Thirty-eight years of change in a tropical forest: plot data from Mpanga Forest Reserve, Uganda

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Abstract

Variations in the composition and structure of mid-altitude, semi-deciduous topical forest in a 0.64-ha plot in Mpanga Forest Reserve, Uganda, are described for a 38-year period to 2006. Repeat surveys of trees in the plot with a girth ≥30 cm at reference height in 1982, 1993 and 2006, following a baseline survey in 1968, indicate only relatively minor fluctuations in density, Shannon diversity, evenness, basal area (BA) and estimated above ground biomass. The largest trees [diameter at breast height (dbh) > 40 cm] and main canopy taxa (e.g. *Celtis mildbraedii*) accounted for the largest fraction of BA. Mortality was the highest amongst taxa classed as early seral, understorey and/or in the smallest size category (dbh = 9.5–20 cm), while new recruits were predominantly understorey taxa. Only one tree was recorded as felled for human use between the surveys of 1968 and 1993. In contrast, a considerable increase in anthropogenic disturbance was evident at the time of the 2006 survey, and illegal logging now poses a substantial threat to future resource availability and carbon storage in what was for a time one of the most protected areas of forest in Uganda.

Key words: Africa, anthropogenic, monitoring, permanent plot, rain forest, selective logging

Résumé

Sont décrites ici les variations de la composition et de la structure d'une forêt tropicale semi-décidue de moyenne altitude, dans une parcelle de 0,64 ha située dans la Réserve forestière de Mpanga, en Ouganda, pendant une période de 38 ans courant jusqu'en 2006. Dans cette parcelle, une surveillance des arbres dont la circonférence est supérieure à 30 cm à la hauteur de référence, répétée en 1982, 1993 et 2006, suite à une première étude réalisée en 1968, indique des fluctuations relativement mineures de la densité, de l'indice de diversité de Shannon, de l'uniformité, de la surface terrière (G) et de la biomasse estimée au-dessus du sol. Les plus grands arbres (dbh > 40 cm) et les taxons principaux dans la canopée (ex. *Celtis mildbraedii*) constituaient la plus grande fraction de G. La mortalitéétait la plus élevée dans les taxons classés comme de début de succession, de sous-bois et/ou dans la catégorie des plus petites tailles (dbh = 9,5–20 cm), alors que les nouveaux recrutements étaient en majorité des taxons de sous-bois. On a rapporté la coupe d'un seul arbre pour une utilization humaine, entre l'étude de 1968 et celle de 1993. Par contre, au moment de l'étude de 2006, une forte augmentation des perturbations d'origine humaine était évidente, et la coupe illégale de bois représente maintenant une menace réelle pour la disponibilité future des ressources et pour le stockage du carbone dans ce qui fut pendant un certain temps une des forêts les mieux protégées d'Ouganda.

Introduction

The dynamics of tropical forests are poorly understood relative to many other vegetation types. This is in part because of their structural and biological complexity and the longevity of many tropical trees, which can greatly exceed those of the researchers (Chambers *et al.*, 2001). A poor level of understanding, however, is also a consequence of the limited number of long-term studies on rates of growth, recruitment and mortality, and variations in these rates as a result of the influence of disturbance factors, such as extreme weather events and anthropogenic activity. Long-term studies, while difficult to maintain, are

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essential in the development and testing of hypotheses regarding processes and rates of ecological recovery following disturbance, both anthropogenic and natural.

Tropical forests have important biological, climatic, hydrological and socio-economic functions, accounting for more than 50% of the Earth's biodiversity (Groombridge & Jenkins, 2003; Clark, 2007), influencing climate, e.g. through the global carbon cycle (Phillips *et al.*, 1998; Lewis, 2006), and providing vital ecosystem and revenue-generating services, such as watershed protection, eco-tourism and acting as sources of forest products (Laurance, 1999; Naidoo & Adamowicz, 2005). Disturbance – both anthropogenic and natural – impacts these functions, and an incomplete understanding of disturbance-related phenomena, such as ecological succession (Sheil, Jennings & Savill, 2000), severely limits attempts to anticipate the effects of future changes in climate conditions and levels of human activity.

Repeat surveys of the same area or areas of vegetation over an extended period of time (tens of years) provide a reliable means of examining the dynamics of tropical forest. In Africa, permanent plots were established in tropical forests in Nigeria in the 1920s (Okali & Ola-Adams, 1987) and Uganda (Budongo Forest) in the 1930s and 1940s (Eggeling, 1947). Later, Maitre (1987), Okali & Ola-Adams (1987) and Swaine, Hall & Alexander (1987a) published permanent plot data from evergreen and semi-deciduous forests in Ivory Coast, dry evergreen mixed deciduous forest in Nigeria and semi-deciduous forest in Ghana respectively. Most recently, Muoghalu (2006) has published data that include the effects of a severe ground fire from a 0.25-ha permanent plot in secondary rain forest in Nigeria.

Of the published permanent forest plot-based studies in Africa, only one location, Budongo Forest, has to date generated data that span more than 30 years (Sheil, 1998, 1999, 2003; Sheil *et al.*, 2000). The permanent plots in Budongo Forest were largely established across what Eggeling (1947) perceived at the time to be a chronosequence relating to ecological succession, from wooded grassland to ironwood (*Cynometra alexandri*) forest. An additional plot was located in an area of swamp forest. A total of twelve plots was originally established, and five of these (four of 1.86 ha and one of 2.12 ha) have been maintained and re-surveyed at intervals, the most recent census taking place in 1992–1993. Commercially non-valuable trees in four of the maintained plots were poisoned in the 1950s and 1960s, while one plot (plot 7) received no such treatment. Notwithstanding difficulties in ensuring data comparability between surveys, some of the conclusions from the work at Budongo Forest (e.g. the importance of large-size trees in forest dynamics locally) could only have been arrived at through analyses of time series data obtained from repeat surveys of the same plots (Sheil *et al.*, 2000).

