

RESTORING ABANDONED PASTURE LAND WITH NATIVE TREE SPECIES IN COSTA  
RICA: AN ECOPHYSIOLOGICAL APPROACH TO SPECIES SELECTION.

By

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To my parents

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Abstract of Thesis Presented to the Graduate School  
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RESTORING ABANDONED PASTURE LAND WITH NATIVE TREE SPECIES IN COSTA  
RICA: AN ECOPHYSIOLOGICAL APPROACH TO SPECIES SELECTION.

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The establishment of trees in the successional trajectory of tropical abandoned pastures into forest communities is confronted with several barriers: dispersal, seed predation, unfavorable conditions for germination, and intense competition once they germinate. In order to aid the restoration of abandoned pastures into forested ecosystems, we must overcome some of these barriers through manipulative efforts.

The present study was designed to characterize the light requirements of six native tree species (light demanding: *Pseudosamanea guachapele* (Kunth) Harms (Fabaceae), *Tabebuia impetiginosa* (Mart. Ex DC.) Standley (Bignoniaceae), *Ceiba pentandra* (L.) Gaertn. (Bombacaceae); shade tolerant: *Bombacopsis quinatum* (Jacq.) Dugand. (Bombacaceae), and intermediate: *Dalbergia retusa* Hemsl. (Fabaceae), *Tabebuia rosea* (Bertol.) DC. (Bignoniaceae) under contrasting light environments and grass competition. Understanding their early establishment requirements could be used in selecting proper light and competition regimen for the success of restoring pastures after abandonment.

Field studies were conducted in the pastures of the Santa Ana Conservation Center in Costa Rica. Two grass competition regimes were selected, one dominated by *Hyparrhenia rufa* (Nees) Stapf (Tall-grass) and another dominated by *Cynodon mlenfluensis* Vanderyst (Short-

grass). Three light treatments were created (100%, 37% and 2% light) using either neutral shade cloth (37% and 2%) or no shade cloth (100%). Growth characteristics, biomass partitioning and light response curves of the seedlings were measured. Overall, *P. guachapele* had the best performance in competing with the grasses followed by *D. retusa*, *T. impetiginosa*, and *T. rosea*, which had similar results regardless of the grass. *C. pentandra* did not do well under tall grass. The 2% light treatment greatly reduced seedling performance for all species and 37% had no effect except for *D. retusa*.

We recommend planting *P. guachapele* as an initial step in reforesting pastures. Once they are established and shade produced by the tree reduces grass cover, *T. rosea*, *T. impetiginosa* and *C. pentandra* can be planted.

## CHAPTER 1 INTRODUCTION

Costa Rican forests have been greatly diminished in the recent past. For example, Sader and Joyce (1988) estimated a 50% decline between 1940 and 1984. The driving forces behind deforestation have generally been the expansion of agriculture and cattle operations (Sánchez-Azofeifa, 2000). The latest estimates are that a 29% of the territory is under closed forest cover and that 30% of that forest is protected by national conservation policies (Sánchez-Azofeifa, Harriss, and Skole, 2001).

Although Costa Rica still has nearly a third of the land area under forest cover, most of it is fragmented and as a result faces further threat of being degraded into even smaller islands. This new landscape is a mosaic of forest patches surrounded by human dominated lands, primarily of agricultural activities. For various reasons, many agricultural areas are being abandoned and left as pastures. Some of these areas are able to regenerate naturally; although the speed at which they restore will depend on the existing vegetation in the pasture, the land use history and the proximity of these to forested areas (Aide, Zimmerman, Pascarella, Rivera, and Marcano-Vega, 2000; Hooper, Legendre, and Condit, 2005; Zimmerman, Pascarella, and Aide, 2000). Several studies have demonstrated that pastures may regenerate naturally into forest within a few decades, but the species composition may be drastically different compared to the original one (Aide et al., 2000; Finegan and Delgado, 2000; Parrotta and Knowles, 1999). Therefore, in order to accelerate restoration and obtain the desired species composition it is necessary to intervene with enrichment planting.

One of the main factors influencing the successional trajectory of abandoned pastures into forest communities is seed dispersal. Since pastures have little or no woody vegetation, the majority of woody species that colonize abandoned pastures are wind-dispersed (Finegan and

Delgado, 2000; Holl, 2002; Holl, Loik, Lin and Samuels, 2000; Toh, Gillespie, and Lamb, 1999; Zimmerman et al., 2000). Those species that eventually colonize also undergo seed predation, unfavorable conditions for germination, and intense competition once they germinate (Camargo, Ferraz, and Imakawa, 2002; Holl and Lulow, 1997; Holl et al., 2000; Wijdeven and Kuzee, 2000).

Consequently, competition with other species is an important factor limiting the establishment of seedlings, following their dispersal barrier (Holl, 1998). The most evident competition is aboveground between the pasture grasses, which in many cases are exotic species and very aggressive and new colonizers. Grass cover greatly reduces light availability (Hooper, Condit, and Legendre, 2002; Vieira, Uhl and Nepstad, 1994), and hence seedling growth. Belowground, competition can have important implications as well, especially where water is scarce and soils are low in nutrients (Chapman, Chapman, Zanne, and Burgess, 2002).

In order to aid the restoration of abandoned tropical pastures into forested ecosystems, we must overcome some of these barriers through manipulative efforts. In doing so, we need to learn more about the performance of native tree species in these extreme environments. For example, what are their capabilities and at what stage of the regeneration process should they be introduced? Can they all be planted in an open pasture at the same time? Should we introduce different species at different stages to mimic the natural successional trajectory? Our knowledge base is limited at this point to answer these questions.

**Objectives.** The present study was designed to characterize the light requirements of six native tree species under contrasting light environments and grass competition. Understanding their early establishment requirements could be used in selecting proper light and competition

regimen for the success of restoring a pasture after abandonment. More specifically the research was designed to

- determine growth characteristics and biomass partitioning of seedlings under three different light environments and two levels of grass competition;
- estimate light response curve parameters under three different light environments and two levels of competition;
- establish the sequence in which the native species should be planted in a pasture.

