Population dynamics of two timber tree species from a tropical dry forest after logging.

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Abstract

Multiple studies have been performed regarding logging in tropical forests. Most studies show that current logging regimes are not sustainable in either extracted species' populations or extracted amounts of timber. We studied the effect of logging and silvicultural treatments on *Acosmium cardenasii* and *Centrolobium microchaete,* two dominant species in the Chiquitania forest in Eastern Bolivia.
Our results show that the population growth rate of *Centrolobium microchaete* is positively influenced when silvicultural treatments are performed following logging compared to the unlogged situation. This makes our study one of the first that shows that the performance of silvicultural treatments followed logging can positively influence population growth rates of extracted species.
Acosmium cardenasii showed increased population growth rates after logging, but when silvicultural treatments were performed, population growth decreased.
We also show the importance of resprouting of harvested individuals of *Centrolobium microchaete*. Resprouting as a mechanism of regeneration is often ignored in population dynamics models, while it may play a major role in the faster regrowth of harvested forests.
We concluded that logging of both species was potentially sustainable for population size, but due to the low density of *Centrolobium microchaete* individuals, was the timber demand in some cutting cycles not fulfilled.

Resumen

Muchos estudios se realizaron sobre aprovechamiento forestal para bosques tropicales. La mayoría de estos estudios demuestran que los regímenes de aprovechamiento no son sostenibles para las poblaciones de especies ni para la sostenibilidad de la cantidad de madera aprovechada. Hemos estudiado el efecto del aprovechamiento y tratamientos silviculturales en dos especies dominantes del bosque Chiquitano (Bosque seco tropical) que se encuentra en el este de Bolivia.
Nuestros resultados muestran que la tasa de crecimiento poblacional de *Centrolobium microchaete* está siendo afectado positivamente por los tratamientos silviculturales aplicados después del aprovechamiento. Lo cual nos convierte en los primeros en demostrar este tipo de relacion.
Acosmium cardenasii mostro un incremento en las tasas de crecimiento poblacional después del aprovechamiento, pero los tratamientos silviculturales aplicados hicieron que el crecimiento de su población disminuya.
También mostramos la importancia de la capacidad de rebrote de individuos aprovechados de *Centrolobium microchaete*. Los rebrotes son un mecanismo de regeneración que son ignorados en modelos de dinámica poblacional, sin embargo, este mecanismo podría acelerar el crecimiento o regeneración de bosques aprovechados.
Concluimos que el aprovechamiento de ambas especies fue potencialmente sostenible para el tamaño de la población, pero debido a la baja densidad de individuos de *Centrolobium microchaete* , la producción de madera en algunos ciclos de corta no fue suficiente para satisfacer la demanda de madera.

Introduction

Tropical forests are considered one of the most diverse ecosystems on Earth (Gentry 1995, Wilson 1995), but they also face many threats, among others clear cutting, conversion and overexploitation (FAO 2001). Among the various types of tropical forests, the wet and evergreen rainforests are more diverse and have traditionally received much more attention compared to the seasonally dry and deciduous forests (Murphy & Lugo 1986, Parker et al.1993). Dry forests in South America cover a large area, stretching from Brazil, Paraguay and Bolivia down to Argentina and Chili. (Killeen et al. 1998) These forests are uniquely positioned between the wet Amazonian forests and the dry Gran Chaco. The largest remaining area of dry 'Chiquitania' forest is found in Bolivia. This ecosystem used to cover up to 30% of the country (Dinerstein et al. 1995) but already 32% of the original area of these forests has been cleared due to timber extraction or conversion to agricultural fields (Camacho et al. 2001, Rojas et al. 2003). The remaining areas remain under threat.

Fortunately, large areas of dry forests are still intact, and there are good prospects for their sustainable management (Fredericksen et al. 2000).

Although the conservation and the economic use of these forests by timber extraction may cause some conflicts (Pinard et al. 1999) the contribution of both of these goals are essential for preservation of these forests (Fredericksen & Pariona 2002). One of the major conflicts between these two parties is the large demand for timber and the slow regeneration of the forest by seedling and sapling recruitment (Mostacedo & Fredericksen 1999). Silvicultural treatments like the removal of competing vegetation by logging or burning can alter both fruit production (Stevens 1987, Zuidema & Boot 2002) and the recruitment of seedlings and saplings in these forests (Fredericksen & Mostacedo 2000, Mostacedo et al. 2001) and preharvesting planning, which was traditionally not performed in these forests, may alter survival in general (Fredericksen & Mostacedo 2000).

Demographic studies have previously proven useful in testing sustainability of extraction of forest products from tropical forests (Harsthorn 1995), both non-timber (Zuidema & Boot 2002, Ticktin 2004) and timber forest products (Olmsted 1995, Hernández-Apolinar et al. 2006, Zhang et al. 2008, Verwer et al. 2008). Extraction is usually regarded sustainable when population growth rates obtained from population matrix models (Caswell 2001) are larger then 1, indicating population growth. More detailed demographic analyses include elasticity (de Kroon et al. 1986), indicating the relative contribution of a vital rate to population growth and Life Table Response Experiments (LTRE; Caswell 2001), which shows differences in vital rates on variation in λ. Elasticity is regarded as a prospective analysis, while LTRE shows retrospective effects (sensu Horvitz et al. 1997). If vital rates with a high elasticity have low LTRE contributions and vice versa, harvest can be regarded as sustainable (sensu Zuidema et al. 2007).

In this study we test sustainability of different timber extraction regimes on the populations of two tree species from the Chiquitania forests; *Acosmium cardenasii* (H. S. Irwin & Arroyo) and *Centrolobium microchaete* (Mart. ex Benth.) Lima ex G. P. Lewis.

Both species are very abundant in the Chiquitania forests and both are able to reproduce vegetatively by means of resprouting from old stumps besides sexual reproduction (Mostacedo, 2007). The difficulties regarding seedling establishment in these forests (Mostacedo et al. 1999) are overcome by this way of reproducing. *Centrolobium microchaete* is regarded as a commercial valuable species (Pinard et al. 1999) and is already exploited for the production of furniture and flooring (Justiniano & Fredericksen 1998). For *Acosmium cardenasii* no exploitation takes place yet and the commercial value was regarded as low (Pinard et al. 1999), but its abundance could make the exploitation profitable. We performed our experiment in 20 hectare big experimental plots that were exposed to different logging

regimes and monitored for 5 years by the Bolivian institute for forest research. The aims of our research were (1) In which way affect different logging regimes vital rates of the exploited species (2) evaluating in which logging regimes populations of exploited species can be sustained and (3) analyzing whether logging negatively affects the most important vital rates.

Material and Methods

Study Site
Data for growth and survival were collected at INPA Parket, a 30,000-ha tract of privately owned seasonally dry tropical forest. This area is located 30 km northeast of the town of Concepción (16° 6' 45" S and 61° 42' 47" W) and 250 km northeast of the city of Santa Cruz de la Sierra, Bolivia. The altitude of this area is approximately 380 m. The canopy of the forest is 20-25 m tall with *Tabebuia impetiginosa* (Mart. Ex DC.) Standl., *Anadenanthera macrocarpa* (Benth.) Brenan, *Astronium urundeuva* (Allemão) Engl., and *Centrolobium microchaete* (Pariona 2006) as dominant species. *Acosmium cardenasii* (≈ 38 trees/ha ≥ 20 cm dbh) and *Anadenanthera* (8 trees/ha ≥ 20 cm dbh) are the most abundant species in the research area (Mostacedo 2007).

Climate
The mean annual temperature at INPA is 24.3 °C and the mean annual precipitation is 1150 mm (range 798-1859 mm/y). From May till October there is a dry season during which most trees lose their leaves. Many tree species in this type of forest flower at the end of the rainy season with another flowering peak at the beginning of the dry season. The major fruiting period is during the mid-dry season.

Study species

Acosmium cardenasii
Acosmium grows up to 25 m with a diameter at breast height (dbh) of 75 cm, which makes it a subcanopy tree (Mostacedo 2007). The geographical range of *Acosmium cardenasii* is restricted to the dry forests in eastern Bolivia, Paraguay and Brazil. It is a shade tolerant species (Pinard 1999) and the most common tree in our research area with a stem density of 159.25 stems/ha of trees bigger than 10 cm. This makes up 38% of the trees in INPA. (Van Andel 2005)
Its seeds are dispersed by explosive dehiscence (ballistochrorous dispersal). Apart from sexual reproduction, *Acosmium cardenasii* can also reproduce vegetatively by root and trunk resprouts. Its high resprouting ability allows it to become a dominant species after low intensity burning and plant removal regimes (Gould et al. 2002). The potential for sustainable use of this species is high because of its abundance and regenerative capacities, but up to now very little harvesting of this species has been performed.

