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# Seedling regeneration, environment and management in a semi-deciduous African tropical rain forest

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## Abstract

**Questions:** How is seedling regeneration of woody species of semi-deciduous rain forests affected by (a) historical management for combinations of logging, arboricide treatment or no treatment, (b) forest community type and (c) environmental gradients of topography, light and soil nutrients?

**Location:** Budongo Forest Reserve, Uganda.

**Methods:** Seedling regeneration patterns of trees and shrubs in relation to environmental factors and historical management types were studied using 32 0.5-ha plots laid out in transects along a topographic gradient. We compared seedling species diversity, composition and distribution patterns along topographic gradients and within types of historical management regimes and forest communities to test whether environmental factors contributed to differences in species composition of seedlings.

**Results:** A total of 85 624 woody seedlings representing 237 species and 46 families were recorded in this rain forest. *Cynometra alexandri* C.H. Wright and *Lasiodiscus mildbraedii* Engl. had high seedling densities and were widely distributed throughout the plots. The most species-rich families were Euphorbiaceae, Fabaceae, Rubiaceae, Meliaceae, Moraceae and Rutaceae. Only total seedling density was significantly different between sites with different historical management, with densities highest in logged, intermediate in logged/arboricided and lowest in the nature reserve. Forest communities differed significantly in terms of seedling diversity and density. Seedling composition differed significantly between transects and forest communities, but not between topographic positions or historical management types. Both Chao-Jaccard and Chao-Sørensen abundance-based similarity estimators were relatively high in the plot, forest community and in terms of historical management levels, corroborating the lack of significant differences in species richness within these groups. The measured environmental variables explained 59.4% of variance in seedling species distributions, with the three most important being soil organic matter, total soil titanium and leaf area index (LAI). Total seedling density was positively correlated with LAI. Differences in diversity of $>2.0$ cm dbh plants (juveniles and adults) also explained variations in seedling species diversity.

**Conclusions:** The seedling bank is the major route for regeneration in this semi-deciduous tropical rain forest, with the wide distribution of many species suggesting that these species regenerate continuously. Seedling diversity, density and distribution are largely a function of adult diversity, historical management type and environmental gradients in factors such as soil nutrient content and LAI. The species richness of seedlings was higher in soils both rich in titanium and with low exchangeable cations, as well as in logged areas that were more open and had a low LAI.

**Keywords:** Albertine rift ecoregion; Analysis of similarity; Chao's Similarity estimators; Continuous regeneration; Ecological resilience; Leaf area index.

**Nomenclature:** Polhill (1952 et seq.), Hamilton (1991).

**Abbreviations:** ANOSIM = Analysis of similarity; CAP = Community analysis package; CCA = Canonical correspondence analysis; dbh = Diameter at 1.3 m; LAI = Leaf area index, NFA = National Forestry Authority, SIMPER = SIMilarity PERcentages.

## Introduction

Sustainable management for timber and other wood products in most African tropical rain forests and woodlands relies on natural regeneration through seedling establishment and resprouting from cut stumps (Peters 1994; Luoga et al. 2002, 2004; Wilson & Witkowski 2003; Neke et al. 2006; Mwavu & Witkowski 2008a). Hence, understanding the natural regeneration processes and dynamics of tree and shrub species has practical applications in sustainable management and in restoration of habitats (Peters 1994; Witkowski & Garner 2000; Botha et al. 2004). Studies on natural regeneration and seedling ecology can provide options for forest development through improvements in recruitment, establishment and growth of desired seedling species (e.g. Whitmore 1996; Teketay 1997; Kyereth et al. 1999). Indeed, determining seedling species diversity, richness and distribution, and how these relate to environmental factors, can help guide the sustainable management of African tropical rain forests, which are important for their economic, conservation and environmental benefits.

While there have been many studies of forest seedling regeneration in tropical and temperate forests (Dalling et al. 1998a; Nathan & Muller-Landau 2000; Wright et al. 2005; Comita et al. 2007), few studies have been undertaken in semi-deciduous tropical forests, particularly in the Albertine Rift Ecoregion of Africa. The Albertine Rift Ecoregion, which includes the Budongo Forest Reserve, is one of Africa's most species-rich and endemic regions in the world (Cordeiro et al. 2007; Plumptre et al. 2007). The Budongo Forest is recognised for both its timber (Sheil 1996) and wildlife conservation value (Plumptre & Reynolds 1994). Over the years, management of this reserve for timber has relied on natural regeneration; tree planting, which was not successful, was abandoned in the 1950s (Philip 1965). Although several studies have been undertaken on seedling regeneration of tree species in Budongo Forest, most have focused on life history and monitoring of mahogany species, which are the key timber species (Sheil 1996; Mwima et al. 2001). There have also been studies on the phenology, population structure and regeneration of tree species that are both timber and primate food sources (Plumptre 1995; Tweheyo & Babweteera 2007; Mwavu & Witkowski 2009).

Despite these studies, little is known about patterns of seedling regeneration for a wide range of other important multiple-use woody species. With the increasing human population, demand for wood products, loss of woodlands in areas surrounding BFR (Mwavu & Witkowski 2008b) and diminishing stocks of species of African mahogany [e.g. *Khaya anthotheca* (Welw.) C.DC., *Entandrophragma* spp.], many more tree species in Budongo Forest Reserve are increasingly being exploited for timber and domestic needs. A large number of timber tree species [e.g. *Antiaris toxicaria* (Pers.) Lesch., *Chrysophyllum* sp., *Pouteria altissima* (A. Chiev) Aubrev. & Pellgr, *Celtis mildbraedii* Engl.] produce fruits that are eaten by primates but, increasingly, more of these species are being used for timber (Plumptre 1995; Tweheyo 2003) and fuelwood. The increased human use pressure and conservation concerns necessitate strengthening of the ecological basis for sustainable management of this forest (Guariguata 2000). Hence, understanding seedling regeneration patterns in these forests is vital for the conservation of important constituent woody species and ecosystems. Environmental factors such as light, temperature and disturbance regimes influence natural regeneration (Herrera et al. 1994; Barnes et al. 1998; Mwima et al. 2001) and can guide conservation efforts. For example, the amount of light that reaches lower canopy layers influences conditions for plant recruitment, growth and reproduction, thus affecting community composition (Kotowski & van Diggelen 2004).

