993a,b; Korning & Balslev, 1994). Attempts to use indigenous tree species in afforestation programmes may be unsatisfactory, because some species are not suited to the environmental conditions at the time of planting or soon after. Such problems have occurred in the Kibale and Mount Elgon National Parks, Uganda (Kuper, 1996). The paucity of information on the biology of the vast majority of tropical forest tree species is the major reason why most afforestation programmes have used only a few, predominantly exotic species (Condit *et al.*, 1993a). Although carbon sequestration can be achieved through planting exotic tree species whose silviculture is well documented, such trees may not cater for the requirements of wildlife and may have undesirable environmental effects. Therefore, the best way forward is for tropical forest biologists and foresters to investigate how to carry out successful afforestation with indigenous trees.

The artificial restoration of deforested lands to their original high diversity is expensive in terms of human energy and money, and may fail to produce the desired ecological complexity (McClanahan & Wolfe, 1993). Given that money for conservation is scarce, we need inexpensive afforestation methods that restore ecological complexity. Some promising methods include the provision of perches for seed dispersing animals (McClanahan & Wolfe, 1993; Robinson & Handel, 1993) and allowing natural succession under tree plantations (Riswan & Kartaniwata, 1988, cited in Bruenig, 1996; Lugo, Parrota & Brown, 1993; Chapman & Chapman, 1996; Fimbel & Fimbel, 1996). Here I describe the partial results of an ongoing natural process which suggests that reforestation can be achieved by fire exclusion alone. The long-term objective of this study is to provide baseline data for monitoring succession rates and growth and mortality rates of trees growing in former grasslands at Ngogo, Kibale National Park. I report the long-term effects of fire exclusion on species diversity, tree density, basal area and the importance of animal seed dispersers in forest succession.

Methods

The study area

The study was conducted at the Ngogo study area in Kibale National Park, approximately 766 km^2 in western Uganda, within the geographical coordinates: 0°13′–0°41′N and 30°19′–30°32′E. The conservation status of Kibale Forest has changed over the years. For details about the park, see Struhsaker (1997) and Chapman & Lambart (2000).

The altitude within the park ranges from 1590 m in the north to 990 m in the south (average elevation at Ngogo is 1350 m). Annual mean rainfall range is 1492–1622 mm and the rain is fairly well distributed throughout the year. However, March–May and September–November are usually the wettest months, while June–July and December–February are usually dry (Struhsaker, 1997). Mean monthly maximum temperatures are 23–24°C and the mean monthly minimum temperature is 16°C (Struhsaker, 1997).

The study plots

The study plots were located in pyrogenic grasslands adjacent to mature forest. When the Ngogo study site was established in 1975 (T. Struhsaker, pers. comm.) the grassland around the camp and within the trail grid-system started receiving protection from fire. The effectiveness of this protection was not uniform across all grasslands, as some burnt at different times. This situation offers an opportunity to investigate the role of fire exclusion in forest succession. The study area map (Fig. 1) shows the vegetation in the study plots as of 1981 (Ghiglieri, 1984).

Plot 1 (0.54 ha) is bordered by a motorable track on the western side and by a fire-break on all other sides. These have not provided a perfect barrier to fire; the plot has burnt frequently, most recently in August 1996 (D. Watts, pers. comm.) and February 1999 (pers. obs.).

Plot 2 (0.5 ha) was an open grassland in 1984 when I started working at Ngogo, and has been perfectly protected from fire since the establishment of the Ngogo Camp in 1975 (T. Struhsaker, pers. comm.).

Plot 3 (1 ha) is part of a larger former grassland. Although it is within the trail system, fires that were presumably set by poachers, used to burn this grassland until the early 1990s. The last fire was on 15 January 1991 (J. Tibisiimwa, pers. comm.). Therefore, it had been unburned for approximately 9 years prior to the beginning of this study.

Plot 4 (1 ha) has been protected the longest. In 1984, this site was an impenetrable thicket (pers. obs.). Judging from the similarity between the vegetation near the camp that

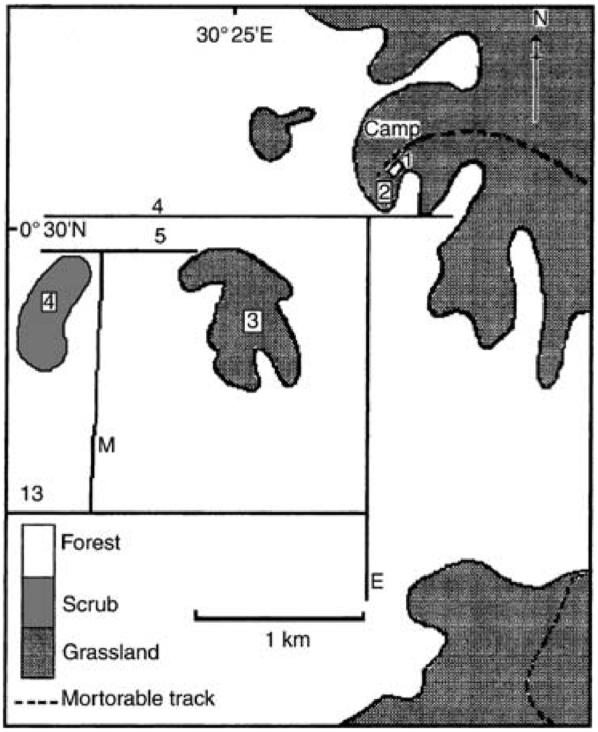

Fig 1 Map of Ngogo study area showing locations of the study plots and vegetation as of 1981

has not been cut or burnt for the last 14 years and the vegetation in Plot 4 in 1984, it had not been burnt since about 1970. Therefore, the period without fire to the beginning of this study is approximately 30 years.