The results of experiments carried out are presented in the two subsequent chapters. In the final chapter, a summary of these findings is presented. Preliminary recommendations for the sequence of planting in restoring an abandoned pastureland and the future research needs are also discussed in the final chapter.

CHAPTER 2  
GROWTH AND BIOMASS ALLOCATION OF TROPICAL TREE SEEDLINGS IN AN  
ABANDONED PASTURE IN COSTA RICA: RESPONSE TO GRASS COMPETITION  
AND VARIED LIGHT REGIMES

**Introduction**

Traditionally, plants have been grouped by light requirements as light demanding and shade tolerant (Swaine and Whitmore, 1988). This is mainly because in a forested environment, light is one of the most varying and dynamic resources for a plant (Chazdon, Pearcy, Lee, and Fetcher, 1996). Plant species also vary in their ability to exploit different light environments in order to optimize growth (Lambers, Chapin, and Pons, 1998). Understanding where species stand in this dichotomy will provide a guide for refining management interventions aimed at improving plant establishment and growth.

Light available to plants may vary greatly when ecosystems are compared. For example, light levels in large open areas, such as pastures, can be much greater than in undisturbed forests (Holl, 1999). Moreover, within each particular ecosystem, measurements of light fluctuate vertically: higher at the canopy and lower at the base of the plants. Consequently, even in pastures competition aboveground with grasses, which in many cases are exotic species and very aggressive, may reduce seedling establishment and seedling growth (Hooper et al., 2002; Vieira et al., 1994). In any event, what is important from a restoration point of view is that species selection needs to be aimed at finding the right match between light availability and plant light requirements for successful establishment and seedling growth.

Furthermore, the growth of tropical tree seedlings in these particular light environments, and their ability to adapt to changes, depends on the complex interaction of morphological and physiological attributes of each species (Garwood, 1996). Light influences growth directly through differences in carbon gain, and indirectly through differences in carbon partitioning

(Veneklass and Poorter, 1998). The focus of this chapter is the growth and biomass allocation response of tree seedlings under the competition conditions posed by existing pastures and under varied light conditions.

Growth analyses are commonly used to understand seedling performance. In particular the relative growth rate (RGR), which represents the increase of plant mass per unit of plant mass, is analyzed as the product of a physiological component, the net assimilation rate (NAR), which stands for the increase in plant mass per unit leaf area, and a morphological component, the leaf area ratio (LAR), which corresponds to the amount of leaf area per unit plant mass. LAR in turn can be broken down into the biomass allocated to leaves, the leaf mass ratio (LMR) or the amount of leaf mass per unit plant mass, and the specific leaf area (SLA) or the amount of leaf area per unit leaf mass. However it is important to consider that growth is the net acquisition of resources from the environment by different parts of the plant and their relative influences will have consequences on growth (Farrar and Gunn, 1998). This is examined by studying plant biomass allocation to various parts of the plant.

The objectives of this study were to (1) determine growth characteristics and biomass partitioning of seedlings in three different light environments and two levels of competition and (2) establish the sequence in which the native species should be planted in a pasture based on the growth and biomass partitioning data.

We hypothesized that light demanding species should exhibit higher relative growth in high light environments, whereas the shade tolerant species should perform better under low light, and the intermediate species should perform best in medium light. All seedlings under Short-grass competition should have higher relative growth rates than under Tall-grass competition.

## Material and Methods

### Study Area

This study was conducted in the pastures of the Santa Ana Conservation Center in Costa Rica, a protected spot in the outskirts of San Jose (9° 56'26.00" N 84° 11'44"10W), in the middle of the fastest urban expansion front in the country. According to the Holdridge Classification, the Santa Ana Conservation Center is located on a Premontane Wet Forest Life Zone. The climate is seasonal, with a dry season that extends from early December to the end of April. The average annual rainfall is 2,467 mm and the average annual temperature is 23.4°C. There are two rainfall peaks: one at the beginning of the rainy season, in May, and the second at the end of the rainy season between October and November. The average maximum temperatures occur during the dry season.

Soils were vertisols with a soil texture of 12.8% sand, 24% silt, and 63.2% clay. Soil pH was 5.5. Nutrient levels based on Bertsch (1986) soil standards showed deficiencies of Potassium (K) and Phosphorous (P). All other nutrient levels were normal (Table A-1).

### Experimental Design

In the pastures of the Santa Ana Conservation Center, two grass competition regimes were selected by creating 18 (3.5 x 3.5 meter) plots in each of two areas: one dominated by *Hyparrhenia rufa* (Nees) Stapf (Tall-grass) and another dominated by *Cynodon mlenfluensis* Vanderyst (Short-grass), both of which had been hand machete once before planting to a height of about 15cm. These grasses are native to tropical Africa. *C. mlenfluensis* is a stoloniferous perennial without underground rhizomes, which can reach heights of 100 cm and *H. rufa*, also perennial, can reach heights that range from 60–240cm (Skerman and Riveros, 1990). In each area three light environments were created: low (2% light), medium (37% light) and high (100% light). Plots were separated by 3 meters to prevent neighbor shading. For the shaded treatments

shade houses 2.5 meters tall were constructed to cover the entire plot using neutral shade-cloth (63% and 98% shade). Each light environment x grass competition treatment was replicated six times for a total of 36 plots. Therefore each plot was a sampling unit for this experiment.

Six species pertaining to different natural life histories were used; light demanding: *Pseudosamanea guachapele* (Kunth) Harms (Fabaceae), *Tabebuia impetiginosa* (Mart. Ex DC.) Standley (Bignoniaceae), *Ceiba pentandra* (L.) Gaertn. (Bombacaceae); shade tolerant: *Bombacopsis quinatum* (Jacq.) Dugand. (Bombacaceae), and intermediate: *Dalbergia retusa* Hemsl. (Fabaceae), *Tabebuia rosea* (Bertol.) DC. (Bignoniaceae) (See Table 2-1). Six individuals of each species were directly planted into the ground in a row under each treatment (light environment and grass competition) for a total of 36 individuals per plot. Species were assigned a row by systematically rotating their position within the plot. Tree seedlings were provided by the Santa Ana Conservation Center nursery, located in the same area. All seedlings were grown under 40% shade in plastic bags (9cm x 18cm) for 11 months. They were planted during the first two weeks of the experiment starting the last week of May 2005 directly into the ground in holes of about 20cm in diameter. One week after planting, damaged seedlings were replaced.

