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The effects of selective logging on forest structure and tree species composition in a Central African forest: implications for management of conservation areas

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Abstract

The forests of Central Africa enjoy world-wide recognition for their spectacular wildlife and also harbor an abundance of high quality timber. With mismanagement and the conversion of large tracts of West African forest to agricultural production, Central African forests are experiencing increased harvesting pressures. This is particularly true for species of African mahogany (*Entandrophragma* spp.).

In the tri-national region of Cameroon, Central African Republic, and Republic of Congo, a widely applied version of the Integrated Conservation and Development Model attributes the dual management objectives of biodiversity conservation and timber production to the same zones. Many conservationists working in the region believe that highly selective timber extraction is the best management scenario to meet these objectives. Conventional wisdom holds that if selective logging does not adequately regenerate *Entandrophragma* spp., loggers will quit the region after having mined the forest.

A comparison between unlogged, 6-month and 18-year post-harvest forest stands indicates lasting effects of highly selective, high grade logging. While there was little difference in tree species composition and diversity between treatments, stem densities of both saplings and trees in unlogged forest were significantly higher than those in forest sampled 18 years after logging. Evidence suggests inadequate recruitment of *Entandrophragma cylindricum* and *E. utile*, the principal timber species, to justify continued timber extraction. Data indicate a significant shift in canopy dominance from shade intolerant to shade bearing species due to insufficient canopy disturbance. Nevertheless, an abundance of other top quality timber species remains after selective removal of African mahogany and these forests will remain attractive to loggers long after the elimination of *Entandrophragma* spp. A better approach to manage timber zones for timber production and conservation would be an adaptive management approach based on increased species selection and canopy disturbance. Zones targeting the conservation of closed forest obligate species should not be logged.

Keywords: African mahogany; Central African Republic; Floristic diversity; Forest management; Guild; Tri-national park

1. Introduction

Tropical forests are recognized for their high biological diversity and role in maintaining global

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climate cycles as well as regional and local weather patterns (Richards, 1952; Whitmore, 1984). At the same time, many cash strapped countries rely on these forests for income generating activities, most notably logging (Eba'a Atyi, 2000; Plumptre, 2001). Unfortunately, examples of mismanagement and forest degradation resulting from poorly planned timber extraction abound (Gartlan, 1989; Uhl et al., 1991; Ashton and Peters, 1999).

The forests of Central Africa constitute the second-largest continuous tropical forest in the world and, in contrast with other areas, still maintain high densities of large mammals (see, e.g., Barnes et al., 1995; Hart and Hall, 1996; Hall et al., 1998; Tutin and Vedder, 2001). However, the lack of options for economic growth in most Central African countries has led to a continued reliance on forests for revenue generation and job creation (Plouvier, 1998). The desire to accommodate both conservation and revenue generation activities from forests has led to the application of the Integrated Conservation and Development Project model, a version of which assigns both timber production and conservation priorities to the same or adjacent forest lands.

An example of such a model is the Dzanga-Sangha Dense Forest Reserve in the Central African Republic, which is part of a tri-national protected area where adjacent protected areas in Congo and Cameroon are loosely managed together as conservation areas (Weber and Rabinowitz, 1996). The contiguous forest from all three of these countries is well known for its very high densities of gorillas, elephants, and other large mammals (e.g., Carroll, 1988a,b; Fay, 1989; Fay and Agnagna, 1992; Turkalo and Fay, 2001). However, parts of the Dzanga-Sangha Reserve and large parts of adjacent forests in Congo and Cameroon are also zoned as timber production areas and commercial logging has been going on for three decades.

In West Africa, there is a long and rich history of forestry research (see, e.g. MacGregor, 1934; Lancaster, 1960; Taylor, 1960; Parren and de Graaf, 1995). Shelterwood, liberation thinning, and enrichment planting techniques have all proven successful in at least some areas for increasing densities of timber species (Nwoboshi, 1987; Okali and Ola-Adams, 1987; Dupuy et al., 1997) but they have often not met the threshold of economic return to justify widespread application (Asabere, 1987). In Central Africa, with the exception of a few selected research projects (see, e.g., Durrieu de Madron and Forni, 1997), virtually no forests are managed according to management plans with preconceived forestry prescriptions. A particularly poignant example is in the Dzanga-Sangha Dense Forest Reserve where timber management consists solely of high grade logging with extraction of approximately 1 stem per hectare of either *Entandrophragma cylindricum* (Sprague) Sprague or *Entandrophragma utile* (Dawe and Sprague) Sprague (Baum et al., 1998). This management practice began in 1972 and continues today (Blom, 2001). The purpose of this study was to examine the effects of this highly selective logging on floristic diversity and forest structure with the goal of interpreting results in the context of the dual management objectives of biodiversity conservation and timber management.

2. Materials and methods

2.1. Site description

This study was carried out between October and December 2000 in the 4380 km^2 Dzanga-Sangha Dense Forest Reserve, southwestern Central African Republic (Fig. 1). This study was carried out in mixed semi-evergreen forest (often referred to as "semi-deciduous"), one of seven forest types recognized to be within the Reserve (Harris, 2002). Satellite imagery and maps of logging history were used to identify forest stands that were believed similar before logging and that encompassed three distinct age classes in logging history. Two stands (unlogged and 18 years post-logging) were located within 6 km of each other in the forest around the Kongana camp. The third stand (6 months post-logging) was approximately 17 km west of Kongana. Additional data discussed in this paper was collected at a fourth site, the Eleme ya Ngombe plot, approximately 9 km north northwest of Bayanga (Hall, 2002). Soils within the region are broadly classed as Oxisols (Juo and Wilding, 1996); Carroll (1997) reported an average annual precipitation of 1365 mm between 1973 and 1985 for Bayanga.

