6 Impacts on biomass, nutrients and water

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6.1 Introduction

Tropical lowland rain forest growing on deeply weathered soils of low fertility, as the mesophytic forest in Suriname, is characterised by a huge standing phytomass. The nutrient capital is mainly stored in the phytomass, nitrogen quite often being an exception (Golley et al. 1975). High annual rainfall, tropical temperatures, a high leaf production, high litterfall and rapid decomposition of the litter at the forest floor, all contribute to a relatively quick cycling of water and nutrients. The dense mat of roots, generally in symbiosis with mycorrhiza fungi growing in the litter layer, recaptures much of the nutrients and thus reduces their loss from the system by leaching.

Such semi-closed cycling systems are considered characteristic for tropical lowland rainforests and it may be expected that they are sensitive to management interferences in the forest such as inherent to the CMS. In order to assess this quantitatively a number of key processes were studied in forests stands subjected to different management interventions and in undisturbed forest (see Table 5.1). We also provide here an overview of the amounts and fluxes of phytomass and nutrients and the flux of water in forest stands treated according to the CMS. In addition, we discuss the results of a computer simulation for the Kabo forest, modelling the input and output of phytomass, nutrients and water.

6.2 Phytomass and nutrients

6.2.1 Methods

In four of the seven forests mentioned in Table 5.1 phytomass was measured. The undisturbed Phytomass Forest in Kabo and the lightly exploited Procter's Forest in Mapane (no unexploited forest is available there) were taken as the controls; the lightly

exploited and refined stand Akintosoela1 and the heavily exploited stand Weyerhäuser (both in Mapane) as treated forests.

In a variable number of 10×10 m plots, the total amounts of phytomass and nutrients were determined by harvesting all above ground phytomass. Fresh and dry weights (subsamples dried at 70 ⁰C for 24 hours) and nutrient concentrations of (samples of) all compartments (leaves, branches, stems) of all individual trees and palms rooting in the plot were measured.

The following parameters were measured on each individual tree (including palms): total tree height, stem height (height till the first major branch), diameter at reference height (DBH or above buttresses), crown length and crown width.

Tree phytomass in each stand was estimated based on relations between stem diameter and dry weight totals of leaves, branches and stems (see below). Most other compartments, such as fine (leaves, flowers, fruits and twigs) and coarse litter (wood > 2 cm diameter), lianas, small trees of < 1 cm dbh, and herbs, were bulked, sampled and analysed for mass and nutrients.

Where relevant, the results based on harvest measurements were compared to those based on regression analysis.

Roots were sampled as bulk in a 50×50×50 cm monolith in the middle of the plot or in a randomly chosen locality just outside the plot. The total soil volume studied in each of the four forest stands did not exceed 3.5 m² surface area against 1500 m² for the assessment of the aboveground phytomass. To improve the root mass estimates based on these small pits, in one large 0.9 m deep pit of 10×10 m in Procter's Forest, all root phytomass > 1 cm diameter was collected, traced to individual trees, and analysed, while smaller roots were bulked and analysed. Roots of all trees in the pit were pooled to establish a relation between dbh and root dry weight. Regressions found here were extrapolated to the other stands.

Amounts of phytomass and concentrations and amounts of nutrients were calculated per compartment, per tree and per plot. Tree phytomass was estimated on basis of the relations between the diameter at reference height of individual stems and the dry weights of the compartments (leaves, branches stem) of these trees. For tree leaves, branches and stems, the best fit, with very high correlation coefficients (see Table 6.1), was found with the function:

$W = k * d^{2b}$ (Eq. 6.1)
in which $k = 10a * EXP (0.5*S^2ln^210)$.
For roots the best fit was:
$W = c + e.d^2$ (Eq. 6.2)

In both formulas W = dry weight in kg, d = dbh in mm, a, b, c, e, S and k are constants (see Table 6.1). Total tree dry weight (leaves, branches, stems, roots) per stand was recalculated using these correlations and the inventory data from the forest stands.

Table 6.1. Correlations between dry weight of tree parts and stem diameter for four differently treated (see Table 5.1) forest stands. For explanation of formulas see text.

	Phytomass Forest	Procter's Forest	Akintosoela1	Weyerhäuser
Leaves: formula used $W = k \cdot d^{2b}$ with $k = 10a \cdot EXP(0.5 \cdot S^2 \ln^2 10)$.				
N	177	499	476	117
a	-3.764	-3.759	-3.680	-2.828
b	0.998	0.964	0.959	0.681
S2	0.087251	0.177532	0.251879	0.219533
R	0.956	0.839	0.778	0.744
Branches: formula used $W = k \cdot d^{2b}$ with $k = 10a \cdot EXP(0.5 \cdot S^2 \ln^2 10)$.				
N	133	285	432	113
a	-4.852	-4.338	-4.076	-3.580
b	1.418	1.280	1.242	1.051
S2	0.138294	0.169339	0.196403	0.254048
R	0.966	0.917	0.88	0.846
Stems: formula used $W = k \cdot d^{2b}$ with $k = 10a \cdot EXP(0.5 \cdot S^2 \ln^2 10)$.				
N	177	497	476	117
a	-3.485	-3.615	-3.797	-3.261
b	1.257	1.258	1.272	1.125
S2	0.042209	0.053816	0.073722	0.076163
R	0.986	0.964	0.950	0.953
Roots: formula used $\log W = c + e \cdot d^2$				
N		22		
c		-5.944		
e		0.0012		
R		0.999		

In each stand plots were selected randomly. Due to the small number of plots, the basal area measured in all harvested plots in a stand did not compare well with the basal area found after inventories of larger areas. In the Phytomass Forest a basal area of 42.8 $m^2.ha^{-1}$ was harvested, whereas in a forest inventory of 5 ha (in 1981) a basal area of 30.5 $m^2.ha^{-1}$ was found. For the other stands values were: Procter's Forest (31.6 and again 31.6 $m^2.ha^{-1}$ on five hectare), Akintosoela (23.8 and 19.2 $m^2.ha^{-1}$ on one hectare) and Weyerhäuser (33.2 and 26.9 $m^2.ha^{-1}$ on one hectare). These differences explain why the tree phytomass data (stems, branches, leaves and roots) differ so much between the two estimation methods. Hence, the correlation method was used for the estimation of tree phytomass (stem, branches, leaves and roots). This is in line with commonly applied methods. A correction simply based on basal area (not shown here) was rejected.

Nutrient concentrations in each sample were analysed and nutrient amounts calculated for each compartment of each tree and for the other bulked samples and compartments. Next, mean concentrations were calculated per compartment (tree leaves, etc.) and

nutrient amounts were calculated for each plot and averaged for each stand. The tree data given here are based on regression analysis; those for the other compartments are based on harvesting totals.

Soil nutrient content was studied in soil pits, but not in all four stands. Soils and the nutrient amounts in the Kabo region and the Mapane region differed (see Table 6.2), and this is reflected in different growth patterns, structures and species compositions of the forest vegetation in the two regions (see Chapter 5).

Table 6.2. Soil nutrient contents in Kabo and Mapane regions, based on soil pits 1.2 m deep.

Region		Kabo	Mapane
Location*		Kabo, Eastern Creek**	Procter's Forest
Number of pits		5	1
Soil organic matter	t.ha^{-1}	99.5	113.1
N	kg.ha^{-1}	8816	9602
P (P-Bray)	kg.ha^{-1}	33.0	10.3
K	kg.ha^{-1}	93.9	183.4
Ca	kg.ha^{-1}	377.7	564.9
Mg	kg.ha^{-1}	226.2	77.7
Source		Poels (1987)	Boxman (unpublished)

* Identical methods used at both locations. * *Located about 1 km east of the MAIN experiment and about 10 km west of Phytomass Forest.

We assume that the soils under Procter's Forest, Akintosoela1 and Weyerhäuser are similar, because these stands are located within 1 km from each other. Even though Procter's Forest is located down the slope, near the Mapane Creek, Weyerhäuser is at the top of the slope, and Akintosoela1 in between, differences in altitude are less than 10 m. With this assumption the effects of treatments (see Table 5.1) on phytomass can be studied by comparing these three forest stands. Procter's Forest and Akintosoela1 were selectively cut in 1966 (about 20 m^3.ha^{-1} removed, De Graaf 1986). Akintosoela1 was refined in 1975; all unwanted trees above 20 cm dbh were poison-girdled, thus reducing the basal area of living trees from 28.3 to 9.8 m^2.ha^{-1}. Dead phytomass was left in the stand. Hence, the exploitation and refinement in Akintosoela1 were somewhat heavier than the normal CMS prescriptions, as carried out in the MAIN experiment (see Section 4.4). In Weyerhäuser, virtually all wood was harvested in 1969, removing 194 m^3.ha^{-1} and there was no follow-up treatment (see 's Landsbosbeheer 1971). This resulted in a residual basal area of 7.7 m^2.ha^{-1} (Boerboom 1970). Keeping in mind that after this treatment stand growth has to start almost from scratch, this stand can be considered as a secondary forest. Thus, Weyerhäuser is taken to indicate what will happen after very severe interferences. In the Mapane region, no untreated forest was available for phytomass assessment. Phytomass assessments were carried out between 1980 and 1982 (see Table 5.1), thus allowing for different regrowth periods after treatment.

6.2.2   Phytomass in undisturbed and lightly exploited forest

With about 574 t.ha^{-1} the total amount of phytomass in Phytomass Forest in the Kabo region was some 15 % larger than that of Procter's Forest (about 492 t.ha^{-1}) in the Mapane region (see Table 6.3, values estimated by regression, and Figure 6.1). Phytomass Forest had a considerable amount of palms. Therefore Phytomass Forest had about 30 % more total leaf mass in comparison to Procter's Forest, although the total weights of tree leaves in these two forests were similar. Phytomass Forest also had about 20 % more fine litter than Procter's Forest, but Procter's Forest had about 40 % more coarse litter.
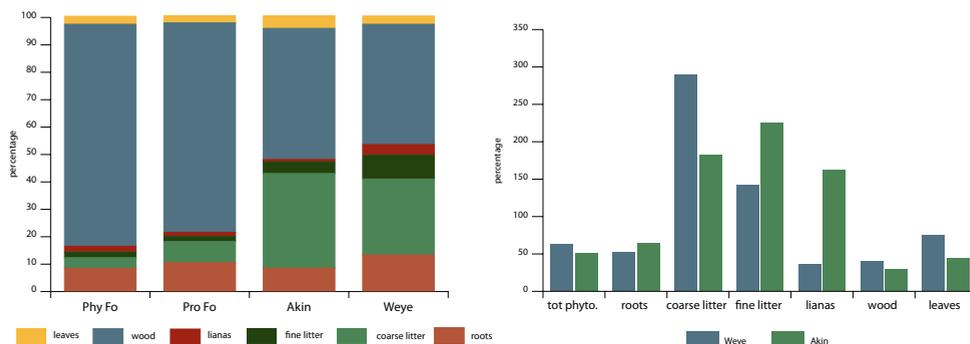

Figure 6.1. Left: Distribution of total phytomass, corrected according to regression analysis, over compartments in four differently treated (see Table 5.1) forest stands. Right: Phytomass of given compartments in Akintosoela1 and Weyerhäuser as a percentage of the same compartment in Procter's Forest. Phy Fo = Phytomass Forest, Pro Fo = Procter's Forest, Akin = Akintosoela1, Weye = Weyerhäuser; tot. phyt. = total phytomass; co. lit. = coarse litter; fi. lit. = fine litter.

The difference in total phytomass of about 82 t.ha^{-1} was mainly due to the difference in wood mass, both in branches and stems. The selective cutting of only about five trees per ha carried out in the Mapane region (De Graaf 1986) may be the main cause, whereas differences in growth and soil conditions may also have contributed. Logging probably also is the cause of the much higher percentage of coarse litter (lying dead stems) in Procter's Forest (see Figure 6.1).

Procter's Forest, while having less above-ground phytomass, had a slightly larger root phytomass than Phytomass Forest (51 respectively 47 t.ha^{-1}).

We calculated the root mass of the 10×10×0.9 m plot that we sampled in Procter's Forest using the relation we had established between dbh and dry weight of roots. We obtained a root mass value of around 161 t.ha^{-1}. This plot, however, was densely stocked compared to the surrounding forest. Therefore we applied a correction based on basal area in the plot and in the surrounding forest. That gave a total tree root mass for the stand (excluding palms) of 45 t.ha^{-1} (Table 6.4). This brings our estimates of tree root mass for both Phytomass Forest and Procter's Forest in the same order of magnitude (Table 6.3).

Table 6.3. Phytomass in t.ha^{-1} per compartment in four differently treated forest stands.
Methods: meas.: harvest over 12, 14, 12 and 2.5 plots of 0.01 ha each; r.a.: idem, tree phytomass only calculated over respectively 5, 5, 1 and 1 ha with regression analysis, other compartments by harvest. Tree phytomass: leaves, stems, branches, roots. For more details see text.

