TREE SPECIES DIVERSITY AND SOIL STATUS OF PRIMARY AND DEGRADED TROPICAL RAINFOREST ECOSYSTEMS IN SOUTH-WESTERN NIGERIA

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ONYEKWELU, J. C., MOSANDL, R. & STIMM, B. 2008. Tree species diversity and soil status of primary and degraded tropical rainforest ecosystems in south-western Nigeria. We investigated the tree species diversity and soil properties of primary (Queen's) and degraded (Elephant and Oluwa) rainforests in south-western Nigeria. Results revealed that differences in soil properties of the sites could not be attributed to the effect of forest degradation since there was no discernable pattern between properties of primary and degraded forest soils. A total of 31 families (26, 24 and 22 in Queen's, Oluwa and Elephant forests respectively) were encountered. Species diversity index, species richness and species evenness were in the order Queen's > Oluwa > Elephant forests and decreased as the level of forest degradation increases, thus indicating that these indices depended on site conditions. Queen's forest had the highest species diversity (51), followed by Oluwa (45) and Elephant forests (31). About 30% of tree species in the three sites were among the endangered tree species in Nigeria, a situation that calls for urgent conservation measures. The similarity of diversity index of the once highly degraded Oluwa forest with that of the primary forest indicates that rainforests have the ability to return to their original 'species rich' situation even after significant degradation, provided that the physical factors of the forest are intact, seed dispersal is present, the site does not become invaded by aggressive weed species and all forms of degradation activities cease or are controlled.

Keywords: Forest degradation, species diversity index, species richness, species evenness, soil properties, conservation measures

ONYEKWELU, J. C. MOSANDL, R. & STIMM, B. 2008. Kepelbagaian spesies pokok dan status tanah ekosistem hutan hujan tropika primer dan ternyahgred di barat daya Nigeria. Kami menyiasat kepelbagaian spesies pokok dan ciri tanah hutan hujan primer (hutan Queen's dan ternyahgred (hutan Elephant dan hutan Oluwa) di barat daya Nigeria. Keputusan menunjukkan bahawa perbezaan dalam ciri-ciri tanah tapak kajian tiada kaitan dengan kesan degradasi hutan. Ini kerana tiada corak yang jelas antara ciri tanah hutan primer dengan hutan ternyahgred. Sebanyak 31 famili (masing-masing 26, 24 dan 22 di hutan Queen's, Oluwa dan Elephant) ditemui. Indeks kepelbagaian spesies, kekayaan spesies dan kesamaan spesies adalah dalam turutan hutan Queen's > hutan Oluwa > hutan Elephant dan nilainya menurun apabila degradasi hutan bertambah. Ini menunjukkan bahawa semua indeks ini bergantung pada keadaan tapak. Hutan Queen's mempunyai nilai kepelbagaian spesies yang tertinggi (51) diikuti hutan Oluwa (45) dan hutan Elephant (31). Lebih kurang 30% spesies pokok di ketiga-tiga tapak merupakan spesies pokok yang terancam di Nigeria dan ini semestinya menuntut agar langkah-langkah pemuliharaan segera diambil. Hutan Oluwa dahulunya merupakan hutan ternyahgred. Namun indeks kepelbagaiannya yang hampir sama dengan indeks hutan primer mencadangkan bahawa hutan hujan mampu kembali ke tahap kekayaan spesies asal walaupun setelah degradasi yang teruk asalkan faktor fizikal hutan tidak berubah, berlakunya penyebaran biji benih, tapak tidak dipenuhi pokok musuh yang agresif dan segala aktiviti degradasi terhenti terus atau terkawal.

INTRODUCTION

One of the well-known characteristics of tropical rainforests is the large number of species that inhabit them. Though accounting for only 7% of the earth's dry surface area, rainforests accommodate 70% of animal and plant species

in world ecosystems (Lovejoy 1997). Between 100 and 300 tree species ha⁻¹ are found in rainforests, a value that is much higher than that of species found in temperate forests. The high species diversity of rainforests is partly responsible for

the intense pressure under which they have been and are still subjected to. About 10 million ha of rainforests are degraded each year, with exploitation, felling damage to residual forests and non-timber forest products collection being the chief causes. Forest degradation is usually accompanied by species extinction, reduction in biodiversity and decrease in primary productivity (Wilcox 1995).

The long-term effect of this pressure is usually destruction of the quality and quantity of rainforests. While destruction in quantity is called deforestation, destruction in terms of quality is called forest degradation. Unlike deforestation, forest degradation does not involve land-use change.

Nigerian rainforest ecosystems occupy 95372 km² (9.7%) of the country's land mass. It is the most densely populated part of Nigeria and source of the bulk of the country's timber needs. These ecosystems have been under intense pressure and had already shown signs of human activity even before colonial times. Trading of Nigerian timbers in international markets as well as rising domestic demand led to unregulated exploitations of forests and timber was removed on a massive scale (Oliphant 1934). This eventually resulted in serious forest degradation leaving less than 5% of the country's rainforest ecosystems as undisturbed forests (Kio *et al.* 1992, Sarumi *et al.* 1996).

Following centuries of degradation, many rainforest ecosystems are severely threatened and persist as forest fragments. Consequently, there is a growing interest in quantifying habitat characteristics such as forest structure, floristic composition and species richness in primary and degraded forests (Myers *et al.* 2000, Gillespie *et al.* 2004). This study investigates tree species diversity and soil properties of primary and degraded rainforest ecosystems in south-western Nigeria.

MATERIALS AND METHODS

Study areas

The study was conducted in Queen's and Elephant forests located within Omo Forest Reserve (6° 35'-7° 05' N and 4° 05'- 4° 40' E) as well as in Oluwa forest located within Oluwa Forest Reserve (6° 55'-7° 20' N and 3° 45'-4°

32' E). Both reserves experienced heavy and repeated timber exploitation during the past 50 years, except for a few inaccessible parts. By early 1970s, Oluwa and Omo Forest Reserves were already seriously degraded and were subsequently designated for industrial plantation establishment. However, only little portions of the reserves have been planted, thus, leaving a considerable portion under natural forest cover.

Queen's forest, with its core area and buffer zone of 460 and 14 200 ha respectively, was constituted a Strict Nature Reserve in 1949 and Biosphere Reserve in 1977 (Isichei 1995, Were 2001). There is no recorded evidence of timber exploitation in Queen's forest. Elephant forest, which is home to forest elephant species (Loxodonta cyclotis) was heavily exploited in the past. However, the Elephant Project which was launched in 1992 substantially reduced timber exploitation activities. In Oluwa Forest Reserve exploitation of natural forest usually occurred prior to plantation establishment, and the remaining natural forest has not been exploited since the commencement of large-scale plantation establishment, though it has been designated for plantation.

Climate and site conditions

Rainy season in both reserves occurs from March till November while the dry season, form December till February. Annual rainfall ranges from 1700 to 2200 mm. Annual temperature and average daily relative humidity in Oluwa and Omo is 26 °C and 80% respectively. Average elevation is 100 m in Oluwa and 123 m in Omo. Soils are predominantly ferruginous tropical, typical of the variety found in intensively weathered areas of basement complex formations in the rainforest zone of south-western Nigeria. The soils are well-drained, mature, red, stony and gravely in upper parts of the sequence. The texture of topsoil in both reserves is mainly sandy loam.