Centrolobium microchaete
Centrolobium microchaete grows up to 18-30 meter in height and is a dominant species in the canopy of our research area. It is a common species in the northern semi-deciduous chiquitano and the transition zone to the more humid forests (Killeen et al. 1993). The density of the *Centrolobium microchaete* is around 7.38 trees/ha for individuals between 5-70 cm dbh, and the species has clumped spatial distribution. It is a very light demanding species (Pinard 1999). *Centrolobium microcahete* produces large amounts of seeds but the regeneration is low (<5 individuals per ha) (Pinard et al. unpublished). This is mainly due to seed predation

(approx. 41.3 %) by parrots and monkey's (Justiniano & Fredericksen 1998) and a large quantity of non-viable seeds. (Kennard, obs. pers.) Resprouting seems the most important way of reproduction (Justiniano & Fredericksen 1998, Mostacedo 2007). Growth of stump sprouts of *Centrolobium microchaete* is about 195 cm/y and sprouts may maintain this rate for up to 4 years (Mostacedo 2007). *Centrolobium microchaete* responds very well to occasional perturbations like timber logging and slash and burn treatments, but less to forest-fires (Gould et al. 2002). These results classify *Centrolobium microchaete* as a fast growing pioneer-species, having a high competitivity in disturbed areas.

Study design
The study on the growth and survival of *Centrolobium microchaete* was conducted at two different blocks at INPA Parket. The first site was within the Long-Term Silvicultural Research Plots (LTSRP) in Block # 1, 5-6 km south of the IBIF field station (16° 18' 26.8"S, 61° 41' 13.5"W). Four large-scale (20 ha) LTRSP's were established by the Instituto Boliviano de Investigación Forestal (IBIF). These plots received different logging regimes; control, normal logging, improved logging and intensive logging. In the normal logging plot the mean amount of tree harvested was 4.3 trees/ha, using standard reduce impact-logging techniques like road planning, directional felling and the retention of 20% of the harvestable trees as seed trees.
In the improved logging plot the amount of trees harvested was the same as in the normal plot, but in this plot silvicultural treatments were performed to increase future crop trees' (FCT) (i.e., well-shaped trees of commercial species 10-40 cm dbh) growth, like liberation of liana cover by cutting the lianas with a machete and liberation of competition from nearby non-commercial trees by poison girdling.
The same logging techniques were used in the intensive management plot, but instead of 4.3 trees/ha, 8.1 trees/ha were harvested. The skidders mechanically scarified the soil surface in an average of 0.6 felling gaps/ha while harvesting where there was no existing regeneration of commercial timber species. After logging silvicultural treatments were performed on FCTs.
In the control plot, no logging took place, nor were silvicultural treatments performed.

Design of the experimental plots
The measurements of trees larger than 10 cm dbh were performed in the LTSRP's in two different blocks each consisting of four plots, one for each treatment. The size of the experimental plots varies between 20 and 27 hectares, dependent upon the logging system used by the concession. The design of the plots is nested within the blocks, and the silvicultural treatments were applied at random. Trees with a dbh larger than 40 cm were monitored in the entire plot. Trees with a dbh between 20 and 40 cm were monitored in a subplot in half of the entire plot. Trees with a dbh between 10 and 20 cm were monitored in four one-hectare sized plots within the subplot. The plots have a network of trails to facilitate the regular measurement and mapping of trees. Logging in the LTRSP's took place in 2002, after which plots were monitored annually from 2002-2007. The annual measurements were done in the same month as the installation, except in 2005 when no measurements were performed. Measurements of seedlings (<10cm dbh) were gathered by Van Andel from 2003-2005 in the same plots as the other growth measurements. For each treatment four 450 x 4 meter long transects were installed, which had a nested design. Seedlings up to 30 cm were measured in spreaded 2 m x 2 m subplots that covered a total of 84 m^2 per transect, seedlings between 30 and 150 cm were measured in four subplots of 2 m x 450 m covering a total of 840 m^2 per transect and saplings up to 10 cm in dbh were measured in four subplots of 4 m x 450 m covering 1680 m^2 per transect. Resprouts measurements were performed from 2002-

2004 in the LTRSP's, resprouts up to 2 m in height and 5 cm dbh were measured in a 4 m x 4 m plot.

Growth rate (γ)
We tested for differences in growth between years and treatments with a 2-way ANOVA. Within years differences between treatments were analyzed using a Tukey HSD test. Adult tree growth rates were calculated from data collected from the LTRSP's. We calculated mean growth rates per size class because very few Hossfeld non-linear regressions had significant results
Seedling and resprout growth was measured over two years, and divided by two to obtain annual seedling growth. We used these calculated growth rates in all models for all years since there were no data for each separate year. Growth of smallest size resprouts lacked in the control treatment, we replaced them with growth of the same size resprouts from the normal treatment. Growth of size two resprouts in the normal treatment was zero, because this was unrealistic we subtituted them with growth of size two resprouts from the control treatment.

Survival rate(σ)
Survival rates were calculated from the same individuals as growth rates. Resprout, seedling and sapling survival rates were corrected per year, these values were used for all years. We calculated survival rates by performing a Binary logistic forward regression in SPSS. *Centrolobium microchaete* stage 1 resprouts' survival rates of the normal treatment were also used for the control treatment. Trees that were recruited and trees that were girdled but still alive were regarded "alive" for the survival analysis.

Sexual reproduction (f)
Data for fruiting probability were obtained from research performed by Mostacedo (2007) in the LTRSP's. We calculated the amount of offspring produced by *Acosmium cardenasii* by dividing the density of seedlings smaller than 10 cm height by the density of reproducing trees larger than 10 cm dbh (Añez et al. 2005).

Vegetative reproduction (v)
All *Centrolobium microchaete* individuals under 10 cm dbh in our research area were resprouts. Previous research has proven that *Centrolobium microchaete* mainly reproduces by resprouting instead of seed production (Mostacedo 2007), therefore we did not include seedlings and saplings in the model for this species. *Acosmium cardenasii* can resprout as well, but no data are available on resprouting frequency, therefore all plants under 10 cm dbh were considered to be originated from seeds.
Number of resprouts produced per tree stump and resprouting probability were obtained from Mostacedo (2007). There were no different treatments in this study, thus we used these data for all treatments and all years. We assumed resprouting to only take place when trees were regarded dead by either logging or natural causes.

Matrix model parameterization and simulations.
We constructed a size-classified projection matrix (Caswell 2001) to simulate and analyze population dynamics. Matrix models have the form: n(t+1) = A x n(t). In this formula n(t) is the population size at time t and A is the transition matrix constructed out of transition probabilities. The population growth rate (λ) is the dominant eigenvalue of the projection matrix. We used seven different size classes in the model; Seedlings and resprout stage 1 (0-

1,50 cm high), Saplings and resprout stage 2 (1,50 cm high till 10 cm dbh) and five reproducing categories (10-20, 20-30, 30-40, 40-50 and >50cm dbh).

We used four transitions in our matrix model; Growth, survival, sexual reproduction and vegetative reproduction by means of resprouting. The formula of the growth transition (G_{ij}) is $G_{ij} = \sigma_j \times \gamma_j$, of the survival transition (P_{jj}) is $P_{jj} = \sigma_j - G_{ij}$, of the sexual production transition (F_{1j}) $F_{1j} = \sigma_j \times f_j$ and of the vegetative reproduction transition (V_{rj}) is $V_{rj} = (1- \sigma_j) \times v_j$. In these equations σ_j is the survival rate of size class j, γ_j represents growth, f_j seedling production rate and v_j resprout production rate. The r represents the smallest resprout class. We modeled population size by constructing separate matrices for the difference treatments at the first, second and third until the fourth year. From the fifth until the 25th year, which is the end of the cutting cycle, we used a matrix with the average vital rates of the three control matrices of the first three years.

