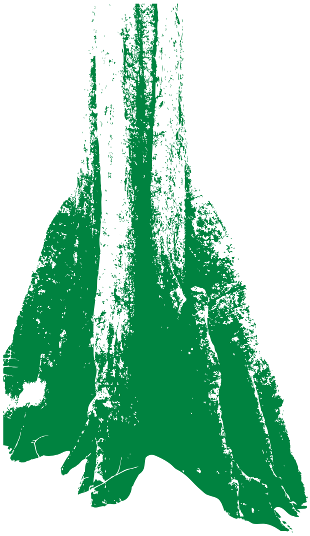


4 Tree growth, recruitment and mortality after logging and refinement

W.B.J. Jonkers

4.1 Introduction

The CELOS Management System should, among others, result in an attractive sustained yield (see Chapter 3). Evidence presented by De Graaf (1986) indicates that forest recovery after selective logging is too slow for this purpose, and that silvicultural interventions are needed (see Chapter 2). The CELOS Silvicultural System (CSS; De Graaf 1986; Jonkers 1987) was primarily meant to speed up the volume increment of the commercial stand, so that the desired sustained yield could be achieved.

This chapter deals with long-term impacts of logging and refinement on the stem diameter increment, mortality and ingrowth[1] of commercial and non-commercial tree species, and on the volume increment of the commercial stand. It is based on the large-scale MAIN experiment at Kabo, supplemented by information from the older CELOS silvicultural experiments Mapanebrug and Akintosoela1 and the Akintosoela2 experiment of the State Forest Service. The CELOS experiments have been established between 1967 and 1978. Until 1983 they were re-measured frequently. Akintosoela2 was created in 1984 in an area which Hendrison (1990) had used earlier for testing the CELOS Harvesting System. Since 1984, each of the experiments has been assessed once between 1995 and 2000. The growth, recruitment and mortality data thus obtained allow a review of the CSS based on the long-term response of the forest to the logging and silvicultural treatments applied.

This chapter provides answers to the following question: how do logging and silvicultural treatments influence tree growth, mortality and recruitment? Or, more specifically:

1 Ingrowth: trees, which had not been included in previous enumerations because they had not yet reached the minimum diameter applied in enumerations. In the MAIN experiment, this minimum size was 15 cm dbh, although smaller trees where recorded in subsamples.

- What is the commercial volume increment resulting from these logging and silvicultural treatments?
- Is the growth of the timber stand such that all timber harvested or killed by logging can be substituted within one cutting cycle of 25-30 years?
- To what extent do trees damaged by logging recover from injury?
- Do non-commercial tree species recover after logging and silvicultural interventions?

4.2 Regeneration, growth and mortality patterns in pristine forest

Light conditions at the forest floor are poor, except where a fallen tree has formed an opening in the canopy. Most tree species depend on such gaps for their regeneration. Seeds of most pioneer species and a few other trees, such as *Goupia glabra*, only germinate in gaps. Other species produce seedlings underneath a closed canopy, most of which die soon after germination. Those which remain may survive for years in dense shade without noticeable growth. When a tree-fall gap is formed, seedlings within the gap start to grow. The response of a given seedling depends on its vitality, the ecological requirements of the species concerned and on local microclimatic conditions. The least vital individuals hardly respond to the changed light conditions. Some tree species develop best in the full sun, but most grow better under more moderate microclimatic conditions. There is considerable variation in light, temperature and humidity between gaps of different sizes and shapes, and also between the edges and the centre of a gap. Chances for growth and survival of a given seedling therefore depend on its ecological requirements, the dimensions of a gap, and its location within the gap.

When a gap newly forms, most of the existing vegetation in the gap area is destroyed by the impact of the falling material. It decays together with the remains of the fallen tree, thus providing nutrients to the seedlings inside the gap as well as to the surrounding trees. Most natural gaps are small, and although light conditions in such gaps are more favourable than under a closed canopy, only a fraction of the sunlight reaches the forest floor. Light and nutrient conditions generally deteriorate with time, because the seedlings increasingly compete with one another and because crowns of surrounding trees gradually close the opening in the canopy. Under such conditions, regenerating trees have to grow as rapidly as possible towards the light in order to ultimately reach the canopy. Thus, seedlings and saplings grow in length rather than in width, which leads to slender stems and narrow and oblong crowns. The growth release usually lasts not longer than a few years as growth is increasingly impeded by suboptimal light conditions in the closing gap, and virtually all small trees will become suppressed sooner or later. Most surviving small trees need a sequence of growth releases to reach the canopy.

Understorey species adapt to the shady conditions in the forest by slowly expanding their branches in lateral directions to reduce self-shading and to capture more light. Canopy and emergent species respond by reducing their physiological activity until light conditions become more favourable for further height increment, that is, until an adjacent small tree perishes or until a new gap is formed near the tree. Most trees die before there is such an opportunity. This pattern of slow but highly variable growth is reflected in the diameter growth of small commercial trees in the MAIN experiment: the mean value was just 0.31 cm.y^{-1} with a standard deviation (S.D.) as high as 0.28 (Jonkers et al. 2005).

When a tree ultimately reaches the canopy, it starts to expand its crown laterally, and the height increment of the stem comes to a halt. At this point, the tree generally attains sexual maturity (Jonkers 1987). Emergent species also start forming large oblique-oriented branches, which allow the tree to grow further in height and to form their characteristic wide-spreading crowns. The diameter growth of the stems increases, but remains highly variable. This is again evident from the results of the MAIN experiment: the mean increment of medium-sized and large commercial trees was just 0.39 cm.y^{-1} with a S.D. as high as 0.29 (Jonkers et al. 2005).

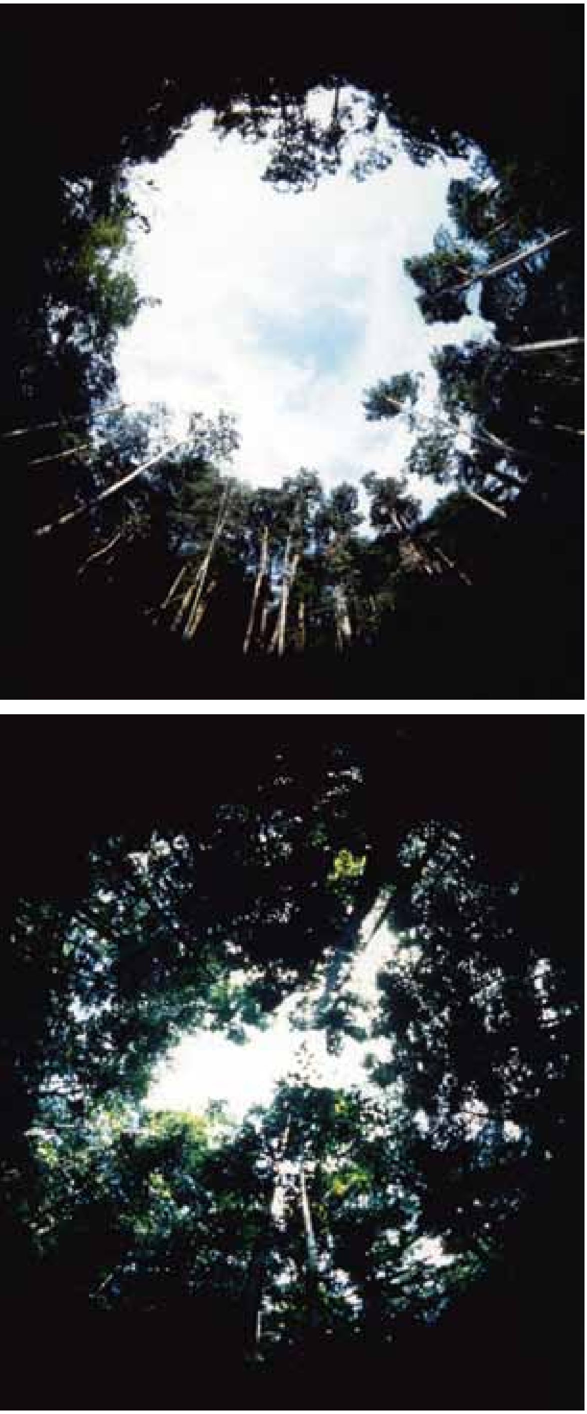


Photo 4.1. Fish-eye lens photos of forest gaps in Guyana. (Photo H. ter Steege)

In large gaps, the pattern is slightly different. In the central part of the gap, light-demanding pioneer trees emerge. These species grow fast and can be so abundant that they effectively suppress regeneration of other trees for decades. Because of their fast growth, some pioneer trees may reach the canopy before the gap is closed. Although their live span tends to be shorter than that of most other tree species, pioneer trees such as *Inga* and *Cecropia* spp. can live longer than half a century (see Section 4.5).

