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Long-term permanent plot observations of vegetation dynamics in Budongo, a Ugandan rain forest

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ABSTRACT. Species composition and turnover that have occurred in a series of permanent sample plots established during the 1930s and 1940s in Budongo, a semi-deciduous Ugandan forest, are reported. The plots were established as part of a sequence first used to describe forest succession, five of which have been maintained and which were last measured in 1992–1993. One plot (plot 7) provides 53 y of data from old-growth pristine forest. Plot 15 was established in wooded grassland at the forest edge and is now closed high forest. Evaluation of the remaining three plots is complicated by silvicultural interventions carried out in the 1950s. Forty species have been added since the first evaluations and a total of 188 tree species (over 80% of Budongo's forest tree flora, and including two exotics) has now been recorded from within the plots. The pattern of shade-tolerance in the original plot series conforms to patterns expected for succession with an increasing proportion of shade-tolerant species with development, and large stems appearing to 'lag behind' smaller stems in this respect. The time series data are less consistent, and while plot 7 increased in the proportion of shade-tolerant stems through time, the proportion of shade-tolerant species actually declines. Stem-turnover (the mean of mortality and recruitment) slowed with implied successional stage. Most species have a higher recruitment than mortality rate and stem numbers have thus increased in all plots. This is most pronounced in the putatively 'early successional' plot. Stem size structure has changed within the plots, with an increased proportion of smaller stems. Species show different rates of turnover and these vary from plot to plot and period to period. In plot 7, the overall mortality rate decreased with initial stem size. Estimates imply that some tree species may easily live longer than 500 y after reaching 10 cm DBH, and that 1000 y is possible. The importance of large trees in determining forest dynamics is illustrated by the finding that death of only seven stems in plot 7 contributed over 60% of net basal area losses recorded over the 53-y observation

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period. Many of the observed patterns were not predicted and could only have been found by long-term studies.

KEY WORDS: Africa, composition, disturbance, monodominant, monitoring, mortality, recruitment, species richness, succession, turnover

INTRODUCTION

The dynamics and stability of species composition of tropical rain forests has long been an ecological preoccupation (Aubréville 1938, Davis & Richards 1934, Richards 1952), but one that continues to receive considerable attention. Since the mid 1970s, the dominant ecological view of tropical rain forests has emphasized cycles of stem death and replacement (Hartshorn 1978, Oldeman 1978, Platt & Strong 1989; Whitmore 1975, 1978). Knowledge of compositional dynamics is central to understanding many ecological processes, including patterns and maintenance of species richness (Connell 1978, Phillips & Sheil 1997, Swaine & Hall 1988) and forest succession (Eggeling 1947a). While the interpretation of available data is contested (Phillips 1995, Phillips & Gentry 1994, Phillips *et al.* 1994, 1997; Sheil 1995a, 1996a, 1997a) there is consensus on the need for more information (Phillips & Sheil 1997). On a more practical level such data provide important information for sustainable natural forest management. It is also a critical area for understanding the possible consequences of recent anthropogenic changes in the tropics, namely deforestation, forest fragmentation and global climatic change. Careful observation and description of tropical forest change provides the material from which specific hypotheses must be formulated and examined.

Satisfactory answers to questions concerning changes in community composition will, in the main, be best achieved from studies that last several generations of the component species of that vegetation. Long-term studies are vital when investigating slow-acting ecological processes and changes, and for evaluating the consequences of rare events (Gaines & Denny 1993).

For temperate herbaceous vegetation, a small number of studies are now available that begin to answer some of these questions (Dodd *et al*. 1995; Watt 1981a,b; Dunnett *et al*. 1998). No such data are available for tropical rain forests, where the generation times of trees may run into decades or centuries. Data on mortality, recruitment and species composition have been published from permanent sample plots (hereafter 'PSPs') from both Old and New World tropical rain forests. A few accounts cover periods of 30–40 years (Burslem & Whitmore 1999, Manokaran & Kochummen 1987), but the overwhelming majority are of much shorter duration. The ecology of long-term change in tropical forests appears to be based more on plausible arguments than upon empirical facts (Finegan 1984).

This study reports analyses of mortality, recruitment and species composition from some of the oldest extant tropical rain forest PSPs. W. J. Eggeling originally established the plots in Budongo forest, Western Uganda during the

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1930s and 1940s (Eggeling 1947a). Five of his 1.86-ha plots have been maintained and remeasured since, most recently in 1992–93. These data therefore represent a rare opportunity for ecologists to examine community change over a relatively long period.

The aim of this paper is to provide baseline information from the five decades of measurements of the Budongo PSPs, to outline the major patterns from the data, and describe the community changes at stem and species levels. This should inform current debates and meta-analyses.

MATERIALS AND METHODS

Study site

The Budongo forest lies in Uganda at 1°37′–2°03′ N and 31°22′–46′ E, at an altitude of 1000–1100 m, just east of the Albertine Rift Valley escarpment. The underlying pre-Cambrian geology has given rise to a gentle topography with deep and ancient (non-volcanic) soils. Annual rain fall is generally between 1200–1800 mm, with most falling during September–November and March–May (see Sheil 1997b). The gazetted area of the Budongo Forest Reserve covers almost 800 km^2 of which *c.* 430 km^2 is closed forest. Despite the homogeneity of the landscape, Budongo has the most forest tree species recorded in a Ugandan forest (Howard 1991, Synnott 1985; Uganda Forest Dept. *pers. comm.*). Fuller descriptions of the Budongo forest are provided by Eggeling (1947a,b), Philip (1965) and Plumptre (1996) and Sheil (1996b, 1998).

Eggeling (1947a) described three main forest types at Budongo (see also Brasnett 1946, Harris 1934). He hypothesized that forest developed from wooded grassland in a progression from 'colonizing', through 'mixed', to 'ironwood' forest (a climax forest dominated by *Cynometra alexandri* C.H. Wright, locally known as 'ironwood'). Tree cover in the south of the forest was reported to have increased since the earliest observations in the 1920s (Eggeling 1947a), and the distribution of forest types prior to logging was consistent with these having a successional origin from forest expansion over several centuries (Eggeling 1947a, Philip 1965). More recent expansion of forest cover is confirmed by aerial imagery (Sheil 1996b). The successional interpretation of the original plot series is crucial, and is dealt with in detail in Sheil (1999a). Apart from a range of evidence that a marked age-gradient across the forest is inevitable, multivariate analysis of the plot series are found to be consistent with four separate predictions of succession in size-structured data (Sheil 1999a). Additional aspects of successional consistency in the plot series are provided in this account.

Sample plots

In the 1930s and early 1940s, Eggeling set up a series of plots in the Budongo forest (Appendix 1). These were numbered from 1–10 according to his successional interpretation, i.e. plot 1 being the earliest developmental stage, plot 10

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Table 1. Vegetation types in the Budongo plots in 1940, and where known in 1992. Listed 15 then 1–10 in the order of Eggeling's (1947a) successional interpretation and using his nomenclature.

Plot	Vegetation in 1940	1992
15	*Terminalia* grassland	Mixed (with *Maesopsis*)
1	Colonizing (Woodland)	nr*
2	Colonizing (with *Maesopsis*)	Mixed
3	Colonizing (with *Maesopsis*)	nr
4	Ecotone to mixed	nr
5	Mixed	Mixed
6	Mixed	Mixed
7	Ecotone to ironwood	Ecotone to ironwood
8	Ecotone to ironwood	nr
9	Ironwood	nr
10	Ironwood	nr
11	Swamp forest	nr

*nr = not recorded.

the most mature (see Eggeling 1947a). Additional plots included plot 15, which was in fact at an earlier developmental stage than plot 1, and plot 11 which was sited on water-logged ground and termed 'swamp forest'. The plots are listed in order of Eggeling's successional series in Table 1. Five of the original plots, numbers 15, 2, 5, 6 and 7, have been maintained since the 1940s. The plots are 1.86 ha in size, except for plot 6, which is 2.12 ha. They have been measured at various times since establishment, most recently in 1992–93.

In the 1950s and 1960s, unmarketable tree species in plots 15, 2, 5, and 6 were poisoned (see Appendix 1 for details). This poisoning was part of an evaluation of ongoing silvicultural operations intended to promote the growth and regeneration of the most valuable timber species, such as *Khaya* and *Entandrophragma* spp. Plot 7 lies in a pristine area designated as a 'nature reserve', and has never received any such treatment.

Measurement conventions are known to have varied to some extent (Appendix 1). Most stem diameters have been measured at 1.3 m, but buttressed, fluted or deformed stems have usually been measured also at higher points (usually 3 m). Where multiple measures have been taken, the highest point has been used in analyses. This is the 'diameter at reference height' (hereafter 'drh'). In the 1992–93 evaluation, stems were measured using all known previous points of measurement. As a minimum, the stems of a fixed list of timber species $\geqslant$ 25 cm drh have been measured on all enumerations (a full species list with authorities is provided in Appendix 2). By contrast, the most comprehensive enumerations have measured all stems $\geqslant$ 10 cm drh for all species. Eggeling (1947a) provides information for all stems $\geqslant$ 10 cm drh (though he did not include plot 15 in his published account). These published data suffer limitations: there are no individual-stem data (only summaries by species and stem size classes); they exclude an end strip from the established plots and refer to plots of 1.49 instead of 1.86 ha; and measurement records are not dated (but were from *c.* 1940, W. J. Eggeling *pers. comm.*). Further information regarding the plots and the assessment methods are available in Eggeling (1947a) and Sheil (1995b, 1996b, 1998).

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Data quality has been comprehensively evaluated (Sheil 1995b), and while some complications have been identified, the quality of the original studies, and in particular the botanical expertise was exceptional as Eggeling was then the botanical authority on Ugandan trees (see Eggeling & Dale 1952). Variation in minimum recorded stem sizes influences the available observation periods for some stem classes and population – in this account these periods have been selected to be illustrative of general patterns without being confounded by methodological changes, or a specific note has been made.

Manipulation and statistical analysis of data

Analysis conventions. Each statistical test is treated as independent of any other. To allow confidence to be assessed under stricter assumptions we quote the full P values when possible (c.f. Day & Quinn 1989, Stewart-Oaten 1995).

Basal area. Basal area (BA) was estimated assuming circular stems, i.e. stem-area = $\pi/4 \cdot \mathrm{drh}^2$. BA turnover figures were derived in a form analogous to that used for stem count estimates (Sheil *et al.* 1995) and are used here as a measure of stand change (ignoring stem growth and recruitment). The lower limit for annualized basal area loss, m_{ba} ($1 \geqslant m_{ba} \geqslant 0$), is estimated as

$$m_{ba} \geqslant 1 - (\mathrm{BA}_t/BA_0)^{1/t} \tag{1}$$

BA_0 is the sum of original basal areas at the beginning of the period ($t = 0$), and BA_t is the BA of surviving stems at the end of the measurement interval, t (in y). Confidence limits cannot be generated. A lower bound for BA loss is provided in units of $\mathrm{m}^2\ \mathrm{ha}^{-1}\ \mathrm{y}^{-1}$ by the inequality

$$m_{ba/\mathrm{ha/y}} \geqslant m_{ba}\ (BA_0/\mathrm{Area}),$$

or

$$m_{ba/\mathrm{ha/y}} \geqslant (1 - (BA_t/BA_0)^{1/t} BA_0)/\mathrm{Area} \tag{2}$$

Mortality and recruitment rates. Both bounded (e.g. mortality) and unbounded (e.g. recruitment) rates were compared by the comparison of two Poisson counts, which assumes that each loss or gain is an independent event (Dobson 1990, Mansfield 1980, Statgraphics-Plus 1993). This approach allows the direct comparison of mortality with recruitment (Sheil 1999b).

Recruitment rate, r, was quantified as

$$r = 1 - (1 - n_r/N_t)^{1/t} \tag{3}$$

where n_r is the count of recruits and N_t is the population count at the end of the measurement interval, in y, t. The reasoning is that this r is equivalent to 'the hypothetical annual mortality rate (m), such that the number of individuals in the population is maintained at equilibrium, given a certain census

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count of recruits'. This formulation is symmetrical in statistical form with the formula used for annual mortality, *m* (see Sheil *et al.* 1995). In all cases we have compared census intervals of similar duration as we cannot yet account for the influence of interval on estimated rate (c.f. Sheil & May 1996).

RESULTS

Species records

With all enumerations combined *c.* 83% of Budongo's known forest tree flora has now been recorded within plots 1–11. Eggeling (1947a) recorded 148 species, ⩾ 10 cm drh in these 11 plots. An additional 40 species have been recorded during the subsequent measurements, these include two exotics. Ninety-eight species originally contributed to stems ⩾ 20 cm drh, 10 more species have subsequently been added. For stems ⩾ 40 cm drh, there were 51 species originally and four have been added.

The 1992–93 census alone added three species to the recorded Budongo tree flora. Two were represented by individual stems in plot 6 – identified as *Xylopia* sp. aff. *rubescens* Oliv. (Annonaceae) and D. Sheil 1295, 1737 sterile, which appears to be an undescribed species (family unknown). The third, *Psidium* sp. (Myrtaceae), an exotic, was present as one individual in plot 15.