We describe patterns of woody seedling regeneration (diversity, density and distribution) in relation to environmental factors, forest communities and historical management types. We tested the following hypotheses: (1) seedling species diversity, richness and density are related to topographic gradients, forest community and historical management type, and (2) variations in seedling distribution in this semi-deciduous tropical rain forest are related to environmental gradients (e.g. light and soil nutrients).

## Methods

### *Study area*

The Budongo Forest Reserve is located on the escarpment east of Lake Albert on the edge of the Western Rift Valley (Howard 1991) in northwestern Uganda. The reserve has an area of about 793 km$^2$ and lies between 1°37′-2°03′N and 31°22′-31°45′E (Fig. 1). The Budongo Forest Reserve was designated as a Central Forest Reserve (CFR) in 1932 (Eggeling 1947). The altitudinal range of the area is 700-1270 m asl, with a mean of about 1050 m, and terrain is gently undulating. Most slopes are gradual and interspersed with rounded ridges (Eggeling 1947). The climate is tropical with two rainfall peaks, from March to May and September to November. The mean annual rainfall is 1500 mm with monthly mean rainfall of $138.5 \pm 66.7$ mm. Dry

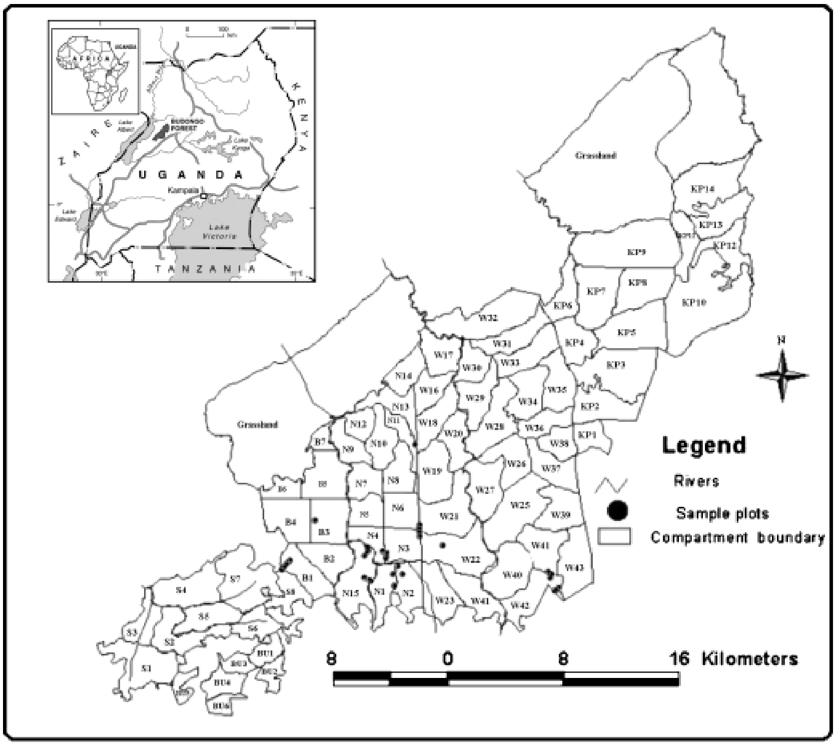


**Fig. 1.** Location (inset) and map of Budongo Forest Reserve, Masindi District, Uganda, showing all management compartments. N, Nyakafunjo; S, Siba; B, Biiso; W, Waibira; KP, Kaniyo Pabidi are the constituent blocks that were further sub-divided and numerically numbered (e.g. N1-N15).

seasons occur from June to August and December to February. Like all equatorial climates, the area is characterised by high temperatures with little daily variation. Maximum temperature recorded in a 24-h period rarely exceeds 32°C and occasionally drops below 24°C (Tweheyo 2003).

All Uganda's natural forest reserves, including the Budongo Forest Reserve, are managed by the National Forest Authority (NFA), which is a central government agency that manages forests and woodlands for economic, conservation and environmental benefits (MWLE 2001). Hence, in Budongo Forest, the three major historical management types are: logged only, both logged and arboricided, and nature reserve (i.e. a control that is not logged or arboricided). Most of the forest compartments have been treated with arboricides and logged at least once, except for a few that from the onset were managed as nature reserves. In some areas, selective logging (both mechanical and pit sawing) has been allowed; in nature reserve areas, logging and any other form of harvesting activity are strictly prohibited. In terms of vegetation characteristics, the Budongo Forest has been broadly classified as a medium altitude, semi-deciduous, moist tropical rain forest because several of the dominant species (e.g. *Celtis* spp., *Maesopsis eminii* Engl., *Ficus* spp.) lose most of their leaves during the dry season (Eggeling 1947; Langdale-Brown et al. 1964), with the exception of the shade-tolerant *Cynometra alexandri* C.H. Wright (Sheil 1997). The deciduous habit is most noticeable during the two dry seasons of the year. The forest is a mosaic of forest types (Mwavu et al. 2008) as a result of forest dynamics, management history (Eggeling 1947; Plumptre 1996) and environmental differences (Mwavu et al. 2008). Generally, the soils are deep with little differentiation into clearly defined horizons, and possess a fine granular structure moulded into larger weakly coherent clods that are friable and porous (Eggeling 1947).