Compartment	Forest stand	Phytomass Forest		Procter's Forest		Akintosoela1		Weyerhäuser	
	Method	meas.	r.a.	meas.	r.a.	meas.	r.a.	meas.	r.a.
Leaves									
	trees	9.5	8.5	5.5	7.9	8.4	7.2	5.2	3.7
	palms	8.0	8.0	1.5	1.5	2.6	2.6	1.0	1.0
	others	0.4	0.4	3.2	3.2	3.9	3.9	2.7	2.7
Total leaves		**17.9**	**16.9**	**10.2**	**12.6**	**14.9**	**13.7**	**8.9**	**7.4**
Wood									
	branches	179.1	133.7	93.3	94.8	79.2	51.2	38.0	30.8
	stems	384.7	326.2	213.1	281.4	129.3	99.7	108.8	78.1
	palms	4.5	4.5	0.0	0.0	0.0	0.0	0.0	0.0
Total wood		**568.3**	**464.4**	**306.4**	**376.2**	**208.5**	**150.9**	**146.8**	**108.9**
Lianas									
	all	10.5	10.5	5.3	5.3	1.9	1.9	8.6	8.6
Total lianas		**10.5**	**10.5**	**5.3**	**5.3**	**1.9**	**1.9**	**8.6**	**8.6**
Litter									
	fine	12.2	12.2	9.7	9.7	13.7	13.7	21.8	21.8
	coarse	22.5	22.5	37.7	37.7	108.9	108.9	68.8	68.8
Total litter		**34.7**	**34.7**	**47.4**	**47.4**	**122.6**	**122.6**	**90.6**	**90.6**
Roots									
	roots	65.3	47.1	26.0	50.8	55.5 *	26.3	24.2	32.5
Total roots		**65.3**	**47.1**	**26.0**	**50.8**	**55.5**	**26.3**	**24.2**	**32.5**
Living phytomass **		**662.0**	**538.9**	**347.9**	**444.9**	**280.8**	**192.8**	**188.5**	**157.4**
Above ground phytomass **		**631.4**	**526.5**	**369.3**	**441.5**	**347.9**	**289.1**	**254.9**	**215.5**
TOTAL PHYTOMASS **		**696.7**	**573.6**	**395.3**	**492.3**	**403.4**	**315.4**	**279.1**	**248.0**

* s.d. 143.8 t.ha^{-1}: one plot 511.5 t.ha^{-1}, including below surface buttresses; the other 11 plots 13.9 $\pm$ 7.2 t.ha^{-1}.
** Living phytomass: leaves, wood, lianas, and roots; above ground phytomass: leaves, wood, lianas, and litter; total phytomass: leaves, wood, lianas, litter, roots.

Variation in root mass was considerable, and this is particularly striking in Akintosoela1 (see Table 6.3 and footnote there).

Table 6.4.   Root phytomass in a 10.0*10.0*0.9 m plot in Procter's Forest and the value corrected on the basis of basal area values in the plot and the surrounding forest.

Root phytomass	t.ha^{-1}	Basal area	m^2.ha^{-1}
Tree roots measured	160.5	Plot	115.0
Palm roots measured	4.2	Stand	31.6
Total roots measured	164.7		
Corrected according to basal area	45.2	Correction factor, used for tree roots only	0.27

6.2.3 Effects of logging and silvicultural treatments on the amounts of phytomass

In Procter's Forest, in 1966, selective logging of about 20 m^3.ha^{-1} was done, just as in Akintosoela1, but there, 9 years after logging, refinement was carried out. In Weyerhäuser virtually all wood was cut in 1969. Thus, the effects of disturbance, as apparent in Akintosoela1 and Weyerhäuser, can be compared with the lightly disturbed Procter's Forest and the undisturbed Phytomass Forest as controls. Furthermore, we assume that the soil at Procter's Forest is similar to that at Akintosoela1 and Weyerhäuser, due to the close proximity of these forest stands. Assessment of the phytomass took place in 1981-82, which was 6 years after refinement in Akintosoela1 and 13 years after cutting in Weyerhäuser.

It should be remembered that logging means that killed phytomass partially remains in the forest and partially is extracted from the forest. The extraction was estimated by Jonkers & Schmidt (1984) for Phytomass Forest to be 3.1 % of the living phytomass and 2.6 % of its total amount of nutrients. Refinement implies that a certain amount of phytomass is killed but that all phytomass remains in the forest.

In Akintosoela1 total phytomass was 315 t.ha^{-1} and in Weyerhäuser 248 t.ha^{-1} which is 36 % and 50 % less than at Procter's Forest, and 45 % and 57 % less than at Phytomass Forest, respectively. In Akintosoela1, tree leaf mass was 9 % more than in Procter's Forest. In Weyerhäuser, tree leaf mass was even less than 50 % of the value obtained in Procter's forest or in Phytomass Forest (Table 6.3), which means a drastic reduction of this stand's photosynthetic capacity.

Six year after refinement, the amount of living wood (standing stems and branches) in Akintosoela1 was 151 t.ha^{-1}, or 40 % of the wood mass in Procter's Forest. Since treatment six to seven years earlier, basal area grew from about 10 m^2.ha^{-1} to about 18.2 m^2.ha^{-1} (De Graaf 1986), indicating that the reduction in tree phytomass was even more than measured and indicated in Figure 6.1. Thirteen years after harvest, the wood mass in Weyerhäuser had increased from about 40 to more than 109 t.ha^{-1}, which is equivalent to 30 % of the wood mass in Procter's Forest. The wood component represents about 80 % of the total phytomass in Procter's Forest, around 50 % in Akintosoela1 and clearly less than 50 % in Weyerhäuser.

This difference is partially compensated by a higher amount of dead wood in the disturbed stands. The amount of coarse litter grew as a result of logging and refinement: living wood became dead wood. To compare the amount of dead wood lying on the

forest floor in the plots with the amount lying in the whole stands, a line sampling method as developed by De Vries (1973, 1979) was used. As the degree of decomposition of the lying stems showed a wide range, thus not allowing for a simple conversion factor from volume to dry weight, the results of the transect sampling (Table 6.5) cannot be compared directly with the data collected in the phytomass plots (see Table 6.3).

Table 6.5. Amount of lying dead wood as assessed by total harvest in 0.01 ha plots and by the line intersect method in four differently treated (see Table 5.1) forest stands.

Method			Forest stand			
			Phytomass Forest	Procter's Forest	Akintosoela1	Weyerhäuser
Plots	area	ha	0.12	0.14	0.12	0.025
Dry weight	mean*	t.ha^{-1}	14.9	36.3	99.2	64.8
	s.d.	t.ha^{-1}	16	49.8	69.5	40
Line	length	m		± 1600	± 1600	
Volume	mean	m^3.ha^{-1}	n.a.	87.6	194.9	n.a.
	variance.	m^3.ha^{-1}	n.a.	12.41	45.30	n.a.
	confidence interval 95 %	m^3.ha^{-1}	n.a.	$61.4 \leq V \leq 113.8$	$98.4 \leq W \leq 291.4$	n.a.
Dry weight**	mean	t.ha^{-1}	n.a.	35.0	78.0	n.a.
	variance		n.a.	4.96	18.12	n.a.
	confidence interval 95 %		n.a.	$24.6 \leq V \leq 45.5$	$39.4 \leq W \leq 116.6$	n.a.

* Data for coarse litter in Table 6.3 (respectively 22.5 t.ha^{-1}, 37.7 t.ha^{-1}, 108.9 t.ha^{-1}, 68.8 t.ha^{-1}) include lying and standing dead wood.

** Assuming a mean dry weight of dead wood of 0.4 t.m^{-3} (living standing wood has a dry weight of 0.65 – 0.75 t.m^{-3}).

The mass of fine litter (mainly leaves) present in Akintosoela1 and Weyerhäuser was far more than in Procter's Forest, respectively 40 % and 125 %. Refinement and heavy exploitation caused a reduction of leaf mass in the canopy (see Table 6.3) and possible caused thereafter a slightly higher litterfall in the first year (see below) and a lower litterfall in the following years. However, because more space and more light, water and nutrients became available, the remaining and newly established trees produced probably more leaves (see Akintosoela1, see also Jonkers 1987). A combination of a quicker turnover of the leaves on the tree and a slower decomposition rate may be of importance too. A different equilibrium between leaf production, leaf fall and leaf decomposition may be the result.

As expected, also the amount of coarse litter was larger in Akintosoela1 (109 t.ha^{-1}) and Weyerhäuser (69 t.ha^{-1}) than in Procter's Forest (38 t.ha^{-1}). De Graaf (pers. comm.) estimated that in Akintosoela1 a stem volume of roughly 200 m^3.ha^{-1} had been killed. In Weyerhäuser, from the 234 m^3.ha^{-1} bole volume (inventory 1964; Boerboom 1964), 194 m^3.ha^{-1} was extracted ('s Landsbosbeheer 1971). After both treatments, large amounts of debris (branches and tops) were left on the forest floor. The main part of this coarse litter was lying dead wood, not yet completely decomposed since the refinement six year earlier or the harvest 13 year earlier.

Standing dead wood, as part of the coarse litter, amounted to only 9.7, 4.0 and 1.4 t.ha^{-1} for Procter's Forest, Akintosoela1 and Weyerhäuser, respectively. These figures are probably underestimations, because harvesting standing dead trees is dangerous and plots with large dead trees were rejected for safety reasons.

Lianas formed only a small part of the total phytomass. Liana mass in Akintosoela1 was very low and not even a third of that in Procter's Forest. Cutting of lianas is part of the CSS prescriptions and was apparently successful. Opening up the canopy due to refinement did not lead to a proliferation of lianas, although it is possible that our decision to reject plots with large standing dead trees could have somewhat biased the measurements here. As expected, as a result of its treatment, phytomass of lianas in Weyerhäuser was substantial larger than in Akintosoela1 and Procter's Forest.

Root phytomass was estimated for Akintosoela1 and Weyerhäuser with the regression relation found for Procter's Forest. Thus calculated, root phytomass was 26 t.ha^{-1} in Akintosoela1 and 32 t.ha^{-1} in Weyerhäuser, which is some 40 – 50 % less than in Procter's Forest (see Table 6.3). The larger amount of roots at Weyerhäuser as compared to Akintosoela1 corresponds to the more vigorous growth at Weyerhäuser. However, it should be noted that the estimation of root mass is difficult.

The above findings can best be summarized by discussing them in terms of the effects of the different treatments on total phytomass. Refinement and regrowth in Akintosoela1 resulted seven years after treatment in only about 60 % of the total phytomass in Procter's Forest. Removing virtually all trees and regrowth in Weyerhäuser resulted 13 years after treatment in about 50 % of the assumed pre-felling phytomass (see Table 6.3 and Figures 6.1 and 6.2). These changes were accompanied by shifts in the fractions of phytomass from living to dead phytomass, resulting in increases in coarse and fine litter, the coarse litter probably being mainly remnants of the killed trees or tree parts. In Weyerhäuser, the living phytomass had increased from about 40 t.ha^{-1} (estimation based on basal area; 's Landsbosbeheer 1971) to nearly 160 t.ha^{-1} (living phytomass) amounting to an average net regrowth of 9.2 t.ha^{-1}.y^{-1}.

It is clear, that both harvest and refinement lead to a reduction of the total phytomass in the tropical rain forest. The regrowth of Weyerhäuser, however, may indicate that the restoration capacity of the tropical rain forest is strong.

6.2.4 Nutrient concentrations and nutrient amounts in undisturbed and lightly exploited forest

Average values of nutrient concentrations per compartment and the total amounts per stand are given in Table 6.6 and Figure 6.3. Concentrations of all nutrients were generally higher in Procter's Forest than in Phytomass Forest, except for calcium (wood, lianas, and roots). These exceptions might be due to differences in species composition or in the soil, though the soil factor does not necessarily seem to directly affect the concentrations in the compartments: The Mapane soils are richer in nitrogen, potassium and calcium and poorer in phosphorus and magnesium as compared to the Kabo soils (see Table 6.2). The data also seem to indicate that the forest stands Akintosoela1 and Weyerhäuser

had slightly higher nutrient concentrations than Procter's Forest (Table 6.6). Thus the disturbed forest stand Akintosoela1, and more strongly so the almost totally disturbed Weyerhäuser with its high N concentration in the leaves that is typical of the high number of pioneer species in that stand, seem to have a better ability to uptake nutrients and perhaps profit from nutrients released from the decomposing dead phytomass.

In all forest stands, leaves had the highest nutrient concentrations (see Table 6.6), except for calcium. Usually calcium concentrations in lianas were highest. Fine litter was also comparatively rich, especially in nitrogen, phosphorus and magnesium, but had lower concentrations than leaves. Wood and coarse litter showed low concentrations, as expected. Concentrations in living wood were either somewhat higher or lower than in coarse litter, suggesting that during the decomposition process of wood enrichment can occur due to invasion of decomposing organisms.

Table 6.6. Concentrations and amounts of nutrients in phytomass as calculated with regression analysis in four differently treated (see Table 5.1) forest stands.