2.2. Sampling methods

Within each forest stand in the Kongana area, a 2.25 km^2 area was chosen within which a sampling

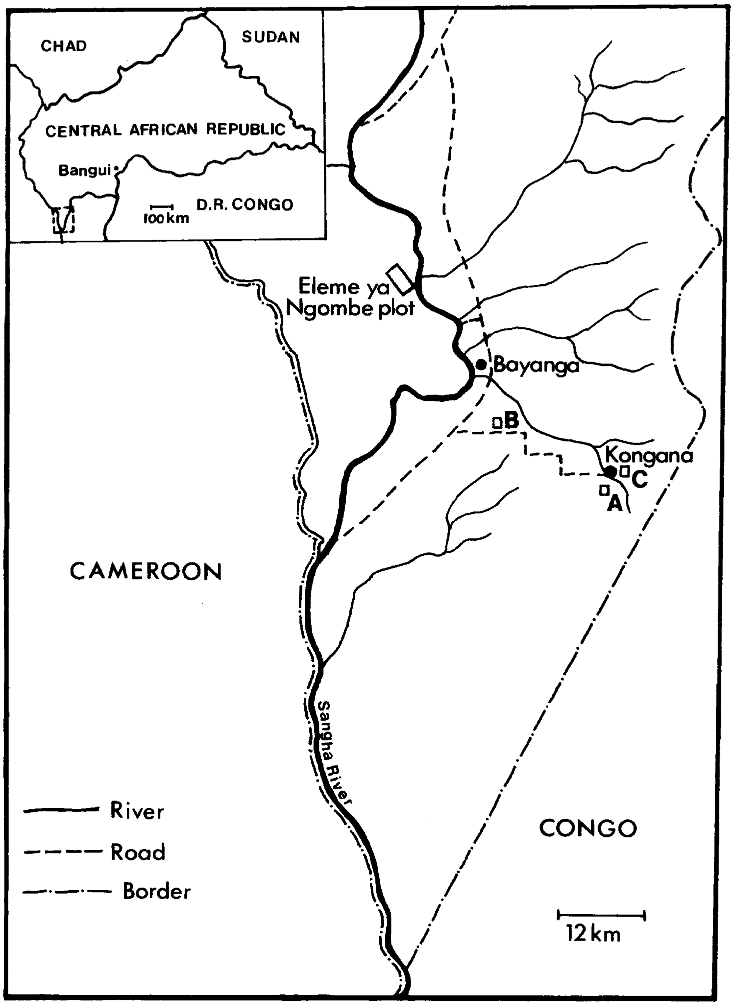

Fig. 1. Map of stands sampled in the Dzanga-Sangha Dense Forest Reserve, Central African Republic: (A) unlogged forest stand, (B) forest stand samples 6 months after logging and (C) forest sampled 18 years after logging.

grid was laid out on the ground. A total of sixteen 30 m × 30 m plots were laid out at 500 m intervals along four parallel 1.5 km transects. This sampling design resulted in no plots being placed in forest directly affected by logging (i.e., logging roads and yards, skid trails, and tree fall gaps caused by felling) in the 6-month post-harvest treatment. Within each plot, diameters were measured and species identified for all trees $\geq$10 cm diameter at breast height (dbh). Diameters were measured at 1.37 m above the ground with the exception that trees with buttresses were measured 50 cm above the buttress. Voucher specimens were made of unknown taxa. Lianas $\geq$10 cm diameter were measured but not identified. Within each 900 m^2 plot, a 10 m × 10 m nested subplot was delineated in the northeastern corner. Here all woody vegetation 2.5–10 cm dbh was measured and identified as above. This class is also referred to as the sapling class in this paper.

A seedling survey was carried out along the transects used to lay out the vegetation plots. Twenty-five 1 m^2 circular plots were censused for seedlings $\leq$50 cm height of *E. cylindricum* and *E. utile*, at 100 m intervals along each transect. One of the biggest sources of mortality in undisturbed forest for seeds of *Entandrophragma* spp. is rodent predation where seeds are eaten and seed wings remain long after predation (Synnott, 1975; J.S. Hall, unpublished data). For this reason, seed wings and fruit capsules were also recorded during this regeneration survey. For the seedling survey, transects were extended an additional 500 m beyond the overstory sampling grid to give a total of one hundred 1 m^2 plots for each stand. A fourth seedling survey was undertaken on the Eleme ya Ngombe plot.

Densities of *Entandrophragma* spp. are notoriously low throughout African forests (see, e.g., CTFT, 1985; Swaine and Hall, 1988; Van Rompaey, 1993) such that one would not expect to identify sufficient numbers of individuals to permit an assessment of future recruitment in a 1.44 ha sample. For this reason, an additional data set was used to assess size class distribution of *Entandrophragma* species (Hall, 2002). In September 1999, an inventory of all *Entandrophragma* spp. was completed on the 100 ha Eleme ya Ngombe plot. Here all *Entandrophragma* spp. $\geq$10 cm dbh were identified, mapped, and diameters measured as above. In addition, each individual was scored with reference to canopy position. Crown class categories were defined as follows:

(1) *Understory*: individuals completely overtopped by adjacent canopy trees.
(2) *Midstory*: individuals whose crowns were partially exposed to direct sunlight overhead.
(3) *Canopy and emergent*: individuals with crowns completely exposed to direct sunlight overhead or above the main canopy stratum.

2.3. Determination of potential timber species

To assess the quality of other timber species inventoried, two sources were used. The Projet d'Amenagement des Ressources Naturelles (PARN) was a World Bank funded inventory project undertaken throughout the forests of the Central African Republic between 1989 and 1993 (PARN, 1995). Foret Ressources Management is a consulting firm that was hired by the current concession holders in Dzanga-Sangha to recommend species and areas to be exploited (Foret Ressources Management, 1999). It is assumed that these sources based their recommendations on the commercial interests of their clients. Thus "class one" (PARN) and "priority" (Foret Ressources Management) species are considered the highest quality and referred to in this paper as "top quality timber species".

2.4. Shade tolerance guilds

Species were classed according to their shade tolerance guilds. Following Hawthorne (1995), pioneers are species for which seedlings need sun to establish. Non-pioneer light demanders (NPLDs) are species that need gaps to develop beyond the sapling stage (Hawthorne, 1995). The shade bearer guild consists of species that can persist and grow in understory shade at the seedling and sapling tree stages.

2.5. Statistical analyses

Stand basal areas and stem densities for both individuals in the 2.5–10 cm and $\geq$10 cm dbh size classes were compared with an analysis of variance (ANOVA). Basal area data was log transformed to meet the underlying assumption of homoscedasticity of residuals. Frequency distributions of percent shade bearer basal area by size class were compared by contingency table analysis. Frequency distributions of *E. cylindricum* seedlings enumerated during seedling inventories were also compared by contingency table analysis. Statistical analyses were completed in S-Plus (Mathsoft, Inc.).

