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# Pioneer and climax tree regeneration following selective logging with silviculture in Suriname

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**Abstract**

In the tropical rain forest of Suriname the occurrence of eight test species, four pioneer and four climax species, was analyzed in a silvicultural field experiment about 20 years old, in three replications of treated forest plots in which 15, 23 and 46 $m^3$ had been extracted. Extraction levels 23 and 46 $m^3$ had been followed immediately by a light or heavy refinement. Actual research was done in the replicated plots of the experiment as well as in primary forest. All measurements were made in the vegetation layer of 3–10 m. In addition to this, total tree density, forest class (a classification used as disturbance indicator) and palm and liana density were measured.

Effects of the extraction and silviculture are still visible after 20 years, but all values of the measurements taken in the present research fall within the same range as that of virgin forest. Climax species are more abundant than pioneers throughout the entire experiment, regardless of treatment. Palm and liana densities, however, show contrasting effects to the severity of treatments in the three replications. It is indicated that natural heterogeneity and the forest's resilience to disturbance are greater than the treatment effects measured in this investigation 20 years later. Conclusion is that the tropical rain forest in Suriname, when treated with the Celos Silvicultural System, does not tend to regress to a more secondary forest as the original primary rain forest structure, composition and dynamics are largely maintained.


*Keywords:* Species composition; Tropical rain forest; Selective logging; Celos Silvicultural System

## 1. Introduction

A number of studies have dealt with the subject of regeneration following selective and conventionally executed logging. In Bolivia, Fredericksen and Mostacedo (2000) found a significant rise in seedling and sapling density 14 months after selection logging. In a Bornean forest, 8 years after selective logging, density and species richness were found lowered as compared to pre-harvest levels, but no major changes in family level taxonomic composition were observed (Cannon et al., 1998). The opposite occurred in the Brazilian Amazon, where after 3–9 years species richness was slightly elevated (Magnusson et al., 1999). In a forest in India, selective felling with limited mechanization had little effect on floristic composition 15 years later and within 20 years the forest was expected to resemble an unlogged forest (Pélissier et al., 1998). In a study in the Philippines, 50 years after selective logging, species richness was the same as in unlogged forest, although species composition was altered (Luna et al., 1999).

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Despite the above-mentioned studies, there are as of yet few controlled replicated long-term experiments that indicate how other approaches than conventional logging affect vegetation development. Research must therefore be carried out in controlled experiments comparing results in replicated treatments consisting of different logging regimes (Simberloff, 1999), focussing on the impact on stand structure and forest biota (Lindenmayer, 1999). An important aspect of this impact is the effect of logging on canopy or gap dynamics, which play an important role in the maintenance of species diversity in rain forests. Felling a single tree results in a gap formation similar to the natural situation, but often more trees are felled in a small area and then the gaps are larger, resulting in far higher light levels (Ter Steege, 1993). According to Van der Meer (1995), it can be hypothesized that when large gaps are clustered and repeatedly disturbed, species richness in these places will decrease since the vigorously growing light demanding species will out-compete other species. One example of an experiment as called for by Simberloff (1999) and Lindenmayer (1999) can be found in Suriname and will be described in this paper.

In Suriname, based on a series of experiments started in 1965, the Celos Silvicultural System (CSS) has been developed by De Graaf (1986), together with Jonkers (1987) and others. The CSS is a cost-effective way of growing more marketable wood in previously exploited neotropical rain forest, based on relatively short felling cycles of 20–30 years (De Graaf, 2000). In a large field trial described by Jonkers (1987), the effect on vegetation structure and mortality of different exploitation and refinement levels as proposed under the CSS have been experimentally tested, starting in 1978.