Vegetation changes through succession

A steady increase of shade-tolerant stems and species are suggested by Eggeling's plot series (Figure 1), guilds have been applied *sensu* Hawthorne 1995, 1996 (see Appendix 2). Along this series, there is a marked increase in the

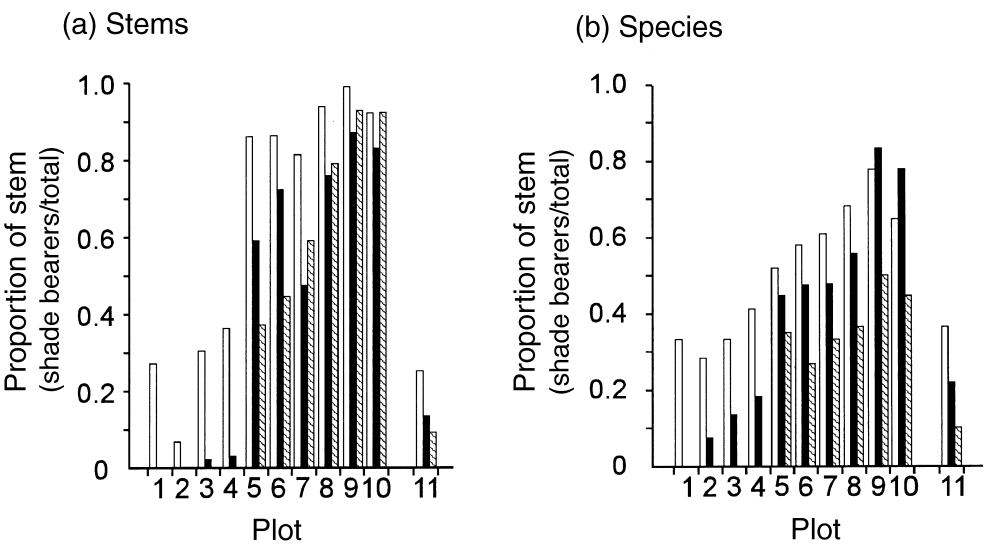


Figure 1. Relative abundance of the 'shade-tolerant' guild in Eggeling's original data set by (a) stems and (b) species in three diameter classes: 10–30 cm (open bars), 30–60 cm (black bars), and ⩾ 60 (hatched bars).

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proportion of shade-tolerant species with successional age, and large stems generally lag behind smaller stems in this respect. Over real time however the pattern is less clear (Figure 2). In plots 15 and 2, few shade-tolerant stems or species occur even by 1992. Plot 7 shows an increase in the proportion of shade-tolerant stems through time, but a slight decline in the proportion of shade-tolerant species.

Plot 15: Eggeling's early successional forest. Twenty-five species were recorded in 1944, rising to 74 species in 1992. This was accompanied by a considerable rise in stem numbers: from 382 to 921 stems ⩾ 10 cm drh. Stems gained and lost by each species in the period prior to silvicultural treatment shows rapid change, with recruitment greater than mortality (Figure 3). Twenty-one species increased stem numbers between 1944 and 1950. Thirteen of these had (⩾ 10 combined gains and losses, of which 12 showed a significant rate imbalance (Table 2).

Plot 15 was located in wooded grasslands at the forest margin in 1944 and reveals changes as forest species established and canopy closure progressed. Originally there were few large stems and some low woodland trees such as *Terminalia* and *Albizia spp.* (mostly *A. zygia*) with a scrubby understorey of *Grewia*, *Piliostigma*, *Erythrina* and *Acacia*, and many *Albizia*, *Terminalia* and *Annona* saplings dominated the plot. Some small *Trema*, *Sapium*, *Dombeya* spp., *Ficus sur*, and two *Maesopsis* stems were also present. By 1950, *Maesopsis* and *Ficus sur* had increased considerably, along with *Harungana*, *Trema*, *Sapium* and *Combretum*, while many additional species (e.g. *Prunus*, *Bridelia* and *Spathodea*) appeared in the smallest stem class. By 1992, there were many large stems, including *Maesopsis, Alstonia*, *Prunus*, *Khaya*, *Milicia* and *Albizia* spp. *Maesopsis* was the only species with large stems (45 stems over 20 cm drh) that was not also represented in the smallest 10–20 cm stem sizes.

Plots 2 and 5: Eggeling's mid successional forest. Both plots received silvicultural treatments in the 1950s and 1960s (Appendix 1), and so statistical analysis of compositional changes are conducted for the period prior to treatment only (plot 2, from 1940–1945; plot 5 1940–1948) and for stems ⩾ 25 cm drh. Species changes in plots 2 and 5 show few marked trends in this brief period (Figure 4).

In the 1940s, plot 2 was dominated by early successional species, mainly *Maesopsis* and *Olea*. *Cordia millenii*, *Sapium*, *Spathodea*, *Terminalia* and *Margaritaria* were also present and reached their highest densities at intermediate size classes. *Maesopsis* declined rapidly in the 1940–45 period (Figure 4). There appeared to be active recruitment of *Caloncoba* and *Erythrophleum*. By the 1960s *Chrysophyllum albidum* had increased markedly and *Maesopsis* and *Cordia* had declined, being represented only by large, relic stems. In 1992 the composition was distinctive when compared with other plots, with notable densities of *Morinda*, *Teclea*, *Diospyros*, *Tetrapleura*, *Antiaris*, *Klainedoxa*, *Olea* and *Erythrophleum*.

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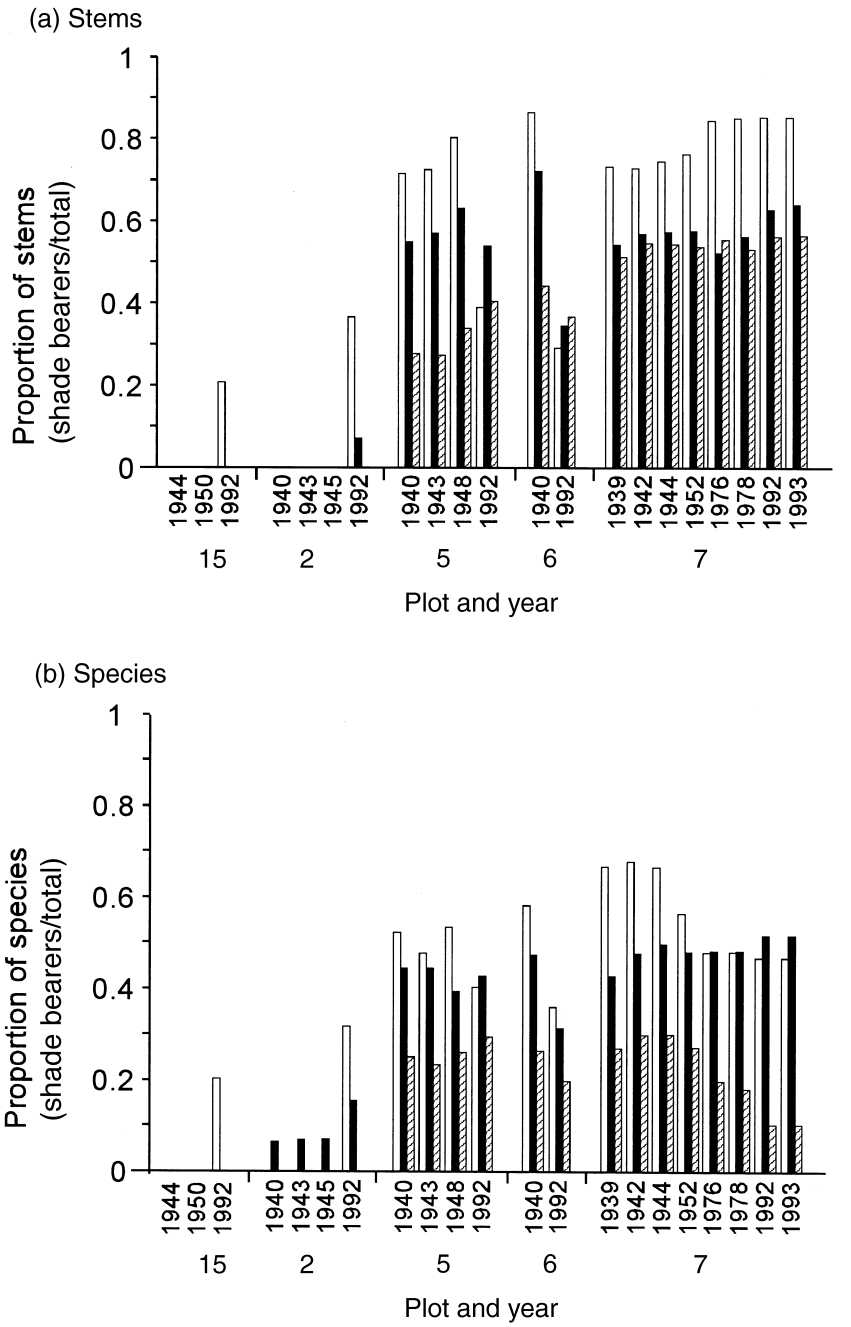


Figure 2. Relative abundance of the 'shade-tolerant' guild over time in plots 15, 2, 5 and 6, by (a) stems and (b) species. Three diameter classes are shown: 10–30 cm (open bars), 30–60 cm (black bars), and ≥ 60 cm (hatched bars). Plot 6 has no early all species record apart from the Eggeling (1947a) data and this is repeated (as '1940') to allow comparison with the 1992 data. All enumerations in which all species were recorded are shown, but the lower diameter class used in some observations is greater than 10-cm which may reduce the value of the 10–30 cm comparisons for these observations (see Appendix 1).

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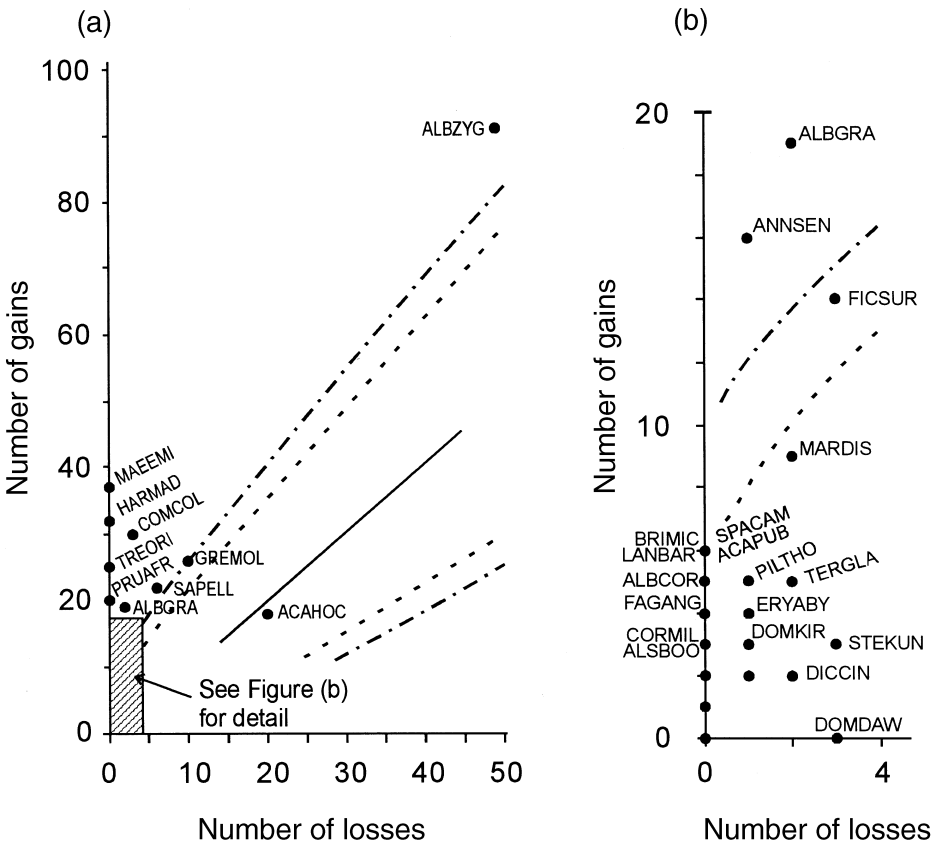


Figure 3. Gains and losses for all species with stems ⩾ 10 cm drh in plot 15 from 1944 to 1950. (a) Covers the most dynamic species, but (b) shows the numerous species having few counts. Confidence lines are derived from interpolating critical values for the comparison of two Poisson counts (see Sheil 1999b, between dotted line: $P > 0.05$; between dash-dot lines: $P > 0.01$). Species are identified by their six-letter codes provided in Appendix 2.

Table 2. Poisson count comparisons of stem gains and losses in plot 15 between 1944 and 1950, of stems ⩾ 10 cm drh for those species where combined losses and gains add to more than 10.