This study provides analysis of a second dataset spanning more than 30 years from a plot-based study in an area of tropical forest in Africa. Data generated from four repeat surveys of a single, permanent plot in Mpanga Forest Reserve, Uganda, over a 38-year period from 1968 to 2006, are described. The interpretations build upon those drawn from a shorter run of data (25 years, 1968–1993) from the same plot (Taylor *et al.*, 1996). Originally the plot at Mpanga was located in an area of forest that was thought relatively inaccessible and therefore to have been little disturbed by humans. However, increases in mortality and declining basal area (BA) increment, as direct results of human activity, are evident in the results of the 2006 survey and provide an unanticipated opportunity to examine the impacts of recent human intervention in the context of longer-term forest dynamics. An important, distinguishing feature of the work at Mpanga described in this study is that one of the co-authors (ACH) conducted all of the four censuses (1968, 1982, 1993 and 2006), ensuring a high level of consistency in enumerations.

Study site

Mpanga Forest Reserve (0°127′N, 32°175′E) is an area of moist semi-deciduous forest that extends over some 450 ha of gently undulating land between 1140 and 1200 m altitude in Mawokota County, southern Mengo, Uganda, 3 km to the southwest of the town of Mpigi (Fig. 1) and 36 km to the west of Kampala (the main Kampala–Masaka road bisects the forest). Mpanga Forest Reserve lies within the Lake Victoria climate zone (Anon, 1967), which is characterized by a bimodal distribution of rainfall. Accurate and up-to-date meteorological data for Mpanga Forest Reserve are not available. However, Dawkins & Philip (1962) estimated mean annual rainfall (50 year mean) and minimum and maximum temperatures at, respectively, 1168 mm and 17.2°C and 26.1°C. Soils in the area are generally red and yellow latosols on hilltops and ridges, grey sandy loams on lower hill-slopes and blue-grey clays and silts on the lowermost hill-slopes