Data collection

Data were collected from 24 temporary sample plots of 20×20 m (eight in each site) laid out systematically across the study sites. Within each plot, trees with diameter at breast height (dbh) \geq 10 cm were identified and their dbh measured. A

 6×6 m subplot was laid out at the centre of each plot. Soil samples were collected in all subplots and tree seedlings and saplings (< 10 cm dbh) were identified and counted. Based on soil profile classification by Smyth and Montgomerry (1962), three soils samples (at 2-m intervals) were collected from each sample plot at four fixed depths of 0-15, 15-30, 30-45 and 45-60 cm using soil auger. Depth of 0-15 cm consisted of O horizon and part of A horizon while the 15–30 cm depth, the remaining part of A horizon. Depths 30–45 and 45–60 cm were B and C horizons respectively. Soils from similar depths within each sample plot were thoroughly mixed and composite samples collected. Samples for bulk density were collected from 0-15 cm only.

Analyses of soil samples

Soil samples were air-dried and ground in a Wiley mill to pass through a 2-mm sieve. Particle size analysis was performed using hydrometer method, with sodium hexameta-phosphate as dispersing agent. The USDA particle size classification was adopted in expressing soil particle size fractions (Soil Survey Staf 2003). Core cylinder samples were dried for two days at 105 °C and bulk density calculated as the ratio of oven-dry weight of soil to cylinder volume. Soil pH was determined using a digital pH meter in 1:2 soil/water solution. Organic matter was estimated by first determining organic carbon using Walkley and Black (1934) method and then multiplying the result by 1.724. Extract for available P was prepared with ammonium fluoride and P determined using molybdenumblue method (Murphy & Riley 1962). Total N was determined using micro-Kjeldahl method with selenium catalyst (Bremner 1965). For determination of exchangeable Ca, Mg, K and Na, soil samples were first leached with 1 N ammonium acetate solution (pH = 7.0). Exchangeable Ca and Mg were determined by atomic absorption spectrophotometer while exchangeable Na and K, by digital flame photometry.

Data analyses

Tree species were categorized into life form using their maximum height (Keay 1989). The percentage of species relative density was computed as:

$$RD = (n_{i}/N) \times 100 \tag{1}$$

where

RD = species relative density

n_i = number of individuals of species i

N = total number of all tree species in the entire community.

Species relative dominance (RDo (%)) was computed using equation (2):

$$RDo = \frac{(\Sigma Ba_i \times 100)}{\Sigma Ba_n}$$
 (2)

where

Ba_i = basal area of individual tree belonging to species i

 $Ba_n = stand basal area.$

The relationship, RD + RDo/2, gave the importance value (IV) for each species. Species diversity index was calculated using Shannon-Wiener diversity index (Kent & Coker 1992):

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i)$$
 (3)

where

H' = Shannon-Wiener diversity index

S = total number of species in the community

p_i = proportion of S made up of the ith species

ln = natural logarithm.

Shannon's maximum diversity index was calculated using equation (4):

$$H_{\text{max}} = \text{In}(S) \tag{4}$$

where

 H_{max} = Shannon's maximum diversity index.

Species evenness in each community was determined using Shannon's equitability (E_{H}) :

$$E_{H} = \frac{H'}{H_{max}} = \frac{\sum_{i=1}^{S} p_{i} \ln(p_{i})}{\ln(S)}$$
 (5)

Sorensen's species similarity index between two sites was calculated using equation (6):

$$SI = \left(\frac{2C}{a+b}\right) * 100 \tag{6}$$

where

C = number of species at sites a and b a, b = number of species at sites a and b.

Test of significance of each soil nutrient, density, species diversity and richness, dbh, basal area and volume production in the three sites was conducted by one way analysis of variance using SPSS for Windows 12.0. Means found to differ significantly were separated using Fishers' least square difference.

RESULTS

There were no significant differences (p < 0.05) in bulk densities of the three sites at 0–15 cm depth, with values ranging from 1.32 to 1.43 g cm⁻³ (Table 1). Silt content significantly increased with soil depth, except at 0–15 cm depth where Queen's and Elephant forests had a significantly higher silt contents than Oluwa forest (Table 1). At all three sites, sand content at 45-60 cm soil depth was significantly lower than the other depths. Except at 0-15 cm soil depth, where Oluwa forest was found to have a significantly lower sand content (p > 0.05) than the other sites, sand content of the three sites were similar (p < 0.05). Oluwa forest showed a significantly higher clay content than both Queen's and Elephant forest, except at 30–45 cm soil depth. Table 1 also shows that soils of the three study sites were slightly acidic, with acidity increasing with increase in soil depth. For depths of > 30 cm, Queen's and Elephant forests had lower pH compared with Oluwa. Organic matter significantly decreased with increasing soil depth but did not differ significantly among the three sites. Available P and exchangeable Na concentrations were significantly higher in Queen's and Elephant forests than in Oluwa while exchangeable K was significantly higher in Oluwa than in Queen's and Elephant forests. Concentrations of exchangeable Mg, Ca and total N were not significantly different across the three sites.

We enumerated 31 families in the three sites, with 26, 24 and 22 of the families occurring in Queen's, Oluwa and Elephant forests respectively (Tables 2–4). About 52% of the families were represented by one species, 16% by two species and 32% by more than two species in the three sites (Tables 2–4). Families with high numbers of different species are Euphorbiaceae,

Sterculiaceae, Meliaceae, Mimosoideae and Apocynaceae.

A total of 76 species were encountered in the three sites, with Queen's forest having the highest number of species (51), followed by Oluwa (45) and Elephant forest (31) (Table 5). Thirty-nine tree species occurred in only one site while 22 were found in two sites. Only 15 tree species existed in all the three sites. Based on FORMECU (1999) classification, 16, 15 and 8 tree species in Queen's, Oluwa and Elephant forests respectively are endangered (Tables 2–4). Average densities are 671, 513 and 508 trees ha⁻¹ in Queen's, Oluwa and Elephant forests respectively.

Species with high relative density (RD) in the study sites included *Diospyros mespiliformis*, *Strombosia pustulata*, *Napoleonaea imperialis*, *Drypetes paxii*, *Celtis zenkeri*, *Sterculia rhinopetala* and *Cola millenii*. Results of importance value (IV) of tree species indicated that *D. mespiliformis*, *Khaya ivorensis* and *Napoleonaea imperialis* have the highest IV in Oluwa, Queen's and Elephant forests respectively (Tables 2–4). More than one species shared dominance in primary and degraded forest communities.

