

Enrichment planting of *Chamaedorea elegans* during forest recovery

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Abstract

Enrichment planting during secondary forest succession could provide a form of income during forest recovery. In southern Mexico, a species of interest for this type of enrichment planting is the understory palm *Chamaedorea elegans*. This palm is native to the rainforests of Central America and popular in the North American and European floral industry. In this study, growth of *C. elegans* palms planted in secondary forests of different ages and in primary forests was examined. Goals were 1) to relate growth performances with abiotic and biotic factors and 2) to determine whether there is an optimal forest age at which palm growth is maximal. The highest total leaf area and net daily assimilation of the palms were found in the younger secondary forests (3-10 years) and appeared to decrease with forest age. Of all measured (a)biotic factors, only light and phosphate availability, and soil clay fraction significantly affected palm growth and of these factors, only phosphate availability could be linked to forest age. While many studies on enrichment planting have focused on light availability, this study shows that for the enrichment planting of *C. elegans* edaphic factors and thus the choice of soil type are at least as important.

Introduction

A few decades ago, the province of Chiapas in southern Mexico was covered, for a large part, by tropical rainforests. Larger tracks of forests are now restricted to a number of protected areas, which make up about 13% of the total land area (source; Government of Chiapas). Most of the remaining landscape consists of a mosaic of small forest remnants, secondary forests and pastures. In addition, a large part of these pastures are now abandoned. Tree planting on abandoned lands could promote forest recovery, and is receiving increasing attention as a way to conserve biodiversity, protect ecological services and stimulate eco-tourism (Florentine et al. 2003; Chazdon 2003). However, as most land in Chiapas is divided in family-owned 'ejidos' (lands), stimulation of forest restoration on these private lands should be combined with some sort of financial compensation. Furthermore, ways to provide income during forest recovery, as well as from primary forests, could provide an alternative to other land uses (eg. clear cutting).

As forest recovery is a long process and environmental conditions can change considerably during forest succession (Finegan 1996; Guariguata et al. 2001), it is unlikely there is one simple activity to satisfy the economic needs of land owners during the whole process of succession. Various means of providing income should be considered and the most profitable way may depend on the successional stage of the forest in question. One activity of particular interest is enrichment planting, which is the introduction of economically valuable species into an ecosystem and thereby increasing the yield of the area (Paquette et al. 2006). Enrichment planting of different species at different times during forest succession could contribute to satisfying yield.

A species of interest for enrichment planting is *Chamaedorea elegans*, a small understory palm, native to the rainforest of Central America. The leaves of *C. elegans*

are harvested from natural populations and exported to Europe and the United States for usage in the floral industry (Current et al. 2001). Its popularity, which is due to the attractiveness and durability of the leaves, makes *C. elegans* a potential candidate for enrichment planting. Before this enrichment planting could take place however, it is necessary to know which succession stage is most suitable for enrichment planting of *C. elegans*. Because the leaf harvest per area will be a product of leaf growth, leaf turn-over rate and plant survival rate, all these parameters should be examined in different forest ages. A research project by W.A. Gudino (in cooperation with Dr. Martinez-Ramos) evaluated the growth of *C. elegans* in forest of different ages and found no significant differences in leaf production or in leaf turn-over rates between the forests, 15 months after planting (unpublished data). However, the trend found indicated a potential reduction of leaf production with forest age. On the other hand, a significant higher survival rate was found in the older secondary forests and primary forests (W.A. Gudino, unpublished data). A possible explanation for these results could be that higher light conditions in younger secondary forests increase assimilation and growth, but excessive irradiance could damage plant tissue (Baker et al. 1994). This could play an especially important role for *C. elegans*, which is an obligate shade plant.

The main objective of this study is to gain more insight in the (a)biotic factors effecting palm growth in forest of different ages, expanding on the work of W.A. Gudino. To evaluate these relations, growth performance of *C. elegans* palms planted in rainforests of different ages were studied, as well as the abiotic and biotic environment on the location of each studied palm. Central research questions were: 1) How is growth performance of *Chamaedorea elegans* related to light and nutrient availability, soil texture, damage by herbivores and competition? 2) Do these factors correlate with forest age? 3) Do the answers to the previous two questions enable me to determine the optimal forest age at which palm leaf production is maximal?

Material & methods

Experimental design

Chamaedorea elegans is a small understory palm occurring in the rainforests of southeastern Mexico, Guatemala, and Belize up to an altitude of 1400 m. It rarely becomes taller than 1.4 m (Hodel, 1992). In this study, net daily assimilation and total leaf area were used as a proxy for palm growth performance. Of the (a)biotic environment, light, nitrogen and phosphate availability, soil texture, organic matter content of the soil and leaf damage caused by herbivores (herbivore damage) were measured.

