EFFECTS OF TRACTOR LOGGING AND BURNING ON BIOMASS PRODUCTION AND NUTRIENT ACCUMULATION IN ACACIA MANGIUM PLANTATIONS IN SABAH, MALAYSIA

N. Nykvist,

Department of Forest Ecology, Faculty of Forestry, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden

Sim Boon Liang

Research & Development Department, Forestry & Timber Division, Sabah Forest Industries, WDT 31, 89858 Sipitang, Sabah, Malaysia

&c

A. Malmer*

Department of Forest Ecology, Faculty of Forestry, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden

Received January 1995

NYKVIST, N., SIM, B.L. & MALMER, A. 1996. Effects of tractor logging and burning on biomass production and nutrient accumulation in Acacia mangium plantations in Sabah, Malaysia. Three 3.8-y-old tropical forest plantations of Acacia mangium, established in different ways, were compared in terms of biomass accumulation and the nutrient contents of different above- and below-ground biomass components. On two soil types, stands established on unburned sites where logs had been manually extracted before planting, growth was faster and biomass accumulation almost double compared with stands subjected to the "normal practice" of tractor log extraction and burning before planting. Sites on which secondary forest, after the "Borneo fire" in 1983, had been subjected to burning before planting, showed the lowest rates of growth and biomass production. Most plant nutrients accumulated rapidly in the plantations. About 80 % of the P in the previous rain forest stand had accumulated after 3.8 y in the above-ground biomass of the best-growing A. mangium plantation. Corresponding figures were 68 % for N, 72 % for K, 47 % for Na, 46 % for Zn, 38 % for S, 24 % for Ca and 23% for Mg whereas the proportion of dry matter biomass accumulated was only 19 %. The fast accumulation can be ascribed to the rapid growth of leaves and small branches by young trees and has important implications for the timing of fertiliser treatments in tropical forest plantations.

Key words: Acacia mangium - forest plantation - biomass production - nutrient accumulation - tractor logging - burning

NYKVIST, N., SIM, B.L. & MALMER, A. 1996. Kesan-kesan pembalakan traktor dan pembakaran ke atas penghasilan biojisim dan pengumpulan nutrien di ladang Acacia mangium di Sabah, Malaysia. Tiga buah ladang hutan tropika Acacia mangium berumur 3.8 tahun yang ditubuhkan dengan cara berbeza, dibandingkan dari segi pengunpulan biojisim dan kandungan nutrien bagi komponen-komponen biojisim di atas dan di bawah tanah yang berlainan. Bagi dua jenis tanah, dirian yang ditubuhkan di atas tapak yang tidak dibakar dimana balak-balak dikeluarkan secara manual sebelum penanaman, pertumbuhannya lebih cepat dan pengumpulan biojisim hampir dua kali dirian yang terdedah kepada "amalan biasa" iaitu pengeluaran balak dengan traktor dan pembakaran sebelum penanaman. Selepas "Kebakaran Borneo" dalam tahun 1983, tapak-tapak di hutan sekunder yang terdedah kepada pembakaran sebelum penanaman, menunjukkan kadar pertumbuhan dan pengeluaran biojisim paling rendah. Kebanyakan nutrien tanaman berkumpul dengan cepat di ladang. Lebih kurang 80% P di dalara dirian hutan hujan terdahulu telah berkumpul selepas 3.8 tahun di dalam biojisim atas tanah ladang Acacia mangium yang paling baik turabesarannya. Angka-angka seterusnya ialah 68% bagi N, 72% bagi K, 47% bagi Na, 46% bagi Zn, 38% bagi S, 24% bagi Ca dan 23% bagi Mg manakala bahagian biojisim bahan kering yang terkumpul hanya 19%. Pengumpulan cepat bolch dianggap disebabkan oleh pertumbuhan cepat daun dan ranting kecil oleh polok-pokok muda dan ini mempunyai implikasi penting ke atas pemilihan waktu yang sesuai untuk rawatan baja di ladang hutan tropika.

Introduction

Due to the shortage of wood, interest in planting fast-growing tree species has increased during the last decades, even in the humid tropics (Evans 1992). However, reviews of information available on the productivity and biomass of tropical forest plantations are rare (Lugo *et al.* 1988), and investigations on nutrient accumulation and allocation to different biomass components are even scarcer.

In Peninsular Malaysia, an area of about 90 000 ha has hitherto been planted with *Acacia mangium*, *Gruelina arborea* and *Parcserianthes falcataria*, on a 10- to 15-year rotation, and a total of 500 000 ha of land area has been planned for forest plantation establishment by the year 2000 (Saifuddin *et al.* 1991).

Forest resources play an important role in the economy of the state of Sabah, accounting for about 40 % of the gross domestic product of the state. Conscious of the necessity to conserve and develop the forest resources, the state government of Sabah plans to implement a large-scale forestry resource programme, including 250 000 ha of forest plantations that should generate about 3 million cubic meters of logs annually by the year 2000. To date, a total of 54 000 ha has been planted by various tree-planting agencies and smallholders.

When the first integrated pulp and paper mill in Malaysia was proposed, the government of Malaysia requested an environmental impact study dealing not only with air and water pollution but also with the ecological consequences of forestry operations.

Six paired catchments were set up in 1985 near the Mendolong nursery, about 35 km from the mill at Sipitang in southwestern Sabah. The objective of the investigation was to study water and nutrient budgets after clear-felling the rain forest and replanting with *Acacia mangium*, which is the most common forest tree species planted in this region. A short summary of results from this paired

catchment study was presented by Nykvist *et al.* (1994). Reducing disturbance, by not using heavy tractors and avoiding burning, resulted in higher wood recovery (Sim & Nykvist 1991) accompanied with less stream s iltation (Malmer 1990) and a 50% reduction in runoff (Malmer 1992) as well as in losses of nutrients in streamwater (Malmer & Grip 1994). This article describes the production and nutrient content of the biomass in the plantations, established using different methods, at 3.8 y of age, which is about half the rotation age for a pulp wood plantation.

Materials and methods

Research area

The research area is situated at 650-750 m.a.s.l. on the foothills of Mount Lumaku in the Crocker Range, 35 km southeast of Sipitang (115.5 °E, 5.0 °N). The slopes are gentle to moderate (< 40%), and the annual rainfall is 3352 mm (1985-1990, Malmer 1992).

The hill dipterocarp forest of the study area was selectively logged in 1981. Part of the area was seriously burnt during the "Borneo fire" in 1983, when large forest areas in Borneo were damaged (Beaman *et al.* 1985, Malingreau *et al.* 1985, Woods 1989, Nykvist 1996). Data on the biomass and nutrient content of the dipterocarp forest of the research area were reported by Sim and Nykvist (1991). They also quantified the biomass of the plantations at 1.6 years of age, comparing the effects of different plantation establishment methods.