**Growth.** An initial census of all plants in the field was made to measure plant height (to the nearest 0.1cm), root collar diameter, (RCD - to the nearest 0.01cm) and leaf number in the second week of July 2005. Ten nursery seedlings were selected randomly for each species and destructively harvested. For each individual, height, RCD, leaf number, biomass allocation (root, stem and leaf) (to the nearest 0.01g) and leaf area (cm<sup>2</sup>) were measured. Leaf area was determined from scanned images of each leaf using *Scion Image* (Scion Corporation, Frederick, Maryland, USA). Plant biomass was determined after drying at 70 °C for 72 hours.

A second and final census was also done during the first week of January 2006 where seedling height, RCD and leaf number of all remaining seedlings were measured the same way as in the first census. Mortality was also recorded. Out of each treatment, at least nine seedlings that had leaves were randomly selected and destructively harvested and measured for biomass allocation (root, stem and leaf) and leaf area using the same method as for the first harvest. At least 1 individual from each plot of 36 was harvested.

## **Analysis**

### **Mortality**

A logistic regression model was used to determine differences in mortality. Live individuals received a score of 1, whereas dead ones received a score of 0. Grass, light and species were used as main effects and, since each plot corresponded to a specific light and grass treatment, our model used the interaction of grass and light with plot nested within it as the random effect.

### **Growth**

Young seedling variability in plant size is difficult to homogenize in experiments; therefore, we conducted an initial census to test for differences among treatments in seedling height and RCD after planting. A two-way ANOVA with grass and light treatments as main effects was used to determine differences between seedling height and RCD. The test indicated that between grasses there were no differences for both seedling height and RCD ( $F_{1,32}=2.32$   $p=0.14$  and  $F_{1,32}=0.25$   $p=0.62$  respectively); for the light treatment there were no differences in height ( $F_{2,32}=0.25$   $p=0.78$ ), however there were differences in RCD ( $F_{2,32}=11.94$   $p<0.0001$ ); Therefore, to compensate for these differences all other analyses were performed with height and RCD as covariates if they were significant in the model.

The growth analyses were done following the “classical” method (Hunt et al., 2002) to calculate mean growth variables over the growth period (using initial and final harvest data): relative growth rate (RGR), net assimilation rate (NAR or ULR), leaf area ratio (LAR), specific leaf area (SLA), leaf mass ratio (LMR), root mass ratio (RMR), and stem mass ratio (SMR) and Root: Shoot allometric coefficient (Table 2-2). Each variable’s mean value over the growth period was compared using a correlation analysis to determine relationships between each treatment. The nonparametric Spearman’s rank correlation coefficients ( $r_s$ ) were used because it is robust to sample distribution problems. Final harvest values for LAR, SLA, LMR, RMR, SMR, and Root:Shoot were compared using a split-plot ANOVA with grass, light and species as main effects and their interactions to determine differences. When the main effects were significant, *post hoc* Tukey's test was carried out for mean separation. Since each plot corresponded to a specific light and grass treatment, our model used the interaction of grass and light with plot nested within it as the random effect. *B. quinatum* was eliminated from this analysis due to the fact that in some treatments they had lost completely their leaves at the time of the second harvest.

All statistical analyses were conducted using JMP version 5.1, SAS Institute 2004.

## **Results**

### **Mortality**

Mortality was low, ranging from 0 to 14%, during the study period (Table2-3). There was no significant difference among any of the treatments.

### **Relative Growth Rate**

The species with the highest relative growth rate (RGR) was *P. guachapele*. This species grew best in 100% and 37% light levels and there was no difference between grass treatments. RGR was positive when grown in 2% light. *D. retusa* and *C. pentandra* shared the second

highest growth rates in 100% and 37% light levels, respectively. *D. retusa* was not affected by the grass treatment, whereas *C. pentandra* performed better in short grass. *T. rosea* and *T. impetiginosa* performed similarly, but the latter was affected more by the tall grass treatment (Figure 2-1).

Relative growth rate overall was correlated to net assimilation ratio (NAR) ( $r_s = 0.96$ ,  $p < 0.001$ ), leaf area ratio (LAR) ( $r_s = -0.60$ ,  $p < 0.001$ ), specific leaf area (SLA) ( $r_s = -0.55$ ,  $p = 0.002$ ) and leaf mass ratio (LMR) ( $r_s = -0.47$ ,  $p = 0.009$ ) (Figure 2-2). When looked at individually under each light treatment, at 100% light there was a strong correlation with NAR ( $r_s = 0.78$ ,  $p = 0.008$ ), but LAR was not significant. At 37% light NAR ( $r_s = 0.95$ ,  $p < 0.001$ ) and LAR ( $r_s = -0.70$ ,  $p < 0.05$ ) and SLA ( $r_s = -0.78$ ,  $p = 0.007$ ) were significant. At 2% light NAR ( $r_s = 0.91$ ,  $p < 0.001$ ) and LAR ( $r_s = -0.62$ ,  $p = 0.06$ ) were significant (Figure 2-3).