	Phytomass Forest		Procter's Forest		Akintosoela1		Weyerhäuser	
	Conc.	Amount	Conc.	Amount	Conc.	Amount	Conc.	Amount
	g/kg	kg.ha^{-1}	g/kg	kg.ha^{-1}	g/kg	kg.ha^{-1}	g/kg	kg.ha^{-1}
Nitrogen								
Leaves	13.1	221.4	16.2	204.1	15.3	209.6	18.4	136.2
Wood	2.9	1346.8	3.8	1429.6	4.2	633.8	4.2	457.4
Lianas	6.4	67.2	7.3	38.7	12.4	23.6	8.6	74.0
Fine litter	12.2	148.8	13.3	129.0	14.2	194.5	14.5	316.1
Coarse litter	3.6	81.0	6.3	237.5	4.5	490.1	2.5	172.0
Roots	7.9	372.1	11.1	563.9	9.3	244.6	4.5	146.3
Total nitrogen		**2237.3**		**2602.8**		**1796.1**		**1301.9**
Phosphorus								
Leaves	0.8	13.5	0.9	11.3	0.9	12.3	0.9	6.7
Wood	0.2	92.9	0.3	91.9	0.5	75.5	0.3	32.7
Lianas	0.4	4.2	1.0	5.3	0.6	1.1	0.5	4.3
Fine litter	0.4	4.9	0.6	5.8	0.6	8.2	0.5	10.9
Coarse litter	0.2	4.5	0.5	18.9	0.3	32.7	0.1	6.9
Roots	0.5	23.6	0.5	25.4	0.4	10.5	0.3	9.8
Total phosphorus		**143.5**		**158.6**		**140.3**		**71.2**
Potassium								
Leaves	9.5	160.6	10.8	136.1	11.6	158.9	11.8	87.3
Wood	2.5	1161.0	2.6	978.1	3.6	543.2	4.1	446.5
Lianas	4.8	50.4	4.8	25.4	6.6	12.5	7.1	61.1
Fine litter	2.5	30.5	2.9	28.1	4.1	56.2	3.0	65.4
Coarse litter	0.6	13.5	1.3	49.0	1.5	163.4	1.1	75.7

Table 6.6. (continued)

	Phytomass Forest		Procter's Forest		Akintosoela1		Weyerhäuser	
	Conc.	Amount	Conc.	Amount	Conc.	Amount	Conc.	Amount
	g/kg	kg.ha⁻¹	g/kg	kg.ha⁻¹	g/kg	kg.ha⁻¹	g/kg	kg.ha⁻¹
Roots	3.5	164.9	4.5	228.6	5.5	144.7	1.4	45.5
Total potassium		**1580.8**		**1445.4**		**1078.9**		**781.5**
Calcium								
Leaves	5.2	87.9	6.3	79.4	8.8	120.6	10.8	79.9
Wood	7.5	3483.0	4.0	1504.8	5.6	845.0	5.0	544.5
Lianas	10.5	110.3	5.3	28.1	13.1	24.9	12.7	109.2
Fine litter	9.1	111.0	6.7	65.0	8.4	115.1	9.9	215.8
Coarse litter	4.4	99.0	4.8	181.0	4.4	479.2	4.4	302.7
Roots	4.1	193.1	1.9	96.5	2.8	73.6	4.4	143.0
Total calcium		**4084.3**		**1954.7**		**1658.4**		**1395.2**
Magnesium								
Leaves	1.6	27.0	2.0	25.2	1.8	24.7	3.5	25.9
Wood	0.5	232.2	0.5	188.1	0.6	90.5	1.0	108.9
Lianas	1.0	10.5	2.1	11.1	1.9	3.6	1.4	12.0
Fine litter	1.4	17.1	1.6	15.5	1.4	19.2	2.0	43.6
Coarse litter	0.5	11.3	0.6	65.3	0.4	43.6	0.5	34.4
Roots	0.7	33.0	1.6	81.3	0.6	15.8	1.2	39.0
Total magnesium		**331.0**		**386.6**		**197.3**		**263.8**

The amounts of nutrients stored in the total plant biomass in Phytomass Forest and in Procter's Forest were of the same order of magnitude. Procter's Forest had about 20 % more N, 10 % more P, 10 % less K and 15 % more Mg. Exception here was again Ca of which, due to a much lower concentration, the total amount stored in Procter's Forest is less than half the amount in Phytomass Forest. The soil in Procter's Forest contained more calcium than the Phytomass Forest soil (Table 6.2). The amounts of nutrients stored in the disturbed forest stands Akintosoela1 and Weyerhäuser were considerably less than those in the non- or little disturbed stands: the amounts of N, P and K all up to 45 - 55 % less, though the decreases in Akintosoela1 were not as drastic as in Weyerhäuser. Amounts of Ca and Mg in the phytomass were also clearly less in Akintosoela1 and Weyerhäuser, but the pattern was not as clear as for N, P and K.

The distribution of various nutrient amounts over the compartments in all four forest stands reflected the differences in phytomass and in nutrient concentrations. These differences were especially clear for Mg and P. The amounts of nutrients stored in leaves were comparable in Phytomass Forest, Procter's Forest and Akintosoela1, but about 30 % lower in Weyerhäuser. In all forests, wood was the most important store for all nutrients, even though it had generally the lowest concentrations. Roots or litter formed the second most important pool. As expected, in the two more strongly disturbed stands

litter was a proportionally much more important pool of stored nutrients than in the other two stands. This is important, because higher percentages of the nutrients stored in the litter layer are likely to enhance leaching.
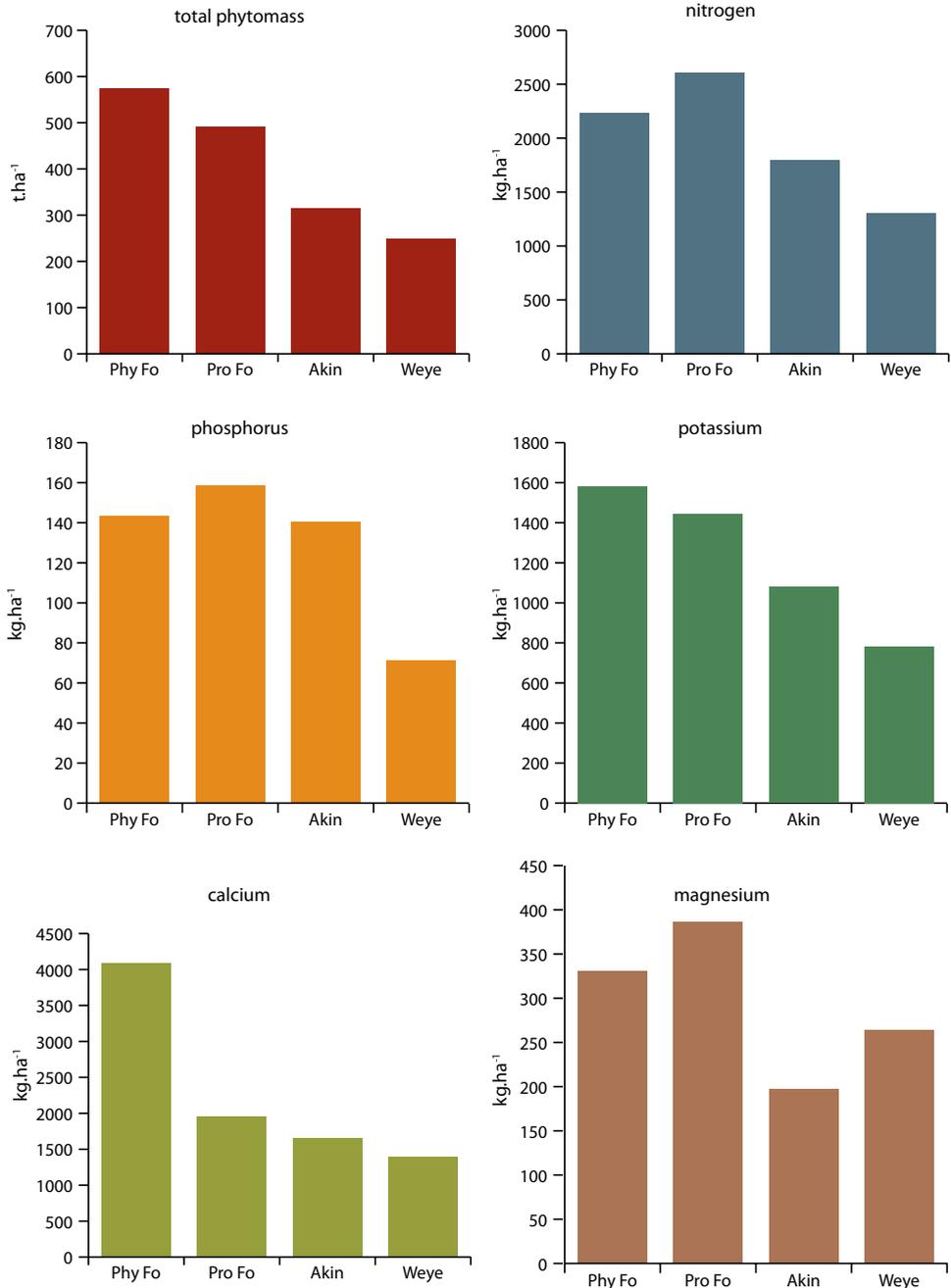

Figure 6.2. Total phytomass and total amounts of N, P, K, Ca and Mg in four differently treated (see Table 5.1) forest stands. Abbreviations see Figure 6.1.
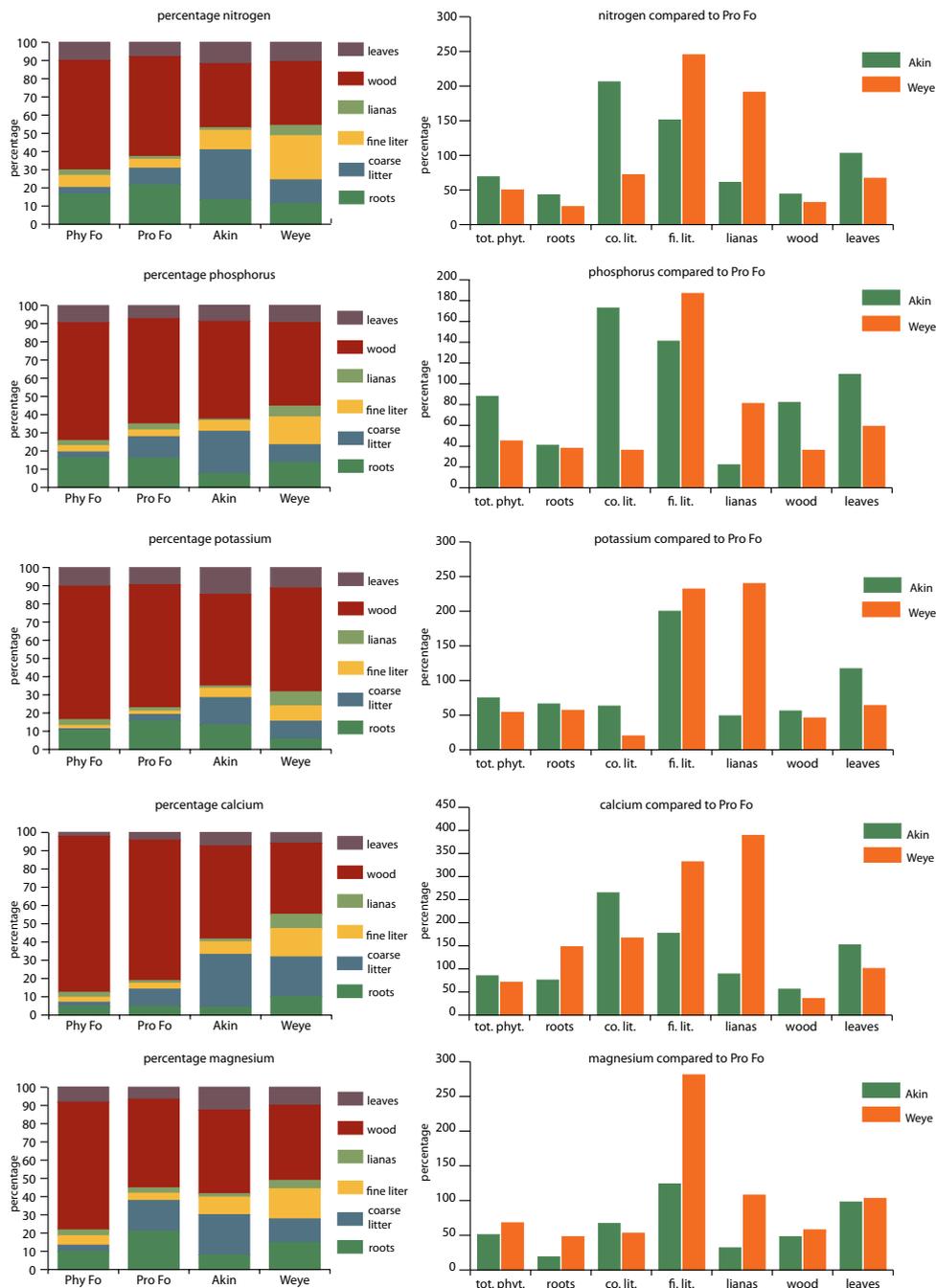
Figure 6.3. Left: Distribution of nutrient amounts stored in relevant compartments as percentage of total phytomass, calculated with regression analysis, in four differently treated (see Table 5.1) forest stands. Right: Amounts of a nutrient in given compartments in Akintosoela1 (Akin) and Weyerhäuser (Weye) as percentage of the same compartment in Procter's Forest. tot. phyt. = total phytomass; co. lit. = coarse litter; fi. lit. = fine litter.

Coarse litter in Akintosoela1 contained 50 % more Ca, 100 % more N and 50 % more P than in Procter's Forest (see Figure 6.3). Coarse litter in Weyerhäuser contained 150 % more Ca, but the same amount of N and P as in Procter's Forest. This could be the result of a higher load of micro-organisms absorbing N and P.

Lianas play a minor role in nutrient capture and storage in these forest stands though their role at Weyerhäuser might be somewhat more important, due to their abundance in that stand.
In general, roots, representing about 10 % of the total phytomass, often contained more than 10 % of the nutrients in the phytomass.

After disturbance the large amount of dead plant material left to decompose most likely made more nutrients available. This, together with the much increased light availability in the remaining vegetation at Weyerhäuser, allowed the abundance and fast growth of the pioneers there, with their typical high concentration of nitrogen and fast leaf turn-over. However, some nutrients, particularly nitrogen and potassium, which are easily leached from the soil, but also magnesium, might become limiting for plant growth. But the concentration data measured by us do not yet clearly indicate such a limiting availability. Unfortunately, however, no soil data of these stands before and after treatment are available.

6.3   Above ground production

6.3.1 Introduction

Primary productivity (the rate of plant biomass production over time) is the main driving force within any ecosystem and forms the basis of estimating the commercial (timber) harvest. This holds also for the humid tropical forests of Suriname as well as for forests managed with the CMS. Nevertheless, this was not fully assessed during the development of the CMS or afterwards. Stem production was mainly assessed as timber production or growth of commercial trees (see Chapter 4). Litterfall, being an indicator of the production of leaves and flower/fruits, and thus a key factor in nutrient cycling, was examined in detail. It is the main flux from the above- to the below-ground nutrient pools. In addition, the production of palms was studied, though in less detail.

