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SUMMARY

In this report an overview is given of the results of the project 'Population Structure, Dynamics and Reproduction of Tropical Tree Species'. These results were obtained during the period August 1990 - April 1994 in Mabura Hill, Guyana.

The main objective of the study is to describe the demographic characteristics of five abundant tree species differing in regeneration strategy. A second objective is to describe the impact of exploitation on the demography of these species.

Most of the study is conducted in permanent plots (2.5-4 ha) in natural forest and in exploited forest (exploited in 1988). The growth, mortality and reproduction is determined for all individuals belonging to the five selected species on a yearly basis. Additional data are collected by monitoring even-aged cohorts and through experiments.

The results are presented for Greenheart (*Chlorocardium rodiei*), a commercial species, and for Clump Wallaba (*Dicymbe altsonii*), a non-commercial species that is co-dominant within the Greenheart forest.

The population structure of both species was affected by logging. For Greenheart this effect was strongest. Nearly 60 % of the adult population was cut; and from the smaller size classes the observed densities were much lower than in the natural forest. Seedlings were more abundant in the exploited plot, and were generally in a better condition. Clump Wallaba lost many large individuals, but the number of saplings was greatly enhanced.

Both species showed higher growth rates in the exploited plot. Clump Wallaba was growing (much) faster than Greenheart in both plots. Still, on a volume per hectare basis, the growth of Greenheart was higher in the natural plot than in the exploited plot. Average seedling growth rates for Greenheart were slightly higher in the exploited plot than in the natural plot, but in general the population was characterized by the loss of many leaves.

Mortality rates were low, and apparently not different for both plots. The data were not considered very reliable on this point. Seedling mortality for Greenheart is higher in the natural plot. A good correlation was found between the number of leaves per decimeter and mortality. Most seedlings in the exploited plot have still a relatively high leaf density, so a deteriorating condition expresses itself primarily in leaf loss, and not as yet in increased mortality.

Reproductive rates for both species seem to be lower in the exploited plot. A larger percentage of the Greenheart population is flowering, and they appear to flower more abundantly, but this can not compensate for the loss of reproductive individuals.

Examples from the cohort study are given to illustrate the slow seed production and germination rates for Greenheart. After one year germination is still not over 50%. Mortality is moderate in the seed stage. Clump Wallaba produces much more seeds, germinates fast and has a very high mortality in the first few months, especially in dark areas. Neither species seems to be very successful in the exploited plot. Greenheart was decimated by rodents; Clump Wallaba by ants and fungi.

The production of stump sprouts provides a potentially promising way of producing Greenheart poles and maybe even trees. Nearly two decades after exploitation, still over half of all stumps bears sprouts, and the (maximum) diameter is much larger than seedlings could possibly reach in that period.

It was concluded on the basis of this limited dataset that the Greenheart population is in a demographic transition in the exploited plot. The life cycle is broken. The sub adult size classes are lacking, so no significant ingrowth can be expected into the exploitable size classes within for forestry interesting time frames. There is a large amount of seedlings, but these seem to be in decline six years after logging, mainly due to low growth rates compared to most other species (Clump Wallaba!). Production of new seedlings is very low, and seems to be insufficient to balance future seedling mortality.

The exploitation intensity employed in the exploited plot (57.0 m³) is too high for Greenheart. The exploitation level should be lower and skidding damage should be greatly reduced in order to reduce damage to the remaining Greenheart stand. Even then an exploitation system that does not incorporate silvicultural treatments seems to be inadequate for sustained Greenheart production.

1. INTRODUCTION

1.1 Overview

Increasingly man has come to realise that the value of the tropical rainforest ecosystem is not limited to its productive use, but that it represents other, sometimes more indirect values, often expressed in terms of species diversity, environmental buffer capacity or existence value (cf. McNeely *et al.*, 1990). The (inherently) destructive nature of forest exploitation operations and subsequent degradation incurred by people colonizing the newly available areas inevitably alters the "values" of the forest. In the first place it affects the production value of the forest itself: a forest exploitation, if not conducted rationally, will eventually result in the decline of the industry that depends on it. In the second place the non-productive values of the forest are affected to such an extent that they may become seriously devaluated.

Many efforts have been done to reconcile the values of the forest as a source of wood with those that prevail in absence of exploitation. The urge to do so has increased recently as the area covered with untouched tropical rainforests dwindles, timber resources approach depletion, and sectors in the general public that emphasize non-productive values of the forest gain strength. This has led to the development of a number of sustainable timber harvesting systems (Lamprecht 1989, Jonkers 1987), of which only polycyclic systems based on a simulation of gap-dynamics (De Graaf 1986, Hartshorn *et al.* 1989) seem to be appropriate in the sense that they aim to conserve other forest values than the production value alone.

There are not many examples where such a system has been applied commercially on a large scale and over a long time, and even less where successfully so. The reasons for this are manifold. One reason that is important in the context of this report is that sustainable silvicultural systems require a relatively advanced level of knowledge about the forest ecosystem and the species in it. While this knowledge is available for a limited number of well studied areas, this is not the case for areas elsewhere. Application of a system that has been developed in another forest type may not have the hoped success if the forest and the (harvested) species are very different.

Forest exploitation in Guyana is legally constrained by observing a minimal felling limit alone, and practically by a limited marketability for most of the timber species. A desire is present to develop the forest as an economic resource of greater importance than in the past, while at the same time conserving all functions of the forest. This objective can not be achieved without employing some form of sustainable forest management. At present efforts are made by large timber companies like DTL and BCL to implement sustainable forest management based on the guidelines set by the Celos Harvesting System that was developed in Suriname (de Graaf 1986, Jonkers 1987, Bodegom & de Graaf 1991). It can not be assumed that the system "works" without adapting it for the specific Guyanese forest situation. The species and soils in Guyana are partially different from those in Suriname. Knowledge of these aspects of the forest resource followed by adaptation of the forest operations will greatly enhance the efficiency of the harvesting system employed. The most severe adaptation is needed when indications exist that sustainability of the forest or of the forest operation can not be ensured without post-exploitation management.

In Guyana, Tropenbos conducts scientific research in order to generate the knowledge that is necessary to facilitate the transition to sustainable forest management.

The emphasis of most studies is to determine the resilience of the forest after disturbance caused by exploitation. Sustainability can be defined in this context as: the minimum requirements for the different forest components to maintain or regain integrity after disturbance. "Minimum requirements" can be read as the maximum permissible exploitation level, but it is worded here from the viewpoint of the forest itself, as its significance is not limited to disturbances caused by forest exploitation alone. The different forest components can variably be taken as 'climate', 'soil', 'water', the 'vegetation', the 'fauna', a certain 'population' or 'species' or even a certain 'individual'. The requirements for these components to maintain integrity may coincide, but that is not necessarily always the case. Impacts that are still acceptable with regard to the soil may be too much for a certain animal species. This leads to the matter how to define 'integrity'. And: if integrity can not be fully maintained, what deviation is permissible? These questions can not be addressed here, and probably not by Tropenbos either. In order to avoid this complex matter an approach is chosen for the purpose of this study that a natural, unexploited situation represents the desired 'integrity' of forest ecosystems, and that exploited situations must be able to return to this state.

It is very difficult to describe the minimum requirements for the integrity of a system as complex as a tropical rainforest. Therefore a number of steps are taken. In the first phase of the Tropenbos Programme, of which this study is a part, an effort was made to describe and define the properties of the various forest components that are relevant in relation to forest exploitation. In many cases variations in the parameters describing these components, like height growth of seedlings, were related to variations in the factors that

change most with exploitation, such as light intensity, nutrient availability, soil compaction, rainfall interception etc. In other cases all these factors were taken together, and 'exploited' situations were compared to 'natural' situations. These basic studies only make sense when they can be used in subsequent studies where the same parameters (like growth) are studied in relation to variation in the whole complex of factors, such as represented by different exploitation intensities. These studies characterise the second phase of the Tropenbos Programme. A last step would be to study the return of the system to the original, natural state. This requires either a long life or a powerful computer, and in a number of studies computer models are used to make projections of the long term effects of exploitation.

1.2 The effects of exploitation on plant population dynamics.

Population dynamics is the study of changes in numbers of individuals in a population and their causes. In plants populations, numbers change as a result of births and deaths; immigrations and emigrations playing a role only in the seed stage of well dispersing species. Birth and death rates can only then be understood if there is insight in the composition of the population in seedlings, adolescents, and reproducing individuals, as well as the factors that govern the transition from one of these stages into the next. (Harper 1977). A complicating factor for tropical tree demography is that in absence of clear annual growth rings it is generally impossible to age a tree accurately, and that tree size is only an imperfect estimator of tree age. Many demographically important events are related to age. Fortunately though it has become clear that a number of events in tree demography are well related to tree size (Harper 1977; Harper and White 1974); and models have become available to describe dynamics of populations organized in size classes or stages (Lefkovitch 1965; Caswell 1989).

The study of the demography of tropical trees is still in its infancy. Studies abound on growth rates of trees. Other studies deal with other aspects of tree demography, such as phenology (Frankie *et al.* 1974; ter Steege & Persaud 1991); seedling establishment and survival (many studies a.o. Augspurger 1983a,b, 1984; ter Steege 1993) and mortality rates (Rankin de Merona *et al.* 1990). There are only a few tree species where a full account is given of all aspects of plant demography, of which the palm *Astrocaryum mexicanum* (Piñero *et al.* 1984; Martinez-Ramos *et al.* 1988) and the trees *Pentaclethra macroleoba* (Hartshorn 1972, 1975) and *Dypterix panamensis* (Clark & Clark 1987; de Steven & Putz 1984) are the best examples for the Neotropics.

Exploitation has a number of consequences for the population dynamics of a species. The initial structure of the population will be altered. In theory, changes in soil properties and microclimate (of which light is most significant), and damage inflicted to the remaining stand will have an effect on the birth rates, on mortality rates and on growth rates of the individuals in the population. It is expected that the effects are greatest just after exploitation, and that in time most parameters gradually return to 'normality'. It is possible though that for some species this will not happen before its population has become extinct at the site.

The impact of exploitation varies with its intensity, frequency and spatial extent (Waide & Lugo 1992), and also whether the species under consideration is exploited itself, or whether it is simply growing in an area that is exploited for other species.

Most studies about silvicultural experiments describe the effect of certain exploitation levels on the growth rates of trees after exploitation, e.g. Jonkers (1987) for Suriname and Prince (1973) for Greenheart in Guyana. Studies on changes in the other parameters are much scarcer if there are any at all. In the next paragraph hypotheses will be formulated for the potential effect of exploitation, based on theoretical considerations in absence of relevant previous work.

The total effect of exploitation on population dynamical parameters is not easily described due to the different natures of the parameters involved. Some effects are 'positive' compared to a natural reference, others are negative. Some last long, others much shorter. In order to overcome this problem it is proposed to express the combined effect of all demographic parameters in terms of population growth rate r . This single parameter makes it possible to compare species populations growing in different environments (e.g. exploited vs. non-exploited) or different species growing in the same environment, regardless of their

species-specific peculiarities.

In population ecological literature it has become customary to obtain a value for r by deriving transition matrices for the populations studied (Caswell 1989). The basic idea is to express dynamics in the population as probabilities to pass from one life stage to another (transition). Transition matrix models will not be discussed in full here, as they will not appear in this report, but mention is made of them because these models will be the tool with which the impact of exploitation will be analyzed at the end of this study. The study is designed to obtain information on the transition probabilities needed for the model, and in this report a first view will be given on the results obtained so far.

Transition models are not in common use as yet to describe the population dynamics of exploited populations, although a few exceptions exist: Usher (1966, 1969); Mendoza & Setyarso (1986). As far as known this study is the first example in which populations from exploited and non-exploited areas are compared.

1.3 Aim of the study

In this report, the results are presented of a study on the population dynamics of two tree species that are affected by exploitation. One, Greenheart (*Chlorocardium rodiei*) is the main harvested species in Guyana. The other, Clump Wallaba (*Dicymbe altsonii*) is the dominant species in many Greenheart-bearing forests, but is not harvested. The study aims to provide a description of the demography of populations of these species in natural and exploited forests. Data are collected on growth, reproduction and mortality of the selected tree species in both habitat types. This knowledge increases the understanding of the behaviour of these species in more complex ecological studies, where exploitation intensity is varied. A population transition model is used to integrate all parameters in one that describes the success of a population; and to make projections of the long term performance of the population.

This report surveys the results obtained up till April 1994. It compares a number of demographic parameters for 1) Greenheart and Clump Wallaba, 2) different disturbance regimes (natural vs exploited).

1.4 Hypotheses.

Changes in plant numbers act upon a certain initial population which can be described in size classes (population structure). The numbers increase by formation of seeds or sprouts (reproduction rate or birth rate) and decrease by deaths (mortality rate). Individuals cycle through the population from birth to death by means of growth (growth rate). These four basic components of population dynamics will subsequently be analyzed in this report.

On the base of theoretical considerations a number of predictions can be made about the behaviour of the species under natural and exploited conditions. This is set out in table 1. The two species used for comparison are introduced in the chapter on materials and methods.

Table 1 Expected effects of exploitation on population dynamical components in Greenheart and Clump Wallaba.

		exploited species Greenheart	non-exploited species Clump Wallaba
component	specification	effect	effect
population structure	adults	selective loss of many individuals	random loss of some individuals
	remaining size classes	random loss of some individuals	
reproduction	subadults	earlier adulthood caused by removal of overstorey	
	healthy adults	higher seed production through better crown illumination	
	damaged adults	lower seed production	
	population	strong reduction in seed bearers	slight reduction in seed bearers
mortality (after exploitation)	larger individuals	increased because of increased crown exposure and root and bole damage	
	seedlings, initial	increased because of sudden change of microclimate; light damage; drying out of seeds	
	seedlings, early successional stages	much reduced due to favourable light conditions	
	seedlings, later successional stages	increased due to shading	low due to higher competitiveness
growth rates	all stages	increased up till moment of overshading	
population growth		lower	higher

1.5 Setup of this report

This report can only give a limited account of the results obtained so far. The dataset is very extensive, and can only be dealt with fully in a series of publications. A choice is made of results that illustrate the effect of exploitation on the demography of two small gap specialists; Greenheart and Clump Wallaba. The population dynamical components mentioned in table 1 will be described for these species.