Species	Losses, n	Gains, n	Change	z	P
Margaritaria discoidea	2	9	+	1.8	0.07
Ficus sur	3	14	+	2.43	0.015
Annona senegalensis	1	16	+	3.40	0.00069
Acacia hockii	20	18	–	0.16	0.87
Albizia grandibracteata	2	19	+	3.49	0.00048
Prunus africana	0	20	+		<0.00001
Sapium ellipticum	6	22	+	2.83	0.005
Trema orientalis	0	25	+		<0.00001
Grewia mollis	10	26	+	2.5	0.012
Combretum collinum	3	30	+	4.53	<0.00001
Harungana madagascariensis	0	32	+		<0.00001
Maesopsis eminii	0	37	+		<0.00001
Albizia zygia	49	91	+	3.47	0.00053
All stems	110	428	+	13.66	<0.00001

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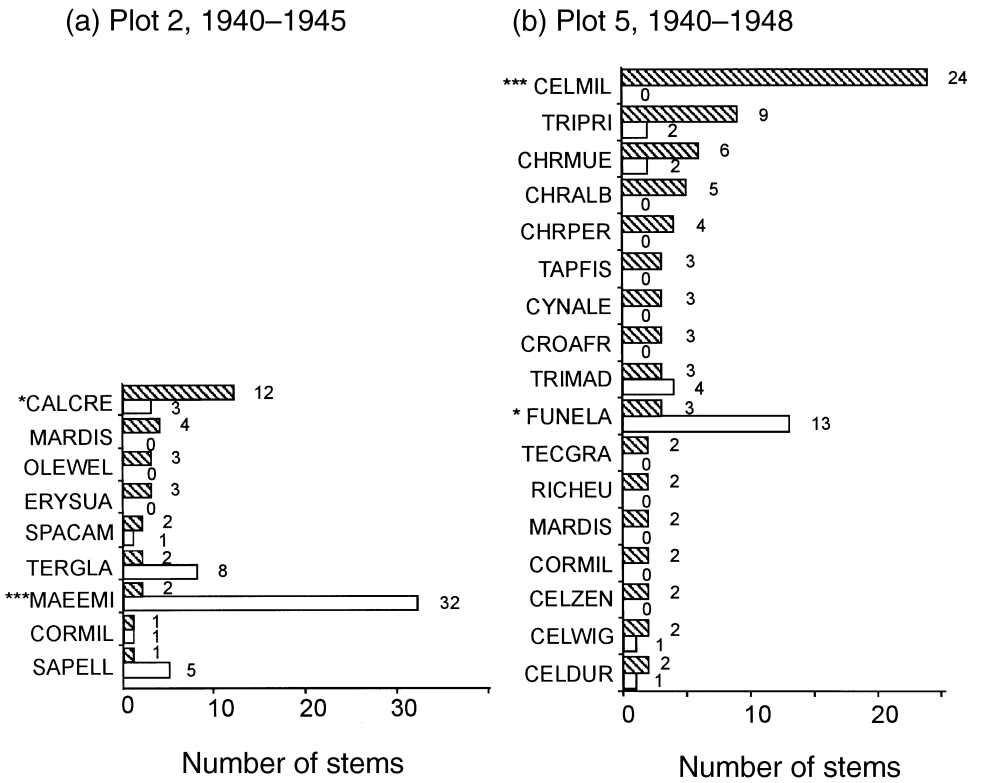


Figure 4. Changes in stem number ⩾ 25 cm drh by species where change is more than a single stem in (a) plot 2 from 1940 to 1945, and (b) plot 5 from 1940 to 1948. Numbers are the counts of gains (hatched) and losses (open). Asterisks denote significant differences: *Calconcoba crepiana,* P = 0.039, *Maesopsis eminii,* P ≪ 0.00001, *Celtis mildbraedii*, P ≪ 0.00001, *Funtumia elastica,* P = 0.024. Species are designated by their six-letter codes provided in Appendix 2.

Many of the original pioneer species had declined but *Margaritaria* and *Caloncoba* appeared to be regenerating, and *Olea* was still represented in all but the smallest stem sizes. *Celtis* spp. had been gained, although apart from *C. durandi,* they had only reached small sizes. There were no *Cynometra* and a general dearth of Sapotaceous canopy species.

None of the 17 species recorded in 1940 in plot 2 with a drh ⩾ 25 cm were lost by 1945, nor were any gained. Nine species had no change in number and eight of these neither gained nor lost stems. There were 235 stems at the start of the period, and 215 at the end, with 50 stem losses and 30 gains (Poisson count comparison, P = 0.034).

The canopy of plot 5 in the 1940s included *Alstonia* and *Chrysophyllum muerense*. *Trichilia prieuriana*, *Croton africana* and *Funtumia elastica* were present in the intermediate sizes. There was considerable regeneration of *Celtis* spp. (particularly *C. mildbraedii,* see Figure 4). *Khaya* and *Entandrophragma* species were present at modest sizes. By the 1960s, there had been an increase in *Chrysophyllum* spp. By 1992 the canopy was mixed, characterized by *Chrysophyllum*

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spp. and *Croton* spp. The abundant species appeared to be recruiting, and *Funtumia elastica*, *Trilepisium*, *Myrianthus arboreus* and *Lychnodiscus* were all well represented amongst the smaller stems where *Cynometra* was also established.

In the two pre-treatment censuses in plot 5 (1940 and 1948), 42 species were recorded, three had been gained in 1948, and one lost, and 12 species had neither gained nor lost stems. There were 228 stems in 1940 and 289 in 1948, with 26 stem losses and 87 gains (Poisson count comparison, $P \ll 0.0001$).

Plot 7: Eggeling's late successional forest. The number of species in plot 7 increased from 49 in 1939 to 60 in 1993. For stems $\geqslant$ 20 cm drh, 25 species increased in abundance over this period, and 13 decreased. The modal change in stem numbers per species was zero (Figure 5), and 11 of these species showed no stem gains or losses at all. Six species were lost, five of which were originally represented by just one stem. Thirteen species were gained, of which 10 were represented by only one stem in 1993. When all of the enumerations in which all species were recorded are considered, 42 stems $\geqslant$ 20 cm drh had been recruited after 1939 and were then lost before 1993. The pattern of overall gains and

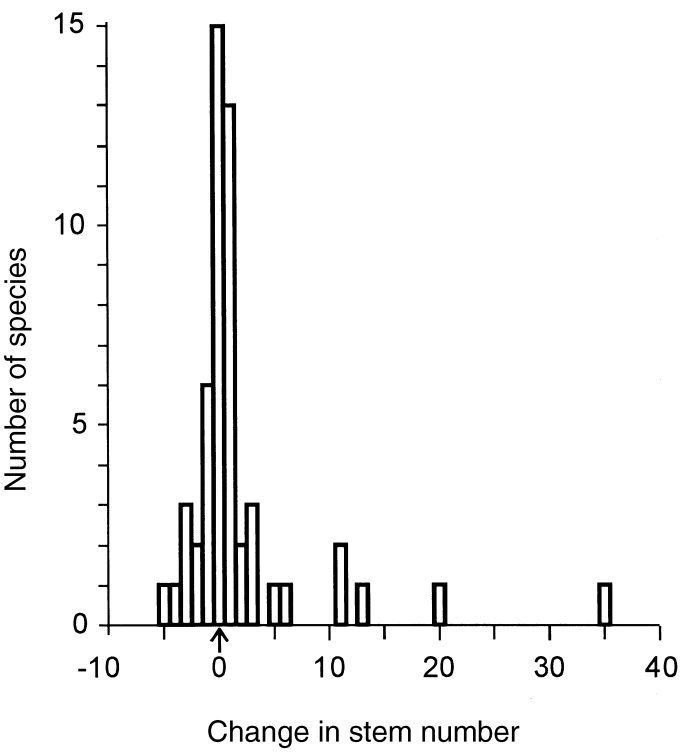


Figure 5. Relative change in frequency of stems $\geqslant$ 20 cm drh by species from 1939 to 1993 in plot 7. The mode is zero, reflecting that 11 species had no stem turnover at all, and the positive skew reflects an increase in total stem number.

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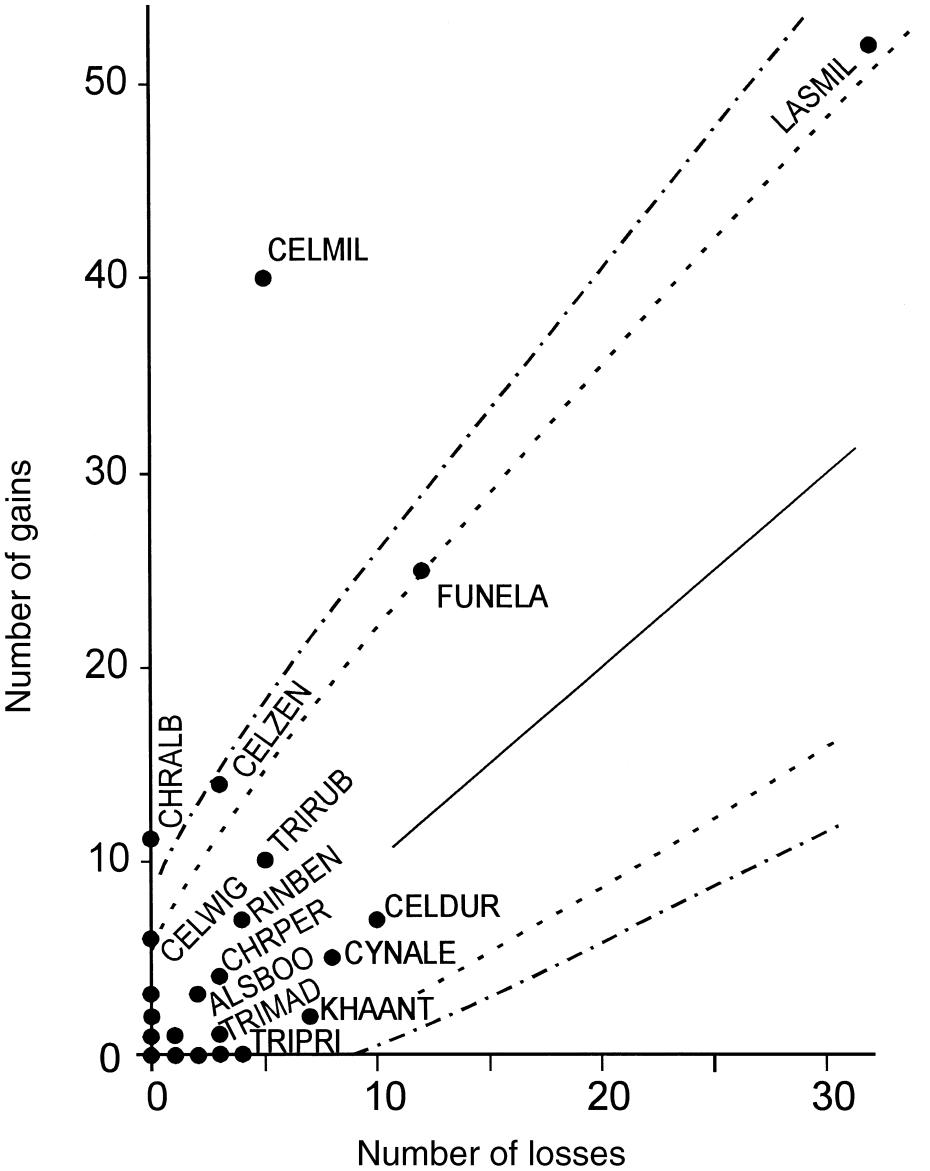


Figure 6. Stem gains and losses for all species in plot 7 of stems ⩾ 20 cm drh, based on the censuses in 1939 and 1993. Confidence lines are derived from interpolating critical values for the comparison of two Poisson counts (see Sheil 1999b, between dotted line: $P > 0.05$; between dash-dot lines: $P > 0.01$). Species are designated by their six-letter codes provided in Appendix 2.

losses is summarized in Figure 6. Recruits and losses in the most abundant species are compared in Table 3.

The canopy of plot 7 in the 1940s was dominated by *Cynometra*, with some large *Alstonia*, *Khaya* and *Entandrophragma* and also some *Trichilia priuriana* and *Celtis durandii*, *Celtis* spp., *Chrysophyllum* spp., *Lasiodiscus*, and *Rinorea* and a

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Table 3. Poisson count comparisons of ⩾ stem gains and losses of stems ⩾ 20 cm drh of the most abundant species in plot 7 from 1939–1993.

Species	Losses, n	Gains, n	Change	z	P
Celtis mildbraedii	5	40	+	5.06	<0.00001
Celtis zenkeri	3	14	+	2.43	0.015
Cynometra alexandri	8	5	−	0.55	0.58
Funtumia elastica	12	25	+	1.97	0.048
Lasiodiscus mildbraedii	32	52	+	2.07	0.038

number of *Belonophora*, *Funtumia elastica* and *Trichilia sp.* By the 1990s, the canopy composition showed few general changes. There were few clear trends in stem size distributions, although *Celtis* spp., *Lasiodiscus*, *Rinorea*, *Trilepsium* and *Coffea* were all actively regenerating. High numbers of small *Funtumia* spp., *Vitex*, *Tabernaemontana* and *Khaya* were present and there was a conspicuous lack of small *Cynometra*.

Data for stems ⩾10 cm drh in plot 7 are available only from 1976 to 1993. In 1976, 981 stems ⩾10 cm drh were recorded, increasing to 1087 in 1993. A total of 125 stems were lost during this period, and 231 were recruited (Poisson count comparison, $P \ll 0.0001$). Sixteen species showed a decrease in stems, and 28 an increase. The four species with a significant imbalance between stem gains and losses all show a net increase (Figure 7).

Mortality and recruitment

The impact of silvicultural interventions is seen as a factor reducing stem numbers in plots 2, 5 and to a lesser extent plot 6, but not in plot 15 (Figure 8). A decline of stem turnover rates (prior to silvicultural treatment) with successional status is indicated in Figure 9. Only four independent data points are available but turnover (the mean of m and r) has perfect rank correspondence to the putative successional sequence, i.e. 15 > 2 > 5 > 7 (exact probability = 1/(4!) = 0.04).