3. Results

3.1. Species composition and diversity

In unlogged forest, a total of 147 taxa were distinguished for trees $\geq$10 cm dbh. Of these, 99 were identified to species, 36 to genus, 9 to family and there were three unknowns; at least 36 families were represented. In the forest sampled 6 months post-harvest, a total of 125 taxa were identified for trees $\geq$10 cm dbh. Of these, 98 were identified to species, 23 to genus, and 4 to family. One hundred twenty nine taxa were recorded in forest 18 years post-logging. Of these, 103 were identified to species, 19 to genus, and 7 to family. Shannon diversity indexes were very similar between forest stands where $H = 1.89, 2.0$ and 1.94 for unlogged, 6 months post-harvest and 18 years

Table 1
Stem density by size class for all species with individuals in the dbh ≥60 cm size class in logging treatments in the Dzanga-Sangha Dense Forest Reserve, Central African Republic[a]

Genus	Species	Stem density per hectare														
		Saplings			Poles			Medium trees			Large trees			All trees		
		UL	L 0.5	L 18	UL	L 0.5	L 18	UL	L 0.5	L 18	UL	L 0.5	L 18	UL	L 0.5	L 18
Afrostyrax	*lepidophyllus*	6.25	6.25	25	3.47	1.39	1.39	0	0	1.39	0	0	0.69	3.47	1.39	3.47
Albizia	sp. 1	0	0	0	0	0	0	0	0	0	0	0	0.69	0.00	0.00	0.69
Albizia	*ferruginea*	0	0	0	0	0	0	0	0	0	0	0.69	0	0.00	0.69	0.00
Amphimas	*pterocarpoides*	0	0	0	0.69	2.08	0.69	0	0	0	0.69	0	0	1.38	2.08	0.69
Anonidium	*mannii*	0	12.5	56.25	2.08	2.78	2.78	0	2.78	3.47	0	0	0.69	2.08	5.56	6.94
Antiaris	*toxicaria*	0	0	0	0	0	0	0	0	0	0	0.69	0	0.00	0.69	0.00
Antrocaryon	*micraster*	0	0	0	0	0	0	0	0	0	0.69	0	0	0.69	0.00	0.00
Bombax	*buonopozense*	0	0	0	0	0	0	0	0	0	0	0.69	0	0.00	0.69	0.00
Celtis	*mildbraedii*	43.75	12.5	18.75	9.03	6.25	4.86	2.08	1.39	1.39	0.69	0	0	11.80	7.64	6.25
Celtis	*tessmannii*	0	0	0	0	3.47	0	0	2.08	0.69	0	2.78	0.69	0.00	8.33	1.38
Cleistopholis	*patens*	0	0	0	0	0	0.69	0.69	0.69	0	1.39	0	0	2.08	0.69	0.69
Coelocaryon	*preussii*	0	0	0	0	0.69	0	0.69	1.39	0	0	0	0.69	0.69	2.08	0.69
Cola	*lateritia*	0	0	0	0.69	2.08	2.78	0.69	0	1.39	0.69	0	0	2.07	2.08	4.17
Dialium	*zenkeri*	0	0	0	0	0	3.47	0	0	0	0	0.69	0	0.00	0.69	3.47
Duboscia	spp.	0	0	12.5	1.39	0	0	1.39	2.78	0.69	0.69	0	1.39	3.47	2.78	2.08
Entandrophragma	*cylindricum*	0	0	0	2.08	0.69	0.69	0	0.69	0	1.39	0.69	0	3.47	2.07	0.69
Ficus	spp.	0	0	0	0	0	0	0	0	0	0.69	0	0.69	0.69	0.00	0.69
Genye		0	0	0	0	0	0	0	0	0	0	0.69	0.69	0.00	0.69	0.69
Hexalobus	sp. 1	0	0	0	0	4.17	0.69	0	1.39	0	0.69	0	0	0.69	5.56	0.69
Irvingia	*excelsa*	0	0	0	0	0	2.08	0	0.69	0.69	0	0	0.69	0.00	0.69	3.46
Irvingia	*grandifolia*	0	0	0	0	0	0	0	0	0	0.69	0	0	0.69	0.00	0.00
Irvingia	*robur*	0	0	0	0	0	0	0	0	0	0	0.69	0	0.00	0.69	0.00
Klainedoxa	*gabonensis*	0	0	0	0	0	0	0	0	0	0	0	1.39	0.00	0.00	1.39
Lophira	*alata*	0	0	0	0	0.69	0	0	0	0.69	0.69	0.69	0	0.69	1.38	0.69
Lovoa	*trichilioides*	0	12.5	6.25	0	1.39	2.08	0	0	0	0	0.69	0	0.00	2.08	2.08
Mammea	*africana*	0	0	0	0	0	0	0	0	0	0.69	0	0	0.69	0.00	0.00
Manilkara	*mabokeensis*	75	75	6.25	13.19	30.56	7.64	0	5.56	0.69	0.69	2.78	2.08	13.88	38.90	10.41
Ongokea	*gore*	0	0	0	0	0	0.69	0	0	0	0.69	0.69	0.69	0.69	0.69	1.38
Oxystigma	*oxyphyllum*	0	0	0	0.69	1.39	0	0	0	0.69	0.69	1.39	0	1.38	2.78	0.69
Pentaclethra	*macrophylla*	6.25	0	6.25	0	2.78	0.69	0.69	2.08	0.69	0.69	0	0	1.38	4.86	1.38
Petersianthus	*macrocarpus*	0	6.25	6.25	0.69	1.39	0	0	4.17	1.39	2.08	0	0	2.77	5.56	1.39
Piptadeniastrum	*africanum*	0	0	0	0.69	0	0	0	1.39	0.69	0.69	0.69	0	1.38	2.08	0.69
Pycnanthus	*angolensis*	0	0	0	0	1.39	0	0	0.69	0.69	0	1.39	0.69	0.00	3.47	1.38
Staudtia	*kamerunensis*	0	6.25	6.25	1.39	12.5	1.39	4.86	2.78	0.69	1.39	0.69	0	7.64	15.97	2.08
Strombosiopsis	*tetrandra*	0	0	0	2.08	0.69	2.78	2.08	1.39	5.56	0	0.69	0.69	4.16	2.77	9.03
Tessmannia	sp. 1	0	0	0	0	0	0	0	0	0	0.69	0	0	0.69	0.00	0.00
Tridesmostemon	*omphalocarpoides*	0	0	0	0	0.69	0	0	1.39	0	0	0.69	0	0.00	2.77	0.00
Unknown	sp. 1	0	0	0	0	0	0	0	0	0	0.69	0	0	0.69	0.00	0.00
Xylopia	sp. 1	0	0	0	0	0	0	0	0	0	0	0	0.69	0.00	0.00	0.69

[a] Saplings: 2.5–10 cm dbh, poles: 10–30 cm dbh, medium trees: 30–60 cm dbh, large trees: dbh ≥ 60 cm; total area sampled for individuals ≥10 cm dbh = 1.44 ha, area sampled for sapling class: 0.16 ha; UL: unlogged forest, L 0.5: forest sampled 6 months after logging, L 18: forest sampled 18 years after logging.