Data were collected within the experiment of W. A. Gudino and Dr. M. Martinez-Ramos. Their experiment consisted of forest plots, around the village of Frontera Corosal, in the province of Chiapas, Mexico (16°45' N, 91°00' W). The mean annual temperature is 25°C and the annual precipitation is approximately 3000 mm with a short dry season (monthly precipitation < 100 mm) from March to May. Plots were located in secondary forests growing for 3, 7 and 20 years after clear cutting and in primary forests. Two independent plots were established in each age-category. To evaluate the effect of competition with the natural ground vegetation, plots were divided in two halves: one half with the original ground vegetation and the other half where this vegetation was removed. In this study, the ground vegetation is defined as all vegetation < 1.5 m total height, which were mainly other palm species, plants of the family Heliconiaceae and young trees. In 2004, seedlings of *Chamaedorea elegans* were planted on each plot half in two rows. The rows were 5 meter apart; individuals in the rows were separated by 1.5 meter. Fieldwork took place in the months January and February 2007.

Light environment and photosynthesis

Three palms were randomly chosen on each plot half. Measurements on photosynthesis were conducted using a portable photosynthesis meter (Li-6400, LiCor). Of each palm, dark respiration and the photosynthetic rate at seven different irradiances were measured on the youngest fully expanded leaf, the oldest leaf and one or two leaves in between, in order to allow interpolation to the leaves not measured. The different irradiances; 700, 150, 90, 60, 45, 30, 15 and 0 PAR, were attained with a red and blue light source (6400-02B LED, LiCor) attached to the leaf chamber. The quantum sensor in the leaf chamber was used to check irradiance levels. Measurements on photosynthesis took place between 8:00 and 11:00 a.m. to prevent a reduction of photosynthesis due to water shortage. Because water shortage during the hottest parts of the day could reduce photosynthetic rates, a measurement of photosynthesis at 700 PAR was repeated on the youngest fully expanded leaf around 12:00 a.m. The reduction (when taking place) would be included in the calculation of the net daily assimilation (see below).

The light availability on a horizontal plane above each palm was estimated by taking hemispheric photographs (fisheye lens, Nikkor). The photos were taken at sunrise 1 meter above the ground using a tripod. Vertical light distribution through the crown of each palm was estimated using a light sensor (9901-013 external quantum sensor, LiCor). Light availability was measured on the tip, centre and base of each leaf and

repeatedly on the horizontal plane above the plant. The latter was used as the reference measurement.

Total leaf area

Leaves of *C. elegans* are compound leaves, existing of up to 40 leaflets (Hodel, 1992). To calculate the surface area of each leaf, the width and length of the longest and smallest leaflet were measured and the total number of leaflets counted. The surface area of an individual leaflets was calculated as having a perfect oval shape, using $(\text{length}/2) \cdot (\text{width}/2) \cdot \pi$. The average surface area of the tallest and smallest leaflet was used as an overall average, assuming a linear decrease in leaflet area from the tallest to the smallest leaflet. Multiplying this average leaflet area with the number of leaflets yielded the leaf area. This was done for all leaves and the summation of leaf areas gave the total leaf area of each palm.

The (a)biotic environment

The damage of each leaf was estimated and used to calculate the average leaf damage per palm. Leaf damage was estimated as the percentage of damaged or disappeared leaf tissue, ranging from 0% for none damaged leaves to more than 90% for highly damaged leaves. Soil samples of the topsoil in a 20 cm radius around each palm were collected, as well as two leaflets from the youngest fully expanded leaf. The leaf samples were dried. The nitrogen and phosphate content of the leaf dry mass was measured using an auto-analyser (Skalar, Breda). Of the soil samples, the organic matter content was analysed using a high temperature oven (550 °C). For the clay and sand fractions of the soil, all organic material was removed by washing 2-gram sub-samples in a 100 ml 6% hydrogen peroxide solution for 60 hours at a temperature of around 70 °C. The remaining soil was analysed in a particle samples (Mastersizer S long bed Ver. 2.18, Malvern Instruments Ltd.). In this study, clay was defined as everything with a grain size smaller than 3.9 µm, the sand as everything with a grain size larger than 63 µm (MacBride, 1994). The category in between, the loam fraction, was not explicitly considered here. All laboratory analysis took place at Utrecht University, the Netherlands.