Results of species similarity index (63.4, 58.3 and 47.4 between Queen's and Elephant forests, Queen's and Oluwa forests, Oluwa and Elephant forests respectively) revealed that tree species in Queen's and Elephant forests are more similar than any other site combinations. Shannon-Wiener diversity index (H') and Shannon's maximum diversity index (H_{max}) followed the order Queen's > Oluwa > Elephant forest (Table 5). Results of Shannon's equitability (E₁₁) revealed that species evenness in the three communities were similar (Table 5), which was confirmed by the difference between H' and H_{max} for each site pair. It has been shown that the lower the difference, the more the evenness of species. Maximum dbh was 180, 108 and 84.8 cm in Queen's, Oluwa and Elephant forests respectively (Tables 2–4) while their respective dbh were 27.3, 22.5 and 21.6 cm (Table 5). Basal area was also higher in Queen's forest than in Oluwa and Elephant forests (Table 5).

There were 54 seedling species (29, 28 and 24 in Oluwa, Queen's and Elephant forests respectively) in the study sites, distributed among 21 families. The families and seedling species in each site were similar to those of the tree category (Tables 2–4 and 6). However, seedling

 Table 1
 Soil chemical and physical properties of the study sites

Soil	Study site				Chemical properties	properties					Physical properties	roperties	
depth (cm)		Hd	OM	Ь	K	Mg	Ca	Z	Na	Sand	Clay	Silt	BD
			(%)	$({ m mg~kg^{-1}})$	(cmol kg ⁻¹)	(cmol kg ⁻¹)	(cmol kg ⁻¹)	%	(cmolkg ⁻¹)	(%)	(%)	(%)	(g cm ⁻³)
0-15	Queen's	$6.3 \pm 0.36a$	$3.72 \pm 0.59a$	$20.27 \pm 4.1b$	$0.26\pm0.04b$	$1.86 \pm 0.28a$	$0.91 \pm 0.13a$	$0.31 \pm 0.08a$	$0.33 \pm 0.03b$	$76.6 \pm 3.9b$	$15.6 \pm 2.4b$	$7.8 \pm 2.9a$	$1.32 \pm 0.16a$
	Oluwa	$6.7\pm0.38a$	$3.32 \pm 0.49a$	$10.77 \pm 1.8a$	$0.50\pm0.14a$	$1.84\pm0.17a$	$0.91 \pm 0.13a$	$0.36 \pm 0.13a$	$0.24 \pm 0.05a$	$70.6 \pm 3.3a$	$21.9\pm2.8a$	$7.5 \pm 3.3a$	$1.36\pm0.24a$
	Elephant	$6.3\pm0.31a$	$3.19\pm0.57a$	$19.89 \pm 4.1b$	$0.27 \pm 0.07b$	$1.70\pm0.45a$	$0.85\pm0.11a$	$0.32 \pm 0.07a$	$0.33\pm0.03b$	$77.6\pm4.5b$	$15.0\pm2.0b$	$7.5 \pm 3.9a$	$1.43\pm0.17a$
15-30	15–30 Queen's	$5.9\pm0.60a$	$2.69\pm0.70b$	$18.00 \pm 3.9b$	$0.21 \pm 0.06b$	$1.81\pm0.24a$	$0.85\pm0.07a$	$0.27 \pm 0.06a$	$0.34 \pm 0.06b$	$69.6 \pm 3.0a$	$18.0\pm 2.7b$	$12.5\pm3.2b$	*pu
	Oluwa	$6.5\pm0.42a$	$2.40\pm0.46b$	$10.23\pm1.3a$	$0.45\pm0.16a$	$1.66 \pm 0.11a$	$0.84 \pm 0.12a$	$0.32 \pm 0.08a$	$0.24 \pm 0.03a$	$68.5\pm4.3a$	$22.9\pm3.8a$	$8.6 \pm 4.2a$	pu
	Elephant	$6.1\pm0.55a$	$2.53\pm0.58b$	$18.52\pm2.7b$	$0.22 \pm 0.08b$	$1.59\pm0.26a$	$0.77\pm0.14a$	$0.27 \pm 0.04a$	$0.35\pm0.06b$	$71.6\pm2.1a$	$17.0\pm4.1b$	$11.5\pm3.7b$	pu
30-45	Queen's	$5.5\pm0.58b$	$1.75\pm0.93c$	$16.83 \pm 3.0b$	$0.15\pm0.03b$	$1.61\pm0.24a$	$0.75 \pm 0.09a$	$0.24 \pm 0.04a$	$0.35\pm0.03b$	$67.2 \pm 3.0a$	$21.0 \pm 4.3a$	$11.8\pm2.7b$	pu
	Oluwa	$6.3\pm0.48a$	$2.25\pm0.46c$	$9.23\pm1.0a$	$0.42\pm0.14a$	$1.63 \pm 0.11a$	$0.83 \pm 0.14a$	$0.31 \pm 0.07a$	$0.27 \pm 0.03a$	$66.0 \pm 6.1a$	$24.6\pm4.7a$	$9.3 \pm 4.5a$	pu
	Elephant	$5.9\pm0.32b$	$1.86\pm0.96c$	$17.33\pm1.0b$	$0.16\pm0.05\mathrm{b}$	$1.55\pm0.33a$	$0.70\pm0.13a$	$0.27\pm0.04a$	$0.37 \pm 0.06b$	$65.9\pm5.6a$	$17.6\pm2.4b$	$16.5\pm6.1c$	pu
45–60	45–60 Queen's	$5.4\pm0.32b$	$5.4 \pm 0.32b$ $1.53 \pm 0.35c$	$15.58 \pm 2.0b$	$0.13\pm0.02b$	$1.56 \pm 0.4a$	$0.71\pm0.11a$	$0.21 \pm 0.02b$	$0.38 \pm 0.06b$	$60.6 \pm 7.7c$	$23.3 \pm 5.6a$	$16.1 \pm 4.3c$	pu
	Oluwa	$6.1\pm0.46a$	$1.76\pm0.44c$	$8.79\pm1.7a$	$0.38 \pm 0.16a$	$1.60\pm0.16a$	$0.77\pm0.08a$	$0.27 \pm 0.05a$	$0.29 \pm 0.02a$	$56.3 \pm 9.5c$	$30.4\pm8.2c$	$13.3\pm9.1b$	pu
	Elephant	$5.5\pm0.53b$	$1.57\pm0.47c$	$16.76\pm1.3b$	$0.15\pm0.06b$	$1.48\pm0.27a$	$0.67 \pm 0.15a$	$0.25\pm0.03ab$	$0.40\pm0.08b$	$59.2 \pm 6.0c$	$21.0\pm5.0a$	$19.8\pm5.3c$	pu

Values are means of eight replicates \pm standard deviation of the mean. OM = organic matter; BD = bulk density of the soil; * nd = not determined Values followed by similar letters are not significantly different at p \leq 0.05.

