REFERENCE

Journal of Tropical Forest Science 5(4): 429 - 439 PERPUSTAKAAN 429 Institut Penyelidikan Perhutanan Malaysia (FRIM) Kepong, 52109 Kuala Lumpur ABOVEGROUND BIOMASS PRODUCTION AND NUTRIENT ACCUMULATION OF A GMELINA ARBOREA PLANTATION IN SARAWAK, MALAYSIA

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HALENDA, C.J. 1993. Aboveground biomass production and nutrient accumulation of a *Gmelina arborea* plantation in Sarawak, Malaysia. A biomass and nutrient content study was carried out on 6.6-y-old *Gmelina arborea*, established on abandoned shifting cultivation sites for the purpose of site rehabilitation. The aboveground biomass of small-litter standing crop, undergrowth and overstorey was determined by destructive sampling of two 10×20 m plots. Total mean aboveground biomass was $92.1 t ha^1$. Biomass comprised 92.3% overstorey, 3.5% undergrowth and 4.2% litter. Aboveground tree biomass was composed of 68.5% stem wood, 8.8% stem bark, 12.3% branches, 5.1%dead branches, 3.0% foliage and 2.3% twigs. The overstorey biomass contained $394 kg ha^1$ K, $236 kg ha^1$ N, $214 kg ha^1$ Ca, $70 kg ha^1$ Mg and $17 kg ha^1$ P. A large proportion of these nutrients (55.1 to 71.7%) was immobilized in the stem wood and bark. Remaining nutrients were immobilized in twigs and branches (14.4 to 25.8%), foliage (8.6 to 20.5%) and dead branches (1.7 to 4.0%). Biomass and nutrient accumulation is compared to those of other *Gmelina* plantations and fallow forests in the tropics.

Key words: Gmelina arborea - aboveground biomass - nutrient accumulation

HALENDA C.J. 1993. Pengeluaran biojisim atas tanah dan pengumpulan nutrien di ladang Gmelina arborea di Sarawak, Malaysia. Satu kajian kandungan biojisim dan nutrien telah dijalankan pada pokok-pokok Gmelina arborea berumur 6.6 tahun yang ditanam atas tanah pertanian pindah yang ditinggalkan untuk tujuan pemulihan tapak. Biojisim atas tanah tanaman dirian sarap kecil, belukar dan tingkat atas ditentukan dengan persempadan menghancur di atas dua plot $10 \times 20m$. Jumlah purata biojisim atas tanah ialah 92.1 $t ha^1$. Biojisim terdiri dari 92.3% tingkat atas, 3.5% belukar dan 4.2% sarap. Biojisim pokok atas tanah mengandungi 68.5% batang kayu, 8.8% kulit batang, 12.3% dahan, 5.1% dahan mati, 3.0% dedaun dan 2.3% ranting. Biojisim tingkat atas mengandungi 394 kg ha⁻¹ K, 236 kg ha⁻¹ N, 214 kg ha⁻¹ Ca, 70 kg ha⁻¹ Mg dan 17 kg ha⁻¹ P. Sebahagian besar dari nutrien-nutrien ini (55.1 ke 71.7%) didapati dari batang kayu dan kulit. Baki nutrien diperolehi dari ranting dan dahan (14.4 ke 25.8%), dedaun (8.6 ke 20.5%) dan dari dahan yang mati (1.7 ke 4.0%). Pengumpulan biojisim dan nutrien diperbandingkan dengan ladang-ladang Gmelina yang lain dan hutan-hutan rang di tropika.

Introduction

Shifting cultivation is one of the most common forms of agriculture in Sarawak. It is practised, as in much of Southeast Asia, mainly as a result of poor soil fertility. After

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abandonment by shifting cultivators, land rapidly revegetates but generally with poor quality secondary forest that has little or no commercial value (Hatch & Lim 1979). In recent years the problem has been aggravated by increased land use pressure resulting in shorter fallow periods and the encroachment of shifting cultivators on to State Forest Reserves. In order to rehabilitate abandoned lands and to discourage further encroachment by shifting cultivators, the Sarawak Forest Department initiated site rehabilitation projects within State Forest Reserves. The means of rehabilitation came in the form of plantation establishment.