Net daily assimilation

The whole-plant net daily assimilation was calculated from the measurements on photosynthesis, light availability during the day and the light distribution through the plant's crown, using the method outlined by Anten & Ackerly (2001). This method uses a non-rectangular hyperbola to characterize light response of net leaf photosynthesis per unit area (P_L):

$$P_L = \frac{(P_{max} + \Phi I_L) - \sqrt{(P_{max} + \Phi I_L)^2 - 4\Phi I_L P_{max}\theta}}{2\theta} - R_d$$

Eqn 1

With P_{max} as the light-saturated rate of photosynthesis, Φ as the quantum yield, θ as the curvature factor and R_d as the dark respiration. The photosynthetic rate at 700 PAR was used as the P_{max} , R_d was measured at 0 par. Φ was calculated from the measurements of photosynthesis at different irradiances. θ was taken constant in this study as 0.8. I_L is the photon flux density (PPFD) on a leaf. I_L is calculated as:

$$I_L = I_0 I_{rL}$$

Eqn 2

Where I_0 is the PFD on the horizontal plane above the palm and I_{rL} the relative light intensity. I_0 was estimated with the program Winphot (ter Steege, 1997) from the canopy fish eye pictures (see above). Light availability was calculated for a complete clear day on January 21st, which was in the middle of the fieldwork period. Program analysis yielded I_0 for 2-minute intervals during the day. I_{rL} was calculated from the measurements on the light distribution through the palm's crown and is expressed as the percentage of light received on a particular leaf in comparison with I_0 . With the estimation of I_0 and I_{rL} , the light availability at the leaf level could be calculated at two minute intervals during the day. The P_L value of each leaf was multiplied with their leaf area and summed to obtain the whole plant carbon gain. Summation of the assimilation during all 2-minute intervals yielded the net daily assimilation of each palm.

Statistical analysis

The data were analysed in three ways. The first was a comparison of the measured properties between the different forest ages and between the treatments. This was done by two statistical analyses; a 'univariate analysis of variance' and a 'repeated measurement analysis'. In both analyses net daily assimilation and total leaf area were logarithmic transformed in order to correct for none-normal distribution. The second approach was combining all data in a regression analysis. Net daily assimilation or total leaf area was taken as dependent factor. Nutrient and light availability, clay-, sand and organic fraction, damage by herbivores, but also the discrete variables forest age, plot and treatment were taken as random factors. Given the 6 palms per treatment per forest age, $n = 48$. Finally, correlations were calculated between all measured properties.

Results

Leaf photosynthetic traits

Maximum photosynthesis, dark respiration and quantum yield of the youngest leaves, as well as of the most productive leaves, did not change significantly with forest age. In addition, removal of the undergrowth did not change photosynthetic parameters (table 1). The repeated measurements around 12:00 a.m., of the maximum photosynthesis on the youngest leaf, indicated no reduction of the photosynthetic rate. The hottest time and therefore potentially driest time of the day however, is around 14:00 p.m. A reduction of photosynthesis could take place around this time, but was not measured in this study.

The (a)biotic environment

The removal of the undergrowth did not significantly effect the whole plant net daily assimilation, total leaf area, or the measured biotic and abiotic factors in any of the forest ages. When combining the data of the two treatments, a significant difference in daily assimilation and total leaf area was found between the youngest forests and the primary forests (fig. 1). Both assimilation and leaf area seemed to decrease with forest age. A higher variance in the total leaf area and daily assimilation was found in the younger forests.

The highest canopy openness was found in the 10-year-old forests. However, the canopy openness of the youngest and the oldest forest, 6 and 100 years respectively, were not significantly different (fig. 2). A higher phosphate and nitrogen concentration in the leaf dry mass was found in the 23 year old forests (fig. 3). Nitrogen concentrations did not differ between the other forests, but phosphate concentrations were significantly different in all forest ages, with lowest concentrations in the primary and 10 year old forests. No significant differences were found in clay (fig. 3), sand, and organic fraction between forests ages, but large differences in texture were found within and between sites (clay fraction ranged from 3 to 50%, sand from 9 to 69%). The average leaf damage was highest in the 23-year-old forests, but did not differ between the other forests (fig. 4).

Regression and correlation analyses

For net daily assimilation, the outcome of regression analysis indicated a model with forest age, canopy openness, phosphate availability and clay fraction as significant factors and an adjusted R^2 of 0.38. A positive relation was found between assimilation and canopy openness & phosphate availability, both forest age and clay fraction were negatively related to assimilation. For total leaf area, significant factors were forest age (negatively) and phosphate availability (positively) with an adjusted R^2 of 0.30. Table 2 summarizes the outcome of the analysis.

Figure 5 depicts all significant correlations found in the total data set, taking forest age, plot and treatment into account as factors. Net daily assimilation was significantly negatively correlated with forest age and positively with total leaf area and canopy openness. The latter correlated with both the soil sand and clay fraction, as with phosphate availability. Phosphate availability in turn correlated with forest age, canopy openness, nitrogen availability, total leaf area and herbivore damage.