4.3 Impact of logging on growth and mortality within the commercial stand

Logging affects tree growth and mortality in various ways. The most obvious direct impact is that trees are killed during the harvest operation: a certain number of large trees are harvested and other trees are destroyed by falling trees or during skidding. In the MAIN experiment, logging was carefully planned and controlled, and unintended logging damage was therefore low. Between 6.8 % and 20.3 % of the commercial trees larger than 5 cm dbh (including harvested trees) died during the logging operation, depending on the logging intensity which varied from 15 to 46 $m^3.ha^{-1}$ (Jonkers 1987). Table 4.1 summarizes how many commercial trees were killed during the logging operation, and gives the stem volumes felled[2] and destroyed.

Table 4.1. Trees felled or destroyed during logging in the MAIN experiment: numbers, basal areas and volumes*

Logging treat-ment **	Felled trees			Destroyed trees***			Total killed***		
	$N.ha^{-1}$	Basal area ($m^2.ha^{-1}$)	Volume ($m^3.ha^{-1}$)	$N.ha^{-1}$	Basal area ($m^2.ha^{-1}$)	Volume ($m^3.ha^{-1}$)	$N.ha^{-1}$	Basal area ($m^2.ha^{-1}$)	Volume ($m^3.ha^{-1}$)
E15	3.36	1.38	19.04	2.76	0.26	3.05	6.12	1.64	22.09
E23	6.08	2.31	31.66	3.51	0.33	3.96	9.59	2.64	35.62
E46	11.49	3.87	52.68	5.48	0.52	6.22	16.97	4.39	58.90

* Volume equation: V = -0.2335 + 0.001125D2 (Jonkers 1987); V = volume in m^3 and D = dbh in cm
** The treatment codes reflect the volumes extracted per ha (E15: 15 $m^3.ha^{-1}$ extracted, etc.)
*** Trees > 15 cm dbh, commercial species only

In addition, 8.9 to 15.0 % of the trees were damaged, but survived (Jonkers 1987). Jonkers (1987) showed that small trees are more vulnerable to destruction and severe damage than large individuals, while minor injury is more common among large trees. The status of the surviving damaged trees was assessed 19 years after logging for those parts of the MAIN experiment which did not receive any silvicultural treatment (Table 4.2). The results showed that trees with mild forms of injury mostly recovered, but trees with severe logging injury had almost twice as much chance either to die within 19 years or to develop a defective stem as compared to trees with minor or no damage. However, the data indicated also that even trees with severe crown or stem injury often developed into good-quality timber trees, although some of these stems may be hollow or decayed inside. So, injured trees apparently have the potential to contribute to future harvests and can be considered as part of the timber resource.

In theory, the growth of the commercial stand should be such, that the stem volume lost during the logging operation is replaced within one cutting cycle. This loss is more than the volume extracted, as the stump, the top end and defective parts of the felled stems are not hauled out and remain in the forest to rot. In addition, some trees of commercial species die during the logging operation due to felling damage. Table 4.1 summarises the main statistics regarding trees felled or destroyed during logging in the MAIN experiment. The commercial volumes to be replaced ranged from approximately 22 $m^3.ha^{-1}$ for the lowest felling intensity to 59 $m^3.ha^{-1}$ for the highest felling intensity. Assuming a 25-year cutting cycle, this would mean that the required annual volume growth should be almost 1 $m^3.ha^{-1}.y^{-1}$ for the lowest logging intensity (E15) and almost 2.4 $m^3.ha^{-1}.y^{-1}$ for the highest one (E46).

2 The volumes felled were considerably larger than the volumes extracted. This is because parts of the felled trees were left in the forest (stumps, top ends and defective parts).

Table 4.2. Recovery and mortality among trees with various degrees of logging damage (MAIN experiment, plots without silvicultural treatment, commercial species; trees >15 cm dbh)

Logging damage (1981)		Number of trees (=100%)	Tree condition in 1999-2000				
Stem injury*	% of crown broken off		Stem quality (%)				Dead / not found (%)
			Good	Adequate	Poor	Broken	
None	0%	1360	12.2	60.9	3.8	3.1	20.0
	1-50%	120	9.2	55.8	8.3	6.7	20.0
	50-99%	48	8.3	43.8	4.2	16.7	27.1
	100%	42	4.8	35.7	0.0	14.3	45.2
	All	1570	11.7	59.3	4.1	4.1	20.9
Minor	0%	58	12.1	62.1	10.3	1.7	13.8
	1-50%	11	9.1	54.5	9.1	27.3	0.0
	50-99%	7	42.9	28.6	0.0	14.3	14.3
	100%	5	0.0	40.0	20.0	0.0	40.0
	All	81	13.6	56.8	9.9	6.2	13.6
Major	0%	25	4.0	44.0	24.0	4.0	24.0
	1-50%	6	0.0	33.3	33.3	16.7	16.7
	50-99%	4	0.0	0.0	25.0	0.0	75.0
	100%	1	0.0	0.0	0.0	0.0	100.0
	All	36	2.8	36.1	25.0	5.6	33.3
All	0%	1443	12.1	60.6	4.4	3.0	19.8
	1-50%	137	8.8	54.7	9.5	8.8	18.2
	50-99%	59	11.9	39.0	5.1	15.3	28.8
	100%	48	4.2	35.4	2.1	12.5	45.8
	All	1687	11.6	58.7	4.8	4.2	20.8

* Major stem injury means that the stem has split, or that the bark has been ripped off over either at least one third of the circumference of the stem or over more than 20 cm of the stem circumference or over a length of at least 2 meters. Minor stem injury means that a smaller piece of the bark has been ripped off.Source: Jonkers et al. (2003)

Volume growth in virgin forest and after logging was investigated in the MAIN experiment. The growth of the commercial volume in a given forest is mainly determined by diameter growth and mortality; volume increment as result of recruitment is so little that it does not merit a separate analysis. Furthermore, volume growth is partially determined by the richness in commercial species, as each commercial tree contributes to volume increment. The forest of the MAIN experiment was - and still is - richer than most forests in Suriname.

Average diameter growth rates per logging intensity and their standard deviations are shown in Table 4.3. The data suggest a positive correlation between logging intensity and tree growth. The differences between the means were rather small and standard deviations were high, however. The evidence is not fully convincing, but it is plausible that logging enhances the growth of commercial trees (see also Section 4.4.1).

Table 4.3. Diameter growth of commercial trees > 15 cm dbh (between the 1982-1983 and 1999-2000 enumerations; MAIN experiment, plots without silvicultural treatment)

Logging treatment	**Number of trees**	**Diameter growth (cm.y^{-1})**	
		Mean	**Standard deviation**
Untouched	452	0.39	0.29
E15	528	0.42	0.33
E23	400	0.44	0.29
E46	484	0.46	0.30

Source: Jonkers et al. (2003)

As trees with severe logging damage are more likely to die within one cutting cycle than other trees, one would expect a positive relation between logging intensity and mortality in the first decades after logging. However, such an impact was not evident and could not be proven. The average mortality for all logging treatments combined was modest; about 21 % over a 17 year period (see Table 4.2), but the differences in mortality between individual plots were enormous (see Table 4.4). Two plots in the intermediate logging intensity (E23) had very high death rates, while mortality in two plots with the highest logging intensity (E46) was negligible. It is unlikely that these differences were due to the harvesting regimes applied, and further statistical analysis was therefore considered redundant. The mortality rates recorded in virgin forest plots were comparable to the average value for logged forest.

Table 4.4. Mortality among commercial trees > 15 cm dbh (between the 1982-1983 and 1999-2000 enumerations; 1-ha plots)

Logging intensity	Replication						Mean	
	1		2		3		Number of trees per ha	Volume (m^3.ha^{-1})
	N.ha^{-1}	m^3.ha^{-1}	N.ha^{-1}	m^3.ha^{-1}	N.ha^{-1}	m^3.ha^{-1}		
Untouched*	13	31.96	16	45.59	18	38.02	15.67	38.52
E15	9	16.84	17	12.17	19	24.31	15.00	17.78
E23	30	55.24	24	66.64	15	22.38	23.00	48.09
E46	9	4.92	17	31.72	8	3.89	11.33	13.51

* Plot 41: Replication 1; Plot 42: Replication 2; Plot 43: Replication 3
Source: Jonkers et al. (2003)

Due to the high variation in mortality, volume growth differed much from plot to plot (Table 4.5). In the virgin forest plots, there was on average hardly any change in commercial volume, as one would expect, although volume increment varied considerably between plots. Volume increment after logging varied even more, from – 36 m^3.ha^{-1} (–2.1 m^3.ha^{-1}.y^{-1}) to +78 m^3.ha^{-1} (+ 4.6 m^3.ha^{-1}.y^{-1}). On average, the volume increment in logged plots amounted to + 1.7 m^3.ha^{-1}.y^{-1}, indicating that the commercial stand recovers after logging.