Interventions may result in changes in litter production and thus may affect the nutrient cycling in the system.

6.3.2 Stem production

The measurement of dbh over longer periods of time allows calculation of changes in stem diameter which can be translated into changes in standing phytomass, using correlations between dry weights of tree parts and stem diameter. Our measurements allowed an assessment of stem production.

Photo 6.1.   Measuring fresh weight stem wood, Mapane, 1982. (Photo P. Schmidt)

In the MAIN experiment (Kabo), based on inventories of three one ha plots per treatment in 1983 and in 2000, wood, branches and leave phytomass can be estimated, including changes therein over time. The inventories contained over 600 trees with dbh >5 cm. Based on these inventories an average net increase in phytomass of 7.8 t.ha^{-1}.y^{-1} was found for untouched forest (MAIN 41, 42, 43), of which 5.2 t stems, 2.5 t branches and 0.1 t leaves (data Jonkers et al., 2005). For harvested and refined forest (MAIN 18, 21, 33) a net average increase of phytomass of 5.0 t.ha^{-1}.y^{-1} was found, of which 3.2 t stems, 1.5 t branches and 0.3 t leaves.

For Mapane, De Graaf (1986) estimated bole volume increments of commercial species after different treatments. In a lightly exploited, non-refined forest experiment at Mapanebrug (comparable to Procter's Forest) this amounted to an average 1.2 m^3.ha^{-1} annually over the period 1974-1980. For the whole stand of Akintosoela1 (lightly harvested and 'heavily' refined), a bole volume increment over six years (1976-1982) of 11.6 m^3.ha^{-1} or on average 1.9 m^3.ha^{-1}.y^{-1} for commercial species of form class I only was found. Assuming an average specific gravity of 0.72 g.cm^{-3} (calculated on the basis of data from Vink 1977), wood production of commercial species in Akintosoela1 was 7.92 t.ha^{-1} or 1.32 t.ha^{-1}.y^{-1}. For commercial species of form class III, it amounted to 1.1 t.ha^{-1}.y^{-1} (see De Graaf 1986), resulting in a total growth of about 2.4 t.ha^{-1}.y^{-1}. In Weyerhäuser, 13 years after clear cutting, 8.0 t.ha^{-1} leaves, 8.6 t.ha^{-1} lianas and 119 t.ha^{-1} wood were present. This implies a wood growth of 119 – 40 = 79 t.ha^{-1} over 13 years, i.e. an average gross annual regrowth of about 6 t.ha^{-1}.y^{-1}.

6.3.3 Litterfall

Total litterfall in Phytomass Forest and in Procter's Forest amounted to 11.7 and 11.3 t.ha^{-1}.y^{-1}, respectively (see Figure 6.4), or 2.5 and 3.0 % of the total living phytomass. The total litter consisted mainly of leaves, complemented by twigs, flowers and fruits (see Figure 6.5) and contained about 300 and 400 kg.ha^{-1} of nutrients (N, P, K, Ca, Mg).
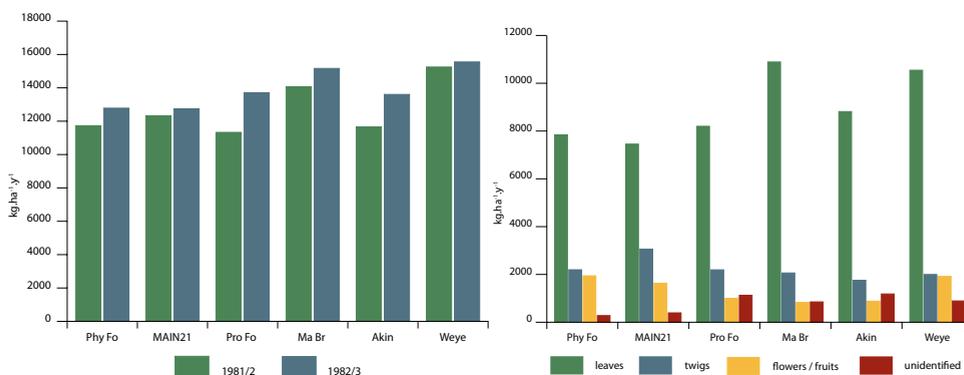

Figure 6.4. Total litterfall in two consecutive years (left) and mean litterfall over two years (right) in six differently treated (see Table 5.1) forest stands. Abbreviations see Figure 6.1.
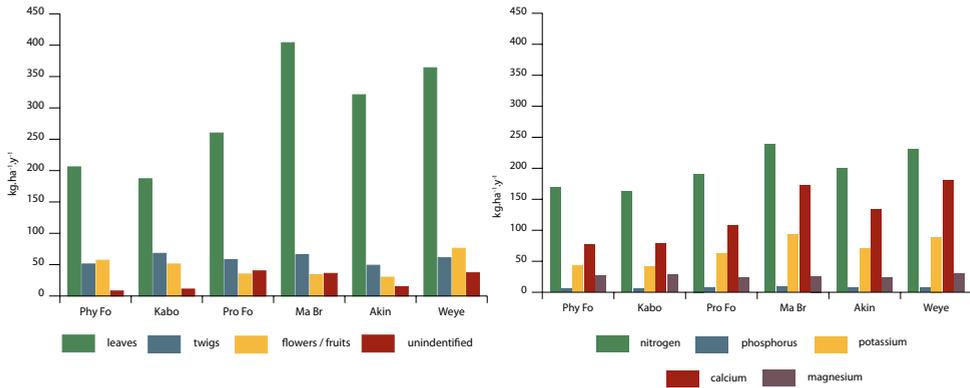
Figure 6.5. Total mineral (N+P+K+Ca+Mg) fall per tree compartment (left) and per element (right) in six differently treated (see Table 5.1) forest stands. Abbreviations see Figure 6.1.

The amount of fine litter on the forest floor in the various stands varied from 9.7 t.ha^{-1} in Procter's Forest, 12.2 t.ha^{-1} in the Phytomass Forest, 13.7 t.ha^{-1} in Akintosoela1 to 21.8 t.ha^{-1} in Weyerhäuser (see Table 6.3). This resulted in turn-over times (amount of litter falling in a year as compared to the amount lying on the forest floor) of 0.8, 1.0, 1.1 and 1.4 years, respectively. This may be an indication for rapid decomposition, which might lead to increased leaching. However, the large mass of fine roots in the top soil and the good growing conditions guarantee a rapid uptake of released nutrients, thus diminishing the danger of leaching.

Interventions in the Kabo region apparently did not influence total litterfall (compare Kabo exploited in 1978 and refined in March 1982 to Phytomass Forest, see Table 6.6 and 6.7). One has to realize that, depending on the species, poisoning of trees results in dying back of these trees over a period of about two years and that the fall of leaves from dying trees is spread over that period of time. In the long run, interventions also seem slightly to enhance litterfall (compare Mapanebrug and Akintosoela1 to Procter's Forest). In the young forest stand Weyerhäuser, litterfall is considerable, but this stand contains an abundance of pioneers which characteristically have a rapid leaf turn-over. As the standing phytomass is less in the treated forest stands (compare Procter's Forest with Akintosoela1 and Weyerhäuser, see Table 6.3), while litterfall and the amount of litter on the forest floor are larger, a higher percentage of the total phytomass and thus the nutrients is involved in the mobile stage of the nutrient cycle. This might enhance the possibilities for leaching of nutrients. On the other hand, it may be possible that the rate of nutrient uptake in this vigorously growing vegetation of the treated stands is faster and more efficient.

Litterfall was unevenly distributed over the year (see Figure 6.6 and 6.7). In the Kabo area (Figure 6.6), litterfall was highest at the beginning of the dry season (Phytomass Forest 1981, 1982; Kabo 1981). This was confirmed by Jonkers (1987), who reported the shedding of old and the flush of new leaves in this period. In Kabo, between February and April 1982, a refinement was carried out, resulting in a slightly higher litterfall in the rest of that year. In 1983, one year after the refinement, leaf fall was less. This was due to the fact that no new leaves were produced by the poisoned trees. It indicated a less

dense canopy, but leaves were still falling during the whole year. This means that over the whole year a canopy is present. As expected, one year after treatment, the amount of twigs, falling from the dead trees, increased. The fall of flowers and fruits seemed to be enhanced, thus confirming the phenological observations by Jonkers (1987). Flowering apparently increased, possibly due to more sunlight reaching the remaining trees.
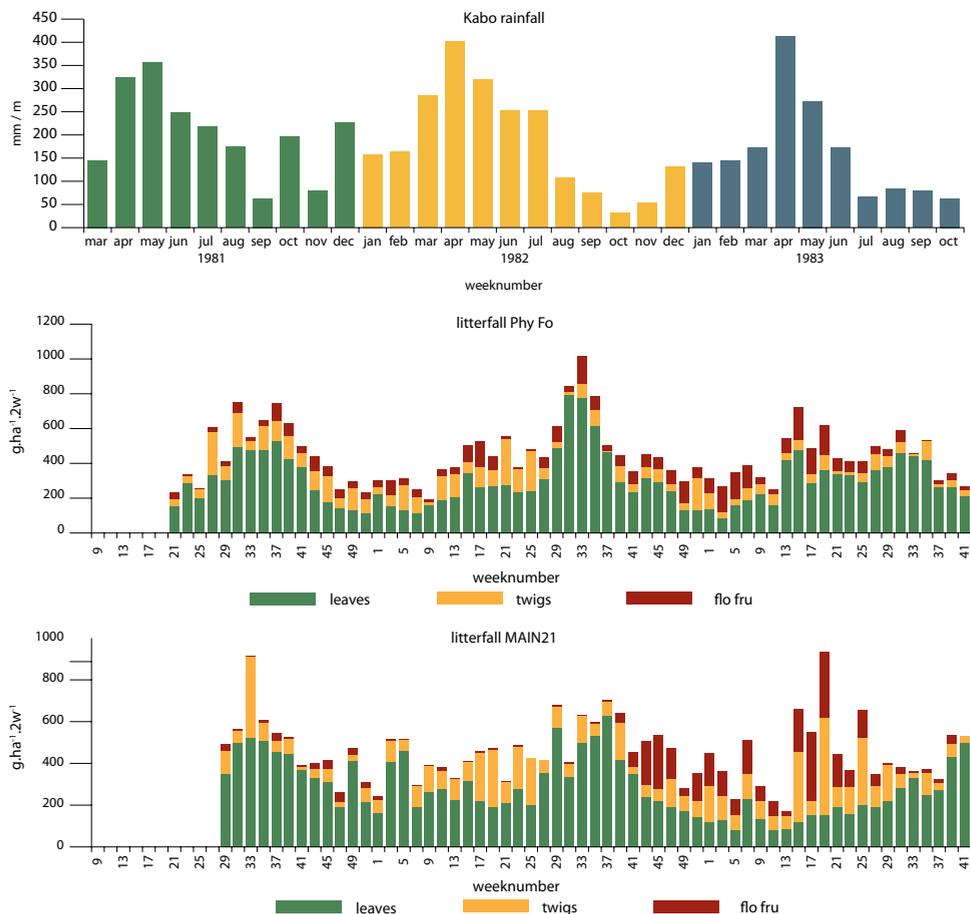

Figure 6.6. Rainfall (in mm per month) and litterfall (leaves, twigs and flowers & fruits) (in gram per hectare per two weeks) in two differently treated (see Table 5.1) forest stands in the Kabo region between March 1981 and October 1983. In MAIN21 a refinement was carried out between February and April 1982. No column in the graph means no data available. Abbreviations see Figure 6.1.

Litterfall in the Mapane region (Figure 6.7) confirmed the observation that litterfall is a bit higher during the dryer periods (Procter's Forest 1981, 1982, 1983; Mapanebrug 1982; Akintosoela1 1982 and Weyerhäuser 1982). The annual rhythm seems to be less smooth in Mapanebrug, Akintosoela1 and Weyerhäuser than in Procter's Forest, which may be due to the higher number of pioneer trees with large leaves, such as *Cecropia* and *Pourouma*. Apart from this observation, no effects of refinements (that had occurred seven years or more before litterfall assessment) and of harvest were observed, indicating a recovery of leaf production to a normal level. Note however the enormous litterfall in