Table 2
Stem densities for top 25 species with individuals in the 2.5–10 cm dbh size class in logging study in the Dzanga-Sangha Dense Forest Reserve, Central African Republic[a]

Genus	Species	Stem density per hectare														
		Saplings			Poles			Medium trees			Large trees			All trees		
		UL	L 0.5	L 18	UL	L 0.5	L 18	UL	L 0.5	L 18	UL	L 0.5	L 18	UL	L 0.5	L 18
Rinorea	*welwitschii*	350	587.5	175	2.08	2.08	0	0	0	0	0	0	0	2.08	2.08	0.00
Thomanderisa	*hensii*	331.25	381.25	368.75	2.778	2.78	0	0	0	0	0	0	0	2.78	2.78	0.00
Diospyros	*bipindensis*	256.25	143.75	112.5	13.89	10.42	9.03	0	0.69	0	0	0	0	13.89	11.11	9.03
Rinorea	sp. 1 and 2	125	137.5	181.25	0	0	0	0	0	0	0	0	0	0.00	0.00	0.00
Microdesmis	*puberula*	112.5	112.5	18.75	0	0	0	0	0	0	0	0	0	0.00	0.00	0.00
Diospyros	*iturensis*	106.25	50	37.5	22.92	4.86	8.33	0	0	0	0	0	0	22.92	4.86	8.33
Grossera	*macrantha*	106.25	31.25	56.25	24.31	17.36	9.72	0	0	0	0	0	0	24.31	17.36	9.72
Dasylepis	*seretii*	87.5	50	43.75	31.25	15.97	6.25	0	0	1.39	0	0	0	31.25	15.97	7.64
Greenwayodendron	*suaveolens*	81.25	56.25	56.25	11.11	6.94	9.03	8.33	2.08	4.86	0	0	0	19.44	9.02	13.89
Manilkara	*mabokeensis*	75	75	6.25	13.19	30.56	7.64	0	5.56	0.69	0.69	2.78	2.08	13.88	38.90	10.41
Dichostemma	*glaucescens*	75	12.5	100	7.64	2.78	15.97	0	0	0	0	0	0	7.64	2.78	15.97
Tabernaemontana	*penduliflora*	68.75	137.5	56.25	0.69	4.86	0.69	0	0	0	0	0	0	0.69	4.86	0.69
Drypetes	*cinnabarina*	68.75	118.75	37.5	2.78	2.08	0.69	0	0	0	0	0	0	2.78	2.08	0.69
Rinorea	*oblongifolia*	68.75	93.75	12.5	6.94	9.72	1.39	0	0	0	0	0	0	6.94	9.72	1.39
Drypetes	*aff. angustifolia*	68.75	43.75	31.25	0.69	0	0	0	0	0	0	0	0	0.69	0.00	0.00
Rubiaceae	spp.	68.75	12.5	25	0	0	4.17	0	0	0.69	0	0	0	0.00	0.00	4.86
Drypetes	sp. 1	56.25	31.25	0	0.69	1.39	0	0	0	0	0	0	0	0.69	1.39	0.00
Drypetes	*polyanthum*	50	18.75	6.25	0	0.69	0	0	0	0	0	0	0	0.00	0.69	0.00
Ritchiea	*aprevaliana*	43.75	18.75	6.25	0	0	0	0	0	0	0	0	0	0.00	0.00	0.00
Celtis	*mildbraedii*	43.75	12.5	18.75	9.03	6.25	4.86	2.08	1.39	1.39	0.69	0	0	11.80	7.64	6.25
Drypetes	*capillies*	43.75	6.25	56.25	0	0	0	0	0	0	0	0	0	0.00	0.00	0.00
Drypetes	*aff. urophylla*	37.5	0	37.5	2.78	2.08	1.39	0	0.69	0	0	0	0	2.78	2.77	1.39
Pancovia	sp. 1 and 2	31.25	43.75	25	11.81	8.33	2.08	1.39	0	0	0	0	0	13.20	8.33	2.08
Cleistanthus	*mildbraedii*	31.25	31.25	18.75	9.03	18.75	5.56	2.78	4.86	0.69	0	0	0	11.81	23.61	6.25
Drypetes	*occidentalis*	31.25	12.5	0	2.78	4.17	2.08	0.69	0.69	0.69	0	0	0	3.47	4.86	2.77

[a] Saplings: 2.5–10 cm dbh, poles: 10–30 cm dbh, medium trees: 30–60 cm dbh, large trees: dbh ≥60 cm; total area sampled for individuals ≥10 cm dbh = 1.44 ha, area sampled for sapling class: 0.16 ha; UL: unlogged forest, L 0.5: forest sampled 6 months after logging, L 18: forest sampled 18 years after logging.

post-harvest, respectively. Of the 40 species represented by at least one stem ≥60 cm dbh in at least one stand, 19 species were shared by all three stands in the logging chronosequence (Table 1). Seventy species with individuals ≥10 cm dbh were found on plots in all three stands and at least 101 species were found in two of the stands. Of the 25 species with the highest densities in the 2.5–10 cm size class, only three were not shared by all three stands (Table 2). The mixed nature of the forest is underscored by the fact that no one species occupied more than 5% of the basal area or 7% of the total stems ≥10 cm dbh in unlogged forest.