Vital rate sensitivity (s) and elasticity (e)
Vital rate sensitivity and elasticity gives an indication of the importance of a particular vital rate to the population growth rate. We calculated vital rates sensitivities by tracing changes in λ to the vital rates included in the calculation of matrix element a_{ij} (Caswell 1989; p. 126–129).We calculated vital rate elasticity by multiplying vital rate sensitivity with the vital rate in consideration, divided by the population growth rate. (Caswell 1989; p. 135)

Survival sensitivity:

$$s_{\sigma j} = \delta\lambda/\delta P_{jj} \times \delta P_{jj}/\delta\sigma_j + \delta\lambda/\delta G_{ij} \times \delta G_{ij}/\delta\sigma_j + \delta\lambda/\delta F_{1j} \times \delta F_{1j}/\delta\sigma_j + \delta\lambda/\delta V_{rj} \times \delta V_{rj}/\delta\sigma_j$$
$$= s_{jj} \times (1- \gamma_j) + s_{ij} \times \gamma_j + s_{1j} \times \sigma_j + s_{rj} \times -v_{rj}$$

Growth sensitivity:

$$s_{\gamma j} = \delta\lambda/\delta P_{jj} \times \delta P_{jj}/\delta\gamma_j + \delta\lambda/\delta G_{jj} \times \delta G_{jj}/\delta\gamma_j$$
$$= s_{jj} \times -\sigma_j + s_{ij} \times \sigma_j$$

Sexual reproduction sensitivity

$$s_{fj} = \delta\lambda/\delta F_{1j} \times \delta F_{1j}/\delta f_{1j}$$
$$= s_{1j} \times \sigma j$$

Vegetative reproduction sensitivity:

$$s_{vj} = \delta\lambda/\delta V_{rj} \times \delta V_{rj}/\delta v_j$$
$$= s_{rj} \times (1-\sigma_j)$$

Vital rate elasticity:
$$e_{xij} = s_{xij} \times x_{ij}/\lambda$$

LTRE analyses
LTRE analyses determines the contribution of changes in vital rates to changes in λ. Such changes in vital rate may result from experimental treatments, habitat differences, year-to-year variation etc. We used fixed effect Life Table Response Experiments at a vital rate level to test the influence of different treatments on $\Delta\lambda$ (Jongejans & de Kroon 2005).
The used formula was:

$$\lambda^m = \lambda^c + a^m$$

$$a^m = (x_j{}^m - x_j{}^c)\ \delta\lambda/\delta x_j\ |_{1/2\ A}{}^m\ _+\ {}_A{}^c$$

In which λ^m is the growth rate of treatment m, λ^c the growth rate of the control treatment which we use as the reference value, and a^m the main effect of treatment m on vital rate $x_j{}^m$. Vital rate LTRE contribution and the matching vital rate elasticity of the control treatment were subsequently correlated and plotted in a graph. The combination of the retrospective scope of LTRE (sensu Horvitz 1997) and the prospective scope of elasticity (sensu Zuidema et al. 2007) reveals if vital rates that are affected by the different logging regimes have an important role in future population growth.

Results

Testing for differences in vital rates
Differences in growth rates of all adult trees between years and between treatments were significant for both *Acosmium cardenasii* (years: F = 208,343 P < 0,001 treatment: F = 137,043 P < 0,001) and *Centrolobium microchaete* (years: F = 30,685 P < 0,001 treatment: F= 25,441 P < 0,001). Per year however not all of the used treatments differed significantly (Table 1).
We combined year 3 and 4 because, as previously mentioned, no data were gathered in 2005. Survival rates among different treatments within a year did not differ significantly (Table 2), there were however no treatments that showed no significant difference in growth rate nor in survival rate (Table 1, 2).

Table 1 Results of Tukey HSD analysis for adult tree growth rates of *Acosmium cardenasii* and *Centrolobium microchaete.* Equal letters in Homogenous subsets indicate no significant difference in between treatment**.**

	Acosmium cardenasii		*Centrolobium microchaete*	
Year 1	Average growth rate	Homogenous subsets	Average growth rate	Homogenous subsets
IN	0,2714	A	0,2240	A
IM	0,2602	A	0,1107	B
N	0,2221	B	0,0517	B
C	0,1487	C	-0,0426	C
Year 2				
IN	0,2328	A	0,0923	A
IM	0,0763	B	-0,0731	B
N	0,1729	C	0,0887	A
C	0,2532	D	0,2764	C
Year 3-4				
IN	0,2812	A	0,1706	A
IM	0,2126	B	0,1338	A
N	0,2747	C	0,2322	B
C	0,2520	D	0,2504	B

Table 2 Results of logistic regression analyses for survival rates. The control treatment was used as reference. Empty boxes indicate no effect of the independent variable.

Acosmium cardenasii	R^2	Constant	DBH	IN	IM	N
Year 1	0,068	4,216	0,047	-2,266	-2,014	-1,717
Year 2	0,013	3,777	0,026	-0,553	-0,455	
Year 3-4	0,448	3,771		-3,768	-0,738	
Centrolobium microchaete						
Year 1	0,286	9,853	-0,106	-4,429	-3,723	3,715

Year 2	0,012	3,338	0	-0,749	
Year 3-4	0,020	3,219		-1,013	-0,621

Population growth rates
Populations growth rates were higher than 1 in almost all treatments and all years indicating population growth (Table 3). Population growth rates for *Acosmium cardenasii* were highest in the control treatment. The annual transient λ however was the highest in the normal treatment; it was even higher than the λ of the control treatments. Population projections indicated that the tree density after 100 years (Fig. 1) was 57.7 % higher than the unlogged control plot. Only in the intensive treatments population declines occurred, but annualized transient growth rates indicated that populations increased in all treatments (Table 3).

Table 3 Population growth rates for treatments and three years. Annualized transient growth rate is the average growth rate modelled over 100 years using a sequence of matrices with the matrix of year 1 in the first year etc. From year 5-24 which is the end of the cutting cycle the control treatment was used.

Acosmium cardenasii	Year 1	Year 2	Year 3-4	Annualized transient
IN	0,980335	1,01672	0,805664	1,039182
IM	1,016684	1,049105	1,052346	1,064862
N	1,028507	1,05503	1,059853	1,072424
C	1,068593	1,061002	1,066318	1,06932

Centrolobium microchaete				
IN	1,036103	1,020652	1,024126	1,021303
IM	1,040629	1,070269	1,083637	1,036425
N	1,011391	0,999046	0,998382	1,017632
C	1,004718	0,998211	1,004681	1,014278