### Leaf Area

At final harvest there was a significant difference in total leaf area in all treatments; light ( $F_{2,8} = 15.56$ ;  $p = 0.002$ ), grass ( $F_{1,8} = 10.62$ ;  $p < 0.01$ ), and species ( $F_{4,8} = 9.09$ ;  $p = 0.005$ ) (Table 2-4). Seedlings grown under light levels 37% and 2% had the same total leaf area whereas leaf area was significantly lower in the 100% light treatment. Seedlings grown in short grass had more leaf area than those in tall grass. *P. guachapele* and *T. rosea* shared the highest leaf area, followed by *C. pentandra* and *T. impetiginosa* and *D. retusa* with the lowest. As for the interactions none were significant. *T. impetiginosa* and *D. retusa* had the same leaf area in all light levels. *P. guachapele* had the highest leaf area in the 37% light treatment and lower, but similar leaf area in the 2% and 100% treatments. *C. pentandra* and *T. rosea* had 37% and 2% with the highest values which were greater than 100%. *C. pentandra* and *P. guachapele* had

higher values in the short grass than tall. *T. rosea*, *T. impetiginosa* and *D. retusa* had same values in short and tall grass.

### **Leaf Area Ratio and Leaf Mass Ratio**

Leaf area ratio and Leaf mass ratio were significantly different in all treatments (Table 2-4). Seedlings grown under 2% light had the highest LAR and LMR followed by 37% and then 100%. LAR and LMR were higher in seedlings grown in short grass compared to tall grass. *T. rosea* and *C. pentandra* had the highest LAR, followed by *T. impetiginosa* and *P. guachapele* and finally by *D. retusa* (Figure 2-4). For LAR, the only interaction with a significant difference was light \*species ( $F_{8,8}=9.30$ ;  $p = 0.002$ ), where *P. guachapele* and *D. retusa* had similar values at 37 and 100%, all other species showed the same trend as with the light treatment.

For LMR, *T. rosea* had the highest values followed by *T. impetiginosa* and *C. pentandra*, then *P. guachapele* and finally by *D. retusa* (Figure 2-4). For the interaction of light \*species, *T. impetiginosa* showed the same trend, but *T. rosea*, *C. pentandra*, and *P. guachapele* had similar values for their 2% and 37% light treatments and their 100% was significantly lower. *D. retusa* showed similar values across light levels. As for the grass \*species interaction *T. impetiginosa*, *P. guachapele*, and *D. retusa* showed similar values in tall and short grasses, *T. rosea* had higher values in short than tall and *C. pentandra* had the inverse.

### **Specific Leaf Area**

Specific leaf area showed significant differences in light ( $F_{2,8}=115.91$ ;  $p < 0.001$ ) and species ( $F_{4,8}=10.43$ ;  $p = 0.003$ ) treatments, but not in grass. There were significant interactions for light \*species ( $F_{8,8}=5.88$ ;  $p = 0.011$ ) only (Table 2-4). SLA exhibited the same trend under light treatment as LAR. However, for species, *D. retusa* and *C. pentandra* shared the highest values followed by *P. guachapele*, *T. rosea* and *T. impetiginosa*, which also had similar values.

For the interaction of light and species all species except *T. impetiginosa* had higher values at 2% and 37% and 100% were less, but similar. *T. impetiginosa* had similar values in all light treatments (Figure 2-4).

### **Root Mass Ratio, Stem Mass Ratio, and Root: Shoot Ratio**

Root mass ratio and root: shoot ratio showed significant difference in light treatments and species. There was a significant interaction between light \*species (Table 2-5). The RMR of seedlings grown under 100% light treatment had the highest value followed by 37% and then 2%. For the species treatment *T. impetiginosa* had the highest followed by *D. retusa*, *P. guachapele*, *C. pentandra* and *T. rosea*. As for the light interaction, *T. impetiginosa* followed the same trend as the light treatment. *D. retusa* had light at 37% the same as 2%. *P. guachapele*, *C. pentandra* and *T. rosea* all had all light levels equal except for 100% and 2% (Figure 2-5). For R:S ratios the light treatments at 37% and 2% similar, but were lower than 100%. *T. impetiginosa* had the highest value followed by *D. retusa* and *P. guachapele* and then by *C. pentandra* and *T. rosea*. *P. guachapele*, *C. pentandra* and *T. rosea* did not differ in the light treatments. *D. retusa* and *T. impetiginosa* had similar ratios at 37 and 2%, which were lower than 100% (Figure 2-5). As for the interaction between grass \*species *T. impetiginosa* was the only one to have Short grass larger than Tall grass, the rest had same values.

For SMR, *C. pentandra* had the highest followed by *T. rosea*, *P. guachapele*, *D. retusa* and *T. impetiginosa* (Figure 2-5). The interaction between light and species ( $F_{8,8}=4.05$ ;  $p = 0.03$ ) (Table 2-5), all species had similar values in all light treatments except *D. retusa*, for which 37% and 2% were similar and greater than 100%. Tall grass had a higher value than short. For grass \*species interaction all species had the same values in both types of grasses (Figure 2-5).

## Discussion

In this study we observed a low mortality in all treatments, which may be due to the short duration of the study (only 26 weeks). Interspecific relative growth rates (RGR) can be ranked into specific groups by patterns in both net assimilation ratio (NAR) and leaf area ratio (LAR) (Veneklass and Poorter, 1998). Light demanding species have higher relative growth rates in both low and high light environments (Kitajima, 1994). However there are discrepancies as to which component, NAR or LAR, determines RGR at low-light and at high-light. For example, in low light conditions Bloor and Grubb (2003) found NAR to be significantly related to relative growth rate and Veneklass and Poorter (1998) suggest LAR. In the light levels that we examined, we did not see a shift from NAR to LAR (Figure 2-3). In all light treatments NAR had a high correlation with RGR. Nonetheless at 37% light LAR becomes significant, but not as significant as NAR. This coincides with the findings of Bloor and Grubb (2003) that under very low light condition RGR is determined by NAR. Light under tall grass canopies can be greatly reduced (Holl, 2002; Hooper et al., 2002) and this, combined with seedling height, could explain why RGRs were correlated mainly to NAR under all light conditions.