*Sampling procedure and data collection*

Within the forest, we identified areas that had been subjected to (1) logging and arboricide treatment (hereafter referred to as logged/arboricided), (2) logging alone (logged only) and (3) those without logging or arboricide treatment (nature reserve), so that all of the major historical management types in this forest were included in the study (Fig. 1). In each historical management type, at least two transects were established along topographic gradients, each providing at least three topographic positions: lower-slope (swamp/riparian), mid-slope, upper-slope and flat/ridge-top positions. Plots of $50 \times 100$ m (0.5 ha) separated by at least 150 m were laid within each available topographic position. Each 0.5-ha plot was further divided into five $20 \times 50$ m contiguous sub-plots, and all tree and shrub (hereafter referred to as "woody plants") seedlings were counted and recorded by species in each sub-plot. As defined for this study, a seedling is a woody individual of $<2.0$ cm dbh and $\leq 1.0$ m high. A total of 32 plots were laid out in the nature reserve, logged/arboricided and logged only areas (6, 19 and 7 plots, respectively). The number of plots per historical management type was related to the corresponding size of the area in the forest. For species that could not be identified in the field, voucher specimens were collected, pressed and subsequently identified at the Botany Department Herbarium, Makerere University (MHU), Kampala, Uganda.

### *Measurement of environmental variables*

#### ***Soil nutrient status***

Soil cores were collected at a depth of 0-15 cm with a soil auger (2-cm diameter) from ten random locations per 0.5-ha plot. Cores were bulked, thoroughly mixed, sub-sampled, air-dried, cleaned of stones and roots fragments and then passed successively through 20- and 2-mm sieves. Soil organic matter, pH and total N were determined using the standard methods in Nelson & Sommers (1982), McLean (1982) and Bremner & Mulvaney (1982), respectively. Elemental constituents (Ca, Mg, Na, P, Li, Si, Ti and Fe) were determined using X-ray fluorescence spectrometry (XRF: Feather & Willis 1976; Thomsen 2002) in the School of GeoSciences, University of Witwatersrand, Johannesburg, South Africa.

#### ***Light availability under the tree canopy***

Light availability under the tree canopy was indirectly measured as leaf area index (LAI) using the LAI-2000 Plant Canopy Analyser (Li-Cor, Lincoln, NE, USA) at 1.0 m above ground level at five random points in each 0.5-ha plot during the growing/rainy season after the trees had regained their full leaf cover. All measurements were taken within 1.5 h of solar noon (i.e. when the sun is close to the zenith in the tropics), while the sky was uniformly overcast, light level was most stable and the contribution of leaf angle to light diffusion was changing as slowly as possible.

### *Data analyses*

#### ***Seedling species diversity and distribution patterns***

Species richness (S) and the Shannon-Wiener index of diversity ($H'$) were computed to quantify and characterise the species diversity patterns of woody seedlings (Magurran 2004) at the 0.5-ha scale. Both diversity metrics were calculated using the Species Diversity and Richness (SDR)® version IV software (Seaby & Henderson 2006).

Differences in seedling density, species richness and diversity in response to (a) historical management type, (b) forest community type (and the interaction between "a" and "b") and (c) topographic position along a transect (bottomland/swamp versus all "upland" slope positions) were compared using a nested ANOVA. The main effects tested were historical management type, forest community type and the interaction between these two factors, with topographic position nested within forest community type. Because all of the comparisons were unbalanced, type III sums of squares were used (SAS® version 8.0; SAS Institute Inc. 2004). Since, for species diversity and richness, none of the interactions were significant ($P > 0.05$), one-way ANOVAs and Tukey multiple comparisons tests were also computed.

To test whether there were significant variations in seedling species composition between *a priori* groupings of plots, ANOSIM (ANalysis Of SIMilarity), a randomization permutation test in the Community Analysis Package (CAP)® 3.1 (Seaby et al. 2006), was also employed. For this analysis, the sample plots were categorised in four different groupings, transect, topographic position, forest community and historical management type. The test statistic ($R_{ANOSIM}$) values generated by CAP 3.1 are relative measures of separation of *a priori* defined groups. Zero (0) indicates that there is no difference among groups, while one (1) indicates that all samples within groups are more similar to one another than to any samples from other groups. A randomization process was used to find the probability of gaining particular values of $R_{ANOSIM}$ by chance. Where a significant difference ($P < 0.05$) was detected, a SIMilarity PERcentage (SIMPER; Clarke 1993) analysis was conducted to determine which species were primarily responsible for the observed difference or similarity (i.e. the species made up 90% of the difference or similarity between or within each group). Chao's abundance-based Jaccard and Sørensen similarity estimators (Chao et al. 2005, 2006) were also computed for the (a) plot, (b) historical management and (c) forest community levels employing EstimateS® Version 8.0 (Colwell 2006).

### *Ordination*

To examine seedling densities and distribution along environmental gradients, a canonical correspondence analysis (CCA) ordination using CANOCO® version 4.5 (ter Braak & Šmilauer 2003) was used. Soil elemental concentrations were log-transformed. The environmental variables were soil nutrients (Ca, Mg, Na, P, Li, Si, Ti, Fe, N), pH, organic matter, historical management type and LAI. The species diversity (Fisher's α-diversity) for individuals with dbh > 2.0 cm (i.e. juvenile and adult trees; Mwavu et al. 2008) was also included as a supplementary environmental variable. A Monte Carlo re-randomisation procedure, with 499 permutations under the reduced model, was used to test the significance of the first canonical axis and then the combination of the first four canonical axes, as a direct test of whether the included environmental variables had a significant effect on variation in species composition. The CCA intra-set correlations (i.e. correlations between environmental variables and ordination axes) were used to infer the relative importance of each environmental variable in predicting species composition (ter Braak 1995). The relationship between seedling densities and LAI at the 0.5-ha plot level was further tested using Spearman rank-order (non-parametric) correlations (Dytham 2003).