Table 2 Family and tree species richness in Queen's forest (primary forest) in Omo forest reserve

F 11-2	C.,	MT 1 b	Life	Conservation	Dbh	(cm)	RD	RDo	IV
Family ^a	Species ^a	Number ^b	$form^{c}$	status ^d	Mean	Max	(%)	(%)	(%)
Meliaceae	Khaya ivorensis	21	VLT	Endangered	106.2	160.0	2.72	25.93	14.32
Ebenaceae	Diospyros mespiliformis	125	LT	Endangered	13.2	27.8	16.30	2.01	9.15
Combretaceae	Terminalia superba	13	LT	Endangered	70.3	180.0	1.63	15.17	8.40
Sterculiaceae	Cola gigantea	21	VLT	-	80.9	140.0	2.72	13.28	8.00
Olacaceae	Strombosia pustulata	79	MT	-	21.2	35.5	10.32	3.20	6.76
Sterculiaceae	Sterculia rhinopetala	38	LT	Endangered	29.9	75.0	4.89	4.18	4.53
Lecythidaceae	Napoleonaea imperialis	50	ST	-	21.1	35.0	6.52	2.06	4.29
Apocynaceae	Funtumia elastica	50	MT	Endangered	17.1	28.0	6.52	1.11	3.82
Euphorbiaceae	$Ricinodendron\ heudelotii$	21	LT	Endangered	35.4	48.0	2.72	2.22	2.47
Meliaceae	Guarea thompsonii	21	VLT	Endangered	23.9	50.0	2.72	1.56	2.14
Sterculiaceae	Triplochiton scleroxylon	8	VLT	Endangered	61.7	90.6	1.09	3.15	2.12
Apocynaceae	Picralima nitida	25	ST	-	17.9	27.0	3.26	0.76	2.01
Myristicaceae	pycnathus angolensis	17	LT	-	28.4	49.8	2.17	1.75	1.96
Ulmaceae	Celtis zenkeri	4	LT	-	95.0	95.0	0.54	3.06	1.80
Irvingeaceae	Irvingia smithii	17	MT	-	36.2	48.5	2.17	1.36	1.77
Euphorbiaceae	Drypetes paxii	21	ST	-	15.1	23.8	2.72	0.43	1.57
Euphorbiaceae	Ricinodendron rautanenii	4	MT	-	87.5	87.5	0.54	2.60	1.57
Mimosoideae	Erythrophleum spp.	4	MT	-	84.0	84.0	0.54	2.39	1.47
Caesalpinioideae	Dialum spp.	17	ST	-	19.7	28.6	2.17	0.66	1.41
Apocynaceae	Hunteria umbellata	17	ST	-	17.7	27.5	2.17	0.49	1.33
Euphorbiaceae	Discoglypremna caloneura	17	MT	_	16.2	20.8	2.17	0.37	1.27
Rubiaceae	Nauclea diderrichii	13	LT	Endangered	30.4	36.0	1.63	0.90	1.27
Moraceae	Ficus exasperata	13	MT	-	16.5	27.6	1.63	0.68	1.16
Lecythidaceae	Napoleonaea vogelii	13	ST	_	17.1	22.8	1.63	0.63	1.13
Rubiaceae	Pausinystalia johimbe	13	MT	_	12.9	15.7	1.63	0.46	1.04
Mimosoideae	Pentaclethra macrophylla	13	MT	_	17.4	24.5	1.63	0.34	0.98
Mimosaceae	Tetrapleura tetraptera	8	MT	_	16.4	21.0	1.09	0.59	0.84
Ebenaceae	Diospyros spp.	8	MT	Endangered	15.0	16.0	1.09	0.47	0.78
Irvingeaceae	Irvingia spp.	4	MT	-	54.5	54.5	0.54	1.01	0.78
Agavaceae	Draceana spp.	8	ST	_	23.5	33.4	1.09	0.44	0.76
Papilionaceae	Pterocarpus spp.	4	MT	Endangered	51.5	51.5	0.54	0.90	0.72
Mimosoideae	Albizia ferruginea	4	LT	-	50.2	50.2	0.54	0.85	0.72
Meliaceae	Khaya grandifoliola	4	LT	Endangered	46.3	46.3	0.54	0.73	0.64
Sapotaceae	Pachystela brevipes	4	ST-MT	-	45.0	45.0	0.54	0.69	0.61
Rubiaceae	Mitragyna ciliata	8	LT	Endangered	13.3	13.5	1.09	0.12	0.60
Burseraceae	Canarium schweinfurthii	4	LT	Endangered	42.1	42.1	0.54	0.60	0.57
Euphorbiaceae	Phyllanthus discoideus	4	MT	Elidaligered	35.0	35.0	0.54	0.42	0.37
Moraceae	Ficus goliath	4	MT	-	35.0	35.0	0.54	0.42	0.48
Moraceae	Musanga cecropioides	4	MT	-	35.0	35.0	0.54	0.42	0.48
Sterculiaceae	Pterygota macrocarpa	4	LT	-	34.5	34.5	0.54	0.42	0.48
	Xylopia aethiopica	4	MT	-	23.0	23.0	0.54	0.40	0.47
Annonaceae	Enantia chlorantha	4	MT	- Endangered	21.4	21.4	0.54	0.16	0.35
Annonaceae	Ceiba pentandra	4	LT	-	55.8	55.8	0.54	0.10	0.34
Bombacaceae	*								
Capparaceae	Boscia salicifolia	4	ST	-	20.5	20.5	0.54	0.14	0.34
Mimosoideae	Albizia zygia	4	MT		21.0	22.0	0.54	0.14	0.34
Euphorbiaceae	Bridelia spp.	4	MT	-	19.0	19.0	0.54	0.12	0.33
Apocynaceae	Alstonia boonei	4	LT	- F., J	35.0	35.0	0.54	0.10	0.32
Boraginaceae	Cordia mellenii	4	ST	Endangered	14.6	14.6	0.54	0.07	0.31
Sterculiaceae	Cola millenii	4	MT	-	14.6	14.6	0.54	0.07	0.31
Tiliaceae	Desplatsia spp.	4	ST	-	13.5	13.5	0.54	0.06	0.30
Capparaceae	Buchholzia coriacea	4	ST-MT	-	11.6	11.6	0.54	0.05	0.29

For Tables 2–4: ^aFamily names and species nomenclature verified using *Trees of Nigeria* (Keay 1989)

^aValues are total number of trees in all sample plots

 $^{^{\}circ}$ VLT = very large trees (height > 50 m); LT = large trees (height > 30 and < 50 m); MT= medium trees (height > 15 and < 30m); ST = small trees (height < 15 m) and SH = shrub

 $^{^{\}rm d}\!$ Only trees classified as endangered by FORMECU (1999) were identified.