The bedrock is mainly sandstones and siltstones with interbedded shales (Malmer 1993). The soils in the research area are Haplic Acrisols with clayey top soil, Gleyic Podsols with sandy top soil and intermediate forms. Top soils are loose with high infiltrability on both soil types. Disturbance by tractors on 24% of the catchment with "normal practice" (W5, Table 1) reduced infiltrability to practically zero, while soil physical changes were not significant in the "minimum disturbance" treatment (W4, Table 1) (Malmer & Grip 1990).

Methods

Plantation establishment

The sizes of the catchments, treatments and vegetation before and after treatments are summarised in Table 1. Two of the catchments in the area that had not been burnt by the "Borneo fire" were clear-felled from November 1987 to January 1988. In one of these catchments (W5) the logs were extracted with crawler tractors, and the slash was burnt before planting, which is a common land-clearing practice in the tropics. In the other catchment (W4), the logs were pulled on wooden sleighs according to the old "Kuda Kuda" method (Brown 1955), and slash in the planting rows was manually removed, and not burned, before planting. Further details on treatments were given by Malmer and Grip (1990). In the area that had been burnt by the "Borneo fire", there were no living trees to be logged. In two of these catchments (W1 and W2), the dead trees and secondary vegetation were cleared and the residues burnt before planting. These two catchments are treated as one in this report.

The spacing of the Acacia mangium was 3×3 m (eq. 1089 trees ha⁻¹) in all catchments. Circle weeding and inter-row slashing were carried out once every three months until the plants were one and a half years old. All logging and silvicultural treatments in this study were carried out by a regular contractor and personnel involved in full-scale operations in the surrounding areas.

Catchment	Size (ha)	Vegetation before treatment	Treatment	Vegetation after treatment
W1+2	6.5	Secondary veg. after 82/83 wild- fire	Felled, no harvest, burned, replanted	A. mangium
W3	18.2	Same as W1+2	Control	Lowland hill dipterocarp 20%, secondary 80 %
W4	3.4	Lowland diptero- carp sel. logged in 1981	Felled, manual harvest, not burned, replanted	A. mangium
W5	9.7	Same as W4	Felled, tractor harvest, burned, replanted	A. mangium
W6	4.5	Same as W4	Control	Lowland hill dipterocarp

Table 1. Characterisation of the Mendolong catchments in Sabah, Malaysia

Biomass sampling

Sampling for this study was carried out in November 1991 when the trees were 3.8 years old in W1+2 and W4 and 3.6 years old in W5. An inventory of the planted catchments was made three years after planting. Based on this inventory, sampling trees from four diameter classes were selected at random along sampling lines (Table 2).

The above-ground biomass other than Acacia mangium was sampled from 10×10 m plots. These plots were situated at a fixed position in relation to the randomly sampled trees. Consequently, in each catchment there were five plots. In each catchment, roots were sampled down to 50-cm depth in five 50×50 cm sample plots, also in a fixed position to the sample trees. If a sample plot ended up

within 50 cm from an Acacia mangium tree, on boulders or on undecomposed logs, it was extended 1 m further along the sampling line.

Catchment	Diameter class (DBH)							
	0-5	5-10	10-15	15-20	Tota			
	cm	cm	cm	cm				
		Tree	s per hectare	2				
W1+2	301	396	231	12	940			
W4	7	341	599	80	1027			
W5	171	472	325	29	997			
		Sa	mple trees					
W1+2	1	2	1	1	5			
W4		1	2	2	5			
W5	1	1	2	1	5			

Table 2. Diameter class distribution and assignment of sample trees to diameterclasses for Acacia mangium in catchments W1+2, W4 and W5 in theMendolong research area, Sabah, Malaysia

Table 3. Mean Acacia mangium growth on Haplic Acrisol and (in parentheses) Gleyic Podzol after different treatments in the Mendolong research area in Sabah, Malaysia. W1+2 plantation was 35 months old and those of W4 and W5 were 37 months old.

Treatment/ Catchment	Stems n ha ^{.1}	DBH ¹ cm	DOMH ² m	BA ³ m² ha ¹	V ¹ m³ha ^{-l}	CAIV ⁵ m ³ ł	MAIV ⁶
Felled, no harvest, burned, replanted/ W1+2	930 (990)	9.3 (5.1)	13.0 (8.3)	7.0 (2.0)	39.0 (7.6)	26.1 (4.2)	13.4 (2.6)
Felled, manual harvest, not burned, replanted/ W4	1070 (940)	11.8 (10.1)	14.0 (13.9)	11.8 (8.4)	73.4 (53.4)	49.7 (36.5)	23.8 (17.8)
Felled, tractor harvest, burned, replanted/ W5	1330 ⁷ (1080)	9.4 (8.4)	13.5 (13.1)	9.4 (5.8)	56.3 (33.1)	44.8 (25.2)	18.5 (10.8)

¹ DBH - Diameter at breast height,

² DOMH - Dominant height,

⁸ BA - Basal area,

⁴ V - Volume,

⁵ CAIV - Current-year annual increment in volume,

⁶ MAIV - Mean annual increment in volume,

⁷ No slope correction in spacing.

The choice for sampling of trees and plots were stratified on catchments and on diameter classes, and not additionally stratified for soil type, to minimise sampling and facilitate sampling layout. However, out of five sampled trees and plots per catchments, more sandy top soils were found in one plot in W1+2, two plots in W4 and two plots in W5, compared with relative areas of 38%, 34% and 62% of sandy top soils for W1+2, W4 and W5 respectively (Grip *et al.* 1994). That means that the more fertile soils were over represented in the least productive catchments W1+2 and W5, whereas poor soils were somewhat over represented in the best productive catchment W4 (Table 3).

For the sample trees, discs were cut from the bottom, middle and top part of the stems and debarked. The tree top, which was less than 2 cm in diameter, was treated as a branch. Leaves, climbers and seeds were separated by hand. The stump (< 10 cm above soil surface) and root crown, cut 50 cm from the centre of the trunk, were treated as one sample category. Root discs were used as subsamples for the root crown and stump.

Total destructive sampling, followed by immediate weighing, was carried out in the field using spring balances (Salter 100 ± 0.5 kg, 50 ± 0.2 kg, and 10 ± 0.05 kg). Subsamples for dry weight determinations of every sampling category were immediately sealed in plastic bags in the field and weighed in the laboratory later in the same day, and again after drying overnight at 105 °C. Total dry weights of different biomass components were calculated from dry weight percentages and total field fresh weights. Based on these figures and the size of the sampling plots or the number of trees per hectare in the corresponding diameter classes, the biomass per hectare could be calculated (Table 4). In the understorey plots the most common species in each plot were analysed separately.

Measurements of leaf area were made on weighed leaves from different heights on all sample trees. The leaf area index was calculated by multiplying the area/dry weight ratio for the sampled leaves and the total dry weight of the leaves.