## Results

### *Seedling species diversity and distribution patterns*

A total of 85 624 seedlings representing 237 species and 46 families were recorded in the survey. The most species-rich families were Euphorbiaceae, Fabaceae, Rubiaceae, Meliaceae, Moraceae and Rutaceae (24, 21, 19, 17, 15 and 14 species, respectively; Appendix S1). Plots varied in species richness of seedlings (26 to 88 species), Shannon-Weiner diversity (H′; 1.46 to 3.54) and density (824 to 18 710 seedlings $ha^{-1}$). At the total forest level, the seedling population was dominated by *Cynometra alexandri* (0.09 individuals $m^{-2}$) and *Lasiodiscus mildbraedii* (0.08 individuals $m^{-2}$). Among the 237 species, 70 (29.5%) were rare, with only two to ten individuals, while 28 (11.8%) were very rare, with only one individual recorded. However, 45 tree and shrub species with hundreds of individuals per plot were found in more than 62.5% of the plots (Appendix S1). The most frequent species were *Chrysophyllum albidum* ($n = 32$, 100%), *Celtis zenkeri* (93.8%), *C. alexandri* (90.6%), *Acalypha neptunica* ($n = 29$, 90.6%) and *Teclea nobilis* (90.6% of the plots). *Lasiodiscus mildbraedii* and *Raphia farinifera* seedlings were usually found clumped around adult trees.

Nested ANOVA showed that only forest community type had an effect on diversity and density. Seedling density was only significantly related to topographic position nested within forest community (Table 1). One-way ANOVA revealed that differences in seedling density ($F_{3,28} = 5.55$, $P = 0.004$) and diversity ($F_{3,28} = 5.00$, $P = 0.006$) for forest communities were significant (Table 2). For historical management types, total seedling densities were higher in logged sites compared to the logged/arboricided and untreated nature reserve sites (Table 2). In contrast, species diversity ($F_{3,28} = 0.75$, $P = 0.49$) and richness ($F_{3,28} = 0.41$, $P = 0.67$) were not significantly different between historical management types (Table 2).

Seedling species composition differed among transects (Global $R_{ANOSIM} = 0.284$, $P = 0.001$), suggesting that plots within transects were more similar than would be expected by chance. Of the 36 transect pair-wise ANOSIM comparisons, 19 were significant, with each pair having a $R_{ANOSIM} > 0.33$ and $P < 0.05$. However, differences were more marked ($R_{ANOSIM} = 1$, $P = 0.029$, average dissimilarity $> 85.0$) for pair-wise tests between two transects within forests dominated by either *Cynometra alexandri* (logged only) or *Khaya anthotheca*. These two forest communities were geographically distant from each other, with one in the eastern and other in the western part of the Budongo Forest Reserve. The species composition of seedlings did not differ between topographic positions (Global $R_{ANOSIM} = -0.02$, $P = 0.602$). Comparing historical management types, the overall ANOSIM showed no significant difference in species composition between groups (Global $R_{ANOSIM} = 0.004$, $P = 0.46$), but the pair-wise comparison between logged only and nature reserve sites were significantly different ($R_{ANOSIM} = 0.354$, $P = 0.001$, average dissimilarity = 64.2%). These results corroborate those of the nested ANOVA diversity analysis (Table 1). The individual species contributing most to significant dissimilarity between logged

**Table 1.** Nested ANOVA examining the variation in seedling alpha-diversity (H′), richness and density of woody plants among historical management types, forest communities and topographic positions (bottomland/swamp versus all upland slope positions) in Budongo Forest Reserve, NW Uganda. *P*-values in bold are significantly different ($P < 0.05$).

| | *df* | SS | MS | *F* | *P*-value |
|---|---|---|---|---|---|
| *Diversity (H′)* | | | | | |
| Historical management type (HMT) | 2 | 0.31 | 0.15 | 0.75 | 0.484 |
| Forest Communities (FC) | 3 | 3.16 | 1.05 | 5.13 | **0.007** |
| HMT∗FC | 1 | 0.11 | 0.11 | 0.53 | 0.475 |
| Topographic position (nested within FC) | 1 | 0.204 | 0.20 | 0.99 | 0.329 |
| *Richness* | | | | | |
| Historical management type (HMT) | 2 | 349.3 | 174.7 | 0.61 | 0.553 |
| Forest Communities (FC) | 3 | 1318.4 | 439.5 | 1.53 | 0.233 |
| HMT∗FC | 1 | 24.3 | 24.3 | 0.08 | 0.770 |
| Topographic position (nested within FC) | 1 | 90.8 | 90.8 | 0.32 | 0.580 |
| *Density* | | | | | |
| Historical management type (HMT) | 2 | 94 80 830 | 47 40 414 | 0.64 | 0.536 |
| Forest Communities (FC) | 3 | 95 03 4798 | 31 67 8266 | 4.28 | **0.015** |
| HMT∗FC | 1 | 35 940 | 35 940 | 0.00 | 0.945 |
| Topographic position (nested within FC) | 1 | 535 6 8776 | 53 56 8776 | 7.24 | **0.013** |

**Table 2.** Means ± SD of woody seedlings density, alpha-diversity (H′) and species richness for sites with different historical management and forest community types in Budongo Forest Reserve, NW Uganda. Different letters for groups under historical management practice type and forest community type in each column indicate significant differences between the groups based on Tukey analysis ($P < 0.05$).

| Grouping | Seedlings (mean ± SD) | | |
|---|---|---|---|
| | Density | Species richness | Diversity (H′) |
| Historical management type | | | |
| *Logged/arboricided* | 5034.13 ± 2871.2$^{a}$ | 60.3 ± 17.6$^{a}$ | 2.782 ± 0.47$^{a}$ |
| *Logged only* | 8884.33 ± 4965.7$^{b}$ | 63.5 ± 15.8$^{a}$ | 2.524 ± 0.34$^{a}$ |
| *Nature Reserve* | 3924.67 ± 1593.7$^{a}$ | 67.5 ± 16.1$^{a}$ | 2.818 ± 0.62$^{a}$ |
| Forest Community type | | | |
| *Pseudospondias microcarpa* swamp | 3065.7 ± 1670.2$^{a}$ | 71.7 ± 12.3$^{b}$ | 3.17 ± 0.25$^{a}$ |
| *Funtumia elastica–Pouteria altissima* | 3176.0 ± 2025.0$^{a}$ | 67.4 ± 19.1$^{b}$ | 3.03 ± 0.71$^{a,b}$ |
| *Lasiodiscus mildbraedii–Khaya anthotheca* | 5947.4 ± 2588.4$^{a,b}$ | 54.4 ± 16.6$^{b}$ | 2.47 ± 0.36$^{b}$ |
| *Cynometra alexandri–Rinorea ilicifolia* | 8884.3 ± 4965.7$^{b}$ | 63.5 ± 15.8$^{b}$ | 2.52 ± 0.34$^{a,b}$ |

only and nature reserve sites were *Lasiodiscus mildbraedii* and *Argomuellera macrophylla* (Table 3). SIMPER analysis of dissimilarity between the historical management types of logged only and nature reserve showed that 20 families, represented by 38 species, made up 90.3% of the observed differences in these communities (Table 3).