However, interspecific variation in RGR with respect to light treatments varied. Overall, *P. guachapele* had the best performance (Figure 2-3). In the high light treatment (100%) *P. guachapele* and *D. retusa* performed better than other species. Gerhardt (1993) found that after six months after planting seedlings, the highest growth rates for the two light demanding species they examined were the individuals grown in a pasture. This means that they were able to compete with grasses above or belowground. *P. guachapele* and *D. retusa* were species with the largest stem height (Table 2-1). If plants were taller in the grass environment, they would have had better access to light. This may be true for *P. guachapele*; however *C. pentandra*, whose height was considerably large, did not perform well in the high light condition.

It is important to note that *P. guachapele* and *D. retusa* are both legumes, and have nitrogen fixing nodules. This could have enhanced their capability to compete with grasses. Jones, Wishnie, Deago, Sautu, and Cerezo (2004) found that the legume species *Inga* spp. had the best comparative performance with 13 other species in pastures in Panama. It is also important to note that *D. retusa* and *P. guachapele* ranked second and third in root mass ratios (RMR) (Figure 2-5), which means that overall they invested more in roots than the other species. This, combined with their nitrogen fixing capabilities, could have given them an advantage when compared to the other species.

Lowering the light level to 37% did not affect the performance of *P. guachapele* or *T. rosea*, but greatly reduced *D. retusa*, and improved *C. pentandra* under short grass (Figure 2-1). Shading can effectively eliminate or hinder grasses, for example Hooper et al. (2002) found that shade eliminated the *Saccharum* exotic grass and enhanced tree regeneration in Panama. In our study, grasses were not eliminated, but shading made them less aggressive. However, the reduction in light could also affect seedling performance, that being the case for *D. retusa*. *C. pentandra* performed better under short grass due to the reduction in competition, but this reduction was not enough under tall grass. Lewis and Tanner (2000) found that a reduction of below ground competition resulted in increased allocation to leaves and in decreased allocation to roots, a trend that we found in *C. pentandra*, *T. impetiginosa*, and *T. rosea* (Figure 2-5). At the lowest light level, shade effectively eliminated grass, but also reduced all species RGRs, except for *P. guachapele*.

Contrary to our expectations of categorizing species solely by light requirements, there was clearly a grass and light effect which varied with species. Therefore, we can not make

generalization as to light requirements. For example, not all light demanding species performed better under high light conditions.

### **Conclusion**

Species differed in their RGR, but overall *P. guachapele* was the best performer. We recommend planting this species as an initial step in reforesting pastures. Once it is established and shade produced by the tree reduces grass cover *T. rosea* (Roble), *T. impetiginosa* and *C. pentandra* can be planted. However, *C. pentandra* may be affected by competition with grasses and/or *P. guachapele*'s presence. Further research is needed to understand how different species will react under *P. guachapele*'s shade and competition. Will its canopy be effective in reducing light quantity to have an effect on grasses? Seedling size may also become a factor in these pasture conditions, which should be examined with the other species of smaller heights that were used.

Table 2-1. Mean (standard error) initial and final height and diameter for each species.

Species	Family	Species code	Initial Height (cm)	Initial Diameter (cm)	Final Height (cm)	Final Diameter (cm)
<i>Ceiba pentandra</i>	Bombacaceae	Ceiba	42.0(0.6)	0.76(0.01)	48.8(1.1)	0.88(0.02)
<i>Dalbergia retusa</i>	Fabaceae	Coco	41.7(1.2)	0.55(0.009)	40.4(1.3)	0.64(0.01)
<i>Tabebuia impetiginosa</i>	Bignoniaceae	Cortez	24.1(0.4)	0.51(0.009)	25.9(0.4)	0.60(0.02)
<i>Pseudosamanea guachapele</i>	Fabaceae	Guaya	46.1(0.9)	0.75(0.01)	52.5(1.3)	0.93(0.02)
<i>Bombacopsis quinatum</i>	Bombacaceae	Pochote	21.9(0.5)	0.61(0.01)	24.5(0.7)	0.78(0.02)
<i>Tabebuia rosea</i>	Bignoniaceae	Roble	28.3(0.4)	0.82(0.01)	33.2(0.5)	0.89(0.02)

Table 2-2. Plant variables derived for growth analysis. M is total dry mass of seedling (g), A is seedling leaf area (cm<sup>2</sup>), L is seedling leaf dry mass (g), S is stem dry mass (g), R is root dry mass (g) and T is time (weeks). Subscripts refer to initial (i) final (f).

Variable	Formula	Units
Relative growth rate (RGR)	$\frac{(\ln M_f - \ln M_i)}{(T)}$	g g <sup>-1</sup> week <sup>-1</sup>
Net assimilation rate (NAR)	$\frac{[(M_f - M_i)(\ln A_f - \ln A_i)]}{[(A_f - A_i)]}$	g cm <sup>-2</sup> week <sup>-1</sup>
Leaf are ratio (LAR)	$\frac{A}{M}$	cm <sup>2</sup> g <sup>-1</sup>
Specific leaf area (SLA)	$\frac{A}{L}$	cm <sup>2</sup> g <sup>-1</sup>
Leaf mass ratio (LMR)	$\frac{L}{M}$	g g <sup>-1</sup>
Stem mass ratio (SMR)	$\frac{S}{M}$	g g <sup>-1</sup>
Root mass ratio (RMR)	$\frac{R}{M}$	g g <sup>-1</sup>
Root to shoot coefficient (R:S)	$\frac{R}{S + L}$	

Table 2-3. Percent mortality of species by treatment (grass and light). See Table 2-1 for species coding.