Centrolobium microchaete had a complete different pattern, with highest λ values in the improved treatment, followed by the intensive treatment. The projected population size after 100 years was 9 times larger than in the control plot (Fig. 1). The density showed a steep increase following logging. In both the normal and the control treatment population declines occurred in some years, but all annualized transient λ's indicated population increases (Table 3).
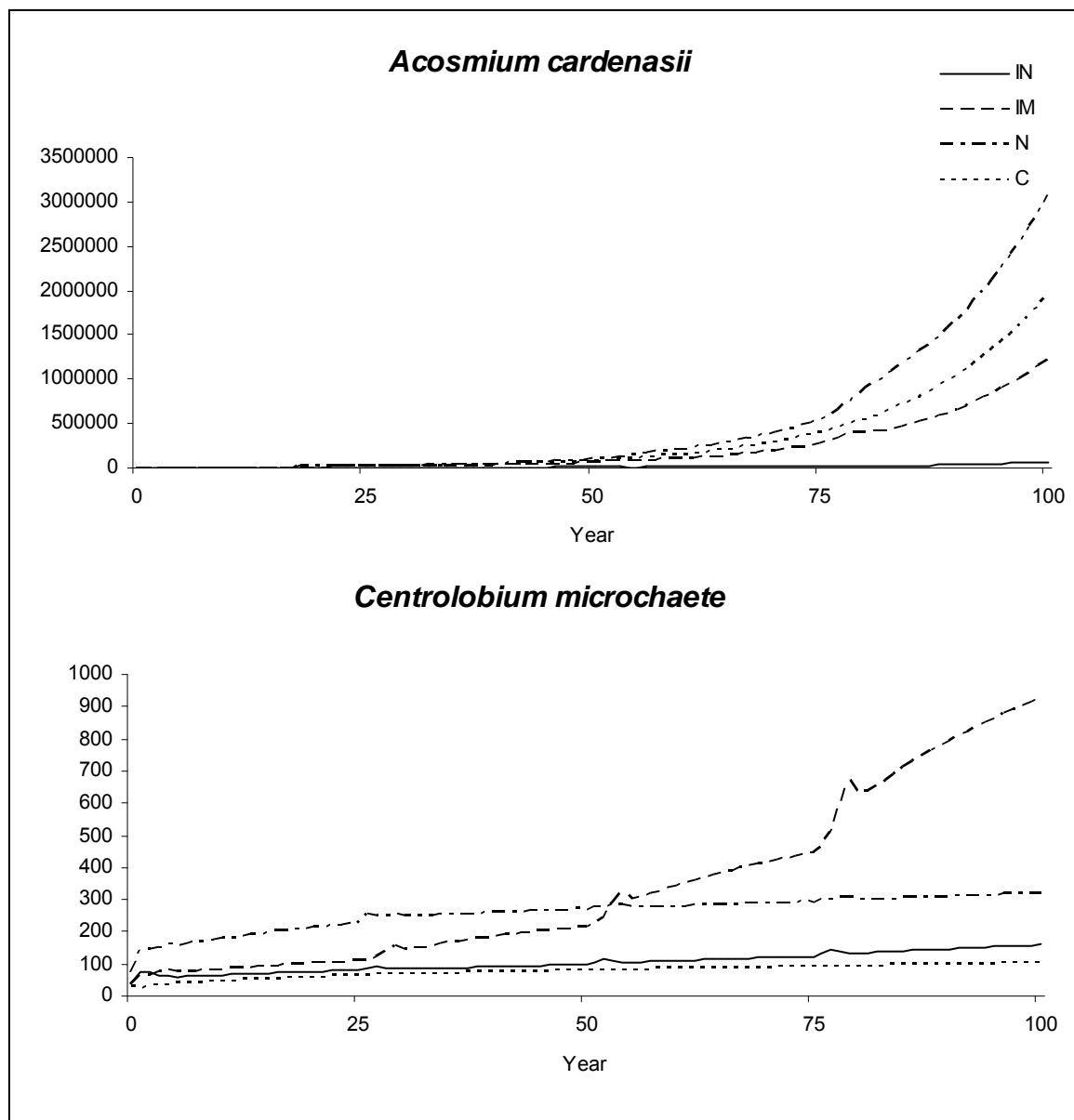
Figure 1 Density per hectare of both species projected for 100 years. Cutting cycle is 25 years and starts at year 0.

The pattern of the density of commercially harvestable trees (Fig. 2) of *Acosmium cardenasii* was similar to total density (Fig. 1). The density of harvestable individuals was 58% higher than the amount in the control plot without any logging. The improved treatment had 42% less commercial harvestable trees, while the intensive treatment even had 96.5% less trees larger than 40 cm dbh. There was no cutting cycle in which the amount of trees planned for harvesting could not be harvested. For *Centrolobium microchaete* however this was not the case in all treatments. Only in the normal treatment in the first three cutting cycles could the required amount of trees be harvested (Fig. 2). In contrast to the total density (Fig. 1), the amount of harvestable individuals after 100 year decreased in all treatments, except the improved treatment, which had a 56.8% increase.
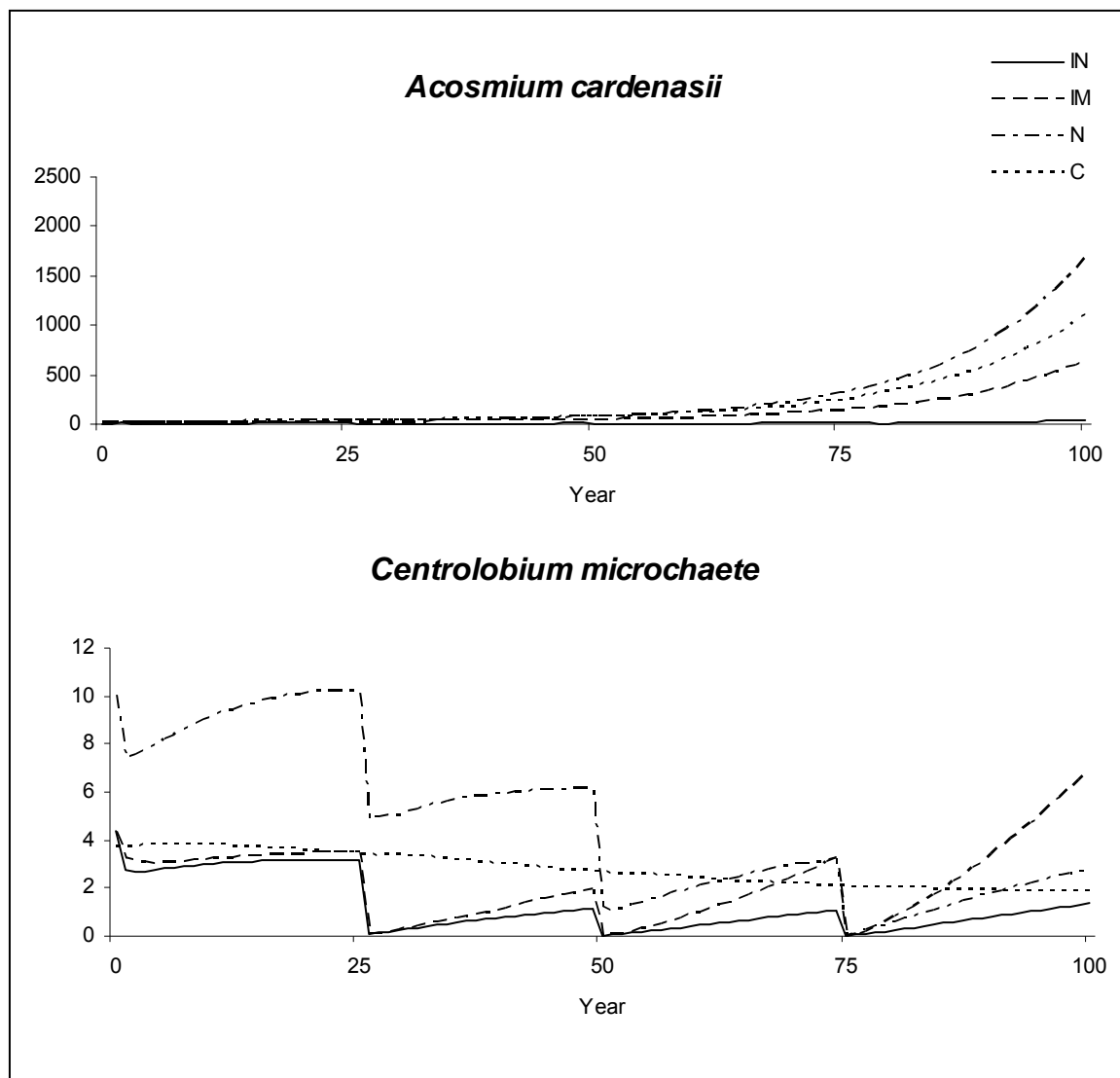
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Figure 2 The amount of harvestable trees (>40cm dbh) per hectare simulated for 100 years with a 25 year cutting cycle.