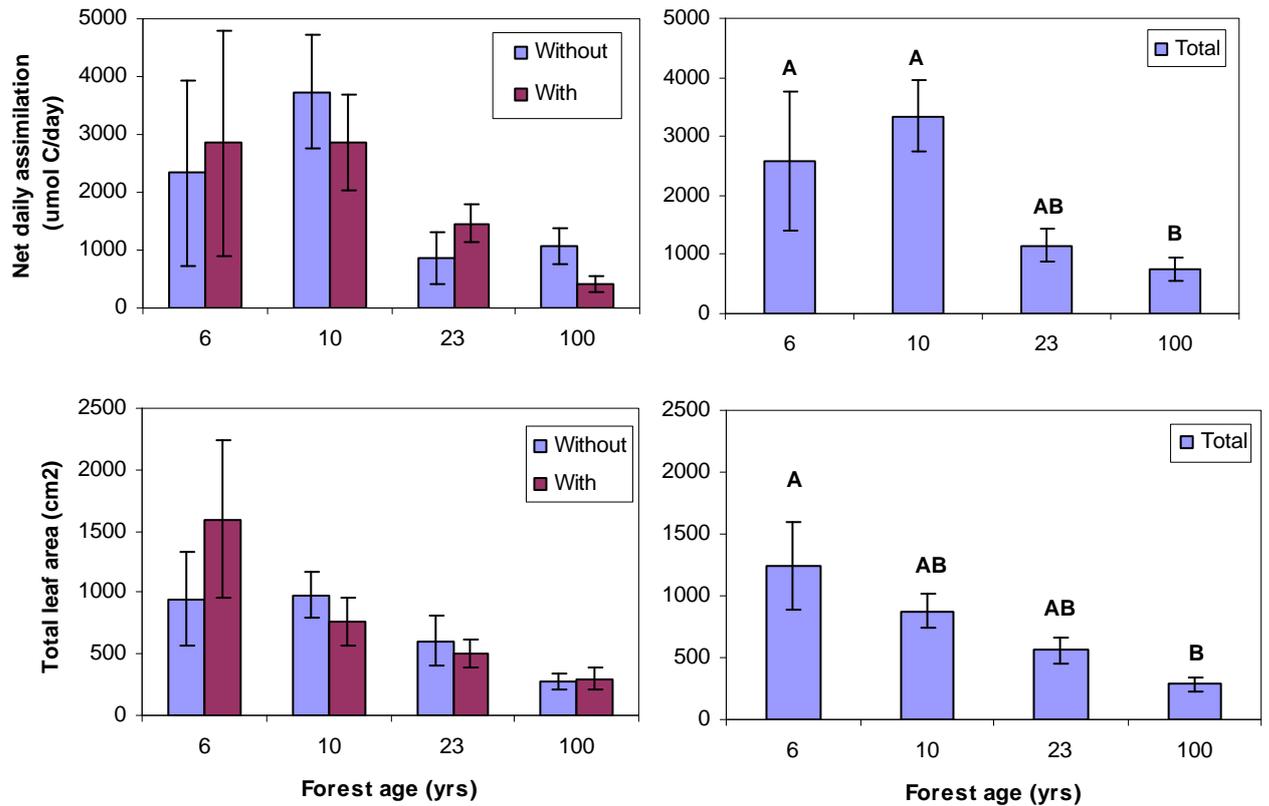


Fig. 1. Net daily assimilation (above) and total leaf area (below) with forest age. No significant differences were found between the undergrowth treatments (figures left). When combining all data, a significantly higher assimilation and total leaf area were found in the younger secondary forests (figures right). Error bars denote the SEM, letters the significant differences.

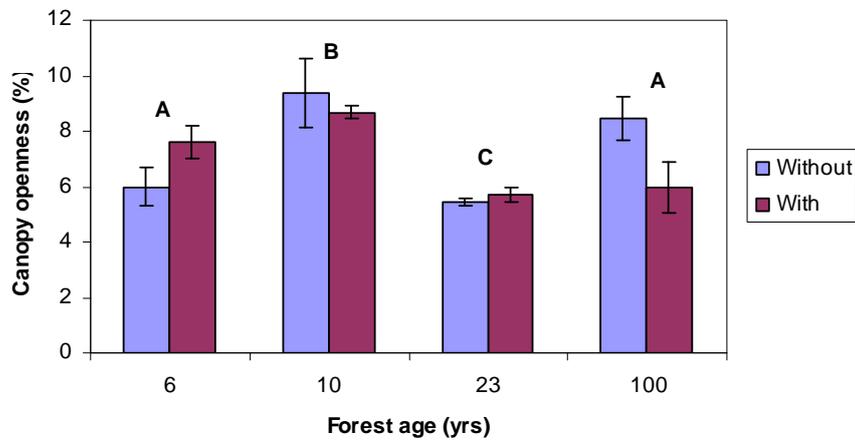


Fig. 2. Canopy openness with forest age. Error bars denote the SEM, letters the significant differences when the data of the two treatments are combined.