The number of species responsible for 90% of the observed similarity in historical management type in logged, logged/arboricided and control based on SIMPER included 11, 22 and 21 species, respectively. A comparison of the dominant species (Table 4) revealed absence of *Thecacoris lucida* in both the nature reserve and logged/arboricided areas. Furthermore, the three species contributing most to the similarity in each historical management type (Table 4) were *L. mildbraedii*, *C. alexandri* and *Argomuellera macrophylla*, indicating their wide distribution throughout the forest, although at varying abundances (Tables 3 and 4). Apart from the tree species *Cynometra alexandri* and *Celtis mildbraedii*, species contributing >2% to the overall similarity per historical management type were understorey species (e.g. *Lasiodiscus mildbraedii* and *Rinorea ardiisiflora*).

Seedling species composition was different in the four forest communities (Global $R_{ANOSIM} = 0.442$, $P = 0.001$), with all pair-wise comparisons significant ($P < 0.05$), except between the *Lasiodiscus mildbraedii-Khaya anthotheca* and *Cynometra alexandri-Rinorea ilicifolia* forests. Indeed, SIMPER similarities within the forest communities were relatively low (24.5-52.2%), whereas SIMPER dissimilarities between forest communities were relatively high (56.8-83.6%).

ANOSIM results were further corroborated by the Chao abundance-based similarity estimators. At the plot level, the Chao-Jaccard similarity estimator ranged from 0.01 to 1.0 (mean ± SD = 0.62 ± 0.21, with 91.3% of plot pairs >0.5), while the Chao-Sørensen ranged from 0.03 to 1.0 (0.74 ± 0.19, with 87.7% of the 496 plot pairs >0.5). At the level of

**Table 3.** Similarity percentage (SIMPER) analysis, highlighting species of woody seedlings contributing most to the dissimilarity between logged only and nature reserve management types in Budongo Forest Reserve, NW Uganda. Species are ranked according to their percentage contribution to the dissimilarity between types, and only those contributing > 1% dissimilarity are shown. The values of average dissimilarity and percentage of cumulative dissimilarity are also given. Average dissimilarity values identify species (ranked by importance) that contribute to the observed assemblage difference between the two historical management type areas, and percentage contribution = average contribution/average dissimilarity between the two areas.

| Species | Average Abundance | | Average Dissimilarity % | % Contribution | Cumulative % |
|---|---|---|---|---|---|
| | Logged only | Nature Reserve | | | |
| *Lasiodiscus mildbraedii* Engl. | 971 | 358 | 10.01 | 15.58 | 15.58 |
| *Argomuellera macrophylla* Pax Laka | 564 | 147 | 6.86 | 10.68 | 26.26 |
| *Cynometra alexandri* C.H. Wright | 561 | 398 | 5.67 | 8.83 | 35.09 |
| *Rinorea ardiisiflora* Kuntze | 321 | 160 | 5.06 | 7.88 | 42.96 |
| *Rinorea ilicifolia* (Oliv.) O. Kuntze | 524 | 9.8 | 5.00 | 7.78 | 50.75 |
| *Thecacoris lucida* (Pax) Hutch | 229 | 13 | 3.39 | 5.27 | 56.02 |
| *Celtis mildbraedii* Engl. | 197 | 14 | 3.24 | 5.04 | 61.06 |
| *Blighia unijugata* Bak | 73 | 8 | 1.66 | 2.58 | 63.64 |
| *Rawsonia lucida* Harv. & Sond. | 111 | 4 | 1.48 | 2.31 | 65.95 |
| *Teclea nobilis* Del. | 97 | 5.3 | 1.47 | 2.29 | 68.24 |
| *Acalypha ornata* Hochst. ex. A. Rich. | 107 | 57 | 1.14 | 1.77 | 70.01 |
| *Rinorea brachyptela* (Turcz) O. Kuntze | 67 | 45 | 1.08 | 1.69 | 71.70 |
| *Tabernaemontana holstii* K.Schum. | 0.0 | 64 | 1.05 | 1.63 | 73.33 |

**Table 4.** Similarity percentage (SIMPER) analysis, highlighting the contribution of each woody species seedling to the overall similarity within each historical management type in Budongo Forest Reserve, NW Uganda. Species are ranked according to their percentage contribution to the similarity within each management type, and only species contributing > 2% are shown. Average similarity and percentage of cumulative similarity are also given. The term "average abundance" represents the average abundance (density) of each species in a group or area, while "average similarity" values identify species (ranked by importance) that are found consistently in the group.