Gmelina arborea is one of several exotic tree species used for rehabilitation of abandoned shifting cultivation sites in Sarawak. Although it was first planted in Sarawak in 1973, relatively little is known of its performance or its effects on the ecosystem. This paper reports the biomass and nutrient content of a 6.6-y-old *Gmelina arborea* plantation and compares it to those of other *Gmelina arborea* and similarly aged fallow forests.

Study area

The biomass plots were located in Niah Forest Reserve, Sarawak, Malaysia situated at 3° 40' N and 113° 44' E. The site is accessed from the Bintulu-Miri Road and is located 106 km from Bintulu, adjacent to the Niah Forest Research Station. Elevation of the site is between 35 to 45 m above sea level. The mean annual temperature of the area is 26° C and the mean annual rainfall, calculated from 1980 to 1985 data (the major growth period of the study trees), was 3209 mm.

The study area was logged in 1970 and 1971 after which it was subjected to shifting cultivation. The shifting cultivators were evicted from the area in 1980 as they were illegally farming on Forest Reserve land. The period of cropping and the number of harvests taken from the study site prior to plantation establishment is not known. However, given the length of time involved it is estimated to have been farmed once or twice, probably in consecutive years. In 1979 a *Gmelina arborea* plantation was established as part of a silvicultural trial to monitor the recovery of abandoned shifting cultivation sites. The biomass study was carried out when the trees were 6.6 y of age.

Methods

Soil sampling

A topographic and soil survey was carried out and two replicate plots, 10×20 m in size, were established on the midslope of a hill with a gradient of 21°. Soil pits were dug at the centre of each plot. A profile description was recorded to a depth of one metre. Soil horizons were delineated based on soil colour and texture and a chemical and physical analysis was carried out for each horizon.

Soil samples were air dried and ground to pass through a 2 mm mesh sieve prior to analysis. Particle-size class analysis was done by pipette method on peroxidetreated samples. Two replicate core samples were taken from each horizon for bulk density analysis as described by Phang (1987). Bulk density was used to calculate elemental weight of each horizon.

The pH was measured on 1:2.5 soil-water mixture using a Pye Unicam pH meter. Total organic C was determined by Walkley and Black's titration method, total N by micro-Kjeldahl digestion method and total P by perchloric acid digestion with vanado-molybdo phosphoric reaction. Cation exchange capacity (CEC) was determined by leaching with 1M ammonium acetate at pH 7. Exchangeable cations K, Ca, Na, and Mg were extracted by leaching with ammonium acetate at pH 7. Methods used are described in detail by Chin (1986).

Biomass sampling

A five per cent survey of the small-litter standing crop and undergrowth vegetation was carried out in each 10×20 mplot. Ten 1×1 msubplots were randomly placed within each larger plot. All litter and aboveground undergrowth vegetation were collected. Litter was taken to the laboratory for sorting and oven drying while undergrowth was sorted into grass, ferns, non-woody and woody plants, and weighed fresh. Three to five random subsamples of each category (depending on quantity of vegetation present) were taken for oven drying at $105^{\circ}C$ for conversion to dry-weight biomass.

All trees within the 10×20 m plots were harvested on an individual basis. Before felling the diameter over bark at breast height (DBH) and mean crown diameter (by projection to the ground) were recorded. Trees were cut to ground level (roots were not included in the harvest) and total height and crown length were recorded. Trees were separated into the following components for immediate weighing: fruit and flowers, foliage, twigs < 1 cm diameter over bark (DOB), branches 1-3 cm DOB, branches > 3 cm DOB, dead branches and stem. Stem bark weights were determined by separating the bark and wood of stem subsamples in the field and weighing separately. The percent bark weight of stems was calculated and used to determine total stem bark biomass.

Weights were recorded to the nearest 10 g for small components using a 10 kg spring scale. Stem sections including bark were weighed to the nearest 100 g using a Salter 50 kg spring scale. Five subsamples (a minimum of 0.5 kg for foliage and 1.0 kg for woody components) were weighed to the nearest 0.1 g using an Ohaus triple beam balance scale. Subsamples were collected randomly and used for dry weight determination at 105° C. All results were expressed in dry weights at 105° C.