Within this large experiment (called Expt 78/5) a study has been done in June and July 2000 on the occurrence of a number of pioneer and climax tree species under increasing levels of disturbance initiated 20 years ago by both logging and silvicultural refinement. In this paper, we report on the results of this study. Apart from pioneer and climax trees, also some stand characteristics have been recorded, amongst which density of palms and lianas. Last named categories were supposed to have a behavior different from that of dicotyledonous trees. More specific questions were: (a) have the indicated pioneer species gained terrain, especially after the most intensive treatments, and (b) what are the effects of the treatments on lianas and palms.

## 2. Methods and materials

### 2.1. Study site

This research has been conducted within the original Expt 78/5 at the Tonka research site, Suriname. This study site is located in the region of the Kabo creek, approximately 100 km southwest of Paramaribo (5°15′N, 55°43′W). It has a level to undulating landscape, about 25–36 m above sea level. The climate is classified as Af under Köppens system, the average rainfall is 2385 mm per year, in the driest month there is on average 98 mm of rainfall. The parent material is the Zanderij sediment of sandy clay loam texture which is well drained but with good water retention capacity. The soil is reasonably homogeneous and was classified (Poels, 1987) as Haplorthox according to the USDA Soil Taxonomy (FAO equivalent: Ferralsol). It is acid and very poor in nutrients but has a good structure. Cation exchange capacity (CEC, at soil pH) in the A-horizon (0–49 cm) ranges from 1.01 to 1.38, in the B-horizon (49–300 cm) this is 0.25–0.65, decreasing with depth. Respective ranges for pH ($H_2O$) are 3.8–4.6 for the A-horizon and 4.8–5.0 for the B-horizon. The pH increases with depth. Organic matter content in the A-horizon lies between 0.81 and 3.52% and between 0.17 and 0.48% in the B-horizon, and decreases with depth. C/N ratio of the soil for the A-horizon varies between 11.8 and 17.8, in the B-horizon between 9 and 14, also decreasing with depth (Jonkers, 1987).

The study site is located in tropical rain forest and a total of 193 vernacular names have been recorded of which 37 are commercial species. Basal area before application of the treatments was about 30 $m^2$ (lower diameter limit 5 cm). The most abundant species are *Dicorynia guianensis* Amshoff, *Qualea rosea* Aubl. and *Dendrobangia boliviana* Rusby. The presence of palms is conspicuous, mainly boegroemaka (*Astrocaryum sciophilum* Pulle) and paramaka (*Astrocaryum paramacca* Pulle), both undergrowth species. Lianas are numerous but very thick individuals are rare (Jonkers, 1987).

### 2.2. Experimental set up of Expt 78/5

In the original experiment, started in 1978, three levels of exploitation and three levels of silvicultural refinement were tested in a $3^2$-factorial experiment replicated three times. Also "virgin forest plots" (VFPs) have been set up in three replications. The experimental replications are made up of nine compartments on which the treatments have been applied. The VFPs are replicated in three separate compartments. A compartment comprises a 1 ha assessment plot surrounded by a 50 m bufferzone. The assessment plot has been divided into one hundred 10 m × 10 m subplots.

The three levels of exploitation removed basal areas of about 1, 2 and 4 $m^2\ ha^{-1}$. This yielded, respectively, about 15, 23 and 46 $m^3\ ha^{-1}$. These treatments were coded E15, E23 and E46. The logging took place in 1979–1980. E46 was considered a non-acceptable high level, too destructive for general application in future forest management practice.

The three levels of silvicultural refinement consisted of: (a) a control, (b) a light refinement, killing unwanted trees >30 cm dbh and reducing basal area to 18 $m^2$, and (c) a heavy refinement, killing unwanted trees >20 cm dbh and reducing basal area to 14 $m^2$. This heavy refinement was considered the utmost yet acceptable when avoiding a change into a forest dominated by pioneer species. Treatments entailed climber-cutting and poison-girdling of non-commercial species and commercial trees with serious defects. These treatments were coded S0, SR18 and SR14 and took place in 1980–1981. The whole experiment has been completely recorded again recently.