weeks 47 and 49 in 1981 in Mapanebrug, Akintosoela1 and Weyerhäuser, which may have been a result of heavy rain and wind in this period. Unfortunately no complete rainfall and wind data are available for this period. For unknown reasons Procter's Forest did not show this pattern.
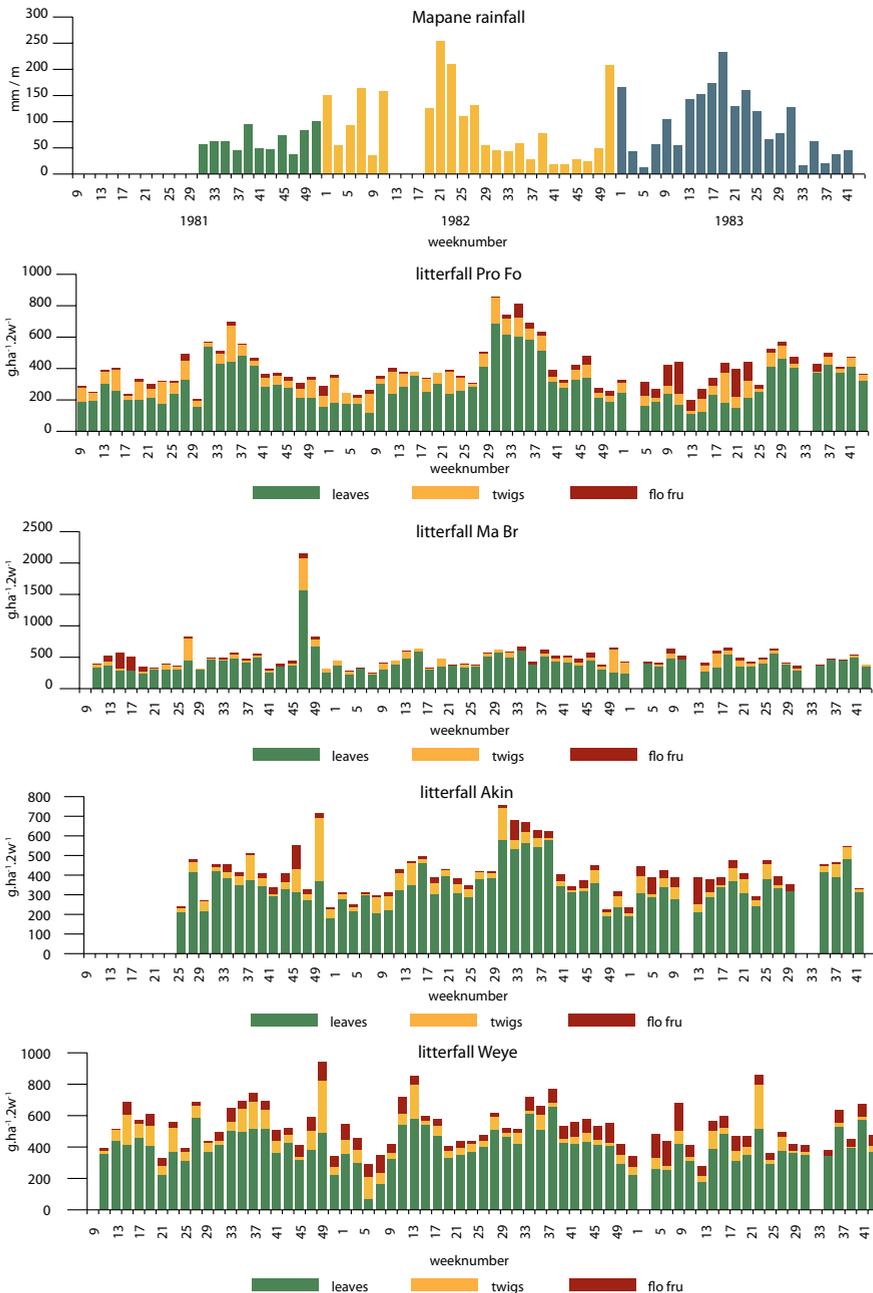

Figure 6.7.   Rainfall in mm per two weeks and litterfall (leaves, twigs and flowers & fruits) (in gram per hectare per two weeks) in four differently treated (see Table 5.1) forest stands in the Mapane region between March 1981 and October 1983. No column in the graph means no data available. Abbreviations see Figure 6.1.

If we take the litterfall figures as a proxy of the net production of leaves, highest production took place in Weyerhäuser (15.4 t.ha^{-1}.y^{-1}) and Mapanebrug (14.6 t.ha^{-1}.y^{-1}). The net primary production in Akintosoela1 (12.6 t.ha^{-1}.y^{-1}), Procter's Forest (12.5 t.ha^{-1}.y^{-1}) and Phytomass Forest (12.3 t.ha^{-1}.y^{-1}) was somewhat less. In MAIN, at Kabo, over a 17 years period, there was a net increase in leaf mass of 290 kg.ha^{-1} annually (calculation based on data from Jonkers et al. 2005). This implies that net leaf production was slightly higher than total leaf fall. It can be assumed that this was also the case in Mapanebrug, Akintosoela1 and Weyerhäuser, as there the vegetation was still growing towards a mature state. There is a larger increase in total biomass in Akintosoela1 and Weyerhäuser, because interferences in the stands were far greater than in MAIN and hence the development was more strongly thrown back.

From the above it can be concluded that in the Kabo region each year on average 12.2-12.5 t.ha^{-1} litter contributes to the mineral cycling. In the Mapane region this is 12.5 t.ha^{-1} for Procter's Forest, 14.6 t.ha^{-1} in Mapanebrug, 12.6 t.ha^{-1} in Akintosoela1 and 15.4 t.ha^{-1} in Weyerhäuser. The litter of all the Mapane stands had higher nutrient concentrations than in the Kabo sites. Given the turn-over rates given above, these nutrients become available within 0.8-1.4 years.

Summarizing, it has been shown that harvest and refinement do affect litterfall and its rhythm somewhat, causing a small reduction during the first year after the intervention, but that litterfall is restored to its original level within a couple of years. The same holds for mineral fall.

6.3.4 Palms

Palm growth formed a small part of the total primary production of our forest stands. They contributed substantially to the litterfall and were probably influenced by the treatments. Palm litter was not included in our litterfall studies but was measured separately. Over a period of one year, from January 1982 till January 1983 at Kabo and November 1981 till November 1982 at Mapane, growth, mortality and weight of palm leaves were studied. Figures 6.8 and 6.9 give the growth and mortality values of leaves of some palm species in five forest stands. In Mapane, the total palm leaf mass varied from a minimum of 0.3 t.ha^{-1} in Procter's Forest, 0.8 in Akintosoela1 and 1.0 in Mapanebrug, to a maximum of 1.2 t.ha^{-1} in Weyerhäuser. From Procter's Forest, Schmidt (1981a, b) reported only 1.5 t.ha^{-1} of total palm phytomass, mainly leaves. The production of leaves varied from 0.04 t.ha^{-1}.y^{-1} (Procter's Forest), to 0.14 in Akintosoela1, 0.17 in Mapanebrug, and 0.2 t.ha^{-1}.y^{-1} (Weyerhäuser) (Van der Steege 1983b).

Ohler (1980) estimated that leaf mass for all palms in Phytomass Forest (Kabo region) amounted to 8.0 t.ha^{-1} with a total palm mass of 12.5 t.ha^{-1}. Schmidt (1981a, b), using correlations between height and total weight for a number of palm species (see Table 6.7), calculated that the amount of palm leaves in the 0-10 m layer in Phytomass Forest was 7.8 t.ha^{-1}. However, Van der Steege (1983b) reported a total leaf mass of only 1.8 t.ha^{-1} (based on one small plot of 0.25 ha and extrapolation). These findings indicate the large variability in palm density in Kabo. In Kabo, the density of palms was much higher than in Mapane, where palms were less dominant.

Palm species studied

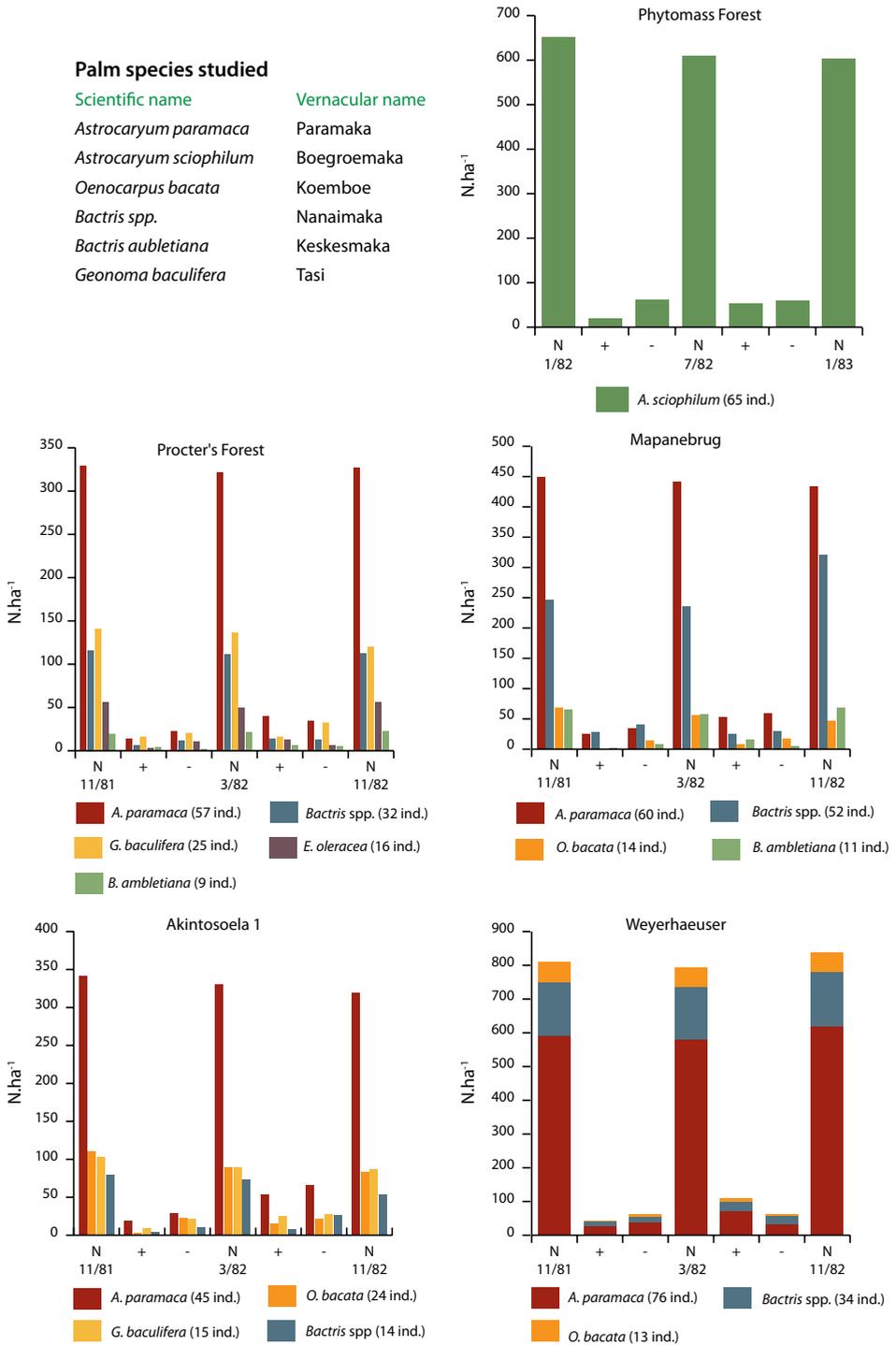| Scientific name	Vernacular name
Astrocaryum paramaca	Paramaka
Astrocaryum sciophilum	Boegroemaka
Oenocarpus bacata	Koemboe
Bactris spp.	Nanaimaka
Bactris aubletiana	Keskesmaka
Geonoma baculifera	Tasi

Figure 6.8. Number of leaves, leaf growth and leaf fall of palms in two six month periods in five differently treated (see Table 5.1) forest stands. Source: Van der Steege (1983b).

Table 6.7. Coefficients of correlation in linear correlations between height (H, in m) and phytomass (W, in kg dry weight) for palm species. Log W = a + b log H.

Region Kabo

W leaf/H	N	a	B	r²
Astrocaryum sciophilum	93	0.7595	2.4290	0.9147
Other palm species	12	-1.1645	2.6343	0.8776
All palms	105	-0.7860	2.4152	0.9003
W total/H				
Astrocaryum sciophilum	93	-0.7888	2.6572	0.9172
Other palms	12	-1.2410	2.8164	0.9235
All palms	105	-0.8195	2.6347	0.9021

Region Mapane

W leaf/H	N	a	B	r²
Astrocaryum paramaca	35	-0.4346	1.5303	0.3957
Other palm species	19	-1.2461	1.7465	0.5993
All palms	54	-1.4754	3.0209	0.7399
W tot/H				
Astrocaryum paramaca	35	-0.4346	1.5303	0.3957
Other palm species	19	-1.1545	2.3059	0.7250
All palms	54	-1.1206	2.5173	0.7517

The leaf production of individual palms was just one leaf per year. This is true for each stand and each species. The average lifespan of a palm leaf ranged from 2.2 year for *Bactis aubletiana* in Procter's Forest to 8.5 year for *Astrocaryum sciophilum* in Kabo. There was variation in lifespan per species over the different forest stands. For example, in Akintosoela1, *Astrocaryum paramaca* leaves had a lifespan of 4.4 years, while in Weyerhäuser this was 6.2 years.
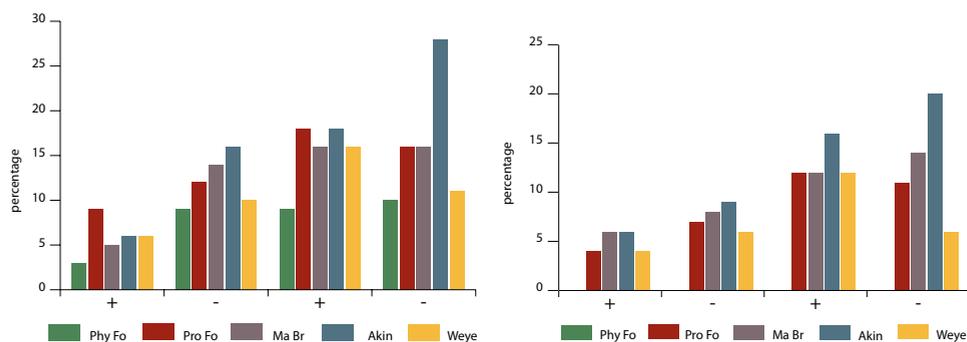

Figure 6.9.   Palm leaf growth and fall for all palms and for *Astrocaryum paramaca* palms in two consecutive six months periods as percentage of the numbers of leaves at the beginning of each period in five differently treated (see Table 5.1) forest stands. Abbreviations see Figure 6.1. The Phytomass Forest was assessed from January 1982 to January 1983; the others from November 1981 till November 1982.

These data do not point to clear conclusions about the impact of the CMS treatments on palms. In order to reduce competition between palms and regeneration, it may be advisable to diminish palm density during refinement.

6.3.5 Total primary production

Table 6.8 gives a summary of the measured, calculated and estimated primary production values in six differently treated forest stands. Unfortunately the production values are incomplete and not always comparable. Different methods were used to obtain the values and they are not available for all the stands.