Data collection

I divided each plot into subplots of 10 m × 10 m, the corners of which were marked permanently by driving 45 cm long plastic pipes into the ground. The pipes were painted white for easy identification on subsequent surveys. I identified and recorded all woody plants $\geq$2.5 cm diameter at breast height (d.b.h. = 1.4 m) to species level. For trees that forked below 1.4 m, I measured their diameter just below the point of branching. In all cases, the point where the measurement was taken was painted with white oil-based paint. I removed climbers and loose bark in the line of measurement before taking measurements. Each tree included in the sample was permanently marked with an aluminium tag bearing a code (made up of the first two letters of its genus and species names) and number. The numbers followed the sequence in which the trees were encountered. Using two tape measures laid along adjacent sides of a subplot, the location of each tree was recorded to the nearest decimetre by x and y co-ordinates. The methods used in this study are described in detail in Whitmore (1989). Voucher specimens of trees that could not be identified in the field were collected for later identification at the Makerere University Herbarium. I recorded the locations and d.b.h. of dead trees in plot 1 that were presumably killed by fire, but did not give them identification numbers. Unless otherwise stated, these were excluded from the analyses.

Data analysis

I measured the species diversity in each plot using the Shannon-Weaver index of diversity (H') (Greig-Smith, 1983) and also calculated Prendergast *et al.*'s (1993, cf. Lwanga, Balmford & Badaza, 1998) indices of relative richness. This involves construction of species accumulation curves smoothed using Krebs' (1989) rarefaction algorithm. The species richness of each plot was compared with the richness of all other plots in a pair-wise manner at the highest sampling scheme (number of 10 m × 10 m subplots) common to each pair of plots. Then, the relative richness index of each plot was calculated as a geometric mean of all pair-wise values.

I used the Kruskal–Wallis one-way ANOVA to test for differences in species richness, number of stems and basal area per unit area among the four study plots. Multiple comparisons between plots (Siegel & Castellan, 1988) were calculated to ascertain which pairs were different.

Many tropical forest tree species are represented by one or just a few individuals, which makes the establishment of clear differences in floral composition difficult (Swaine, Liebermann & Putz, 1987; Milton, Laca & Demment, 1994). Therefore, I assigned most species to ecological guilds and conducted analyses on these. The ecological guilds were: seed dispersal syndromes (based on Hamilton, 1981; Beentje, 1994; Katende, Birnie & Tengnäs, 1995; Whitmore, 1998), forest dependence (Katende *et al.* 1995; Hamilton, 1981; Beentje, 1994) and ecological succession (i.e. pioneer versus climax; Swaine & Whitmore, 1988). I used Paired t-tests to test for differences in stem density and basal area among the guilds, and Spearman rank correlations to test the hypothesis that the proportion of stems and basal area of climax species increases with duration of fire exclusion. In all tests, the 10 m × 10 m

Table 1 Summary data of the four study plots indicating plot size, duration of protection, sampling period, the different indices of diversity and results of the Kruskal–Wallis one-way ANOVA on species density, stem density and basal area. Superscripts indicate values that were shown by multiple comparisons to be different ($P = 0.05$)

Plot number	1	2	3	4	χ^2	*P*
Plot size (ha)	0.54	0.5	1	1	–	–
Duration of protection from fire (year)	0.58	25	9	≈30	–	–
Sampling period	1999	1999	2000	2000	–	–
Species richness	9	49	49	70	–	–
Shannon–Weaver diversity index H′	1.55	2.57	2.74	3.24	–	–
Relative richness index	0. 1775	1.7323	1.4074	2.3131	–	–
Number of species per subplot	1.407^{a}	7.24^{b}	4.98^{b}	11.03^{c}	186.57	<0.001
Number stems per subplot	4.407^{a}	17.96^{c}	12.03^{b}	20.32^{c}	111.68	<0.001
Basal area per subplot	0.053^{a}	0.198^{c}	0.134^{b}	0.288^{c}	71.26	<0.001

subplot was used as the sample unit and significance levels were one-tailed. It was rare that I could not assign a species to guilds, and excluded them from analyses based on guilds.

I defined density as the number of individuals per hectare; basal area was defined as the area occupied by a cross-section of a stem at breast height; frequency was the number of sample units (10 × 10 m) in which a species was found. I calculated relative density and relative basal area as percentages of the sum of values of all species in the plot.