For the investigation reported on here, only part of the large (148) hectare experiment could be visited, so measurements have only been made in three compartments per replication, i.e. in forest that received a light treatment (code E15-S0; 60 subplots), a medium treatment (code E23-SR18; 60 subplots) and a heavy treatment (code E46-SR14; 60 subplots), as well as in the three VFP compartments (also totaling to 60 subplots).

### 2.3. Measurements and data analysis

For the fieldwork, eight tree species were selected as test species. Of these species, density was measured in a 20% random sample of the 100 subplots per treatment per replication. The test species were selected on the grounds that they are either strongly light demanding or shade tolerant in their early life, and that they are the most common species in the study area (according to Jonkers, 1987, and/or Schulz, 1960). Both commercial and non-commercial species were selected since this may have an effect on regeneration after exploitation, see Table 1 for the test species used. Apart from the recording of these eight species, also the densities of all species encountered were recorded.

All measurements concerning the density of trees were made in the vegetation layer of 3–10 m. The reason for this is that older and larger, mature trees are not suitable as test subjects since they often have a slow response to changes in the micro-climate (Zagt, 1997). Seedlings are suitable but need to be studied in a longer time frame, not in a single visit, for demographic processes to take effect. Selecting the undergrowth layer of 3–10 m eliminates the mature trees and seedlings from the measurements and thereby ensures that micro-climate is still a strong determinant of species composition and that demographic processes have had ample time to take effect. This is in accordance with Magnusson et al. (1999). If the application of the treatments still continues to have an effect on forest composition after 20 years, in addition to a short-lived stimulus of pioneer regeneration directly after logging, this is where it can be detected more easily than in other forest strata.

Additionally, a number of stand characteristics were recorded in the same 20% random sample. Total tree density in the 10 m × 10 m plots in the research layer was measured and with the help of the database of the

Table 1
The eight test species used in this research

| | |
|---|---|
| *Light demanding* | |
| Commercial | *Goupia glabra* Aubl. (Celastraceae) |
| | *Loxopterygium sagotii* Hook (Anacardiaceae) |
| Non-commercial | *Inga alba* Willd. (Mimosaceae) |
| | *Cecropia sciadophylla* Mart. (Cecropiaceae) |
| *Shade tolerant* | |
| Commercial | *Dicorynia Guianensis* Amshoff (Caesalpiniaceae) |
| | *Qualea. Rosea* Aubl. (Vochysiaceae) |
| Non-commercial | *Dendrobangia boliviana* Rusby (Icacinaceae) |
| | *Lecythis corrugata* Mori (Lecythidaceae) |

Celos Research Institute forest class was analyzed. Forest class is a (non-numerical) variable that was designed as a general disturbance indicator (Jonkers, 1987). It covers, per subplot: (1) high forest with a maximum of two individuals of secondary tree species of more than 2 m high; (2) a gap as a result of treefall; (3) a skid trail; (4) high forest with three or more individuals of secondary tree species of more than 2 m high. In addition to this, the density of palms and lianas in the subplots was recorded. This was not an intended part of this research, but since in the field strong differences were observed, it was decided to incorporate this into the present research without any prior hypotheses.

Since it was often found that there was a strong interaction between replication and treatment, the three replications were analyzed separately where necessary. This was done because completely contrasting responses to treatments occurred which would go unnoticed if the replications were analyzed simultaneously as usual. Where applicable an analysis of variance (ANOVA) has been applied after examination of the assumptions of normality (Kolmogorov–Smirnov test) and equal variance (Levene's test). When these assumptions were not valid, and this could not be solved by a transformation of the data, the non-parametric tests that were used to replace the ANOVA and the *t*-test are, respectively, the Kruskal–Wallis test and the Wilcoxon signed rank test. When an ANOVA of all three replications was not possible but a Kruskal–Wallis test was inadequate because of a too large influence of the density differences between replications, then the three replications were also analyzed separately. Contrasts have been examined with a Tukey test and non-numerical data (forest class) were analyzed with a $\chi^2$-test.