Table 4.5. Volume increment* of commercial species (change in volume of trees > 15 cm dbh between the 1982-1983 and 1999-2000 enumerations; no silvicultural treatment)

Logging intensity	Replication			Mean
	1	2	3	
	Volume increment in 17 years ($m^3.ha^{-1}$)			
Untouched**	15.49	9.16	-15.72	2.98
E15	34.65	47.92	46.22	42.93
E23	-24.50	-36.19	34.82	-8.62
E46	44.68	40.38	78.10	54.39

* Volume equation: V = -0.2335 + 0.001125D2 (Jonkers, 1987); V = volume in m^3 and D = dbh in cm ** Plot 41: Replication 1; Plot 42: Replication 2; Plot 43: Replication 3 Source: Jonkers et al. (2003)

These mean values suggest that a sustained yield of about 20 $m^3.ha^{-1}$ once every 25 years can be achieved without any silvicultural treatment in this particular forest, but the variation in mortality was such, that this cannot be proven. Moreover, because the MAIN experiment is a lot richer in commercial species than most forests in Suriname, it is likely that 25 years is generally insufficient to sustain such a yield without additional measures such as silvicultural treatment.

Actions to reduce logging damage in addition to the measures already applied in the MAIN experiment may also lead to higher sustained yields, although Table 4.1 shows that the potential for further damage reduction is limited. The CELOS Harvesting System (Hendrison, 1990) and other RIL methods are not meant to enhance the growth of individual trees, but should have a beneficial effect on the volume growth of the entire commercial stand as more trees, seedlings and saplings survive logging to form the growing stock. Evidence from the Akintosoela2 experiment showed indeed that the CHS resulted in significantly more new, young timber trees in the 5-15 cm diameter class than conventional logging (Jansen et al., 2005), but this experiment had been subject to too much unscheduled disturbance to prove an eventual effect on the volume increment of the entire commercial stand.

4.4 Impact of silvicultural treatment on growth and mortality of commercial species

The CELOS Silvicultural System is meant to enhance the growth of commercial timber species by eliminating part of the competing vegetation (see Chapter 3). In this section, the impact of silvicultural treatment on increment and mortality is elaborated.

Treatment intensities varied not only within the experiments because different diameter limits were tested, but also between experiments because of differences in forest composition (see Chapter 5) and in criteria for trees to be eliminated. In all experiments, not only trees of non-commercial species were killed, but also trees of commercial species which did not meet certain standards. These standards differed from one experiment to another. When the oldest pilot experiment (Mapanebrug) was established in 1967, the idea was that the research would lead to a monocyclic management system. Hence, all trees above the refinement limit were killed, except trees of commercial species which were likely to be still in good condition at the end of the rotation of 60-80 years, that is, good quality stems which were less than 50 cm in diameter (Boerboom 1965, appendix 32). In experiment Akintosoela1, which was established in 1975, this 50 cm upper diameter limit for commercial species was not applied, but poor stem form and other defects remained reasons to reject and eliminate timber trees (Staudt 1977). In the MAIN experiment, all trees of commercial species were retained, except for a few visibly hollow or extensively decayed stems and split or broken trunks (Jonkers 1983, 1987). Furthermore, when the Mapanebrug experiment was established, there were only 31 entries on the commercial species list, while a list of 58 species was applied in the other experiments. Hence, in refinements with a 20 cm diameter limit, basal area was reduced to about 7 $m^2.ha^{-1}$ in Mapanebrug, to 9.8 $m^2.ha^{-1}$ in Akintosoela1 (De Graaf 1986) and to about 14 $m^2.ha^{-1}$ in the MAIN experiment (Jonkers 1983)[3]. For comparison: the basal area in undisturbed forest is about 30 $m^2.ha^{-1}$.

Photo 4.2. Measuring a stem diameter above the buttresses. (Photo K.E. Neering)

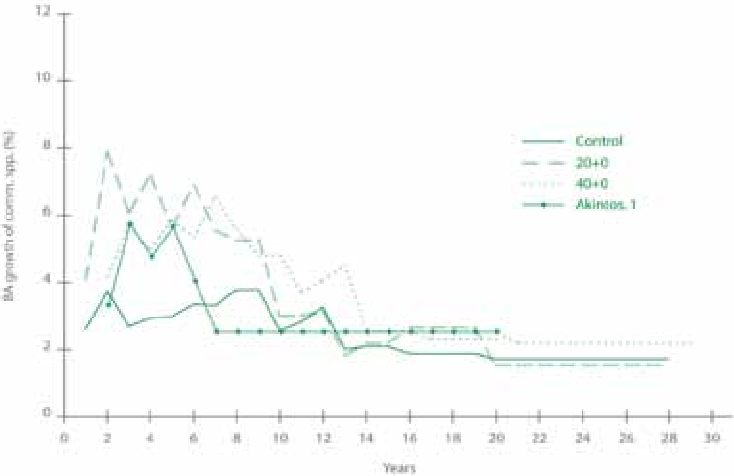
The treatments applied in the State Forest Service's experiment Akintosoela2 were less rigorous than in the 20-cm diameter limit refinements in other experiments. Diameter limits of the five most intensive treatments were meant to be in accordance with De Graaf's CSS prescriptions, that is, a basal area of 12.5 – 15 $m^2.ha^{-1}$ should remain after refinement. However, the basal area calculations were based on trees larger than 25 cm in diameter only, and not on all trees exceeding 10 cm in diameter as was meant by De Graaf (see Van Bodegom & De Graaf 1991). Hence, diameter limits applied ranged from 25 cm to 50 cm (Jansen et al. 2005). In addition, the experiment included a refinement with a diameter limit of 65 cm and a control treatment.

4.4.1 Growth of medium-sized and large trees

The bulk of the commercial volume increment has to be brought about by the diameter growth of medium-sized and large commercial trees, that is, stems exceeding 15 cm in diameter. In Mapanebrug and Akintosoela1, the refinements with a 20-cm diameter

3 The true difference in treatment intensity between the Mapane experiments and the MAIN experiment is even larger, as De Graaf based his basal area calculations on all trees larger than 5 cm in diameter, while Jonkers' estimate is based on trees exceeding 15 cm in diameter.

limit, or rather, the drastic reductions in biomass resulting from these treatments, led initially to average diameter growth rates of about 0.9 $cm.y^{-1}$ for such medium-sized and large stems (see De Graaf 1986; Jonkers 1987). However, after about eight years, diameter increment rates dropped rapidly to pre-refinement levels and basal area growth of commercial species fell to a mere 2 % of the pre-treatment basal area (Poels et al. 1995; De Graaf et al. 1999, see Figure 4.1). But in those Mapanebrug plots where a second refinement had been applied, diameter growth remained high for another 8 years, as predicted by De Graaf (1986). In the absence of such a second treatment, the forest in Akintosoela1 produced a sufficient volume of marketable timber for the next harvest, but only marginally so: 19 years after refinement, there was about 40 $m^3.ha^{-1}$ of harvestable timber in the stand, assuming a low minimum felling diameter of 45 cm (De Graaf et al. 1999). De Graaf et al. (1999) therefore concluded that "a treatment scheme as prescribed in the CSS should not be abandoned after one treatment if a sustained yield is to be implemented".



Note: Treatments presented are the control treatment (no refinement after logging) and refinements with 20 and 40 cm diameter limits without follow-up.

Figure 4.1. Basal area growth of commercial species in Mapanebrug and Akintosoela1: changes in time, expressed as percentage of the basal area in year 1 (source: Poels et al. 1995).

The much milder treatments applied in Akintosoela2 also stimulated diameter growth, but the response was substantially less than in Mapanebrug and Akintosoela1. In order to get statistically meaningful results, Jansen et al. (2005) lumped the seven treatments in two classes: all refinements with diameter limits of 25 to 40 cm together in class I, and the control treatment and refinements with higher diameter limits in class II. The difference in diameter growth between these two classes was small but statistically significant for all species groups, and the mean diameter increment of all species combined was just 0.038 $cm.y^{-1}$ faster after the heavier refinements. This treatment effect may seem negligible, but in relative terms it is an increase by 16 %. According to Schneider's law, this is equivalent to a 33 % increase in volume growth (Jansen et al. 2005). The annual volume increment of surviving commercial trees was about 1.4 $m^3.ha^{-1}$ in untreated plots and 1.9 $m^3.ha^{-1}$ in plots with relatively heavy refinements (Jansen et al. 2005).