Table 3 Family and tree species richness in Elephant forest (degraded forest) in Omo forest reserve

Family ^a	Species ^a	Number ^b	Life form ^c	Conservation status ^d	Dbh	(cm)	RD	RDo	IV
,	1				Mean	Max	(%)	(%)	(%)
Lecythidaceae	Napoleonaea imperialis	113	ST	-	18.1	48.5	18.49	12.14	15.32
Olacaceae	Strombosia pustulata	75	MT	-	24.5	44.5	12.33	14.64	13.48
Ebenaceae	Diospyros mespiliformis	75	LT	Endangered	16.9	34.5	12.33	6.80	9.56
Euphorbiaceae	Drypetes paxii	75	ST	-	15.8	34.7	12.33	5.76	9.04
Bombacaceae	Ceiba pentandra	13	LT	-	50.6	84.8	2.05	11.75	6.90
Sterculiaceae	Cola millenii	33	MT	-	14.9	30.5	5.48	2.32	3.90
Apocynaceae	Picralima nitida	21	ST	-	22.4	45.6	3.42	3.66	3.54
Capparaceae	Buchholzia coriacea	21	ST-MT	-	20.3	31.5	3.42	2.68	3.05
Irvingeaceae	Irvingia smithii	4	MT	-	68.9	68.9	0.68	5.29	2.99
Euphorbiaceae	Phyllanthus discoideus	8	MT	-	42.0	50.8	1.37	4.10	2.73
Apocynaceae	Hunteria umbellata	17	ST	-	23.5	33.0	2.74	2.64	2.69
Moraceae	Musanga cecropioides	21	ST-MT	-	18.5	22.0	3.42	1.95	2.69
Boraginaceae	Cordia mellenii	13	ST	Endangered	29.1	36.8	2.05	2.93	2.49
Ulmaceae	Celtis zenkeri	13	LT	-	28.3	37.8	2.05	2.90	2.48
Combretaceae	Terminalia superba	13	LT	Endangered	26.3	44.6	2.05	2.85	2.45
Moraceae	Ficus exasperata	4	MT	-	54.0	54.0	0.68	3.25	1.97
Euphorbiaceae	Ricinodendron heudelotii	4	LT	Endangered	48.5	48.5	0.68	2.62	1.65
Rubiaceae	Pausinystalia johimbe	8	MT	-	25.2	33.0	1.37	1.55	1.46
Apocynaceae	Funtumia elastica	8	MT	Endangered	24.6	25.6	1.37	1.35	1.36
Tiliaceae	Desplatsia spp.	8	ST	-	23.9	28.0	1.37	1.31	1.34
Agavaceae	Draceana mannii	13	MT	-	13.0	14.6	2.05	0.57	1.31
Euphorbiaceae	Discoglypremna caloneura	8	MT	-	20.1	23.5	1.37	0.93	1.15
Myristicaceae	pycnathus angolensis	4	LT	-	38.0	38.0	0.68	1.61	1.15
Annonaceae	Cleistopholis patens	8	LT	-	15.3	16.5	1.37	0.52	0.95
Burseraceae	Canarium schweinfurthii	4	LT	Endangered	31.6	31.6	0.68	1.11	0.90
Meliaceae	Lovoa trichilioides	4	LT	Endangered	31.2	31.2	0.68	1.09	0.89
Annonaceae	Enantia chlorantha	4	MT	Endangered	23.0	23.0	0.68	0.59	0.64
Rutaceae	Zanthoxylum zanthoxyloides	4	ST	-	20.5	20.5	0.68	0.47	0.58
Sterculiaceae	Cola gigantea	4	VLT	-	18.5	18.5	0.68	0.38	0.53
Lecythidaceae	Napoleonaea vogelii	4	ST	-	10.0	10.0	0.68	0.11	0.40
Mimosoideae	Albizia zygia	4	MT	-	10.5	10.5	0.68	0.12	0.40

of species like Daneillia ogea, Mansonia altissima, Mallotus oppositifolius, Piptadeniastrum africanum, and Moringa oleifera were not represented in the tree category. Regeneration of Draceana spp. and Diospyros spp. was high in all sites. However, regeneration of Funtumia elastica, D. ogea and Hunteria umbellate was high at Oluwa forest only, Napoleonaea vogelii and M. oleifera at Queen's forest only while that of Napoleonaea spp. and Desplatsia spp. were moderate at Elephant forest.

DISCUSSION

The high temperature and rainfall in rainforest regions have been linked to rapid decomposition and leaching of nutrients from upper soil horizon (Cossalter & Pye-Smith 2003). Consequently,

tropical rainforests, which are inherently poor in soil nutrients, have developed very efficient nutrient cycling system. Nutrients in decomposing organic matter are returned to the soil, reabsorbed and stored in aboveground tree components. When rainforest soils are exposed by deforestation or degradation, the consequences include soil structure degradation, impaired soil nutrients and soil compaction. However, our results suggest that soil nutrient pool is not seriously degraded as long as the site remains under forest cover. The difference in soil nutrients of the three study sites could not be attributed to the effect of forest degradation since there was no discernable pattern between soil properties of primary and degraded forests. The observed differences appeared to be

 Table 4
 Family and tree species richness in the degraded natural forest in Oluwa forest reserve