| Historical management type | Average Similarity | Seedling Species | Average Abundance | Average Similarity | % Contribution | Cumulative % |
|---|---|---|---|---|---|---|
| Logged/arboricided | 32.97 | *Lasiodiscus mildbraedii* Engl. | 409 | 6.38 | 19.34 | 19.34 |
| | | *Cynometra alexandri* C.H. Wright | 412 | 5.12 | 15.52 | 34.86 |
| | | *Argomuellera macrophylla* Pax Laka | 228 | 3.07 | 9.31 | 44.17 |
| | | *Acalypha neptunica* Muell. Arg. | 160 | 2.96 | 8.99 | 53.16 |
| | | *Rinorea ardiisiflora* Kuntze | 285 | 2.36 | 7.16 | 60.32 |
| | | *Tabernaemontana holstii* K.Schum. | 63 | 1.77 | 5.38 | 65.69 |
| | | *Acalypha ornata* Hochst. ex. A. Rich. | 109 | 1.3 | 3.94 | 69.63 |
| Logged only | 52.24 | *Lasiodiscus mildbraedii* Engl. | 971 | 11.2 | 21.45 | 21.45 |
| | | *Argomuellera macrophylla* Pax Laka | 564 | 10.89 | 20.85 | 42.3 |
| | | *Cynometra alexandri* C.H. Wright | 561 | 10.02 | 19.19 | 61.49 |
| | | *Rinorea ardiisiflora* Kuntze | 321 | 3.94 | 7.55 | 69.04 |
| | | *Celtis mildbraedii* Engl. | 197 | 3.07 | 5.88 | 74.92 |
| | | *Acalypha ornata* Hochst. ex. A. Rich. | 107 | 2.18 | 4.17 | 79.09 |
| | | *Thecacoris lucida* (Pax) Hutch. | 229 | 2.03 | 3.88 | 82.97 |
| | | *Acalypha neptunica* Muell. Arg. | 78 | 1.39 | 2.65 | 85.62 |
| Nature Reserve | 39.85 | *Cynometra alexandri* C.H. Wright | 398 | 9.98 | 25.05 | 25.05 |
| | | *Lasiodiscus mildbraedii* Engl. | 358 | 7.63 | 19.16 | 44.2 |
| | | *Argomuellera macrophylla* Pax Laka | 147 | 3.2 | 8.03 | 52.23 |
| | | *Acalypha neptunica* Muell. Arg. | 85 | 2.65 | 6.66 | 58.89 |
| | | *Rinorea ardiisiflora* Kuntze | 160 | 1.82 | 4.56 | 63.45 |
| | | *Tabernaemontana holstii* K.Schum. | 64 | 1.75 | 4.4 | 67.85 |
| | | *Belonophora hypoglauca* (Welw. ex Hiern) A. Chier. | 38 | 1.33 | 3.33 | 71.18 |
| | | *Acalypha ornata* Hochst. ex. A. Rich. | 57 | 1.07 | 2.69 | 73.88 |
| | | *Bequeartiodendron oblanceolatum* (S. Moore) Hiene | 37 | 0.86 | 2.17 | 76.04 |

historical management type, both of the similarity indices showed highest similarity between the nature reserve and logged/arboricided areas, and lowest between the nature reserve and logged only areas (Table 5). In addition, both indices showed highest similarity between the *Lasiodiscus mildbraedii*-

**Table 5.** Chao Jaccard and Sørensen estimators based on abundances of woody seedlings for (a) historical management types and (b) forest community types in Budongo Forest Reserve, NW Uganda. Forest communities: A: *Pseudospondias microcarpa* swamp forest; B: *Funtumia elastica–Pouteria altissima* forest; C: *Lasiodiscus mildbraedii–Khaya anthotheca* forest; D: *Cynometra alexandri–Rinorea ilicifolia* forest.

| Grouping | Chao similarity estimators | | | | | |
|---|---|---|---|---|---|---|
| | Jaccard | | | Sørensen | | |
| *(a) Historical management type* | | | | | | |
| | Logged only | Nature Reserve | | Logged only | Nature Reserve | |
| Logged/ arboricided | 0.95 | 0.96 | | 0.98 | 0.98 | |
| Logged only | | 0.92 | | | 0.96 | |
| *(b) Forest community type* | | | | | | |
| | B | C | D | B | C | D |
| A | 0.90 | 0.93 | 0.78 | 0.95 | 0.96 | 0.88 |
| B | | 0.86 | 0.75 | | 0.93 | 0.86 |
| C | | | 0.95 | | | 0.98 |

*Khaya anthotheca* and *Cynometra alexandri*-*Rinorea ilicifolia* forest types, and lowest for *Funtumia elastica*-*Pouteria altissima* and *Cynometra alexandri-Rinorea ilicifolia* forest types (Table 5).

*Seedlings in relation to environmental factors*

Relative influence of the environmental variables on seedling abundance can be inferred from the CCA ordination (Fig. 2) and intra-set correlations (Appendix S2). The first environmental axis was strongly correlated with LAI, Ti, Mg, organic matter and N, while the second axis was correlated with pH, Si and Ca (Appendix S2, Fig. 2). Species diversity for individuals of >2.0 cm dbh (i.e. saplings, poles and trees) was strongly correlated with Axis 2 in the CCA (Fig. 2). Overall, the three most important environmental variables were OM, Ti and LAI. The contours/isolines depicting seedling species diversity (Fig. 2) increased in magnitude in the direction of the arrow representing increasing species diversity for plants of >2.0 cm dbh. This suggests that seedling diversity is also a function of adult tree/shrub diversity. The CCA further revealed that seedlings of *Rinorea ilicifolia*, *Thecacoris lucida*, *Rawsonia lucida* and *Argomuellera macrophylla* were mainly associated with a high LAI (results not shown); these species are common under low-light conditions below the forest canopy. Similarly, seedling density and LAI were negatively correlated ($r_s = -0.46$, $P = 0.007$). Seedlings of species such as *Raphia farinifera*, *Pseudospondias microcarpa*, *Cleistopholis patens* and *Glyphaea brevis* were exclusively associated with the swamp forest community; while seedlings of *Senna spectabilis* were exclusively associated with the upland *Senna spectabilis*-dominated forest community.