In the MAIN experiment, temporal changes in growth could not be investigated, as there were only two enumerations after silvicultural treatment: one about 1 year after the treatment and one 17 years later, but the experiment allowed a more detailed analysis of long-term impacts of a first refinement than the other trials, also because three levels of silvicultural treatment had been combined with three logging intensities. The levels of silvicultural treatment applied were a control treatment (no refinement, code S0) and refinements with diameter limits of 20 cm (code SR14) and 30 cm (code SR18). The SR codes reflect the basal areas which were expected to remain after application of the treatments (Jonkers 1983). The logging intensities are indicated by the codes E15, E23 and E46, which reflect the average harvested timber volumes (15, 23 and 46 $m^3.ha^{-1}$ respectively).

Average growth rates per combination of logging intensity and silvicultural treatment (Table 4.6) suggest that higher intensities of logging and refinement lead to faster diameter growth of the remaining trees, and that refinement has more impact than logging. All mean growth rates were substantially higher than the mean rate recorded in the virgin forest plots, which amounted to 0.39 $cm.y^{-1}$ (S.D. = 0.29) (see previous section) and slightly inferior to the average growth rates recorded in Akintosoela1 over a 19-year period. Because differences in growth rate between the logging intensities were small and standard deviations were high, the overall impact of logging on diameter growth could not be proven with Analysis Of Variance (ANOVA, $p = 0.08$). Differences between the lowest logging intensity (E15) on the one hand and the intermediate and the highest logging intensities (E23 and E46) on the other hand were substantial, but the differences between the growth rates of the two highest logging intensities were small. The conclusion is the same as the one presented in Section 4.3: the evidence is not statistically proven, but it is likely that logging enhances the growth of commercial trees.

Table 4.6. Diameter growth of commercial trees > 15 cm dbh in $cm.y^{-1}$ (between the 1982-1983 and 1999-2000 enumerations; 2.25-ha plots of the MAIN experiment)

Refinement	Logging intensity											
	E15			E23			E46			All		
	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.
S0	528	0.42	0.33	400	0.44	0.29	484	0.46	0.30	1412	0.44	0.31
SR18	560	0.51	0.33	498	0.55	0.30	453	0.56	0.34	1511	0.54	0.32
SR14	516	0.55	0.40	467	0.60	0.34	420	0.60	0.35	1403	0.58	0.37
All	1604	0.49	0.36	1365	0.53	0.32	1357	0.54	0.33	4326	0.52	0.34

N: number of trees
Source: Jonkers et al. (2005)

Refinement resulted in mean growth rates of 0.5 – 0.6 $cm.y^{-1}$. The differences between treatments proved statistically significant when tested with ANOVA ($p = 0.008$). The t-tests showed that especially the differences between the untreated plots (S0) on the one hand and each of the refinement treatments on the other hand were highly significant ($p = 0.000$), but the difference between both refinements (SR14 and SR18) was highly significant as well ($p = 0.001$). This result confirms earlier claims (De Graaf

1986; Jonkers 1987) that the diameter growth of medium-sized and large commercial trees is stimulated by refinement, and that a 20-cm diameter limit refinement leads to faster growth than a 30-cm diameter limit treatment.

Photo 4.3. Numbering the tree and marking the point at which the diameter is measured. Mapane, 1982. (Photo P. Schmidt)

Remarkable are the high standard deviations (0.3 – 0.4 cm.y^{-1}) found for each combination of logging intensity and silvicultural treatment and also for the virgin forest plots. This means that the growth rates of individual trees were often substantially higher or lower than the mean. A closer examination of the data revealed, that 5 – 10 % of the trees had grown less than 0.1 cm.y^{-1} while the fastest growing individuals had an increment of about 2 cm.y^{-1}. An effort was made to find explanations for these differences in growth rate. One obvious explanation is that some species grow faster than others. This was indeed the case, and variation in growth rate within species was generally somewhat less than for all species combined (Table 4.7). However, the diameter increment of the two most common species, *Qualea rosea* and *Dicorynia guianensis*, was more variable than the growth of all commercial trees. These species were also the common commercial species with the fastest average growth[4].

Table 4.7. Diameter growth rates of common commercial species (trees > 15 cm dbh; MAIN experiment).

Scientific name	Vernacular name	Treatment	N*	Mean dbh growth (cm.y^{-1})	Standard Deviation (cm.y^{-1})
Manilkara bidentata	Bolletri	virgin forest plots	47	0.27	0.16
		logged, no refinement	202	0.30	0.16
		logged, refinement SR18	157	0.42	0.18
		logged, refinement SR14	153	0.44	0.20
Goupia glabra	Kopi	virgin forest plots	24	0.36	0.17
		logged, no refinement	6	0.38	0.26
		logged, refinement SR18	72	0.46	0.30
		logged, refinement SR14	53	0.49	0.27
Virola michelli	Hoogland baboen	virgin forest plots	34	0.33	0.18
		logged, no refinement	86	0.37	0.22
		logged, refinement SR18	84	0.51	0.27
		logged, refinement SR14	109	0.52	0.25

4 Higher average growth rates were recorded for some less common species, such as *Parkia nitida* and *Simarouba amara*.

Scientific name	Vernacular name	Treatment	N*	Mean dbh growth ($cm.y^{-1}$)	Standard Deviation ($cm.y^{-1}$)
Tetragastris altissima	Rode sali	virgin forest plots	36	0.42	0.24
		logged, no refinement	69	0.40	0.22
		logged, refinement SR18	111	0.48	0.21
		logged, refinement SR14	88	0.55	0.27
Dicorynia guianensis	Basralokus	virgin forest plots	84	0.44	0.29
		logged, no refinement	287	0.51	0.32
		logged, refinement SR18	348	0.50	0.32
		logged, refinement SR14	267	0.62	0.48
Qualea rosea	Bergi gronfolo	virgin forest plots	40	0.53	0.38
		logged, no refinement	300	0.57	0.36
		logged, refinement SR18	350	0.69	0.35
		logged, refinement SR14	358	0.71	0.37

* N: number of trees
Source: Jonkers et al. (2005)

Variation in diameter increment is apparently mostly due to other factors, such as the vitality of individual trees and competition from neighbouring trees, lianas and other plants. The impact of competition from neighbouring trees is reflected in the following regression equation:

$$\delta dbh = 0.657 - 0.201\ BA_{0\text{-}5} - 0.069\ BA_{5\text{-}10} - 0.104\ BA_{10\text{-}15} \qquad p = 0.000 \qquad \text{(Eq. 4.1)}$$

where δdbh = diameter increment in $cm.y^{-1}$, $BA_{0\text{-}5}$ = competing basal area (in m^2) within 5 m distance from the stem, $BA_{5\text{-}10}$ = basal area (in m^2) at 5-10 m distance and $BA_{10\text{-}15}$ = basal area (in m^2) at 10-15 m distance (BA derived from 1982-1983 data).

This equation shows indeed that diameter growth is negatively correlated to the density of the surrounding vegetation. The impact of competition is substantial and is not confined to the immediate vicinity of the tree. This applies both to light and root competition. Jonkers (1987) analyzed crown dimensions and reported that considerable light competition over distances exceeding 10 m may be expected from trees of approximately 50 cm dbh and larger and evidence presented in Section 5.5.2 indicates that root systems can extend to at least 30 m from the stem. Because of this, and because competition changed considerably over the 17 years recording period during which competing trees either grew larger or died, equation 4.1. explains only a small part of the variation in tree growth (R^2=0.05).

Diameter growth also depends on tree size. Relatively small trees are generally shaded by larger trees and are therefore likely to suffer more from competition than large individuals. On the other hand, large trees may grow less fast in diameter than smaller individuals because they may become less vital with increasing age and also because a tree has to increase its annual volume growth substantially when it gets larger if it is to maintain the same diameter increment.

Regression analyses were conducted for each silvicultural treatment to analyse the relation between diameter increment on the one hand and the stem diameter and the square of the stem diameter on the other hand. This led to the following equations:

For logged forest, no refinement:
$\delta dbh = 0.2485719 + 0.0089114\ dbh - 0.0000767\ dbh^2$ $\quad p = 0.000 \quad$ (Eq. 4.2)

For logged forest, after refinement SR18:
$\delta dbh = 0.3868536 + 0.0075807\ dbh - 0.0000757\ dbh^2$ $\quad p = 0.000 \quad$ (Eq. 4.3)

For logged forest, after refinement SR14:
$\delta dbh = 0.4338468 + 0.0076187\ dbh - 0.0000775\ dbh^2$ $\quad p = 0.004 \quad$ (Eq. 4.4)

where δdbh = diameter increment in $cm.y^{-1}$ and dbh = stem diameter in cm (1982-1983 data).