At the end it will be investigated to what extent the results correspond to the original objectives, and why an extension of the project is expected to add to the results.

The time frame imposed on the completion of this interim report did not allow for an extensive review of the literature, nor for elaborate statistical testing of the results.

2. METHODOLOGY

2.1 Study site

The study was conducted in the Mabura Hill Ecological Reserve (natural habitat) and an adjacent exploited area that was exploited in 1988. The area is described in detail in ter Steege (1993) and Jetten (1994). The forests may be considered representative for a large part of the central Forestry Belt of Guyana.

The tree populations were studied in plots within this area. The soil type is described as Kasarama loamy sands. The forests of the study sites in their natural state are dominated in the overstorey by Clump Wallaba, Greenheart and Black Kakaralli (*Eschweilera sagotiana*), in the understorey by Karishiri (*Oxandra asbecki*) and Yarri yarri (*Duguetia neglecta*) (Fanshawe 1954). Exploitation has led to a change in the floristic make-up of the exploited area, resulting in a patchy environment of remaining forest islands and secondary vegetation with local dominance of immature Kabukalli (*Goupia glabra*) and *Renealmia orinocense*.

Both study sites are in relatively flat terrain. The exploited area gives way to a more swampy forest type at the fringes.

2.2 Study species

In total five species are involved in the study (table 2). They were selected on the basis of commercial value, abundance and chosen to cover the spectrum of regeneration strategies from pioneer to small gap specialist to understorey species (Lieberman et al. 1985). Only two species, Greenheart and Clump Wallaba, will be compared in this report. Both are 'small gap specialists' representing a large percentage of the total stand. To some extent they may be considered competitors, and exploitation as a case in which the commercial species has a large competitive disadvantage compared to the other. A change in relative abundance between the two would certainly affect the future commercial attractivity of the forest to a large extent. Another obvious difference between the two is that Clump Wallaba possesses stem sprouts which are a means of vegetative reproduction. This is not the case in Greenheart.

Table 2 List of the species studied and introduction of species codes.

SPECIES	VERNACULAR NAME	CODE	REGENERATION STRATEGY	COMMERCIAL USE
<i>Chlorocardium rodiei</i>	Greenheart	GH	small gap specialist	yes
<i>Dicymbe altsonii</i>	Clump Wallaba	CW	small gap specialist	no
<i>Duguetia neglecta</i>	Yarri Yarri	YY	understorey	no
<i>Goupia glabra</i>	Kabukalli	KB	(late) pioneer	yes
<i>Cecropia obtusa</i>	Congo Pump	CE	pioneer	no

2.2.1 Greenheart

Greenheart (*Chlorocardium rodiei* (Schomb.) Rohwer, Richter & van der Werff) is the main commercial species of Guyana. Because of this its population structure is well known (Richards 1952, Fanshawe 1954; Prince 1973, ter Steege 1990 and many timber cruise reports). More relevant demographic information is reviewed in ter Steege 1990, and will be referred to later in the text.

Greenheart occurs mainly in Guyana on brown sandy loams and on laterite. It has been exploited for a long period, and at present exploitation covers the larger part of its natural range. The only legal protection is the minimum felling diameter of 12 inches (28 cm).

2.2.2 Clump Wallaba

Clump Wallaba (*Dicymbe altsonii* Sandw.) is the main non-commercial species in many 'Greenheart-forests' on sandy loams. It is also frequent in white sand forests. In spite of its abundance it is a relatively unknown species, although Fanshawe (1954) mentions it as the namebearer of one of the faciations in the Eschweilera-Licania association. It seems to be equally restricted in its range as Greenheart (Cowan & Lindeman 1989). There is no commercial use for Clump Wallaba.

2.3 Plot lay-out, tree marking and measurements.

The lay-out of the demographic plots follows in general terms the recommendations of Alder & Synnott (1992). There are two plots (table 3), a 'natural' plot and an 'exploited' plot.

The exploited plot is larger than the natural plot to compensate for the losses in the larger size classes. Individuals smaller than 10 cm dbh (diameter at breast height, taken at 1.30) are studied in a 1.35 ha intensive studyplot only. The area was exploited in 1988. Exploitation was apparently not performed according to a logging plan, as a large amount of cut trees were not removed from the forest (or even the timber landing), and the relative contribution of skidtrails to the total area seems unnecessarily high. There is no indication however that this plot does not represent a standard exploitation scenario at the time. Details on exploitation intensity are presented in the results. In the natural plot an area of 0.5 ha serves as an extension for the measurement of larger trees (cf. table 5)

Table 3 Layout of the demographic plots and introduction of plot codes. The exploited plot has an intensively studied area (int) and a larger extensively studied area (all; this includes int) for large trees only.

PLOT NAME	PLOT CODE	AREA (ha)	PHYSICAL SUBDIVISION	# SAMPLE PLOTS FOR SEEDLINGS	DIMENSION (m x m)	CENSUS INTERVAL
natural	NA	2.50	10x10m	38	5x5	1 year
exploited	EX -int	1.35	30x30m	10	2.5x10	1 year
	EX-all	3.98	30x30m	0		1 year

The plots are semi-permanently marked with wooden poles and flagging tape. All trees meeting certain size requirements are located in the plot (with reference to the grid system), marked at the point of diameter measurement with a double ring made with spray paint or normal paint and issued with a reference number written on a plastic label. Big trees have their labels attached with a galvanised nail, smaller trees with a metal wire around the stem. (Problems of strangling occasionally occur in fast growing saplings in the exploited plot.). The point of measurement is taken at breast height (1.30 m), determined according to established standards (Alder & Synnott 1992). In the case of buttresses, stem irregularities or sprouts (Clump Wallaba) at reference height, the point of measurement is taken higher.

Population censi are taken at yearly intervals. Mortality is determined. Diameter is measured with a pi-

graduated tape (trees over 4 cm diameter), with a caliper (trees under 3 cm diameter) or both (between 3 and 4 cm). The instruments are read to the nearest tenth of a millimeter. Height is determined directly with a tape or measuring pole for individuals up to c. 4.5 meter, and with a Suunto clinometer for taller trees. Due to large error margins clinometer readings are made only once in the whole study period, though. This means that no length growth is determined for trees taller than 4.5 m. All details with a potential effect on growth or mortality rate are recorded qualitatively. This concerns hollowness, tree inclination, infestation with lianas, termites or fungi, crown damage and herbivory. It is determined whether observed damage is 'natural' or caused by exploitation.

Table 4 Crown position scores adapted from Dawkins (1958). These give a semi-quantitative estimate of the light climate of an individual crown. Highly subjective, they still give a fast and easy indication of the light environment of a tree.

CROWN POSITION CODE	DIRECT LIGHT FROM ABOVE	DIRECT SIDE LIGHT
5	fully exposed	from > 45°
4	> 50 % exposed	from < 45°
3	< 50 % exposed	from < 45°
2	not exposed	high (2h), medium (2m) or low (2l) amount
1	not exposed	not exposed

The tree environment is described in a number of ways for every tree. A semi-quantitative estimation is made of the crown illumination or 'crown position' (Dawkins 1958, modified; table 4). A code is given for the position of the crown with respect to the canopy (in the understorey, in the canopy, in a secondary canopy (gaps), liberated). Finally it is indicated whether the tree is growing in the mature phase, viz. building phase, viz. young gap phase of the forest (for the natural plot); or in a forest remnant, in disturbed habitat or on a skid trail (for the exploited plot).

Sampling plots for seedlings and small saplings were laid out at random. Table 5 gives the size limits below which trees were only measured in seedling plots. The enumeration procedures are similar to those of larger trees, with a few exceptions. Tree coordinates are not determined. The number of leaves, and for Greenheart also the number of branches and cotyledons is counted. Leaf density, the number of leaves per decimeter stem height is derived from these data, and is used as a measure for vitality.

The plots were laid out in 1991. The first enumeration took place from September 1991 to May 1992. The exploited plot, due to its size and inaccessibility, has become fully operational only from the second enumeration in 1993. Table 6 tabulates which data are obtained from the enumerations. For population structures, the results obtained for the second enumeration were used for presentation in this report. Growth is calculated for the interval between the first two enumerations. For a number of trees negative growth-rates were observed. When this obviously concerned measuring errors, the data were omitted (similarly unusual positive growth rates were omitted); when the 'growth' was slightly negative the data were set to zero (no growth).

Table 5 Minimum size requirements for measurements in the full plot areas. All remaining individuals are measured in sample plots. Species - and plot abbreviations according to tables 2 and 3. a/p is absence/presence.

SPECIES	FULL PLOT	PLOT EXTENSION
GH	> 0.65 m height	> 1.30 m height (NA) > 10 cm dbh (EX)
CW	> 1 cm dbh (a/p only) > 2.5 cm dbh	> 5 cm dbh (NA) > 10 cm dbh (EX)

Table 6 Overview of the data obtained from the enumerations of the demographic plots. In all cases comparisons are made between the exploited and the natural plot.

ATTRIBUTE	PARAMETER	METHOD	REPORTED HERE ON:
population structure	tree density	yearly count	GH, CW
mortality	# dead individuals	yearly count	GH, CW
	volume removed	volume equation	GH
growth	diameter	yearly measurement	GH, CW
	height; seedlings and saplings	yearly measurement with tape/ clinometer	GH
	# leaves	count	GH

2.4 Reproduction rate

The reproduction rates of trees are difficult to determine accurately, as fecundities may vary greatly between individuals in a population, between populations and between years. Moreover, the densities of the species under study makes it virtually impossible to study individual fecundity (which is the required input in the transition model). Several approaches are taken to overcome these problems. Due to their specific peculiarities (seed size, length of fruiting season), the methods vary per species. The methods are summarized in table 7.

Table 7 Overview of data obtained for tree reproduction.

ATTRIBUTE	PARAMETER	SPECIES STUDIED	METHOD
maturity; reproductive activity	# flowering/ fruiting trees	GH, CW	count
timing of flowering	flower density	CW	weekly samples of littertraps
timing of fruiting	fruit density	CW	weekly samples of littertraps
	fruit density	GH	weekly samples of sample plots
fecundity	# fruits per tree	GH	sampling of isolated trees
	# fruits per m ²	GH	weekly samples of sample plots
	# fruits per m ²	GH, CW	systematic sample of 1000 1 m ² plots
	# fruits per m ²	CW	weekly samples of littertraps

Tree maturity is determined by checking the trees for flowers or fruits in the fruiting season. This is done yearly. The number of fruits produced per tree could only be determined for a small sample of 16 isolated trees (for Greenheart only), which were visited weekly in the fruiting season. The number of fruits under the tree was determined.

Estimates for tree fecundity on a population basis were made in several different ways. For Greenheart with its lengthy fruiting season weekly visits were made to the 38 5x5m sample plots used for seedlings (par. 2.3), which were augmented with 5 additional plots. Seeds were marked for subsequent cohort studies (par.2.5). This procedure is repeated yearly. Clump Wallaba flowering and fruiting was sampled weekly in 1993 in 19 randomly placed littertraps (0.25-0.64 m² each). Flowering and fruiting was expressed in numbers of flowers and fruits per m² . Finally, systematic samples of 1 m² each were made in every 5x5m subplot within the demographic plots, thus obtaining an estimated seed density based on 1000 samples (200 in 1991). In this report the sample will be treated as being random, although strictly this was not the case. Systematic samples were made three times from 1991.

Estimation of reproduction rates in the exploited plot is hampered by the difficulty of the terrain and the general lack of seeds, which makes it difficult to collect sufficiently large datasets. Consequently, most of the information will be based on the natural plot.

2.5 Cohort studies.

Cohorts are populations of even-aged individuals, and cohort studies are for many tropical trees the only way to assess age-specific demographic events, if only for the very first life phase. The main purpose of cohort studies in this project is to evaluate the effect on growth and mortality of the various light environments available to seedlings in the forest, and what effect these have on the spatial distribution of seedling populations and on the development of populations of uneven-structured individuals. Moreover it provides estimates for germination rates of seeds and early survival of seedlings.

The activities are summarized in table 8 in the same way as in previous paragraphs. They concentrate exclusively on Greenheart and Clump Wallaba. Yarri Yarri seedling cohorts are small, and Congo Pump and Kabukalli seedling cohorts virtually absent. These are covered as much as possible in the regular demographic enumerations.

Greenheart cohorts 1991 (seeds not marked as these were produced too early in the study period); 1992; 1993 and 1994 are marked from the onset of fruiting in all 43 sample plots in the natural plots. Bi-monthly checks are made of death, germination, height, number of leaves, branches and cotyledons, disease, light and condition.

Clump Wallaba cohorts 1991 (only 8 small plots) and 1993 (35 sample plots of 2.5x2.5m) are marked in a similar way as Greenheart. The measurements are initially much more frequent but less elaborate than in the case of Greenheart, due to large numerical changes but virtually absent changes in plant size. Only presence, number of leaflets and condition are recorded.

The signalled lack of seeds and seedlings in the exploited plots made it necessary to introduce artificial cohorts of 16 (GH) to 25 (CW) seeds in each of 16 sample plots equally distributed in open gaps, skid trails, disturbed areas and forest remnants. The measurements are the same as in the natural plot.

Table 8 Overview of data collected from cohort studies.