Results

Species richness

Species richness was highest in plot 4, which had the longest duration of fire exclusion, and lowest in plot 1, which had the shortest duration (Table 1). Richness was the same for plots 2 and 3, despite different periods of fire exclusion. However, plot 2 was only half the size of plot 3. The Shannon–Weaver diversity index H′ was higher for plot 3 than plot 2 despite the much longer protection for

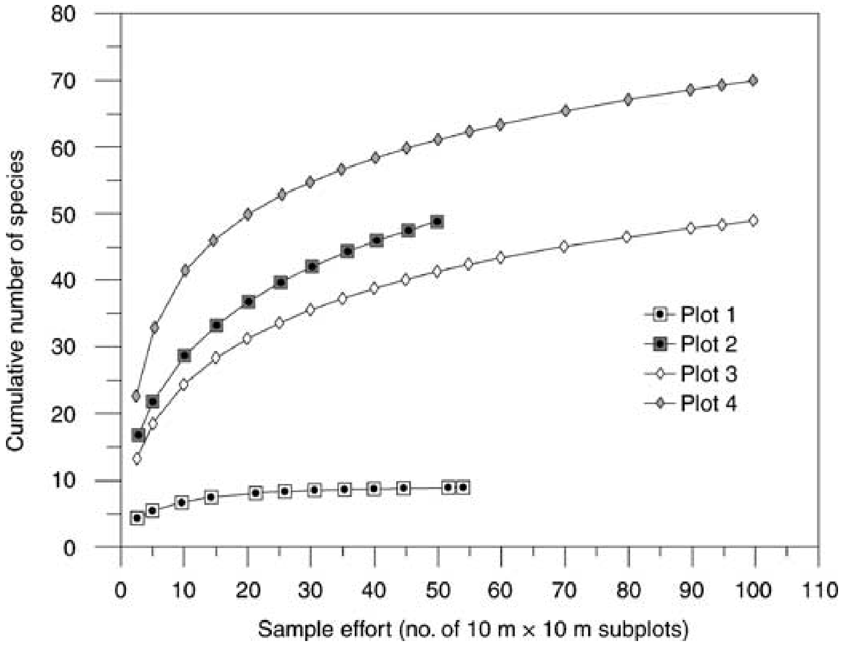

Fig 2 Species accumulation curves as a function of sampling effort in the four study plots

plot 2. Nonetheless, relative richness scores (Prendergast *et al.*, 1993) which control for differences in sampling effort, increased with duration of fire exclusion (Fig. 2). The number of species per subplot varied significantly among the plots (Table 1). *A posteriori* multiple comparison tests revealed that the species richness was highest in plot 4, followed by plots 2, 3 and 1. The difference between plots 2 and 3 was not significant.

Stem density and basal area

The number of stems per subplot also varied significantly between plots (Table 1). Multiple comparison tests indicated that stem density did not differ between plots 2 and 4. However, stem density in these two plots was significantly higher than in plots 1 and 3. Stem density was significantly higher in plot 3 than in plot 1. Variation in basal area followed exactly the same pattern as stem density (Table 1).

Plots 1, 2, 3 and 4 had 441, 1796, 1203 and 2032 stems/hectare, respectively. Stem density values varied among species (Table 2). In plot 1, 93.4% of the total stem density was contributed by the five most common species (*Maesa lanceolata, Acacia hockii, Hoslundia opposita, Albizia grandibracteata* and *Erythrina abyssinica*). In plot 2, the five commonest species, *A. grandibracteata, M. lanceolata, Warburgia ugandensis, Diospyros abyssinica* and *Flueggea virosa* contributed 63.9% of total stem density. The top five species in plot 3, *H. opposita, A. grandibracteata, Vernonia auriculifera, Harrisonia abyssinica* and *Bridelia micrantha* contributed 61.8% of the plot's stems. In plot 4, the top five species *D. abyssinica, Teclea nobilis, Clausena anisata, Turraea floribunda*, and *Celtis africana* contributed only 48.1% of all stems.

Total basal area for plots 1, 2, 3 and 4 was 5.3, 28.7, 13.4 and 19.8 m^2/ha, respectively. Again, this was not divided equally among species and a species' relative basal area did not necessarily reflect its contribution to stem density (Table 2). Ranked on the basis of basal area, the top five species in plot 1, *Erythrina abyssinica, M. lanceolata, Entada abyssinica, H. opposita* and *A. hockii*, contributed 95.1% of total basal area. In plot 2, the top five species, *A. grandibracteata, F. virosa, M. lanceolata, Erythrina abyssinica*, and *Spathodea campanulata* contributed 86.2%. The top five species in plot 3, *A. grandibracteata, H. opposita, Dombeya nairobensis, Vernonia auriculifera* and *Harrisonia abyssinica* accounted for 75.1% of basal area. The top five species in plot 4, *Dombeya mukole, Olea welwitschii, D. abyssinica, Sapium ellipticum* and *T. nobilis* accounted for 50.4%.