Chemical analysis

Analyses of nutrient concentrations were conducted at the Environmental Research Laboratory at the Department of Forest Ecology in Umeå, Sweden. A total of 354 vacuum dried and ground biomass samples were analysed for total phosphorus, potassium, calcium, magnesium, manganese, copper, zinc, iron, aluminum, sulphur and boron using ICP-emission technique after wet combustion treatment (Emteryd 1989). Concentrations of nitrogen and carbon were determined by elementary analysis after dry combustion.

Differences in element mean concentrations in the different components of biomass between catchments and between soil types were tested using the Tukey-Kramer multiple test (Kramer 1956) following tests for homogeneity in variance. Multivariate statistics to include concentrations of catchments and soil types were not made due to too low number of samples analysed in each component of biomass.

Biomass compartment			Catchment	
· · · · · · · · · · · · · · · · · · ·		W1+2	W4	W5
Above-ground parts	of trees			
Leaves		1.09	2.42	1.55
Climbers		0.55	L	0.92
Seeds		J.	0.26	_1
Live branches	<0.5 cm	0.81	1.17	0.95
	0.5-2 cm	2.42	3.98	3.78
	>2 cm	0.54	2.66	0.34
Dead branches		0.55	4.30	0.73
Stem bark		2.52	7.20	2.75
Stem wood		7.31	22.65	11.96
Total tree biomass above ground		15.80	44.65	22.99
Understorey		6.36	5.35	7.38
Stumps and roots sar	npled to 50 cm dep	th		
Stump and root	crown	2.77	7.43	3.05
Roots	50-20 mm	0.88	_1	0.22
	20- 5 mm	1.25	0.96	0.97
	5-2 mm	1.12	1.19	0.98
	<2 mm	11.06	1.61	3.19
	Total roots	14.31	3.76	5.36
Total stumps and roots		17.08	11.19	8.41
Total biomass		39.90	61.19	38 74

Table 4. Biomass dry weight (t ha¹) of different compartments of 3.8-y-oldplantations of Acacia mangium in different catchments of Mendolongresearch area in Sabah, Malaysia

' < 0.10 t ha''.

Results and discussion

Forest inventory

The growth rates of the Acacia mangium plantations in the different catchments are shown in Table 3. The volume of 3-y-old plantations on Acrisol was $73.4 \text{ m}^3 \text{ ha}^1$ in the manually logged, unburnt area (W4) and 56.3 m³ ha⁻¹ for the tractor logged and burnt area (W5). On Podzol soil the corresponding figures were 53.4 and $33.1 \text{ m}^3 \text{ ha}^{-1}$ respectively.

On Acrisol the mean annual increment in volume was $23.84 \text{ m}^3 \text{ ha}^1 \text{ y}^1$ for W4 and $18.5 \text{ m}^3 \text{ ha}^1 \text{ y}^1$ for W5, a difference of $4 \text{ m}^3 \text{ ha}^1 22 \%$. On the other hand, current-year annual increment in volume was $49.7 \text{ m}^3 \text{ ha}^1 \text{ y}^1$ for W4 and $44.8 \text{ m}^3 \text{ ha}^1 \text{ y}^1$ for W5, which is only a difference of 10 %, indicating that the difference in growth rate between the manually logged/unburnt and tractor logged/burnt catchments decreased with time.

The impact of the "Borneo fire" seemed to be more pronounced, as indicated by the poor growth rate in W1+2 where the current-year annual increment in volume was only 26.1 m³ ha⁻¹ y¹ on Acrisol and 4.2 m³ ha⁻¹ y¹ on Podsol.

In Figure 1, the relation between diameter at breast height (DBH) and age for *Acacia mangium* plantations in the tropics on a variety of soils is presented in the form of a scatter diagram. The relatively low fertility of the Mendolong soils is illustrated by their over-representation in the lower half of the scatter.



Figure 1. Scatterplot of diameter at breast height (DBH) versus age for *Acacia mangium* plantations in the tropics from Lim (1993) and for the present stands on different soils

Biomass production

The above- and below-ground biomass for standing crops of *Acacia mangium* plantations in the differently treated catchments can be found in Table 4. The dry matter contents of the above-ground parts of the *Acacia mangium* trees were 45 t ha⁻¹ for the manually logged, unburnt catchment (W4) and 23 t ha⁻¹ for the tractor logged, burnt one (W5). In W1+2, which was damaged by the "Borneo fire" in 1983 and then burned again before planting, the dry matter content was only about 16 t ha⁻¹. Almost 4 t of the dry matter in W4 consisted of dead branches as compared with about 0.6 t for the other catchments, indicating that the rate of

self pruning was higher in W4. The leaf area index for the *Acacia* trees was 0.97, 2.95 and 1.83 ha ha⁻¹ for catchments W1+2, W4 and W5 respectively. Before clear-felling, the leaf area index of the natural forest was 6.7 ha ha⁻¹ (Sim & Nykvist 1991).

When establishing forest plantations in the humid tropics after clear-felling, the slash is burnt before planting. The biomass growth of the *Acacia mangium* plants in the burnt catchment (W5) at Mendolong was low compared with that on other plantations of *Acacia mangium* in the tropics, indicating that the fertility of the soils in the Mendolong experimental area was low (Table 5).

Stand	Age (y)	MABI (t ha ⁻¹ y ⁻¹)	Source
	0.7	0.3	Kurosaki 1988
W1+2	1.6	1.5	Sim & Nykvist 1991
W4	1.6	6.5	,
W5	1.4	3.9	
	3.5	15.5	Lim & Mohd. Basri 1985
	3.5	18.31	Lim 1985
W1+2	3.8	4.1	This study
W4	3.8	11.8	
W5	3.6	6.3	
	4	21.0	Lim 1988
	4	12^{2}	Yantasath et al. 1992
	4	$32^{2,3}$	Yantasath <i>et al.</i> 1992
	4.5	$18.2^{3,4}$	Lim 1986
	5.0	12.8	Ruhiyat 1989
	6.8	18.1	Halenda 1989

 Table 5. Mean annual increment of above-ground tree biomass (MABI) for some

 Acacia mangium plantations in the humid tropics

¹ Projected for plantation condition,

² Converted from freshweight data by multiplying by 0.4,

* 10 000 stems per ha,

⁴ Regular fertilisation of cocoa planted in between the trees.

The biomass of stumps and root crowns was much higher and the biomass of fine roots (< 2 mm) sampled to 50 cm depth was much lower in W4 than in the other catchments (Table 4). The explanation for the comparatively greater biomass of fine roots in W1+2 is probably that the biomass of grasses, ferns and herbs was greater in W1+2. In initial studies of *Acacia mangium* stands between two and six years old, Lim (1992) found the average biomass of roots to be about 4 t ha⁻¹, which corresponds well with the root biomass in the most productive catchment, W4 (Table 4).