ATTRIBUTE	PARAMETER	METHOD
germination	# germinated seeds	weekly (CW) - bimonthly (GH) monitoring of natural (NA) or introduced (EX) cohorts
survival	# dead seedlings	idem

2.6 Spatial distribution of seedlings

The spatial distribution of seeds is entirely determined by the distribution of reproducing adults and their seed dispersal strategy. After dispersal, environmental factors start having an impact on the germinating seeds. The spatial distribution of many of those, like light, proximity to sources of pathogens and herbivores (other seedlings, adult trees) and secondary dispersers is heterogeneous, which causes the original spatial distribution of the seeds to be modified (cf. Augspurger 1983a, Janzen 1970, Connel 1971). It is likely that after a number of years the surviving seedlings are distributed according to the occurrence of gaps in the area.

To study this phenomenon, the cohorts mentioned in par. 2.6 are chosen to cover the forest in all its structural stages, from young gaps to building phases and mature phases. Apart from this, the systematic sampling procedure that is used to describe the initial seed distribution (see par 2.5), is repeated yearly for at least the two most recent Clump Wallaba cohorts that are available. Table 9 summarizes the methods.

Table 9 Data obtained for study of spatial distribution of seedlings in time.

ATTRIBUTE	PARAMETER	SPECIES	METHOD
original distributon	# seeds per m ²	CW, GH	systematic sample of 1000 1m ² plots
mortality	# deaths per m ²	CW, GH	cohort study (§2.5)

2.7 Sprout production.

Greenheart produces sprouts on cut stumps. This was studied a in areas of varying age since exploitation. The number of surviving sprouts per stump, the relation between stump diameter and number of sprouts, and the size class distribution of sprouts were determined. Some aspects of this study are reported here.

3. RESULTS AND DISCUSSION

3.1 Population structure.

The population structures of Greenheart and Clump Wallaba are presented in fig. 1 and 2 respectively. The trees were distributed over equal classes of 8.95 cm, starting from 2.5 cm dbh (not shown in the graph). The density of Greenheart above the felling limit (classes over 29.4 cm dbh) were comparable between the natural plot and the exploited plot before exploitation. Exploitation removed 59.6% (57.0 m³ volume; 5.47 m² basal area) of the trees above this limit (table 10,11). The remaining population of trees from these classes tends to show defects (rot, forks, bad shape etc.) which makes them unsuitable for future harvesting.

The two plots are markedly different in the amount of trees in the 11.5-29.4 cm classes. These size classes are much more common in the natural plot than in the exploited plot. Table 10 shows that the same trend is present in the size classes below 11.5 cm. The densities for these smaller size classes in the natural plot are similar to those reported elsewhere (reviewed in ter Steege 1990), although populations differ slightly with respect to the size class with highest density. Similarly, a survey in other exploited areas in the former DWL concession south of Mabura Hill revealed that these smaller ('subadult') size classes are poorly represented in these areas too (table 11). This is explained by the nature of the exploitation carried out at these sites. The cutting of the trees to some extent, but especially skidding causes a lot of damage to

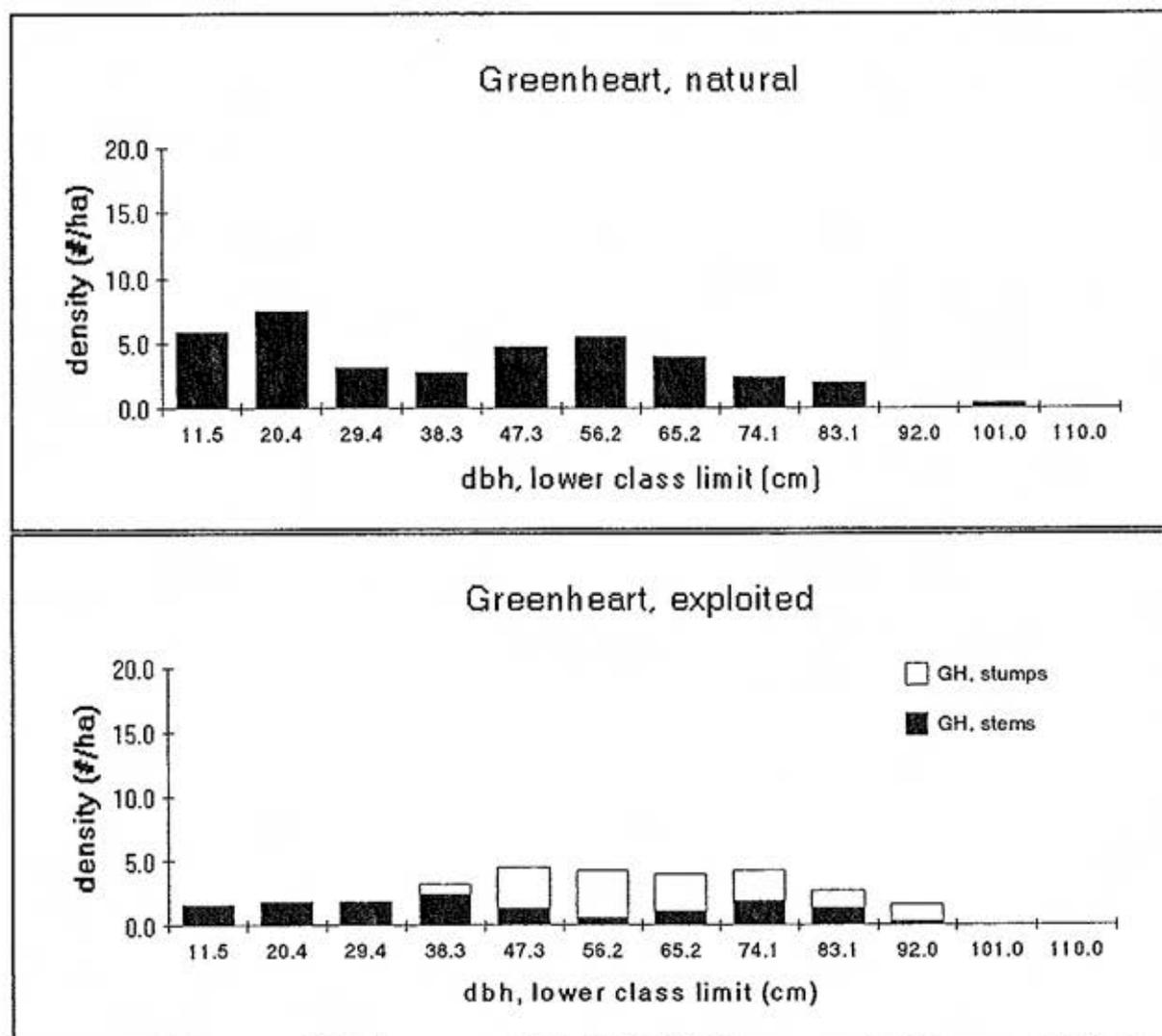


Figure 1 Population structures of Greenheart in the natural plot (above) and in the exploited plot (below).

the remaining stand of smaller Greenhearts. This profoundly affects future exploitation prospects.

Table 10 Summary statistics and density of small size classes for Greenheart and Clump Wallaba in the natural and exploited plots. Data presented as densities (#/ha).

SIZE CLASS (cm dbh)	GH, NA	GH, EX	CW, NA	CW, EX
0-1	31.6	34.1	not available	
1-2.5	20.6	8.5	512.5	2036.0
2.5-11.5	11.1	6.8	129.6	378.1
11.5-29.4	13.4	3.4	22.1	22.5
> 29.4	24.9	10.6	48.2	15.1
stumps		15.6		1.3

The population structure for Clump Wallaba (figure 2, table 10) has a similar shape as for Greenheart for the larger size classes, but the tree is about twice as common, and big trees are more frequent. The direct impact of exploitation is limited to a few cut trees (somewhat surprisingly Clump Wallaba ranks second after Greenheart in number of cut trees in the exploited plot, notwithstanding its commercial uselessness). Logging damage in the higher size classes is apparent from the graph in the form of a strong reduction in tree density above 29.4 cm. This is partly true, as many large Clump Wallabas can be seen lying in the plot, but to some extent this is also due to a deficiency in the dataset. Some larger trees that were

more difficult to measure are still absent from the dataset. An assessment of the number of trees fallen during exploitation is not completed as yet. Trees smaller than 29.4 cm are much more common than

Table 12 Population structure (#/ha) and exploitation levels for Greenheart in four areas. See text for details. *based on ter Steege (1990), with 5 cm deduction for trees cut below dbh; and 6% bark-deduction. **excludes stump sprouts.

	EX	EKUK1	EKUK2	EKUK3
area sampled (ha)	1.35/ 3.78	1.08	0.80	0.99
1-2.5	4.8**	0.0	0.0	3.0
2.5-11.5	6.8	0.0	0.0	1.0
11.5-29.4	3.4	4.6	1.3	11.1
> 29.4	10.6	46.3	12.5	27.3
stumps	15.6	28.7	30.0	36.4
extracted volume (m ³)*	57.0	85.4	101.8	80.6
extraction rate (%)	59.6	38.3	70.6	57.1

Greenhearts of that size. The exploited and natural plots differ markedly from each other in that the number of saplings in the exploited plot is much higher. This is explained by a greatly enhanced growth and survival rate for Clump Wallaba seedlings in the exploited plot shortly after exploitation. Apparently this species benefits more than Greenheart from the increased light availability caused by exploitation.

The Greenheart population seems to be heavily damaged in the exploited plot. In order to investigate whether this was a local phenomenon or a phenomenon more frequently observed in exploited areas, a comparison was made with exploited populations from three areas in the Ekuk logging compartment. These forests grew on similar soils, but exploitation was more recent (1-2 yrs before measurement vs 5 yrs for the exploited plot). The results are summarized in table 11.

Some caution should be observed when interpreting these data. The

exploited plot is 'older', so some ingrowth might have taken place in the lower size-classes (stem sprouts are omitted from the data).

The study intensity is much lower than in the exploited plot, possibly causing some smaller Greenhearts to be overlooked in the other areas. Only Greenheart stumps are included in the calculations (as no volume equations were available for other species). This is a bias against the exploited plot, the plot with most cut non-Greenhearts (2.4/ha). The value of a volume equation for stumps is questionable. Most trees are cut

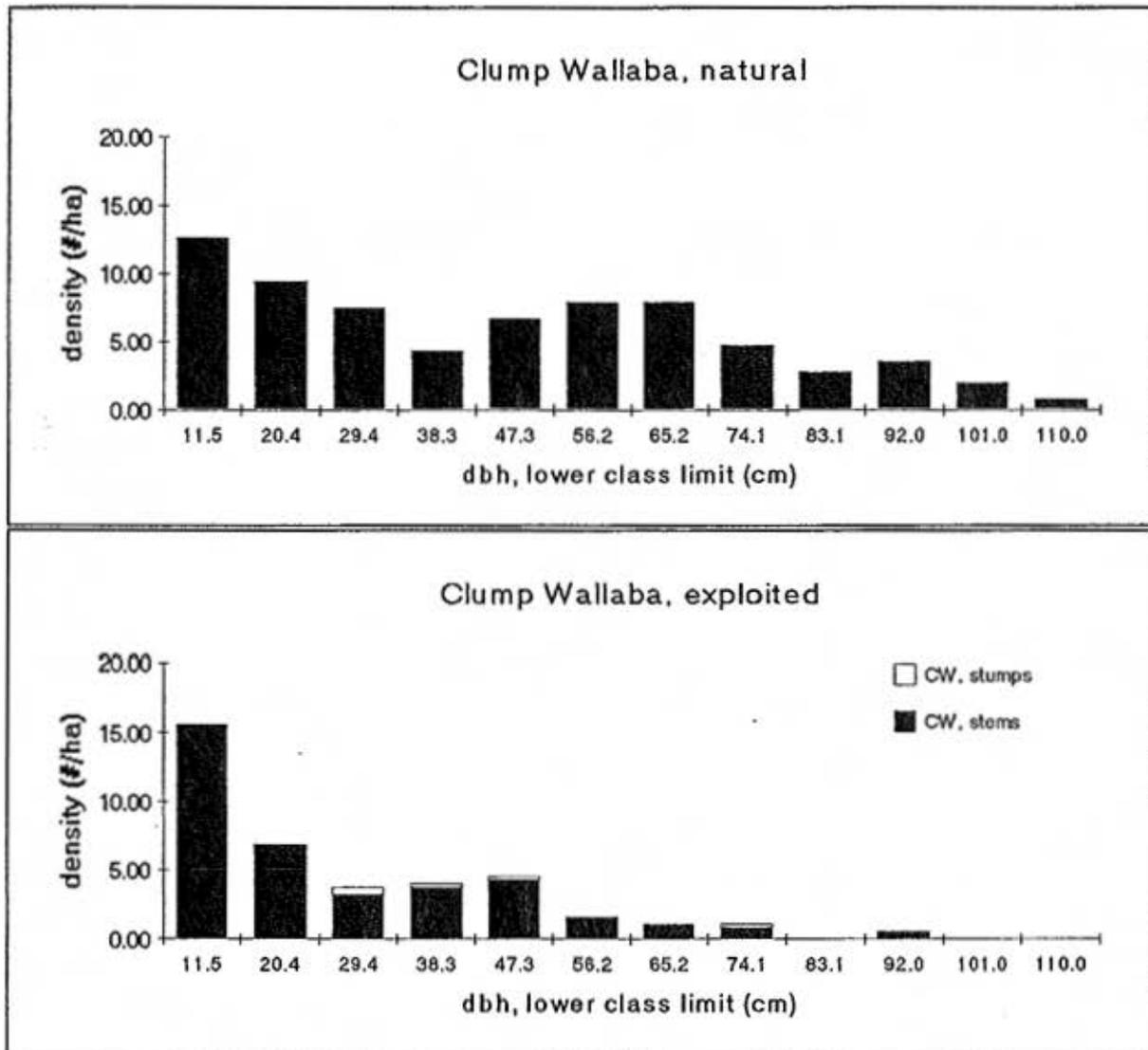


Figure 4 Population structures of Clump Wallaba in the natural plot (above) and in the exploited plot (below).

below dbh (on which the equation is based), and for small trees the error is large. For purposes of comparison it can still be used though.