Annualized mortality and recruitment rates of species are high in plot 15 prior to silvicultural treatment (between 1944 and 1950 for recruitment *and* mortality in stems ⩾10 cm drh): averaging 5.3% $y^{-1}(m)$ and 14.1% $y^{-1}(r)$. The considerable variation amongst species is shown in Figure 10. Those species with the smallest initial populations have the greatest potential for percentage rate increases. There is a significant relationship between mortality and recruitment rates amongst those 15 species where non-zero estimates are available for both ($\tau = 0.488$, $P = 0.013$). Analysis of mortality and recruitment rates per species for plots 2, 5 and 6 are not shown as data for these plots covers only the short periods prior to silvicultural interventions.

Stems ⩾ 20 cm drh in plot 7 were evaluated for imbalances between mortality and recruitment (Table 4). One hundred and thirteen of the stems recorded in 1939 had been lost by 1993, while 212 were gained ($m = 1.05$ % y^{-1} and $r =$

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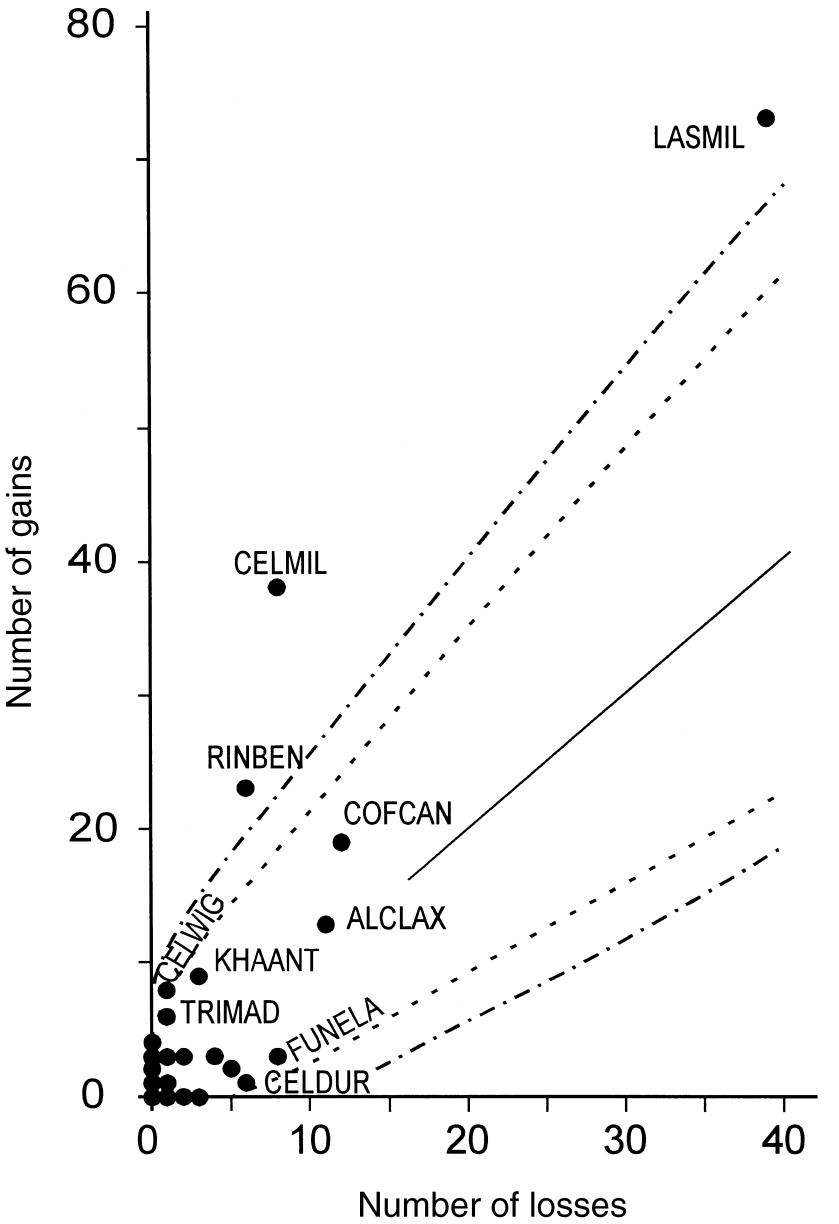


Figure 7. Gains and losses for all species with stems ⩾ 10 cm drh in plot 7 from 1976 to 1993. Note different scales on the axes. Confidence lines are derived from interpolating critical values for the comparison of two Poisson counts (see Sheil 1999b, between dotted line: $P > 0.05$; between dash-dot lines: $P > 0.01$). Species where differences between gain and loss were significant by comparison of two Poisson counts are: *Lasiodiscus mildbraedii*, $P = 0.0018$; *Celtis mildbraedii*, $P = 0.00019$; *Rinorea beniensis*, $P = 0.002$; and *Celtis wightii*, $P = 0.046$. Species are designated by their six-letter codes provided in Appendix 2.

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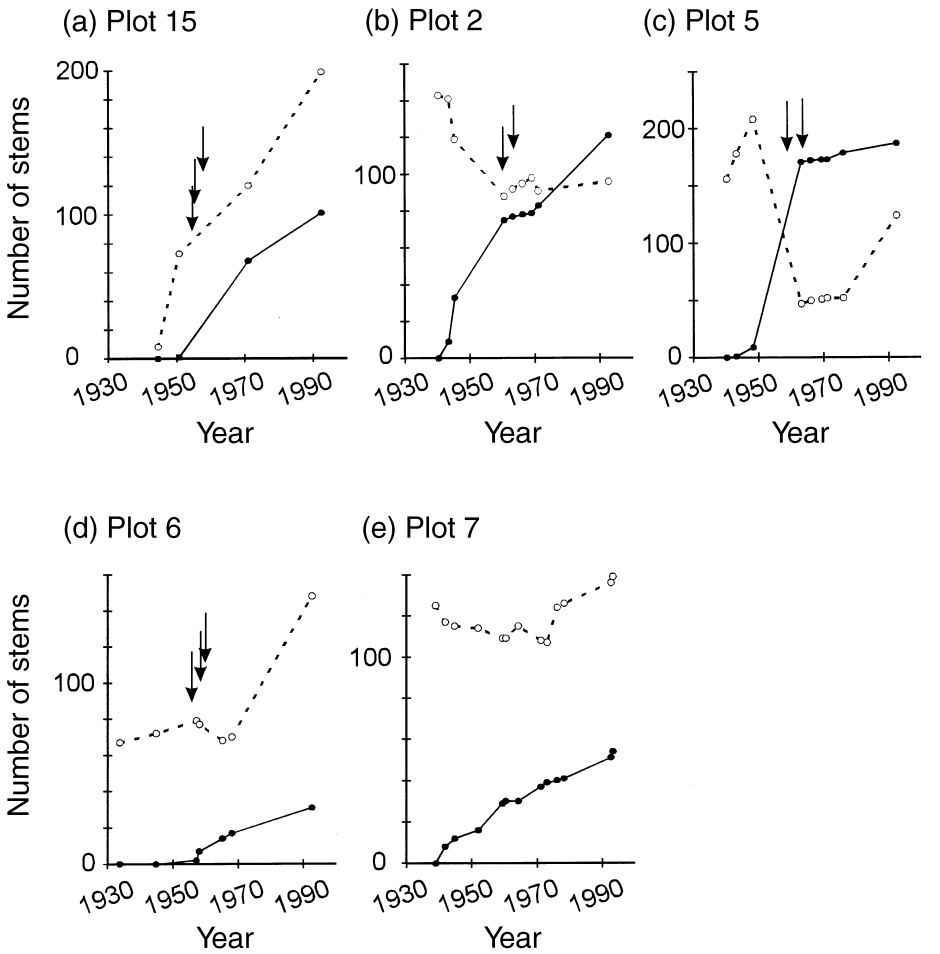


Figure 8. Stem number (open circles) and cumulative stem loss (filled circles) for the minimum inclusive population (i.e. timber species ⩾ 25 cm diameter) for all plots at all dates. The timing of silvicultural treatments is indicated. For plot 6 the survivorship up to 1957 may be confounded by lost data on stems that died before that date.

1.64% y^{-1} with 95% confidence intervals of 0.89–1.23% y^{-1} and 1.45–1.84% y^{-1} respectively). Recruitment was consistently higher than mortality throughout the measurement period, with the imbalance being most pronounced in recent times but both varied between species (Figure 11). For the 11 species where both gains and losses occurred in stems ⩾ 20 cm drh, there is a significant rank correlation between calculated m and r values (n = 11 species, $\tau = 0.46$, $P = 0.039$). Mortality is significantly lower than the plot average for *Cynometra* and higher than average for *Funtumia elastica* ($P = 0.016$ and 0.0057, n = 8 and 12 respectively, by Poisson count comparisons). Stem size had little detectable influence on mortality in most species, but the smaller stems of *F. elastica* had significantly higher survival than larger ones ($P = 0.018$, by Wilcoxon test, n = 15).

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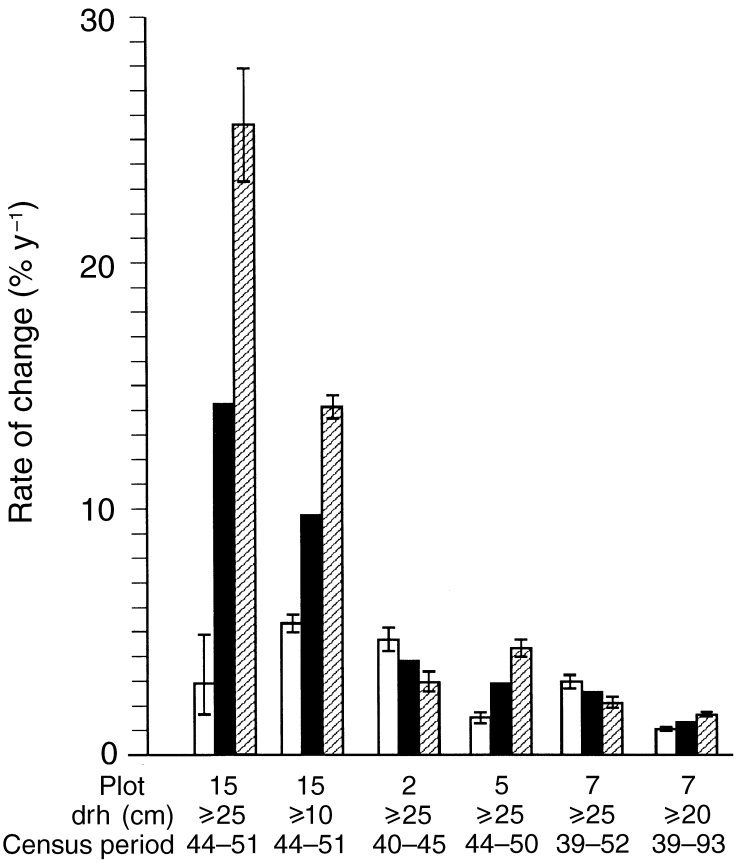


Figure 9. Overall mortality, *m*, (open bars), recruitment, *r*, (hatched bars) and mean, [(*r*+*m*)/2] (black bars) in the plots prior to silvicultural treatment. Note the different minimum stem sizes for plots 15 and 7, and different time intervals in plot 7. Bars on the mortality and recruitment indicate the 75% confidence limits calculated from the F distribution.

In plot 7 there was an increase in the density of small stems, but no significant change in size class distribution in plots 2 and 5 in the shorter period prior to silvicultural intervention (Table 5).

The relationships between initial stem size and subsequent mortality were examined for plots 15, 2 and 5 prior to interventions but no clear pattern is seen except the high rate recorded for the smallest stems in plot 15 (Figure 12). For plot 7, a pattern of decreasing mortality with increasing size is apparent (Figure 13), and a rank correlation for *m* against initial size class is significant ($n = 5$, $\tau = -0.95$, $P = 0.023$). This reduced mortality in larger stems sizes is seen over shorter periods but is significant only for the period 1939–52 ($n = 5$, $\tau = -0.80$, $P = 0.05$).