Nutrient sampling

Nutrient analysis of vegetation was carried out by taking random subsamples of each vegetation component. Subsamples were washed with a wetting agent, air dried and then ground in a Wiley mill to pass through a 1.0 mm mesh sieve. Total P was determined using H_2SO_4/HNO_3 digestion method; total N by micro-Kjeldahl

procedure; and total K, Ca and Mg by dry ashing and extraction by dilute HC1. Nutrient accumulation for each tissue type was calculated by multiplying biomass per *ha* by the appropriate nutrient concentration.

Results and discussion

Soils

Table 1 gives a representative profile description of the soils underlying the *Gmelina* plots. The soil is a Red-Yellow Podzolic in the Merit family and Begunan series. It has a brown sandy clay loam topsoil overlying a brownish yellow clay. The FAO World Soil Map Legend (FAO 1974) classifies these soils as Dystric Nitosols or Ferric Acrisols (Tie 1982). The USDA (1975) classifies them as clayey, mixed, isohyperthermic, Typic Paleudults or Dystropepts. Table 2 gives the results for the physical analysis of each horizon and Table 3 the chemical analysis. The soils were extremely acidic and nutrient content was low to moderately low but typical of other Red-Yellow Podzolic soils in Sarawak (Andriesse 1972).

Great Group		: Red-Yellow Podzolic	Drainage	:	Moderately well drained			
Family		: Merit	Topography	:	Hilly			
Series		: Begunan	Slope	:	21°			
Parent M	aterial	: Sandstone	Position	:	Midslope			
Horizon	Depth (cm)	Description						
Al	0 - 8	Sandy clay loam; brown moderately hard grits; a medium pores; clear an	(10YR 4/3); friable when bundant fine and many me d wavy horizon boundary t	moist; r edium re to:	noderate medium crumb; few oots; abundant fine and many			
B21	8 - 58	Clay; brownish yellow (10YR $6/8$); firm when moist; moderate medium subangular block structure; many soft gravels; few fine and medium roots; few fine pores; merging and was horizon boundary to:						
B22	58 - 100	Clay; brownish yellow (10 when moist; moderate r	ownish yellow (10YR 6/8); firm many soft gravels.					

Table 1. Soil profile description

Growth rates

Growth rates of the *Gmelina* overstorey are given in Table 4. Mean height and DBH were 16.6 m and 17.3 cm respectively. Mean crown length and mean crown diameter were 6.0 m and 5.6 m respectively. (Spacing was $3.7 \times 3.7 m$ or 750 trees ha^1). Compared to other *Gmelina* in Malaysia, these values are average to slightly below average. Freezaillah and Sandrasegaran (1966) reported an average height of 23.5 m and DBH of 18.5 cm for 7-y-old *Gmelina* in West Malaysia. Tan and Jones (1982) reported average dominant height of 5-y-old *Gmelina* in Sabah at 18 m. On more fertile sites the average dominant height was 24 m but dropped to 14 m on poorer

	Size class and particle diameter (mm)											
Horizon	orizon Depth Total (% of < 2m (cm)			2 <i>mm</i>)	$m) \qquad \qquad \text{Sand } (\% \text{ of } < 2mm)$							
		Sand	Silt	Clay	VC	С	М	F	VF	(g cm ³)		
Al	0-8	50.4	22.6	27.0	0.5	1.0	1.4	17.0	30.5	1.32		
B21	8-58	34.0	19.3	46.7	2.6	2.3	1.6	8.4	19.1	1.46		
B22	58-100	31.4	20.5	48.1	2.9	4.0	2.6	5.1	16.8	1.40		

Table 2. Soil physical analysis

Note: VC = very coarse, C = coarse, M = medium, F = fine, VF = very fine.

Hori-	Depth	pН	С	Total	C/N	Total		Exc	hangeabl	e cations		CEC	Base
zon	(<i>cm</i>)	(H ₂ O)	(%)	N (%)	N (%)	P (%)	Ca	Mg (Na meg/100	K g)	Sum		sat'n
A1	0-8	4.3	2.41	0.21	12.05	0.02	3.34	1.72	0.30	0.14	5.50	16.00	34.38
B21	8-58	3.7	0.51	0.10	5.20	0.01	0.47	0.32	0.21	0.14	1.14	16.71	6.82
B22	58-100	3.7	0.14	0.08	1.75	0.01	0.23	0.10	0.15	0.14	0.62	17.26	3.59

Table 3. Soil chemical analysis

Table 4. Grov	wth rates	of the	overstorey
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	Height (range)	Diameter (range)	Mean crown	Mean crown diameter	
(<i>m</i>)		(<i>cm</i>)	(<i>m</i>)	(<i>m</i>)	
Mean	16.6 (9.4-20.4)	17.3 (7.5-25.3)	6.0	5.6	
MAI	2.5 (1.4-3.1)	2.6 (1.1-3.8)	0.9	0.8	

sites. Tan and Jones (1982) produced growth curves using height over age related to three site index classes. The growth rates of *Gmelina* in this study were similar to the lowest site index group in the Sabah study.