Stump and root biomass as a percentage of the total above- and below-ground biomass was 44 % for W1+2, 18 % for W4 and 22 % for W5. Before clear-felling the rain forest, the stump and root biomass ratio was 39 % (Sim & Nykvist 1991). This high figure was due to the great number of buttresses in the rain forest. Andrae and Krapfenbauer (1979) reported a figure of 20 % for a 4-y-old plantation of *Eucalyptus saligna* which had decreased to 14 % by the time that the stand had reached an age of 8 y (Andrae 1982). In a young plantation of *Pinus caribaea*, the percentage was 18.5, which was reasonably close to the value of 21.1 % obtained in an earlier study (Egunjobi & Bada 1979). Considerably higher figures for root biomass have been obtained by Parrotta (1989). In a 3-y-old stand of *Albizia lebbek* with 2500 trees per ha, the root biomass amounted to 37 % of the total tree biomass. Corresponding figures for stands with 10 000 and 40 000 trees per ha were 41 and 58 % respectively.

Table 6. Total above-ground biomass of the ten most common plant species besidesAcacia mangium, 3.8 y after planting. Means of fives sample plots $(10 \times 10 \text{ m})$ per catchment. Figures (in parentheses) are numbers of sample plots in which
the plant species were found.

Species	Catchment	14/4	1475
Nephrolepis biserrata (fern)	2854 (5)	766 (5)	1587 (5)
Saccharum spp. (grass)	803 (3)		
Mikania cordata (vine)	719 (4)		
Eupatorium odoratum (herb)	482 (5)		
Imperata cylindrica (grass)	473 (5)		
Pteridium spp. (fern)	457 (3)		
Ficus spp. (tree)	98 (3)	204 (3)	554 (5)
Zingiher spp. (herb)	65 (4)	180 (5)	137 (5)
Musa spp. (herb, banana)	60 (2)	209 (2)	223 (3)
Melastoma malabathricum (shrub)	47(1)		
Callicarpa spp. (tree)		781 (4)	750 (4)
Bamboo spp. (grass)		639 (5)	113 (2)
Dicranopteris linearis (fern)		385 (5)	870 (4)
Pandanus spp. (shrub)		184 (3)	
Cyathea spp. (tree fern)		133 (3)	115 (4)
Smilux spp. (tree)		113 (4)	
<i>llex</i> spp. (tree)			648 (1)
Macaranga spp. (tree)			227 (5)
Other species	304	1756	2154
Total	6362	5350	7378

The biomass of the understorey (Table 6) had increased by about 3.5 t ha⁻¹ in W4 and by about 4.0 t ha⁻¹ in W5 since the investigation was carried out 2.2 y earlier (Sim & Nykvist 1991). The corresponding increase of biomass in W1+2 was only 0.2 t ha⁻¹. However, the species composition of W1+2 has changed considerably. In 1991, the understorey species with the greatest biomass were *Nephrolepis biserrata*, *Saccharum* spp. *Mikania cordata*, *Eupatorium odoratum*, *Imperata cylindrica* and *Pteridium* spp. Of these six species, only *Nephrolepis biserrata, Eupatorium odoratum*, and *Imperata cylindrica* were found among the ten most common species 2.2 y earlier (Sim & Nykvist 1991). *Nephrolepis biserrata* had increased with time from about 1100 to about 2800 kg ha⁻¹, but *Eupatorium odoratum* and *Imperata cylindrica* had decreased by about 400 and 150 kg ha⁻¹ respectively.

Platteborze et al. (1971) found that Nephrolepis biserrata, Eupatorum odoratum, Dicranopteris linearis and Mikania cordata were abundant in plantations of Pinus caribaea in West Malaysia. That area was probably covered with grass (Imperata cylindrica) prior to planting. According to Platteborze (1970) Dicranopteris linearis is generally associated with slow growing Pinus caribaea in West Malaysia. He found, however, that the main reason for the slow growth of these trees was not the abundance of this fern, but the low content of phosphorus in the soil. Platteborze et al. (1971) found a significant correlation between growth of Pinus caribaea and the amount of available soil phosphorus but no similar correlation for nitrogen or potassium. Dicranopteris linearis, which is one of the most common plant species in forest clearings in Malaysia, was found in W4 and W5 but not in W1+2 which was burnt by the "Borneo fire" in 1983 and reburnt before planting in March 1988.

Among the ten most common species of ground vegetation found in 1989, only Hornstedtia sp., Dinochloa sp., Uncaria sp. and Blumea sp. were not found in the 1991 sampling. Species among the most common in 1991 but not among the ten most common species two years earlier were Saccharum spp., Mikania cordata, Pteridium spp, Zingiber spp. (wild ginger), Musa spp. (wild banana), Callicarpa spp., Bamboo spp., Dicranopteris linearis, Pandanus spp., Cyathea spp. (tree fern) and Ilex spp.

Element concentrations in various biomass components

Macronutrient concentrations in the above- and below-ground biomass are given in Appendix 1. Very few statistical differences (p < 0.05) were found between the catchments in mean concentrations of elements analysed for any of the biomass components investigated. However, for phosphorus, calcium, magnesium and sulphur, mean concentrations in tree biomass components were generally greatest in W1+2 and smallest in W4, with statistical differences detected in fine and small roots for magnesium. In the most common understorey plant in the catchments, viz. *Nephrolepis biserrata*, the mean concentration of magnesium was also statistically greater in W1+2 than in W4 and W5. Malmer (1993) and Grip *et al.* (1994) also found that levels of leaching of calcium, magnesium, sulphur and silica, from control catchments, were positively related to the areal percentage of clay top soil, which they related to richer dark shales interbedded in the sand and siltstones of the bedrock of the area.

The finest fractions of Acacia branches (< 5 mm) had significantly lower concentrations of nitrogen and potassium on sandy top soils; means were 0.97% N and 0.98% K on sandy top soil versus 1.51% N and 1.83% K on clay top soils. Other nutrient rich parts, like leaves and bark of Acacia, showed a similar, but weak and non-significant trend in concentrations of N, K and P and a weak inverse trend for C. The narrow 95% confidence interwall (Appendix 1) for the high means

of N concentrations for Acacia leaves mirrored the N-fixation (Galiana et al. 1995). That confidence interval of only 2-4%, compared to up to 72% for other elements, can be interpreted as a higher dependence of uptake, for all other nutrients than N, on the variable site qualities. However, as leaves did not show significant differences in concentrations between sandy and clayey top soils, other micro site factors like amounts of slash decomposing, amounts of ash, moisture regime, compactness of soils, etc. also probably played a role for biomass nutrient uptake and concentrations.

The greatest concentrations of nitrogen, phosphorus, potassium, magnesium, sulphur, sodium and manganese were found in the leaves. For calcium the concentration was greatest in the bark, whereas the highest concentrations of aluminium, iron, silicon and zinc were found in fine roots.