Grass	Light	Species	Mortality
Tall	100%	Ceiba	3%
Tall	100%	Coco	6%
Tall	100%	Cortez	0%
Tall	100%	Guaya	0%
Tall	100%	Roble	0%
Tall	37%	Ceiba	0%
Tall	37%	Coco	3%
Tall	37%	Cortez	3%
Tall	37%	Guaya	3%
Tall	37%	Roble	3%
Tall	2%	Ceiba	14%
Tall	2%	Coco	8%
Tall	2%	Cortez	6%
Tall	2%	Guaya	0%
Tall	2%	Roble	3%
Short	100%	Ceiba	3%
Short	100%	Coco	3%
Short	100%	Cortez	8%
Short	100%	Guaya	3%
Short	100%	Roble	0%
Short	37%	Ceiba	0%
Short	37%	Coco	11%
Short	37%	Cortez	0%
Short	37%	Guaya	0%
Short	37%	Roble	0%
Short	2%	Ceiba	11%
Short	2%	Coco	14%
Short	2%	Cortez	0%
Short	2%	Guaya	3%
Short	2%	Roble	14%

Table 2-4. Split-plot ANOVA for Total Leaf Area, LAR, LMR and SLA with respect to each treatment and their interactions.

Treatment	Variable			
	Total Leaf Area	LAR	LMR	SLA
Grass	$F_{1,8}=10.62; p < 0.01$	$F_{1,8}=5.48; p = 0.047$	$F_{1,8}=5.93; p = 0.041$	$F_{1,8}=1.66; p < 0.23$
Light	$F_{2,8}=15.56; p = 0.002$	$F_{2,8}=281.58; p < 0.001$	$F_{2,8}=55.31; p < 0.001$	$F_{2,8}=115.91; p < 0.001$
Grass*light	$F_{2,8}=2.96; p = 0.11$	$F_{2,8}=1.75; p = 0.23$	$F_{2,8}=0.094; p = 0.91$	$F_{2,8}=1.05; p = 0.40$
Species	$F_{4,8}=9.09; p = 0.005$	$F_{4,8}=24.41; p < 0.001$	$F_{4,8}=9.09; p = 0.005$	$F_{4,8}=10.43; p = 0.003$
Species*Light	$F_{8,8}=2.61; p = 0.098$	$F_{8,8}=9.30; p = 0.002$	$F_{8,8}=2.90; p = 0.077$	$F_{8,8}=5.88; p = 0.011$
Species*Grass	$F_{4,8}=1.64; p = 0.26$	$F_{4,8}=1.30; p = 0.35$	$F_{4,8}=2.68; p = 0.11$	$F_{4,8}=0.77; p = 0.58$

Table 2-5. Split-plot ANOVA for RWR, SMR and R:S with respect to each treatment and their interactions.

Treatment	Variable		
	RWR	SMR	R:S
Grass	$F_{1,8}=0.0007; p = 0.98$	$F_{1,8}=5.50; p = 0.047$	$F_{1,8}=1.77; p = 0.22$
Light	$F_{2,8}=61.9; p < 0.001$	$F_{2,8}=1.10; p = 0.37$	$F_{2,8}=29.80; p < 0.001$
Grass*light	$F_{2,8}=0.28; p = 0.76$	$F_{2,8}=0.089; p = 0.91$	$F_{2,8}=0.13; p = 0.88$
Species	$F_{4,8}=55.63; p < 0.001$	$F_{4,8}=52.44; p < 0.001$	$F_{4,8}=73.11; p < 0.001$
Species*Light	$F_{8,8}=4.14; p = 0.03$	$F_{8,8}=4.05; p = 0.03$	$F_{8,8}=3.61; p = 0.044$
Species*Grass	$F_{4,8}=2.69; p = 0.11$	$F_{4,8}=1.97; p = 0.19$	$F_{4,8}=2.12; p = 0.17$

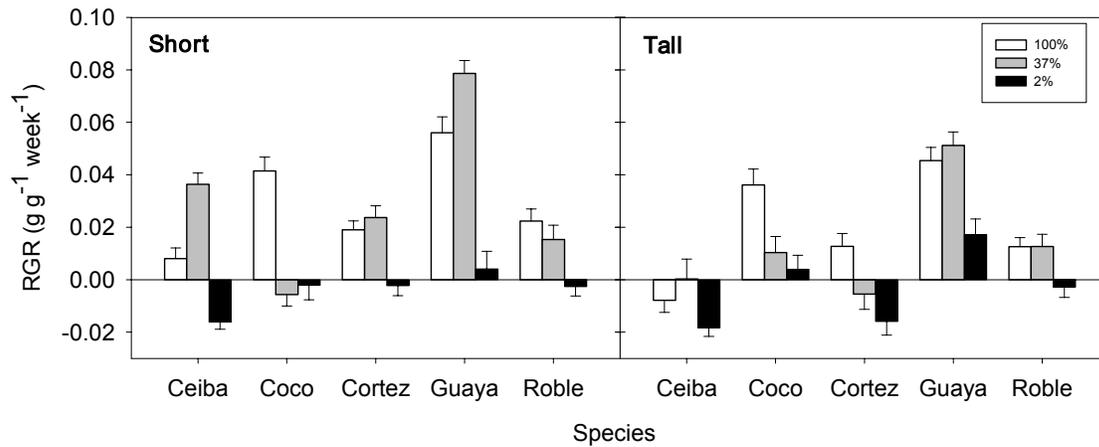


Figure 2-1. Mean values of relative growth rate and standard errors over the growth period for each species in the three light treatments (100%, 37% and 2%) and grass treatments (short and tall). See Table 2-1 for species coding.