The tendency found in the exploited plot repeats itself in the other areas: apart from a reduction in the large size-classes there is a near elimination of the smaller size classes. In terms of total extracted volume the exploited plot seems to be at the lower side of the spectrum, whereas the extraction rate (% stems logged) is average. There seems to be a relation between extracted volume and remaining density of stems between 2.5 and 29.4 cm (data not shown), but the dataset is too small to draw conclusions.

Irrespective of the ability of Greenheart to recover from exploitation or not, the level of damage inflicted on its population in the exploited plot has consequences for a possible next cycle of exploitation. The basis for the second coupe should be formed by trees entering the class of 30 cm, the lower cutting limit. These trees nearly vanished during the first coupe. The remaining larger trees are largely defective. The consequence is that for commercial purposes this area has no significance in the next few decades.

Does this damage have consequences for the future of the species in this area? Not necessarily. Studies with matrix models have indicated that the long term behaviour of populations does not depend on their initial structure, but on their vital (growth-, mortality- and reproduction-) rates. When these are favourable, and the restoration period (*i.e.* till the next cut) long enough, the population may recover. When exploitation comes back with the same intensity in regular cycles, this will have a profound influence on the vital rates, and thus on the long term behaviour of the population. The next chapters will deal with the vital rates of Greenheart and Clump Wallaba.

The main results of this paragraph are summarized in table 13.

Table 13 Overview of differences between the natural and exploited plots with respect to population structures. The exploited plot is compared with the natural plot, so 'less' means 'less than in natural plot'.

ATTRIBUTE	GH	CW
density, adults (> 30 cm dbh)	less	less
density, adolescents (10-30 cm dbh)	less	same
density, saplings (< 10 cm dbh)	less	more

3.2 Growth.

Growth of both Greenheart (fig. 3) and Clump Wallaba (fig. 4) seems to be higher for most classes in the exploited plot compared to the natural plot. Whether this is significantly so is difficult to say, as the samples for the exploited plot remain small (due to incomplete first enumeration).

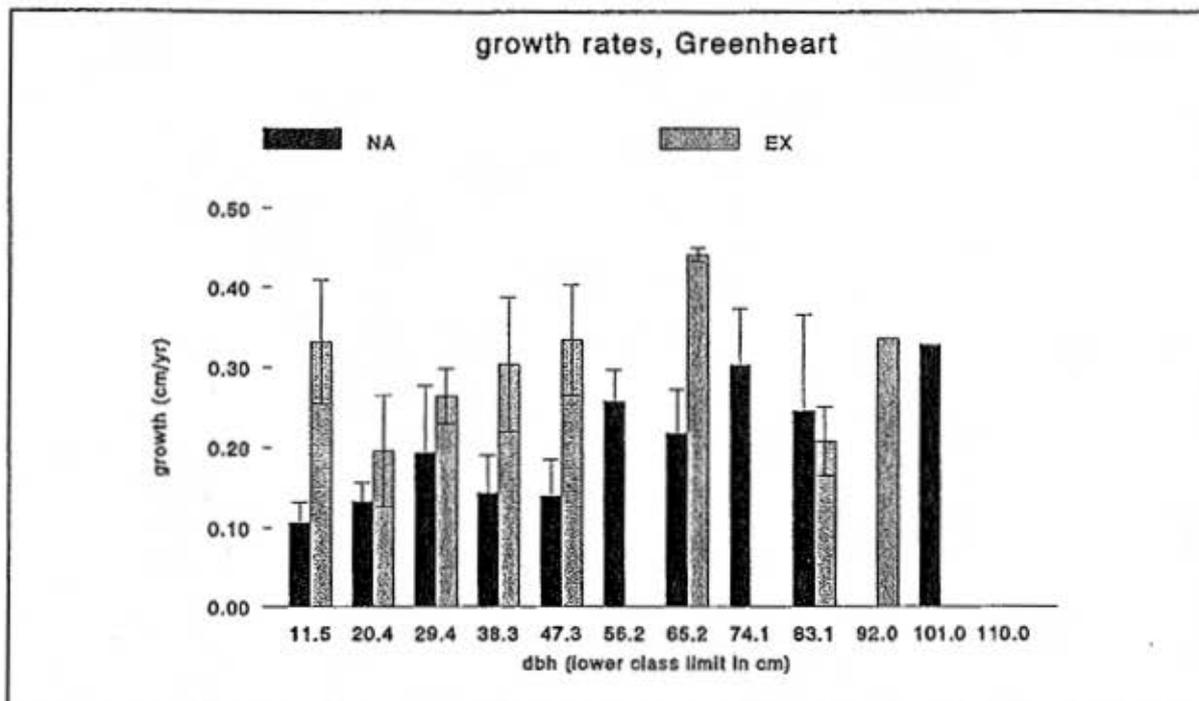


Figure 3 The diametrical growth rate per size class for Greenheart in the natural and exploited plots. For some size classes no data were available.

Average growth rates are presented in table 14, expressed for diameters and for volumes (*vide ter Steege* 1990). On average, growth rates for Greenheart > 11.4 cm in the exploited plot are slightly less than double compared to the natural plot, whereas Clump Wallaba grows more than twice as fast. These favourable figures for Greenheart are reverted when total yearly volume increase is calculated. Due to the poor condition of the remaining stand, and to the small size of it, volume increase in the natural plot exceeds that of the exploited plot.

Comparison of the distribution of growth rates is also instructive, as it gives a good impression of the variability of growth (figure 5). It is clear that Greenheart growth rates never exceed 0.6 cm/yr even in the exploited plot; and that more than 40% of the trees in the natural plot does not show any significant growth at all. The range in growth rates is much wider in Clump Wallaba, with even in the natural plot a number of very fast growing trees (> 1 cm/yr). In the exploited plot more than 25% of the trees have that growth rate.

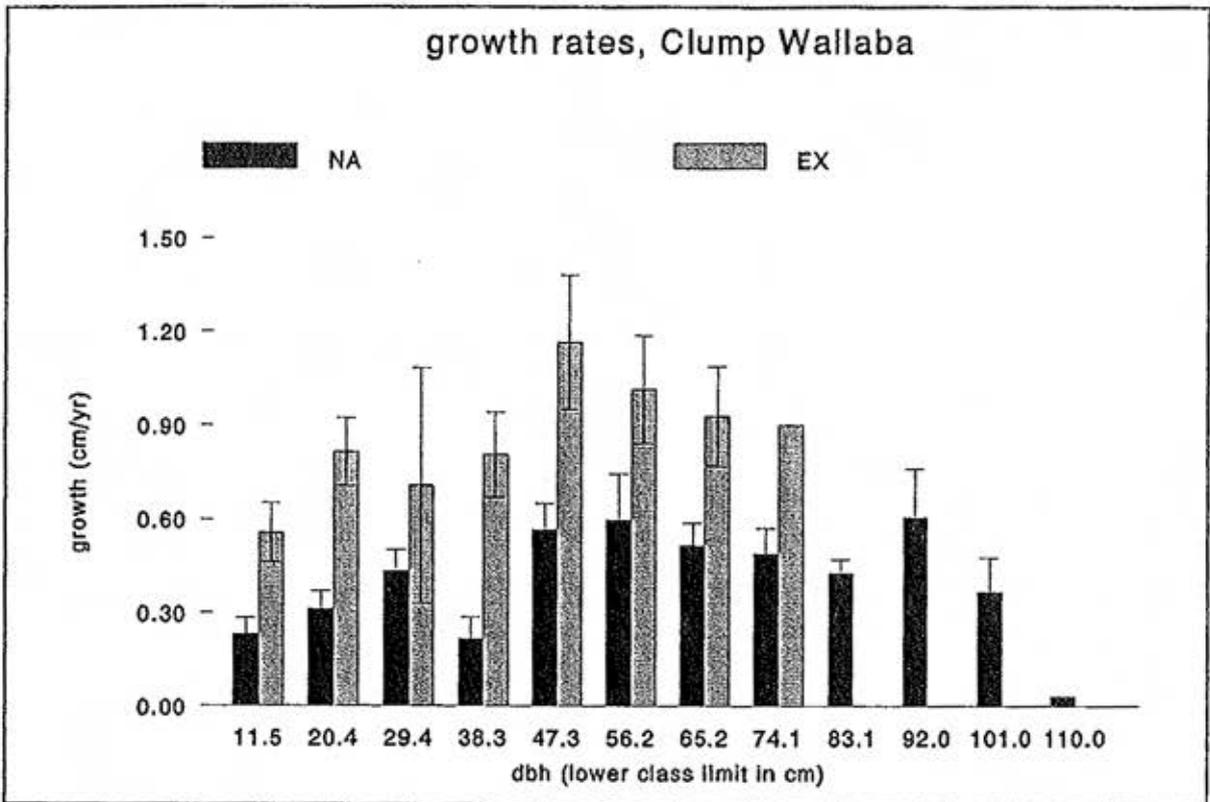


Figure 4 The diametrical growth rate per size class for Clump Wallaba in the natural and exploited plots.

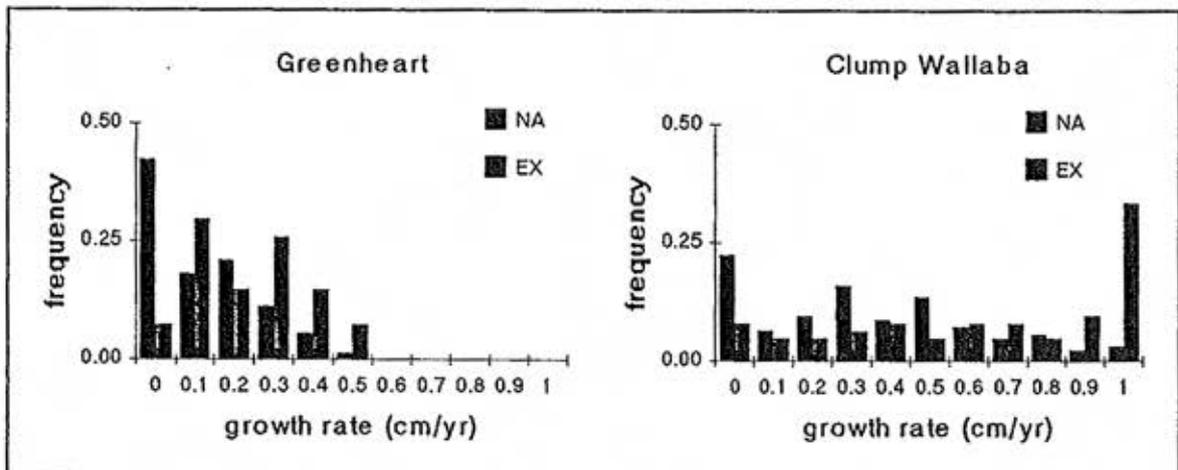


Figure 5 Distribution of growth rates for Greenheart and Clump Wallaba. Only trees > 29.4 cm are considered.

Table 14 Average growth rate (\pm s.e.) for all trees >11.5 cm (for volumes >29.4 cm), expressed as diametrical resp. volume growth for Greenheart and Clump Wallaba. There is no volume equation available for Clump Wallaba.

SPECIES	DBH-GROWTH (cm,yr)		VOLUME GROWTH (m ³ /yr)		VOLUME INCREASE (m ³ /ha, yr)	
	NA	EX	NA	EX	NA	EX
GH	0.181 ± 0.016	0.289 ± 0.025	0.0276 ± 0.003	0.0329 ± 0.004	0.497 ± 0.081	0.348 ± 0.043
n	71	27	45	20		
CW	0.406 ± 0.027	0.800 ± 0.058				
n	125	63				

The observed growth rates for Greenheart in the natural plot are generally somewhat below the values obtained in increment plots elsewhere in Guyana (reported in ter Steege 1990, fig. 39). The results for the exploited plot seem to agree well with those given there for exploited but untreated forest. The reported values for trees in treated forest are never attained in the exploited plot.

It can be concluded that growth of individual trees is enhanced in the exploited plot when compared with the natural plot. Growth for Clump Wallaba is always faster than for Greenheart. There seems to be no clear relation between size and diameter growth. Even though it has to be stressed that the volume approximations can not be considered very accurate, they show that growth on a population level is not higher in the exploited plot. This is simply caused by a lack of trees. If exploitation would be less intense, the 'population effect' might be positive as well, although the individual growth rates might be lower than found here in the exploited plot due to a lesser opening of the canopy.

Comparison with growth rates cited in Jonkers 1987 (table 5.5, p. 97) for trees measured during development of the CELOS system in Suriname reveals that Greenheart ranks among the slowest growing species in the region, both in natural forest and in exploited forest. (The exploited forests in Suriname had different exploitation levels than in this study; all of them lower). Clump Wallaba grows as fast as the fastest growers in Suriname in the natural plot, and tops all of them in the exploited forest.

Table 15 Overview of differences between the natural and exploited plots with respect to growth rates. The exploited plot is compared with the natural plot, so 'less' means 'less than in natural plot'.

ATTRIBUTE	GH	CW
diameter growth	more	more
volume growth (population)	less?	?
number of stagnant trees	less	less

3.3 Mortality.

Mortality rates in adult trees are generally low, and because of the haphazard nature of death, large samples and long time series are necessary to make a proper estimate of death rates. In the present study it will hardly be possible to give an accurate estimate for size-related mortality. The results presented in table 16 give an indication of the mortality observed during the first measuring period. The data for trees below 11.5 cm are added for reference. For the size class over 11.5 cm these figures are based on one and two dead

Table 16 Mortality rates observed for Greenheart and Clump Wallaba. *for CW: 1-2.5 cm.