Prospective sustainability analysis

The survival of saplings and reproductive trees with a diameter of 10-20 dbh of *Acosmium cardenasii* in the control treatment showed the highest elasticities (Figure 3). Growth of seedlings and saplings had a higher elasticity than the reproductive classes. Individuals of 10-20 cm dbh also had the highest fecundity elasticity. The pattern of *Centrolobium microchaete* was quite different, whereas elasticities of adult classes' survival were negative due to the assumption in the model that resprouting only took place in dead trees. This assumption caused a negative effect of survival on reproduction, leading to a negative elasticity value. The highest elasticity growth rates of *Centrolobium microchaete* growth rates of the non-reproductive classes to reproductive classes, similar to *Acosmium cardenasii*. These elasticities of *Centrolobium microchaete* however were smaller than those of *Acosmium cardenasii*. Reproduction elasticity rates are low, even lower than of *Acosmium cardenasii*.
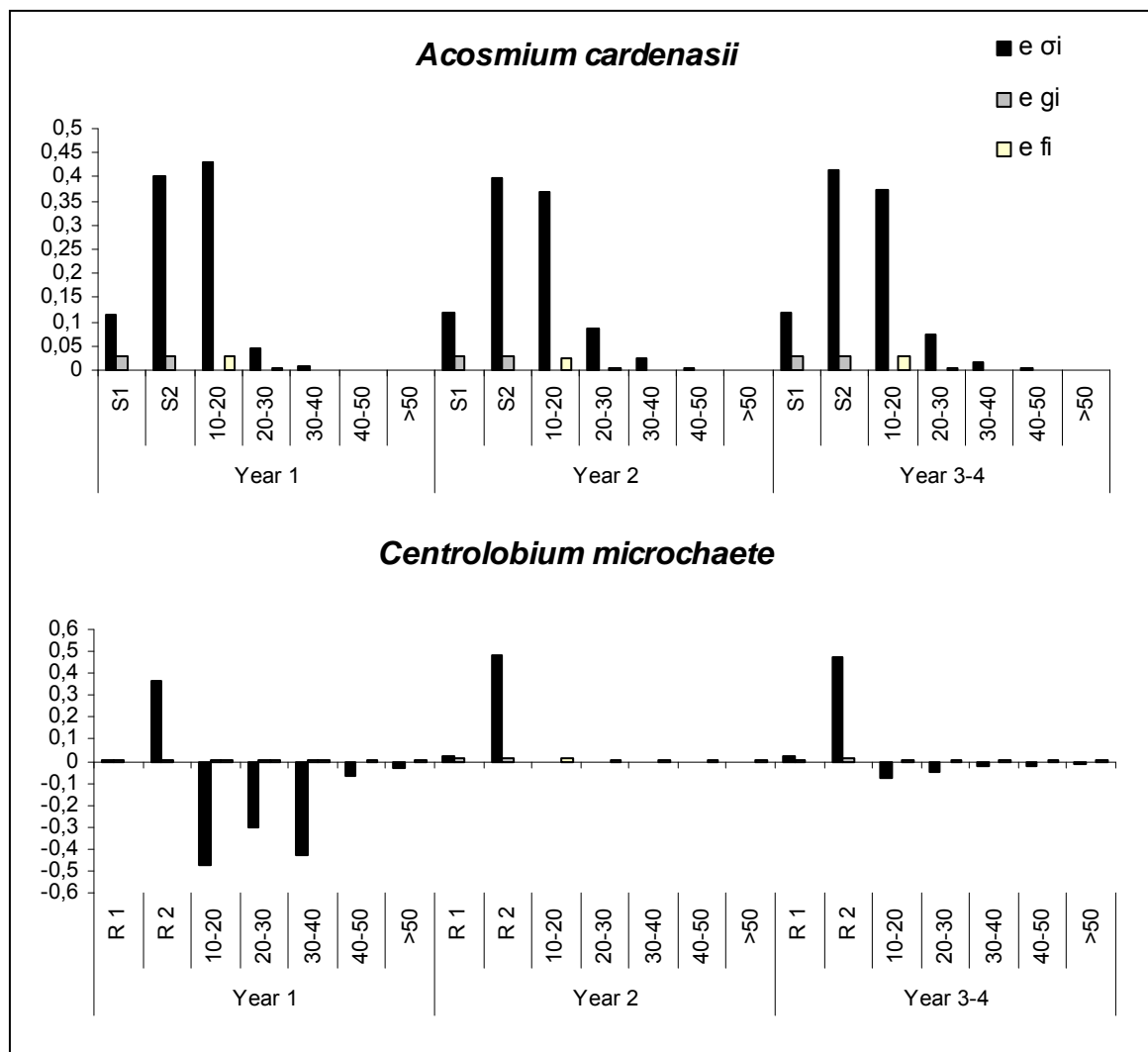
Figure 3 Vital rate elasticities in the control treatments for both species. S1, S2, R1 and R2 represents seedling , sapling, resprout 1 and resprout 2.