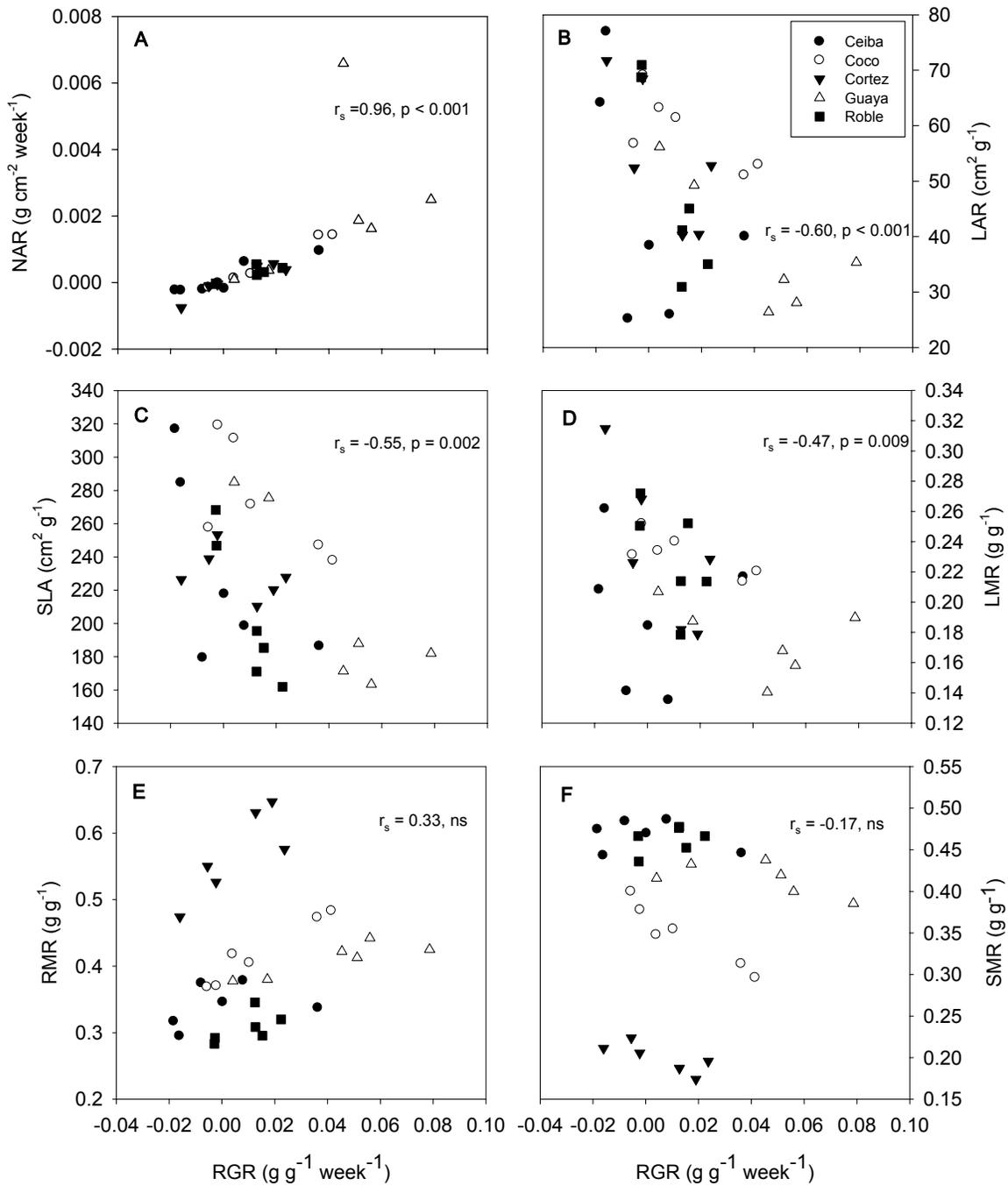


Figure 2-2. The overall relationship between relative growth rate (RGR) and growth variables for all treatments. A) Net assimilation rate. B) Leaf area ratio. C) Specific leaf area. D) Leaf mass ratio. E) Root mass ratio. F) Stem mass ratio. Mean values over growth period of 26 weeks. Spearman's rank correlations estimated and significance based on ( $p < 0.05$ ). See Table 2-1 for species coding.