Family ^a	Species ^a	Number ^b	Life form ^c	Conservation status ^d	Dbh	(cm)	RD	RDo	IV
,	1				Mean	Max	(%)	(%)	(%)
Ebenaceae	Diospyros mespiliformis	100	LT	Endangered	15.1	30.2	17.01	5.84	11.42
Ulmaceae	Celtis zenkeri	46	LT	-	29.8	66.5	7.48	10.27	8.87
Annonaceae	Cleistopholis patens	21	LT	-	39.0	108.0	3.40	14.31	8.86
Olacaceae	Strombosia pustulata	63	MT	-	16.2	27.5	10.20	3.66	6.93
Euphorbiaceae	Ricinodendron heudlotii	13	LT	Endangered	48.0	108.0	2.04	11.21	6.63
Myristicaceae	Pycnathus angolensis	29	LT	-	34.2	74.3	4.76	5.50	5.13
Moraceae	Ficus exasperata	8	MT	-	47.7	92.0	1.36	7.91	4.63
Capparaceae	Buchholzia coriacea	25	ST-MT	-	18.8	35.0	4.08	2.28	3.18
Meliaceae	Entandrophragma cylindricum	13	VLT	Endangered	31.1	62.0	2.04	3.97	3.00
Apocynaceae	Hunteria umbellata	21	ST	-	16.3	29.5	3.40	1.37	2.39
Euphorbiaceae	Phyllanthus discoideus	8	MT	-	40.5	52.0	1.36	3.23	2.29
Mimosoideae	Albizia zygia	13	MT	-	27.5	37.0	2.04	2.19	2.12
Sterculiaceae	Sterculia rhinopetala	13	LT	Endangered	25.0	35.4	2.04	1.77	1.90
Lecythidaceae	Napoleonaea paviflora	17	ST/SH	-	16.5	22.0	2.72	1.03	1.88
Bignoniaceae	Cordia mellenii	13	ST	Endangered	23.6	33.2	2.04	1.65	1.85
Euphorbiaceae	$Bridelia\ micranthe$	8	MT	-	35.6	38.8	1.36	2.32	1.84
Sterculiaceae	Cola gigantea	17	VLT	-	21.4	41.8	2.72	0.95	1.84
Euphorbiaceae	Drypetes spp.	17	ST	-	12.7	16.0	2.72	0.66	1.69
Euphorbiaceae	Drypetes paxii	17	ST	-	15.0	19.5	2.72	0.67	1.69
Euphorbiaceae	Bridelia spp.	13	MT	-	19.0	29.0	2.04	1.13	1.59
Sterculiaceae	Cola nitida	13	ST	-	17.3	18.0	2.04	0.82	1.43
Caesalpinioideae	Erythrophylleum ivorensis	8	MT	-	23.0	35.0	1.36	1.22	1.29
Irvingiaceae	Klainedoxa gabonensis	8	LT	-	25.5	26.0	1.36	1.18	1.27
Capparaceae	Boscia salicifolia	8	ST	-	24.5	25.0	1.36	1.09	1.23
Rutaceae	Fagara macrophylla	8	ST-MT	-	22.0	28.0	1.36	0.95	1.15
Sterculiaceae	Sterculia tragacantha	8	MT	Endangered	18.7	23.7	1.36	0.68	1.02
Rutaceae	Zanthoxylum zanthoxyloides	4	ST	-	38.3	38.3	0.68	1.34	1.01
Sterculiaceae	Pterygota spp.	8	LT	-	17.0	20.0	1.36	0.54	0.95
Papilionoideae	Baphia nitida	8	ST	-	16.1	19.1	1.36	0.49	0.92
Moraceae	Myrianthus arboreus	4	ST	-	33.4	33.4	0.68	1.02	0.85
Ulmaceae	Holoptelea grandis	4	LT	Endangered	33.0	33.0	0.68	0.99	0.84
Meliaceae	Guarea thompsonii	4	VLT	Endangered	32.1	32.1	0.68	0.94	0.81
Caesalpinioideae	Berlinia corioceae	4	ST	Endangered	31.8	31.8	0.68	0.92	0.80
Apocynaceae	Funtumia elastica	4	MT	Endangered	33.1	33.1	0.68	0.85	0.77
Bignoniaceae	Spathodea campanulata	4	MT	-	29.0	29.0	0.68	0.77	0.72
Sapotaceae	$Chrystophyllum\ { m spp.}$	4	MT	-	29.0	29.0	0.68	0.77	0.72
Simaroubaceae	Hannoa klaineana	4	LT	-	29.0	29.0	0.68	0.77	0.72
Rubiaceae	Pausinystalia talbotii	4	MT	-	25.0	25.0	0.68	0.57	0.62
Meliaceae	Lovoa trichilioides	4	LT	Endangered	22.0	22.0	0.68	0.44	0.56
Meliaceae	Khaya ivorensis	4	VLT	Endangered	21.1	21.1	0.68	0.42	0.55
Annonaceae	Enantia chlorantha	4	MT	Endangered	18.7	18.7	0.68	0.32	0.50
Moraceae	Musanga spp.	4	ST	-	19.0	19.0	0.68	0.33	0.50
Chrysobalanaceae	Maranthes glabra	4	LT	-	18.3	18.3	0.68	0.31	0.49
Caesalpinioideae	Brachystegia eurycoma	4	LT	Endangered	16.7	16.7	0.68	0.25	0.47
Papilionaceae	Pterocarpus spp.	4	MT	Endangered	11.1	12.0	0.68	0.11	0.39

Study site	Density (trees ha ⁻¹)	No. of families	No. of species	No. of endangered species	Mean dbh (cm)	Basal area (m²ha-1)	H'	H_{max}	\mathbf{E}_{H}	D
Queen's forest	671 a	27	51 a	16	27.3 b	85.4 b	3.31	5.16	0.66	1.85
Oluwa forest	513 b	24	45 a	15	22.5 a	35.9 a	3.12	5.04	0.60	1.92
Elephant forest	508 b	22	31 b	8	21.6 a	29.4 a	2.82	4.98	0.57	2.16

Table 5 Summary of the results of various analyses conducted for the three study sites

Values followed by similar letters are not significantly different ($p \le 0.05$).

 $H' = Shannon-Wiener diversity index; H_{max} = Shannon's maximum diversity index; E_{H} = Shannon's equitability (species evenness); D = difference between the diversity index (H') and its maximum value (H_{max})$

inherent in the parent materials of soils of the two forest reserves. Soil properties of the three study sites are comparable or better than those of other rainforest sites in Nigeria as reported by

Ola-Adams & Hall (1987).

The Nigerian rainforest ecosystem is dominated by members of Sterculiaceae (e.g. Cola spp., Sterculia spp.), Moraceae (Antiaris africana, Ficus spp.), Ulmaceae (Celtis spp., Holoptelea grandis), Meliaceae (e.g. Entandrophragma spp., Khaya ivorensis) and species like Nauclea diderrichii, Erythrophleum ivorense, Brachystegia eurycoma and Terminalia superba (Richards 1939, Isichei 1995, Were 2001), which is consistent with our findings (Tables 2–4 and 6). In addition, our results indicate that members of Apocynaceae (Funtumia elastica, Hunteria umbellate), Euphorbiaceae (Bridelia spp., Drypetes spp., Ricinodendron spp.) families and species like *Diospyros* spp., *Napoleonaea* spp. and Strombosia pustulata are important parts of the floristic composition of the study sites. The occurrence of different dominant species across the different sites could be attributed to the effect of forest degradation. The lower importance value of K. ivorensis in Oluwa and Elephant forests compared with Queen's forest is a consequence of logging in the degraded forests. The absence of regeneration of *K. ivorensis* at all three sites could not be immediately explained. Unless measures to promote the regeneration of this species are undertaken, it is feared that its status may soon change from being endangered to extinct. Although *Draceana* spp. are not currently one of the dominant species of the study communities, the abundance of their regeneration indicates that they may become future dominant members. Also, the high regeneration of Daneillia ogea, Boscia salicifolia, Moringa oleifera, Mallotus oppositifolius and Desplatsia spp. shows that they may also emerge as future dominant species.

Species richness is an index of biodiversity and our results indicated that Queen's and Oluwa forests had similar species richness, which was higher than that of Elephant forest. This implies that species richness decreases as the intensity of forest degradation increases. The lower species richness in Elephant forest could be attributed to the effect of repeated timber logging (Webb & Peralta 1998). Species richness values in Queen's and Oluwa forests are comparable with that of some rainforest sites in Nigeria, e.g. 56, 55 and 54 tree species ha⁻¹ were found in Sapoba, Shasha and Ala forest reserves respectively (Lowe 1997, Adekunle 2006).

The trend of Shannon-Wiener diversity indices (H') showed that Queen's forest was the most diverse of the three study communities, followed by Oluwa and lastly by Elephant forests. As with species richness, species diversity also decreases as the level of forest degradation increases. The H' values of 3.34–3.66 for some rainforest sites in Nigeria (Adekunle 2006) are similar to that of Queen's and Oluwa forests but higher than that of Elephant forest. Values of H' for the study sites were lower than their maximum diversity indices, an indication that all species in these sites did not have equal area abundance. From E₁₁ values obtained in this study, we conclude that trees species are most evenly distributed in Queen's forest followed by Oluwa and Elephant forests. This subsequently suggests that species distribution is also affected by level of forest degradation.