SIZE CLASS (cm dbh)	GH, NA (%)	GH, EX (%)	CW, NA (%)	CW, EX (%)
0-2.5*	2.25	0.00	1.95	1.57
2.5-11.5	0.00	0.00	2.41	0.39
> 11.5	2.04	0.00	0.57	0.00

trees respectively, so no large significance should be attached to the percentage value given. Still, these figures compare well to mortality rates published in Rankin de Merona *et al.* (1990) for a number of Neotropical forests. For trees over 10 cm dbh mortality ranged between 1.13 and 2.93% in that study.

For larger trees no mortality has been observed in the exploited plot up till now. Apparently the forest has stabilized after exploitation;

usually mortality rates remain high for the first few years after exploitation before they level off.

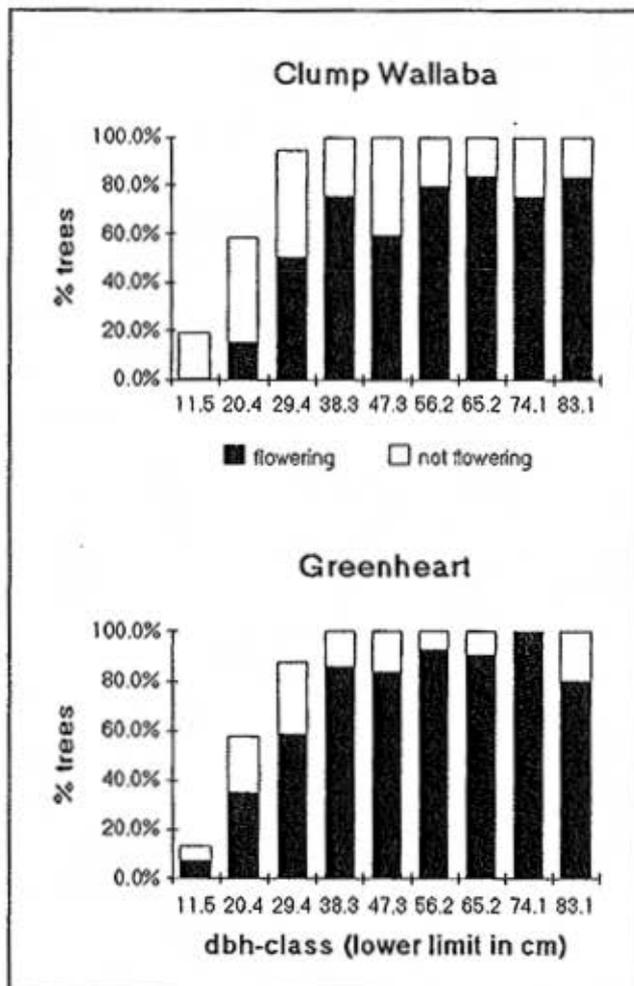


Figure 6 Percentage of individuals per size class reaching into the canopy and flowering activity in 1993 for Clump Wallaba and Greenheart in the natural plot.

3.4 Reproduction

In the period 1991-1994, Greenheart flowered and fruited every year, whereas Clump Wallaba seemed to jump years. It flowered and fruited in 1991 and 1993. In 1992 and 1994 very few trees could be observed flowering, and none in the study plots. Greenheart fruits take about a year to mature; Clump Wallaba fruits mature within 13 weeks after flowering.

Both species become reproductive after they reach the canopy. Occasionally, Greenheart already flowers before that moment. For both species more than half of the individuals is in the canopy for the 20.4-29.4 size class (figure 6), but only above 38.3 cm all individuals belong to the canopy.

Flowering activity (% flowering individuals) is higher in Greenheart in most size classes, and it starts flowering at a much smaller size. There is an interesting difference between the exploited plot and the natural plot in that flowering activity in the exploited plot is always higher (actually, all individuals flower every year, table 17). Observations indicate that flowering seems to be more abundant too in the exploited plot. The hypothesis put forward in table 1 that the trees reach maturity at a smaller size in the exploited plot could not reliably be tested due to the lack of small trees in the plot.

Table 17 Flowering activity for Greenheart and Clump Wallaba. Clump Wallaba only flowered in 1993. n = number of (canopy) trees observed.

YEAR	GH, NA	GH, EX	CW, NA	CW, EX
1992	75.7 %	100 %		
1993	73.3 %	100 %	66.7 %	65.3 %
1994	81.7 %	100 %		
n	70-75	19-20	135	32

The flowering activity of Clump Wallaba is the same for both plots. Visual inspected indicated that flower abundance was less in the exploited plot than in the natural plot.

In figures 7 and 8 the production of flowers (CW only) and fruits in time is given. The data for Greenheart were obtained in sample plots, those for Clump Wallaba with littertraps.

For Greenheart there exists a considerable variation from year to year, not only in numbers of seeds produced ($\pm 513-1398$), but also in

the timing of seed production. In 1992 the median of overall seed production was in week 9, but the medians for individual plots (trees) ranged from week 6 to week 12. For 1993 these figures were week 14, week 7 and week 18 respectively, so seed production was much later in that year. The data for 1994 are not completed as yet.

An outstanding feature of Greenheart seed production is its long duration: more than half a year, excluding a small fruiting period in October. Clump Wallaba fruits within five weeks time (figure 8), and follows much closer on flowering.

No similar data were collected for the exploited plot, but there seem to be no differences with respect to timing of flower and fruit production.

Another striking difference between Clump Wallaba and Greenheart is the amount of seeds produced. Individual tree fecundity was only determined for Greenheart. The production of 16 trees in 1992 varied widely between 0 and 578; with a median (for producing trees only) of 50 seeds. Clump Wallaba, with much smaller seeds (dry weight = $7.68g \pm 0.17$; $n=96$ for CW vs. $18.29g \pm 1.43$; $n=24$ for GH) is likely to have a higher fecundity.

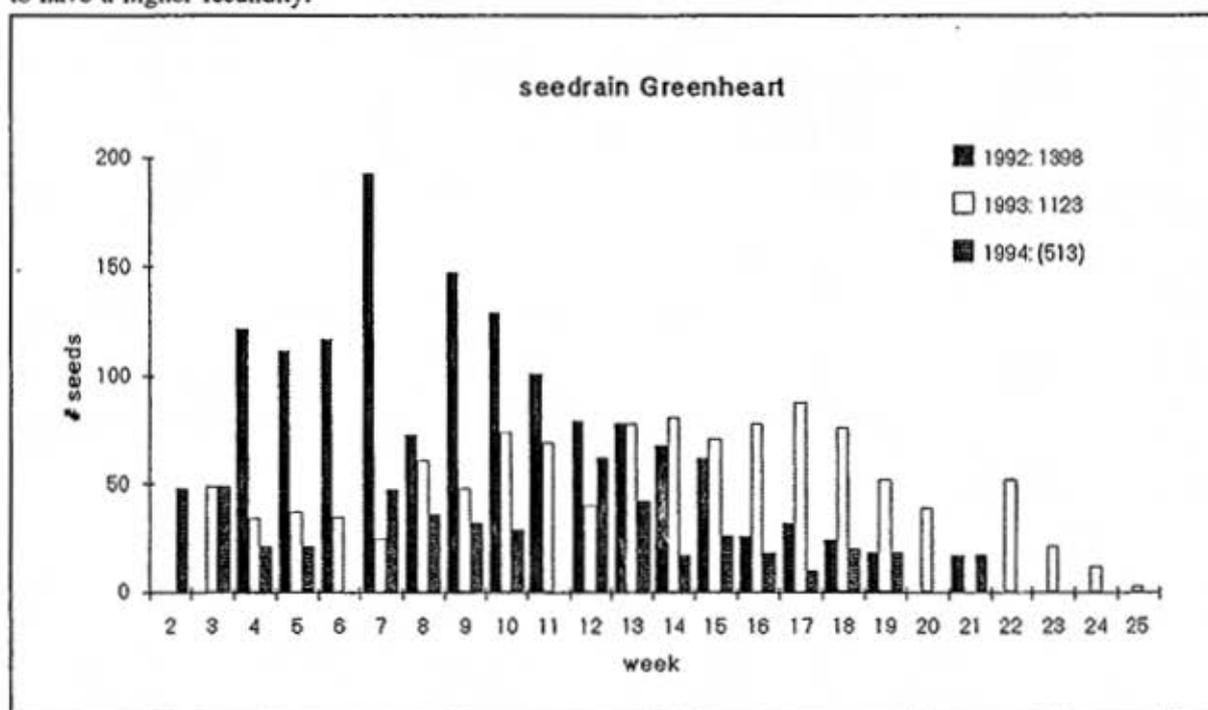


Figure 7 Seed production of Greenheart in 1992-1994 in 43 5x5m sample plots in the natural plot. Time is in standard weeks. Seedrain for 1994 included until May 24.

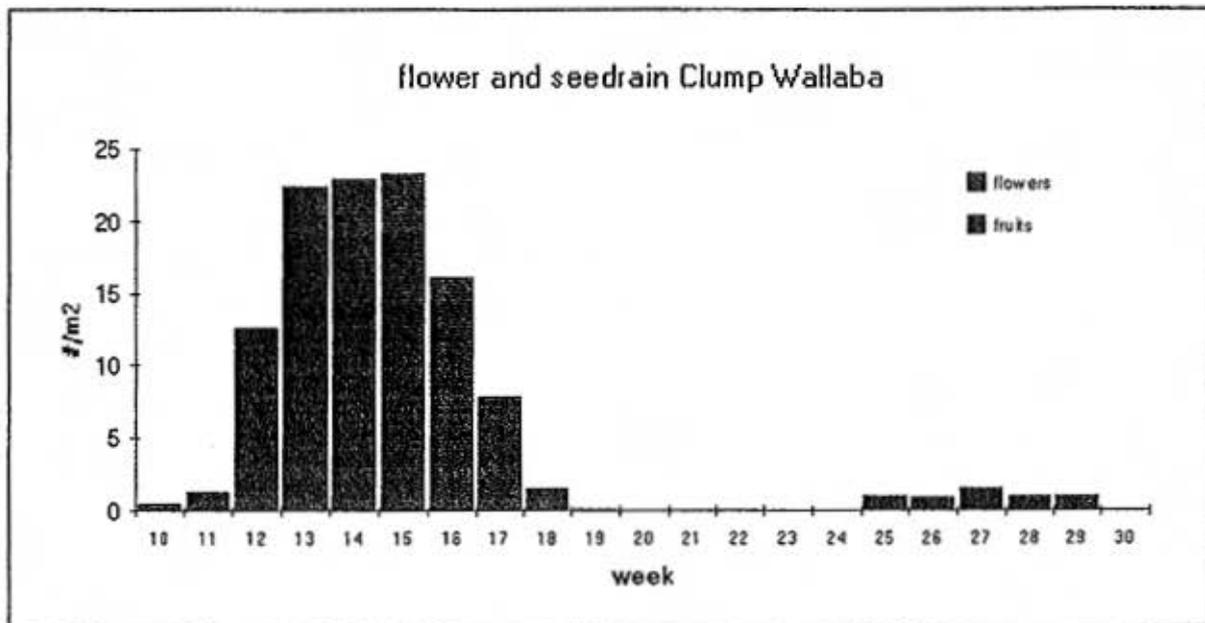


Figure 8 Flower and seed production of Clump Wallaba in 19 littertraps ($\pm 0.5 \text{ m}^2$) in 1 ha of the natural plot in 1993. Time is in standard weeks.

On a population level, estimates of fecundity were obtained by sampling 1000 1 m^2 plots in the natural plot (table 18). These results clearly indicate that the seed densities of Clump Wallaba are much higher than for Greenheart. Maximum densities are more similar. This is due to the poor dispersal capacity of Greenheart, which leads to an accumulation of seeds around the parent tree. In apparent contradiction with figure 7, the total seed production for Greenheart was higher in 1993 than in 1992. The high figure for 1992 in the sample plots is caused by a disproportionate contribution to the seedrain of only two plots, where production was higher in 1992 than in 1993. For both Clump Wallaba and for Greenheart, in the 'good' years there were more plots with seeds, and the average number of seeds in these plots was higher.

Table 18 Average seed density for Greenheart and Clump Wallaba. Note that not all species are sampled in the same years, and that the sampling intensity for Clump Wallaba in 1991 was less.

NATURAL PLOT

SPECIES	YEAR	# PLOTS SAMPLED	$P(x > 0)$	AVERAGE DENSITY (#/m ²)	S.E.	MAXIMUM DENSITY
GH	1992	994	0.156	0.401	0.013	14
	1993	995	0.214	0.650	0.021	30
CW	1991	200	0.850	5.655	0.400	30
	1993	995	0.774	3.981	0.205	46

EXPLOITED PLOT

CW	1991	146	0.541	2.493	0.205	24
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When Clump Wallaba produces seed, the aspect of the understorey changes completely. With a density of up to 57.000 seedlings per hectare that germinate immediately, its seedlings dominate the vegetation of this stratum. Greenheart is also common (6.500 seeds per hectare) but is not as dominating as Clump Wallaba.

Similar data for the exploited plot still have to be collected. Greenheart seed densities appear to be very low, as can be concluded from the regular demographic enumerations of sample plots (less than 10 seeds in all ten 25 m² plots together). Clump Wallaba was sampled once in 1991, and had lower seed densities than in the natural plot. Observations indicate that seed densities for 1993 were even lower than that, in spite of a flowering activity that was comparable to that of the natural plot (figure 6).

The conclusion of these data is that a comparison of reproduction between the two plots is complex. A summary of differences between both plots is given in table 19, stressing that many data are very speculative at most.

Table 19 Overview of differences between natural and exploited plots for some reproduction-related characteristics of the trees. EX is compared with NA, so 'more' means 'in EX more than in NA'.