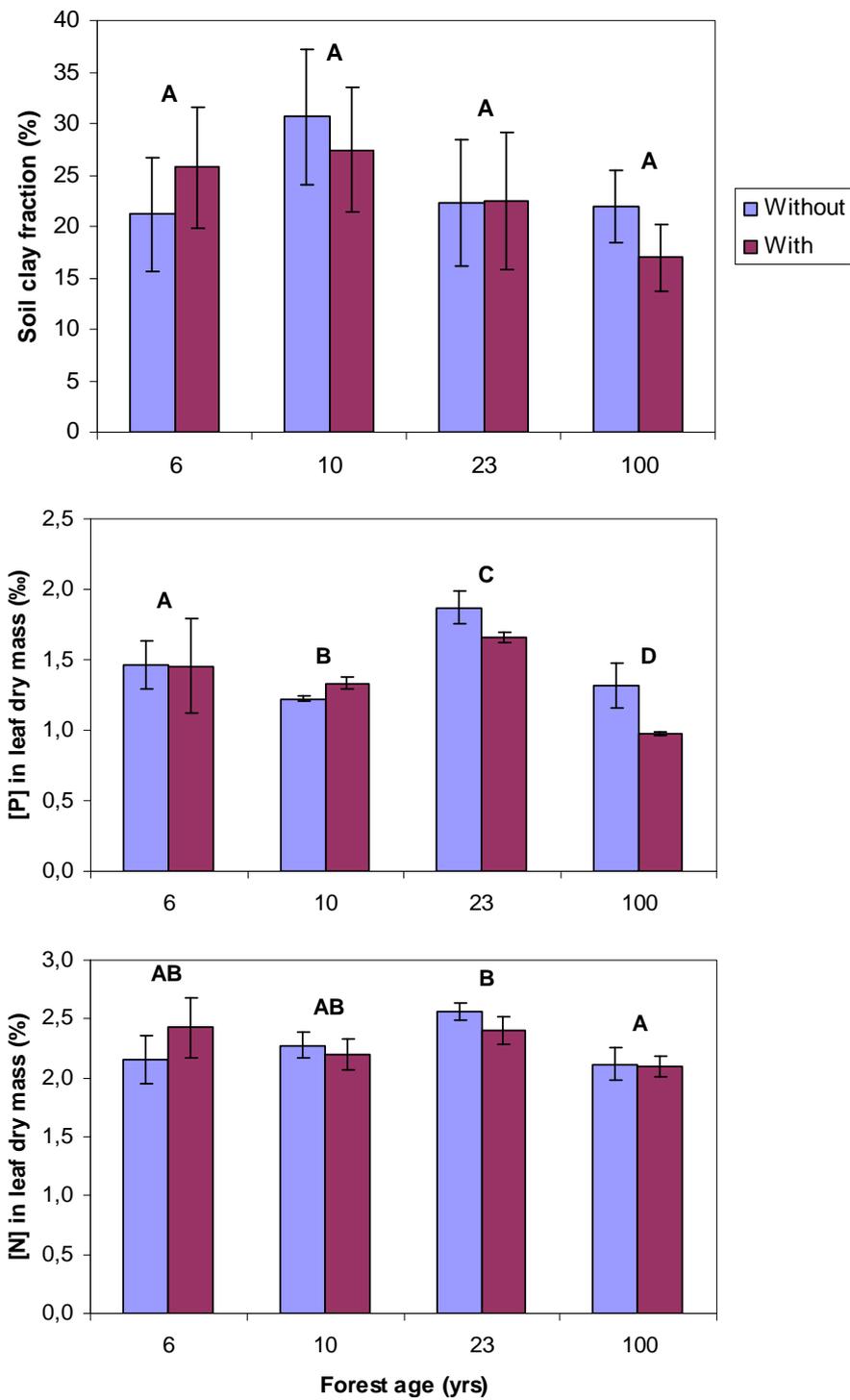


Fig. 3. Clay fraction and the phosphate & nitrogen concentration in the leaf dry mass with forest age. Error bars denote the SEM, letters the significant differences when the data of the two treatments are combined.