It has been reported that 58 (10.4%) of 560 tree species in Nigerian forests are endangered (FORMECU 1999). Since there are 22 endangered species in our study area, it is evident that a high number of trees in rainforest ecosystems of Nigeria are currently endangered. This is to be expected given the long history and the almost uncontrolled nature of logging as well as the high volume of timber removed from these

Table 6 Family, species and frequency of occurrence of seedlings within 6×6 m subplots in the study site

	Queen's forest			Oluwa forest			Elephant forest	
Family ^a	$\mathrm{Species}^a$	$ m Number^b$	${ m Family}^a$	${ m Species}^a$	$Number^b$	Family	Species	$\mathrm{Number}^{\mathrm{b}}$
Agavaceae	Draceana mannii	70 (8)	Agavaceae	Draceana spp.	80 (8)	Ebenaceae	Diospyros mespiliformis	(9) 88
Lecythidaceae	Napoleonaea vogelii	60 (3)	Ebenaceae	Diospyros spp.	(9) 09	Lecythidaceae	Napoleonaea spp.	28 (6)
Ebenaceae	Diospyros mespiliformis	35 (5)	Apocynaceae	Funtumia elastica	(9) 09	Agavaceae	Draceana mannii	26 (8)
Moringaceae	Moringa oleifera	20 (1)	Caesalpinioideae	Daneillia ogea	60 (1)	Tiliaceae	Desplatsia spp.	20 (1)
Apocynaceae	Hunteria umbellata	15 (4)	Apocynaceae	$Hunteria\ umbellata$	55 (3)	Lecythidaceae	Napoleonaea vogelli	16 (1)
Lecythidaceae	$Napoleonaea\ { m spp}.$	12 (3)	Agavaceae	Draceana arborea	50 (1)	Euphorbiaceae	Drypetes paxii	15 (2)
Sterculiaceae	Cola gigantea	10(3)	Capparaceae	Boscia salicifolia	35 (2)	Apocynaceae	Picralima nitida	12 (1)
Euphorbiaceae	Mallotus oppositifolius	10(2)	Capparaceae	Buchholzia coriacea	20 (1)	Apocynaceae	Hunteria umbellate	10 (4)
Mimosoideae	Piptadeniastrum africanum	10(2)	Lecythidaceae	Napoleonaea imperialis	13 (1)	Rubiaceae	Pausinystalia johimbe	8 (1)
Ebenaceae	Diospyros spp.	8 (3)	Capparaceae	Buchholzia spp.	8 (3)	Capparaceae	Buchholzia coriacea	3 (2)
Euphorbiaceae	Drypetes spp.	5 (1)	Sterculiaceae	$Pterygota { m spp.}$	6 (2)	Mimosoideae	Piptadeniastrum africanum	3 (1)
Moraceae	Myrianthus arboreus	5 (2)	Euphorbiaceae	Drypetes spp.	5 (2)	Sapotaceae	Pachystela brevipes	3 (1)
Apocynaceae	Alstonia boonei	5 (1)	Sterculiaceae	Pterygota macrocarpa	4 (2)	Sterculiaceae	Pterygota macrocarpa	3 (1)
Sapindaceae	Bliphia sapida	5 (1)	Papilionoideae	Baphia nitida	3 (3)	Euphorbiaceae	Discoglypremna caloneura	2 (1)
Apocynaceae	Funtumia elastica	4 (2)	Sterculiaceae	Mansonia attissima	3 (2)	Sterculiaceae	Cola gigantean	2 (1)
Euphorbiaceae	Ricinodendron heudelotii	3 (1)	Sterculiaceae	Sterculia rhinopetala	1 (2)	Papilionoideae	Afrormosia spp.	1 (1)
Irvingeaceae	Irvingia spp.	3 (1)	Sterculiaceae	Triplochiton scleroxylon	1 (2)	Papilionoideae	Baphia nitida	1 (2)
Mimosoideae	Albizia zygia	3 (1)	Myristicaceae	pycnathus angolensis	2 (2)	Papilionoideae	Lonchocarpus sericceus	1 (1)
Combretaceae	Terminalia superba	2 (2)	Ulmaceae	Cettis zenkeri	2 (2)	Euphorbiaceae	Mallotus oppositifolius	1 (1)
Sterculiaceae	Cola nitida	2 (1)	Caesalpinioideae	Brachystegia eurycoma	1 (1)	Sterculiaceae	Sterculia rhinopetala	1 (1)
Sterculiaceae	Pterygota macrocarpa	2 (2)	Euphorbiaceae	Bridelia spp.	1 (1)	Ulmaceae	Celtis zenkeri	1 (1)
Sterculiaceae	Sterculia rhinopetala	2 (1)	Papilionoideae	Lonchocarpus sericceus	1 (2)	Ulmaceae	Celtis mildbraedii	1 (1)
Sterculiaceae	Triplochiton scleroxylon	2 (2)	Rubiaceae	Rothmannia hispida	1 (2)	Unknown 1	Unknown 1	1 (1)
Unknown 2	Unknown 2	2 (2)	Sapindaceae	Lynchnodiscus reticulatus	1 (2)	Unknown 2	Unknown 2	1 (2)
Bignoniaceae	Newbouldia laevis	1 (1)	Sapindaceae	Lecaniodiscus cupanioides	1 (2)			
Capparaceae	Boscia salicifolia	1 (1)	Sterculiaceae	Cola gigantea	1 (2)			
Myristicaceae	pycnathus angolensis	1 (1)	Sterculiaceae	Cola nitida	1 (2)			
Unknown 1	Unknown 1	1 (1)	Mimosoideae	Entada abyssinica	1 (1)			
			Moraceae	Milicia regia	1 (1)			

^aFamily names and species nomenclature after *Trees of Nigeria* (Keay 1989) ^bValues in parentheses are the number of 6×6 m sample plots (total = 8 per study site) in which the seedling (s) of the corresponding species was found.

ecosystems. It has been reported that rainforests of West and Central Africa are among the most important areas of threatened species across Africa (Burgess *et al.* 2005).

Our results indicate that Elephant forest has the least number of families and species, species density, species diversity and species evenness. Consequently, though Elephant forest has remained under forest cover, its composition and biological functions appears to have been compromised due to degradation. The current degraded status of Elephant forest could be attributed to repeated logging activities, since it is the most logged of the three sites. Although some logged forests could be as rich as unlogged ones depending on the logging method employed, the general trend is that unlogged forests contain more species and are more diverse than logged ones (Webb & Peralta 1998, Foody & Cutler 2003). Other scientists have shown that logging may impact most on species evenness, with logged forests being more uneven than unlogged forests (Chapin et al. 2000, Putz et al. 2000).