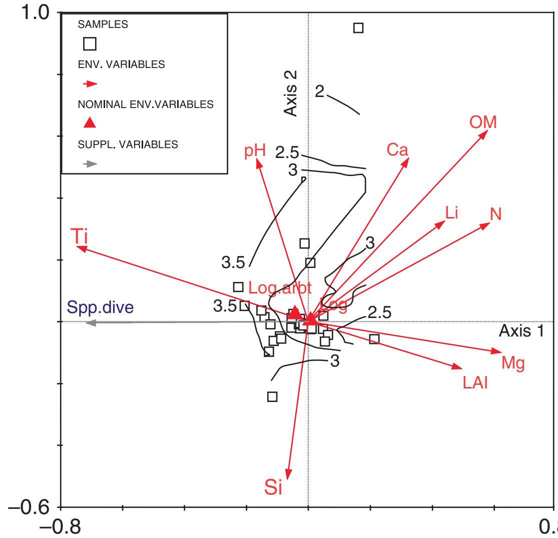


**Fig. 2.** Canonical correspondence analysis ordination showing environmental variables (arrows), historical management types (▲) and sampling plots in Budongo Forest Reserve, NW Uganda. Species density data were used; first axis is horizontal, second axis is vertical. Spp.dive, species diversity (Fisher's α-diversity) for individuals with dbh >2.0 cm (i.e. saplings, poles and trees). Isolines show the relationship of seedling species diversity (Shannon's diversity) of sample plots to environmental factors: organic matter (OM), leaf area index (LAI) and historical management type (logged (Log) or logged/arboricided (Log.arbt)), and species diversity of individuals with dbh >2.0 cm. Some of the environmental variables with shorter arrows are suppressed in the ordination space for more clarity in the ordination diagram. The length of the arrows is proportional to their importance and directions of the arrows show their correlation with the axes.

The combination of the first four canonical axes of the CCA explained 31.9% of the variance in species data, and 59.4% of the variance in the species-environment relation. The first and second axes of the CCA (eigenvalues 0.323 and 0.285, respectively) explained 18.5% of the variance in species data, and 34.4% of the species-environment variation (Table 6). The Monte Carlo permutation test was significant for both the first canonical axis ($F = 1.851$, $P = 0.02$) and the combination of the first four canonical axes ($F = 1.412$, $P = 0.002$), indicating that the first four CCA axes significantly explained the species-environment relations.

**Table 6.** Summary of canonical correspondence analysis results for species of woody seedlings in the Budongo Forest Reserve, NW Uganda.

| Axes | 1 | 2 | 3 | 4 | Total Inertia |
|---|---|---|---|---|---|
| Eigenvalues | 0.323 | 0.285 | 0.243 | 0.199 | 3.288 |
| Species–environment correlations | 0.945 | 0.918 | 0.896 | 0.854 | |
| Cumulative percentage variance | | | | | |
| of species data | 9.8 | 18.5 | 25.9 | 31.9 | |
| of species–environment relation | 18.3 | 34.4 | 48.1 | 59.4 | |
| Sum of all eigenvalues | | | | | 3.288 |
| Sum of all canonical eigenvalues | | | | | 1.767 |

## Discussion

### *Seedling species diversity and distribution patterns*

Topographic gradients, forest communities and historical management types influence the density, diversity and distribution of woody seedlings of the semi-deciduous tropical rain forest of Budongo Forest Reserve, Uganda. The density, alpha-diversity and richness of seedlings differed significantly among the different habitats of the Budongo Forest Reserve, with some species widely distributed and others restricted to specific environments. Other studies also report similar relationships of seedling composition relative to disturbance history and site conditions, but also attribute some patterns of seedling distribution to chance colonization in early succession (Lertzman et al. 1996).

Logging for timber in the Budongo Forest Reserve has had an impact on forest structure because total seedling density was higher in logged versus nature reserve areas. In tropical rain forests, high light availability in gaps promotes seed germination and growth of seedlings of most canopy and understorey species (Balderrama & Chazdon 2005), so that seedling dynamics in canopy gaps may be related to logging or other activities that would create forest openings (Denslow et al. 1998) and recruitment of seedlings to saplings (Dupuy & Chazdon 2006). In the Budongo Forest Reserve, disturbances from selective logging and subsistence harvesting are common, and these activities lead to a mosaic of forest community types (e.g. Plumptre 1996; Mwavu et al. 2008). The resulting habitat heterogeneity may provide opportunities for establishment of new individuals and species (Sousa 1984), favour the coexistence of species with different life histories and ecological requirements, and thus contribute to the maintenance of community diversity (Barkham 1992). The high density of seedlings in the logged *C. alexandri*-dominated forest has also been reported for sheltered well-shaded sites, as compared to exposed open sites, in a tropical dry forest in Ghana (Lieberman & Li 1992). However, the pronounced rainfall seasonality experienced in the Budongo Forest Reserve might create some similarities to drier forests in terms of seed production, germination, survival and seedling development (Khurana & Singh 2000), which consequently influence seedling regeneration. Drought and other seasonal effects affect species population densities and stand structure of forest seedling banks because these factors have different effects on different species (e.g. Delissio & Primack 2003; McLaren & McDonald 2003). Fruit production by woody species in the Budongo Forest Reserve varies from year to year, with some trees not producing any fruit in some years (Tweheyo & Babweteera 2007). After periods of low-fruit production, it is more likely that low numbers of seedlings will be found within the forest (Condit et al. 1995; Middleton 2009).

Woody seedlings were common in the understorey of the Budongo Forest Reserve, which implies that the dense seedling bank (Whitmore 1996) can act as a source of material for regeneration. However, about 119 woody species resprout after tree or shrub damage (Mwavu & Witkowski 2008a). Moreover, the Budongo Forest Reserve is undergoing a continuous regeneration phase because over 45 species had a high density of seedlings that were widely distributed. Continuous regeneration refers to the growth of shade-tolerant seedlings and saplings beneath canopies lacking obvious gaps, leading to continuous replacement of older trees (Veblen & Stewart 1980). Seedling abundance patterns might also be related to past patterns of light distribution within forest stands (Nicotra et al. 1999), but no specific information regarding such a pattern is known for this reserve.