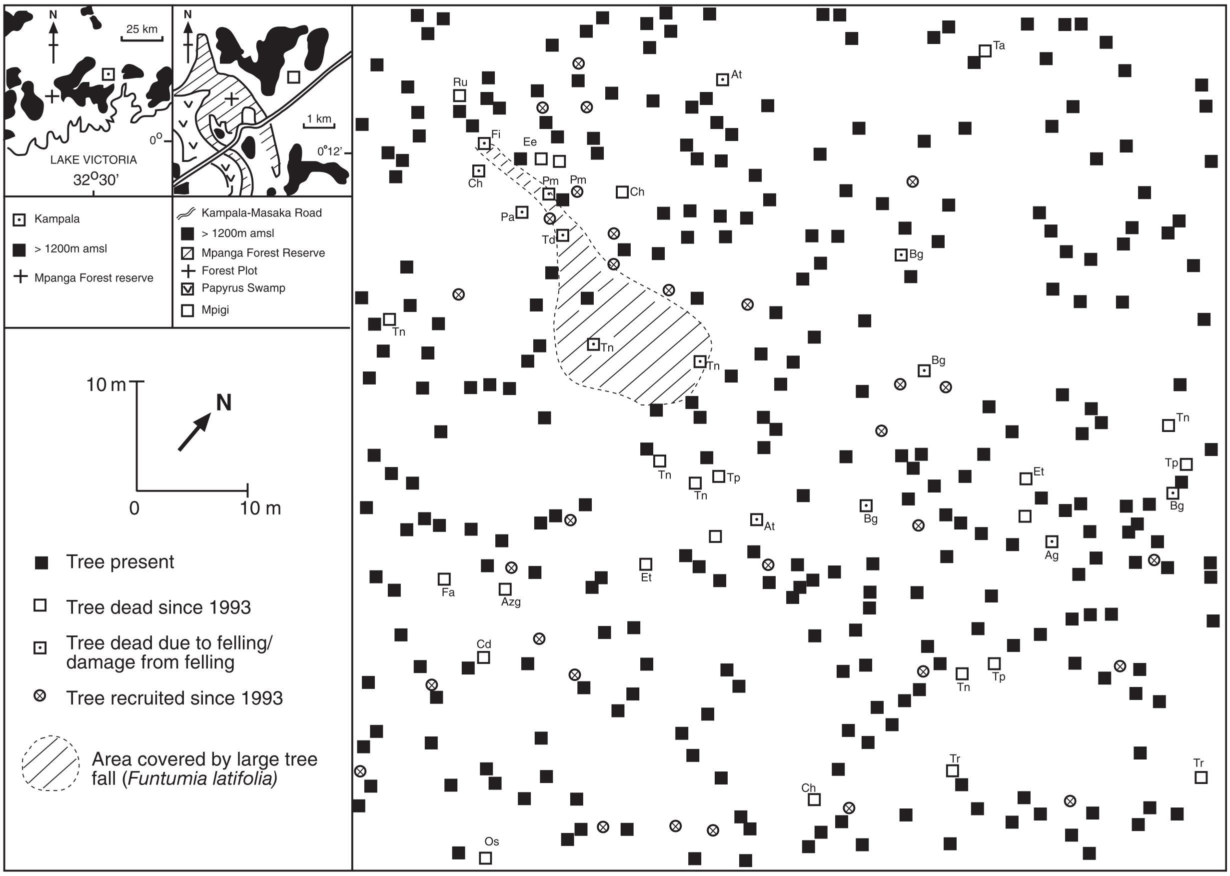

Fig 1 Location of the permanent plot in Mpanga Forest Reserve, Uganda, and spatially displayed plot data from the 2006 survey. Trees that had died between the 1993 and 2006 surveys, including those removed or damaged by humans, are identified. At, *Antiaris toxicara*; Azg, *Albizia zygia/grandibracteata*; Bg, *Belanophora glomerata*; Cd, *Celtis durandii*; Ch, *Tabernaemontana holstii*; Et, *Euphorbia teke*; Fa, *Fagara angolensis*; Fl, *Funtumia latifolia*; Os, *Oxyanthus speciosus*; Pa, *Pycnanthus angolensis*; Pm, *Pseudospondias microcarpa*; Ta, *Treculia africana*; Td, *Trichilia dregeana*; Tn, *Teclea nobilis*; Tp, *Trichilia prieurreana*; Tr, *Trichilia rubescens*. For a more detailed figure showing topography and vegetation cover in the vicinity of the plot at Mpanga, see Taylor *et al.* (1996)

and in valley bottoms (Thomas, 1945; Langdale-Brown, 1960). Forest at Mpanga is classified as lowland forest (Lind & Morrison, 1974; Hamilton, 1989) and belongs to White's (1983) Lake Victoria regional mosaic phytochoria (drier peripheral semi-evergreen Guineo-Congolian rain forest). Dawkins & Philip (1962) provided a detailed description of composition: *Albizia, Antiaris, Celtis africana, Celtis durandii* and members of the Meliaceae (such as *Entandrophragma* and *Lovoa*) characterized the canopy of regenerating forest with *Teclea* prominent in the understorey; *Aningeria, Antiaris, Celtis mildbraedii, Celtis zenkeri, Morus* and large *Entandrophragma* were the main canopy-formers in long-established forest, with *Albizia ferruginea, Albizia glaberrima* and *Albizia zygia* also present. *Teclea* was said to be less common as an understorey tree than in regenerating forest, while sub-canopy synusia tended to be dominated by *Trilepisium* and *Trichilia*.

Forest at Mpanga was gazetted for protection as a Research Forest Reserve in 1951, dedicated to research on the productivity of indigenous forest trees. An 80 × 80 m (0.64 ha) permanent sample plot was laid out in 1968 by ACH on a gentle well-drained slope in a relatively inaccessible, representative area of dryland forest. In 1968, the plot contained taxa associated with both long-established and regenerating forest: *Antiaris toxicaria, C. mildbraedii, C. zenkeri, Entandrophragma* spp. and *Pseudospondias microcarpa* were conspicuous in the canopy; *Funtumia latifolila, Trilepisium madagascariense* and *Trichilia prieureana* were common understorey taxa. *Albizia* spp., *Fagara angolensis* and young individuals of *Antiaris, Entandrophragma*, and *Newtonia buchananii* were present where the canopy was more open. A single, large fig tree (*Ficus mucosa*) was emergent above the main canopy. The plot was re-surveyed in 1982 and 1993 (Taylor *et al.*, 1996) and again in June–July 2006.

Taylor *et al.* (1996:594) concluded that the main changes in forest composition over the period 1968–1993 were due to long-term ecological recovery following previous disturbance, in all likelihood the activities of pit-sawyers. According to Sangster (1950), pit-sawing was formerly widespread at Mpanga, with *Entandrophragma angolense, Lovoa brownii* and *Piptadeniastrum africanum* the most popular species felled. More recently, since about 1990, a thriving wood-carving industry has developed along the Kampala–Masaka road, and drum-making alone now provides employment locally for more than 300 people (Samula, 2001). Nearby forests such as Mpanga are convenient sources of raw materials. Drum-makers are highly selective in the wood they use, the wood having to meet their own requirements as woodworkers and those of musicians; according to Omeja, Obua & Cunningham (2004), drum-makers near Mpanga utilize the trees *Antiaris toxicara*, *Ficus exasperata*, *Ficus mucoso, Funtumia* spp. and *Polyscias fulva*.

Methods

Field methods

Only trees with a minimum circumference of 30 cm girth at reference height [1.3 m above the ground, and equivalent to 9.5 cm diameter at breast height (dbh)] were included in the original survey in 1968 and in subsequent repeat surveys. In the case of buttressed trees, two measurements of girth were taken: one at 1.3 m; and a second, when possible, above the buttresses. For those trees with particularly large buttresses, the measurement of girth directly above the buttressing was replaced with a visual estimate of trunk diameter. The approximate locations of tree falls were recorded, and a note made of any evidence of human impact.

Each tree enumerated was assigned to one of four ecological guilds on the basis of field experience and on information in Dawkins & Philip (1962) and Hamilton (1981): (i) understorey species (mature phase, shade-tolerant tree species of the lower woody strata of primary forest); (ii) main canopy species (mature phase, light-demanding, relatively long-lived species forming the main canopy of primary forest); (iii) emergent species (mature phase, light-demanding, long-lived species growing above the main canopy of primary forest to more than 30 m, usually with spreading crowns); and (iv) seral species (relatively short-lived species requiring gaps for germination and establishment, showing rapid growth and including taxa of both primary and regenerating forests that in some cases may persist to form part of mature forest). A fifth category (unknown) was reserved for unidentified species.