3.2. Stand structure

Forest sampled 18 years post-harvest had significantly lower densities of individuals in the 2.5–10 cm dbh ($F = 6.04, \text{d.f.} = 2, P < 0.05$) and 10 cm ≤ dbh ($F = 6.74, \text{d.f.} = 2, P < 0.05$) size classes than either the unlogged stand or the stand sampled 6 months post-harvest (Table 3). There were no significant differences in liana densities between treatments in either the 2.5–10.0 cm dbh and ≥10 cm dbh size classes. In addition, no significant differences in basal area were found between unlogged and logged forest stands (unlogged = 30.5 ± 3.76(S.E.), 6 months post-logging = 29.8 ± 2.31(S.E.), and 18 years post-logging = 24.4 ± 1.87(S.E.) $m^2\ ha^{-1}$).

Table 3
Stem density for trees and shrubs 2.5–10 cm dbh and ≥10 cm dbh in selectively logged forest in the Dzanga-Sangha Dense Forest Reserve, Central African Republic[a]

Time since logging	Stem density for 2.5–10 cm dbh size class (stems ha^{-1})	Stem density for ≥10 cm dbh size class (stems ha^{-1})
Unlogged	2937.5 a	451.4 a
6-Month post-logging	2806.25 a	450.7 a
18 years post-logging	2212.5 b	359.7 b

[a] Letters denote significant differences by Tukey test for ANOVA in S-Plus, $n = 16$ samples.

3.3. Shade tolerance guilds

Statistically significant differences were found between frequency distributions of percent shade bearers between logging treatments ($\chi^2 = 11.48$, d.f. $= 4, P < 0.05$). This is clearly due to the differences between percent shade bearers in the 18-year post-harvest treatment and the other treatments (Fig. 2).

3.4. Timber species

3.4.1. Seedling inventory of exploited species

Forest sampled 18 years post-logging was the only forest stand within which no *E. cylindricum* seedlings

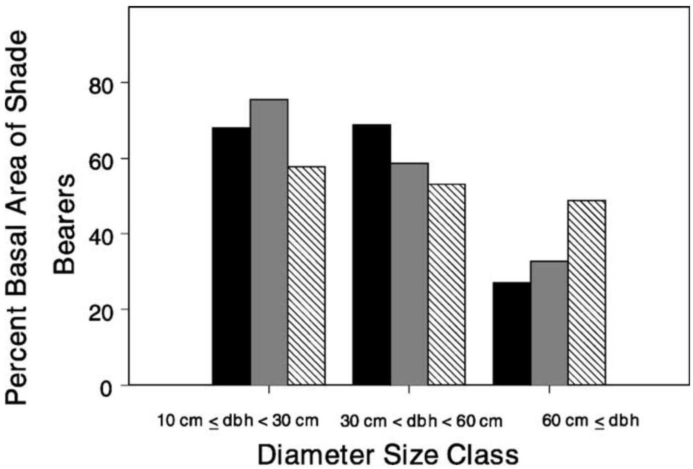

Fig. 2. The percentage of shade bearers in unlogged, 6 months and 18 years post-harvest forest treatments in the Dzanga-Sangha Dense Forest Reserve, Central African Republic (dark shading: unlogged stand, gray shading: 6 months post-logging stand, diagonal hatching: 18 years post-harvest stand).

Table 4
Frequency distribution and seedling density for *E. cylindricum* seedlings detected during regeneration survey in logging study in the Dzanga-Sangha Dense Forest Reserve during the months of October–November 2000

	0	1	>1	Density (stems ha^{-1})
Unlogged forest	92	5	3	1800
18 years post-harvest	100	0	0	0
6-Month post-harvest	81	14	5	5926
Eleme ya Ngombe plot	53	17	25	9684

were found in plots (Table 4). However, some seedlings were detected outside of the plots. There was significant variability between frequency distributions of *E. cylindricum* seedlings on plots in the two unlogged forest stands sampled (Kongana unlogged and Eleme ya Ngombe, $\chi^2 = 34.35, \text{d.f.} = 2, P < 0.05$). While 47% of the plots sampled at Eleme ya Ngombe contained seedlings of *E. cylindricum*, only 8% of those sampled in Kongana unlogged forest contained seedlings of *E. cylindricum*. Contingency table evaluations found significant differences among the three logging treatments ($\chi^2 = 22.22, \text{d.f.} = 2, P < 0.05$).

3.4.2. Saplings and trees

Both logged timber stands contained individuals of one or more harvested timber species (*E. cylindricum* and *E. utile*, Table 5) but densities were too low to permit statistical comparisons.

No statistically significant differences were observed between number of top quality timber trees ≥10 cm dbh between treatments but 80% of these species were shade intolerant. No individuals of top quality timber species in the 2.5–10 cm dbh size class were found in unlogged forest; however, they were found in both logged treatments (Table 5).

3.4.3. Size class distribution of exploited species

In unlogged forest near Kongana, 3.2 individuals of *E. cylindricum* ≥10 cm dbh were found per hectare. In a similar survey undertaken on Eleme ya Ngombe plot, Harris and Hall (unpublished data) found 3.1 individuals per hectare of *E. cylindricum* in the same size classes. In the 10–30 cm dbh size class, densities of *E. cylindricum* were 2.1 and 1.9 individuals per hectare for Kongana unlogged and Eleme ya Ngombe, respectively. *E. utile* was rare in both these forest stands. The similarities of these data sets suggests that the 100 ha census of *E. cylindricum* and *E. utile* ≥10 cm dbh on the Eleme ya Ngombe study site can be used as a reasonable substitution for size class distribution of these species in unlogged forest at Kongana.

During the census at Elembe ya Ngombe, 324 and 16 individuals ≥10 cm dbh were identified of

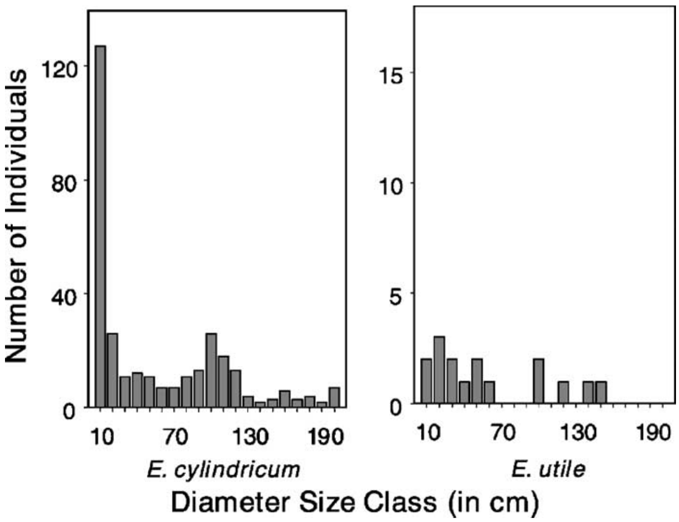

Fig. 3. Size class distribution of *E. cylindricum* and *E. utile* ≥10 cm dbh on the 100 ha Eleme ya Ngombe plot in the Dzanga-Sangha Dense Forest Reserve, Central African Republic.