Biomass and nutrient content

The biomass and nutrient contents of the overstorey, undergrowth, litter and the underlying soil (depth to one metre) are given in Table 5. Total aboveground biomass of the *Gmelina* plantation was 92.1 $t ha^1$. The overstorey made up 85 $t ha^1$ or 92.3% of the total biomass. Litter and undergrowth made up the remaining biomass at 3.9 $t ha^1$ (4.2%) and 3.2 $t ha^1$ (3.5%) respectively.

Nutrient content of the total aboveground biomass was highest for K followed by N and Ca and smaller amounts of Mg and P. Nutrient accumulation was only a fraction (ranging from 0.9% for P to 39.7% for K) of that in the underlying soil. As site recovery continues it is expected that this proportion (with the exception of N) will increase to a greater amount than that in the soil, as is the case during fallow forest recovery (Nye & Greenland 1960, Sabhasri 1978).

Litter

A large proportion (86%) of the litter material was produced by the tree storey in the form of foliage and twigs while the remainder (14%) was composed of fern and grass material. The large percentage of leaf and twig litter indicates the importance of the overstorey with regard to returning nutrients to the topsoil. Litter decomposition rates appeared to be relatively rapid, thus emphasizing that overstorey litter plays an important part in nutrient cycling and improving the surface soil through continual addition of organic matter. The dominant nutrient in the small-litter standing crop was Ca followed by N and Mg and smaller amounts of K and P (Table 5).

		the	e Gmelina ar	<i>borea</i> planta	tion		
Vegetation	Biomass		N	Р	K	Ca	Mg
Гуре	t ha ⁻¹	%		kg	g ha⁻'		
Litter	3.9	4.2	47.0	1.5	5.0	57.0	18.1
Undergrowth	3.2	3.5	32.6	1.8	63.6	17.5	8.7
Overstorey	85.0	92.3	236.2	16.9	394.0	214.4	69.7
Total	92.1	100.0	315.8	20.2	462.6	288.9	96.5
Soil	-	-	15284	2262	1164	1775	622

Table 5. Total aboveground biomass and nutrient accumulation of

Undergrowth

Undergrowth played a minor role in the *Gmelina* plantation biomass, contributing only 3.5% to the total aboveground biomass. It is expected that with increased crown closure the undergrowth biomass will decrease due to competition for sunlight. The amount of nutrients taken up by the undergrowth was relatively small. Nutrients in the undergrowth would generally be available for recycling since most of the undergrowth consisted of short lived grass and fern species.

Overstorey

Biomass and nutrient accumulation of the overstorey, by component, are given in Table 6. The largest amount of biomass was contained in the stem at 65.7 $t ha^1$, of which 58.2 $t ha^1$ was stem wood and 7.5 $t ha^1$ was bark. Branches > 1 cm DOB comprised the next greatest biomass at 10.5 $t ha^1$ followed by dead branches (4.3 $t ha^1$), foliage (2.5 $t ha^1$) and twigs < 1 cm DOB (2.0 $t ha^1$). Percentage weights of these components are given in Table 6. Calculations using data from Chijioke (1980) give the following percentage ranges of biomass distribution for *Gmelina* : 2.0-3.5% foliage, 8.8-24.1% branches, 5.2-12.0% bark and 65.0-84.1% stem wood. The *Gmelina* in this study has a biomass allocation that generally falls in the middle of these ranges, except for stem wood biomass which was at the lower end of the range at 68.5%.