Compared with the natural rain forest before clear-felling and planting, concentrations of plant nutrients in leaves from *Acacia mangium* plantations in the same catchment were higher for nitrogen, phosphorus and potassium and lower for calcium and magnesium, although the differences were statistically significant only for nitrogen. The N/P ratio, for all catchments, in *Acacia* leaves (23.5) compared to that of *Neprolepis* (13.0) also mirrored the N-fixation by the *Acacia mangium*. Concentrations of plant nutrients in *Acacia mangium* leaves from the Mendolong research area were similar to those in plantations in East Kalimantan, Indonesia (Ruhyat 1989). In both areas, the bedrock consisted of sandstones, mudstones and shales with low contents of plant nutrients.

Concentrations of plant nutrients in leaves are often used as indicators of the nutritional status of plants. Srivastava (1993) summarised foliar analyses of *Acacia mangium* from different investigations. Compared with the critical levels given, the mean foliage concentrations in our study were low in phosphorus, magnesium and boron (Table 7). However, in an investigation from South Kalimantan, Indonesia, Simpson (1992) found that *Acacia mangium* grew fast at foliar concentrations of phosphorus as low as 0.08 % which is lower than the critical value of less than 0.13 % given by Srivastava (1993). In contrast to our figures, which represent mean concentrations for all leaves collected from five trees, the leaf samples used for foliar analyses made by Srivastava (1993) and Simpson (1992) were collected from upper-crown branches, following the standard sampling procedure for foliar analyses.

In the understorey there were also some aluminium-accumulating plants in which foliar concentrations of aluminium exceeded 0.1 %. Aluminium concentrations in leaves, shoots, stem and roots of *Melastoma malabatricum* were 0.6, 0.5, 0.2 and 0.4 % respectively. This plant belongs to a family, many members of which are known to accumulate aluminium. Aluminium concentrations of 0.65, 0.41, 0.24 and 0.16 in the leaves of the fern *Dicranopteris linearis* indicate that there were also other aluminium-accumulating species in the catchments. Concentrations of aluminium in other plants were mostly less than 0.01 %; e.g. for *Acacia mangium* leaves they were $0.003\% \pm 0.001\%$.

Element	Mean o	concentration (% or	ppm)	Diagnost	ic levels
	W1+2	W4	W5	Critical	Satisfactor
N %	3.08(0.11)	3.19(0.07)	3.12(0.14)	not known	>3
Р%	0.15(0.04)	0.11(0.08)	0.14(0.01)	< 0.13	0.13-0.15
К %	1.37(0.14)	1.64(0.10)	1.55(0.39)	<0.6	>1.0
Ca %	0.52(0.06)	0.42(0.09)	0.41(0.10)	<0.2	
Mg %	0.10(0.03)	0.11(0.04)	0.12(0.02)	<0.11	0.15-0.20
s %	0.21(0.04)	0.21(0.02)	0.20(0.01)	<0.10	
Mn ppm	130(80)	190(80)	130(20)		
Na ppm	140(60)	230(150)	110(90)		
Zn ppm	30(10)	20(10)	20(-)	10	
Cu ppm	8(6)	10(-)	8(6)	3	
B ppm	6(17)	6(7)	4(7)	<10	
Fe ppm	80(30)	80(20)	80(20)		
Al ppm	30(10)	30(10)	30(10)		
Sippm	12(6)	30(20)	30(10)		

Table 7. Mean foliage concentrations, with 95 % confidence intervals (in parentheses)in this study and proposed diagnostic levels of Acacia mangium foliage basedon unpublished information by Mead (Srivastava 1993)



Figure 2. Amounts of nitrogen, potassium and phosphorus in above- and below-ground biomass of *Acacia mangium* plantations 3.8 y after planting in different catchments in the Mendolong research area, Sabah, Malaysia. See Table 1 for different treatments before planting.



Figure 3. Amounts of magnesium, sulphur and calcium in above- and below-ground biomass of *Acacia mangium* plantations 3.8 y after planting in different catchments in the Mendolong research area, Sabah, Malaysia. See Table 1 for different treatments before planting.

Amounts of elements in the biomass

Catchment W4, with no soil disturbance or burning before planting, had the greatest total planted-tree biomass (Table 4), and also contained the greatest amounts of nitrogen and potassium (Figure 2). For the other macronutrients, such as phosphorus, calcium, magnesium and sulphur, amounts in the total biomass were greatest in W1+2 owing to their high concentrations in roots, especially in the smallest ones (Figures 2 and 3). The biomass in catchment W5, which was subjected to both soil disturbance and burning before planting, contained the smallest total amounts of all macronutrients.

For the above-ground biomass, amounts of all macronutrients, except magnesium, were highest in W4. Compared with the W1+2 biomass, that of W5 contained smaller amounts of all nutrients except nitrogen. The greater amounts of nitrogen in W5 can be attributed to the fact that the nitrogen-fixing tree *Acacia mangium* grew faster in this catchment than in catchment W1+2.

Estimating the accumulation of plant nutrients in the biomass is even better than foliar analysis for assessing soil fertility. The mean annual accumulation of plant nutrients in the above-ground tree biomass was therefore calculated by dividing amounts of plant nutrients in the tree biomass by stand age. Figures obtained in this way for *Acacia mangium* plantations in the Mendolong research area were then compared with corresponding figures for other *Acacia mangium* plantations in Table 8. Phosphorus accumulation by plants was lower in the fastest growing plantation (W4) in the Mendolong than in the other plantations, indicating that the availability of this plant nutrient in the soils of the Mendolong research area was low (unpublished).

Stand ¹	Age	Ν	Р	K	Ca	Mg	Source
	(y)						
	0.7	4		I	1	0.2	Kurosaki 1988
W1+2	1.6	13	0.6	11	6	0.9	
W4	1.6	53	2.4	66	24	4.4	Sim & Nykvist 1991
W5	1.4	40	2.1	29	14	2.7	
W1+2	3.8	29	1.2	20	21	2.8	
W4	3.8	76	2.4	57	34	5.9	This study
W5	3.6	42	1.4	27	19	2.8	
	4.5	78	15.4	50	35	4.8	Lim 1986
	5.0	64		38	30	5.8	
	6.0	50		38	35	5.3	Ruhiyat 1989
	7.0	52		45	28	5.7	•
	6.8	91	4.9	44	59	7.1	Halenda 1989

Table 8. Mean annual accumulation of plant nutrients in the above-ground treebiomass (above-ground nutrient amount divided by plantation age) forsome Acacia mangium plantations in humid tropics

¹See Table 1 for stand descriptions.



Figure 4. Amounts of sodium, manganese and silicon in above- and below-ground biomass of *Acacia mangium* plantations 3.8 y after planting in different catchments in the Mendolong research area, Sabah, Malaysia. See Table 1 for different treatments before planting.