Data analysis

Permanent plot data were analysed in accordance with published procedures. Shannon diversity and evenness measures were determined using the method described in Magurran (2004). Above ground biomass (AGB) was computed from the biomass-regression model (model II) for moist tropical forests with no height measures (Chave *et al.*, 2005) using a figure of 0.56 tonnes m^{-3} for wood specific gravity. This figure is the rough estimate quoted for African forest trees in Brown (1997): the estimate is in broad agreement with measurements of wood specific gravity for 20 of the taxa recorded at Mpanga included in the World Agroforestry's wood density database (range from 0.25–1.10 tonnes m^{-3}), and for an additional six species recorded at Mpanga provided by Marie Noel (unpublished data), which range from 0.40 to 0.78 tonnes m^{-3}. Calculation of the rate relative BA increment, or the annual change in BA divided by the initial BA for each year, followed Hamilton *et al.* (2002), while calculation of annual rates of mortality and recruitment for BA and stems followed Sheil, Burslem & Alder (1995) and Lewis *et al.* (2004a), with final estimates census corrected in accordance with Lewis *et al.* (2004b). Corrected annual turnover, effectively the difference between recruitment and mortality, was established using the method described in Phillips & Gentry (1994).

Results

Changes in structural characteristics

Overall, data from the four repeat surveys indicate relatively stable conditions ecologically from 1968 to 2006, with only relatively minor fluctuations evident in density,

Table 1 Summary of changes in the permanent plot at Mpanga Forest Reserve, Uganda, for the period 1968–2006

	Year of survey			
Parameter	1968	1982	1993	2006
No. individuals per plot	294	332	326	314
Density (ha^{-1})	459	519	509	491
Species richness (ha^{-1})	44 (2)	45 (4)	47	45
Shannon diversity	3.146	3.175	3.168	3.117
Shannon evenness	0.826	0.829	0.823	0.819
Basal area (BA, m^2 ha^{-1}) [all trees, i.e. total BA pool]	39.05	40.91	42.13	41.22
Basal area (BA, m^2 ha^{-1}) [nonbuttressed trees only]	20.55	22.35	23.45	23.51
Estimated above ground biomass (kg ha^{-1}) [all trees]	524,820	543,102	560,353	548,640

Shannon diversity, evenness, BA and AGB (Table 1). A total of 416 individual trees, assigned to 50 taxa (Table 2), was enumerated during the four repeat surveys, with a further five individuals remaining unidentified. The number of living trees recorded in 2006 was about 8% higher than in 1968, while BA increased by about 6% during the same period, although highest levels of BA (and of AGB) were recorded in 1993 (BA in 1993 was *c.* 8% > 1968). Two-hundred and fifteen trees, divided among 26 species, first recorded in 1968 were alive in 2006 (Table 3): *Trilepisium madagascariense* and *Trichilia prieureana* (both understorey taxa) were the most common among the ever-presents, followed by the main canopy-former *Celtis mildbraedii*. Growth rates varied greatly within and between species represented among the ever-presents, with mean rates over the 38-year-long survey period ranging from a low of 1.8 cm^2 year^{-1} (*Entandrophragma cylindricum*, n = 3) to a high of 19.35 cm^2 year^{-1} (*Zanha golungensis*, n = 4).

The majority of trees enumerated in the plot had dbh ≤ 40 cm (Fig. 2), although trees with dbh > 40 cm account of the largest share of BA (ranging from 64–72%). The overall rate of BA change was negative over the period 1968–2006 for trees in the smallest (9.5–20 cm) and largest (>40 cm) dbh categories, but positive for trees in dbh class > 20–40 cm. The proportion of BA accounted for by main canopy taxa remained largely constant, at about 50%, throughout the survey period, with one species, *Celtis mildbraedii*, comprising about one-third of the total BA in each of the censuses. The proportion of BA accounted for by seral taxa declined over the course of the survey, while that for understorey species increased. BA gains exceeded BA losses for all but one of the census periods, with1993–2006 the exception: annual rates of change of BA for the periods 1968–1982, 1982–1993, 1993–2006 and 1968–2006 were, respectively, 0.13, 0.11, −0.07 and 0.06 m^2 ha^{-1} year^{-1}. The rate of relative BA increment decreased from 0.34% year^{-1} (1968–1982) to 0.27% year^{-1} (1982–1993) to −0.17% year^{-1} (1993–2006) and was 0.15% year^{-1} for the entire survey period (1968–2006).

Human impact

There was considerable increase in the number of trees in the plot felled by people during the period 1993–2006 when compared with the previous censuses (1982–1993). In 1993, only a single individual tree was recorded as having been removed by humans since the census of 1982, and of the 36 trees recorded as dead since the previous survey only three were members of taxa that are valued locally in construction and wood-working industries, while no felling of trees or damage by humans was recorded in the plot in either the 1968 or 1982 surveys. The tree recorded in 1993 as having been felled (*Polyscias fulva*, dbh = 16.9 cm in 1983) was too small for its loss to have a major influence on plot statistics. Altogether, ten individuals in the plot had been felled between 1993 and 2006 (five *Belanophora glomerata*, two *Antiaris toxicaria*, and one each of *Albizia gummifera* group, *Belanophora hypoglasca* and *Funtumia latifolia*) and a further seven had been killed as a result of the felling of other trees. In all, more than 6% of the BA present in the plot in 1993 had been lost by 2006, either directly or indirectly as a result of illegal selective felling; this loss more than accounted for any growth in total BA during the same period. Furthermore, an additional thirteen trees had been severely damaged, either directly or indirectly by the activities of woodcutters, of which seven were *Belanophora glomerata*.