ATTRIBUTE	GH	CW
minimum reproductive size	smaller??	??
% flowering trees (flowering activity)	more	same
number of flowering individuals (population)	less	less
number of flowers per tree	more?	less?
seed production per tree	??	??
total seed production (population)	less	less
maximum seed density	less	less

3.5 Greenheart seedlings

Up till now the smallest individuals that were enumerated in the complete plot areas escaped the attention. In this chapter an overview will be given of the demography of Greenheart seedlings between 0.65 and 2.50 meter height. These seedlings (and young saplings) form the pool from which the future population is drawn. (This is also the case for Clump Wallaba, but these are so numerous that analysis was not feasible as yet). First the population structure will be given for these seedlings on the basis of a number of parameters: height, number of leaves and leaf density (number of leaves per decimeter stem height). Then growth and mortality of these seedlings will be analysed with reference to these same parameters.

Inspection of figure 9 shows that Greenheart seedlings are more numerous in the exploited plot, and that they are taller on average. This last is caused by the fact that 1) the growth conditions these seedlings have experienced were better (more light); and 2) these seedlings are on average older than in the natural plot, and have grown for a longer period. In the continuation of this chapter it will be contended that in contrast with the natural plot mortality is generally low, but that there is hardly any new input of seedlings from new seedling cohorts, so on average the seedlings must be older than in the natural plot.

Larger seedlings tend to have more leaves (figure 10), but there are large standard errors, indicating that certainly not all large seedlings have many leaves. There seems to be a difference between the two plots in number of leaves, with seedlings from the exploited plot having more leaves than seedlings from the same size in the natural plot. This becomes clear in figure 11, where the distribution of seedlings over leaf density classes is given. Leaf density could be considered as a measure for vigour or health: the more leaves, the more potential for growth, and the less the risk for death. The vast majority of seedlings in the natural plot has less than two leaves per decimeter, and none more than eight. In the exploited plot very high leaf densities occur (only possible through branching). There is no strong relationship between seedling height and average leaf density in either plot (data not shown).

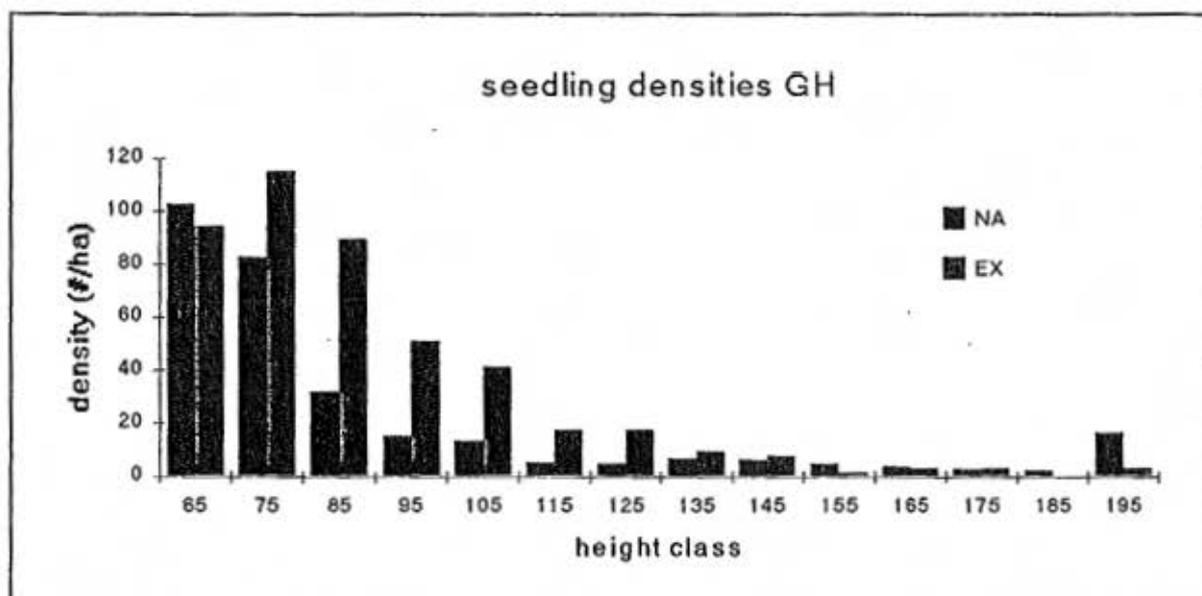


Figure 9 The density of Greenheart seedlings per height class (lower class limits in cm) in the natural and exploited plots. Data based on seedlings with reliable data for 1991 and 1992; $N_{NA} = 789$; $N_{EX} = 325$.

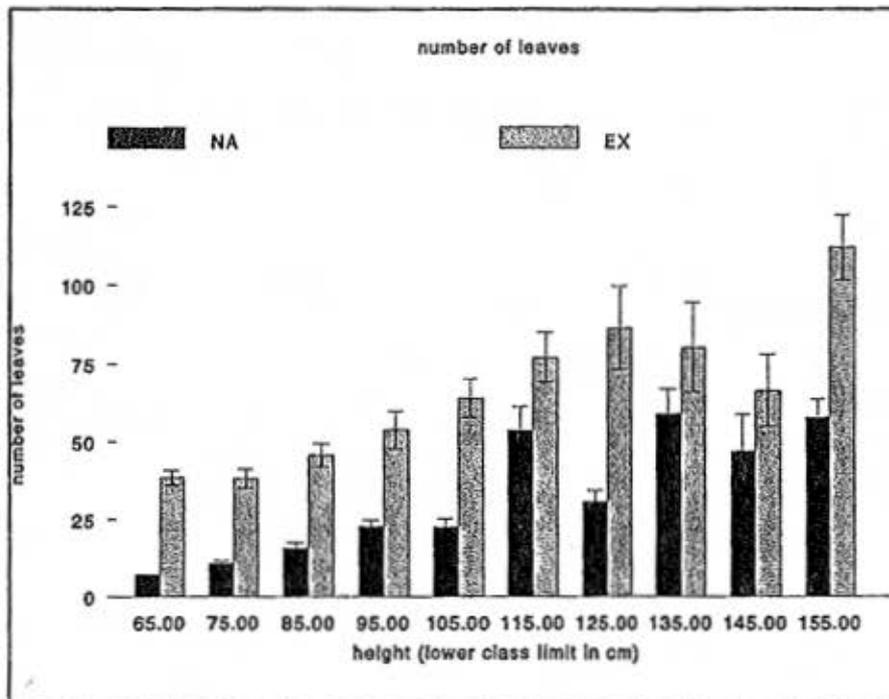


Figure 10 The average number of leaves (\pm s.e.) per seedling per size class for the natural and exploited plots. Classes over 1.55 m joined.

The data presented up till now give a favourable picture of the number and condition of Greenheart seedlings in the exploited plot.

Whether they are really faring well should become apparent from their mortality and growth rates.

Mortality is presented in figures 12 and 13, and in table 20. There is a problem to determine mortality accurately for these small seedlings, as a relatively large amount of seedlings was 'not found' at re-enumeration. It is likely that a disproportionately large fraction of these seedlings was actually dead at that moment. For now, the mortality rates

are calculated with omission of the 'not found' seedlings, and should be considered as a slight underestimation of real mortality rates. Annual mortality was more than twice as high in the natural plot than in the exploited plot. Leaf density seems to be an excellent predictor for seedling vigour, as seedlings with less than 1 leaf per decimeter face a very high mortality risk over the next year (figure 12). This is especially the case in the exploited plot, where competition pressure may be higher, and where many seedlings have a large structure to maintain. The data indicate that many seedlings were much more vigorous in the past, then gradually lost most of their leaves, but retained a large stem and many branches which consume a large part of photosynthates. No mortality was observed for seedlings with many leaves (leaf density > 6). Light has a positive effect on survival, especially in the exploited plot (figure 13). The mechanism is probably that low light conditions affect leaf density, and that below a certain leaf density threshold the seedlings die.

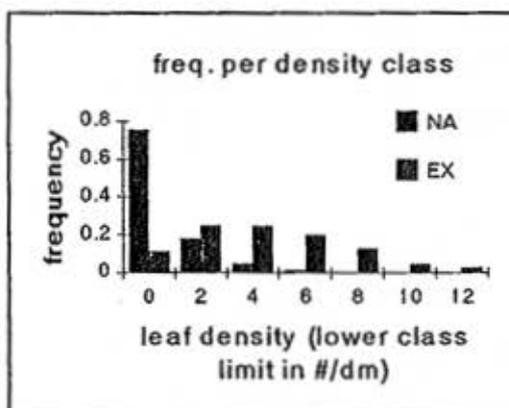


Figure 11 Frequency of Greenheart seedlings in leaf density classes (in #leaves per decimeter).

Table 20 Mortality rates for Greenheart seedlings between 0.65 and 2.50 m height in the natural and exploited plots.

PLOT	N	MORTALITY	S.E.
NA	789	23.9 %	1.5 %
EX	325	10.2 %	1.7 %

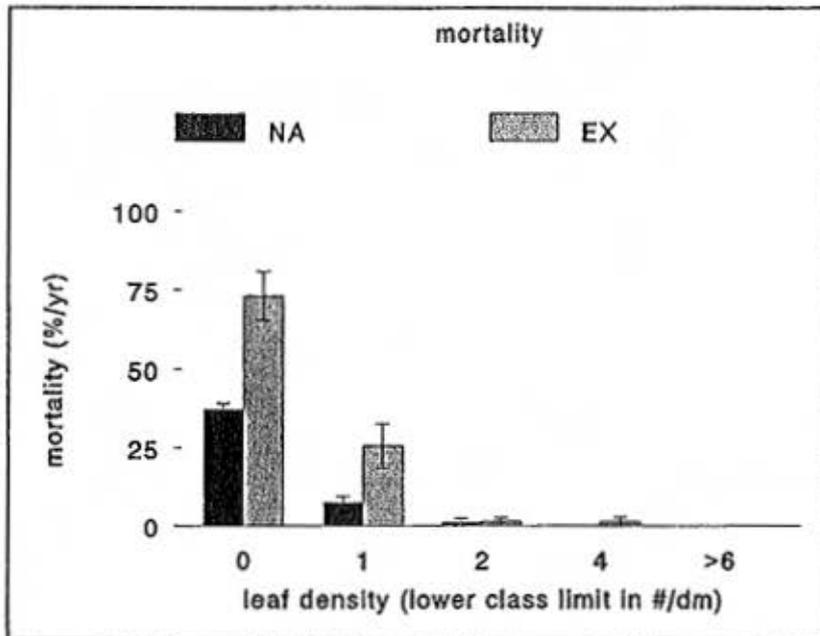


Figure 12 Mortality rates (in %/yr) per density class for Greenheart seedlings in the natural and exploited plots. Class 0-2 has been split in 0-1 and 1-2.

In the exploited plot the seedlings have initially been able to build a large structure with many leaves, but after a secondary canopy of fast growing species closed above them most are not able to maintain their large structure. Death comes only after a long period of decline, and most seedlings in the exploited plot are still in that phase. This is illustrated in the next section, where growth data are presented.

Data on growth of seedlings are not fully analysed as yet, but some preliminary results are given here in figures 14 and 15. The large standard errors make it difficult to draw definite conclusions, but the general impression obtained from these graphs is that height

growth is limited in both plots, that there is hardly any change in leaf numbers in the natural plot, but that in the exploited plot the seedlings loose on average 20-45% of their leaves in one year. The large standard errors are caused by the fact

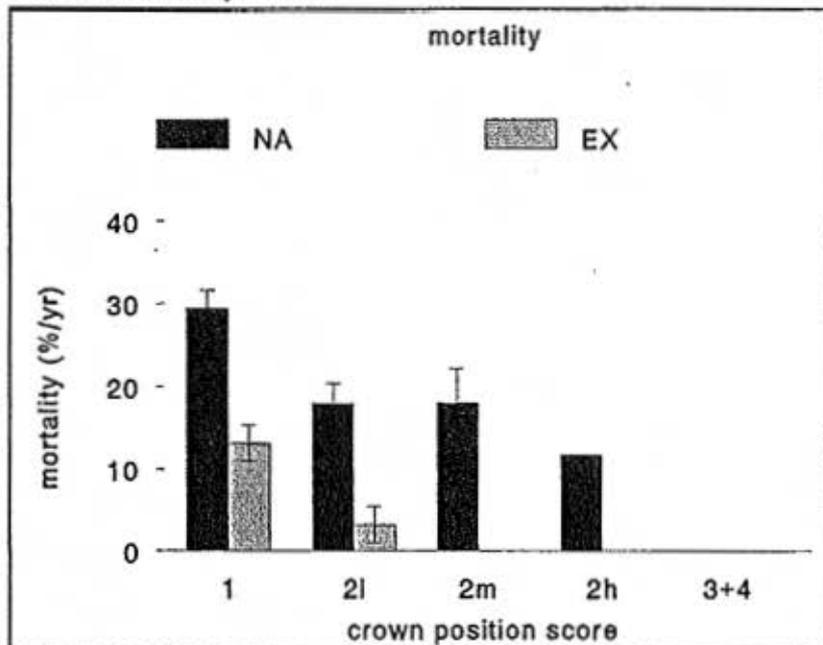


Figure 13 Mortality rates (in %/yr) per Dawkins crown position class (light) in the natural and exploited plots. Standard error bars omitted if $n < 30$.

that growing and not-growing individuals are treated together, which gives the seeming paradox of an (on average) positive height growth and negative leaf growth. Data on the relation between growth and light are possibly instructive, but not given here.