Frequency

Frequency indicates how the species are dispersed and is an ecologically meaningful parameter for species represented by several individuals in a plot. In plot 1, none of the common species *M. lanceolata, A. hockii* and *H. opposita* occupied more that 18 of the 54 subplots, suggesting a clumped distribution. The commonest species in plot 2, *A. grandibracteata*, had 332 stems in 90% (45 subplots) of the sample units. *M. lanceolata* and *W. ugandensis* were represented in at least 50% of the subplots. *Hoslundia opposita* and *A. grandibracteata*, the two commonest species in plot 3, occurred in 76 and 60 sample units, respectively. The five commonest species in plot 4, *D. abyssinica, T. nobilis, C. anisata, T. floribunda* and *C. africana* occurred in at least 58% of the subplots.

The importance of animal dispersal agents in forest succession

I assigned all species in the sample to their respective modes of dispersal (Table 3). The differences in the number of stems of animal and non-animal dispersed species were not significant for plots 1 and 3, which had been protected from fire for relatively short periods (Table 4a). Animal dispersed species were more common than non-animal dispersed species in plot 2 but this difference was only weakly significant (Table 4a). In plot 4, which had been protected from burning the longest, animal dispersed species were significantly more abundant than non-animal dispersed species (Table 4a).

No significant differences in the basal areas of animal and non-animal dispersed species were detected in plots 1 and 2, but the differences were significant for plots 3 and 4 (Table 4b). However, whereas the basal area of non-animal dispersed species was greater than that of animal dispersed species in plot 3, the converse was true in plot 4 (Table 4b).

Time as an important factor in forest establishment

I classified all species in the sample as pioneer or climax species (Table 3). The relationship between the duration of fire exclusion and the proportion of climax species stems was positive and highly significant ($r_s = +1.0$,

Table 2 Species represented in plots 1, 2, 3 and 4, showing basal area/ha, stem density/ha, frequency and number of stems

	Basal area				Density				Frequency				Number of stems			
Species	Plot 1	Plot 2	Plot 3	Plot 4	Plot 1	Plot 2	Plot 3	Plot 4	Plot 1	Plot 2	Plot 3	Plot 4	Plot 1	Plot 2	Plot 3	Plot 4
Acacia hockii	0.572		0.217		96		21		18		12		52		21	
Aeglopsis eggelingii		0.003		0.140		4		92		2		52		2		92
Albizia coriaria		0.317	0.085			8	11			3	10			4	11	
Albizia grandibracteata	0.190	11.84	4.490	0.799	19	664	223	61	7	45	60	26	10	332	223	61
Aningeria altissima				0.005				4				4				4
Antiaris toxicaria			0.001	0.001			1	1			1	1			1	1
Balanites wilsoniana		0.018	0.036	0.287		6	5	22		2	4	15		3	5	22
Bequaertiodendron oblancelatum				0.003				1				1				1
Bersama abyssinica		0.021	0.015	0.142		4	2	33		1	1	30		2	2	33
Blighia unijugata		0.033	0.002	0.039		16	2	17		4	1	14		8	2	17
Bosquiea phoberos				0.009				2				2				2
Bridelia micrantha		0.104	0.349	0.001		6	59	1		2	31	1		3	59	1
Cassipourea ruwensorensis		0.002		0.011		2		5		1		5		1		5
Celtis africana	0.001	0.022	0.019	0.252	2	6	3	94	1	3	2	61	1	3	3	94
Celtis durandii		0.150	0.001	0.755		26	1	37		10	1	30		13	1	37
Chaetacme aristata			0.155	0.261			4	19			3	18			4	19
Chrysophyllum albidum		0.008		0.022		8		15		3		10		4		15
Citropsis articulata				0.002				1				1				1
Clausena anisata		0.087	0.094	0.525		18	12	129		5	8	60		9	12	129
Clerodendron sp.		0.004				2				1				1		
Cola gigantea				0.002				2				2				2
Conopharyngia holstii		0.062	0.004	0.408		16	5	69		3	5	37		8	5	69
Croton macrostachyus			0.002				1				1				1	
Dasylepis eggelingii			0.001	0.005			1	1			1	1			1	1
Dichrostachys cinerea	0.047	0.030	0.016	0.061	13	10	3	4	3	4	3	4	7	5	3	4
Diospyros abyssinica		0.129	0.077	1.446		94	35	413		24	14	82		47	35	413
Dombeya mukole		0.017	0.120	3.368		4	15	65		2	12	43		2	15	65
Dombeya sp.		0.484	1.571			8	58			3	26			4	58	
Dovyalis macrocalyx		0.002	0.017	0.036		2	3	16		1	3	14		1	3	16
Dovyalis macrocarpa				0.005				2				2				2
Dovyalis sp.			0.005				1				1				1	
Dovyalis spinosissima				0.151				11				9				11
Elaeodendron buchananii		0.001		0.172		2		18		1		14		1		18
Entada abyssinica	1.084	0.164	0.247		7	2	11		4	1	6		4	1	11	
Erythrina abyssinica	1.515	0.952	0.130	0.438	19	24	6	5	6	6	5	5	10	12	6	5
Fagara angolensis		0.010				2				1				1		
Fagaropsis angolensis		0.131	0.027	0.255		60	4	39		18	3	31		30	4	39