The contribution of large trees to forest dynamics

Plot 7 provides a rare opportunity to assess changes in BA in pristine mature forest over 54 y (1939–1993). The estimated loss of BA for all stems ⩾ 20 cm

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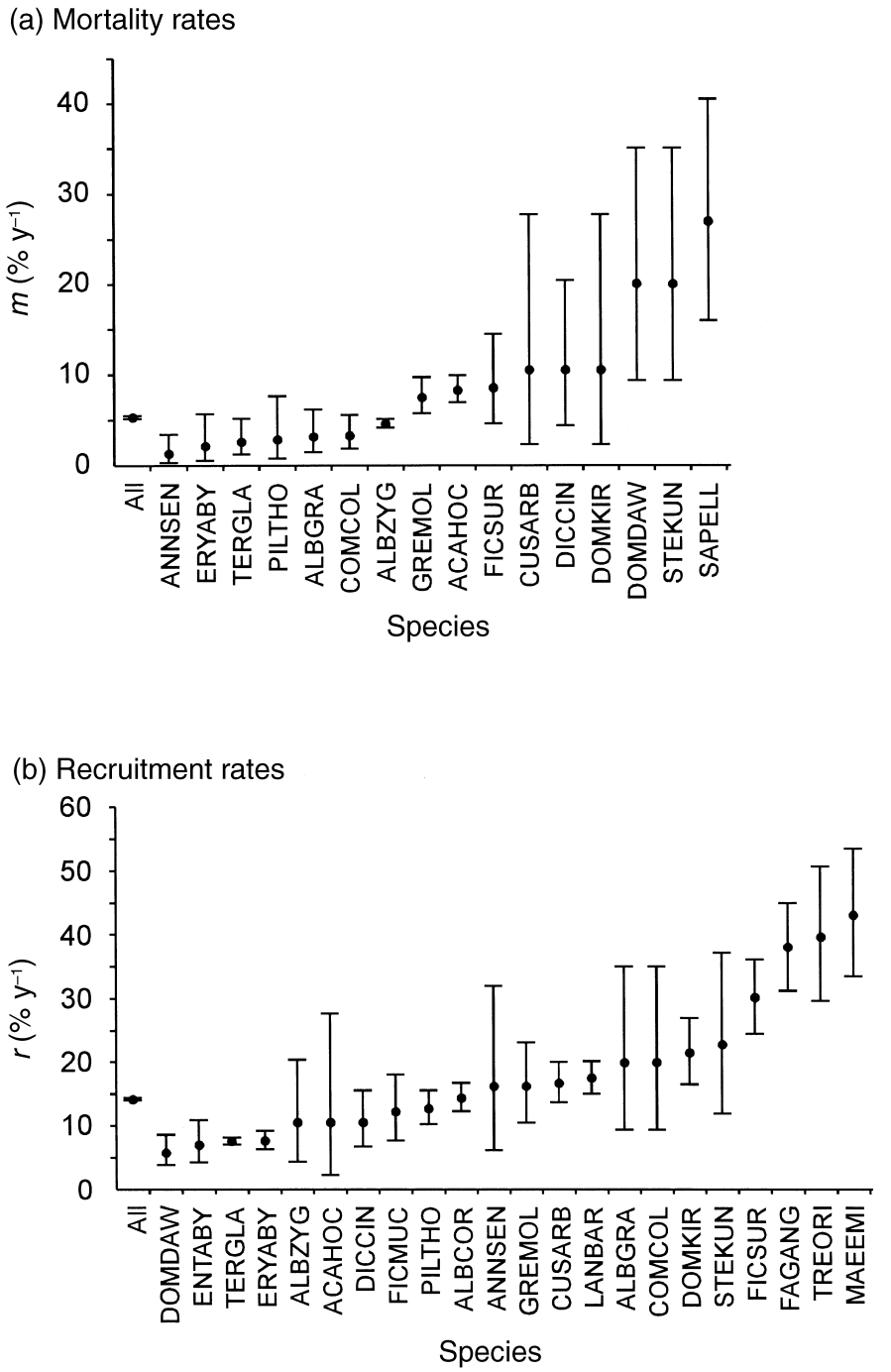


Figure 10. (a) Annual mortality, and (b) recruitment rates in plot 15 from 1944 to 1950, stems ⩾ 10 cm drh. Species are ordered lowest to highest. Bars indicate the 75% confidence limits calculated from the F distribution. Species are identified by their six-letter codes provided in Appendix 2, and 'ALL' refers to all stems combined. Species are designated by their six-letter codes provided in Appendix 2.

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Table 4. Poisson count comparisons recruitment and mortality rates for all stems ⩾ 20 cm drh in plot 7 over different periods.

Period	Losses, n	Gains, n	Change	z	P
1939–1952	43	61	+	1.67	0.096
1952–1976	68	92	+	1.82	0.069
1976–1993	42	99	+	4.72	<0.00001
1939–1993	113	212	+	5.43	<0.00001

drh is > 0.28 m^2 ha^{-1} y^{-1}. The loss in the 20–30 cm class is 8% of the total mortality, the 60–100 cm class provides nearly 20% of annual loss while the ⩾ 100 cm class contributes over 60% (> 0.175 m^2 ha^{-1} y^{-1}) of BA loss. This 60% was the result of a loss of only 7 stems that were ⩾ 100 cm drh in 1939. This pattern is consistent through each period: between 1939 and 1952, four stems ⩾ 100 cm drh died but this was 76% of all the BA lost; from 1952 to 1976, five stems died contributing 55% of all BA lost; and from 1976 to 1993, three stems contributing 69% of all BA lost.

These estimates of changes in BA are imprecise as many of the largest stems are fluted or buttressed. A careful (non-automated) comparison, where measures were matched stem by stem to try to use the same point of measurement for each stem at each enumeration, showed that the BA of all stems ⩾ 40 cm drh has remained approximately constant, being 58 m^2 ha^{-1} in 1939, and 63 m^2 ha^{-1} in 1992 (with error approximately ± 10%, estimated by taking different points of measurement on fluted *Alstonia* stems).

DISCUSSION

Species records

Analysis of the species records raises several questions. In Ugandan terms, Budongo has a rich tree flora. This is despite the limited altitude and topographic ranges of the forest, and its rather uniform soils. Budongo's history of succession and disturbance is probably not exceptional. Part of the explanation may lie in the relatively long history of botanical research that has been conducted at Budongo, with the species list rising as the forest becomes increasingly well studied. In any case, over 80% of Budongo's tree flora has now been recorded from Eggeling's PSPs, which cover less than 0.05% of the forest area (12 plots of 1.86 ha in 430 km^2). Even given that the plots were located to represent a range of forest types, and that the plots have had a long history of intensive botanical study, this seems notable.

Edaphic factors, such as a stream bed in plot 6, are clearly important in determining local species composition. By providing a record of temporal changes in species abundance, the PSP data imply that many of the patterns in forest composition are also a result of temporal processes (site history, succession) that are linked to stem turnover. All of the plots show an increase in species numbers over time. The increase in species in the plots is associated

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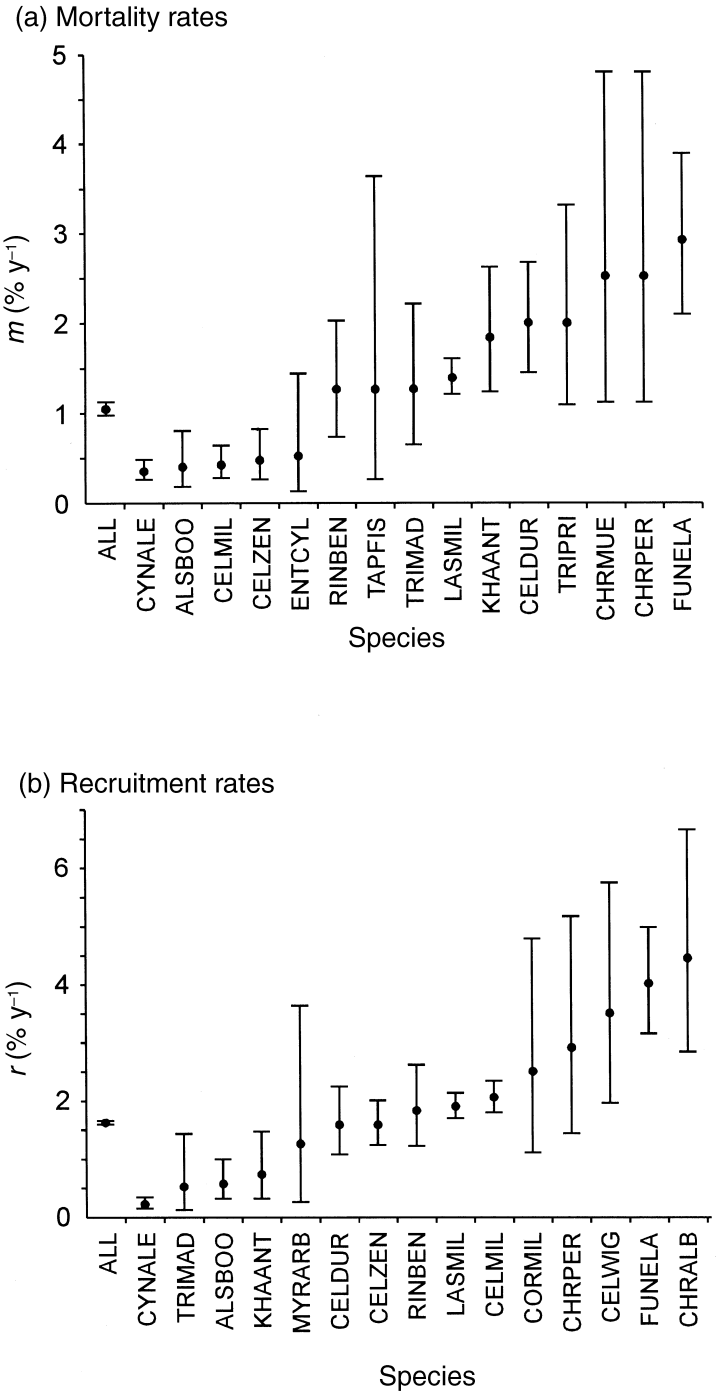


Figure 11. Annualized mortality and recruitment rates for species gaining or losing at least one stem ⩾ 20 cm drh in plot 7 from 1939–1993. Species are ordered lowest to highest. Bars indicate the 75% confidence limits calculated from the F distribution. Species are designated by their six-letter codes provided in Appendix 2, and 'ALL' refers to all stems combined.

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Table 5. Analysis of changes in stem-size distribution between census periods by Kolmogorov–Smirnov two sample tests. D–N is the maximum difference between cumulative distribution functions, and K–S is the test statistic. The number of stems in each analysis can be read from Appendix 1.

Plot	Period	Minimum drh size (cm)	D–N	K–S	P
5	1948–92	20	0.139	1.77	0.0039
7	1939–93	20	0.123	1.51	0.021
15	1944–50	10	0.217	3.53	< 0.00001
15	1950–92	10	0.152	3.03	< 0.00001

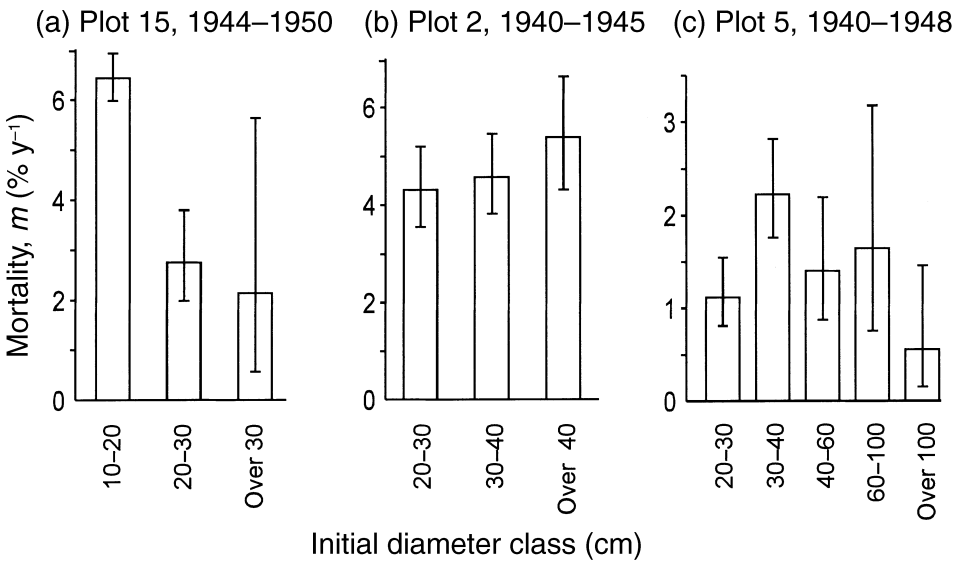


Figure 12. Mortality by original diameter class (cm) in plots 15, 2 and 5, prior to silvicultural treatment. Note the different size-classes and time intervals. Bars indicate the 75% confidence limits calculated from the F distribution.

with, and partly caused by an increase in stems. This is mostly a result of species that were already known from other parts of the forest becoming newly established within these plots. For example, before 1992, *Tetrorchidium* had only been recorded as one stem in the 'swamp' sited plot 11 (Eggeling 1947a), but was recorded in two non-swamp plots in 1992. There are shifts in relative densities and some previously absent species are now widespread. *Trichilia martineaui* for example, occurred in four of the five plots in 1992—though recorded once before in the forest, it had not been found during an intensive previous study on *Meliaceae* and was considered very rare (Styles 1974, Styles *pers. comm.*).