Table 5
Stem density by size class of top quality timber species encountered in logging study in the Dzanga-Sangha Dense Forest Reserve, Central African Republic[a]

Genus	Species	Stem density per hectare															Shade tolerance
		Saplings			Poles			Medium trees			Large trees			All trees			
		UL	L 0.5	L 18	UL	L 0.5	L 18	UL	L 0.5	L 18	UL	L 0.5	L 18	UL	L 0.5	L 18	
Entandrophragma	*angolense*	0	6.25	0	0.69	1.39	0.69	0	0.69	0.69	0	0	0	0.69	2.08	1.38	NPLD
Entandrophragma	*candollei*	0	0	0	0.69	2.08	1.39	0	0	0	0	0	0	0.69	2.08	1.39	NPLD
Entandrophragma	*cylindricum*	0	0	0	2.08	0.69	0.69	0	0.69	0	1.39	0.69	0	3.47	2.07	0.69	NPLD
Entandrophragma	*utile*	0	0	0	0	0	0.69	0	0	0	0	0	0	0.00	0.00	0.69	NPLD
Erythrophleum	*ivorense*	0	0	0	0.69	0	0.69	0	0	0	0	0	0	0.69	0.00	0.69	NPLD
Lophira	*alata*	0	0	0	0	0.69	0	0	0	0.69	0.69	0.69	0	0.69	1.38	0.69	Pioneer
Lovoa	*trichilioides*	0	12.5	6.25	0	1.39	2.08	0	0	0	0	0.69	0	0.00	2.08	2.08	NPLD
Nesogordonia	*papaverifera*	0	12.5	6.25	2.78	0	3.47	2.78	0	1.39	0	0	0	5.56	0.00	4.86	SB
Oxystigma	*oxyphyllum*	0	0	0	0.69	1.39	0	0	0	0.69	0.69	1.39	0	1.38	2.78	0.69	SB
Pterocarpus	*soyauxii*	0	6.25	18.75	2.08	2.08	3.47	0.69	0	2.08	0	0	0	2.77	2.08	5.55	NPLD

[a] Top quality: species classed by PARN (1995) and/or Foret Ressources Management (1999) as their highest priority exploitation class; saplings: 2.5–10 cm dbh, poles: 10–30 cm dbh, medium trees: 30–60 cm dbh, large trees: dbh $\geq$ 60 cm; total area sampled for individuals $\geq$10 cm dbh = 1.44 ha, area sampled for sapling class: 0.16 ha; UL: unlogged forest, L 0.5: forest sampled 6 months after logging, L 18: forest sampled 18 years after logging; shade tolerance follows guilds defined in Hawthorne (1995).

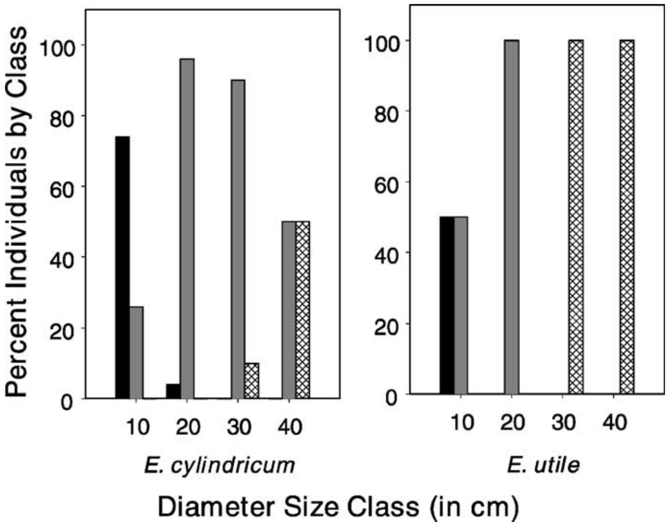

Fig. 4. Percent individuals by crown and diameter class of *E. cylindricum* and *E. utile* $\geq$10 cm dbh on the 100 ha Eleme ya Ngombe plot in the Dzanga-Sangha Dense Forest Reserve, Central African Republic (dark shading: understory, gray shading: midstory and cross-hatching: canopy and emergent individuals; $n = 324$ for *E. cylindricum* and $n = 16$ for *E. utile*).

E. cylindricum and *E. utile*, respectively. *E. cylindricum* exhibited a bimodal size class distribution and *E. utile* did not (Fig. 3). *E. cylindricum* had 100 more individuals in the 10 cm diameter size class than in the second peak at 100 cm. Both species exhibited a pronounced shift in canopy position with increased diameter between the 10 and 40 cm diameter classes (Fig. 4).

4. Discussion

4.1. Tree species composition and diversity

Inventories of woody vegetation exhibited a high degree of species overlap between the stands in the logging sequence. As noted above, no plots in the 6-month post-logging stand were placed in forest actually affected by logging. The fact that the species diversity index for the forest 18 years post-logging fell between what amounts to two unlogged forest samples highlights the natural variability within the forest. These data suggest that the low level timber extraction practiced in the Dzanga-Sangha Dense Forest Reserve has minimal impact on levels of tree species diversity. Malcolm and Ray (2000) assessed the impacts of timber exploitation by looking at differences in forest structure and floristic and rodent diversity in the same forest. In their study, Malcolm and Ray (2000) compared forest along primary and secondary logging roads and skidder trails with unlogged forest and concluded that primary and secondary roads have a significant impact on floristic diversity. In this study, the unit of study was the forest stand, which is a more appropriate unit of study when assessing the impacts of logging on floristic diversity within a forest.