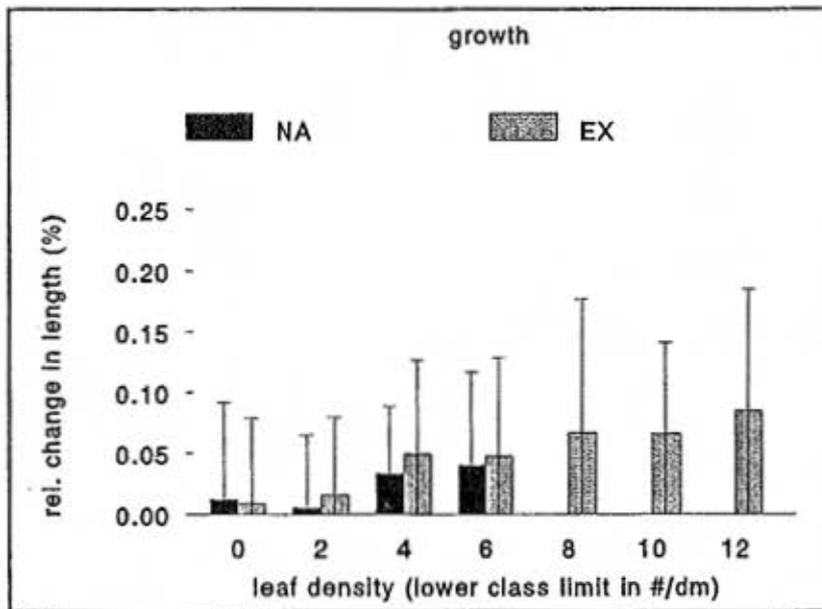


Figure 14 Relative height change in %/yr per density class for Greenheart seedlings in the natural and exploited plots.

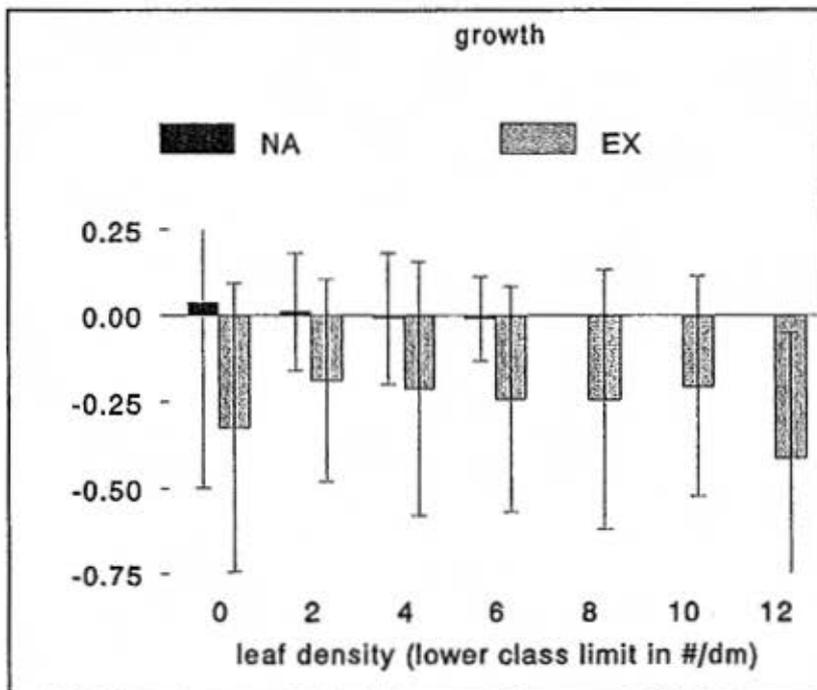


Figure 15 Relative change in number of leaves in %/yr for Greenheart seedlings in the natural and exploited plots.

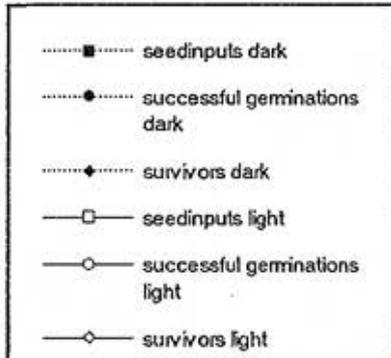
Some conclusions based on these data are summarized in table 21. The seedling populations of Greenheart in the exploited plot are clearly in a period of transition. During the 'open' early phase of succession after exploitation they had a period of strong growth and (possibly) low mortality. After they became overshadowed their fortunes turned around, as they were left with an anachronistic physical structure, one that is not suitable any more for the reigning conditions. Most of these seedlings date probably back to pre-exploitation times (concentrations of seedlings around tree stumps bear testimony to now removed trees). However, the time of mass mortality has not arrived as yet, and average seedling vigour is still better than in the natural plot. From the previous paragraph it became apparent that the input of new seedlings in the population is limited, so in the long run (a few years from now) a collapse of the seedling populations might be expected. This implies that reports on favourable seedling development in areas that were exploited just before have to be interpreted with care.

Table 21 Overview of differences between the natural and exploited plots in terms of seedling growth and survival (GH only). EX is compared with NA, so 'more' means 'in EX more than in NA'

ATTRIBUTE	GH
number of seedlings per hectare	more
number of branches and leaves per seedling	more
seedling height	more
leaf density (#/dm)	more
mortality	less
growth (height)	more?
growth (number of leaves)	less

3.6 Seedling cohorts.

Results on the germination and survival of cohorts of seedlings that germinated in 1993 can only be illustrated with some examples. In the natural plot, a plot in the understorey ('dark') is compared with a plot in a (small) gap ('light') for both species. Presentation of all data for all plots from all years (1991-4) is not possible at the moment.



Legend for figures 16 & 17

The dataset for the exploited plot is much smaller, so here cohorts from all 'dark' plots together are compared with those from all 'light' plots together. Greenhearts from 1993 were still germinating one year after, so no data on growth are presented. Clump Wallabas germinated much quicker, but did not grow afterwards.

The total seed-production of Greenheart in the two 5x5 m sample plots in the natural plot was 84 for the dark plot and 125 for the light plot. Seed production took about 4 months in these two plots; the first seedlings were observed early August, 3-7 months later (figure 16). By May 1994, at a moment that the next cohort was already produced, germination was still not completed in the light plot (31.2 % of the original 125 seeds), whereas nearly all remaining seeds in the dark plot had germinated (52.4 % of 84).

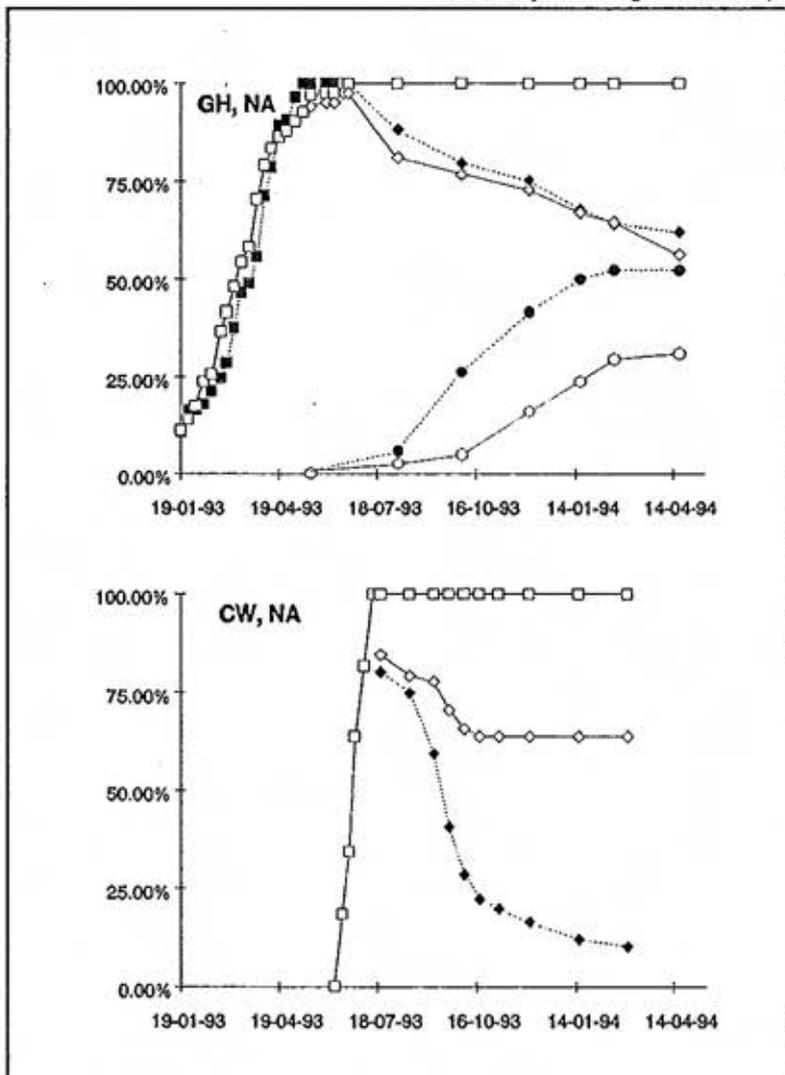


Figure 16 Seedproduction, survival and germination as % of total seed input of GH (top) and CW (bottom) in the natural plot. Legend given separately. X-axis is the same for both graphs.

The onset of germination was faster in the dark plot, but from October germination rates in both plots are similar. Mortality is hardly different between the two plots, and totals around 45% after one year.

The results for Clump Wallaba in the natural plot indicate that seed production (not measured but calculated with data from figure 8), germination (not indicated as such but easily inferred from the graph) and death are much faster processes. Germination success is between 80 and 85% of 166 (dark) and 58 (light) seeds. Both plots experience a period with high mortality caused by fungi, but the losses for the dark plot are heavier. At the moment mortality stops in the light plot, it stabilizes at a lower-than-before rate in the dark plot. Accumulated losses are 89.7 (dark) and 36.2% (light), even before a year is passed. Mortality in the dark plot is very high, and probably represents the highest mortality observed in any of the sampling plots.

The results for the exploited plot (figure 17) look somewhat different. Both cohorts are introduced (so there is no line for seed production); 300 (dark) and 75 (light) for Clump Wallaba, and 208 (dark) and 48 (light) for

Greenheart. Results are given for all introduced seedlings summed. Survival for Greenheart is not given after November 1993, as some plots were decimated by rodents, and the cohorts had to be supplemented. Germination of the original cohort is still indicated in the graph. The germination rates seem somewhat lower than in the natural plot, especially in the light (which is represented here by large clearings, where seeds tend to dry out). Survival is mainly determined by the distribution of rodents in the plot area and not comparable with the natural plot (where rodent predation is a minor mortality cause).

The germination rate of Clump Wallaba in the exploited plot could be determined, and was higher in the dark (59.7%) than in the light (38.7%). Mortality takes its toll already before germination is completed. In the dark this is mainly caused by harvester ants eating the cotyledons. In some light plots the seeds dry out completely and die. Those who escape this fate will germinate and have a very high survival afterwards. Seedlings in the dark continue to be eliminated at a very high rate by fungi. By early March 1994 mortality was 86.7 (dark) and 65.3 % (light).

It is still too early to draw conclusions about differences between the two plots with respect to growth and survival of new seedlings. Greenheart appears to be slow in all aspects of its demography. Mortality

causes are different in both plots, and at least in the exploited plot somewhat haphazard in character, impeding clear conclusions.

Initially, Clump Wallaba faces a very high mortality, both when there is too little light (exploited plot, the extreme case in the natural plot) or when there is too much. After this critical phase mortality slows down (although only very slightly so in EX) or stops. It remains even then much more common than Greenheart seedlings of the same age.

Observations on the other cohorts studied in this project indicate that, for Greenheart in the natural plot, mortality is high after germination, to such an extent that hardly any seedlings of cohort 1991 survive outside gaps. Growth is negligible even in gaps. Out of an estimated 3000 seeds produced in the cohorts 1991-1993 in the sample plots, less than 20 have to date recruited into the for this study important 65 cm height class. Mortality rates for Clump Wallaba are low about a year after germination, and in gaps the seedlings start to grow. Results from the density study (par. 2.9) indicate that under optimal conditions (large gaps) the seedlings may reach a height of 1.8 m in 1.5 years, whereas this is only about 60 cm in understorey conditions.

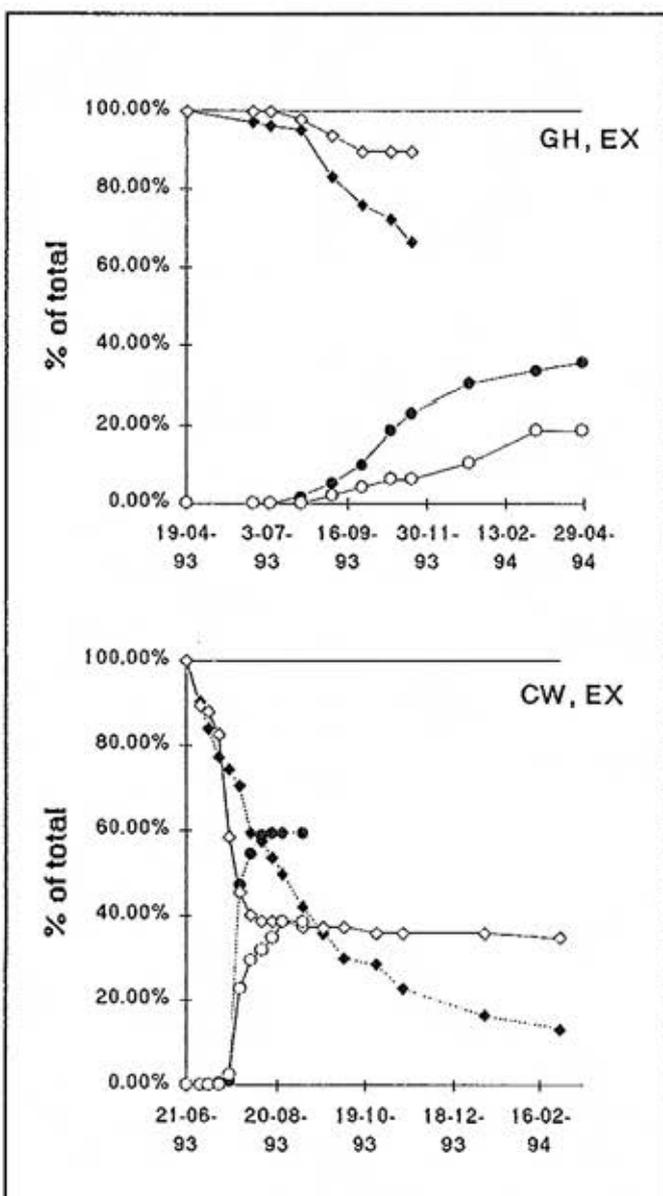


Figure 17 Survival and germination as % of total seed input of GH (top) and CW (bottom) in the exploited plot. Legend given separately on the previous page. X-axis is different for both graphs.