In the absence of human disturbance, mature, continental tropical rain forests are usually considered resistant to invasion by exotic species (Rejmánek 1996, Whitmore 1991). Two exotic species have been recorded from the

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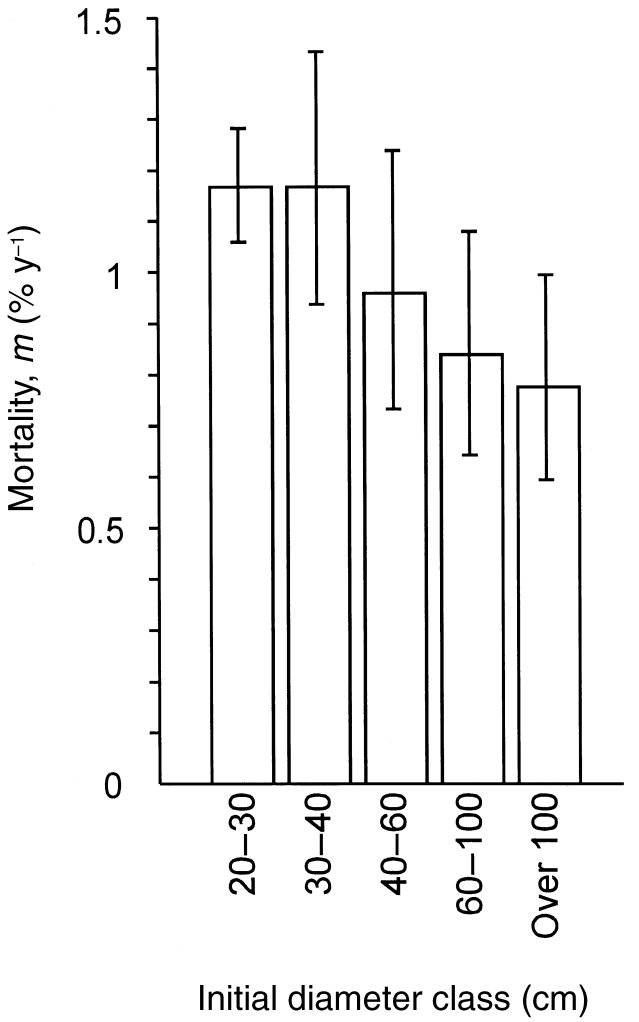


Figure 13. Long-term mortality rates from plot 7, by original diameter class (cm). Bars indicate the 75% confidence limits calculated from the F distribution.

Budongo PSPs, both of which were new records for the plots in 1992. *Cassia spectabilis* DC. colonizes gaps and more open forests, and would increase under any regime that increased disturbance (e.g. logging). *Psidium* occurs in closed forest at a low density and if truly shade-tolerant, may increase. A third species, *Broussonetia papyrifera* (L.) Vent., is another naturalized exotic in the Budongo forest (Sheil 1994). *Broussonetia* fruits are eaten by various animals and the tree regenerates well in open areas such as road sides. In closed forest it expands slowly by suckering and tree-fall sprouting, dominating the understorey such that whenever gaps occur they pre-empt all other species. Such spread is slow and *Broussonetia* does not yet occur in any of the PSPs.

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Species changes through succession

The advancement of the forest edge in plot 15 during the first measurement period is reflected by the rapid increase in both stems and species. Not only forest species, but also savanna species (e.g. *Annona*, *Piliostigma*, *Terminalia* and *Cussonia*) increase. The early observations in plots 2 and 5 by contrast reveal few obvious trends apart from the marked imbalances between recruitment and mortality. In plot 2, mortality is higher than recruitment, and there is marked decline in *Maesopsis* while *Caloncoba* increases. In plot 5, recruitment is higher than mortality, there is a loss of *Funtumia elastica* and an increase of *Celtis mildbraedii*.

In plot 7, there was an increase in species numbers and a large increase in smaller stems. No species showed significant decline, and both light-demanding and shade-tolerant species increase in abundance (*Celtis mildbraedii*, *C. zenkeri*, *Chrysophyllum albidum*, *Lasiodiscus* and *Funtumia elastica*). Recruitment and mortality were correlated for common species, as has been shown in several other studies (e.g. Lieberman *et al.* 1985a, Swaine *et al.* 1987a, Swaine & Hall 1988).

Stem turnover

The silvicultural treatments in plots 2, 5 and 6 had a marked effect. Not just 'weed' species but also commercial stems were lost, most notably in plot 5. Plot 6 eventually showed marked increases in stems of timber species through recruitment (Figure 8), which was the intended effect of the silvicultural treatment (see Dawkins 1954, 1955; Philip 1965). In the early successional plot 15, the loss of stems by treatment is obscured by the rapid recruitment of new stems.

Stem-turnover rates declined with implied successional stage (Figure 9). A slowing of vegetation dynamics in late successional stages has been reported from other vegetation types (Bornkamm 1981, Prach 1993). The proximate cause is the increasing proportion of shade-tolerant species (Figure 1) which are generally more long-lived.

Rates of recruitment and mortality often appear out of balance, with recruitment normally outstripping mortality (Figure 9). The generality of this phenomenon suggests a forest-wide explanation, of which one of the most likely candidates is the local loss of elephants (Sheil 1998, and unpubl. data).

Large trees and mortality

Larger stems have had lower than average mortality in plot 7, and the phenomenon is consistent over both long and short periods. Published analyses of mixed tropical tree populations $\geqslant$ 10 cm DBH have generally failed to detect a relation between size and mortality (e.g. Condit *et al*. 1993, Gentry & Terborgh 1990, Kohyama 1991, Lieberman *et al*. 1985b, Lieberman & Lieberman 1987, Manokaran & Kochummen 1987, Milton *et al*. 1994, Swaine 1989, Swaine *et al.* 1987a). Where a relationship has been found, mortality has usually been greater at intermediate (e.g. Carey *et al*. 1994) or large sizes (e.g. Mervart

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1972), and is often associated with drought (Hubbell & Foster 1990, Leighton & Wirawan 1986, Seth *et al.* 1960, Tang & Chang 1979), although Hartshorn (1990) found higher drought mortality in smaller stems. Droughts and variation in water access appear a plausible explanation for the distribution of deaths amongst tree size classes, but the argument is equivocal, with upper canopy trees being more exposed to desiccation but also being likely to have deeper roots. Leaf fall strategies are also likely to be relevant: most of Budongo's canopy species are deciduous while understorey species are mostly evergreen. Other causal factors may include increased vulnerability of smaller stems to lethal damage (e.g. tree falls, Clark & Clark 1991; or elephants, Laws *et al.* 1975); higher mortality in small stems may be due to an increased proportion of them being below their compensation point compared with large stems; species with a large maximum size may have reduced long-term mortality (the species with lowest mortality indeed achieve large size).

Average mortality in plot 7 (1.0% y^{-1}) is far lower than that generally reported for other tropical forests, where values of around 2–3% y^{-1} are typical (Swaine *et al.* 1987b). The large proportion of species for which neither stem deaths nor recruits occurred also illustrates this relative stasis. The inherent slow dynamics of this plot confers a passive slowness to change, which should be distinguished from dynamic stability based on equilibrium replacement.

Large stems dominate basal area losses. In plot 7, 60% of all basal area lost in a 54-y period was provided by only seven individual stems (ignoring collateral damage to other stems). Stochastic patterns of mortality of large stems will thus dominate not only basal area and biomass change, but also canopy cover, and associated factors (e.g. regeneration and growth).

Tree longevity

The plot 7 data imply considerable longevity for larger trees. This is explored in crude terms assuming a constant probability of annual death equivalent to the recorded annual mortality (i.e. estimated t = ln[remaining fraction]/ ln[1-annual loss], see Sheil & May 1996 for a more critical examination of this assumption). For example, if trees over 1 m drh have an *m* value between one and 0.6% y^{-1} (see Figure 13) the half-life is *c.* 70–120 y, and one in a hundred trees are expected to survive for 460–750 y. A low mortality of *c.* 0.4% y^{-1} (e.g. *Cynometra*, Figure 11) implies a 172-y half-life with one in a hundred such stems surviving 1150 y. These could be conservative estimates as long-term survivorship is generally underestimated by shorter-term evaluations (Sheil & May 1996), however senescence and rare mortality-causing events have not been considered. Note also that these estimates are for trees that are already 1 m in diameter which for *Cynometra* can conceivably take 100–500 y, (using median growth rates per-size class for 10 to 100 cm drh trees gives *c.* 350 y growth data from Sheil 1997c). Not enough stems are included to justify more sophisticated modelling but it does appear that, barring catastrophes, stems will readily survive several centuries. These estimates could potentially be tested using isotope-based techniques.

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Trends in plot 7

Eggeling's (1947a) successional model predicts that there should be a relative increase in shade-tolerant stems and species. In plot 7 however, although there is a relative increase in shade-tolerant stems the proportion of shade-tolerant species actually declined (Figure 2). The absolute increase in both stems and species offers an explanation: the original species already included the most common shade-tolerant taxa, so all 'newly recruited' species are less shade-tolerant even though the original more shade tolerant species showed a greater increase in stems. The imbalance between recruitment and mortality rates has resulted in plot 7 reaching a stem density higher than *any* of Eggeling's (1947a) original plots (from 472 to 586 stems $\geqslant$ 10 cm drh ha^{-1}, a rise of 24%) and more than twice the 236 stems $\geqslant$ 10 cm drh ha^{-1} in Eggeling's most 'successionally advanced' plot (plot 10). One potential explanation for this increase is a 'large-tree-fall' effect. The death of these large stems implies an increase in canopy openness with associated increased light penetration (c.f. Jennings *et al.* 1999). However, several lines of evidence suggest that community behaviour in this plot has not been dominated by canopy gaps. The basal area of larger stems has remained constant and high ($c.>$ 55 m^2 ha^{-1}); most of the recruited stems are of shade-tolerant species, growth rates have not increased (Sheil 1997c), and there is little evidence of the patchy recruitment expected if recruitment were centred on canopy gaps (Sheil 1996b). The decline in understorey herbivores (e.g. elephants, a major cause of mortality for slow growing understorey stems, Laws *et al.* 1975), remains the most plausible explanation for the increased stem densities.

The value of long-term studies

Long-term tropical forest dynamics are currently not well described or understood. Despite the impressive sample sizes generated by large PSPs, most of our current perspectives are built on very short-term observations. The relationship between short-term observations and longer-term processes are difficult to assess without adequate observations. What is a fluctuation and what is a trend? In this study we have been able to record changes over 50 y. These data have already been valuable in demonstrating the uncertain relationships between short and long term measures of stem turnover (Sheil 1995a,b; Sheil & May 1996), stem growth (Sheil 1995a, 1997b,c) and changes in species richness (Sheil 1998, in press) – and have also suggested the poor predictive power of the elegant hypotheses which have proliferated without reference to real forest change (Sheil 1999c).

The results given here further emphasize the complexity of forest change underlying the role of stochastic processes such as large tree falls, the probable longevity of some stems, and also the probable significance of a range of influences upon vegetation structure and composition. We have identified so many specific details and factors that may have influenced the forests that it may appear that the results have little generality to other sites. However, if we start

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by noting that every site is a product of local history we will recognize that increasing knowledge about any site (not just Budongo) defines the particular not the general (c.f. Sheil 1996a). By identifying influences we are characterizing what matters in the long-term – a factual basis about long-term change.

Prior to the measurements reported here, much of the data and four of the plots had been assumed lost. The study has now provided detailed data on a changing forest. Several of the findings, such as the increase in the proportion of shade-tolerant species and stems in the early successional plots are consistent with established theory. Nevertheless, the data provide an example of tropical rain forest succession that is unique because it is time-series data (with rates of change quantified) rather than a succession inferred from a spatial series or model. Other findings, such as the increased stem density, proportion and number of shade-tolerant species and the overwhelming contribution of a small number of trees to basal area loss in the primary forest plot (plot 7) were less expected and could not have been found other than by long-term observation. While some of these results may be local others may reflect more widespread processes, the generality of which can only be judged by the evaluation of other long-term data.

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Appendix 1. Summary of the measurement history and management of the Budongo permanent sample plots.

Plot	Measurement conventions				Descriptive data		[6]Management and notes
	[1]Date	[2]Min d (cm)	New recruits measured	Species measured	[3]Stem N	[4]BA (m^2 ha^{-1})	
15	1944	9.7		All	425	5	
	1950	9.7	Yes	All	761	12	Poisoning > 19.4 cm, 1955, 1956, 1958 or 1959.
	1971	8.8	Yes	Timber only	201	13	Total BA lost 8–15 m^2 ha^{-1}
	1992	9.8	Yes	All	927	35	Mapped
2	1940	23.9		All	257	13	
	1943	24.3	Yes	All	250	14	
	1945	24.7	No	All	219	12	
	1960	10.2	Yes	Timber only	131	8	Poisoned stems > 9.7 cm (1960)
	1963	9.8	Yes	Timber only	135	9	Poisoned stems > 39 cm (1964)
	1966	9.7	Yes	Timber only	141	10	Total BA lost 6–10 m^2ha^{-1}
	1969	10.3	No	Timber only	152	11	
	1971	10.4	Yes	Timber only	145	11	
	1992	9.7	Yes	All	985	21	Mapped
5	1940	21.3		All	259	36	
	1943	24.3	Yes	All	273	37	
	1948	16.6	Yes	All	448	51	
	1963	10.8	Yes	Timber only	67	11	Poisoned stems > 9.7 cm (1960)
	1966	9.8	Yes	Timber only	75	12	Poisoned stems > 39 cm (1964)
	1969	10.2	Yes	Timber only	81	12	Total BA lost 25–30 m^2 ha^{-1}
	1971	10.2	Yes	Timber only	83	12	
	1976	11.2	Yes	Timber only	81	13	
	1992	9.6	Yes	All	810	24	Mapped
6	1933	23.9		Timber only	90	13	Survivors till 1957 only measured
	1944	25.0	No	Timber only	90	14	Survivors till 1957 only measured
	1957	15.0	Yes	Timber only	106	16	Poisoned > 9.7 cm (1956)
	1958	10.8	Yes	Timber only	112	16	Poisoned > 9.7 cm (1958 & 1959)
	1965	6.1	Yes	Timber only	100	16	Total BA lost 15–25 m^2 ha^{-1}
	1968	8.2	No	Timber only	99	16	
	1992	9.6	Yes	All	849	29	Mapped

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Appendix 1. *Continued.*

Plot	Measurement conventions				Descriptive data		[6]Management and notes
	[1]Date	[2]Min d (cm)	New recruits measured	Species measured	[3]Stem N	[4]BA (m^2 ha^{-1})	
7	1939	15.0		All	278	63	
	1942	19.4	No	All	255	58	
	1944	19.4	Yes	All	261	61	
	1952	15.4	Yes	All	322	45	
	1959	9.9	Yes	Timber only	250	42	
	1960	9.9	No	Timber only	247	42	
	1964	8.3	Yes	Timber only	273	43	
	1971	8.5	Yes	Timber only	293	42	
	1973	8.3	No	Timber only	287	42	
	1976	8.7	Yes	All	988	54	
	1978	8.8	No	All	982	54	
	1992	10.0	Yes	All	1090	50	
	1993	10.0	No	All	1087	50	Mapped

[1]Underlining shows the end of the measurement series for 'untreated' forest.
[2]Min d = smallest diameter measured.
[3]Stem N = number of stems measured.
[4]BA = basal area for all measured stems at highest point of measurement.
[5]Total BA lost is estimated from graphical examination.