Table 2 Full scientific names, including authorities, of taxa recorded in the forest plot, 1968–2006

- Anacadiaceae
  - *Pseudospondias microcarpa* (A. Rich.) Engl.
- Apocynaceae
  - *Funtumia latifolia* (Stapf.) Schltr
  - *Tabernaemontana holstii* K. Schum.
- Araliaceae
  - *Polyscias fulva* (Hiern) Harms
- Boraginaceae
  - *Ehretia cymosa* Thonn.
- Burseraceae
  - *Canarium schweinfurthii* Engl.
- Euphorbiaceae
  - *Euphorbia teke* Scweinf. ex Pax.
- Leguminosae
  - *Newtonia buchananii* (Baker f.) Gilb. and Bout.
  - *Albizia gummifera* (J.L. Gmel.) C.A. Sm
  - *Albizia zygia/grandibracteata*
- Meliaceae
  - *Entandrophragma angolense* (Welw.) C.DC.
  - *Entandrophragma cylindricum* (Sprague) Sprague
  - *Lovoa brownii* Sprague
  - *Trichilia dregeana* Sond.
  - *Trichilia prieureana* A. Juss.
  - *Trichilia rubescens* Oliv.
  - *Turraea* sp.
- Monimiaceae
  - *Xymalos monospora* (Harv.) Baill
- Moraceae
  - *Antiaris toxicaria* Lesch.
  - *Ficus mucoso* Welw.
  - *Morus lactea* Mildbr.
  - *Treculia africana* Decne
  - *Trilepisium madagascariense* DC.
- Myristicaceae
  - *Pycnanthus angolensis* (Welw.) Warb.
  - *Staudtia kamerunensis* Warb.
- Olacaceae
  - *Strombosia scheffleri* Engl.
- Rubiaceae
  - *Belanophora hypoglauca* (Welw. ex Hiern) A. Chév.
  - *Belanophora glomerata* M.B. Moss
  - *Oxyanthus speciosus* DC.
  - *Rubiaceae* sp.
- Rutaceae
  - *Fagara angolensis* Engl.
  - *Fagara leprieurii* (Guill. & Perr.) Engl.
  - *Teclea nobilis* Delile
- Sapindaceae
  - *Blighia unijugata* Bak.
  - *Sapindaceae* sp.
  - *Zanha golungensis* Hiern

Table 2 (Continued)

- Sapotaceae
  - *Afrosersalisia cerasifera* (Welw.) Aubrév.
  - *Aningeria altissima* (A. Chév) Aubrev. & Pellegr.
  - *Bequaertiodendron natalense* (Sond.) Heine & J.H. Hemsl.
  - *Manilkara dawei* (Stapf.) Chiov.
  - *Mimusops bagshawei* S. Moore
  - *Pachystela brevipes* (Baker) Engl.
- Sterculiaceae
  - *Leptonychia mildbraedii* Engl.
- Ulmaceae
  - *Celtis brownii* Rendle
  - *Celtis durandii* Engl.
  - *Celtis mildbraedii* Engl.
  - *Celtis zenkeri* Engl.
  - *Chaetacme aristata* Planch.
- Violaceae
  - *Rinorea ilicifolia* (Welw. ex. Oliv.) Kuntze

Although still alive at the time of the census in 2006, damaged trees are likely to have an increased probability of mortality and of not featuring in future censuses when compared with undamaged individuals.

Mortality and recruitment rates

Mortality was numerically highest among early seral (e.g. *Albizia zygia/grandibracteata*) and understorey (e.g. *Euphorbia teke, Teclea nobilis* and *Trilepisium madagascariense*) taxa and individuals in the smallest dbh category (dbh = 9.5–20 cm) (Fig. 3). Corrected mortality rates for the census periods 1968–1982, 1982–1993 and 1993–2006 were also the highest for trees in the dbh category 9.5–20 cm (respectively, 0.95%, 1.53% and 1.43% year^{-1}) and the lowest for trees in the largest dbh category, >40 cm (respectively, 0.48%, 0.40% and 0.33% year^{-1}). Trees in the intermediate size category (dbh > 20–40 cm) had corrected mortality rates for the census periods 1968–1982, 1982–1993 and 1993–2006 of, respectively, 0.92%, 1.28% and 1.03% year^{-1}. Annual basal area mortality rate (BAMR) fluctuated throughout the survey, peaking in 1993–2006.

Proportionately, when total numbers of tree deaths in a particular category by 2006 are expressed in terms of total numbers of trees in the same categories in 1968, early seral (51%), followed by understorey (42%) and main canopy (11%) taxa and individuals in the smallest dbh category (45%) are the most susceptible to mortality. Two species (*Belanophora glomerata* and *Teclea nobilis*) showed

Table 3 Growth rates (cm^2 year^{-1}) for nonbuttressed individuals of most common taxa (i.e. taxa that have >2 individuals in the plot at the time of any one census period) present throughout the entire 38-year-long census period (1968–2006)

Taxon	Ecological guild	No. individuals present throughout 1968–2006	Growth rate (cm^2 year^{-1}) 1968–2006 *mean* and [range] if no. individuals present > 1
Albizia gummifera group	S	1	26.19
Aningeria altissima	S	7	*2.75* [0.17–9.12]
Antiaris toxicaria	S	6	*3.42* [0.51–7.34]
Belanophora glomerata	U	4	*2.45* [1.42–4.34]
Blighia unijugata	U	1	0.5
Celtis durandii	U	1	12.36
Celtis mildbraedii	MC	24	*5.68* [0–29.53]
Celtis zenkeri	MC	1	1.31
Entandrophragma cylindricum	S	3	*1.80* [0.0–4.43]
Euphorbia teke	U	3	*3.57* [1.80–5.66]
Fagara angolensis	S	1	2.93
Funtumia latifolia	U	12	*10.89* [4.72–16.31]
Lovoa brownii	U	1	2.99
Manilkara dawei	MC	2	*3.69* [2.48–4.90]
Mimusops bagshawei	MC	4	*6.21* [1.71–10.99]
Morus lactea	MC	2	*5.89* [5.25–6.54]
Newtonia buchananii	S	2	*16.01* [14.94–17.07]
Oxyanthus speciosus	U	5	*2.54* [0.43–4.45]
Pycnanthus angolensis	S	2	*3.57* [1.41–5.73]
Sapindaceae indetermined	U	3	*3.66* [1.27–6.83]
Tabernaemontana holstii	U	3	*5.34* [2.45–5.92]
Teclea nobilis	U	5	*3.55* [2.09–5.90]
Trichilia prieureana	U	29	*5.85* [0.0–18.17]
Trichilia rubescens	U	12	*2.62* [0.43–7.27]
Trilepisium madagascariense	U	30	*4.54* [0.0–15.58]
Zanha golungensis	U	4	*19.35* [0.98–38.69]

Ecological guilds: MC, main canopy; S, seral; U, understorey.