Retrospective sustainability analysis

We performed a LTRE-analysis in which the effect of the different logging treatments on the vital rates was compared to the unlogged control treatment. LTRE analysis showed that all vital rates of *Acosmium cardenasii* were severely negatively affected in the intensive treatment (Figure 4). The improved treatment had an overall negative effect, except the fecundity of the smallest size adult trees. In the normal treatment the growth of seedlings is strongly negatively affected, but the growth of saplings shows the opposite effect. In the first year the vital rates are in all treatments negatively affected, but in the following years these effects diminish. Growth of seedlings is highly negatively affected in the normal treatment, but the growth of saplings is slightly positively influenced by this treatment. In the second, third and fourth year there was hardly any effect of the normal treatment. The improved treatment had the smallest negative LTRE effect in the first four years, thus the smallest negative impact, this in contrast to the population growth rate in the first four years (Table 3) which was highest for the normal treatment. *Centrolobium microchaete* showed positive LTRE contributions in all treatments, but differences between the control and the normal treatment were minimal. The intensive treatment on the other hand had, especially in the first year, a positive influence on the growth of size two resprouts. These higher growth rates occurred both in the intensive and improved treatment, but the negative growth effect on
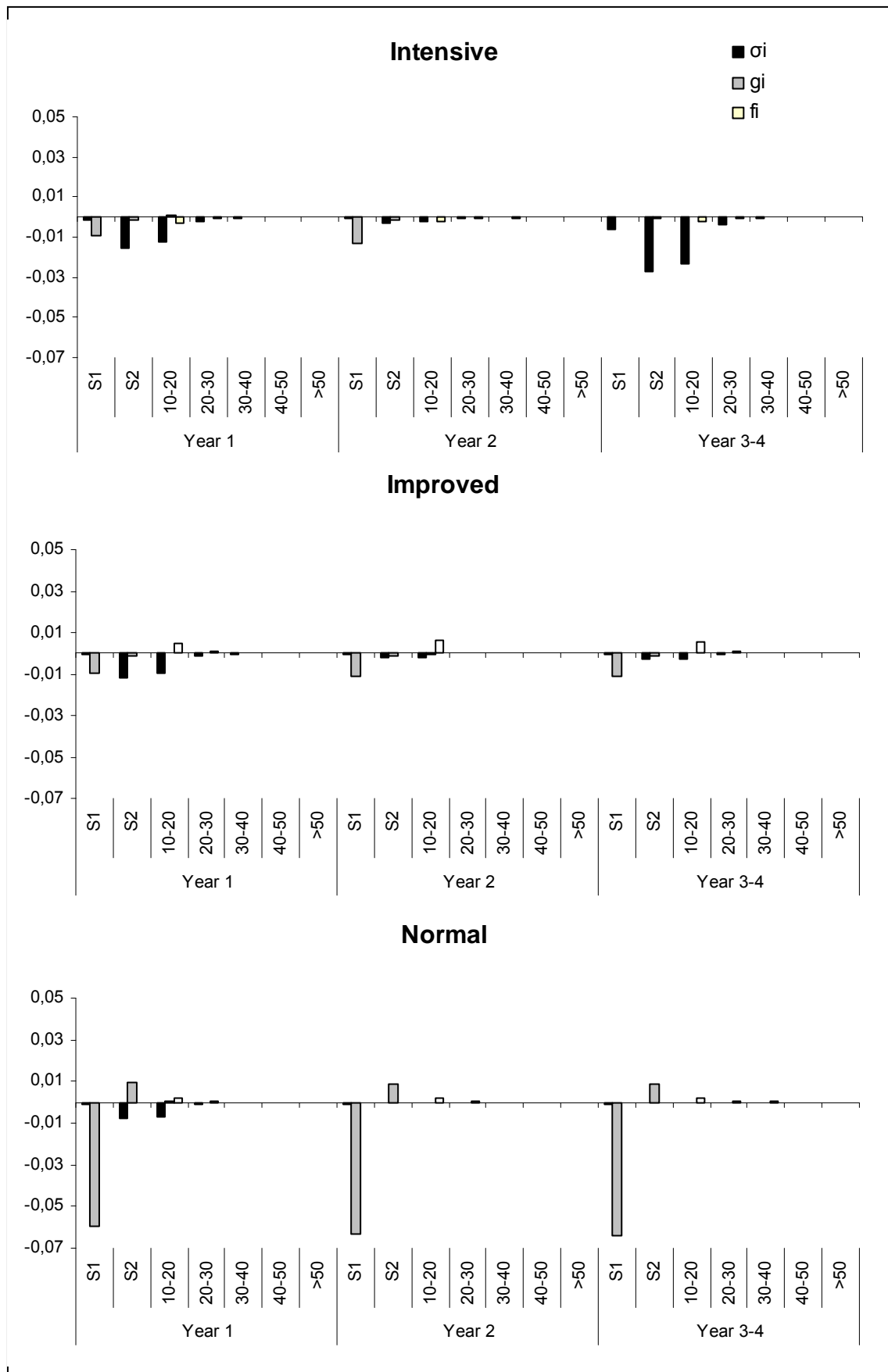
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Figure 4 Vital rate LTRE analysis of *Acosmium cardenasii* for intensive, improved and normal treatment compared to control treatment.
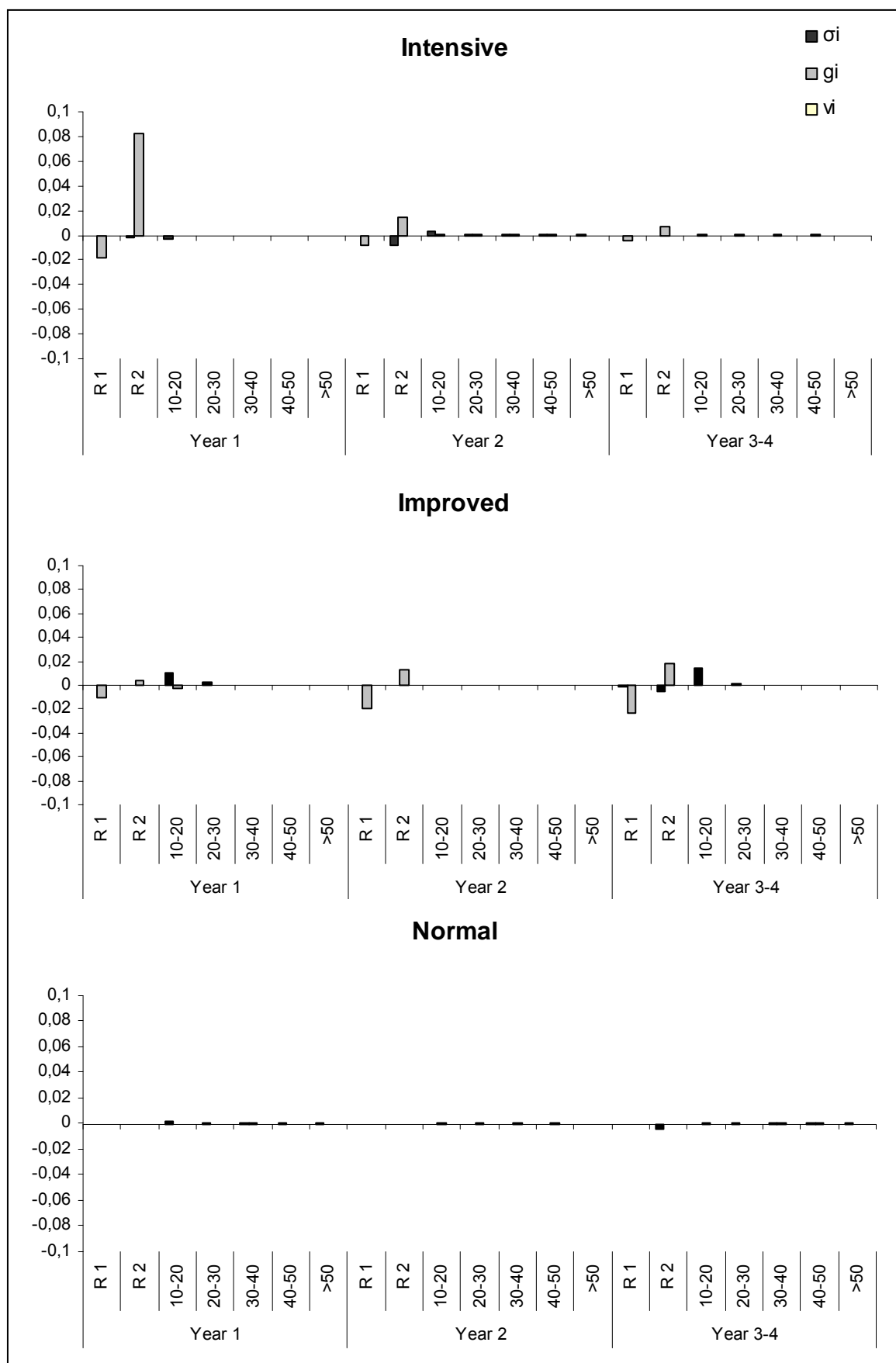
Figure 5 Vital rate LTRE analysis of *Centrolobium microchaete* for intensive, improved and normal treatment compared to control treatment.
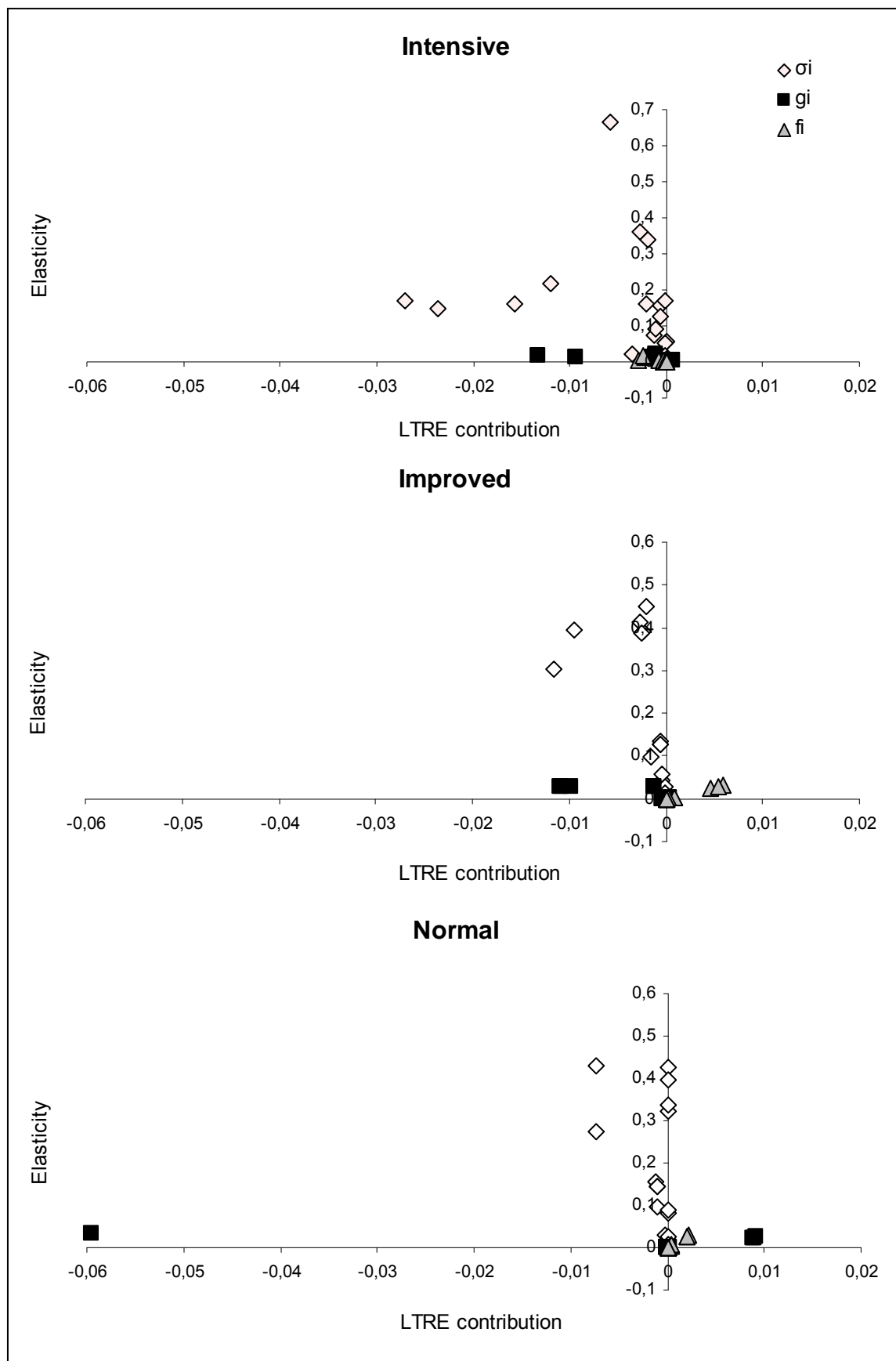
Figure 6 Vital rate LTRE contributions and vital rate elasticity of control treatment for three treatments of *Acosmium cardenasii* for all years. Kendal rank correlations are: IN: $\tau = -0.702$, P > 0.001. IM: $\tau = -0.382$, P > 0.001, N: $\tau = -0.075$, P = 0.215
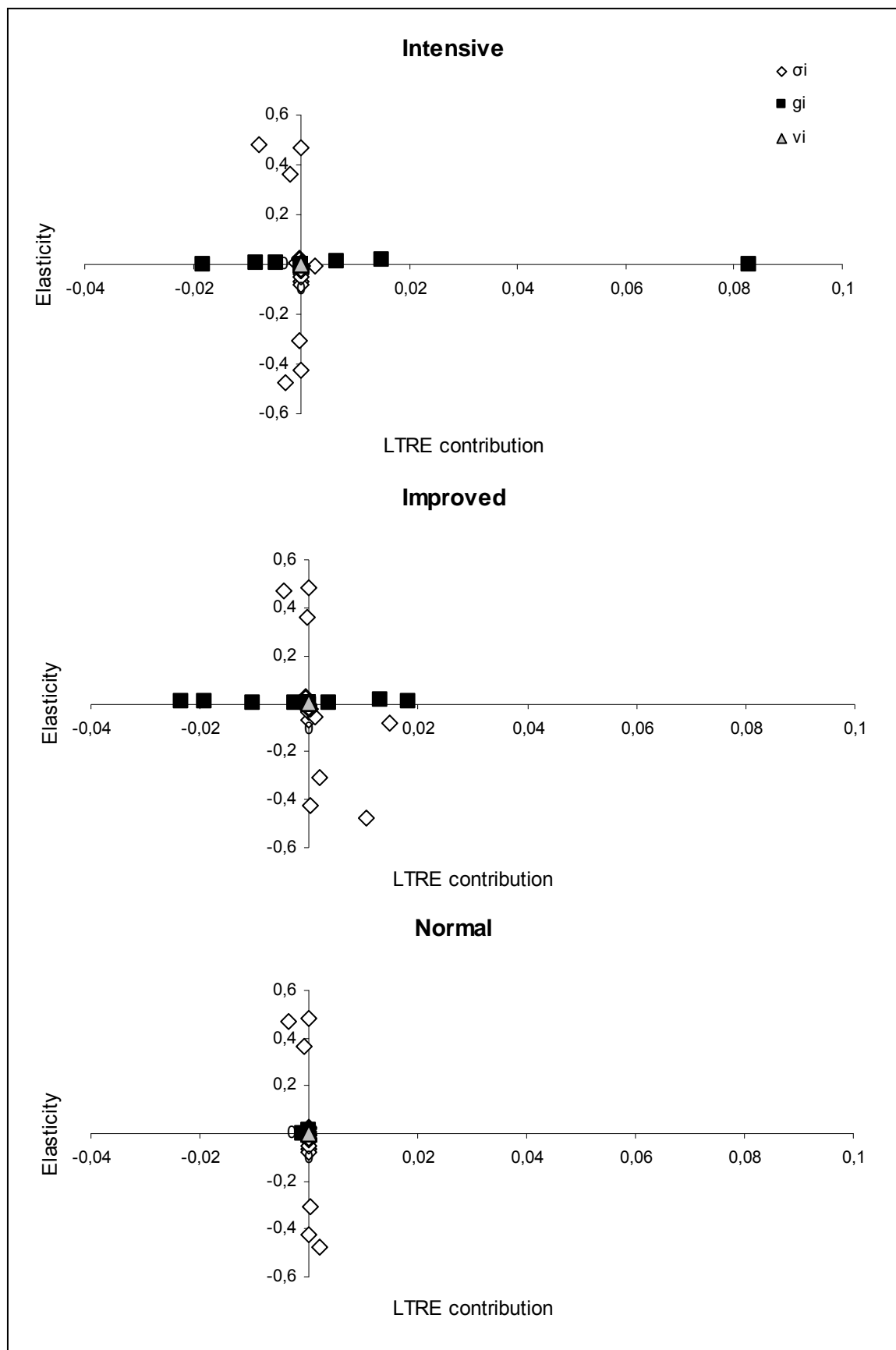
Figure 7 Vital rate LTRE contributions and vital rate elasticity of control treatment for three treatments of *Centrolobium microchaete* for all years. Kendal rank correlations are: IN: τ = -0.147, P = 0.065. IM: τ = -0.505, P > 0.001, N: τ = -0.376, P <0.001