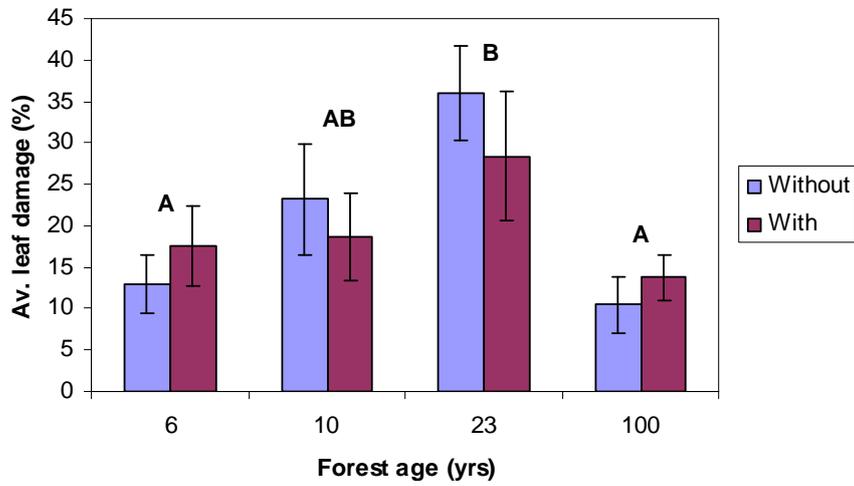


Fig. 4. Average leaf damage with forest age. Error bars denote the SEM, letters the significant differences when the data of the two treatments are combined.

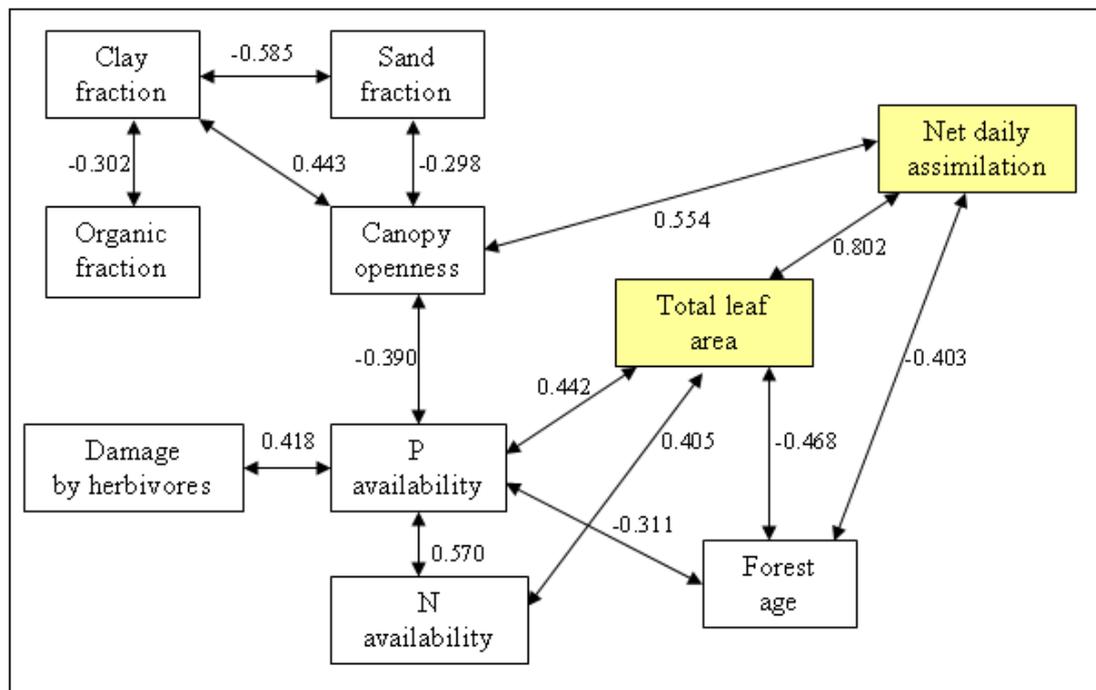


Fig. 5. All observed significant correlations (Pearson's cc.).

Table 1. Measured photosynthetic parameters of the most productive leaves. P_{max} = the maximum photosynthesis (at 700 PAR), Rd = the dark respiration (at 0 PAR). Values in parentheses are SEM (n = 6).