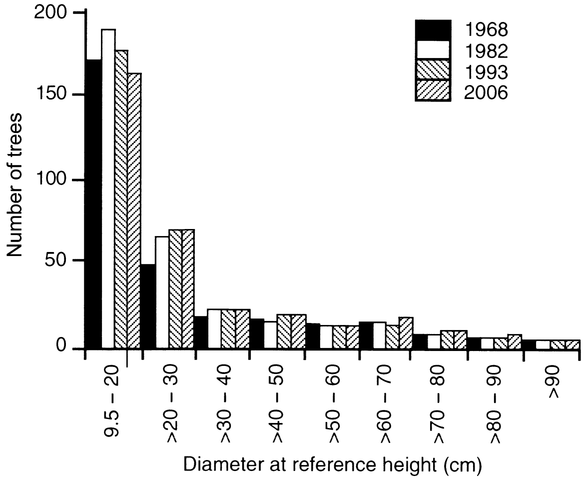

Fig 2 Frequency of trees according to different dbh classes for the four surveys of the 0.64-ha forest plot at Mpanga (1968, 1982, 1993, 2006)

increased mortality over the course of the survey period. As mentioned previously, one of these taxa (*Belanophora glomerata*) is valued locally as a source of poles for building.

Annual stem recruitment rate (SRR) was at its highest in 1968–1982 and lowest in 1993–2006: stem recruitment exceeded stem mortality in 1968–1982 and for the overall survey period (1968–2006), but losses outweighed gains in 1982–1993 and 1993–2006. Rising numbers of individuals recorded as having died since the previous census, and the annual stem mortality rates, both of which peaked in 1993–2006, were the opposite of stem recruitment and SRR. Annual BA recruitment rate showed a steady decline throughout, indicating falling mean growth rates, although the overall rate (0.96% year^{-1}) was higher than the overall rate of BAMR (0.78% year^{-1}), reflecting a slight net increase in BA over the 38-year survey period. Corrected annual turnover for 1968–2006 was 2.3% year^{-1} (stems) and 0.87% year^{-1} (BA).

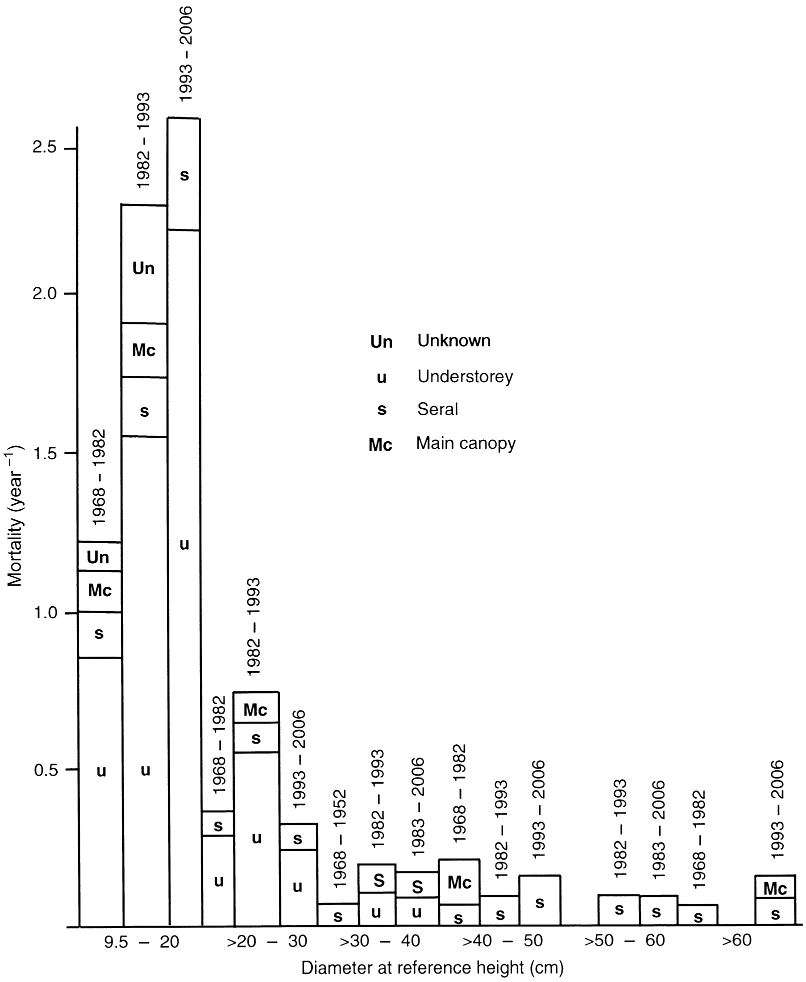

Fig 3 Mortality rates according to different dbh in the 0.64-ha forest plot at Mpanga. Mortality data are expressed in terms of the number of dead trees since the previous survey for categories of dbh values, divided by the number of years since the previous survey, and have been partitioned according to ecological guild [MC, main canopy; S, seral; U, understorey; Un, unknown (see text for more information)]

No new individuals were recorded during the 38-year survey period for five of the 28 most common taxa (Table 4). New recruits were predominantly understorey taxa: *Euphorbia teke*, *Oxyanthus speciosus* and *Tabernaemontana holstii* were the most commonly represented among the new recruits, with numbers of new recruits to these species generally exceeding mortality. The numbers of new recruits were also high for *Blighia unijugata* and *Celtis mildbraedii*, although there was little or no mortality for these two species. Of the taxa favoured locally by woodcutters, only *Antiaris toxicaria* and *Belanophora glomerata* were recorded as new recruits during the survey: no new recruits were reported for *Belanophora glomerata* since the 1982 census; although three individuals of *Antiaris toxicaria* were recruited from 1968 to 2006, another three individuals of this taxon were lost over the same period.