Because of low densities per subplot, all calculations were made with the number of individuals and not a measure of biomass. With low numbers, random fluctuations in biomass are unlikely to be averaged out, so this would give more statistical error than clear results. Also because of low densities, the individual climax and pioneer species were grouped together and have not been analyzed separately.

## 3. Results

### 3.1. Tree species densities

In an analysis of the densities of pioneer and climax tree species, no significant treatment effect could be seen in the pioneer species in replication 1 ($p = 0.601$), nor in replication 3 ($p = 0.309$). Replication 2, however, did show an effect ($p = 0.021$). It can be seen in Fig. 1 that the medium treatment has a higher

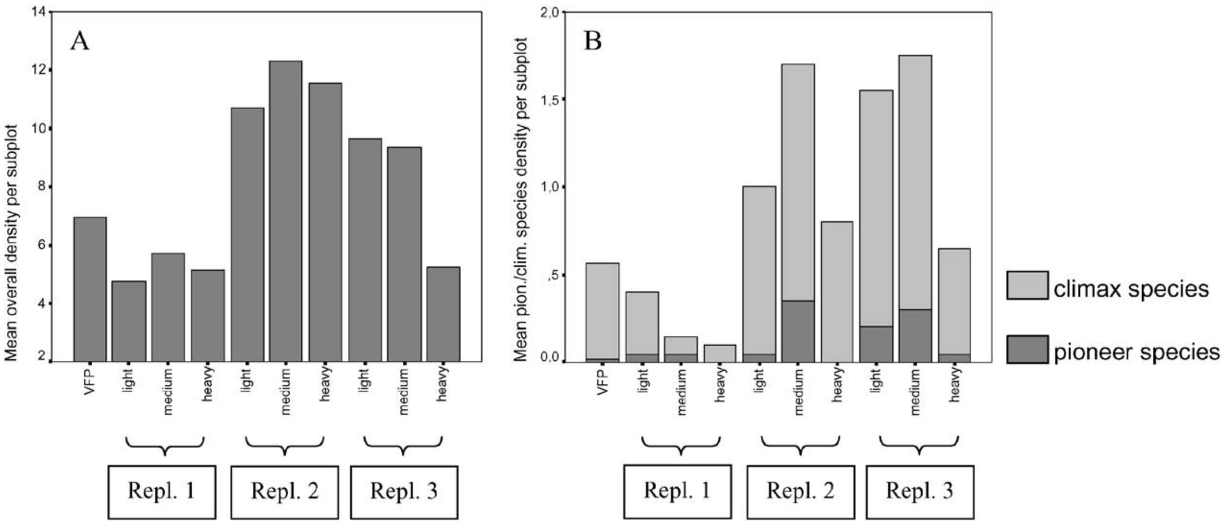


Fig. 1. Mean density in the research layer per 10 m × 10 m subplot for all replications and treatments of: (A) all species and (B) the selected pioneer and climax species in the tropical rain forest of Kabo, Suriname.

number of pioneer species, the same goes for replication 3. The climax species showed no significant treatment effect in any of the replications ($p =$ 0.292, 0.392 and 0.169), though in the graph the medium treatment again shows the highest number of (climax) species in replications 2 and 3 (Fig. 1B).

There is a significant difference in density between pioneer and climax species, throughout the entire experiment, ($p < 0.001$). In replication 1, without stratifying according to treatment, there is a difference in density between pioneer and climax species ($p = 0.021$), the climax species being slightly more abundant. Replication 2 also shows an overall difference in density ($p < 0.001$), and in replication 3 the situation is the same as in replication 2 ($p < 0.001$). Each time the climax species are more abundant than the pioneer species (Fig. 1B).