Although plots with high-light availability (low LAI) were expected to have high numbers of seedlings, this was not always the case. Plots with low numbers of seedlings were generally characterised by a thick herbaceous layer and ground vegetation that might suppress regeneration of seedlings through competition for space, water and light. In contrast, areas with higher herbaceous cover in old Afromontane forest fragments in South Africa had increased seedling density (Lawes et al. 2005). However, competition from herbaceous species was found to be a significant factor leading to increased mortality in large gaps in a tropical wet forest in

Costa Rica (Dupuy & Chazdon 2006). Similarly, beneath the dense herbaceous fern cover in temperate forests, increased seedling mortality and decreased growth of tree seedlings were found, which was attributed to competition for light (George & Bazzaz (1999).

Although many species of seedlings were widely distributed in this study area, the seedlings of some species, notably *Lasiodiscus mildbraedii* and *Raphia farinifera*, were clumped around adult conspecifics. This clumping pattern might have occurred because seeds of many tropical tree species are only dispersed over short distances (Guariguata & Pinard 1998; Dalling et al. 2002). Moreover, movement of propagules/seeds determines the potential species composition of a particular habitat (Harper 1977), and a lack of seed dispersal can limit forest regeneration (Holl 1999; Middleton 1999). The importance of both seed dispersal and seedling establishment in regeneration of tree species and maintenance of diversity in both temperate and tropical forests have been highlighted in many studies (e.g. Dalling et al. 1998a; Lambers et al. 2002; Wang & Smith 2002). Furthermore, in the Budongo Forest Reserve, some species, notably *Raphia farinifera*, *Rinorea ilicifolia*, *Glyphaea brevis*, *Neoboutonia melleri, Rawsonia lucida* and *Thecacoris lucida*, were restricted to particular environments. The limited distribution of these species can be explained partially by the presence of ecological gradients in soil moisture, organic matter and pH (Nigatu & Tadesse 1989).

### *Seedling regeneration in relation to environmental factors*

CCA ordination pointed to the importance of environmental gradients in soil nutrients and LAI in maintaining variations in seedling regeneration among the different habitats of the Budongo Forest Reserve. CCA axes 1 and 2 explained 18.5% of the variation in species, and 34.4% of the species-environment relationship (Table 6); the first canonical axis and the combination of the four canonical axes were significant. As a rule of thumb, eigenvalues $>0.30$ indicate strong gradients for these axes (ter Braak 1995). Thus, in this study, with eigenvalues of 0.32 for the first axis, the measured environmental variables substantially influenced the observed seedling distributions, abundances, diversity and richness, where organic matter, Ti and LAI were the most important environmental variables. Hence, the important mechanisms that influence forest seedling regeneration operate through the soil system (soil nutrients) and ground and canopy vegetation through the influence of LAI on light availability below the canopy. The importance of environmental differences in seedling regeneration is corroborated by the significant ANOSIM for comparisons of transects, suggesting that the similarities within, and differences between, transects are not just a result of chance. Furthermore, recent studies clearly indicate the potential for niche partitioning among tropical forest tree seedlings along gradients of light availability (Montgomery & Chazdon 2002; Poorter & Arets 2003).

In this study, seedling species diversity increased with increasing Ti concentration, but decreased with higher amounts of exchangeable cations (e.g. Mg and Ca) and organic matter (see Fig. 2). Hence, seedling diversity was higher in areas with less fertile soils in this area. Similarly, Costa Rican forests had a negative correlation between soil nutrient availability and tree species richness (Huston 1980). In Ecuador, soil Ca and Mg also affected species distribution of seedlings. Furthermore, results of this study are in agreement with Huston's (1979) general hypothesis of species diversity, which postulates that diversity should be highest under conditions of relatively low-nutrient availability (excluding extremely deficient sites). The increasing soil Ti concentration with increasing tree species diversity may be attributed to a "vegetation effect" (i.e. vegetation recycles a significant quantity of Ti, increasing its mobility in the soil; see Cornu et al. 1999), although this relationship cannot be clearly explained in this study. Moreover, species diversity of the $>2.0$-cm dbh plants as a supplementary environmental variable also explained the variation in observed seedling distributions, abundances and diversity in the Budongo Forest Reserve. Comita et al. (2007) also found that tree seedling species abundance was largely a function of reproductive adult abundance, although this relationship cannot be clearly demonstrated here.

### *Conclusions and future directions*

Analysing the diversity, density and distribution of seedlings can reveal information on species regeneration, yet few studies have been undertaken in semi-deciduous African tropical forests, particularly in the Albertine Rift Ecoregion. Although this study represents a short-term study of seedling diversity, abundance and distribution, the results offer insight into the patterns of seedling regeneration in semi-deciduous tropical rain forests. We found high densities of seedlings per ha, wide distributions for a variety of species, significant variations in seedling distributions among transects, and among forest communities and among historical management types; hence, there was substantial variability in seedling regeneration among species. Patterns of seedling regeneration in the Budongo Forest Reserve are a reflection of adult tree diversity, historical management type and environmental gradients in soil nutrients and light. Hence, the important mechanisms influencing seedling regeneration operate through both edaphic and canopy vegetation characteristics. Most species in this study had high-seedling densities and frequencies, indicating that the forest is likely undergoing continuous regeneration. With some species having restricted habitat preferences and regenerating only through seedlings, it may be necessary to ensure that such seed trees are not removed from logged areas. Further studies are also required (a) to evaluate spatial and temporal patterns of seed rain and seed banks as stocks with regenerative potential and (b) for seedling survival and recruitment of woody species in relation to disturbance and tree life history features for conservation planning and management in the Budongo Forest Reserve and other semi-deciduous tropical rain forests.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Species list arranged alphabetically by family for woody seedlings recorded in 32, 0.5-ha plots within Budongo Forest Reserve, NW Uganda. Plot frequency (expressed as a percentage of the overall number of plots sampled) and overall density (individuals per ha) for each species are included.

**Appendix S2.** The CCA inter-set and intra-set correlations of environmental variables of the first four axes for woody seedling abundance in Budongo Forest Reserve, NW Uganda.

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