3.7 Sprout formation on Greenheart stumps.

Greenheart is capable of producing a large number of stump sprouts after being cut. Observations in the exploited plot indicated that these sprouts seemed to grow fast and to survive well. Apparently these sprouts benefit from the large root system of the mother tree, and the high light intensity just after exploitation. On the basis of these observations a study was made to compare the occurrence and size of stump sprouts across stumps of different age (Malta & Rijks, 1993). The results are summarized in table 22.

The majority of stumps produces coppice already in the first year after exploitation, and this seems to continue for a while after. After 15-20 years (exact exploitation date unknown) still more than half of the stumps has sprouts, but the average number of sprouts per sprouting stump is lower. Already within a year sprouts are produced with a diameter (at 50 cm height) of over 2 cm. After 15-20 years the maximum diameter observed was 8.2 cm.

Table 22 Characteristics of sprouts on Greenheart stumps in areas varying in age since exploitation. Diameter was measured at 50 cm height. Data after Malta & Rijks 1993.

PLOT AGE (yr)	N	FRACTION WITH SPROUTS	AVERAGE NUMBER OF SPROUTS	AVERAGE DIAMETER OF LARGEST (cm)	MAXIMUM DIAMETER OF LARGEST (cm)
1	51	79 %	3.9	1.2	2.4
5	52	74 %	7.6	1.9	3.4
8	57	89 %	3.9	3.0	5.9
15-20	52	56 %	2.3	3.3	8.2

Compared to seedlings the performance of stump sprouts seems to be much better. They gain height and diameter faster, and they can postpone the moment of overshadowing much longer. The scant data on growth of the largest sprouts of several stumps in the exploited plot (which is the 5-year old plot of table 22) suggest diametrical growth rates (dbh) in the order of 0.5 cm/yr, about five times as fast as saplings of similar size.

It is unknown whether these sprouts can maintain these growth rates, whether they will eventually produce a mature Greenheart tree, and whether the timber characteristics of such a tree will be comparable to normal trees. Nevertheless, the performance of sprouts in an environment where the rest of the Greenheart population is under pressure makes it interesting to investigate the possibilities of producing timber by coppicing. There is ample room for improving growth of these sprouts by thinning the sprouts (leaving only one or two large ones), and by liberating the sprout from competing secondary vegetation after a few years in order to maintain growth rates at a high level.

3.8 Spatial patterns.

The seed densities produced by mature Greenheart and Clump Wallaba trees in the natural plot were found to be very variable spatially. Despite its abundance, Greenheart seeds were found in only 15-22% of all 1000 1 m² plots laid out systematically in that plot (table 18), with density ranging between 1 and 30/m². Clump Wallaba is more common and a slightly more efficient disperser, but for this species too the variability from place to place is high. In par. 3.7 and 3.8 it was shown that growth and/or survival of seedlings varies according to light availability. Light availability is also a parameter varying in space. Regeneration of a species will only occur in places where seedlings are present and where the conditions are favourable for a long enough period.

Specific data on this subject are not analysed as yet, but data on the distribution of seeds and seedlings just after seed dispersal are available and are given in figure 18. Both species show a patchy distribution in the plot. Areas with high densities indicate the location of very fertile adults.

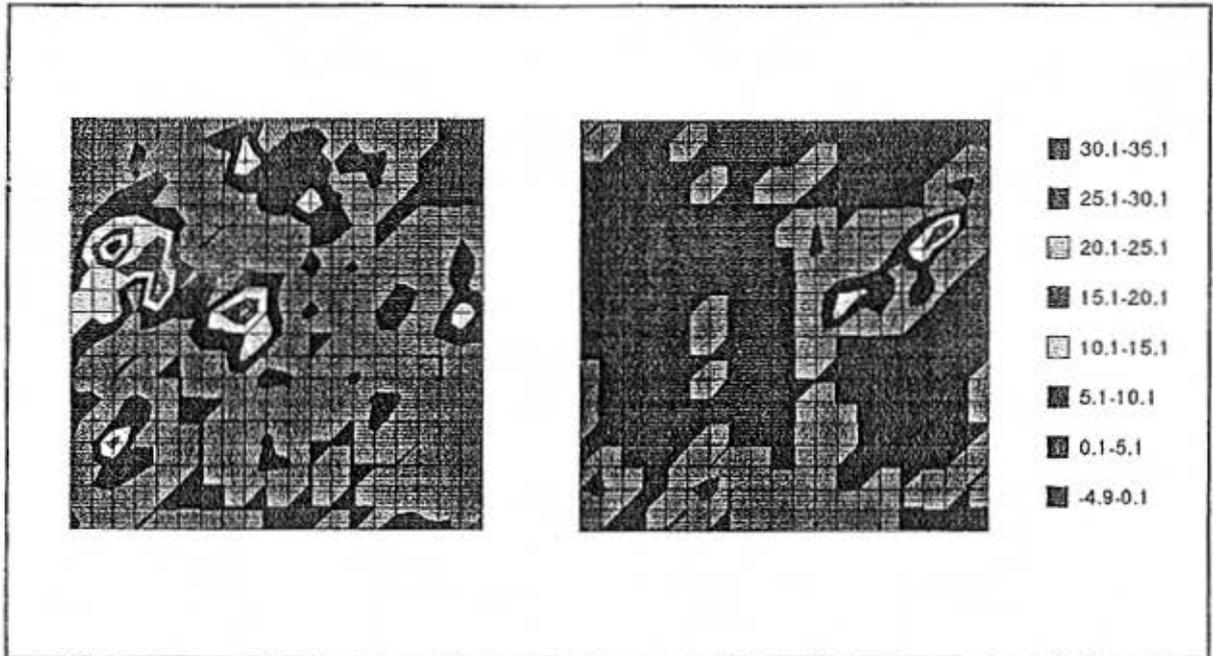


Figure 18 Distribution of Clump Wallaba seedlings (left) and Greenheart seeds (right) of cohorts 1993 in one hectare of the natural plot. Both axes run from 2.5-97.5 m.

3.9 Evaluation of original expectations.

In par 1.4, table 1, a number of expectations were formulated with respect to the effect of exploitation on the components of population dynamics. With the data collected and analysed in chapter 3 it is possible to investigate to what extent the expectations are supported by evidence, and also where the present study has detected large variability, thus requiring additional data for more definite conclusions. The same table 1 is

	exploited species Greenheart	non-exploited species Clump Wallaba	GH	CW	ADD. STUDY REQ.
COMPONENT	EXPECTED EFFECT	EXPECTED EFFECT	RESULTS	RESULTS	
structure	selective loss of many individuals	random loss of some individuals	<i>confirmed</i>	<i>confirmed</i>	
	random loss of some individuals below felling limit		<i>losses >> than expected</i>	<i>not denied</i>	
reproduction	earlier adulthood caused by removal of overstorey		<i>??</i>	<i>not confirmed</i>	X
	higher seedproduction through better crown illumination		<i>not denied</i>	<i>not confirmed</i>	X
	lower seedproduction (population)		<i>confirmed</i>	<i>confirmed</i>	
	strong reduction in seedbearers	slight reduction in seedbearers	<i>confirmed</i>	<i>confirmed</i>	
mortality (after exploitation)	increased because of increased crown exposure and root and bole damage		<i>not confirmed</i>	<i>not confirmed</i>	X
	increased because of sudden change of microclimate; light damage; drying out of seeds (initial)		<i>not analysed yet</i>	<i>not analysed yet</i>	X
	much reduced due to favourable light conditions (early succession)		<i>confirmed</i>	<i>confirmed</i>	
	increased due to overshading	low due to high competitiveness	<i>not confirmed as yet</i>	<i>confirmed</i>	X
growth rates	increased up till moment of overshading		<i>confirmed</i>	<i>confirmed</i>	X
population growth	lower	higher	<i>not analysed yet</i>	<i>not analysed yet</i>	X

Table 23 Evaluation of expected effects of exploitation on population dynamics in Greenheart and Clump Wallaba. 'Not confirmed' means 'expectation not supported'. 'X' means that more data are necessary to support the evidence.

repeated as table 23, with a summary of conclusions based on the previous sections. The full scope of the study is of course much wider, but some results with direct relevance for forest management become apparent from this table.

4. IMPLICATIONS FOR MANAGEMENT; THE CELOS SYSTEM.

The exploitation as done in the exploited plot does not allow a second harvest in the next several decades. This result is not so surprising, considering the exploitation intensity. More important is that Greenheart as a population is hardly functional any more. The normal processes of regeneration are interrupted, and there is no pool of young individuals left that might compensate for a temporary lack of reproductive input. The environmental conditions imposed by exploitation (a very dark and very dense stand of secondary vegetation) are not optimal for a fast development of a new pool of saplings, even though the conditions in the first few years after exploitation have been supportive for the development of a large population of healthy seedlings. Although no data are available from the situation just after exploitation, it seems likely that very few seedlings that form the seedling population now are from post-exploitation seed cohorts. The same holds for Clump Wallaba (and is evident in the cohort study in the exploited plot), but Clump Wallaba seedlings, as opposed to Greenheart, respond strongly to increased light levels, and do not get overshadowed as soon. The 'wave' of Clump Wallaba recruits is now 1-4 cm in dbh (see tab. 10) and strongly growing (about 0.45 cm/yr, which is very fast for such small trees).

So it seems that for both Greenheart and Clump Wallaba successful reproduction is not possible at the moment, and also that mortality for trees over 10 cm dbh is negligible. The key for Clump Wallaba's success, and Greenheart's demise is 1) the fast growth rate of the former; and 2) the fact that exploitation was selectively directed against Greenheart, and not Clump Wallaba. The lack of sub-adults prevents Greenheart from recapturing some canopy space and reinstating some reproductive potential soon (as opposed to Clump Wallaba), and the slow growth of the seedlings prevents it (in the longer term) from producing new subadults. The life cycle is broken.

Adaptations in logging technique should ensure that the demographical mechanics of the population are maintained. They should be specifically directed at prevention of excessive losses in the sub-adult size classes (and preferably also of adults, in order to maintain a reasonable seed input in the population), and a reduction of the differences in growth rates between competing species. The first point translates easily in controlled extraction techniques. The last point requires some explication. Greenheart, just like most other species, responds to exploitation with increased growth rates (fig. 3). The maximum growth rates however remain relatively low compared to Clump Wallaba (fig. 5) and even more so compared to really fast growing pioneer species (like Congo Pump). This means that among seedlings and saplings growing up on skidtrails and in heavily disturbed areas, Greenheart will always be at a competitive disadvantage. High potential growth rates can only be expressed if the conditions are suitable, *i.e.* under high light availability in large gaps. The lower the light availability, the smaller the differences in growth, the longer it takes before Greenheart becomes overshadowed (cf Boot, 1993). If smaller gaps are created during exploitation, the effect that is now observed in the exploited plot (declining seedling populations) will not occur, or only much later. A consequence is that it takes much longer to produce a mature Greenheart in this manner (because growth rates are lower). So even though this might be beneficial for the Greenheart population in the long run, for the forester it isn't because there is still no firm base for a new coupe, 20-30 years later.

Reality tells that an exploitation system that imposes a strong selective disadvantage on only one species that is characterised by an extremely slow growth rate cannot be sustained without balancing these disadvantages with selective advantages.

Comparison with the results that led to the development of the CELOS system in Suriname are instructive in this respect (Jonkers 1987). On the basis of table 5.5 (p. 97), where the growth rates of commercial species were compared between natural and exploited forests, he concludes: "Tree growth stimulated by logging is therefore insufficient and forest management systems based only on such an effect cannot be recommended in Suriname". Greenheart grows slower than most of these species.

Selective advantages for commercial species proposed for the CELOS system consist of elimination of competing trees (liberation) in a few steps, over a period of 20-25 years. This system seems to have positive effects on the development of commercial trees after logging. In order to be effective for the Guyanese situation, a few requirements should be met. The exploitation intensity should be much lower than in the exploited plot of this study. Exploitation should not be directed at one species alone, that has to bear the full load of negative effects. Damage caused by extraction should be drastically reduced, in order to maintain a population to be liberated. Longer cycles should be allowed for recovery, as the growth rate of at least Greenheart is slow. Considering the poor competitiveness of Greenheart seedlings, a liberation treatment designed especially for them should be considered. (If proliferation of secondary vegetation is not heavy with reduced exploitation intensities, then such a treatment is not necessary. In the case of the exploited plot in this study, it is probably the only sensible treatment that can be done now).

One proposed treatment for exploited forests is seeding Greenheart, or transplanting Greenheart seedlings. Although it is true that seedinputs in the population are much reduced, both in quantity and in space, it is clear from par. 3.7 that subsequent losses will be high. Such a treatment is probably not effective without accompanying liberation from competing individuals.

These options can be worked out better with the population transition model. This will be done later in this study.

Finally, attention is drawn to the sprouts that grow on Greenheart stumps. Even without measures such as thinning and liberation, these sprouts have a high growth rate that is maintained during a long period. Even if it would prove impossible to grow trees of suitable quality from sprouts, they might still produce wood for other purposes, like poles or piles.

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