Amounts of sodium, manganese, silica, aluminium, iron and zinc in above- and below-ground biomass are shown in Figures 4 and 5. The high values obtained for aluminium, iron and zinc in below-ground biomass could have partly been due to difficulties in removing all small mineral soil particles from fine roots before analysis.

Great amounts of plant nutrients were taken up and stored in the above- and below-ground biomass of planted trees and ground vegetation during the first years after clear-felling. To roughly estimate the rate of accumulation of plant nutrients in the vegetation, amounts were calculated as percentages of amounts in the rain forest biomass before clear-felling (Table 9). The element showing the highest relative rate of accumulation was phosphorus. In the fastest growing *Acacia mangium* plantation (W4), 80 % of the amount of P bound in above-ground biomass in the previous rain forest had accumulated in above-ground plantation biomass after 3.8 y. Other elements showing this pattern were nitrogen, potassium, sodium, zinc and sulphur. Corresponding figures for these elements were 68 % (N),

Age	Stand	BM ¹	N	Р	к	Ca	Mg	s	Al	Fe	Si	Mn	Na	Zn	Cu
(y)								%							
Above	e-ground bi	omass													
1.6	W1+2	3	17	48	34	7	16	17	6	9	2	6	3	23	
1.6	W4	5	21	32	35	7	8	15	8	7	1	5	4	20	
1.4	W5	3	19	34	27	6	9	15	27	14	1	7	2	21	
3.8	W1+2	9	37	79	51	21	24	26	10	13	2	13	15	32	29
3.8	W4	19	68	80	72	24	23	36	25	20	3	16	47	4 6	49
3.6	W5	12	48	66	49	18	18	24	33	18	3	19	17	36	30
Belov	v-ground bi	omass													
3.8	W1+2	9	24	55	35	12	47	53	58	27	8	12	129	80	75
3.8	W4	6	11	11	12	7	5	16	23	11	3	4	59	16	10
3.6	W5	5	12	17	12	6	5	14	30	16	2	3	37	27	13
Total	biomass														
3.8	W1+2	9	30	68	44	17	34	36	43	24	3	12	42	62	56
3.8	W4	14	38	49	47	17	15	28	23	13	3	12	50	27	26
3.6	W5	8	29	44	34	13	13	21	31	16	3	13	22	30	20

Table 9. Biomass (BM) and amounts of elements in biomass of Acacia mangium plantations, in per cent of the
corresponding figures for the rain forest before clear-felling the Mendolong research area in Sabah,
Malaysia. See Table 1 for stand descriptions.

¹ BM = Biomass.

72 % (K), 47 % (Na), 46 % (Zn) and 36 % (S). At the same time the accumulation of biomass in W4 was only 19 % of the biomass in the previous rain forest. For most other elements, percentages were close to the biomass value, except for silica, which was only 3 %. The high figure for nitrogen was probably due to nitrogen fixation by *Acacia mangium*, while the low accumulation of Si can be ascribed to the relatively low production of stem wood during the first years.



Figure 5. Amounts of aluminium, iron and zinc in above- and below-ground biomass of *Acacia mangium* plantations 3.8 years after planting in different catchments in the Mendolong research area, Sabah, Malaysia. See Table 1 for different treatments before planting.

The uptake and storage of elements by the plantation were considerably lower in the below-ground biomass as compared with the above-ground biomass, except for W1+2 which had the greatest below-ground biomass of the compared catchments. Total accumulations of phosphorus and magnesium in the above- and below-ground biomass were, in fact, greater in W1+2 than in the fastest growing plantation (W4), despite the considerably lower biomass in W1+2 (Table 4). The roots of grasses, ferns and herbs colonising W1+2 after burning seemed to tie up the nutrients more effectively than did the ground vegetation of the catchments not damaged by the "Borneo fire", which could explain why tree growth was poorest in W1+2. Uhl and Jordan (1984) compared the nutrient amounts in above- and below-ground secondary vegetation five years after forest cutting and burning with values for the previous forest. The secondary vegetation had 16 % as much total biomass, 15 % as much N, 23 % as much P, 39 % as much K, 48 % as much C and 45 % as much Mg. Corresponding values for the fastest growing plantation (W4) in our study were lower for calcium and magnesium whereas those for nitrogen, phosphorus and potassium were higher. This fast accumulation of nutrients can be ascribed to the rapid build-up of the tree crown rather than woody biomass during the initial stage of tree growth. An indication of this was that W4 had almost half of the leaf area index (2.95) of the previous rain forest (6.7, Sim & Nykvist 1991) in less than four years.

Acknowledgements

Funding for this study was provided by Sabah Forest Industries Sdn. Bhd. (SFI) and the Swedish Agency for Research Cooperation with Developing Countries (SAREC) in a joint project between SFI and the Department of Forest Ecology of the Swedish University of Agricultural Sciences. The authors are grateful to local SFI staff in Mendolong for biomass sampling and to the staff of Environmental Research Laboratory at the Department of Forest Ecology for chemical analyses, as well as to reviewers for constructive ideas.

References

- ANDRAF, F. 1982. Zweitinventur eines Eucalyptus saligna-Bestandes Sudbrasilien. Zentralblatt für das gesamte Forstwesen 99: 193-219.
- ANDRAE, F. & KRAPFENBAUER, A. 1979. Untersuchungen über Biomassen und Nährstoffverhältnisse in einer vierjährigen Aufforstung mit Eucalyptus saligna Smith in Santa Maria, R. S. Brasilien. Zentralblatt für das gesamte Forstwesen 96 : 1 - 29.
- BEAMAN, R.S., BEAMAN, J.H., MARSH, C. & WOODS, P. 1985. Drought and forest fires in Sabah in 1983. Sabah Society Journal 8: 10 - 30.
- BROWN, G.S. 1955. Timber extraction methods in N. Borneo. Malayan Forester 18: 121-132.
- EGUNJOBI, J.K. & BADA, S.O. 1979. Biomass and nutrient distribution in stands of *Pinus caribaea* L. in the dry forest zone of Nigeria. *Biotropica* 11: 130 135.
- EMTERYD, O. 1989. Chemical and Physical Analysis of Inorganic Nutrients in Plant, Soil, Water and Air. Swedish University of Agricultual Sciences, Department of Forest Ecology, Umeå, Sweden, Stencil No. 10. 181 pp.

EVANS, J. 1992. Plantation Forestry in the Tropics. Second edition. Clarendon Press, Oxford. 472 pp.

GALIANA, A., MALLET, B., BALLE, P., N'GUESSAN KANGA, A. & DOMENACH, A-M. 1995. In-situ nitrogen fixation of Acacia mangium inoculated with bradyrhizobium. Pp. 92 - 100 in Schulte, A. & Ruhiyat, D. (Eds). Proceedings International Congress on Soils of Tropical Forest Ecosystems. 3rd Conference on Forest Soils (ISSS-AISS-IBG). Volume 7. Mulawarman University Press, Samarinda, Indonesia.