Table 6.8. Summary of measured, calculated or estimated primary production values in phytomass (dry weight in t.ha^{-1}.y^{-1}) or as carbon (between brackets, t.ha^{-1}.y^{-1}) in six differently treated (see Table 5.1) forest stands. N.a. means no data available.

	Phytomass Forest	MAIN 41, 42, 43	MAIN 18, 21, 33	Procter's Forest	Mapane Brug	Akintosoela1	Weyerhäuser
	Untouched	Untouched	Lightly expl. & ref.	Lightly expl.	Lightly expl. & refined	Lightly expl. & heavily ref.	Nearly clear cut
	t.ha^{-1}.y^{-1}	t.ha^{-1}.y^{-1}	t.ha^{-1}.y^{-1}	t.ha^{-1}.y^{-1}	t.ha^{-1}.y^{-1}	t.ha^{-1}.y^{-1}	t.ha^{-1}.y^{-1}
Total litterfall[1]	12.3	12.5	12.5	12.5	14.6	12.6	15.4
Palm leaves[2]	0.2	n.a.	n.a.	0.05	0.17	0.14	0.2
Wood	n.a.	(2.4)[7] 5.2[3]	(1.5)[7] 3.2[3]	n.a.	n.a.	(1.2) 2.5[4]	(2.9) 6,1[6]
Branches	n.a.	(1.3) 2.5[3]	(0.7) 1.5[3]	n.a.	n.a.	(0.3) 0.7[5]	(1.4) 2.9[5]
Leaves	n.a.	(0.03) 0.1[3]	(0.1) 0.3[3]	n.a.	n.a.	(0.1) 0.3	(0.2) 0.4
Total	**n.a.**	**20.3**	**17.5**	**n.a.**	**n.a.**	**16.2**	**25.0**

1. Measured in litter traps.
2. Measured on individual palms.
3. Based on data from Jonkers et al. (2005).
4. Calculated from an annual bole volume growth of 1.9 m^3.ha^{-1}.y^{-1} (De Graaf 1986) with an average specific gravity of 0.72 g.cm^{-3} (Vink 1977).
5. Based on the assumption that the branch production equals 48 % of wood production as in MAIN21
6. Calculated from standing total stem weight after 13 year minus the same at the start.
7. Average carbon content factors used: leaves 41.5 %; wood 47 %. Source Ajtay et al. (1979).

The production value in undisturbed Kabo (MAIN 41, 42, 43) of 20.3 t.ha^{-1}.y^{-1} is of the same order of magnitude as found in literature (average 23 t.ha^{-1}.y^{-1}, Ajtay et al. 1979). However, the total amount of phytomass calculated by Jonkers et al. (2005) is, with 550 t.ha^{-1}, higher than found through destructive methods and corrected using correlation factors (see Table 6.3).

Litterfall in all stands is of the same order of magnitude, with highest value for Weyerhäuser (15.4 t.ha^{-1}.y^{-1}) with its many rapidly growing pioneer trees.

Lower values for litterfall were reported from other tropical forests in the same geographical region: 5.47 t.ha^{-1}.y^{-1} in lower montane rainforest in Puerto Rico, 5.87 t.ha^{-1}.y^{-1} in forest on Oxisols in Venezuela, and 11.3 t.ha^{-1}.y^{-1} in moist forest in Panama (Jordan 1989). Such lower values are as expected for the montane forest and the forest on Oxisols, as in those forests trees typically grow leaves with a lower specific leave area and a greater longevity, resulting in a slower turn-over rate.

The total primary production (25 t.ha^{-1}.y^{-1} of which 9 is wood production, see Table 6.8) in Weyerhäuser is relatively high compared to the average value found for all tropical rainforest. This high production can be attributed to the vigorous growth of the vegetation after the severe interference and rapid decomposition of leaves. Values of 4.9 t.ha^{-1}.y^{-1} for wood production were found in Venezuela and Puerto Rico (Jordan 1989).

The data suggest that the undisturbed forest of Kabo is not in a steady state but still increasing in phytomass. The treated forests of Akintosoela1 and Weyerhäuser are also increasing in phytomass. They have not yet reached the amount of phytomass as previous to the treatments.

Jonkers et al. (2005) found that twenty-two years after logging the phytomass of commercial species was often larger than before felling, but the total phytomass had generally not yet recovered fully. His results suggest that refinement had a positive impact on the phytomass growth of species that were considered commercial at the start of the experiment, while the phytomass growth of other species after refinement was similar to the increment in untreated forest. The results were highly variable, however, and large differences between treatments could not always be explained as resulting from the treatments applied. They also found that the phytomass in the three undisturbed plots in Kabo varied.

Net phytomass increase in individual plots varied from a mere 0.4 t.ha^{-1}.y^{-1} to 6.4 t.ha^{-1}.y^{-1}, under different logging and refinement regimes.

The data of Jonkers et al. (2005) also suggested a negative correlation between pre-felling phytomass and phytomass increment. In Chapter 4, it was already shown that natural variation in mortality had a considerable impact on the variation in volume increment. This effect of mortality is also reflected in the changes in phytomass: the high mortality in replication 2 and in plots with the intermediate logging intensity E23 led to considerably less phytomass increment than elsewhere. In other plots, the phytomass in 2000 generally exceeded pre-felling values. Given the fact that by far most nutrients in these forest ecosystems is contained in the living and dead phytomass this increment in phytomass indicates that logging and silvicultural treatment do not result in losses of nutrients.

The impact of logging and refinement on carbon sequestration will be discussed in Section 6.6.

Poels (1987, see also below) in his simulation model also found that the undisturbed forest ecosystem in Kabo, and to a lesser extent the treated forest, is accumulating nutrients. There is no equilibrium at present; the forest is still growing towards its mature stage. This accumulation takes place in the phytomass as well as in the soil.

6.4   Decomposition of leaves and wood

Decomposition is one of the main processes in the cycling of minerals in tropical rainforest ecosystems. Decomposition rates depend on the type of plant material, biological activity in the soil and on environmental factors such as microclimate and soil moisture. Logging and refinement may affect these characteristics.

Decomposition rates of leaves differed from species to species (see Figure 6.10). After 28 weeks (June-December 1982), 68 % of *Tetragastris* leaves had decomposed and 62 % of the leaves of *Inga* (see Van der Steege 1983a). Lowest rates were found in a heavily exploited stand, which was subsequently planted with *Pinus caribaea*, with 44 % loss of weight for *Tetragastris* and 50 % for *Inga*. In the other two stands (refined 14 and 8 years before) decomposition values were higher than in this *Pinus* stand, but lower than in Procter's Forest. Highest rates were found in the most pristine forest stand, Procter's Forest. Fastest loss of weight took place in the first weeks, mainly because of nutrient leaching. In a second observation period (from October 1982 to March 1983), lower decomposition rates were found.
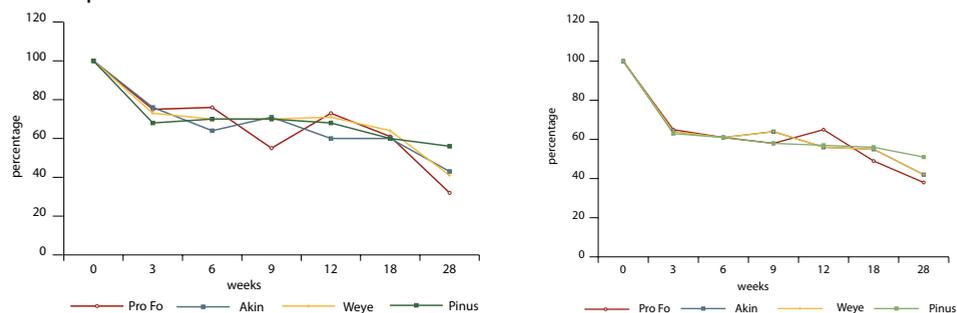

Figure 6.10.   Decomposition rate expressed as percentage remaining dry weight of leaves of *Tetragastris altissima* (left) and *Inga edulis* (right) in four differently treated (see Table 5.1) forest stands. Abbreviations see Figure 6.1; Pinus: *Pinus caribaea* stand, 13 years after clear cut. (Source Van der Steege 1983a).

Mixed natural litter showed lower decomposition rates than freshly cut leaves of single species. After 28 weeks only about 50 % of the mixed litter was decomposed in contrast to the freshly cut and air dried leaves of *Tetragastris* (68 %) and *Inga* (62 %; see above). Freshly cut leaves are richer in nutrients than fallen leaves. Mineral contents are known to decrease with aging of the leaves (Grubb & Edwards 1982; Mason 1976), resulting in lower decomposition rates.

In both observation periods there was a positive correlation between decomposition rate and rainfall. Within one month, small roots and hyphae had penetrated the litter bags. The rate of fungal invasion was positively correlated with the amount of rainfall. Concentrations of minerals in litter seemed to fluctuate during the decomposition

process. At the start they diminished, but later nitrogen and phosphorus increased slightly. This was probably caused by the uptake of these minerals by micro-organisms, which contributed to the decomposition process.

Wood decomposition was much slower than leaf decomposition. After 36 weeks, loss in weight was only 33 % and 21 % for wood of Tetragastris and Inga, respectively.

Only a slight influence of treatments, in the form of slowing down of the decomposition process, could be detected seven years or longer after refinement. This indicates that the danger of leaching is not high.

6.5   Water and nutrient cycles

As part of the CSS research, studies were carried out on the impact of interferences on the total water and nutrient cycles for a whole forest at Kabo. These cycles were studied at the scale of the soil profile and at the scale of entire watersheds. At the level of the soil profile, the following fluxes can be distinguished: aerial input from rain and dust, input from decomposing organic matter and from weathering of minerals. Output takes place in deep drainage, in surface run-off of water and in erosion of soil and litter material.

At the scale of a watershed the same fluxes can be distinguished, although the output is generally combined. The output was measured at the downstream end of the watershed where the creek removes water of both deep drainage and surface drainage from the area, as well as sediment and organic matter resulting from erosion (for details, see Poels 1987).

6.5.1 Water cycle

The hydrology of a small catchment area of 295 ha was studied. In this catchment, two small tributaries of the Ingipipa Creek of similar size, the Eastern Creek and the Western Creek, are present. A dam with a measuring weir was built a short distance from the confluence of both tributaries.

Photo 6.2.   Weir to measure water flow, Kabo, 1982.
(Photo K.E. Neering)

Data were collected on rainfall, evaporation, discharge, topography, soil, substratum and groundwater. The water balance during a period of four years and nine months was simulated using an adapted version of the computer model WOFOST4 (Van Keulen & Wolf 1986) with inputs of measured weather and soil data.

The hydrological year started on November 1 and lasted till October 31 of the next year. Reason for this is that around November 1, the discharge in the creek was lowest and often zero. As a consequence, the discharge in a given twelve-months period (hydrological

year) is the result of the rainfall in the same twelve-months period, facilitating the construction of a water balance.

Computer simulation using the input of these measured data was used to make estimates of other components of the water balance that are difficult to measure. Input to the programme was, next to rainfall and discharge, pan evaporation (Epan), which represents the drying power of the atmosphere for each day. By varying the Pan factor, the ratio between the real water use of the forest and the pan evaporation, it was tried to simulate a discharge corresponding with the measured discharge. The water use of the forest was then divided in transpiration and interception by analysing simulated total water amounts in the system at the beginning and the end of each rainy season, when discharges reached a certain low level (Poels 1987). If the simulated amount of water in the system after a rainy season was lower than before that season, interception was set at a too high level, and vice versa. The calculations were repeated with a new value for interception. After several iterations, a balance was found whereby the extra water use by interception was found. This interception loss is defined as the additional water use on rain days compared with the transpiration that would have occurred under the same climatic conditions but with dry days. The following results were obtained (see Table 6.9):

Table 6.9. Water balance totals (mm) per hydrological year at the end of each hydrological year.

Hydrological year	1	2	3	4	5	Annual mean
	1979/80	1980/81	1981/82	1982/83	1983/84	
Measured						
Rainfal	1967	2467	2348	1791	1703	2143
evaporation (EPan)	1461	1551	1478	1528	1143	1504
Discharge	296	600	865	294	177	514
Rainfall-discharge	1671	1867	1483	1497	1526	1629
Simulated						
PET**	1659	1732	1673	1713	1292	1694
Interception	218	239	245	232	177	233
effective rainfall	1750	2228	2104	1559	1526	1910
Transpiration	1423	1478	1441	1269	919	1403
Discharge	345	586	855	319	201	526
interception+transpiration	1641	1717	1686	1501	1096	1636
changes in storage	-19	164	-193	-29	406	-19
transpiration/PET	0.86	0.85	0.86	0.74	0.71	0.83
(interception+transpiration)/PET	1.00	0.99	1.01	0.88	0.85	0.97
Measured – simulated						
discharge	-49	14	10	-25	-24	-12. 5

Average rainfall and discharge were respectively 2,143 mm and 514 mm per year, resulting in a water use by the vegetation (transpiration and interception) of 1,629 mm per year on average. Length and intensity of the dry season (the period with less than

100 mm rain per month) varied between two and five months per year. The length of the dry period with no or very little discharge varied between zero and eight months per year.

There are large differences between the years, especially in discharge. This is caused by the forest that tries to maintain transpiration at a level corresponding with weather conditions other than precipitation (temperature, radiation, wind speed).

After several simulation runs a good matching between measured and simulated discharges (and measured and simulated groundwater levels) was found. From these simulations, reasonable estimates of transpiration and interception could be derived. Total water use of the forest (transpiration + interception) nearly equals potential evapotranspiration (PET) (factor 0.97).