Total tree species density in the research layer (all species, not just the test species) only showed a significant treatment effect for replication 3 ($p = 0.003$) (replication 1: $p = 0.602$; replication 2: $p = 0.470$). In examining the contrasts, the light treatment differed from the heavy treatment ($p = 0.005$) as did the medium treatment ($p = 0.01$). As shown in the graph, the heavy treatment in replication 3 has the lowest sapling density of the three treatments (Fig. 1A). The graph also shows clear differences in tree density (in the research layer) between replications, with replication 1 having the lowest density.

### 3.2. Forest class

In analyzing forest class, two groups were made: primary forest (forest class 1) and disturbed forest (forest classes 2–4). In order to quantify the correlation between treatment level and forest class, the test statistic Cramér's $V$ has been calculated, the value of which lies between 0 and 1, indicating the strength of the relationship (0: not correlated; 1: perfectly correlated). Forest class was significantly affected by treatment level in replications 2 ($p < 0.001$; $V = 0.701$) and 3 ($p = 0.013$; $V = 0.382$), but not in replication 1

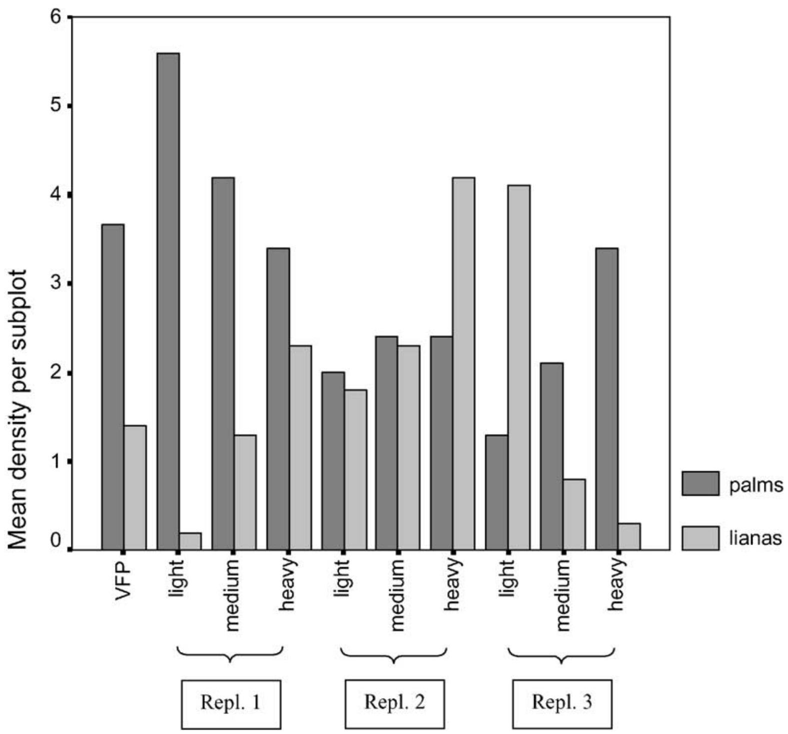


Fig. 2. Mean density of palms and lianas in the research layer per $10\,m \times 10\,m$ subplot for all replications and treatments in the tropical rain forest of Kabo, Suriname.

($p = 0.393$). These results indicate that in the heavier treatments, more disturbed forest is created and that this effect can still be seen after 20 years.

### 3.3. Palm density

An analysis of palm density in replication 1 showed a significant treatment effect ($p = 0.019$). The heavy treatment differed significantly only from the light treatment ($p = 0.014$). In replication 2 no significant treatment effect could be seen ($p = 0.129$), replication 3 on the other hand, did show a strong effect ($p < 0.001$). An examination of contrasts showed that all three treatments were significantly different from each other (light/medium: $p = 0.021$; light/heavy: $p < 0.001$ and medium/heavy: $p = 0.046$). The graphical representation in Fig. 2 shows that there is a completely opposite effect from the different treatments. Where in replication 1 palm density decreases with higher exploitation intensity, the opposite occurs in replications 2 and 3. A *t*-test of difference in mean palm density (regardless of treatment) showed that replication 1 has a significantly higher palm density than does replication 3 ($p < 0.001$). This was so already before the experiment started (De Graaf, pers. comm.).