Ficus asperifolia		0.005				4				2				2		
Ficus exasperata		0.002				2				1				1		
Flueggea virosa		9.718	0.298	0.727		92	25	40		22	20	29		46	25	40
Funtumia latifolia		0.003	0.003	0.145		2	3	9		1	2	8		1	3	9
Glyphaea brevis				0.001				1				1				1
Harrisonia abyssinica	0.024	0.342	0.592	0.237	7	58	66	15	3	23	34	13	4	29	66	15
Hoslundia opposita	0.755	0.219	2.588	0.183	91	46	271	29	17	18	76	17	49	23	271	29
Kigelia moosa			0.022	0.328			1	38			1	28			1	38
Lindackeria bukobensis		0.001		0.002		2		1		1		1		1		1
Lovoa swynnertonii				0.004				2				2				2
Maerua duchesnei			0.003				1				1				1	
Maesa lanceolata	1.120	1.750	0.007		187	202	1		17	27	1		101	101	1	
Markhamia platycalyx		0.047	0.070	0.011		8	13	1		3	3	1		4	13	1
Maytenus gracilipes		0.003	0.016	0.041		2	5	17		1	4	15		1	5	17
Maytenus undata				0.109				22				18				22
Millettia dura		0.213		0.830		46		28		6		10		23		28
Mimusops bagshawei				0.024				12				9				12
Monodora myristica			0.001	0.013			1	6			1	5			1	6
Morus lactea		0.003				2				1				1		
Ocimum suave			0.001	0.001			1	1			1	1			1	1
Olea welwitschii		0.394		2.645		8		24		3		19		4		24
Oncoba spinosa				0.038				4				4				4
Pancovia turbinata				0.001				1				1				1
Pavetta hymenophylla		0.003		0.005		2		6		1		5		1		6
Peddiea fischeri		0.011	0.005			8	3			4	3			4	3	
Piptadeniastrum africanum				0.018				2				2				2
Premna angolensis				0.053				4				4				4
Prunus africana				0.030				1				1				1
Pseudospondias microcarpa				0.003				1				1				1
Psychotria lauracea		0.020	0.013	0.226		24	12	54		9	8	35		12	12	54
Pterygota mildbraedii		0.273	0.237	0.028		8	54	9		4	14	9		4	54	9
Randia malleifera				0.013				8				8				8
Randia urcelliformis		0.005	0.013	0.012		4	3	8		2	3	7		2	3	8
Rhus natalensis			0.174				31				20				31	
Ritchiea albersii				0.002				1				1				1
Rytigynia beniensis				0.033				21				19				21
Sapium ellipticum			0.003	1.257			3	10			2	8			3	10
Spathodea campanulata		0.502	0.555			4	5			2	5			2	5	
Tabernaemontana ventricosa		0.070		0.088		40		23		13		23		20		23
Tetrapleura tetraptera				0.003				2				1				2

Table 2 continued

Species	Basal area				Density				Frequency				Number of stems			
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 1	Plot 2	Plot 3	Plot 4	Plot 1	Plot 2	Plot 3	Plot 4	Plot 1	Plot 2	Plot 3	Plot 4
Teclea nobilis		0.127	0.167	1.247		78	43	221		22	16	76		39	43	221
Treculia africana				0.002				3				3				3
Trichilia splendida				0.003				2				2				2
Trimelia grandifolia			0.001	0.060			1	4			1	4			1	4
Turraea floribunda				0.344				120				58				120
Uvariopsis congensis		0.071	0.011	0.074		60	13	36		19	8	28		30	13	36
Vangueria apiculata		0.004	0.028	0.075		2	2	18		1	2	16		1	2	18
Vernonia amygdalina		0.063	0.006			2	2			1	2			1	2	
Vernonia uriculifera			0.823				125				39				125	
Vitex amboniensis				0.009				3				3				3
Warburgia ugandensis		0.267	0.081	1.232		96	31	45		29	17	32		48	31	45
Total	5.307	28.71	13.40	19.76	441	1796	1203	2032					238	898	1203	2032

df = 3, $P < 0.001$). The proportion of basal area contributed by climax species was also positively related to the duration of fire exclusion but was not significant ($r_s = +0.800$, df = 3, $P = 0.1$).

I grouped species that were restricted to different types of forests (e.g. forest interior, forest generalist and forest edge; Table 3) as forest dependent species. I classified facultative forest inhabitants and those found in open habitats as forest non-dependent species. The proportion of forest dependent species in a plot was significantly correlated with duration of fire exclusion ($r_s = +1.0$, df = 3, $P < 0.001$). The relationship between the proportion of basal area contributed by forest dependent species and the duration of protection from fire was also positive, but was non-significant ($r_s = +0.800$, df = 3, $P = 0.1$).