Photosynthesis parameters	Treatment	
	With undergrowth	Without undergrowth
P_{max} (molC/m²/s)		
6yrs	3.62 (0.48)	4.32 (0.61)
10yrs	4.13 (0.22)	4.23 (0.35)
23yrs	3.61 (0.29)	2.69 (0.20)
100yrs	3.73 (0.49)	4.53 (0.78)
Rd (molC/m²/s)		
6yrs	-0.48 (0.08)	-0.70 (0.25)
10yrs	-0.74 (0.18)	-0.39 (0.09)
23yrs	-0.46 (0.08)	-0.47 (0.12)
100yrs	-0.38 (0.07)	-0.63 (0.10)
Quantum yield		
6yrs	0.037 (0.00)	0.058 (0.00)
10yrs	0.060 (0.01)	0.055 (0.00)
23yrs	0.046 (0.00)	0.031 (0.00)
100yrs	0.047 (0.01)	0.050 (0.01)

Table 2. Results of linear regression analysis. The data of the net daily assimilation and total leaf area were logarithmic transformed.

Dependent variable: net daily assimilation (Ln)		
<i>Factors</i>	<i>Standardized coefficients</i>	<i>Sig.</i>
(constant)	4.270	.000
Forest age	-0.322	.014
Canopy openness	0.576	.000
Phosphate availability	0.352	.012
Clay fraction	-0.319	.022
Dependent variable: total leaf area (Ln)		
(constant)	5.307	.000
Forest age	-0.336	.011
Phosphate availability	0.381	.004

Discussion

Net daily assimilation and the total leaf area of the palms appeared to be smaller in older secondary and primary forests. This result is consistent with the trends found by W.A. Condino, who studied the growth of *C. elegans* for two years in the same forest plots as used in this study. Her results were not significant however. A reason why the current study indicated a stronger reduction could be because these measurements were taken later on after the initiation of the experiment. As *C. elegans* is a relative slow grower, differences in leaf production could become more prominent as time continues (Hodel, 1992). One other important point is that this study only calculated net daily assimilation and total leaf area and does not estimate growth directly. Growth reflects the difference in biomass between two time points in the past. Net assimilation on the other can be seen as the potential growth in the near future; it is an estimation of the carbon fixation, part of which is usable for future growth. Total leaf area doesn't reflect growth either, but is a useful indicator of differences in standing biomass at a particular time point. A future project is planned to combine the data of growth and net daily assimilation of *C. elegans* and to evaluate their relation in field conditions.

Interestingly, the study of W.A. Gudino found higher survival rates in the older secondary (23yrs) and primary forests. As mentioned in the introduction, the reduction of growth, but increment of survival rates with forest age was hypothesized to be a consequence of a decrease of light availability with forest age. Higher light conditions in the younger secondary forests could increase assimilation and growth, but excessive irradiance could also damage plant tissues. As *C. elegans* is an obligate shade plant, the negative consequences of high irradiances could be especially severe. While the light harvesting capacity of shade tolerant plants is more or less comparable to that of shade intolerant plants, its carboxylation capacity is much reduced (Lambers et al. 1998). This implies that at high light availability light capture is greatly in excess of its use in photosynthesis. On the molecular level it has been assumed that the excessive energy during this imbalance destroys the Mn-cluster of the oxygen-evolving complex of photosystem II (Murata et al, 2007). This destruction also takes place at low irradiances, but could exceed repairing capacity at very high irradiances and result in structural damage of photosystem II, reducing assimilation and plant fitness on the long term (Baker et al. 1994; Kyle et al, 1985). Interestingly, no reduction of light availability (canopy openness) with forest age was found. Light availability in the younger forests was not significantly higher than in the primary forests. It is therefore difficult to explain the growth and survival patterns by differences in light availability between the forests. It is important to point out however that the survival rates were measured two to three years before the measurements on light availability took place. Therefore, differences in light levels could have been greater when survival was measured and could have been more equalized by the time the canopy openness was measured.

When ignoring forest age and combining all data, a significant positive correlation was found between net daily assimilation and light availability. It should be noted though that net daily assimilation was calculated from the measurements on photosynthesis and light availability. Therefore, a correlation between assimilation

and light availability is to be expected, without indicating direct causality. Interestingly, no correlation was found between total leaf area and canopy openness and could have been expected when light availability determines the major part of growth performance. However, this result could also be explained by the fact that not only leaf production but also leaf turn over increase with light availability. It remains therefore unclear to what extent light plays a role in determining growth rates of the palms.

As mentioned, survival rates were also difficult to link with light availability. Because the environmental conditions on the location of died plant were not studied, the possibility remains that these palms were growing on spots with (excessive) high light availability. Negative correlations between survival and canopy openness have been found for natural populations (Martinez-Ramos unpublished data) For the palms measured, no significant differences were found in photosynthesis parameters (P_{max} , R_d , quantum yield), indicating no severe photo-inhibition was taking place. The average leaf damage was slightly higher in the 23 year old forests, but did not differ between the other forests. Survival rates are therefore also difficult to relate with differences in herbivore pressure. What determines survival rates remains unclear.