Discussion

A demand for raw materials, particularly in the wood working and construction industries, appears to have driven the felling of trees, and damage to neighbouring trees, during the period 1993–2006. One of the larger trees felled (*Funtumia latifolia,* dbh = 49 cm in 1993) had been cut into blanks for drums, and two of the other large-sized trees felled (both *Antiaris toxicaria*, dbh = 57.9 cm and dbh = 68.7 cm) are likely to have been cut down for the same purpose. During the 2006 survey, it was obvious that those responsible for cutting the trees had carefully toured the whole plot site (and adjoining areas of forest) to extract stems of a rather inconspicuous understorey tree (*Belanophora glomerata*), which according to nearby inhabitants is an important source of building poles. The

Table 4 Absolute mortality and recruitment numbers per census period by most common taxa (i.e. taxa that have >2 individuals in the plot at the time of any one census period)

Taxon	Ecological guild	No. individuals recruited (died) during the census period 1968–1982	1982–1993	1993–2006	1968–2006
Albizia gummifera group	S	0 (0)	0 (0)	0 (1)	0 (1)
Albizia zygia/grandibracteata	S	0 (3)	1 (3)	0 (1)	1 (7)
Aningeria altissima	MC	2 (1)	0 (1)	1 (0)	3 (2)
Antiaris toxicaria	S	1 (1)	0 (0)	2 (2)	3 (3)
Belanophora glomerata	U	5 (0)	0 (1)	0 (5)	5 (6)
Blighia unijugata	U	4 (0)	0 (0)	1 (0)	5 (0)
Celtis durandii	U	0 (0)	0 (1)	0 (1)	0 (2)
Celtis mildbraedii	MC	4 (0)	0 (1)	1 (0)	5 (1)
Celtis zenkeri	MC	0 (0)	1 (0)	0 (0)	1 (0)
Entandrophragma cylindricum	S	0 (1)	1 (1)	0 (0)	1 (2)
Euphorbia teke	U	14 (4)	0 (6)	2 (3)	16 (13)
Fagara angolensis	S	0 (1)	0 (1)	0 (1)	0 (3)
Funtumia latifolia	U	0 (1)	0 (1)	0 (1)	0 (3)
Lovoa brownii	U	2 (2)	0 (1)	0 (0)	2 (3)
Manilkara dawei	MC	0 (1)	0 (1)	0 (0)	0 (2)
Mimusops bagshawei	MC	0 (0)	1 (0)	0 (0)	1 (0)
Morus lactea	MC	1 (2)	1 (0)	0 (0)	2 (2)
Newtonia buchananii	S	1 (0)	1 (0)	0 (1)	2 (1)
Oxyanthus speciosus	U	5 (0)	3 (2)	1 (2)	9 (4)
Pseudospondias microcarpa	MC	0 (0)	0 (0)	0 (1)	0 (1)
Pycnanthus angolensis	S	0 (0)	1 (0)	0 (1)	1 (1)
Sapindaceae indetermined	U	1 (0)	0 (1)	2 (0)	3 (1)
Tabernaemontana holstii	U	5 (0)	7 (0)	6 (4)	18 (4)
Teclea nobilis	U	3 (2)	1 (4)	1 (9)	5 (15)
Trichilia prieureana	U	3 (2)	3 (0)	3 (3)	9 (5)
Trichilia rubescens	U	3 (1)	4 (0)	4 (2)	11 (3)
Trilepisium madagascariense	U	3 (2)	1 (6)	3 (2)	7 (10)
Zanha golungensis	U	1 (0)	0 (0)	0 (0)	1 (0)

Ecological guilds: MC, main canopy; S, seral; U, understorey.

stem of a specimen of *Canarium schweinfurthii*– the only one in the plot – had also been cut to provide incense used in churches and traditional ceremonies.

Increased human impact since 1993 when compared with the period 1968–1993 is perhaps somewhat surprising, given the relatively recent economic and political history of Uganda. During the 20 or so years of economic and political turmoil in the country since the late 1960s, poaching, encroachment and unauthorized logging, facilitated by weak policing – and indeed the direct involvement of government, army and police officials in illegal activities, are commonly believed to have led to the degradation of Uganda's natural resource base (GDA, 1974; Hamilton, 1984; Howard, 1991; NEMA, 1996; Naughton-Treves, 1999). By comparison and on the basis of the plot data presented here, Mpanga Forest Reserve seems to have been relatively little impacted during this period, presumably because the prevailing conditions at the time restricted development of woodworking and construction enterprises in the vicinity of the forest and a market for finished timber products. As the economy of Uganda picked-up in the late 1980s and 1990s, so have demands on forests, and the effects of this increased demand are clearly evident even in supposedly closely protected areas of forest such as Mpanga Forest Reserve.