Size-class distribution of selected species

I plotted the size-class distribution of potentially tall trees (at maturity) for all species represented by at least 100 stems in all four plots combined. These included one wind dispersed species, *A. grandibracteata*, and three animal dispersed species, *D. abyssinica*, *C. africana* and *W. ugandensis* (stand curves can be requested from the author). In general the stand curves for *A. grandibracteata* were an inverted J-curve in all plots but the species was represented very poorly in plot 1 (recently burnt) and plot 4 (tending towards mature forest). *Diospyros abyssinica* was totally absent in plot 1. It was represented by the two and three smallest size classes in plots 2 and 3, respectively. The species was very abundant in plot 4 but 98% (405 trees) of the trees were less than 17.5 cm d.b.h. The largest tree was only 28.7 cm d.b.h. Like *D. abyssinica*, *W. ugandensis* was absent from plot 1 and represented by the three smallest size classes in plots 2 and 3. In plot 4, the three smallest size classes accounted for 75% (34 trees) of the trees. The largest tree in the plot was 59.2 cm d.b.h. The paucity of *C. africana* trees in plots 1, 2 and 3 renders the interpretation of the stand curves difficult. The species was represented by a single tree in plot 1 and by two individuals in plots 2 and 3. The stand curve in plot 4 was an inverted J- curve and the largest tree was 17.7 cm d.b.h.

The impact of fire on forest succession

Forty-one trees belonging to six species: *Acacia hockii*, *Albizia grandibracteata*, *Dichrostachys cinerea*, *Flueggea*

Table 3 Combined list of species encountered in all study plots showing growth form, and ecological guilds, mode of seed dispersal and habitat affinity

Species	Growth form	Dispersal	Habitat aff	Eco type
Acacia hockii	S/ST	Wind	Oh	Pioneer
Aeglopsis eggelingii	S/ST	Animal	Fg	Climax
Albizia coriaria	TT	Wind	Fn	Pioneer
Albizia grandibracteata	TT	Wind	Fn	Pioneer
Aningeria altissima	TT	Animal	Fg	Climax
Antiaris toxicaria	TT	Animal	Fn	Climax
Balanites wilsoniana	TT	Animal	F	Climax
Bequaertiodendron oblancelatum	ST	Animal	F	Climax
Bersama abyssinica	ST	Animal	Fn	Climax
Blighia unijugata	ST/TT	Animal	Fg	Climax
Bosquiea phoberos	TT	Animal	Fg	Climax
Bridelia micrantha	S/ST	Animal	Fn	Pioneer
Cassipourea ruwensorensis	ST	Animal	F	Climax
Celtis africana	TT	Animal	Fg	Climax
Celtis durandii	TT	Animal	F	Climax
Chaetacme aristata	S/ST	Animal	Fg	Climax
Chrysophyllum albidum	TT	Animal	F	Climax
Citropsis articulata	S/ST	Animal	F	Climax
Clausena anisata	S/ST	Animal	Fn	Climax
Clerodendron sp.	S	Ud	Ud	Ud
Cola gigantea	TT	Animal	F	Climax
Conopharyngia holstii	ST	Animal	F	Climax
Croton macrostachyus	S/ST	Animal	Fn	Pioneer
Dasylepis eggelingii	S/ST	Animal	Fn	Climax
Dichrostachys cinerea	ST	Self	Oh	Pioneer
Diospyros abyssinica	TT	Animal	F	Climax
Dombeya mukole	ST	Self	fe	Pioneer
Dombeya sp.	S/ST	Self	fe	Pioneer
Dovyalis macrocalyx	S	Animal	fe	Climax
Dovyalis macrocarpa	S	Animal	fe	Climax
Dovyalis sp.	S	Animal	Fn	Climax
Dovyalis spinosissima	S/ST	Animal	Fn	Climax
Elaeodendron buchananii	ST/TT	Animal	F	Climax
Entada abyssinica	ST	Wind	Oh	Pioneer
Erythrina abyssinica	ST	Self	Oh	Pioneer
Fagara angolensis	TT	Animal	F	Climax
Fagaropsis angolensis	TT	Animal	Fg	Climax
Ficus asperifolia	S	Animal	Fn	Climax
Ficus exasperata	TT	Animal	Fn	Pioneer
Flueggea virosa	S/ST	Animal	Fn	Pioneer
Funtumia latifolia	TT	Wind	F	Climax
Glyphaea brevis	S/ST	Animal	Fg	Climax
Harrisonia abyssinica	ST	Animal	Fn	Climax
Hoslundia opposita	S	Animal	Fn	Pioneer
Kigelia moosa	ST	Animal	Fn	Climax
Lindackeria bukobensis	ST	Animal	Fn	Climax
Lovoa swynnertonii	TT	Wind	F	Climax
Maerua duchesnei?	ST	Animal	Fg	Ud
Maesa lanceolata	S/ST	Animal	Fn	Pioneer
Markhamia platycalyx	ST	Wind	Fn	Pioneer
Maytenus gracilipes	S	Animal	fe	Climax