Restoration of biodiversity in degraded tropical forests is a challenge to forest managers and conservationists. The regeneration of native tree species following forest degradation could be constrained by a number of factors including low seed availability, predation of seeds and seedlings, competition with grasses and other non-woody vegetation, soil degradation and unfavourable microclimate (Holl & Kappelle 1999, Hardwick et al. 2004, Shono et al. 2006). Where these factors are prevailing, restoration may be difficult, otherwise the degraded forest site may recover fairly well as was demonstrated by one (Oluwa forest) of the study communities. Bearing in mind that Oluwa forest was once highly degraded, its comparable results with that of Queen's forest (primary) is an indication that rainforest ecosystems possess the potentials of recovering from degradation and returning to their original species-rich situation, even after significant degradation. However, this necessitates that physical factors of the forest be intact, seed dispersal be present and the site does not become invaded by aggressive weed species, and that all forms of degradation activities ceases or are controlled as was the situation in Oluwa forest for over three decades. Murphy et al. (1995) reported a relatively rapid recovery of a tropical dry forest in Puerto Rico that was cut and allowed to recover without disturbance for 13 years. The potential of degraded rainforests to recover from degradation calls for reconsideration of the current practice in Nigeria whereby degraded forests are usually clear-felled and converted into monoculture forest plantations. These forests should be left to recover and instead we propose that abandoned agricultural sites, waste lands and degraded coalmine sites be used for plantations.

The results of this study revealed the potential of conservation measures in restoring degraded rainforests. The urgent need for conservation measures is underscored by the many endangered species in the study areas, uncontrolled and high rate of logging and deforestation (344 684 ha year-1). Since the frequency of logging impacts greatly on biodiversity and damage to remnant stand is often proportional to the amount of timber removed, the frequency and intensity of logging operations in Nigeria's rainforests must be reduced and subsequent logging operations be planned on sustainable yield basis. Other conservation measures could be the strict enforcement of the prohibition of roundwood and semi-finished timber products export by the Federal Government of Nigeria, prohibition of exploitation of endangered species and application of reduced impact logging.

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REFERENCES

ADEKUNLE V. A. J., 2006. Conservation of tree species diversity in tropical rainforest ecosystem of southwest Nigeria. *Journal of Tropical Forest Science* 18: 91–101.

Bremner, J.M., 1965. Total nitrogen. Pp. 1149–1178 in Black, C. A. (Ed.) *Methods for Soil. Analysis, Part 2: Chemical and Microbiological Properties*. Am. Soc. Agro., Inc.,

Burgess, N., Küper, W., Mutke, J., Brown, J., Westaway, S., Turpie, S., Meshack, C., Taplin, J., McClean, C. & Lovett, J. C., 2005. Major gaps in the distribution of protected areas for threatened and narrow range Afrotropical plants. *Biodiversity and Conservation* 14: 187–894.

- Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack M. C. & Diaz, S. 2000. Consequences of changing biodiversity. *Nature* 405: 234–242.
- Cossalter, C. & Pye-Smith, C. 2003. Fast-Wood Forestry: Myths and Realities. CIFOR Publication, Bogor.
- FOODY, G. M. & CUTLER, M. E. J. 2003. Tree biodiversity in protected and logged Bornean tropical rain forests and its measurement by satellite remote sensing. *Journal of Biogeography* 30: 1053–1066.
- FORMECU. 1999. Forest Resources Study, Nigeria. Revised National Report Volume 2. Prepared for FORMECU by Beak and Geomatics International, Ibadan.
- GILLESPIE, T. W., BROCK, J. & WRIGHT, C.W. 2004. Prospects for quantifying structure, floristic composition and species richness of tropical forests. *International Journal of Remote Sensing* 25: 707–771.
- HARDWICK, K., HEALEY, J. R., ELLIOTT, S., BLAKESLEY, D. 2004. Research needs for restoring seasonal tropical forests in Thailand: accelerated natural regeneration. *New Forests* 27: 285–302.
- Holl, K. D. & Kappelle, M. 1999. Tropical forest recovery and restoration. *Tropical Ecology* 14: 378–379.
- ISICHEI, A. O. 1995. Omo biosphere reserve, current status, utilisation of biological resources and sustainable management. UNESCO South-South Cooperation Programme. Paper 11.
- Keay, R. W. J. 1989. *Trees of Nigeria*. Oxford University Press, Oxford.
- Kent, M. & Coker, P. 1992. Vegetation Description and Analysis: A Practical Approach. Belhaven Press, London.
- KIO, P. R. O., ABU, J. E. & LOWE, R. G. 1992. High Forest Management in Nigeria. Draft report for IUFRO Centeniell meeting in Eberswalde.
- LOVEJOY, T. E. 1997. Biodiversity: what is it? Pp. 7–14 in Reaka-Kudla et al. (Eds.) Biodiversity II: Understanding and Protecting Our Natural Resources. Joseph Henry Press, Washington, D.C.
- LOWE, R. G. 1997. Volume increment of natural moist tropical forest in Nigeria. Commwealth Forestry Review 76: 109–113.
- Murphy, P. G., Lugo, A. E., Murphy, A. J. & Nepstad, D. C. 1995. The dry forests of Puerto Rico's south coast. In: Lugo *et al.* (Eds.) *Tropical Forests: Management and Ecology*. Springer Verlag, Berlin.
- Murphy, J. & Riley, J. P. 1962. A modified single solution for determination of phosphate in natural water. *Analytica Chemica* Acta 27: 31–36.

- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Ola-Adams, B. A. & Hall, J. B. 1987. Soil-plant relations in a natural forest inviolate plot at Akure, Nigeria. *Journal of Tropical Ecology* 3: 57–74.
- OLIPHANT, F. M. 1934. Report on the commercial possibilities and development of the forest of Nigeria. Sessional Paper No. 7. Government Printer, Lagos.
- Putz, F. E., Dykstra, D. P. & Heinrich, R., 2000. Why poor logging practices persist in the tropics. *Conservation Biology* 14: 951–956.
- RICHARDS, P. W. 1939. Ecological studies on the rain forest of Southern Nigeria. I. The structure and floristic composition of the primary forest. *Journal of Ecology* 27: 1–61.
- SARUMI, M. B., LADIPO, D. O., DENTON, L., OLAPADE, E. O., BADARU, K. & UGHASORO, C. 1996. Nigeria: Country Report to the FAO International Technical Conference on Plant Genetic Resources. http://www.fao.org/ag/AGP/AGPS/Pgrfa/pdf/nigeria.pdf, Leipzig.
- Shono, K., Davies, S. J. & Kheng, C. Y. 2006. Regeneration of native plant species in restored forests on degraded lands in Singapore. *Forest Ecology and Management* 237: 574–582.
- Smyth, A. J. & Montgomerry, R. F. 1962. Soils and Land Use in Central Western Nigeria. Government Printer, Ibadan.
- WALKLEY, A. & BLACK, I. A., 1934. An examination of the Degtjareff method for determining soil organic matter and a proposed mordification of the Chromic Acid Titration Method. *Soil Science*, 37: 29–38.
- Webb, E. L. & Peralta, R. 1998. Tree community diversity of lowland swamp forest in Northeast Costa Rica, and changes associated with controlled selective logging. *Biodiversity and Conservation* 7: 565–583.
- Were, J. L. R. 2001. Nigerian Lowland Forests. www. worldwildlife.org/wildworld/profiles/terrestrial/at/at0123_full.html.
- WILCOX, B. A. 1995. Tropical forest resources and biodiversity: the risks of forest loss and degradation. *Unasylva* 46: 43–49.
- Soil Survey Staff 2003. *Keys to Soil Taxonomy*. Ninth edition. United States Department of Agriculture, Natural Resources Conservation Service, Washington, D. C.