resprout size 1 growth as well. The survival rate of resprouts and trees of 10-20 cm dbh was less affected in the intensive treatment than in the intensive treatment. The improved treatment had the highest positive LTRE effect. Fecunditie values were equal across all treatments and years and therefore did not contribute to Δλ.

Prospective and retrospective sustainability analysis combined
We plotted the vital rate LTRE contributions and control vital rate elasticity. Low LTRE contributions and high elasticities indicate sustainability and vice versa (sensu Zuidema et al 2007). The comparison of effects of the treatments on the population growth rate in a retrospective way (LTRE) with the importance of the vital rates for the population growth rate in a prospective way (elasticity) gives a better prediction of future effects of logging on the population. If a low elasticity vital rate is heavily affected by a treatment, the impact of logging is buffered, leading to little effect on the population growth rate and vice versa. Figure 6 shows that multiple survival rates in multiple years were negatively affected by the intensive treatment (Figure 3 & 4) in *Acosmium cardenasii*. These survival rates had both substantial elasticity values, but were severely negatively influenced. This leads to little prospects for sustainability. In the improved treatment survival rates with an even higher elasticity value were negatively affected, but these impacts were survival rates in the first year following logging. In the normal treatment the same high elasticity survival rates from the first year were the least impacted of the three treatments, but the growth of seedlings is highly negatively affected although its elasticity is relatively low.
In all three treatments the high elasticity survival rates of size two resprouts (Figure 3,5,7) of *Centrolobium microchaete* were negatively impacted. In the improved treatment and to a smaller extent in the normal treatment the survival of individuals of 10-20 cm dbh was positively affected (Figure 5), but these vital rates have large negative elasticity values (Figure 3) indicating little sustainability as well.

Discussion

The influence of timber extraction on populations dynamics has been extensively studied in tropical forests, but population dynamics of extracted dicotyledon timber species themselves following logging are remarkably scarce (Schulze et al. 2008, Hernandez-Apolinar et al. 2006, Zhang 2008). The influence of different logging intensities and silvicultural treatments on dicotyledon timber species is even studied to a lesser extent (Verwer et al. 2008). As far as we know this is one of the first studies investigating the effect of different logging regimes and performed silvicultural treatments on population dynamics of extracted trees belonging to different ecological functional groups.

Logging versus no logging
My results show that both *Acosmium cardenasii* and *Centrolobium microchaete* respond positively to logging, showing higher population growth rates (Table 1) and total population density (Fig. 1). This is probably due to the higher light availability after logging and soil scarification caused by skidders. Both factors have been known to have a positive effect on regeneration of light demanding species from tropical forests. (Dickinson et al. 2000, Fredericksen & Mostacedo 2000, Fredericksen 2002) That logging has a positive effect on a light demanding species like *Centrolobium microchaete* (Pinard 1999, Mostacedo et al. 1999) is therefore not surprising, but my results indicate that an intermediate (Markesteijn, 2002) to shade tolerant species (Pinard 1999) like *Acosmium cardenasii* may also benefit from light logging regimes. In contrast to the total population density there was a declining trend in the density of harvestable trees (Fig. 2) of *Centrolobium microchaete* in both the logged an

unlogged situation. In the unlogged situation this trend occurred in all years, while in the normal treatment the main reason for the decline was the extraction of individuals followed by an increase in the density of harvestable units until the start of the next cutting cycle. After more than three cutting cycles however there were not enough harvestable trees to meet up to the demand. *Acosmium cardenasii* is less affected directly by the extraction because of its high density of harvestable individuals. This high density also buffered the amount of harvestable units after 100 years.

In the unlogged situation the most important vital rates were survival of small trees and to a smaller extent growth of juvenile trees and the reproduction of the smallest adult tree class (Fig. 3). Especially in the first year after logging a higher mortality of all reproductive classes leads to a major increase for population growth. In the following years is mortality of less importance to population growth.

The negative elasticity values of the survival of adult trees is caused by the assumption in our model that vegetative reproduction of this species only takes place in dead trees.