- GRIP, H., MALMER, A. & WONG, P. 1994. Converting tropical rainforest to forest plantation in Sabah, Malaysia. I. Dissolved nutrient dynamics and losses from control catchments streams. *Hydrologi*cal Processes 8: 179 - 194.
- HALENDA, C.J. 1989. Biomass estimation of Acacia mangium plantations using allometric regression. NFT Research Reprints 7:49-51.
- KRAMER, C.Y. 1956. Extension of multiple range tests to group means with unequal numbers of replications. *Biometrics* 12:307-310.
- KUROSAKI, T. 1988. A Study of Nutrient Contents of Acacia mangium. Forest Research Centre, Sandakan, Sabah, Malaysia. Publication No. 51.
- LIM, M.T. 1985. Biomass and Biomass Relationship of 3.5-y-old Open-grown Acacia mangium. Occasional Paper No. 2. Faculty of Forestry, Universiti Pertanian Malaysia, Serdang, 13 pp.
- LIM, M.T. 1986. Biomass and productivity of 4.5-year-old Acacia mangium in Sarawak. Pertanika 9:81 87.
- LIM, M.T. 1988. Studies of Acacia mangium in Kemasu? Forest, Malaysia. I. Biomass and productivity. Journal of Tropical Ecclogy 4: 293 - 302.
- LIM, M.T. 1992. Research on growth and yield, litter production and nutrient cycling in *Acacias*. Pp. 72 75 in Awang, K. & Tylor, D.A. (Eds.) *Tropical Acacias in East Asia and the Pacific*. Winrock International, Bangkok, Thailand.
- LIM, M.T. & MOHD. BASRI, H. 1985. Biomass accumulation in a naturally regenerating lowland secondary forest and an *Acacia mangium* stand in Sarawak. *Pertanika* 8(2): 237-242.
- LUGO, A.E., BROWN, S. & CHAPMAN, J. 1988. An analytical review of production rates and stemwood biomass of tropical forest plantations. *Forest Ecology and Management* 23: 179-200.
- MALINGREAU, J.P., STEPHENS, G. & FELLOWS, L. 1985. Remote sensing of forest fires: Kalimantan and North Borneo in 1982-1983. Ambio 14: 314 - 321.
- MALMER, A. 1990. Stream suspended sediment load after clear-felling and different forestry treatments in tropical rainforest, Sabah, Malaysia. Pp. 62 - 71 in Ziemer, R.R., O'Loughlin, C.L. & Hamilton, L.S. (Eds.) Research Needs and Applications to Reduce Erosion and Sedimentation in Tropical Steeplands. IHAS Publications 192.
- MALMER, A. 1992. Water yield changes after clear-felling tropical rainforest and establishment of forest plantation in Sabah, Malaysia. *Journal of Hydrology* 134 : 77 94.
- MALMER, A. 1993. Dynamics of hydrology and nutrient losses as response to establishment of forest plantation. A case study on tropical rainforest land in Sabah, Malaysia. Ph.D. thesis, Swedish University of Agricultural Sciences, Department of Forest Ecology. 182 pp.
- MALMER, A. & GRIP, H. 1990. Soil disturbance and loss of infiltability caused by mechanized and manual extraction of tropical rainforest in Sabah, Malaysia. *Forest Ecology and Management* 38: 1-12.
- MALMER, A. & GRIP, H. 1994. Converting tropical rainforest to forest plantation in Sabah, Malaysia. II. Changes in dissolved nutrient dynamics and losses in stream water from treated catchments. *Hydrological Processes* 8: 195 - 209.
- NYKVIST, N. 1996. Regrowth of secondary vegetation after the 'Borneo fire' of 1982 1983. Journal of Tropical Ecology 12: 307 - 312.
- NYKVIST, N., GRIP, H., SIM, B.L., MALMER, A. & WONG, F.K. 1994. Nutrient losses in forest plantations in Sabah, Malaysia. *Ambio* 23: 210 215.
- PARROTTA, J. A. 1989. The influence of management practices on the biogeochemical stability of tropical fuelwood plantations. *Tropical Ecology* 30 : 1-12.
- PLATTEBORZE, A. 1970. A soil and vegetation study under a *Pinus caribaea* plantation in West Malaysia. *Malayan Forester* 33: 243 - 257.
- PLATTEBORZE, A., EE, C.S. & SUNDRALINGAM, P. 1971. A preliminary study of the correlation between the N, P and K contents of the soil and growth of *Pinus caribaea* var. *hondurensis* in West Malaysia. *Malayan Forester* 34: 113 - 132.
- RUHIYAT, D. 1989. Die Entwicklung der standörtlichen Nährstoffvorräte bei naturnaher Waldbewirtschaftung und im Plantagenbetrieb, Ostkalimantan (Indonesien). Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen und Subtropen, Heft 35:1-206.

- SAIFUDDIN, S., ABDUL RAHIM, N. & MUHAMMAD FARID, A.R. 1991. Watershed Research in Forest Plantation. I. Establishment and Physical Characteristics of Bukit Tarek Watershed. FRIM Research Pamphlet No. 110. 51 pp.
- SIM, B.L. & NYKVIST, N. 1991. Impact of forest harvesting and replanting. *Journal of Tropical Forest Science* 3(3): 251 284.
- SIMPSON, J.A. 1992. An assessment of the soils and nutrient status of trial plantations in the Indonesia-Finland project at Riam Kiwa, South Kalimantan, Indonesia. Report prepared for Enso Forest Development, Ltd., Helsinki, Finland.
- SRIVASTAVA, P.B.L. 1993. Soils and fertilizer requirements. Pp. 120 147 in Awang, K. & Taylor, D.A. (Eds.) Acacia mangium - Growing and Utilization. MPTS Monograph Series No. 3. Winrock International and FAO, Bangkok, Thailand.
- UHL, C. & JORDAN, C.F. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. *Ecology* 65: 1476 - 1490.
- Woobs, P. 1989. Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica* 21: 290 - 298.
- YANTASATH, K., PATANAYIBUL, S., SUPATANAKUL, W., UNGYICHIAN, I. & CHANTRASIRI, S. 1992. Field trials and multipurpose testings of selected fast-growing, nitrogen fixing trees in Thailand. *Thailand Journal of Agricultural Science* 25: 141 - 169.

Appendix 1

Mean element concentrations (%) in biomass of leaves, branches, stems and roots from Acacia mangium and the fern Nephrolepis biserrata in differently established A.mangium plantations on former tropical rain forest land in Mendolong research area, Sabah, Malaysia. The treatments used and the vegetation present before and after treatments are described in Table 1. The stands were 3.8 (W1+2 and W4) and 3.6 (W5) years old when measured. n = 5 for all components and stands except those stated in footnotes. Means with 95 % confidence intervals in parentheses.