4.2. Stand structure

Timber extraction does appear to have a lasting impact on forest structure as both tree and sapling densities were significantly lower in forest sampled 18 years post-harvest than unlogged forest. In addition, basal area of forest 18 years post-extraction was 19% lower than that of unlogged forest. The fact that basal area of these two forest stands was not significantly different is attributable to the natural occurrence of abundant forest gaps in unlogged forest. This high frequency of gaps resulted in a high variance associated with basal area estimates. Increased sampling effort would undoubtedly lead to significant differences between treatments. The fact that basal area and both sapling class and tree densities were virtually identical between the unlogged stand and the stand sampled 6 months post-extraction is not surprising. The actual forest canopy damage caused directly by similar logging operations in this region was found to be 6.8% by Wilkie et al. (1992) in Congo and 5% by Jardin (1995) in Cameroon. The low sampling frequency resulted in none of the overstory sampling plots being placed in forest directly cleared by logging in the recently logged forest.

The markedly lower basal area of forest 18 years post-logging is likely the result of canopy destabilization, factors related to physiological stress associated with sudden crown exposure (see, e.g., Parrotta et al., 2002), and damage to the residual stand that results in tree death after the completion of timber extraction. The significantly lower density of individuals in the 2.5–10 cm dbh size class recorded in this study between unlogged and 18-year post-harvest stands is most likely due to a combination of factors. The most obvious cause of low densities would be mortality resulting from logging, including physiological stress of sudden crown exposure (Smith et al., 1997). Rapid site occupation and establishment of the ground story by dense herbaceous vegetation in the Zingiberaceae or Marantaceae would preclude seedling establishment and survival of all but the most shade tolerant of species. The slow growth rates of shade bearing seedlings would result in slow seedling recruitment to the sapling class. At the same time, saplings in the logged forest exposed to direct sunlight that overcame the physiological stress of increased sunlight would recruit into the small tree size classes.

4.3. Shade tolerance guilds

In addition to the statistically significant differences in stem densities and marked differences in basal area between unlogged and 18 years post-logging treatments, there was a significant shift in the frequency distribution of percent basal area occupied by shade bearing species between treatments. Whereas shade bearing species occupy approximately one-quarter of the basal area of the largest diameter size class ($\geq$60 cm dbh) in the unlogged forest stand, these species occupy almost half of the basal area in the forest sampled 18 years post-logging (Fig. 2). This suggests that the highly selective logging practiced here favors diameter growth of shade bearing canopy and intermediate stratum trees. However, the percent basal area occupied by shade bearers in the small and medium tree size classes is somewhat lower in this logged forest than in unlogged forest, suggesting that increased light in lower strata resulting from logging operations favored establishment and growth of pioneer and non-pioneer light demanding species.

4.4. Timber species

4.4.1. Seedling inventory of exploited species

The two seedling data sets collected in unlogged forest in this study clearly show the variability in fruiting success between forest stands within a relatively small area in a given year. No seed wings were found within the unlogged Kongana regeneration plots and there was no evidence of a substantial *Entandrophragma* spp. fruiting event within this forest stand in the year before this study. However, during the same period in 1997 an *E. cylindricum* seedling carpet similar to what was found during this survey at Eleme ya Ngombe was observed at Kongana (J.S. Hall, personal observation). Within this context, the statistically significant differences between seedling frequency distributions of the three logging treatments cannot be attributed to timber exploitation.

4.4.2. Saplings and trees

Sapling densities of top quality timber species were low in all three stands. No saplings of these species were detected in unlogged forest and densities were similar in both logged forest stands (Table 5). Given the time elapsed since logging in the 6-month post-harvest sequence, these saplings represent pre-harvest background densities. It is notable that no saplings of either of the two species exploited (*E. cylindricum* and *E. utile*) were detected during sampling in any of the three treatments. Petrucci and Tandeau de Marsac (1994), in a comparison between commercially logged, commercially logged and thinned, and unlogged forest 9 years post-treatment, found densities of *E. cylindricum* regeneration (1.0–10 cm dbh) to be lower in commercially logged forest than their unlogged control. Thus there appears to be a general lack of seedling recruitment to the sapling stage of *Entandrophragma* spp. following high-grade selective logging when no additional silvicultural treatment is applied in forests of the Central African Republic. The lack of statistically significant differences of top quality timber trees ≥10 cm dbh between stands underscores the fact that these forests remain relatively well stocked with timber after high-grade logging.

4.4.3. Size class distribution of *Entandrophragma spp.*

The densities of *Entandrophragma* spp. recorded in this study are similar to those recorded throughout tropical Africa for these species (see, e.g., Hall, 1977; CTFT, 1985; Swaine and Hall, 1988). Because the number of individuals of these species in intermediate tree size classes is often not recorded in low intensity sampling, they may be assumed missing and thus not recruiting. However, in a comprehensive review, Swaine and Hall (1988) found that there is no evidence of insufficient recruitment in unlogged forest when appropriate spatial scales are assessed. The larger data set acquired on the Eleme ya Ngombe plot support their assertion.

Entandrophragma spp. are classed by Hawthorne (1995) as NPLDs and recent empirical work by Hall et al. (in press) has shown that seedlings of these species grow best in the light conditions of small to intermediate sized gaps. Hawthorne (1995) found *Entandrophragma* spp. tree crowns of small and intermediate trees in Ghana to have higher than average background crown class values of light exposure suggesting that only sapling and pole sized individuals that are at least partially exposed to direct sunlight recruit to intermediate tree size classes. Swaine et al. (1987) and Ashton (1981) point out that only the fastest growing individuals of smaller trees destined for the canopy will actually survive and recruit to subsequent size classes. The dramatic differences in crown classes and densities observed in this study between *Entandrophragma* spp. 10–20 and 30–40 cm dbh on Eleme ya Ngombe plot (Fig. 4) suggest that only the relatively small subset of trees in the lower size class whose crowns are exposed to direct sunlight actually recruit to intermediate tree size classes. It is reasonable to assume that trees with exposed crowns have higher than average growth rates for all trees ≥10 cm dbh that may lead to accelerated passage times through intermediate tree size classes and thus account for the observed diameter distributions on the 100 ha plot. This assertion is supported by data presented in Keay (1961) who found a virtual doubling of diameter growth rate for *E. cylindricum* between his 10–19 and 19–39 cm diameter increment size classes. Growth rates doubled again between his 19–39 and 39–87 cm dbh size classes (Keay, 1961).