Of the high elasticity vital rates the survival of saplings and smallest size adult trees of *Acosmium cardenasii* are slightly negatively affected by logging in the first year following logging (Fig. 4).

Growth of seedlings is severely negatively affected by logging, but these data were measured in year 2 and 4 therefore no trend in time can be analyzed. *Centrolobium microchaete* is hardly affected by logging. The pattern of the prospective and retrospective analyses combined (Fig. 6 & 7) indicates that for both species the normal treatment has a sustainable pattern e.g. no high elasticity vital rates are severely negatively influenced and vice versa. Allthough we didn't incorporate sexual reproduction of *Centrolobium microchaete* in our model, sustainability could be accomplished. In the control treatment however sexual reproduction could be more important than resprouting because of the negative effect of logging on seed production in this species (Soriano 2005). Nonetheless our results show that both species will not only survive logging, but will even benefit from it.

Logging intensity and silvicultural treatments
The two species react totally differently to the various logging intensities and silvicultural treatments. *Acosmium cardenasii* is negatively influenced by performed silvicultural treatments expressed in the smaller total population growth rate in the improved treatment (Fig. 1). Especially growth and survival of the smallest classes is negatively influenced by the silvicultural treatments (Fig. 4), vital rates which have high elasticities (Fig. 3), reproduction on the other hand increases when silvicultural treatments are performed.

Intensified logging detoriates the negative effects of the improved treatment (Fig. 4), whereas reproduction decreased too in contrast to the improved treatment. This decrease of seedlings and saplings is in accordance with previous research in semi-deciduous forests in Mexico. (Dickinson et al. 2000)

Centrolobium microchaete on the other hand is positively influenced by the performed silvicultural treatments, leading to higher population growth rates with a growth boost the first years following logging (Fig.1). Without performing silvicultural treatments there was according to our projections no sustainability accomplished in the amount of harvestable units (Fig. 2), since the only treatment with no decrease of harvestable units after 100 years is the improved treatment. Increased growth of second size resprouts occurred, but growth of the smallest size resprouts decreased when silvicultural treatments were performed (Fig. 5), these results are similar to previous research in Chiquitania forests (Pariona et al. 2003).

Survival of the smallest adult classes is also positively influenced in the improved treatment, potentially leading to more harvestable trees. According to our model however should this

negatively influence population growth rate. The main factor contributing to the higher population growth rate of the improved treatment is the growth rate of the largest resprouts in this class. The growth rate for this size class is based on only three individuals caused by a lack of measurements. When population size for this treatment is projected using the value of the intensive treatment, population size and structure are similar, but the LTRE contributions graph pattern stays similar, indicating the susceptibility of λ to errors compared to the LTRE contributions graph. (Zuidema et al. 2002)

Intensified logging lead to the complete disappearance of adult trees larger than 40 cm dbh after two logging cycles (Fig. 2), whereupon the timber demand could not be fulfilled per cutting cycle. Intensified logging improved the growth of the largest resprouts, but decreased growth of the smallest resprouts (Fig.5). These effects faded in the following years. Other vital rates were hardly affected.

The pattern of the prospective and retrospective analyses combined indicates that *Acosmium cardenasii* has some high elasticity vital rates that are negatively influenced by silvicultural treatments (Fig. 6) and even to a higher extent in the intensive treatment in which silvicultural treatments were performed combined with more intensive logging.

The patterns of *Centrolobium microchaete* are quite similar, only in the improved treatment are some vital rates with a high negative elasticity positively influenced, indicating on the one hand little sustainability. As previously mentioned these vital rates refer to the increased survival of the smallest adult trees potentially leading to more harvestable trees, thus more sustainability in the timber production.

Something that has to be taken into consideration regarding the performed population projections is that the effect of silvicultural treatments on the survival rates of both species lasts up to year 4 (Fig. 4 & 5). The effect of intensified logging is for *Acosmium cardenasii* even most notable in year 3-4. While the effect of only logging seem to fade-out within four years. This may indicate that the effect of both the improved and the intensive treatment exceeds the duration of the logging influence of the normal treatment. This leads to a longer lasting logging regime impact than we incorporated in our projection model. This is in accordance with previous research that showed that logging effects on population dynamics can last up to 15 years in tropical forests (Smith & Nichols 2005). If this is the case regarding our population projections would the population density in the intensive and improved treatment of *Acosmium cardenasii* be even lower than our current projections (Table 3, Fig 1 & 2), while *Centrolobium microchaete* would have higher population densities, especially in the improved treatment.

Importance of resprouting on population dynamics
This study shows the importance of vegetative reproduction for population dynamics following logging. According to this study *Centrolobium microchaete* can be harvested sustainably based entirely on vegetative reproduction. This form of regeneration is known from several other studies usually regarding more wet forests where resprouting frequencies are usually lower (Paciorek et al. 2000, Gorchov et al. 1993) than in the chiquitania forest (Mostacedo 2007). This maybe an adaptation of species from chiquitania forests to forest fires and other disturbances (Bond & Midgley. 2001). The higher resprouting frequencies of species in these forests combined with the higher growth rates of resprouts compared to seedlings (Mostacedo 2007) may pose better prospects for sustainable logging in these high disturbance adapted forests than forests that are prone to less disturbances. As previously mentioned, *Acosmium cardenasii* has a high resprouting frequency as well (Mostacedo 2007), but unfortunately we did not have those data on this at our disposal. This may indicate that regeneration of *Acosmium cardenasii* is higher in logged regimes than the predictions of our model.

Conclusion, recommendations and further research
Our study shows that timber harvesting can positively influence population growth of the harvested species. This influence may differ among species, *Acosmium cardenasii* for example shows a higher population growth rate when logging takes place. *Centrolobium microchaete* in contrast requires the performance of silivcultural treatments for sustainable management. These results are consistent with those expected for shade-tolerant and light-demanding species like the two species were classified. (Pinard 1999)

In contrast to our results did *Centrolobium microchaete* show no significant increase of regeneration after silvicultural treatments in moist forests (Peña-Claros et al. 2008). This emphasizes the differences in regeneration of the same species in different ecosystems (Sist & Brown 2004, Putz & Fredericksen 2004) therefore should the general application of this study in different ecosystem be taken with caution.

Our results also show the importance of resprouting for the regeneration of *Centrolobium microchaete*, this way of regeneration, which is faster than regeneration by means of seed production, leads to faster replacement of the harvested individuals. The harvested trees of *Centrolobium microchaete* are all over 40 cm dbh, which is the minimal cutting diameter (MCD) (Añez & Poorter). Since *Centrolobium microchaete* reproduces by means of resprouting, in which the amount of offspring produced is equal for all reproductive classes (Mostacedo 2007), are there possibilities of adapting the MCD for this species. This could lead to more production with probably little effect on the population. The enactment in the Bolivian law to secure regeneration by means of leaving 20% of trees above the MCD for seed production (MDSP 1996) is according to our model of little effect on regeneration of *Centrolobium microchaete*.

In contrary to previous research in tropical forests (Olmsted et al. 1995, Hernandèz-Apolinar et al. 2006) this study shows that survival rates of light demanding species like *Centrolobium microchaete* can be altered due to logging, showing the importance of field research.

The fast growth and regeneration of both *Acosmium cardenasii* and *Centrolobium microchaete* sustains populations of both species after logging and the amount of timber extracted from these forests. Several studies have shown that current cutting cycles do not sustain timber production (Silva et al. 1995, Dauber et al. 2005, Keller et al. 2007) and may cause a shift in the ecology of the extracted forest (van Gardingen et al. 2006). Our results show however that our two species, who are dominant in our study site are positively influenced, which may indicate that the ecology of the forest will not be radically changed after logging. This may, as previously mentioned, be due to the high frequency of disturbances that occur in these forests.

A point of discussion and further research is the very high population growth rate of *Acosmium cardenasii*. The lack of density dependant competition (Freckleton et al. 2003) could explain the extremely high population growth rates that we calculated in our model, especially for *Acosmium cardenasii*, but another reason maybe the assumption that seedlings up to 10 cm in height were first year offspring, while they might be older. This leads to an overestimation of the offspring produced per tree.

Furthermore more research is required in these forests to insure sustainability regarding the duration of logging effects and the effects of stochasticity in precipitation which has a major influence on growth and survival in these forests (Dauber et al. 2005).

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