These equations are all statistically significant and show indeed a relation between diameter growth and tree size. The curves are rather flat, however, with slight peaks between 40 – 60 cm dbh, and explain only a small part of the variation ($R^2 < 0.10$). Trees in the 40 – 60 cm diameter class grew on average about 0.1 $cm.y^{-1}$ faster than trees of 15-20 cm dbh. A similar analysis of the Akintosoela1 data gave comparable results (see De Graaf et al. 1999).

4.4.2 Growth of small trees

The diameter increment of small commercial trees (5-15 cm dbh) shows trends comparable to those found for larger ones. In Mapanebrug and Akintosoela1, the drastic reductions in living biomass led initially to average diameter growth rates of commercial trees of about 0.7 $cm.y^{-1}$ (see De Graaf 1986; Jonkers 1987). After about eight years, diameter increment rates dropped fast to pre-refinement levels. Where a second refinement had been applied, however, diameter growth remained high for another 8 years (Poels et al. 1995; De Graaf et al. 1999).

Data from the MAIN experiment again suggest that higher intensities of logging and refinement lead to faster growth, and that refinement has a larger impact than logging (see Table 4.8). All mean growth rates except one were higher than the average rate recorded in the virgin forest plots, which amounted to 0.31 $cm.y^{-1}$. The differences in growth rate between the logging intensities were small and standard deviations were high. Again, the impact of logging on diameter growth could not be proven with ANOVA ($p = 0.68$). The differences between the lowest logging intensity (E15) on the one hand and the intermediate and the highest logging intensities (E23 and E46) on the other hand were again substantial, while the differences between the growth rates of the two highest logging intensities were once more very small.

Table 4.8. Diameter growth of commercial trees 5-15 cm dbh in cm.y^{-1} (between the 1982-1983 and 1999-2000 enumerations)

Refinement	Logging intensity											
	E15			E23			E46			All		
	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.
S0	170	0.31	0.28	138	0.33	0.23	145	0.36	0.28	453	0.33	0.28
SR18	185	0.42	0.31	185	0.45	0.30	156	0.48	0.33	526	0.45	0.31
SR14	171	0.42	0.29	167	0.52	0.31	140	0.54	0.32	478	0.49	0.31
All	526	0.38	0.30	490	0.44	0.32	441	0.46	0.32	1457	0.43	0.30

N: number of trees
Source: Jonkers et al. (2005)

Refinement resulted in mean growth rates of 0.42 – 0.54 cm.y^{-1}. The differences between treatments proved statistically significant when tested with ANOVA (p = 0.038). The t-tests conducted showed that especially the differences between the untreated plots (S0) on the one hand and each of the refinement treatments on the other hand were highly significant (p = 0.000), as was the difference between both refinements (SR14 and SR18) (p = 0.011).

Standard deviations were again very high (0.3 – 0.5 cm.y^{-1}) for all combinations of logging intensity and silvicultural treatment and also for the virgin forest plots (0.28 cm.y^{-1}). Growth rates of individual trees varied from 0.0 cm.y^{-1} to 1.4 cm.y^{-1}. Regression analyses showed a significant correlation between diameter growth and tree size; trees of 14 - 15 cm dbh grew on average about twice as fast as the ones of 5 - 6 cm dbh. Once more, this explained the variation in growth only partially.

4.4.3 Mortality

Mortality in undisturbed tropical rain forest is modest: on average 1 % of the trees are dying annually (see e.g. Swaine et al. 1987), but higher values of 2-3 % have also been reported (e.g. Condit et al. 1995). Expressed in terms of wood volume or biomass, losses due to mortality are in the same order of magnitude as gains due to growth of surviving trees and this makes mortality a crucial parameter for sustainability. The CELOS Silvicultural System does not include specific measures to reduce mortality and is in fact based on the assumption that mortality of commercial trees does not increase substantially after silvicultural treatment. However, logging and silvicultural treatment influence the chances of trees to survive in various ways; they lead for instance to less competition among trees but also to increased exposure to adverse weather condition, and this may lead to an increase or a decrease in mortality.

Because of the low incidence of mortality, it is hard to soundly quantify it; one needs a long period and large numbers of trees to obtain statistically sound results, especially when the spatial and temporal variation in mortality is considerable. This is often the case: extreme weather conditions may generate temporal peaks in mortality, and the fall of a large tree usually destroys several other trees, thus causing a local increase in death rate. The recording period of the MAIN experiment is adequate for a reliable assessment, but the numbers of trees may be somewhat meagre for analyses per combination of treatments and per species category.

Mortality among the species, which were considered commercial in 1978, is summarised in Tables 4.9 and 4.10. In the replications, about one out of the 95 trees per hectare died annually during the 17-year recording period. Variation between plots was large, but differences between the means for treatments were modest, and there was not the slightest sign of a correlation between mortality on the one hand and logging or refinement intensity on the other hand. Mortality in the virgin forest plots was slightly less than in the logged and refined plots, 15.67 trees.ha^{-1} in 17 years, due to the somewhat lower stocking in these plots (87 trees.ha^{-1}).

Table 4.9. Mortality among commercial species (1978 list) between the 1982-1983 and 1999-2000 enumerations (1-ha plots); number of trees > 15 cm dbh

Refinement	Logging intensity							
	E15		E23		E46		All	
	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.
S0	15.00	5.29	23.00	7.55	11.33	4.93	16.44	7.35
SR18	20.00	3.61	21.33	8.96	15.67	6.43	19.00	6.34
SR14	20.00	6.00	16.67	5.69	18.33	6.03	18.33	5.32
All	18.33	5.05	20.33	7.11	15.11	5.90	17.93	6.24

N.ha^{-1}: number of trees per hectare
Source: Jonkers et al. (2005)

Mortality was also expressed as stem volume loss per annum. This led to substantial differences between means per treatment and between means per combination of treatments (Table 4.10), although there was again no indication of a correlation between mortality on the one hand and logging or refinement intensity on the other. The average loss in the three replications was 2.13 m^3.ha^{-1}.y^{-1}; in virgin forest plots the loss was even higher: 2.53 m^3.ha^{-1}.y^{-1} (standard deviation 0.43 m^3.ha^{-1}.y^{-1}). Differences between treatments could not be proven with ANOVA ($p > 0.05$) and are probably mostly due to chance.

Table 4.10. Mortality among commercial species (1978 list) between the 1982-1983 and 1999-2000 enumerations (1-ha plots), expressed as stem volume growth. Trees > 15 cm dbh

Refinement	Logging intensity							
	E15		E23		E46		All	
	dV	S.D.	dV	S.D.	dV	S.D.	dV	S.D.
S0	-1.26	0.37	-3.19	1.48	-0.96	1.01	-1.80	1.39
SR18	-2.20	0.22	-3.36	1.92	-1.63	0.25	-2.40	1.24
SR14	-2.60	0.66	-2.38	1.04	-1.61	0.60	-2.20	0.82
All	-2.02	0.72	-2.98	1.39	-1.40	0.69	-2.13	1.16

dV: volume growth in m^3 per hectare per year. Source: Jonkers et al. (2005)

4.4.4 Ingrowth and regeneration

Photo 4.4. A new sprout helped a poison- girdled tree to survive. (Photo J. Wirjosentono)

Sustainable rainforest management means, among others, that mortality among species of commercial value should be compensated by ingrowth, that is, trees reaching a size of 15 cm dbh, to secure future harvests. Furthermore, there should remain sufficient advance regeneration (trees smaller than 15 cm diameter). During one cutting cycle of 25 years, those trees of commercial species which were felled or killed during logging operations should be replaced by ingrowth of the same group of species. Furthermore, commercial trees, which died during the recording period, should also be replaced by ingrowth. The required ingrowth can thus be estimated as follows:

- The numbers of commercial trees > 15 cm dbh, which died during logging, were estimated by Jonkers (1987) at 7.1 trees.ha^{-1} for exploitation level E15, at 11.9 trees.ha^{-1} for exploitation level E23 and at 19.1 trees.ha^{-1} for exploitation level E46. As the period between the 1982-1983 and 1999-2000 enumerations covers 67 % of the 25-year cutting cycle, at least two-third of this loss due to felling has to be replaced by ingrowth during this period.
- One can assume the same mortality for all treatments, that is 18 trees.ha^{-1} during the 17 years recording period.
- This means that the ingrowth should be at least 22.8 trees.ha^{-1} for exploitation level E15, 26.1 trees.ha^{-1} for exploitation level E23 and 31.1 trees.ha^{-1} for exploitation level E46.

The recorded ingrowth in undisturbed forest amounted to just 14.67 trees.ha^{-1} in 17 years. Hence, ingrowth after logging should be much more than in untouched forest.