Nitrogen and phosphate content of the leaf dry mass were used to estimate the availability of these nutrients. Although the availability of both nutrients were higher in the 23 year old forests, no significant differences were found in nitrogen availability between the other forest ages. Phosphate availability on the other hand, seemed to decrease with forest age (with the 23 year old forest as an exception), which was also found in a correlation analysis. And although leaf N contents did not correlate with forest age, nitrogen and phosphate contents correlated significantly and positively with each other. This is in agreement with the general view that nutrient availability in the soil decreases as succession proceeds (Jordan 1985). This is because more and more nutrients are transferred from the soil to the above ground biomass and the complex nutrient conserving mechanisms of most rain forest plant species prevent loss of nutrients to the soil (Jordan, 1985). Regression analysis showed that phosphate had a significant positive effect on total leaf area. It could therefore be hypothesized that the palms planted in older secondary forests and primary forest were growing on soils with a lower nutrient availability (and hence the differences in growth).

Although nutrient availability might decrease during succession in the same forest plot, nutrient availability can vary considerably between forests areas, independent of their succession stage (Castilho et al. 2006). This variance can be due to a number of factors, ranging from variance in soil texture, slope or proximity to rivers (Jordan, 1985). Of all potential factors effecting nutrient availability, only the soil texture and soil organic matter content were measured. No significant correlations were found between sand fraction or soil organic matter content and the availability of nitrogen or phosphate, but a marginally significant correlation was found between the clay fraction and the phosphate availability ($p = 0.09$). Multiple studies pointed out that total soil phosphate concentrations increase with clay fraction (Lopez Camelo et al. 1996; Rodier et al. 1994; Hassink 1997). This higher phosphate concentration is assumed to result from the greater physical protection of organic matter in fine-texture soils (Jenkinson, 1998; Van Veen et al. 1990). However, the opposite trend is the case for plant extractable phosphate, which is generally higher in sandy soils (Silver et al.

2000). This is explained by the ability of phosphate to bind with exchangeable Al and Fe of the mineral soil in more aerated sandy soils (Silver et al. 2000). Because phosphate concentration in the leaf dry mass represents available phosphate, the latter seems to be the case in this study.

In addition to its effects on nutrient availability, soil texture also influences many other environmental conditions (Silver et al. 2003). For example, coarser soils are generally quicker dehydrated, whereas clay rich soils are able to hold water and tend to be moister (Williams et al. 2002). Regression analysis points out a direct negative effect of clay on assimilation. A similar result was found by Castilho et al. (2006), who studied the above ground biomass of trees and palms in relation to soil gradients (including texture) in central Amazonian rainforests and found that palm biomass was higher in sandy soils than on clay soils. Because *C. elegans* is normally found on grounds with a good drainage, it could be expected that clay fraction of the soil also affect plant growth in this way (Garwood et al. 2005). Unfortunately, this study does not include any measurements on drainage and water availability, and the potential effects of these on plant performance. Finally, a significant correlation was also found between sand- & clay fraction and canopy openness (-0.298 and 0.443 respectively). How soil texture effects canopy openness is not clear, but could be due to the above mentioned effects on water drainage and nutrient availability. So, soil texture seems to effect assimilation in multiple ways and appears to be important to consider when designating areas for enrichment planting.

In summary, the decrease of net daily assimilation and total leaf area with forest age is difficult to explain when looking at the average values of the measured biotic and abiotic factors per forest age. This could be due to the high variance of these factors within each forest age category, especially in the younger secondary forests. Correlation and regression analysis points out the importance of canopy openness, clay fraction and phosphate availability on daily assimilation and total leaf area. Interestingly, the undergrowth removal did not appear to effect daily assimilation, total leaf area or any of the (a)biotic factors. However, the effects of this treatment on survival rates are not studied and could make this activity useful.

Several studies have been conducted on enrichment planting in tropical secondary forests. The main focus of most studies has been on the effects of canopy openness, planting direction, line width and the method of maintenance on plant growth and survival (Ramos et al. 1992; Adjers et al. 1995; Montagnini et al. 1997; Pena-Claros et al. 2002). Therefore, the current knowledge about optimizing enrichment planting yields, as reviewed by Paquette et al. (2006), is restricted to the adjustment of canopy closure (thinning of stands) and reducing understory competition. This study however shows that for the enrichment planting of *C. elegans*, edaphic factors and thus the choice of soil type are at least as important. It is therefore imaginable that the yield of the enrichment planting of other species and in other biomes could increase if knowledge about edaphic preferences of the species of interest is included.

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