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Appendix 2. Species names, codes, guilds and basic parameters.

Species nomenclature mostly follows *Flora of Tropical East Africa* (Various Authors 1952, *et seq.*), or from advice and determinations provided by staff at the Royal Botanic Gardens, Kew. Authorities follow the recommendations in Brummitt & Powell (1992). Codes are formed from the the first three letters of the generic and specific names, giving each species a unique six letter code. 'Guild' follows Hawthorne (1995, 1996), and are given by numbers here, 1: Pioneers, 2: Non-pioneer light-demanders (NPLDs), 3: Shade-bearers, 4: Swamp species, 5: Savanna species, 6: Strangler fig species, 0: Unclassified. Height is the characteristic mature height of the species, derived from Eggeling & Dale (1952) and Hamilton (1991). Number of observations is from Eggeling (1947a) and plot 15 in 1944, these figures are used to derive the successional index. This index is based on simple (single-axis) weighted averaging (see e.g. Hill 1973, Ter Braak & Barendregt 1986) by species for each stem $\geqslant$ 10 cm drh in Eggeling's (1947a) data and plot 15 (in 1944) along the plot sequence 15 then 1–10. This index can be considered as the 'mean plot' for that species along the sequence ($= \Sigma$ (count of species in plot n_i) $\times$ $[n_i+1]/\Sigma$ (count of species), where plot 15 is considered n_0, plot 1 is n_1, etc.).

Species codes in bold font signifies those species included on the list of 'timber desirables' and measured on all dates when encountered, the rest are historically considered both as 'undesirables' and as 'weed' species.

Code	Scientific name	Guild	Height (m)	No. obs.	Successional index
ACAHOC	*Acacia hockii* De Wild. Fabaceae subfam. Mimosoideae	5	4	48	1.00
ACAPUB	*Acanthus pubescens* (Oliv.) Engl. Acanthaceae	1			
ACASIE	*Acacia sieberiana* DC. Fabaceae subfam. Mimosoideae	5			
AIDMIC	*Aidia micrantha* (K.Schum.) F. White. Rubiaceae	3			
ALACHI	*Alangium chinense* (Lour.) Harms. Alangiaceae	1			
ALBCOR	*Albizia coriaria* Oliv. Fabaceae subfam. Mimosoideae	5	35	6	2.33
ALBFER	*Albizia ferruginea* (Guill. & Perr.) Benth. Fabaceae subfam. Mimosoideae	2			
ALBGRA	*Albizia grandibracteata* Taub. Fabaceae subfam. Mimosoideae	2	30	11	1.00
ALBGLA	*Albizia glaberrima* (Schum. & Thonn.) Benth. Fabaceae subfam. Mimosoideae	1			
ALBZYG	*Albizia zygia* (DC.) J. F. Macbr. Fabaceae subfam. Mimosoideae	2	30	200	1.16
ALCLAX	*Alchornea laxiflora* (Benth.) Pax & K. Hoffm. Euphorbiaceae	3	10	219	7.11
ALLDUM	*Allophylus dummeri* Baker f. Sapindaceae	0	10	5	6.60
ALSBOO	*Alstonia boonei* De Wild. Apocynaceae	1	40	50	6.82
ANIALT	*Aningeria altissima* (A. Chev.) Aubrév. & Pellegr. Sapotaceae	2	50	9	6.78
ANNSEN	*Annona senegalensis* Pers. subsp. *senegalensis* LeThomas. Annonaceae	5	20	13	1.00
ANTLAC	*Antidesma laciniatum* Muell. Arg. var. *membranaceum* Muell.Arg. Euphorbiaceae	3	10	8	2.13
ANTMIC	*Antrocaryon micraster* A.Chev. & Guill. Anacardiaceae	2	35	2	4.00
ANTTOX	*Antiaris toxicaria* Leschenault var. *usambarensis* (Engl.) C.C.Berg. Moraceae	2	45	3	8.33
BALDAW	*Balsamocitrus daweii* Stapf. Rutaceae	3	20	2	7.50
BALWIL	*Balanites wilsoniana* Dawe & Sprague Balanitaceae	2			
BAPPAR	*Baphiopsis parviflora* Baker f. Fabaceae subfam. Caesalpinoideae	0			
BAPWOL	*Baphia wollastonii* Baker f. Fabaceae subfam. Papilionoideae	3	20	3	6.67
BAPKEW	Unknown (D.Sheil 1295, 1737 matched with Drummond & Hemsley 4576 (1953))	0			
BEIUGA	*Beilschmiedia ugandensis* Rendle. Lauraceae	3			
BELHYP	*Belonophora hypoglauca* (Welw. ex Hiern) A.Chev. Rubiaceae	1	15	35	7.83

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Appendix 2 *Continued*

Code	Scientific name	Guild	Height (m)	No. obs.	Successional index
BEQOBL	*Bequaertiodendron oblanceolatum* (S.Moore) Heine & Hemsley. Sapotaceae	3	20	25	6.68
BERABY	*Bersama abyssinica* Fresen. subsp. *abyssinica* var. *holstii* (Guerke) Verdc. Melianthaceae	1			
BLIUNI	*Blighia unijugata* Bak. Sapindaceae	3			
BLIWEL	*Blighia welwitschii* (Hiern) Radlk. Sapindaceae	2	25	1	6.00
BOMBUO	*Bombax buonopozense* P. Beauv. subsp.*reflexum* (Sprague) A. Robyns. Bombacaceae	1	50	1	3.00
BRIMIC	*Bridelia micrantha* (Hochst.) Baill. Euphorbiaceae	1			
CALCRE	*Caloncoba crepiana* (De Wild. & T. Durand) Gilg. Flacourtiaceae1	1	10	469	2.93
CANSCH	*Canarium schweinfurthii* Engl. Burseraceae	2			
CASGUM	*Cassipourea gummiflua* Tul. var. *ugandensis* (Stapf.) J.Lewis. Rhizophoraceae	2	25	3	5.00
CASMAN	*Cassia mannii* Oliv. Fabaceae subfam. Caesalpinioidae	1	25	1	3.00
CASSPE	*Cassia spectabilis* DC. Fabaceae subfam. Caesalpinioidae	1			
CATALT	*Cathormion altissimum* (Hook.f.) Hutch. & Dandy. Fabaceae subfam. Mimosoideae	4			
CELAFR	*Celtis africana* Burm.f. Ulmaceae	1	30	8	2.13
CELDUR	*Celtis durandii* Engl. (Arguably = the Malagasy species *Celtis gomphophylla* Baker).Ulmaceae	2	25	75	5.72
CELMIL	*Celtis mildbraedii* Engl. Ulmaceae	3	45	705	7.27
CELWIG	*Celtis wightii* Planch. Ulmaceae	3	25	447	5.97
CELZEN	*Celtis zenkeri* Engl. Ulmaceae	2	40	105	7.75
CHAARI	*Chaetachme* [*Chaetacme*] *aristata* Planch. Ulmaceae1	1	10	10	5.90
CHLEXC	*Milicia excelsa* (Welw.) C.C.Berg [*Chlorophora excelsa* (Welw.) Benth. & Hook.f.]. Moraceae	1	45	3	5.67
CHRALB	*Chrysophyllum albidum* G.Don. Sapotaceae	3	45	93	6.40
CHRMUE	*Chrysophyllum muerense* Engl. Sapotaceae	3	40	51	6.82
CHRPER	*Chrysophyllum perpulchrum* Mildbr. ex Hutch.& J.M.Dalz. Sapotaceae	3	35	47	6.79
CLAANI	*Clausena anisata* (Willd.) Benth. Rutaceae	1	8	7	3.71
CLAHEX	*Claoxylon hexandrum* Muell. Arg. Euphorbiaceae	3			
COFCAN	*Coffea canephora* Froehner. Rubiaceae	3	6	1	6.00
COLGIG	*Cola gigantea* A. Chev. Sterculiaceae	2	35	10	6.50
COMCOL	*Combretum collinum* Fresen. subsp. *binderanum* (Kotschy) Okafor. Combretaceae	5	10	16	1.00
CONLON	*Connarus longistipitatus* Gilg. Connaraceae	0	12	2	6.00
CORAFR	*Cordia africana* Lam. Boraginaceae	5			
CORMIL	*Cordia millenii* Bak. Boraginaceae	1	35	15	4.67
CRABRO	*Craibia brownii* Dunn. Fabaceae subfam. Papilionoideae	3			
CRASCH	*Craterispermum schweinfurthii* Hiern. Rubiaceae	3	10	1	6.00
CROAFR	*Crossonephalis africanus* (Radlk.) Leenh.Sapindaceae	3	25	61	6.31
CROMAC	*Croton macrostachyus* Hochst. ex A.R.Delile. Euphorbiaceae	2	25	1	2.00
CROMEG	*Croton megalocarpus* Hutch.Euphorbiaceae	2	40	1	7.00
CROSYL	*Croton sylvaticus* Hochst. ex Krauss. Euphorbiaceae	1	10	2	8.00
CUSARB	*Cussonia arborea* A.Rich. Araliaceae	5	6	2	1.00
CYNALE	*Cynometra alexandri* C.H.Wright. Fabaceae subfam. Caesalpinioidae	3	50	423	9.38
DESCHR	*Desplatsia chrysochlamys* (Mildbr. & Burret) Mildbr. & Burret. Tiliaceae	3			
DESDEW	*Desplatsia dewevrei* (De Wild. & T.Durand) Burret. Tiliaceae	3			

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Appendix 2 *Continued*

Code	Scientific name	Guild	Height (m)	No. obs.	Successional index
DIAEXC	*Dialium excelsum* Steyaert. Fabaceae subfam. Caesalpinioidae	2	40	3	8.67
DICARB	*Dictyandra arborescens* Hook.f. Rubiaceae	3	10	3	5.67
DICCIN	*Dicrostachys cinerea* (L.) Wight & Arn. subsp. *cinerea*. Fabaceae subfam. Mimosoideaeae	1	15	4	1.00
DIOABY	*Diospyros abyssinica* (Hiern) F.White. Ebenaceae	1	30	170	3.80
DISPEN	*Discopodium penninervium* Hochst. Solanaceae	5			
DOMDAW	*Dombeya dawei* Sprague. Sterculiaceae	5	3	4	1.00
DOMKIR	*Dombeya kirkii* Mast. Sterculiaceae	5	15	19	2.42
DOVABY	*Dovyalis abyssinica* (A.Rich.) Warb. Flacourtiaceae	0			
DRYUGA	*Drypetes ugandensis* (Rendle) Hutch.Euphorbiaceae	3	15	21	6.52
DURREP	*Duranta repens* L. Verbenaceae	1			
EKESEN	*Ekebergia senegalensis* A.Juss. Meliaceae	2			
EHRCYM	*Ehretia cymosa* Thonn. Boraginaceae	1	20	7	3.86
ENTABY	*Entada abyssinica* A.Rich. Fabaceae subfam. Mimosoideae	5	12	1	1.00
ENTANG	*Entandrophragma angolense* (Welw.) C.DC. Meliaceae	2	55	1	11.00
ENTCYL	*Entandrophragma cylindricum* (Sprague) Sprague. Meliaceae	2	55	10	6.70
ENTUTI	*Entandrophragma utile* (Dawe & Sprague) Sprague. Meliaceae	2	55	6	7.67
ERYABY	*Erythrina abyssinica* DC. subsp. *abyssinica*. Fabaceae subfam. Papilionideae	1	15	8	1.00
ERYEXC	*Erythrina excelsa* Bak. Fabaceae subfam. Papilionideae	1	30	2	7.00
ERYFIS	*Erythroxylum fischeri* Engl. Erythroxylaceae	1			
ERYSUA	*Erythrophleum suaveolens* (Guill. & Perr.).Fabaceae subfam. Caesalpinioidae	2	35	56	3.32
EUPTEK	*Euphorbia teke* Schweinf. ex Pax. Euphorbiaceae	5			
FAGANG	*Fagaropsis angolensis* (Engl.) Dale. Rutaceae	0	30	1	1.00
FICDEN	*Ficus desistipulata* De Wild. Moraceae	0			
FICEXA	*Ficus exasperata* Vahl. Moraceae	1			
FICLUT	*Ficus lutea* Vahl. Moraceae	6			
FICMUC	*Ficus mucuso* Ficalho. Moraceae	1	40	1	1.00
FICPOL	*Ficus polita* Vahl subsp. *polita*. Moraceae	5			
FICSAN	*Ficus sansibarica* ?(need fertile). Moraceae	6	30	1	11.00
FICSAU	*Ficus saussureana* DC. Moraceae	4			
FICPSE	*Ficus pseudomangifera* Hutch.Moraceae	6			
FICSUR	*Ficus sur* Forssk. Moraceae	1	25	8	1.75
FICTHO	*Ficus thonningii* Bl. Moraceae	5			
FICVAR	*Ficus variifolia* Warb. Moraceae	1			
FLAIND	*Flacourtia indica* (Burm.f.) Merrill. Flacourtiaceae	5	10	2	5.00
FUNAFR	*Funtumia africana* (Benth.) Stapf. Apocynaceae	2	30	197	4.88
FUNELA	*Funtumia elastica* (Preuss) Stapf. Apocynaceae	2	30	129	6.22
GLYBRE	*Glyphaea brevis* (Spreng.) Monachino. Tiliaceae	3	8	2	7.00
GRESUA	*Greenwayodendron suaveolens* (Engl. & Diels) Verdc. subsp. *suaveolens*. Annonaceae	3	25	3	9.00
GREMOL	*Grewia mollis* Juss. Tiliaceae	1	2	26	1.00
GUACED	*Guarea cedrata* (A.Chev.) Pellegrin. Meliaceae	3	45	8	5.63
HALSTI	*Hallea stipulosa* (DC.) J.F.Leroy. Rubiaceae	4	30	1	7.00
HARMAD	*Harungana madagascariensis* Poir. Guttiferae	1	20	1	1.00
HOLGRA	*Holoptelea grandis* (Hutsch.) Mildbr.Ulmaceae	1	40	29	4.86
HOSOPP	*Hoslundia opposita* Vahl. Labiatae	1			
KEEZAN	*Keetia zanzibarica* (Klozsch) Bridson subsp. *gentilii* (De Wild.).Rubiaceae	1			
KHAANT	*Khaya anthotheca* (Welw.) C.DC. Meliaceae	2	50	32	7.22
KHAGRA	*Khaya grandifoliola* C.DC. Meliaceae	2			