In the MAIN experiment, the minimum amounts for ingrowth were met where silvicultural treatment had been applied, but logging without silvicultural treatment resulted often in inadequate ingrowth (see Table 4.11). The impact of logging intensity on ingrowth could not be proven, but the positive effect of silvicultural treatment could be shown with ANOVA (p = 0.046). The differences between both refinement treatments (SR18 and SR14) on the one hand and the control treatment (S0) on the other hand were also significant when tested with Fisher's t-test (p = 0.03 and p = 0.04 respectively). However, the difference between the effects of both refinement treatments was not evident (p = 0.69).

Table 4.11. Ingrowth of commercial species (1978 list) between the 1982-1983 and 1999-2000 enumerations (1-ha plots; ingrowth > 15 cm dbh)

Refinement	Logging intensity							
	E15		E23		E46		All	
	$N.ha^{-1}$	S.D.	$N.ha^{-1}$	S.D.	$N.ha^{-1}$	S.D.	$N.ha^{-1}$	S.D.
S0	21.33	13.50	32.00	7.21	28.67	13.80	27.33	11.34
SR18	41.33	18.50	42.33	20.21	42.67	17.04	42.11	16.14
SR14	36.67	10.50	51.00	28.51	49.00	20.52	45.56	19.53
All	33.11	15.52	41.78	19.65	40.11	17.51	38.33	17.38

$N.ha^{-1}$: number of trees per hectare
Source: Jonkers et al. (2005)

This leads to the conclusion that in a 25-year cutting cycle logging without silvicultural treatment often led to ingrowth levels insufficient to compensate losses incurred due to logging and mortality, while the significantly higher ingrowth after both refinement treatments was more than adequate. Apparently, silvicultural treatment is required to ascertain an adequate amount of ingrowth.

The advanced regeneration (saplings) of commercial species, recorded in 1982-1983 and 1999-2000, is given in Table 4.12. Apparently, sapling densities increased considerably in the silviculturally treated plots. The changes in sapling densities in plots without silvicultural treatment was also positive, but distinctly less spectacular. This indicates that silvicultural treatment has a strong beneficial effect on the regeneration, but that adequate sapling densities can also be obtained without such treatment.

Table 4.12. Number of saplings of commercial species in relation to logging intensity and silvicultural treatment. MAIN experiment, replications 2 and 3 only. Sample size: 0.08 ha per combination of treatments.

Logging intensity	Silvicultural treatment	$N.ha^{-1}$		Change
		1999-2000	1982-1983	
E15	S0	412.5	275.0	137.5
	SR18	700.0	587.5	112.5
	SR14	650.0	362.5	287.5
	All	587.5	408.3	179.2
E23	S0	687.5	387.5	300.0
	SR18	875.0	425.0	450.0
	SR14	837.5	362.5	475.0
	All	800.0	391.7	408.3
E46	S0	537.5	425.0	112.5
	SR18	787.5	412.5	375.0
	SR14	900.0	462.5	437.5
	All	741.7	433.3	308.3

Logging intensity	Silvicultural treatment	N.ha^{-1}		Change
		1999-2000	1982-1983	
All	S0	545.8	362.5	183.3
	SR18	787.5	475.0	312.5
	SR14	795.8	395.8	400.0

N.ha^{-1}: number of saplings per hectare
Source: Jonkers et al. (2005)

4.4.5 Volume increment

An important objective of sustainable forest management is to achieve a volume increment of commercial species sufficient to compensate losses incurred during logging. These losses are more than the volumes extracted, as the stumps, the top ends and defective parts of the felled stems are not hauled out and remain in the forest to rot. In addition, some trees of commercial species die during the logging operation due to felling damage. The volumes to be replaced add up to about 23.5 $m^3.ha^{-1}$ for the lowest felling intensity and to 58.7 $m^3.ha^{-1}$ for the highest felling intensity. Assuming a 25-year cutting cycle, this would mean that the required annual volume growth amounts to 0.9 $m^3.ha^{-1}$ for the lowest logging intensity (E15), 1.4 $m^3.ha^{-1}$ for the intermediate intensity (E23) and 2.4 $m^3.ha^{-1}$ for the highest one (E46).

Volume growth depends not only on diameter growth, mortality and ingrowth, but also on the density and the size class distribution of the commercial stand[5]. When a variable is determined by such a variety of parameters, of which some have little or no relation to the treatments applied, one may expect a large amount of unexplained variation. This makes volume increment less fit for statistical testing than diameter growth. Mortality and the original composition of the forest determine volume increment to a large extent, and are major sources of unexplained variation.

Logging affects volume increment in various ways. On the one hand, it opens up the canopy and may therefore stimulate the growth and survival of the remaining commercial trees. On the other hand, it reduces the number of commercial trees and therefore the growth potential of the commercial stand. The effect of logging intensity on volume increment may therefore be either positive or negative.

5 The volume increment per unit area is the sum of the volume increments of individual trees and therefore dependent on the number of trees per unit area. Individual large trees contribute substantially more than small trees. This can be explained as follows:

- The volume equation for the MAIN experiment is: $V = -0.2335 + 0.001125D^2$ (Jonkers 1987); where V = volume in m^3 and D = dbh in cm.
- This means that the relation between volume increment (dV), the stem diameter and diameter growth (dD) is: $dV = 0.001125*dD*(2D + dD)$.
- As dD << D as a rule and as dD changes only slightly with increasing D, volume increment dV increases almost proportionally with D.

Silvicultural treatment stimulates volume increment through increased diameter growth and recruitment. The impact of refinement on mortality was less evident and rather erratic, however, and this will partially blur the overall effect on volume growth.

Volume increment in relation to the treatments is summarised in Table 4.13. The increment in the virgin forest plots was negligible, as expected. In plots where logging was not followed by silvicultural treatment, volume increment was mostly positive, although the relation between harvest intensity and volume increment remained unclear. It seems that a modest sustained yield can be achieved without any silvicultural treatment, but this could not be proven (see also Section 4.3).

Table 4.13. Volume increment* among commercial trees > 15 cm dbh (between the 1982-1983 and 1999-2000 enumerations; 1-ha plots of the MAIN experiment)

Logging intensity	Silvicultural treatment	Volume increment ($m^3.ha^{-1}.y^{-1}$) due to		
		Tree growth and ingrowth	Mortality	Total
Untouched	None	2.55	-2.54	0.01
E15		3.61	-1.26	2.35
E23		2.30	-3.20	-0.90
E46		3.89	-0.96	2.93
E15	SR18	4.21	-2.20	2.01
E23		3.56	-3.36	0.20
E46		3.56	-1.62	1.94
E15	SR14	4.47	-2.60	1.87
E23		4.61	-2.38	2.23
E46		3.47	-1.61	1.86
All	None**	3.27	-1.81	1.46
	SR18	3.78	-2.40	1.38
	SR14	4.19	-2.21	1.98

* Volume equation: $V = -0.2335 + 0.001125D^2$ (Jonkers, 1987); V = volume in m^3 and D = dbh in cm

** Except untouched plots

Source: adapted from Jonkers et al. (2005)

There is a positive relation between refinement intensity and the volume gains due to tree increment and ingrowth. Volume losses due to mortality were somewhat higher in the silviculturally treated plots than in plots without silvicultural treatment, but there is no indication that these losses are treatment-related. Mortality was indeed a major source of unexplained variation: average volume loss due to mortality amounted to 2.1 $m^3.ha^{-1}.y^{-1}$, but losses in individual plots ranged from 0.37 to 4.32 $m^3.ha^{-1}.y^{-1}$. The evidence indicates that one refinement with a 20-cm diameter limit is sufficient to secure a second yield of at least 25 $m^3.ha^{-1}$ after 25 years.

Photo 4.5. Stereoscopic photo of an untreated forest in Mapane region about 20 years after logging. (Photo N.R. De Graaf)

Photo 4.6. Stereoscopic photo of a forest in Mapane region 7 years after refinement. (Photo N.R. De Graaf)

4.5 Impact of silvicultural treatment on other tree species

Species, which were not on the list of commercial species in the 1970s, can be grouped into four categories:

- Timber species, which were not on the original list but which are currently on the market. This category is referred to below as "Commercial B";
- Potentially commercial species ("Commercial P"), that is, other species which are included in the CELOS list of commercial species (CELOS 2002) because they may become marketable in the future;
- Non-commercial pioneer species; and
- Other non-commercial species.