### 3.4. Liana density

Liana density, simultaneously analyzed in all replications, showed no significant treatment effect ($p = 0.454$). A separate analysis of the replications showed that there is a significant effect in replications 1 ($p = 0.012$) and 3 ($p = 0.002$). The effect in replication 2 just falls outside of statistical significance at the $\alpha = 0.05$ level ($p = 0.054$). The graph (see Fig. 2) again shows an opposite effect. In replications 1 and 2 there is an increase in lianas with higher exploitation level, the opposite occurs in replication 3. A test for differences in mean density showed a significant difference ($p = 0.018$) between replications, replication 1 having the lowest and replication 2 having the highest density. Replication 3 is in between.

## 4. Discussion

A well-known characteristic of rain forests is their heterogeneity. This heterogeneity also applies to the site of Expt 78/5. In replication 1, total tree density (in the research layer) is the lowest of all replications (Fig. 1A). This replication also has the highest palm density and the lowest liana density of all replications. Replication 2 has the highest total tree density. Together with replication 3, it has a low density of palms but in liana density it has an intermediate position. Total tree density takes an intermediate position in replication 3, which has about the same relatively low density in palms as replication 2, but has the highest liana density of all replications. The recent findings presented here concur with the older findings of Jonkers (1987).

Other studies investigating the effect of logging on the occurrence of species or species composition were found not suitable to be compared with the results obtained in this study. This also goes for the studies mentioned in Section 1. Some of them have taken place in SE Asia, where the high share of commercially valuable Dipterocarpaceae leads to much higher harvesting levels and a different reaction (regeneration) after exploitation. Also, the object of the investigation is always the impact of a single conventionally executed logging activity and not the combined effect of a low harvest, low impact operation followed by silvicultural treatment that intervenes in the competitive relationship between species. Therefore, no comparisons will be made here to other studies.

When looking at total tree species density and the density of the eight investigated pioneer and climax species in the selected size-class, i.e. between 3 and 10 m high, a pattern can be seen (Fig. 1A and B). Usually, the medium treatment has the highest density of saplings and young trees, and the heavy and the light treatments have a lower position. The heavy treatment often even has a lower density than has the light treatment. Creating more gaps by harvesting more trees, and by doing so increasing radiation at lower levels, does not lead to a higher density of young trees in the lower strata of the forest. Initially, it does rise but in the heaviest treatment it tends to drop rapidly. The heaviest treatment is the treatment where the heaviest exploitation damage can be expected (felling damage, soil compaction, etc.), which might account for this effect. In the heavy treatment, a lot of advance regeneration may have been destroyed during the harvesting operation. This mortality was higher than in the other treatments since proportionally more trees were harvested as a result of the fact that smaller trees had to be harvested. There were not enough large trees to extract 46 $m^3$ in big logs only (De Graaf, pers. comm.).

When comparing the pioneer species with the climax species it becomes clear that the latter are significantly more abundant, especially in replications 2 and 3. Even in the heaviest treatment, the climax species are more abundant in each of the replications, though in replication 1 it does not reach statistical significance. This indicates that a forest microclimate was maintained in which mainly primary forest species could regenerate. In a simulation study, Huth and Ditzer (2001) found that it is mainly conventional logging on short felling cycles that promotes pioneer species regeneration, the effects of which can be mitigated by reduced impact logging (as was applied in this experiment). The effect of silvicultural interventions clearly differs from that of logging.

The variable forest class indicates that the heavier the treatment is (exploitation and refinement), the more damage is done to the forest (more gaps, skid trails and secondary forest). Even though forest class 2 (a gap as a result of treefall) of course also occurs in untouched forest as part of the natural dynamics, a significant increase in this does indicate the creation of more disturbed forest.