Table 3 continued

Species	Growth form	Dispersal	Habitat aff	Eco type
Maytenus undata	ST	Animal	fe	Climax
Millettia dura	S/ST	Self	fe	Climax
Mimusops bagshawei	TT	Animal	F	Climax
Monodora myristica	TT	Animal	F	Climax
Morus lactea	TT	Animal	F	Climax
Ocimum suave	S	Ud	Oh	Pioneer
Olea welwitschii	TT	Animal	Fg	Climax
Oncoba spinosa	S/ST	Animal	Fn	Climax
Pancovia turbinata	ST	Animal	F	Climax
Pavetta hymenophylla	S	Animal	F	Climax
Peddiea fischeri	S/ST	Animal	Fn	Climax
Piptadeniastrum africanum	TT	Wind	Fg	Climax
Premna angolensis	ST	Animal	fe	Climax
Prunus africana	TT	Animal	Fg	Climax
Pseudospondias microcarpa	TT	Animal	Fg	Climax
Psychotria lauracea	S	Animal	F	Climax
Pterygota mildbraedii	TT	Wind	fe	Climax
Randia malleifera	S/ST	Animal	F	Climax
Randia urcelliformis	S/ST	Animal	F	Climax
Rhus natalensis	S/ST	Animal	Fn	Pioneer
Ritchiea albersii	S/ST	Ud	Fg	Ud
Rytigynia beniensis	S	Animal	fe	Climax
Sapium ellipticum	ST/TT	Animal	Fn	Pioneer
Spathodea campanulata	ST	Wind	Fg	Pioneer
Tabernaemontana ventricosa	ST	Animal	F	Climax
Teclea nobilis	ST	Animal	Fn	Climax
Tetrapleura tetraptera	TT	Animal	F	Climax
Treculia africana	TT	Animal	Fg	Climax
Trichilia splendida	TT	Animal	F	Climax
Trimelia grandifolia	ST	Animal	Fn	Ud
Turraea floribunda	ST	Animal	fe	Climax
Uvariopsis congensis	ST	Animal	F	Climax
Vangueria apiculata	S/ST	Animal	fe	Climax
Vernonia amygdalina	S/ST	Wind	Fn	Pioneer
Vernonia uriculifera	S/ST	Wind	Fn	Pioneer
Vitex amboniensis	ST	Animal	F	Climax
Warburgia ugandensis	TT	Animal	F	Climax

S = shrub, ST = short tree, TT = tall tree; Oh = open habitat, Fg = forest generalist, Fn = forest non-dependent, fe = forest edge, F = forest interior, ud = undetermined.

virosa, *Maesa lanceolata* and one unidentified, were killed by fire in plot 1. The diameter of the dead trees at breast height ranged from 2.5 to 18.8 cm.

Discussion

Results from this study strongly suggest that the re-establishment of tropical rain forests on formerly deforested land is possible without human intervention. As McClanahan & Wolfe (1993) noted, artificial attempts to restore deforested lands to their original high diversity ecosystem are expensive and labour intensive and may fail. Artificial forest restoration (for carbon dioxide sequestration) in areas of Kibale National Park formerly occupied by agricultural encroachers (Kuper, 1996) has been costly and has had little success. Afforestation programmes using indigenous tropical forest trees generally fail because of ignorance about the basic biology of most

Table 4 (a) Results of paired *t*-tests comparing differences between number of stems animal and nonanimal dispersed species in the four study plots

	Mean number of stems				
Plot number	Animal dispersed	Non-animal dispersed	*t*-values	df	Significance
1	2.8704	1.537	1.68	53	ns
2	10.04	7.90	2.22	49	$P < 0.1$
3	6.52	5.50	1.82	99	ns
4	18.44	1.86	17.43	99	$P < 0.001$

(b) Results of paired *t*-tests comparing differences between basal areas of animal and nonanimal dispersed species in the four study plots

	Mean basal area				
Plot number	Animal dispersed	Non-animal dispersed	*t*-values	df	Significance
1	0.019	0.0341	−1.71	53	ns
2	0.138	0.1490	−0.15	49	ns
3	0.0483	0.0857	−3.14	99	$P < 0.01$
4	0.1405	0.0570	5.32	99	$P < 0.001$

of these species (Hubbell & Foster, 1992; Condit *et al.*, 1993a,b; Korning & Balslev, 1994). The site-matching technique used in the Kibale reforestation programme (Kuper, 1996) ignored some important ecological principles and this may explain its low success rate. Reforestation programmes need to recognize that succession is a community-controlled process (Odum, 1969) and that seed-germination requirements and tolerances (Lebrón, 1980) are important determinants of the new vegetation. Furthermore, environmental requirements vary among plant species. This particularly applies to light requirements, which can also vary with age (Fox, 1976). Fifty-six (77%) of the species recorded here were forest dependent species (Table 3) that established without human assistance. Therefore, given our limited knowledge of the complex nature of forest succession and inadequate funding, the most appropriate and lowest cost method of restoring deforested lands is to allow natural succession. Manual planting should be limited to severely degraded lands prone to soil erosion in the absence of vegetation cover.