Trees of these species were supposed to be killed during refinement if they exceeded the diameter limit. In the MAIN experiment, the numbers of poison-girdled "Commercial B" trees were rather modest, 2.1 and 7.2 trees.ha^{-1} in refinements SR18 and SR14, respectively. Some of those were still alive in 1999-2000 (1.0 trees.ha^{-1} in each treatment). The numbers of poison-girdled "Commercial P" trees were much higher, 9.1 and 17.9 trees.ha^{-1}. Again, a few of those survived until 1999-2000 (1.3 and 1.4 trees.ha^{-1}). "Non-commercial pioneer species" were less common; 1.9 and 10.2 trees.ha^{-1} were poison-girdled in refinements SR18 and SR14, respectively. Relatively many of them were still alive in 1999-2000 (1.0 trees.ha^{-1} in refinement SR18 and 3.2 trees.ha^{-1} in refinement SR14). The numbers of poison-girdled "Other non-commercial species" trees were much higher (19.7 and 36.2 trees.ha^{-1}), and only few of them were found alive in 1999-2000 (1.7 and 1.4 trees.ha^{-1}).

Table 4.14. Mortality among other currently commercial species (not on the 1978 list) and species with commercial potential between the 1982-1983 and 1999-2000 enumerations (1-ha plots; trees > 15 cm dbh)

Refinement	Logging intensity							
	E15		E23		E46		All	
	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.
Other currently commercial species								
S0	3.00	2.00	2.00	0.00	5.00	2.83	3.29	2.06
SR18	2.50	2.12	1.50	0.71	4.00	2.83	2.67	1.97
SR14	3.00	0.00	2.00	1.41	2.33	0.58	2.43	0.79
All	2.86	1.46	1.83	0.75	3.57	2.07	2.80	1.64
Potentially commercial species								
S0	5.00	2.65	9.00	1.73	3.00	1.00	5.67	3.12
SR18	9.33	4.16	10.33	7.09	5.33	3.06	8.33	4.95
SR14	7.33	0.58	5.67	1.53	10.67	1.15	7.89	2.42
All	7.22	3.11	8.33	4.27	6.33	3.81	7.30	3.71

N.ha^{-1}: number of trees per hectare
Source: Jonkers et al. (2005)

Mortality of "Commercial B" and "Commercial P" species after the 1982-1983 enumeration is summarised in Table 4.14. The loss in the "Commercial B" category was somewhat lower in the silviculturally treated plots than in the untreated plots. This was expected, since many trees had been poison-girdled and were already dead before the 1982-1983 enumeration. Mortality among "Commercial P" species, however, was higher in silviculturally treated forest, because most poison-girdled trees died after the 1982-1983 enumeration. Mortality in the virgin forest plots (4.33 and 6.67 trees.ha^{-1} for "Commercial B" and "Commercial P", respectively) was slightly higher than in untreated logged forest, which was probably due to a difference in initial stocking. There was no clear relation between logging intensity and mortality.

The losses in the category "Commercial B" were also expressed in volume terms, as the species concerned are at present of commercial value. Between the refinement and the 1982-1983 enumeration, mortality amounted to 4.0 and 7.6 m^3.ha^{-1} for refinements SR18 and SR14, respectively. Thereafter, losses in the silviculturally treated plots were modest (Table 4.15), amounting to 1.8 and 3.4 m^3.ha^{-1} in 17 years. This adds up to 5.8 m^3.ha^{-1} for refinement SR18 and 11.0 m^3.ha^{-1} for refinement SR14. The volume lost in the control treatment (S0) amounted to 6.8 m^3.ha^{-1} and therefore exceeded the losses during and after refinement in treatment SR18, but not those incurred in refinement SR14.

Table 4.15. Mortality among other currently commercial species (not on the 1978 list) between the 1982-1983 and 1999-2000 enumerations (1-ha plots), expressed as stem volume growth. Trees > 15 cm dbh

Refinement	Logging intensity							
	E15		E23		E46		All	
	dV	S.D.	dV	S.D.	dV	S.D.	dV	S.D.
S0	-0.51	0.46	-0.13	0.12	-0.51	0.30	-0.40	0.35
SR18	-0.09	0.05	-0.05	0.03	-0.18	0.17	-0.11	0.10
SR14	-0.15	0.12	-0.07	0.07	-0.31	0.36	-0.20	0.24
All	-0.29	0.34	-0.08	0.07	-0.33	0.28	-0.24	0.28

dV: volume growth in m^3 per hectare per year

Mortality of "Non-commercial pioneer" and "Other non-commercial" species after the 1982-1983 enumeration is summarised in Table 4.16. The losses in these categories were somewhat lower in the silviculturally treated plots than in the untreated plots, in spite of the high number of poison-girdled trees still alive during the 1982-1983 enumeration. It seems that in silviculturally treated forest mortality among "Other non-commercial species" was mainly a delayed effect of poison girdling, as relatively few trees which had not been poison-girdled died. Mortality in the virgin forest plots was comparable to rates in untreated logged forest (5.56 and 21.33 trees.ha^{-1} for "Non-commercial pioneer species" and "Other non-commercial species", respectively), and there was again no clear relation between logging intensity and mortality. It is remarkable that more than 50 % of the trees of pioneer species, which were larger than 15 cm dbh in 1982, were still alive in 2000. These species apparently are not as short-lived as is often thought.

Table 4.16. Mortality among species without commercial potential in the period between the 1982-1983 and 1999-2000 enumerations (1-ha plots); number per hectare of trees > 15 cm dbh

Refinement	Logging intensity							
	E15		E23		E46		All	
	$N.ha^{-1}$	S.D.	$N.ha^{-1}$	S.D.	$N.ha^{-1}$	S.D.	$N.ha^{-1}$	S.D.
Non-commercial pioneer species								
S0	8.67	2.52	6.00	2.65	9.00	0.00	7.89	2.32
SR18	4.00	1.73	5.00	1.73	8.00	4.58	5.67	3.16
SR14	4.00	2.65	6.50	3.54	7.67	4.73	6.00	3.63
All	5.56	3.09	5.75	2.25	8.22	3.35	6.54	3.10
Other non-commercial species								
S0	15.00	5.57	31.00	11.53	20.33	4.93	22.11	9.84
SR18	15.00	6.00	22.33	6.03	23.67	12.50	20.33	8.57
SR14	21.00	8.72	22.33	9.29	18.33	4.16	20.56	6.93
All	17.00	6.69	25.22	9.09	20.78	7.41	21.00	8.24

$N.ha^{-1}$: number of trees per hectare. Source: Jonkers et al. (2005)

The average growth rates of trees in category "Commercial B" were low, ranging from 0.17 $cm.y^{-1}$ in logged forest without silvicultural treatment to 0.27 $cm.y^{-1}$ after refinement (SR14). Most species in this category were rather rare (fewer than 1.5 $trees.ha^{-1}$ > 15 cm dbh prior to silvicultural treatment). The only common one, *Lecythis corrugata*, was also the slowest grower with mean rates ranging from 0.12 $cm.y^{-1}$ in the virgin forest plots to 0.22 $cm.y^{-1}$ after refinement (SR14). The average growth rates of trees in category "Commercial P" were substantially higher, ranging from 0.30 $cm.y^{-1}$ in the virgin forest plots to 0.43 $cm.y^{-1}$ after refinement (SR14). The mean increments varied considerably among species. Most common species were slow growers. By far the fastest growing species was Sclerolobium albiflorum with mean growth rates as high as 1.3 – 1.9 $cm.y^{-1}$.

The mean increments in the category "Non-commercial pioneer species" deviated very little from the rates in the "Commercial P" category and ranged from 0.30 $cm.y^{-1}$ in the virgin forest plots to 0.46 $cm.y^{-1}$ after refinement (SR14). Average growth rates of individual pioneer species were mostly close to these mean values, except for Pourouma spp., which grew faster.

The mean increments in the category "Other non-commercial species" ranged from 0.20 $cm.y^{-1}$ in the virgin forest plots to 0.27 $cm.y^{-1}$ after refinement (SR14). Most species in this rest category are understorey species with mean growth rates of 0.1 - 0.2 $cm.y^{-1}$. The fastest growing species was again a *Sclerolobium* species: the canopy tree *S. melinonii* with rates of 0.7 – 0.9 $cm.y^{-1}$.

In all categories and in most individual species diameter growth was highly variable with standard deviations in the order of magnitude of 80 % of the mean values. Furthermore, the growth rates of individual species indicate that virtually all species respond to logging and silvicultural treatment with increased diameter growth.

Trees of "Commercial B" species, which died during or after logging and silvicultural treatment, should preferably be replaced by ingrowth within one cutting cycle. The average ingrowth figures for the various combinations of logging and refinement intensities are given in Table 4.17, together with their standard deviations. Ingrowth generally did not reach the desired levels in plots where no silvicultural treatment had been applied. This may indicate slow recovery, but it may also be due to long-term variation in ingrowth; ingrowth in virgin forest plots, which in 17 years amounted to 3.00 trees.ha^{-1} (S.D. = 1.73), was also less than the mortality in the same period (4.33 trees ha^{-1}). Ingrowth after silvicultural treatment was generally adequate.