Palm density is the first variable that shows an opposite effect in Fig. 2 (i.e. replication 1 versus replications 2 and 3). In replication 1, palm density decreases with heavier treatment, in the other replications it rises. The reason for this could well be the original difference in density as measured by Jonkers. Where there are a greater number of palms, more damage will occur during exploitation and refinement. This might cause a decline in numbers. Replications 2 and 3 have a much lower density of palms and here less damage will occur while the increased light under heavier treatment might stimulate regeneration and growth and thus cause a rise in numbers.

Liana density also shows a contrasting effect. However, it should be noted that palm density and liana density are not independent. A heavy palm cover can suppress not only tree regeneration but also the development of lianas (Jonkers, 1987; Van Roosmalen, 1980). It is, however, impossible without further experimentation to distinguish between the effect of decreased tree density as a result of treatment (more light) and the effect of increased palm density (less light) or vice versa. It appears (see Fig. 2) that in replication 1, where the high palm density decreases, lianas have been given a chance to increase in numbers. In replication 3, where the low palm density has significantly risen with treatment severity, the high liana density appears to have been forced back. In replication 2, with its low palm and relatively high liana density, both seem to rise with increasing treatment (but not significantly). Replication 2 does have the highest total and commercial tree density and harvesting may have been slightly more severe here, offering an opportunity to both palms and lianas.

An important aspect of this research is to look not only at the difference between the treatments but also at the difference between virgin forest and treated forest. As can be seen in Figs. 1 and 2, values as measured in this research for total tree density, pioneer and climax species density and palm and liana density in treated forest, fall within the same range as those measured in the VFPs. Standard deviation (SD) of total tree density in the VFPs is 5.49, in treated forest this ranges from 2.27 to 5.69. For pioneer and climax species, density and palm and liana density these SDs are, respectively, 0.13/0.22–0.75; 0.93/0.31–2.04; 1.74/0.92–1.90 and 1.89/0.42–2.85. Also forest class in treated forest does not exceed much that of the VFPs. The average forest class in the VFPs is $1.27 \pm 0.45$, for treatment E15-S0 this is $1.13 \pm 0.34$, for treatment E23-SR18 this is $1.45 \pm 0.59$ and for treatment E46-SR14 this is $1.80 \pm 0.82$. Even though an average value for a non-numerical variable in itself is meaningless, the rise in these values does indicate that more disturbed forest is created with increasing exploitation intensity but that when given time the forest approaches values of virgin forest again, at least as far as the measured data is concerned.

## 5. Conclusion

The heaviest treatment as applied approximately 20 years ago has been quite severe and was indeed meant to be overdone. In this treatment basal area has been reduced from about 30 to 14 $m^2$, so half the stand has been removed. After application of this treatment the forest looked detrimental (De Graaf, pers. comm.), but since then the forest has had time to recover.

From the data as measured in the short period of fieldwork, it can be concluded that the effects of the CSS on the trees in the lower strata and the measured stand characteristics fall within the range of natural dynamics. There is more disturbed forest but this is mainly in the heaviest treatment and there appear to be slightly more pioneer species in two of the three replications, but the differences with the VFPs are minimal. Furthermore, natural heterogeneity appears to be stronger than treatment effects, accounting for differences in, for example liana density. This has also been observed by Magnusson et al. (1999), who found that differences in species composition between logged–unlogged plots are almost as large as differences between all plots. The regenerative power of the forest shows that forests are resilient to disturbance.

The tropical rain forest in Suriname treated with the CSS appears not to regress to a more secondary forest and as the original primary rain forest structure, composition and dynamics are largely maintained, the conservation potential of such a forest remains high. It should be noted, however, that only one rotation has been completed and no complete set of treatments has been applied. The state of the forest after more than one rotation should be investigated in (the existing) long-term plots where selective logging may be continued as intended under the CSS.

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