Over a period of 6.6 y total overstorey biomass growth was low to moderately productive in comparison with other tropical plantations. Total mean biomass was 85.0 $t ha^1$ or a mean annual biomass increment (MABI) of 12.9 $t ha^1 y^1$. Wycherley (1969) calculated a MABI of 13.9 ± 1.00 $t ha^1 y^1$ for the 8.8-y-old *Gmelina* reported by Freezaillah and Sandrasegaran (1966). Rose and Salazar (1983) reported a MABI of 14 $t ha^1 y^1$ for 5-y-old *Gmelina* in Costa Rica. Chijioke (1980) reported total

	Bion t ha	nass ¹ %	N	P	K g ha ¹	Ca	Mg
Leaves	2.50	3.0	48.48 (20.5)*	2.80 (16.6)	33.71 (8.6)	22.39 (10.4)	12.75 (18.3)
Twigs	1.98	2.3	12.26 (5.2)	0.90 (5.3)	19.97 (5.1)	8.00 (3.7)	3.44 (4.9)
Branches > 1 cm DOB	10.46	12.3	36.04 (15.2)	3.46 (20.5)	71.49 (18.1)	23.00 (10.7)	8.34 (12.0)
Dead branches	4.31	5.1	9.41 (4.0)	0.42 (2.5)	6.66 (1.7)	7.16 (3.3)	1.94 (2.8)
Stem wood	58.22	68.5	82.12 (34.8)	6.30 (37.4)	192.57 (48.9)	68.64 (32.0)	17.74 (25.4)
Stem bark	7.50	8.8	47.92 (20.3)	2.98 (17.7)	69.56 (17.6)	85.22 (39.7)	25.51 (36.6)
Stem total	65.72	77.3	130.04 (55.1)	9.28 (55.1)	262.13 (66.5)	153.86 (71.7)	43.26 (62.0)
Total	84.97	-	236.23	16.86	393.96	214.41	69.72
Mean annual accumulatior	- 1	-	35.80	2.55	59.69	32.49	10.56

Table 6. Mean biomass and nutrient accumulation of the overstorey by component in $kg ha^1$ and percent

* Numbers in parenthesis are percentages of total aboveground tree nutrient accumulation.

aboveground biomass for 5.5 to 6-y-old *Gmelina* at 55.9 to 122.0 $t ha^{1}$ in Brazil and 63.4 to 136.7 $t ha^{1}$ in Nigeria.

Evel *et al.* (1983) state that a reasonably high average growth rate for plantations in the humid tropics is 7.5 $t ha^1y^1$ or stem wood. The *Gmelina* in this study exceeds that at 10.0 $t ha^1y^1$ of stem wood biomass. However, Chijioke (1980) reports stem wood MABI ranging from 9.3 to 20.8 $t ha^1y^1$ for *Gmelina* in Brazil and Nigeria, indicating that stem wood productivity in this study is at the lower end of the productivity potential for *Gmelina arborea*.

Since the *Gmelina* in this study was planted for site rehabilitation purposes, it is of interest to compare it to biomass productivity of fallow forests. Seven to ten-y-old fallow forest overstorey, in the same location and on the same soil type as the *Gmelina* plantation, had a mean biomass of 84.1 t ha¹ and ranged from 62 to 106 t ha¹ (Halenda 1989). In addition, the fallow forest produced a small-litter standing crop of 7.4 t ha¹, almost twice that of the *Gmelina* plantation. This indicates that site rehabilitation using *Gmelina* may not always be an improvement over natural regeneration, in terms of biomass and litter production. In the long run *Gmelina* has the advantage of being a marketable species whereas most secondary forest species are not considered merchantable at the present time. However, if the aim of plantation establishment is solely for the purpose of site rehabilitation, then fallow forest should be considered as a comparably effective rehabilitation establishment and it minimizes disturbance to the site.

Overall accumulation of nutrients in the biomass was highest for K, followed by large amounts of N and Ca and much smaller amounts of Mg and P in that order. Nutrient contents, by components, are given in Table 6, showing the quantities of different nutrients immobilized by various parts of the overstorey. A large proportion, 55.1 to 71.7%, of all nutrients were immobilized in the stem wood and bark. A further 14.4 to 25.8% of nutrients were immobilized in branches > 1 cm DOB and twigs < 1 cm DOB combined. The remaining nutrients were held in foliage (8.6 to 20.5%) and dead branches (1.7 to 4.0%). The latter two components are important in that they contribute nutrients to the forest floor when they fall as litter material. Mean annual accumulation of nutrients ranges from 2.5 $t ha^{1}$ for P to 59.7 $t ha^{1}$ for K.