Table 4.17. Ingrowth of other currently and potentially commercial species (not on the 1978 list) between the 1982-1983 and 1999-2000 enumerations (1-ha plots; ingrowth > 15 cm dbh)

Refinement	Logging intensity							
	E15		E23		E46		All	
	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.
Currently commercial species (not on the 1978 list)								
S0	3.00	1.00	4.33	1.53	3.33	1.53	3.56	1.33
SR18	4.00	1.73	9.00	2.00	7.67	4.93	6.89	3.59
SR14	6.67	2.89	7.67	2.52	9.67	2.89	8.00	2.74
All	4.56	2.40	7.00	2.74	6.89	4.08	6.15	3.24
Other species with commercial potential								
S0	5.00	2.00	10.00	6.56	6.33	2.08	7.11	4.23
SR18	9.00	3.00	15.67	5.51	9.00	7.94	11.22	6.06
SR14	11.67	8.02	12.67	0.58	13.00	1.73	12.44	4.16
All	8.56	5.27	12.78	4.94	9.44	5.10	10.26	5.24

N.ha^{-1}: number of trees per hectare
Source: Jonkers et al. (2005)

The category "species with commercial potential" ("Commercial P") includes a wide variety of timber species, which are not harvested presently but which may become marketable in the future (see Comvalius 2001; CELOS 2002). Therefore, forest management should preferably allow the option to restore the pre-felling stocking of such species before the end of the second cutting cycle. The average ingrowth figures for the various combinations of logging and refinement intensities are given in Table 4.17, together with their standard deviations. Ingrowth was very variable, but it generally reached the desired levels. "Commercial P" trees lost due to logging, refinement and natural mortality will probably be compensated by ingrowth within one cutting cycle where no silvicultural treatment had been applied and within two cutting cycles in silviculturally treated forest. Ingrowth in virgin forest plots, which in 17 years amounted to 6.33 trees.ha^{-1} (S.D. = 2.89), was slightly less than the mortality in the same period (6.67 trees.ha^{-1}).

Shortly before refinement, there were on average 18.3 trees.ha^{-1} of "Non-commercial pioneer species" in the three replications. Most of these species are rather short-lived, so mortality was high: 40 % died in 17 years in plots where no silvicultural treatment had been applied while in silviculturally treated forest, some 40-50 % died between 1982 and 2000, depending on the treatment. Furthermore, one may assume that 1-2 trees.ha^{-1} were destroyed during logging operations, depending on felling intensity. So, an ingrowth level of 8-11 trees.ha^{-1} would fully compensate mortality plus losses due to logging.

It was expected that ingrowth in the replications would be more than sufficient to compensate mortality and that it would exceed the ingrowth in the virgin forest plots, which amounted to 6.67 trees.ha^{-1} (S.D. = 3.06). This certainly was the case; ingrowth was usually abundant, but varied considerably between plots with the same treatments (Table 4.18). Furthermore, the means suggest a sharp rise in ingrowth with increasing exploitation and refinement intensity. Effects of logging intensity and silvicultural treatments on ingrowth proved indeed significant when tested with ANOVA ($p < 0.05$), and the t-tests showed significant differences between refinement treatment SR14 and the silvicultural control treatment S0 ($p = 0.03$) and also between logging intensities E15 and E46 ($p = 0.003$). Differences between logging intensity E23 on the one hand and E15 and E46 on the other hand, and between refinement treatment SR18 on the one hand and treatments S0 and SR14 on the other could not be proven with the t-test ($p > 0.05$).

Table 4.18. Ingrowth of species without commercial potential between the 1982-1983 and 1999-2000 enumerations (1-ha plots; ingrowth > 15 cm dbh)

Refinement	Logging intensity							
	E15		E23		E46		All	
	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.	N.ha^{-1}	S.D.
Non-commercial pioneer species								
S0	13.33	14.57	29.00	13.00	58.00	30.79	33.44	26.79
SR18	37.00	20.22	55.33	16.50	72.67	22.48	55.00	23.14
SR14	40.33	15.95	69.67	37.00	111.33	44.11	73.78	42.98
All	30.22	19.53	51.33	27.78	80.67	37.67	54.07	35.15
Other non-commercial species								
S0	20.33	13.65	25.67	2.08	22.33	8.50	22.78	8.44
SR18	29.67	3.21	31.00	7.94	34.00	7.00	31.56	5.85
SR14	48.00	9.64	30.00	1.73	24.00	5.57	34.00	12.20
All	32.67	14.87	28.89	4.86	26.78	8.24	29.44	10.12

N.ha^{-1}: number of trees per hectare. Source: Jonkers et al. (2005)

Shortly before refinement, there were on average 79.5 trees.ha^{-1} of "Other non-commercial species" in the three replications. Mortality was not high where no silvicultural treatment had been applied, 22 trees.ha^{-1} died in 17 years, while in silviculturally treated forest, some 33-44 trees.ha^{-1} died between 1982 and 2000, depending on the treatment. Furthermore, one may assume that 3-7 trees.ha^{-1} were killed during logging operations, depending on felling intensity. So, ingrowth levels in the order of 27 trees.ha^{-1} (no silvicultural treatment), 38 trees.ha^{-1} (refinement SR18) and 49 trees.ha^{-1} (refinement SR14) would fully compensate both mortality and fatal logging damage.

Here, it was expected that ingrowth in the replications would compensate only part of the mortality and logging damage, especially in silviculturally treated forest, and that it would exceed the ingrowth in the virgin forest plots, which amounted to 18.33 trees.ha^{-1} (S.D. = 5.51). This was to some extent true; it takes the "Other non-commercial species" apparently more than 17 years to recover from losses due to logging and refinement (see Table 4.18), but tree densities at the end of the 25-year cutting cycle will probably be comparable to pre-felling densities.

Table 4.18 suggests that logging intensity hardly had any impact on ingrowth of these species and that silvicultural treatment had a stimulating effect. An influence of logging intensity on ingrowth could indeed not be proven ($p >> 0.05$), while the effect of silvicultural treatment could be shown with ANOVA ($p = 0.025$). Also, the differences between both refinement treatments (SR18 and SR14) on the one hand and the control treatment (S0) on the other were significant when tested with Fisher's t-test ($p = 0.02$ and $p = 0.04$, respectively). A difference between the effects of refinement treatments SR14 and SR18 could not be proven ($p = 0.60$).

4.6 Consequences for the CELOS Management System

The experimental results show that both logging and silvicultural treatment stimulate the diameter growth and recruitment of tree species and that tree growth increases with logging and refinement intensities. This applies for both commercial and non-commercial tree species. The relation between logging and refinement on the one hand and mortality on the other hand is less straightforward: during timber harvesting and silvicultural treatment, many trees are killed, but in the years thereafter, mortality is rather erratic. Still, volume increment of commercial species is generally positive, indicating a recovery of the commercial stand.

In the MAIN experiment, the forest is richer in commercial timber than most natural forests in Suriname. Under these conditions, the rate of recovery is such that:

- A modest sustained yield of about 15 m^3.ha^{-1} once every 25 years can probably be achieved without silvicultural intervention;
- A higher production level of approximately 25 m^3.ha^{-1} once every 25 years will require one refinement with a diameter limit of 20 cm; and
- If one wants to achieve a sustained yield of about 40 m^3.ha^{-1} in a 25-years' cutting cycle, one refinement is not sufficient and at least one follow-up treatment will be needed.

In poorer stands, diameter growth rates after logging will be similar as in better stocked stands, but volume increment will be less as there is less growing stock. Hence, silvicultural treatment will be necessary in such forest if one wants to produce sustainably. Such stands will generally contain more non-commercial trees than richer forest, and the intensity of the 20-cm diameter limit refinement will therefore be higher. The Mapane experiments show that this may result in a dramatic increase in the growth of individual trees and to a volume increment comparable to the rate obtained in the MAIN experiment, and also that a second treatment is required after eight years to maintain growth at this level.

First refinements with a 20-cm diameter limit yielded good results in all experiments. The evidence presented gives no reason for major changes, in spite of the considerable proliferation of pioneer species. Applying a lower diameter limit will result in even larger numbers of pioneer trees and is therefore undesirable, and higher diameter limits did not adequately stimulate the growth of the commercial stand. However, Jonkers' (1987) suggestion to use a limit of 20 cm in the vicinity of commercial stems and a higher limit elsewhere (see Section 3.3) may be considered as protection measure for very poorly stocked parts of the forest. Commercial trees with logging damage should be preserved during the first refinement: most of them will either die or recover, and it is therefore not advisable to kill them.

Furthermore, the findings suggest that the second refinement should focus on reducing competition from pioneer species and a few other fast growing non-commercial species rather than on eliminating slow growing understorey trees. In addition, trees with very serious defects can be eliminated.

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