Component	Stand	Element concentration (%)							
·		N	Р	К	Ca	Mg	S		
Leaves	W1-2	3.08	0.15	1.37	0.52	0.10	0.21		
		(0.11)	(0.04)	(0.14)	(0.06)	(0.03)	(0.04)		
	W4	3.19	0.11	1.64	0.42	0.11	0.21		
		(0.07)	(0.08)	(0.10)	(0.09)	(0.04)	(0.02)		
	W5	3.12	0.14	1.55	0.41	0.12	0.20		
		(0.14)	(0.01)	(0.39)	(0.10)	(0.02)	(0.01)		
Branches < 5 mm	W1+2	1.44	0.07	1.61	0.54	0.06	0.13		
diameter		(0.27)	(0.03)	(0.38)	(0.15)	(0.02)	(0.02)		
	W4	1.33	0.06	1.65	0.36	0.05	0.16		
		(0.37)	(0.02)	(0.53)	(0.12)	(0.02)	(0.03)		
	$W5^1$	1.50	0.08	1.82	0.30	0.08	0.11		
Branches 5-20 mm	W1+2	0.52	0.02	0.50	0.72	0.10	0.05		
diameter		(0.11)	(0.01)	(0.15)	(0.34)	(0.04)	(0.01)		
	W4	0.61	0.02	0.66	0.39	0.08	0.05		
		(0.19)	(0.01)	(0.29)	(0.13)	(0.05)	(0.02)		
	$W5^2$	0.47	0.01	0.28	0.40	0.04	0.02		
		(0.25)	(0.01)	(0.21)	(0.20)	(0.02)	(0.01)		
Branches > 20 mm	$W1 + 2^2$	0.36	0.01	0.28	0.67	0.08	0.03		
diameter		(0.05)	(0.00)	(0.14)	(1.15)	(0.13)	(0.01)		
	$W4^2$	0.31	0.01	0.19	0.29	0.05	0.02		
		(0.09)	(0.00)	(0.06)	(0.07)	(0.02)	(0.00)		
	$W5^2$	0.64	0.02	0.45	0.66	0.06	0.04		
		(0.19)	(0.00)	(0.25)	(0.34)	(0.02)	(0.02)		
Dead branches	$W1+2^{2}$	0.56	0.01	0.26	1.05	0.08	0.05		
		(0.09)	(0.00)	(0.16)	(0.47)	(0.05)	(0.01)		
	W4	0.45	0.01	0.23	0.45	0.07	0.03		
		(0.08)	(0.00)	(0.09)	(0.14)	(0.02)	(0.00)		
	W51	0.58	0.01	0.23	0.51	0.04	0.03		
Stem bark	W1+2 ³	1.22	0.04	0.68	1.32	0.13	0.11		
		(0.16)	(0.01)	(0.13)	(0.28)	(0.05)	(0.02)		
	W43	1.23	0.03	0.66	0.81	0.08	0.13		
		(0.14)	(0.01)	(0.18)	(0.16)	(0.03)	(0.01)		
	• W54	1.51	0.04	0.61	1.02	0.07	0.11		
		(0.15)	(0.01)	(0.16)	(0.21)	(0.03)	(0.01)		

(continued)

Appendix 1 (continued)

Component	Stand		Elen	nent conce	ntration (%	b)	
-		N	Р	K	Ca	Mg	S
Stem wood	W1+2 ³	0.23	0.01	0.25	0.11	0.04	0.02
		(0.03)	(0.00)	(0.13)	(0.03)	(0.01)	(0.00)
	W4 ⁸	0.25	0.01	0.29	0.06	0.02	0.02
		(0.03)	(0.00)	(0.15)	(0.01)	(0.01)	(0.00)
	W5⁴	0.25	0.01	0.25	0.08	0.03	0.02
		(0.06)	(0.00)	(0.14)	(0.02)	(0.01)	(0.00)
Stump/root crown	W1+2	0.36	0.01	0.20	0.18	0.04	0.04
•		(0.13)	(0.01)	(0.14)	(0.06)	(0.02)	(0.02)
	W4	0.36	0.01	0.13	0.12	0.02	0.04
		(0.08)	(0.00)	(0.05)	(0.05)	(0.00)	(0.01)
	W5	0.40	0.01	0.15	0.12	0.02	0.04
		(0.16)	(0.00)	(0.04)	(0.08)	(0.00)	(0.01)
Roots < 2 mm	W1+2 ⁵	1.01	0.06	0.78	0.26	0.38	0.21
		(0.20)	(0.00)	(0.10)	(0.07)	(0.11)	(0.06)
	$W4^5$	1.38	0.04	0.61	0.28	0.14	0.20
		(0.23)	(0.01)	(0.12)	(0.10)	(0.03)	(0.01)
	$W5^5$	1.35	0.05	0.62	0.30	0.11	0.14
		(0.13)	(0.02)	(0.13)	(0.17)	(0.04)	(0.02)
Roots 2 - 5 mm	W1+2 ⁵	0.88	0.05	0.80	0.19	0.29	0.18
		(0.16)	(0.01)	(0.22)	(0.02)	(0.14)	(0.05)
	W4 ⁵	0.98	0.03	0.81	0.32	0.14	0.16
		(0.13)	(0.01)	(0.22)	(0.13)	(0.05)	(0.05)
	W5 ⁵	1.03	0.03	0.76	0.31	0.08	0.12
		(0.34)	(0.01)	(0.34)	(0.12)	(0.02)	(0.03)
Roots 5 - 20 mm	W1+2 ⁵	0.94	0.04	0.52	0.32	0.38	0.19
	T4749	(0.09)	(0.00)	(0.16)	(0.16)	(0.12)	(0.03)
	W42	0.77	0.03	0.82	0.82	0.10	0.10
	1.753	(0.35)	(0.02)	(1.34)	(1.52)	(0.04)	(0.04)
	W5-	1.08	0.03	0.51	0.33	0.09	0.11
		(0.62)	(0.02)	(0.23)	(0.13)	(0.08)	(0.05)
Nephrolepis	W1+2	1.32	0.13	2.43	1.18	0.50	0.20
		(0.43)	(0.07)	(0.66)	(0.34)	(0.23)	(0.06)
	W4	1.39	0.09	2.46	0.42	0.28	0.17
		(0.40)	(0.04)	(0.93)	(0.08)	(0.11)	(0.02)
	W5	1.32	0.09	1.96	0.40	0.27	0.15
		(0.43)	(0.06)	(0.81)	(0.31)	(0.13)	(0.04)

- $n = 2^{1} n = 2^{2} n = 4^{2}$
- ³ n = 14
- n = 14n = 12
- n = 125 n = 6