4.4.4. Timber management

These data have profound implications for recruitment of *Entandrophragma* spp. and forest management. Densities of both *E. cylindricum* and *E. utile* in forest sampled 18 years post-logging suggest a very long re-entry time in order to harvest these species. Data presented in Table 5 suggest only moderate recruitment of top quality timber species in logged forest for small and intermediate size class trees. The data presented for top quality timber trees ≥60 cm dbh reflect the low background densities and spatial variability in the distribution of quality timber. However, these data suggest that if ecological considerations were ignored, stands currently being harvested for timber could be re-entered relatively soon after exploitation if loggers were interested in top quality timber other than *E. cylindricum* and *E. utile*. In fact, vast tracts of forest within the region are currently being inventoried with the intention of subsequent harvests of species other than these two African mahoganies (J.S. Hall and D.J. Harris, personal observation).

The data presented in Figs. 3 and 4 suggest that relatively few *Entandrophragma* spp. represented in the 10–20 cm dbh size class actually recruit to the higher size classes. Even with high recruitment, the very low densities of intermediate size trees and recorded growth rates of 0.53–0.7 cm increment per year (Durrieu de Madron et al., 2000) suggest that it will be a very long time before *E. cylindricum* and *E. utile* alone will provide sufficient densities and volumes to justify re-entry. This is supported by Keay (1961) who projected 100-year rotations for *Entandrophragma* spp. in Okumu Forest, Nigeria. However, Petrucci and Tandeau de Marsac (1994) and Dupuy et al. (1997) have shown that liberation thinning following logging can both increase regeneration establishment of *Entandrophragma* spp. and dramatically increase recruitment of quality timber species. An application of these methods in the Dzanga-Sangha region should have similar effects and improve *Entandrophragma* and other top quality timber species production.

4.5. Management objectives

The management objectives of the Dzanga-Sangha Dense Forest Reserve and adjacent conservation areas in Cameroon and Congo extend far beyond timber production and job creation. This region has long been recognized for its extraordinary fauna and conservation importance (Carroll, 1988a,b; Ray and Hutterer, 1996; Blom, 2001). Problems of immigration and commercial hunting associated with timber exploitation are well known in Central Africa and can have devastating impacts on conservation areas (Wilkie et al., 1992, 2000; Curran, 1993; Noss, 1998). The limited success of management strategies to mitigate these problems make the coexistence of these activities problematic where conservation is the top priority. Nevertheless, both timber production and biodiversity conservation are stated management objectives in or adjacent to conservation projects throughout the region, including the Dzanga-Sangha Dense Forest Reserve (Baum et al., 1998).

Based on a conclusion that canopy disturbance was responsible for the negative effects of logging, Malcolm and Ray (2000) proposed reduced canopy disturbance as the best way to meet the dual objectives of timber production and conservation. Data presented herein suggest that up to 75% of the basal area of canopy trees is represented by individuals of shade intolerant species at the seedling, sapling, and/or small tree size classes in unlogged forest. The extraction of very low volumes of timber appear to have resulted in a significant shift towards a higher representation of shade bearers in the canopy and significantly lower densities of sapling and tree size class individuals for all guilds. There is little evidence of improved regeneration of *Entandrophragma* spp. and recruitment of *Entandrophragma* spp. and other top quality timber post-logging as presently practiced. In a floristically similar forest to the one studied here, Petrucci and Tandeau de Marsac (1994) obtained improved recruitment of top quality timber species and projected a reduction in stand recovery time by 50% through liberation thinning that reduce basal area by an additional 25% post-harvest. If the reduced stand densities of saplings and trees in 18-year post-harvest forest found in this study are a function of the occupation of growing space by existing vegetation as suggested above, then carefully planned increased canopy disturbance rather than decreased disturbance may be a better alternative to maintaining long term forest structure and floristic diversity. However, this should proceed with caution until predictions can be verified.

The data presented herein show that timber extraction within Dzanga-Sangha already has one of the lowest initial impacts of mechanized logging operations in the region (see, e.g., Ola-Adams, 1987; Petrucci and Tandeau de Marsac, 1994; Jardin, 1995). The significantly lower sapling class and tree stem densities between unlogged and 18-year post-harvest stands suggest that without careful attention, stem mortality will increase after logging. However, the shade intolerant nature of the *Entandrophragma* spp. and other top quality timber species saplings and small trees (Table 5) results in a lack of the increased recruitment necessary to continue long term management for these species. Nevertheless, the fact that individuals of most top quality timber species were not harvested suggests that these forests will remain attractive to forestry operations in the future, particularly as markets change to reflect the disappearance of *Entandrophragma* spp. from timber production areas within the region.

Ironically, the best strategy to manage these forests for top quality timber production and maintain long-term forest structure, stem densities, and floristic composition appears to be increased but targeted stand manipulation. If selective application of liberation treatments results in forest recovery after two decades as projected by Petrucci and Tandeau de Marsac (1994), this may also be the best long-term strategy to maintain forest structure outside protected areas. However, data presented in Malcolm and Ray (2000) suggest that the levels of canopy disturbance advocated as being the best way to manage for timber production and maintain forest structure over the long term here will lead to the disappearance of a suite of closed forest obligate small mammals. Further, Plumptre (2001) cautions that selective logging results in reduced densities and, in some instances, the disappearance of many closed forest obligate species of birds. Thus it is clear that timber production is not an appropriate management alternative in areas designated for conserving such species. Nevertheless, managing forests for quality timber production remains one of the best alternatives for meeting the dual goals of biodiversity conservation and revenue generation in areas adjacent to protected areas. Meeting these management objectives in the Dzanga-Sangha region will require respecting the integrity of core conservation areas while managing the matrix within which these areas are found for quality timber.

5. Conclusions

Timber extraction, as presently being practiced in the Dzanga-Sangha region of southwestern Central African Republic and adjacent Congo and Cameroon is little more than a mining operation. There is inadequate recruitment of harvested species and evidence suggests that without post-harvest treatment structural changes will last several decades. Because evidence from other studies suggests that disturbance from logging leads to the disappearance of closed forest obligate species of birds and small mammals, it is an inappropriate activity in this region where strict biodiversity conservation is the priority. Nevertheless, data suggest that carefully planned, increased canopy disturbance will lead to accelerated stand recovery and improved recruitment of top quality timber species. For this reason, well managed forestry appears to be an appropriate revenue generating activity for zones adjacent to protected areas where the overriding management objective is to maintain forest structure and tree species composition over the long term.

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