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Appendix 2 *Continued*

Code	Scientific name	Guild	Height (m)	No. obs.	Successional index
KIGAFR	*Kigelia africana* (Lam.) Benth. (prob to *K.moosa* Sprague, Bidgood *pers. comm.*). Bignoniaceae	2			
KLAGAB	*Klainedoxa gabonensis* Engl. Irvingiaceae	2	50	10	5.70
LANBAR	*Lannea barteri* (Oliv.) Engl. Anacardiaceae	5	12	3	1.00
LANWEL	*Lannea welwitschii* (Hiern) Engl. var. *welwitschii*. Anacardiaceae	1	30	2	6.50
LASMIL	*Lasiodiscus mildbraedii* Engl. Rhamnaceae	3	15	753	9.09
LEPDAP	*Leptaulus daphnoides* Benth. Icacinaceae	3	10	2	8.00
LEPMIL	*Leptonychia mildbraedii* Engl. Sterculiaceae	3	10	2	6.50
LEPSEN	*Lepisanthes senegalensis* (Poir.) Leenh. Sapindaceae	3	15	11	6.73
LINBUK	*Lindackeria bukobensis* Gilg. Flacourtiaceae	3			
LINJOH	*Linociera johnsonii* Baker. Oleaceae	3	15	3	2.67
LOVTRI	*Lovoa trichilioides* Harms. Meliaceae	2			
LYCCER	*Lychnodiscus cerospermus* Radlk. Sapindaceae	3	15	6	7.17
MACSCH	*Macaranga schweinfurthii* Pax. Euphorbiaceae	1			
MAEDUC	*Maerua duchesnei* (De Wild.) F.White. Capparidaceae	3	8	59	10.20
MAEEMI	*Maesopsis eminii* Engl. Rhamnaceae	1	40	177	3.76
MAJFOS	*Majidea fosteri* (Sprague) Radlk. Sapindaceae	2	35	6	6.33
MAMAFR	*Mammea africana* Sabine. Guttiferae	3	30	1	7.00
MANDAW	*Manilkara dawei* (Stapf.) Chiov. only discriminated at Budongo after 1957. Sapotaceae	3			
MARDIS	*Margaritaria discoidea* (Baill.) Webster. Euphorbiaceae	1	25	121	3.70
MARLUT	*Markhamia lutea* (Benth.) K.Schum. Bignoniaceae	1	25	7	3.57
MONANG	*Monodora angolensis* Welw. Annonaceae	3	15	1	8.00
MONMYR	*Monodora myristica* (Gaertn.) Dunal. Annonaceae	3			
MONORO	*Monanthotaxis orophila* (Boutique) Verdc. (in Rabongo only). Annonaceae	0			
MORLAC	*Morus lactea* (Sim) Mildbr. Moraceae	1	45	16	4.94
MORLUC	*Morinda lucida* Benth. Rubiaceae	1	12	2	6.00
MULCRA	*Multidentia crassa* (Hiern) Bridson & Verdc. Rubiaceae	0			
MYRARB	*Myrianthus arboreus* Beauv. Cecropiaceae	3	10	24	5.71
NUXCON	*Nuxia congesta* Fres. Loganiaceae	5			
ONCSPI	*Oncoba spinosa* Forsk. Flacourtiaceae	5			
OCHAFZ	*Ochna afzelii* R.Br. ex Oliv. Ochnaceae	5			
OCHMEM	*Ochna membranacea* Oliv. Ochnaceae	3	3	6	3.17
OLEWEL	*Olea welwitschii* (Knobl.) Knobl. Oleaceae	1	45	185	3.28
OURDEN	*Ouratea densiflora* De Wild. & T.Durand. Ochnaceae	3			
OXYSPE	*Oxyanthus speciosus* DC. subsp. *globosus* Bridson. Rubiaceae	3	10	1	5.00
PARFIL	*Parkia filicoidea* Oliv. Fabaceae subfam. Mimosoideaeae	2	30	1	7.00
PARGUI	*Paropsia guineensis* Oliv. Passifloraceae	1			
PAVMOL	*Pavetta molundensis* K.Krause. Rubiaceae	3	7	2	4.50
PEDFIS	*Peddiea fischeri* Engl. (in Rabongo only).Thymeliaceae	1			
PHOREC	*Phoenix reclinata* Jacq.Palmae	5			
PHYINF	*Phyllanthus inflatus* Hutch.Euphorbiaceae	0	8	2	6.50
PICNIT	*Picralima nitida* (Stapf.) T.Durand & H.Durand. Apocynaceae	3	8	1	8.00
PILTHO	*Piliostigma thonningii* (Schumach.) Milne-Redh. Fabaceae subfam. Caesalpinoideae	5	10	6	1.00
PIPAFR	*Piptadeniastrum africanum* (Hook.f.) Brenan. Fabaceae subfam. Mimosoideaeae	2	50	2	6.00
PITMAN	*Pittosporum mannii* Hook.f. Pittosporaceae	3	10	4	2.00

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Appendix 2 *Continued*

Code	Scientific name	Guild	Height (m)	No. obs.	Successional index
PREANG	*Premna angolensis* Guerke. Verbenaceae	1	25	14	3.71
PRUAFR	*Prunus africana* (Hook.f.) Kalkman. Rosaceae	1	35	7	5.00
PSEMIC	*Pseudospondias microcarpa* (A.Rich.) Engl. Anacardiaceae	4	40	5	7.00
PSIGUA	*Psidium guajava* L. Myrtaceae	5			
PSYPAR	*Psydrax parviflora* (Afzel.) Bridson. Rubiaceae	1	12	3	3.33
PTEMIL	*Pterygota mildbraedii* Engl. Sterculiaceae	2	50	40	4.00
PYCANG	*Pycnanthus angolensis* (Welw.) Exell. Myristicaceae	2			
RAUVOM	*Rauvolfia vomitoria* Afzel. Apocynaceae	1			
RICHEU	*Ricinodendron heudelotii* (Baill.) Pierre ex Pax. Euphorbiaceae	1	45	3	6.33
RINBEN	*Rinorea beniensis* Engl. Violaceae	3	10	226	8.58
RINBRA	*Rinorea brachypetala* (Turcz.) Kuntze. Violaceae	3			
RINILI	*Rinorea ilicifolia* (Oliv.) Kuntze. Violaceae	3			
RINOBL	*Rinorea oblongifolia* (C.H.Wright) Chipp. Violaceae	3			
RITALB	*Ritchiea albersii* Gilg. Capparaceae	3	10	1	8.00
ROTURC	*Rothmannia urcelliformis* (Hiern) Bullock ex Robyns. Rubiaceae	3	10	1	6.00
ROTWHI	*Rothmannia whitfieldii* (Lindl.) Dandy. Rubiaceae	3	5	1	4.00
SAPELL	*Sapium ellipticum* (Krauss) Pax. Euphorbiaceae	1	25	52	2.87
SCHARB	*Schrebera arborea* A.Chev. Oleaceae	1			
SECVIR	*Securinega virosa* (Roxb. ex Willd.) Baill. Euphorbiaceae	1			
SPACAM	*Spathodea campanulata* P.Beauv. Bignoniaceae	1	20	48	2.88
SPOPRE	*Spondianthus preussii* Engl. var. *glaber* (Engl.) Engl. Euphorbiaceae	4			
STAKAM	*Staudtia kamerunensis* Warb. Myristicaceae	0	30	1	7.00
STEDAW	*Sterculia dawei* Sprague. Sterculiaceae	2	30	1	5.00
STEKUN	*Stereospermum kunthianum* Cham. Bignoniaceae	5	9	4	1.00
STRMIT	*Strychnos mitis* S.Moore. Loganiaceae	3	35	19	9.84
STRSCH	*Strombosia scheffleri* Engl. Olacaceae	3	30	1	8.00
SURPRO	*Suregada procera* (Prain) Croizat. Euphorbiaceae	3	20	18	5.67
SYZGUI	*Syzygium guineense* (Willd.) DC. Myrtaceae	0			
TABHOL	*Tabernaemontana holstii* K.Schum. Apocynaceae	3	10	88	5.15
TAPFIS	*Tapura fischeri* Engl. Dichapetalaceae	3	20	85	7.45
TECGRA	*Teclea grandifolia* Engl. Rutaceae	3	15	15	6.53
TECNOB	*Teclea nobilis* A.R.Delile.Rutaceae	3	25	11	3.36
TERGLA	*Terminalia glaucescens* Benth. Combretaceae	5	10	47	1.89
TETDID	*Tetrorchidium didymostemon* (Baill.) Pax & K.Hoffm. Euphorbiaceae	1			
TETTET	*Tetrapleura tetraptera* (Schum. & Thonn.) Taub. Fabaceae subfam. Mimosoideae	1	30	3	6.33
TREAFR	*Treculia africana* Decne. subsp. *africana* var. *africana*. Moraceae	2			
TREORI	*Trema orientalis* (L.) Bl.Ulmaceae	1	15	4	2.75
TRIDRE	*Trichilia dregeana* Sond.Meliaceae	0	40	2	6.00
TRIMAR	*Trichilia martineaui* Aubrev. & Pellegrin. Meliaceae	2			
TRIPRI	*Trichilia prieuriana* A.Juss. Meliaceae	3	25	46	6.39
TRIRUB	*Trichilia rubescens* Oliv. Meliaceae	2	15	202	5.28
TRIMAD	*Trilepisium madagascariense* DC. (=*Bosqueia phoberos*). Moraceae	2	30	49	6.73
TURFLO	*Turraea floribunda* Hochst. Meliaceae	1	10	50	3.12
UVACON	*Uvariopsis congensis* Robyns & Ghesquiere. Annonaceae	3	15	56	4.57
VANAPI	*Vangueria apiculata* K.Schum. Rubiaceae	1			
VANMAD	*Vangueria madagascariensis* Gmelin. Rubiaceae	1	10	2	4.00
VERAMY	*Vernonia amygdalina* Del. Compositae	1			

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Appendix 2 *Continued*

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VITFER	*Vitex ferruginea* Schumach.& Thonn. subsp. *ferruginea*. Verbenaceae	2	15	6	6.00
VITDON	*Vitex doniana* Sweet. Verbenaceae	5			
VOATHO	*Voacanga thouarsii* Roem. & Schultes. Apocynaceae	4			
XYLPAR	*Xylopia parviflora* (A.Rich.) Benth. Annonaceae	2			
XYLRUB	*Xylopia rubescens* Oliv. Annonaceae	4			
ZANGOL	*Zanha golungensis* Hiern. Sapindaceae	5			
ZANGIL	*Zanthoxylum gilletii* (De Wild.) Waterm. Rutaceae	1			
ZANLEP	*Zanthoxylum leprieurii* Guill. & Perr. Rutaceae	1	20	7	4.57
ZANRUB	*Zanthoxylum rubescens* Hook.f. Rutaceae	1	13	1	7.00
ZANMIL	*Zanthoxylum mildbraedii* (Engl.) Waterm. Rutaceae	1			

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