The extra water use caused by interception, not the total interception, was estimated to be 230 mm.y^{-1} (difference between measured rainfall and effective rainfall) by a total water use of 1,640 mm.y^{-1} (see Table 6.9). As expected, during the dry season moisture stress occurs and transpiration is reduced.

It can be concluded that the water use of the forest at Kabo was very high (76 % of the total rainfall). Similar high values were found in Brazil and Malaysia, but much lower values in forests in Ivory Coast and Venezuela (40-54 % and 38–56 %, respectively, see Bruijnzeel 1991).

6.5.2 Model of organic matter and nutrient flow

An attempt was made to draw up a flow and pools diagram of the phytomass and of two nutrients in major compartments of the undisturbed forest of Kabo, based on the first results of the field experiments, the calculations of the various phytomass values and on some estimated values (Boxman et al. 1985, 1987). This flow diagram was compared to a forest stand two years after treatment. It showed that in spite of the accumulation of decaying dead phytomass and the reduction of living phytomass, logging and silvicultural treatment had resulted at most in a slight increase in the leaching of nutrients. It seemed that the CMS does not lead to serious chemical impoverishment of the ecosystem. Based on this preliminary finding a more detailed study was undertaken by making a simulation model.

The effects of the CMS on the nutrient cycle were studied in detail over a longer period of time, in the catchments of the Eastern Creek, an area of 140 ha of undisturbed forest, and at the Western Creek, an area of 155 ha of forest under the CSS (Poels 1987). Changes in the nutrients in the organic matter cycle were studied by determining the amounts of nutrients in the phytomass and by measuring litter amounts and the composition of litter and soil. Measured data were combined in a model of organic matter and nutrient flows. Changes in nutrients in the hydrological cycle were studied by measuring and analyzing rainfall and creek discharges and also the mineral concentration in rain and creek water.

A computer simulation was made of the amounts, flows and decomposition of organic matter in a plateau soil bearing 540 t.ha^{-1} of living phytomass, in which a stem wood harvest of 15 t.ha^{-1} was followed one year later by a refinement during which 40 % of the phytomass was killed. Figure 6.11 presents the data of the simulation of organic matter pools (t.ha^{-1}) and flows (t.ha^{-1}.y^{-1}) in undisturbed forest and changes during exploitation and refinement. Figure 6.12 gives the nutrients in phytomass and soil organic matter before and after treatment (kg.ha^{-1}). The input data on phytomass are comparable to those presented in Table 6.3 except for the amount of roots, which Poels estimated higher. They were derived from an experiment in the direct vicinity of the MAIN experiment that is not discussed here.

The findings of this simulation study are (Figure 6.11 and 6.12):
- After harvest and before refinement litter amounts and nutrients in litter and soil were slightly higher in the treated western catchment area than in the untreated eastern catchment area.
- Even though 22 months after refinement litter amounts in the treated area increased further, the nutrient amounts in the litter had increased only slightly. Nutrient amounts in the soil had not increased at all, and even decreases were measured. Refinement did not cause significant changes in nutrient amounts in litter or soil. But as the number of living trees was reduced through refinement the amount of nutrients available for the remaining living trees was increases, pointing to a 'fertilizing effect'.
- In the three-year period after the harvest, there was an extra release from the litter of about 150 kg N, 900 kg Ca, 70 kg Mg, 400 kg K and 30 kg P per ha. These nutrients were not retained in the upper 120 cm of the soil.
- In case the vegetation after refinement has a higher mean nutrient concentration than the undisturbed vegetation, which is possible because of the increased production of fresh leaves and twigs combined with a larger nutrient supply than without treatment, the extra release of nutrients would have been less than the amounts quoted above.
- The simulation showed that the weight of the living phytomass reached its lowest level one year after refinement. The amounts of nutrients in living and dead phytomass were at their lowest levels about two years after refinement. The amount of total phytomass, both living and dead, was still decreasing four years after refinement.
- Almost two years after refinement, groundwater samples from auguring to a depth of 7.5 m in the treated catchment did not have higher concentrations of nutrients than groundwater samples from the untreated catchment area. It seems therefore that most of the extra nutrients released by refinement had already passed through the soil and the upper groundwater layers on their way to the creek where some will be extracted by the swamp vegetation.

From a comparison of the amounts of nutrients coming in by rain water and flowing out by the creek, it appeared that there was a net export from the catchment of Si, Na and Mg and a small net accumulation of Ca, K and P in the untreated catchment area of 9, 12 and 0.5 kg.ha^{-1}.y^{-1} respectively. In the treated catchment the accumulation was slightly

less. This means that of the large release of nutrients caused by treatment, only a very small proportion was exported by creek water, at least during the first two years after refinement. If evapotranspiration of the catchment had been reduced by the treatment, the difference in outflow would be somewhat larger.
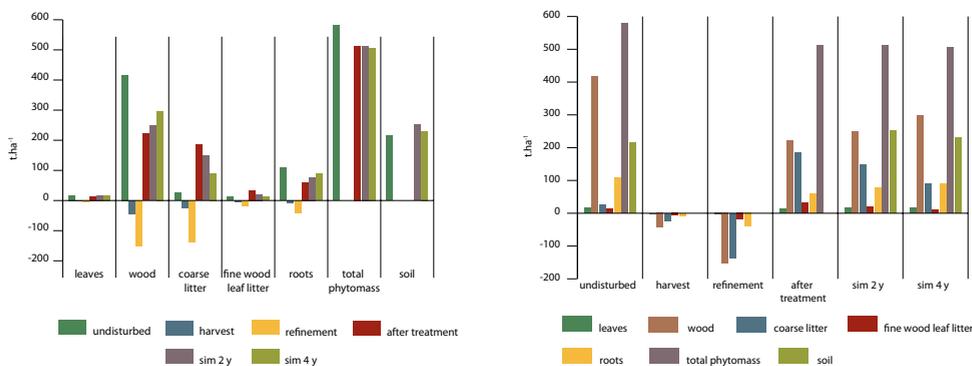

Figure 6.11.   Organic matter pools in undisturbed forest and simulated changes two and four years after exploitation and refinement. Adapted from Poels (1987).

Some considerations based on the above are:

Nutrients leaching to the groundwater can still be picked up by deep roots at several metres depth and probably can even be regained from the groundwater by such roots. A certain loss of nutrients from the plateau and upper slopes is still to be expected as a result of treatment. Nutrient enrichment of foot slopes and valley bottoms will then occur and only small amounts will leave the catchment via the creek water.

The main conclusion from Poels' results of the field experiments and the model output is that: "Forest treatment according to the CELOS Silvicultural System does not result in an unacceptable loss of nutrients from the system. Silviculture based on the natural forest on the brown loamy and sandy soils of the Zanderij formation, is a form of land use of which sustained yields can be expected. As this land use also leads to economic returns (De Graaf 1986), this or similar forest systems could also be of value in other parts of the tropical forest areas, where comparable conditions exist" (Poels 1987). Presently, the forest is not at equilibrium. The area was covered with savanna vegetation during the last glacial period and during that period the soil was intensively leached (see Schulz 1960). Since then, a gradual nutrient accumulation is taking place.

This conclusion is not undisputed, however. In a critical review on nutrient input-output budgets of tropical forest ecosystems analyzing methodological aspects, analytical problems and procedural deficiencies in computation of budgets, Bruijnzeel (1991) doubted that the Suriname forest indeed is accumulating calcium and potassium to such an extent as found by Poels. Bruijnzeel (1989, 1991) based his comment on the difficulties that were met in collecting and analyzing representative precipitation samples as well as the possibilities of unrecorded deep flow through the sandy valley fills.
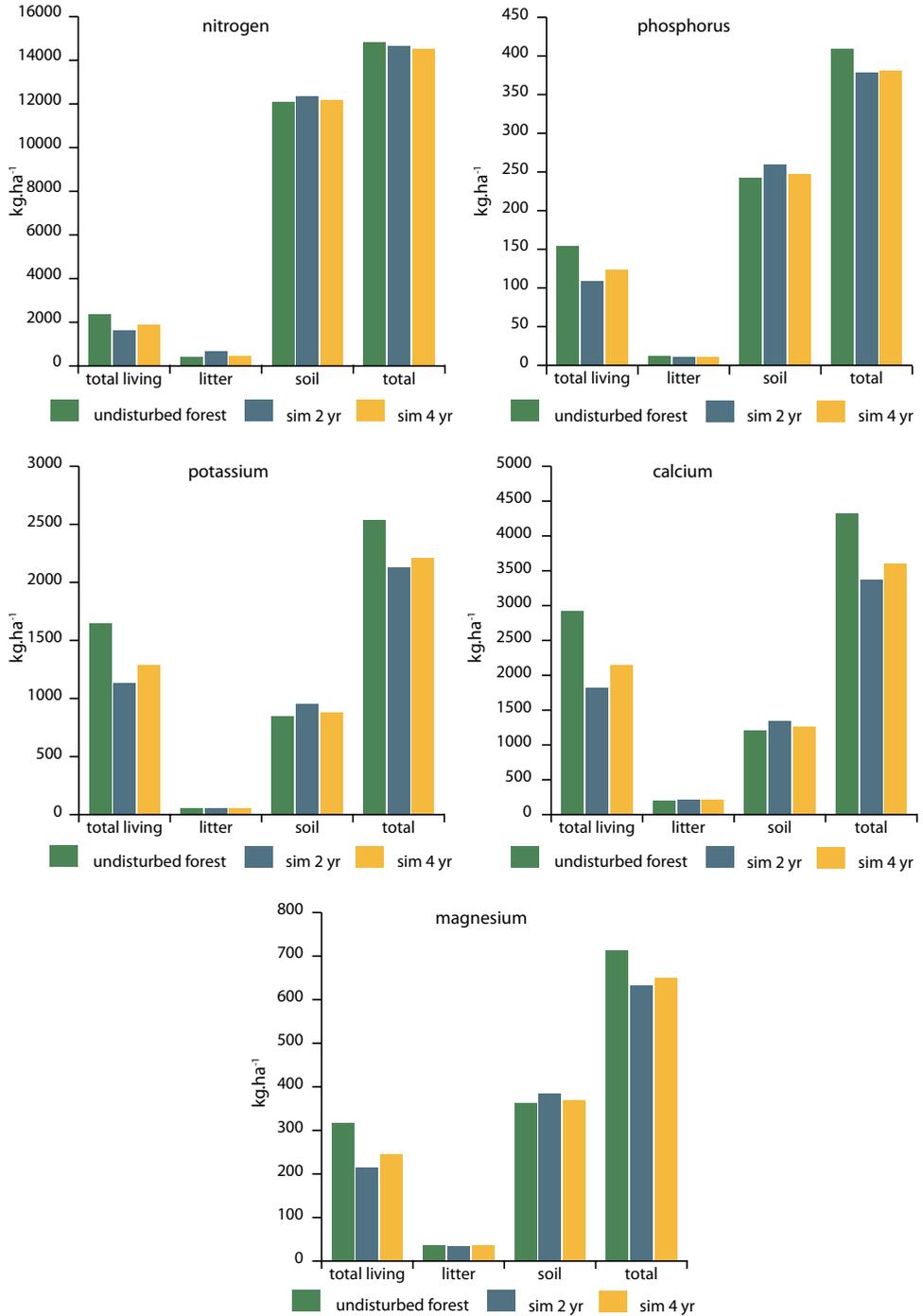
Figure 6.12. Amounts of nutrients in phytomass and soil organic matter and simulated values two and four years after exploitation and refinement. (Source Poels 1987).

6.6   Carbon sequestration

From the dry-weight production data presented in Table 6.8, an impression of carbon accumulation can be obtained by converting these values into carbon content. In undisturbed forest in Kabo, the net increase in total living phytomass of 7.8 t.ha^{-1}.y^{-1} corresponded to an accumulation of 3.6 t.ha^{-1}.y^{-1} of carbon. In Akintosoela1, the net increase amounted to 1.6 t.ha^{-1}.y^{-1} of carbon accumulating, while in Weyerhäuser the net increase in carbon was 4.5 t.ha^{-1}.y^{-1}.

Table 6.10.   Dry weight and carbon[1] stored in total living and dead phytomass in forest under the CMS. Source data see Figure 6.11 and Poels (1987).

	Total living phytomass		Total dead phytomass	
	Dry weight	carbon	Dry weight	carbon
	t.ha^{-1}	t.ha^{-1}	t.ha^{-1}	t.ha^{-1}
Undisturbed forest	542.5	**267.2**	38.1	**19.1**
after treatment (harvest and refinement)	294.7	**140.7**	218.5	**109.2**
Simulation two years after treatment	342.7	**165.7**	170.4	**85.2**
Simulation four years after treatment	403.4	**193.1**	102.6	**51.3**

1. Average carbon content factors used: leaves 41.5%, wood 47%, coarse and fine litter 50%, roots 52%. (Source Ajtay et al. 1979)

The simulated data from Figure 6.11 (MAIN experiment, source Poels 1987), allow the following observations (see Table 6.10): Four years after treatment there was an increase of 52.4 t.ha^{-1} carbon in living phytomass, or an accumulation (uptake out of the atmosphere) of 13.1 t.ha^{-1}y^{-1} of carbon. Dead phytomass (coarse and fine litter) increased due to treatment by 89.1 t.ha^{-1} of carbon. During the four years after treatment, it was diminished by 57.9 t.ha^{-1} as a result of decomposition, leading to an emission of 14.7 t.ha^{-1}.y^{-1} of carbon. Thus, there is not yet a net carbon accumulation in the system.

The situation will gradually change to a position whereby the net increase in phytomass will be greater that the decomposition, resulting in a net carbon sequestration. If we assume a same decomposition rate as in the first four years, which may be high, then it is possible that already after six to eight years after treatment the treated plots form a net sink for carbon. This net sequestering will take place till the forest reaches a steady state.