Human impact since 1993 has had a noticeable, if small, effect on BA and on estimated AGB. Determinations of BA from the four repeat surveys described here exceed the estimate of Dawkins & Philip's (1962) for long established dryland forest at Mpanga (31.4 m^2 ha^{-1} for trees with a dbh ≥ 9.5 cm), but are within the range of values derived from a variety of tropical forest types listed in Swaine, Lieberman & Putz (1987b). The mean annual dbh increment (0.14 cm year^{-1} for nonbuttressed trees overall, but falling to 0.13 cm year^{-1} for the 184 individual, nonbuttressed trees that have been present throughout the entire survey period), is towards the lower end of the range of growth rates reported for tropical forest by Silva, de Carvalho & Lopes (1989).

Estimated AGB is slightly higher than reported for tropical lowland rainforest in Malaysia (Hoshizaki *et al.*, 2004) and about 60% higher than calculated for tropical moist forest in northeast Brazil (Rolim *et al.*, 2005). The mean rate of increase in AGB from 1968 to 2006, 0.63 Mg ha^{-1} year^{-1}, is within the range determined from a pantropical dataset for the period 1958–1996 (0.77 ± 0.44 Mg ha^{-1} year^{-1}), although measurements from central and South America dominate the latter estimate (Phillips, 1998:439). Increasing AGB over the first 25 years of the Mpanga Forest Reserve survey (1.4 Mg ha^{-1} year^{-1}), within the ranges computed for humid forest types in central and South America (Phillips, 1998; Baker *et al.*, 2004), represents a progressive enlargement of the amount of stored carbon [carbon is generally assumed to account for about 50% of dry biomass of a tree (Chave, 2005)]. However, this trend was reversed and the size of carbon sink reduced during the subsequent census period (1993–2006), when the activities of woodcutters contributed to a substantial fall in AGB (−0.9 Mg ha^{-1} year^{-1}).

Growth rates averaged according to the different ecological guilds, and relative differences in mortality among these groupings, are in agreement with results from forests in lowland southeast Asia (Manokaran & Kochummen, 1987; Primack & Hall, 1991; Ashton & Hall, 1992) and central America (Lieberman *et al.*, 1985; Lieberman & Lieberman, 1987). However, higher incidences of mortality among individuals in the smallest size-class are in contrast to the findings from Kade in Ghana (Swaine *et al.*, 1987a), where mortality was observed to be independent of size-class, and from Pasoh in Malaysia (King, Davies & Noor, 2006) where death rates among understorey, canopy and emergent taxa were the highest for the largest size class. Phillips & Gentry (1994), Phillips (1996), Lewis (2004a) and Phillips *et al.* (2004) report a doubling of both stem recruitment and mortality rates across the tropics from the 1950s to the 1990s, based on enumerations of trees with dbh ≥ 10 cm in permanent forest plots, with recruitment rates slightly higher than mortality. According to the forest plot data from Mpanga Forest Reserve, however, although the census corrected mortality rate in 1993–2006 was more than 50% greater than in 1968–1982, the census corrected recruitment rate was almost 50% less. It is possible that the relatively large number of new recruits recorded in 1982, more than twice the number recorded in subsequent censuses, was due to recording error and in particular to the missing of several of the smallest-sized trees when the plot was first delineated and surveyed in 1968. Subsequent declines in recruitment may represent an in-filling of the forest canopy, as recovery from earlier impacts by pit-sawyers proceeds (Taylor *et al.*, 1996), leading to fewer opportunities for small trees to grow large (with impacts of the activities of woodcutters since 1993 not yet evident in recruitment rates). A gradual closing of the forest canopy may explain the initial increase in mortality rate following 1968–1982, especially as seral and understorey taxa accounted for more than 80% of the 36 recorded tree deaths in 1993.

The results presented here provide a first, detailed insight into the rain forest impacts of economic development in central and southern Uganda, and a means of monitoring these impacts over coming years within the context of variations over the preceding 25 years of results. Anthropogenic disturbance of areas of vegetation set-aside for conservation is likely to become an increasing concern for conservationists. Relatively low levels of disturbance may be important in the maintenance of rich biodiversity now and in the future (Robbins *et al.*, 2006) and even degraded areas of forest in Africa have the potential to sequester large amounts of carbon (Glenday, 2006). Although at 0.64 ha the plot in Mpanga Forest Reserve is small, the effects of anthropogenic disturbance that it records, occurring in an area specifically set aside for conservation, have important implications for future resource availability and carbon storage in Ugandan forests more generally. Simply put, if commercially valuable trees can be almost entirely stripped – illegally and over the last decade or so – from a relatively inaccessible part of a supposedly protected forest, then the future prospects for Uganda's forest resource base would appear bleak.

Conclusions

Thirty-eight years of data from repeat surveys of a permanent plot in Mpanga Forest Reserve, Uganda, reveal relatively minor fluctuations in density, Shannon diversity, evenness, BA and AGB. The overall trend in the data to 1993 indicated recovery from an earlier period of anthropogenic disturbance, most likely the activities of pit-sawyers prior to the commencement of the plot-based surveys in 1968. A second phase of anthropogenic disturbance, in the form of selective logging to meet local wood-working and construction demands and associated damage to remaining trees, is clearly evident in the most recent survey data (2006). This second phase of disturbance – if representative of forests in the Mpanga Forest Reserve (and there seems no good reason why this should not be the case) and if left unchecked – is likely to impact severely carbon storage and future resource availability in what was for a time one of Uganda's most heavily protected forests. Ironically, however, if further disturbance can be prevented then the permanent plot referred to in this study potentially can provide an almost unprecedented opportunity to monitor recovery within the context of a relatively long-time series of data, and a basis for testing ecological theories. One example of the latter is the intermediate disturbance hypothesis (Huston, 1994), according to which low-level disturbance should, in time, lead to increased biodiversity.

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