Table 7 compares the *Gmelina* overstorey nutrient accumulation to that of *Gmelina* in Brazil and Nigeria and fallow forest in Sarawak. The amounts of nutrients per tonne of biomass per *ha* have been calculated for easier comparison. The order of nutrient accumulation of the overstorey in this study was K>N>Ca>Mg>P; however, this was not the case for other plantations. In Brazil the order was N>K>Ca>Mg>P, while in Nigeria K was accumulated in the highest amounts, P in the lowest amounts and accumulation of other nutrients varied. The order of nutrient accumulation in both fallow forests was, however, the same as the *Gmelina* plantation in this study. This may be a reflection of similar soil types with similar nutrient status.

The nutrient content of the *Gmelina* in this study is above the average of other plantations for N, K and Ca, average for Mg, and below average for P. However, this is not reflected in the biomass which is 7.6 t ha¹ below the average. Low P

Location	Age y	Biomass t ha ⁻¹	N	Р	K kg ha'	Ca	Mg	Reference
Gmelina arb	orea							
Sarawak	6.6	85.0 (2.8)	236 (0.2)	17 (4.6)	394 (2.5)	214 (0.8)*	70	This study
Brazil	6	122.0 (2.9)	352 (0.5)	63 (1.7)	208 (1.5)	185 (0.6)	79	Chijioke (1980)
Brazil	6	55.9 (2.3)	128 (0.4)	22 (1.7)	93 (0.7)	42 (0.7)	39	-
Nigeria	5.5	136.7 (3.0)	408 (0.4)	49 (7.6)	1039 (4.0)	$553 \\ (0.4)$	51	Chijioke (1980)
Nigeria	5.5	63.4 (2.5)	$\begin{array}{c} 158 \\ (0.2) \end{array}$	12 (5.3)	336 (1.0)	66 (1.5)	92	
Mean	92.6	(2.7)	(0.3)	(4.2)	(1.9)	(0.8)		
Fallow Fore	st							
Sarawak	7-10	84.1 (3.4)	284 (0.2)	14 (4.5)	377 (2.9)	244 (1.4)	- 122	Halenda (1989)
Sarawak	10-14	30.9 (4.0)	124 (0.2)	6 (6.1)	189 (3.6)	113 (0.7)	22	Koopmans & Andriesse (1982)

Table 7. Overstorey	[,] biomass a	and nutrien	t accumulati	on of	other	Gmelina	arborea
	and	fallow fores	ts in the trop	ics			

* Numbers in parentheses are the amounts of nutrients per tonne of biomass (kg ha⁻¹).

accumulation in the biomass of this study is not surprising since P levels in the soil were also low. Since P accumulation is the only nutrient below the average, P may be the most limiting factor to better biomass production of the *Gmelina* in this study.

Compared with 7 to 10-y-old fallow forest the amount of nutrients per tonne of biomass was similar for P and K but were higher for N, Ca and Mg in the fallow forest. In a 10 to 14-y-old fallow forest only P and Mg were similar while N, K and Ca were higher in the fallow forest. However, higher nutrient accumulation did not result in higher biomass production as indicated in Table 7. This suggests that although indigenous species may be somewhat more efficient in accumulating or capturing nutrients, *Gmelina* may be more efficient in using nutrients to produce biomass.

Conclusions

Based on biomass production, the *Gmelina arborea* plantation was found to be an adequate method of rehabilitating abandoned shifting cultivation sites. The total aboveground biomass after 6.6 y was 92.1 t ha^1 . The overstorey attained a mean biomass of 85.0 t ha^1 and made up 92.3% of the aboveground biomass. The

undergrowth and small-litter standing crop made up the remaining biomass at 3.2 $t ha^{1}$ (3.5%) and 3.9 $t ha^{1}$ (4.2%) respectively.

Overstorey biomass was below the average biomass production of *Gmelina* plantations reported elsewhere, but comparable to similarly aged fallow forest in the same area.

The order of nutrient accumulation in the overstorey was as follows: K>N>Ca>Mg>P. Nutrient accumulation ($t ha^1$ per tonne of biomass) was above the average for N, K and Ca; average for Mg; and below average for P when compared to other plantations. Fallow forests appear to be more efficient in capturing nutrients than *Gmelina* plantations; however, *Gmelina* appears to be more efficient in using captured nutrients to produce overstorey biomass.

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