6.7   Discussion and conclusions

Harvest and refinement will, even if carried out carefully and with respect for the forest according to RIL and FSC instructions and regulations, damage the forest ecosystem. Harvested trees will be exported out of the forest and so will reduce the amount of phytomass and the nutrient capital. Also, harvest and refinement will kill and damage (parts of) trees and other plants. This phytomass will remain in the forest, however, and decompose over a considerable period of time. Leaves of the refined trees will fall within one year, augmenting the litter layer with some 50 %; small branches will become available within one or two years but thick branches will take longer and dead stems

can remain standing for at least ten years and maybe longer.

Directly after these interventions, the ecology of the forest is altered: more light will reach the under-storey of the forest at various places. The amount of water reaching the forest floor will increase due to changes in interception. Temperature conditions inside the forest will change too, as will the impact of strong winds. This will result in changes in species composition, as was discussed in Chapter 5, in timber growth, as was discussed in Chapter 4, and in growth in terms of phytomass and in nutrient cycling, as discussed in this Chapter.

Harvest and refinement reduce the amount of living phytomass. The findings presented above show that, as a result of our experimental treatments, harvesting and refinement lead to a substantial reduction of the living phytomass (compare Figure 6.13). A considerable proportion thereof is transformed, however, into dead phytomass and remains in the forest ecosystem. How large these proportions are depends on the intensity of the treatments, as can be concluded from a comparison of the data in Table 6.3. Due to the interventions the ecological conditions inside the forest change. But these conditions are mainly more favourable for growth than the conditions

Photo 6.3. Measuring fresh weight saw dust, Mapane 1982. (Photo P. Schimdt)

in the undisturbed forest: In the treated forest light, water and nutrient availabilities for the remaining trees are higher. The improved availability is higher soon after the interventions and then gradually decreases as the forest canopy restores itself. As the results from Procter's Forest, Akintosoela1 and Weyerhäuser show, the severity of the intervention has a considerable effect on regrowth. While the forest at Akintosoela1 gradually restored towards a forest somewhat similar to Procter's Forest, it is clear that a heavy refinement will postpone a total recuperation for a considerable period of time. And the intervention at Weyerhäuser was so severe that pioneers could massively establish and they changed the character of the forest substantially, so that recuperation to somewhere similar to the undisturbed forest is a very long-term and complex process. Nevertheless, based on our results we tend to conclude that, due to the interventions, the growing potential of the tropical rain forest ecosystem at Mapane is not damaged by the first harvest and first refinement as prescribed in the CMS system. However, a second refinement and a second harvest have not yet been carried out, and therefore our conclusion remains preliminary.
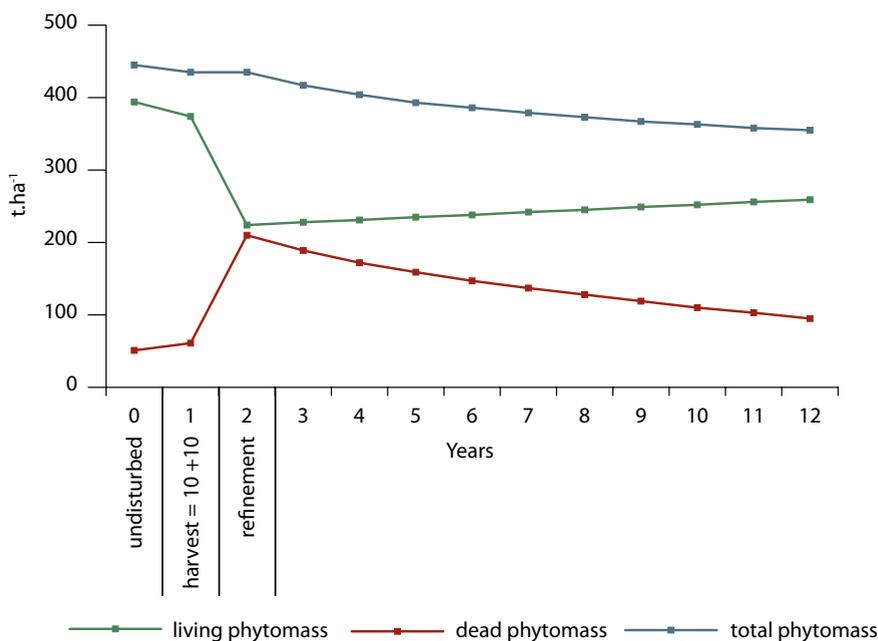
Figure 6.13. Prediction of development of living, dead and total above ground phytomass (dry weight) in the forest stand Akintosoela1 under the CMS.
Assumptions:
Undisturbed forest: Procter's Forest, see Table 6.3.
Harvest: 10 t.ha^{-1} exported from stand, 10 t.ha^{-1} damaged.
Refinement: 40% of living phytomass killed.
Growth: 3.5 t.ha^{-1}.y^{-1} (see Table 6.8: Akintosoela1) over ten years.
Decomposition rate: year 3 10%, year 4 9%, year 5 8%, year 6 and following years 7%.

In this whole process nutrients play a key role. As in many other tropical rain forest ecosystems, in Suriname the soils are poor, notably in phosphorus and magnesium (see Table 6.2) and nutrients liberated from the dead phytomass in the decomposition process can leach, if uptake by the vegetation is slower than the release.

Nitrogen is available in abundance, though it is present in much larger quantities in the soil than in the phytomass (Tables 6.2 and 6.6). Moreover, legumes, of which some species may develop symbioses with nitrogen-fixing bacteria (Pons et al. 2007), form an important part of the forest vegetation (see Table 5.3). Altogether, we expect no problems with regard to the nitrogen availability in these types of forest under CSM application.
Phosphorus is available in the systems under study, as elsewhere in the region, in minimal amounts (Table 6.2 and Poels 1987). Poels (1987) found, during the first years after treatment, no extra discharge of phosphorus in creek water in a basin where harvest and refinement were carried out. However, in acid soils extractable (soluble) P, which usually is considered the phosphorus that is readily available for rapid plant uptake, is often a very small percentage of the total P. The ratio of relatively soluble and insoluble forms of P in the soil might be affected by the CMS. Thus, the small amounts indicate that phosphorus is a weak link in the nutrient cycle, and should be monitored whenever the CMS is applied.

Potassium is a highly mobile element, and it was, according to Poels (1987), leached out of the system in 'relatively large amounts'. This occurred mainly during the first year after refinement; in the second year outflow reached more or less normal levels again.

Though a substantial amount of Calcium is present, compared to other elements a large amount (80 %) is bound in wood and coarse litter, the decomposition of which is slow. On the other hand, the presence of high amounts of Calcium in the soil does not guarantee a high availability. Often, only a small percentage of total Calcium is exchangeable, i.e. available for plants and it is prone to leaching. Poels (1987) found an extra outflow of calcium due to refinement up to two years after treatment (see also Jordan 1989).

Magnesium, like phosphorus, is present in relatively small amounts only. Poels (1987) found no clear effect on the outflow of this element due to refinement. Nevertheless, this element should be monitored carefully too.

In the first three years after treatment there is a "fertilizer effect" through increased decomposition of mainly leaves and fine litter falling from the refined trees. These components have the highest nutrient contents, and their release stimulates growth of the vegetation. In this period chances of leaching are high. Nutrient concentrations in wood are much lower than those of leaves, and decomposition of wood and coarse litter is much slower. Therefore, the amount of nutrients, released per unit material per unit of time, is less (see Table 6.6). Only at a later stage of regrowth nutrients released by decomposing wood begin to play a minor role.

An aspect which has not been studied in the CMS experiments is their impact on the presence of mycorrhizae. Root-mycorrhizae symbioses are adaptations to low nutrient conditions, and play an important role in the prevention of leaching. Refinement, that results in killing their host plants, may kill mycorrhizae, resulting both in nutrient losses and in diminished uptake capacity. A rapid and strong development of fine roots and associated mycorrhizae at the soil surface soon after harvest and refinement will minimise losses of nutrients.

At the long term it appears that, as from three years after refinement, the total aboveground phytomass remains more or less constant (Figure 6.13). This does not hold automatically for the nutrient content too. Moreover, the CMS cycle may include a second refinement ten year after the first one and should lead to a second harvest after 25 years. This was not executed in the present CSM study. Thus, even if the results of the first interventions as prescribed in the CMS look promising, it remains to be seen that the growing potential of the forest as indicated by phytomass and nutrient content will stay at the same level. Proper ecological monitoring of any practical application of the CMS is therefore recommended.

References

Ajtay, G.L., Ketner, P. & Duvigneaud, P. 1979. Terrestrial primary production and phytomass. In: Bolin, B., Degens, E.T., Kempe, S. & Ketner, P., (eds.). The global carbon cycle. Scope 13. John Wiley, Chichester UK, pp. 129-181.

Boerboom, J.H.A. 1964. De natuurlijke regeneratie van het Surinaamse mesofytische bos na uitkap. Landbouwhogeschool, Wageningen, The Netherlands.

Boerboom, J.H.A. 1970. Ecologie. CELOS kwartaalverslagen 16, 64-70.

Boxman, O., De Graaf, N.R., Hendrison, J., Jonkers, W.B.J., Poels, R.L.H., Schmidt, P. & Tjon Lim Sang, R. 1985. Towards sustained timber production from tropical rain forests in Suriname. Netherlands Journal of Agricultural Sciences 33, 125-132.

Boxman, O., De Graaf, N.R., Hendrison, J., Jonkers, W.B.J., Poels, R.L.H., Schmidt, P. & Tjon Lim Sang, R. 1987. Forest land use in Suriname. In: Van Beusekom, C.F., Van Goor, C.P. & Schmidt, P. Wise utilization of tropical rain forest lands. Tropenbos Scientific Series 1. Tropenbos, Ede, The Netherlands, pp. 119-129.

Bruijnzeel, L.A. 1989. Moist tropical forest nutrient cycling, the hydrological framework. In: Proctor, J. (ed.). Mineral nutrients in tropical forest and savanna ecosystems. Blackwell Scientific Publications, Oxford, pp.383-416.

Bruijnzeel, L.A. 1991. Nutrient Input-Output Budgets of Tropical Forest Ecosystems, A Review. Journal of Tropical Ecology 7, 1-24.

De Graaf, N.R. 1986. A silvicultural system for natural of tropical rain forest in Suriname. Ecology and management of tropical rain forest in Suriname, I. PhD Thesis, Agricultural University Wageningen, The Netherlands 250 pp.

De Vries, P.G. 1973. A general theory on line intersect sampling with application to logging residue inventory. Mededelingen Landbouwhogeschool Wageningen 73 (11), 1-23.

De Vries, P.G. 1979. Line intersect sampling, statistical theory, application and suggestions for extended use in ecological inventory. In: Cormack, R.M, Patil, G.P. & Robson, D.S. (Eds.). Sampling biological populations. Statistical ecology series, pp. 1-70.

Golley, F.B., McGinnis, J.T., Clements, R.G., Child, G.I. & Duever, M.J. 1975. Mineral cycling in a tropical moist forest ecosystem. University of Georgia Press, Athens, USA. 248 pp.

Grubb, P.J. & Edwards, P.J. 1982. Studies of mineral cycling in a montane rainforest in New Guinea: III The distribution of mineral elements in the above-ground material. Journal of Ecology 70, 623-648.

Jonkers, W.B.J. 1987. Vegetation structure, logging damage and silviculture in a tropical rain forest in Suriname. Ecology and management of tropical rain forest in Suriname, III. PhD Thesis, Agricultural University, Wageningen. The Netherlands, 172 pp.

Jonkers, W.B.J. & Schmidt, P. 1984. Ecology and timber production in tropical rainforest in Suriname. Interciencia 9, 290-297.

Jonkers, W.B.J, Tjon, K. & Wirjosentono, J. 2005. Long-term changes in selectively logged and silviculturally treated tropical rain forest in Suriname, analysis of the 1978-2000 data of Experiment 78/5. Internal report. CELOS, Paramaribo, Suriname and Wageningen University, Wageningen, The Netherlands.

Jordan, C.F. (ed.), 1989. An Amazonian rainforest. The structure and function of a nutrient stressed ecosystem and the impact of slash-and-burn agriculture. Man and biosphere Series volume 2, Unesco and the Parthenon Publishing Group, Paris, France and Carnforth, UK. 176 pp.

's Landsbosbeheer, 1971. Jaarverslag 1969. Paramaribo, Suriname.

Mason, C.F. 1976. Decomposition. Studies in biology, 74. Edward Arnold, London, United Kingdom. 38 pp.

Ohler, F.J.M. 1980. Phytomass and mineral content in untouched forest. CELOS Rapporten 132, CELOS, Paramaribo, Suriname.

Poels, R.L.H. 1987. Soils, water and nutrients in a forest ecosystem in Suriname. Ecology and management of tropical rain forest in Suriname, II. PhD Thesis, Agricultural University Wageningen, The Netherlands, 253 pp.

Pons, T.L., Perreijn, K., van Kessel, C. & Werger, M.J.A. 2007. Symbiotic nitrogen fixation in a tropical rainforest: 15N natural abundance measurements supported by experimental isotopic enrichment. New Phytologist 173, 154-167.

Schmidt, P. 1981a. Productie ecologie. CELOS kwartaalverslag 59 (1981-III), pp. 11-16.

Schmidt, P. 1981b. Productie ecologie. CELOS Kwartaalverslag 60 (1981-IV), pp. 12-19.

Van der Steege, J.G. 1983a. Strooiselafbraak in vier verschillende bosopstanden. Exp. 82/9 Research report, typoscript. 31 p. + Annexes.

Van der Steege, J.G. 1983b. Bladproductie en bladfytomassa van een aantal palmsoorten van het tropisch regenbos van Suriname. CELOS reports no. 138, 33 pp. + Annexes.

Vink, A.T. 1977. Surinam timbers. State Forest Industries, Paramaribo, Suriname, 253 pp.