Studies at Kanyawara, about 12 km north-west of Ngogo, but in the same continuous forest, suggest that forest regeneration following large scale disturbance due to logging is slow or arrested (Chapman & Chapman, 1997; Chapman *et al.*, 1999). The vegetation in Kibale may not be adapted to sustain disturbance on this scale, perhaps because natural large scale disturbance like earthquakes, hurricanes and forest fires have been rare (Chapman *et al.*, 1999). However, the results given here indicate that the forest can colonize pyrogenic grasslands derived from slash and burn agriculture, close to mature forest. Such conditions seem to enhance the regeneration of some forest tree species. At Kanyawara, Struhsaker *et al.* (1989) found no poles (7–14 cm d.b.h) of five species (*Aningeria altissima*, *Celtis africana*, *Lovoa swynnertonii*, *Mimusops bagshawei* and *Newtonia buchananii*) in the mature forest. In the present study, poles of *C. africana* were fairly abundant in some study plots, suggesting that the species is adapted to regenerating in colonizing forests. Other forest species that appear to benefit from similar conditions include *Diospyros abyssinica*, *Warburgia ugandensis Fagaropsis angolensis* and *Olea welwitschii*. Although extensive 'carpets' of *D. abyssinica* seedlings cover the floor of the mature forest soon after the fruiting season, saplings and poles are extremely rare. Saplings were abundant in plots 2, 3 and 4 (Table 2), suggesting that the species establishes better in forests colonizing former grasslands. Occasionally, saplings and poles of *W. ugandensis* are found in large gaps at Ngogo, but these occur at much higher densities in former grasslands such as plots 2, 3 and 4 (Table 2). Some *W. ugandensis* trees in plot 4 were fairly large (up to 59.2 cm d.b.h), but were not mature. *Warburgia ugandensis* appears to grow quickly; two individuals planted from seedlings at Ngogo camp by T.M. Butynski in 1981 have attained diameters of 37.5 and 52.5 cm in 19 years.

Small scale farming was recommended as a management tool for maintaining habitat diversity in Tiwai Forest (Oates, 1999); unfortunately, due to the political instability in Sierra Leone, the conservation project at Tiwai was terminated before any lessons could be learned on the implementation and benefits of small scale farming in forest conservation.

Results reported here suggest that disturbance by slash and burn agriculture has helped to rejuvenate the forest and maintain species diversity. The destructive activities of African megafauna might also have had such effects Kortlandt (1985). These possibilities are concordant with the current thinking that large scale disturbances are critical to the dynamics of ecosystems (Boucher, 1990).

The role of animal dispersal agents in forest succession

The results show that animals can provide a cheap means of restoring vegetation on deforested lands provided seed sources are available in their home ranges. The stem density of animal dispersed plant species was significantly higher than that of their non-animal dispersed counterparts in plots 2 and 4. The mere presence of animal dispersed plant species in plots 1 and 3 also suggest that animals contribute towards forest succession by dispersing seeds in grasslands. Soil seed banks are one possible source of propagules for the re-vegetation of disturbed areas (Ewel, 1980; Whitmore, 1998). The animal dispersed trees found in the study plots were certainly not from seed banks; these areas had been grasslands for a long time and were frequently burned. Furthermore, some of the species involved (e.g. *Balanites wilsoniana, Diospyros abyssinica, Chrysophyllum albidum, Uvariopsis congensis*, etc.) are large seeded species that require animal dispersal and have recalcitrant seeds that cannot persist long in the soil.

Large frugivores such as chimpanzees and baboons are important seed dispersers in Kibale (Wrangham, Chapman & Chapman, 1994). In addition to other seed dispersers such as elephants, hornbills and civets, these two species are common at Ngogo. Chimpanzees and baboons forage or travel in grasslands and thickets where they inadvertently disperse seeds. Saplings of *C. albidum, U. congensis* and *W. ugandensis* in the plots were typically associated with clusters of suppressed seedlings/saplings of the same species, suggesting that the seeds were deposited in a lump. Baboons and chimpanzees typically defecate seeds in large clusters. Other frugivorous primates: mangabeys, redtails and blue monkeys, also used the study plots. Although some monkeys and chimpanzees are known to eat small seeded fruits such as *F. virosa* and *M. lanceolata*, birds appear to be the major dispersers of these small seeded species with fleshy fruits.

Elephants are also important long-distance seed dispersers in Kibale. They eat a large variety of fruits and range widely. In Kibale, elephants are the sole dispersers of the large (88 mm long) seeds of *Balanites wilsoniana* (Ghiglieri *et al.*, 1982; Chapman, Chapman & Wrangham, 1992). This species was fairly conspicuous in plot 4 (Table 2), indicating that elephants had a role in re-vegetation there.

The role of fire in forest succession

Fire is an important factor in inhibiting forest succession in the grasslands of Kibale National Park (Kuper, 1996). The proportion of stems of climax species in an area was closely related to the duration of fire exclusion. In plot 1, fire killed 41 trees, some larger than 10 cm d.b.h. Fire both reduces tree cover and potentially curtails the further input of seeds from elsewhere. Trees in open areas provide perches for avian seed dispersers (Robinson & Handel, 1993 and McClanahan & Wolfe, 1993). Some of the trees that were killed by fire (e.g. *M. lanceolata*) produce fruit edible to monkeys and birds. Besides contributing to the seed rain of the area being recolonized, such trees also attract frugivores that bring in more seeds, thus increasing the species richness. By removing the tree cover that colonizing tree species provide, fire delays or even prevents the establishment of shade tolerant species.

In summary, this study suggests that the forest is capable of recolonizing grasslands without human intervention, provided that seed sources and dispersers are available; that some forest tree species are better suited to colonizing pyrogenic grasslands close to mature forest; and that fire is the most important factor hindering forest succession in grasslands.

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