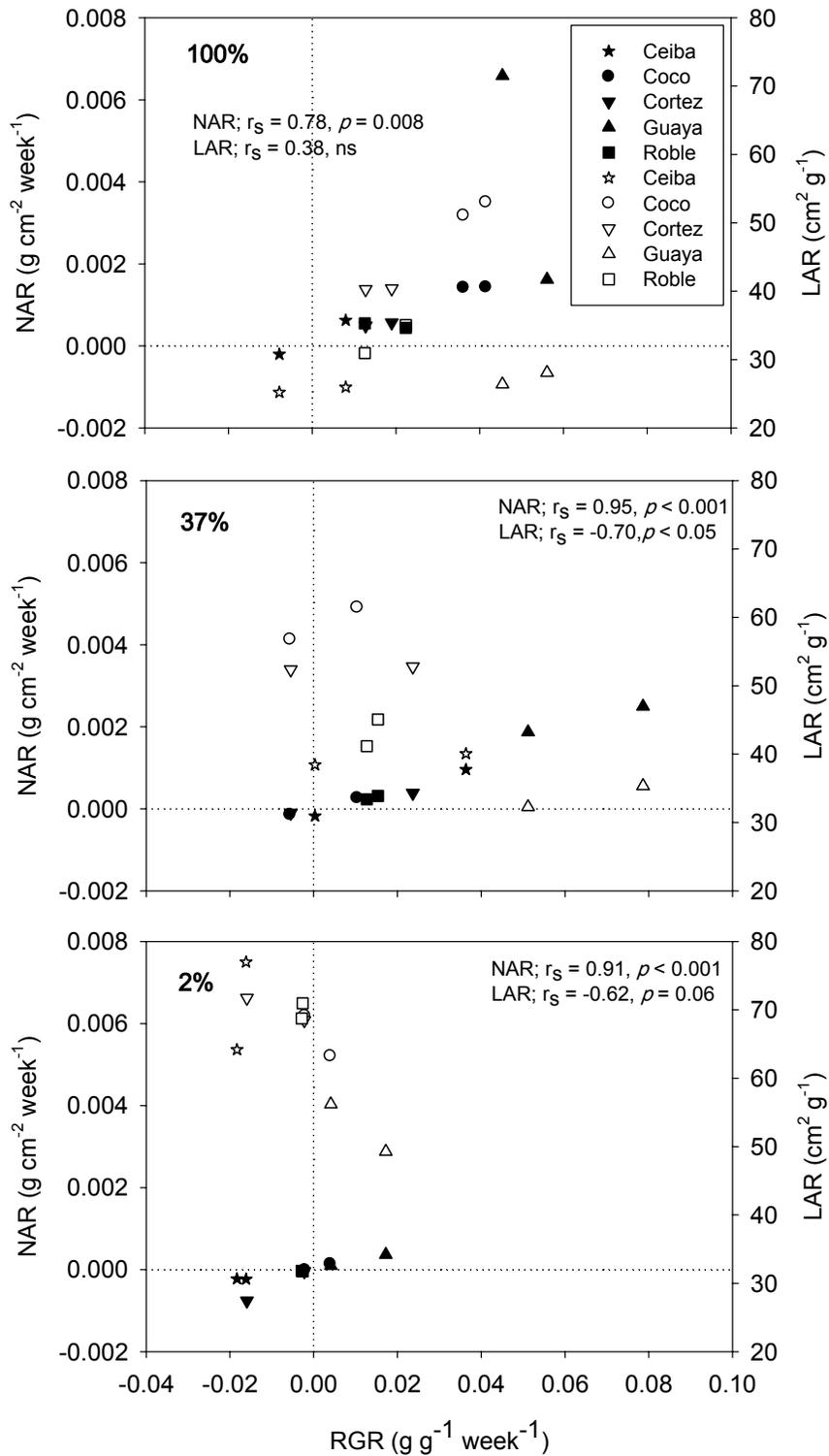


Figure 2-3. Relationship between mean values over growth period of 26 week for relative growth rate (RGR) and net assimilation rate (NAR) -dark symbols, and leaf area ratio (LAR) -white symbols, for each light treatment (100%, 37% and 2%). Spearman's rank correlations estimates and significance based on ( $p < 0.05$ ).

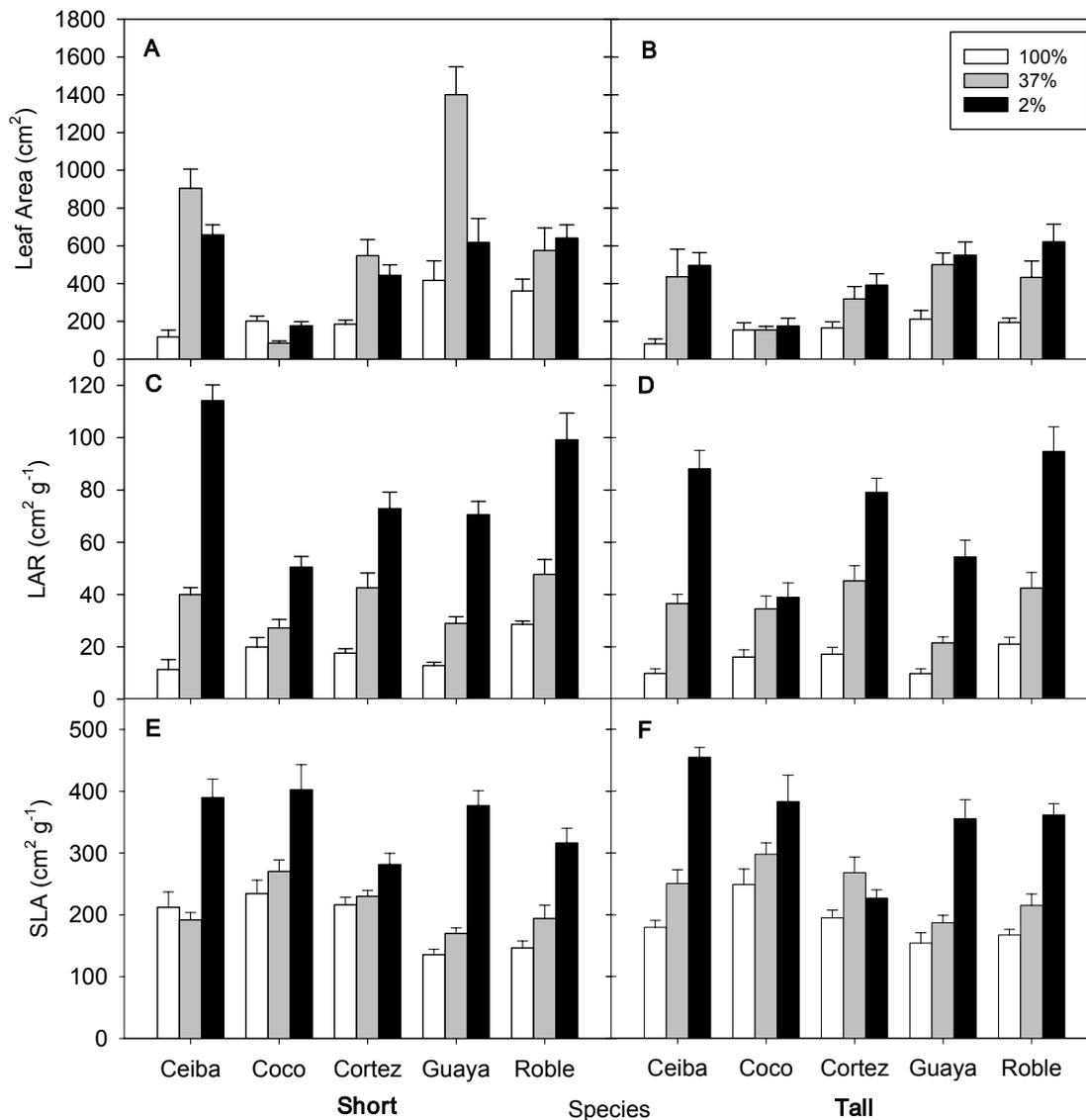


Figure 2-4. Growth variables: Leaf area, leaf area ratio (LAR) and specific leaf area (SLA) for each species grown under low (2%), medium (37%), and high (100%) light condition in each of the grass treatments, short and tall. A) Leaf area short grass. B) Leaf area tall grass. C) Leaf area ratio short grass. D) Leaf area ratio tall grass. E) Specific leaf area short grass. F) Specific leaf area tall grass. Mean values and standard errors obtained from final harvest. See Table 2-1 for species coding.

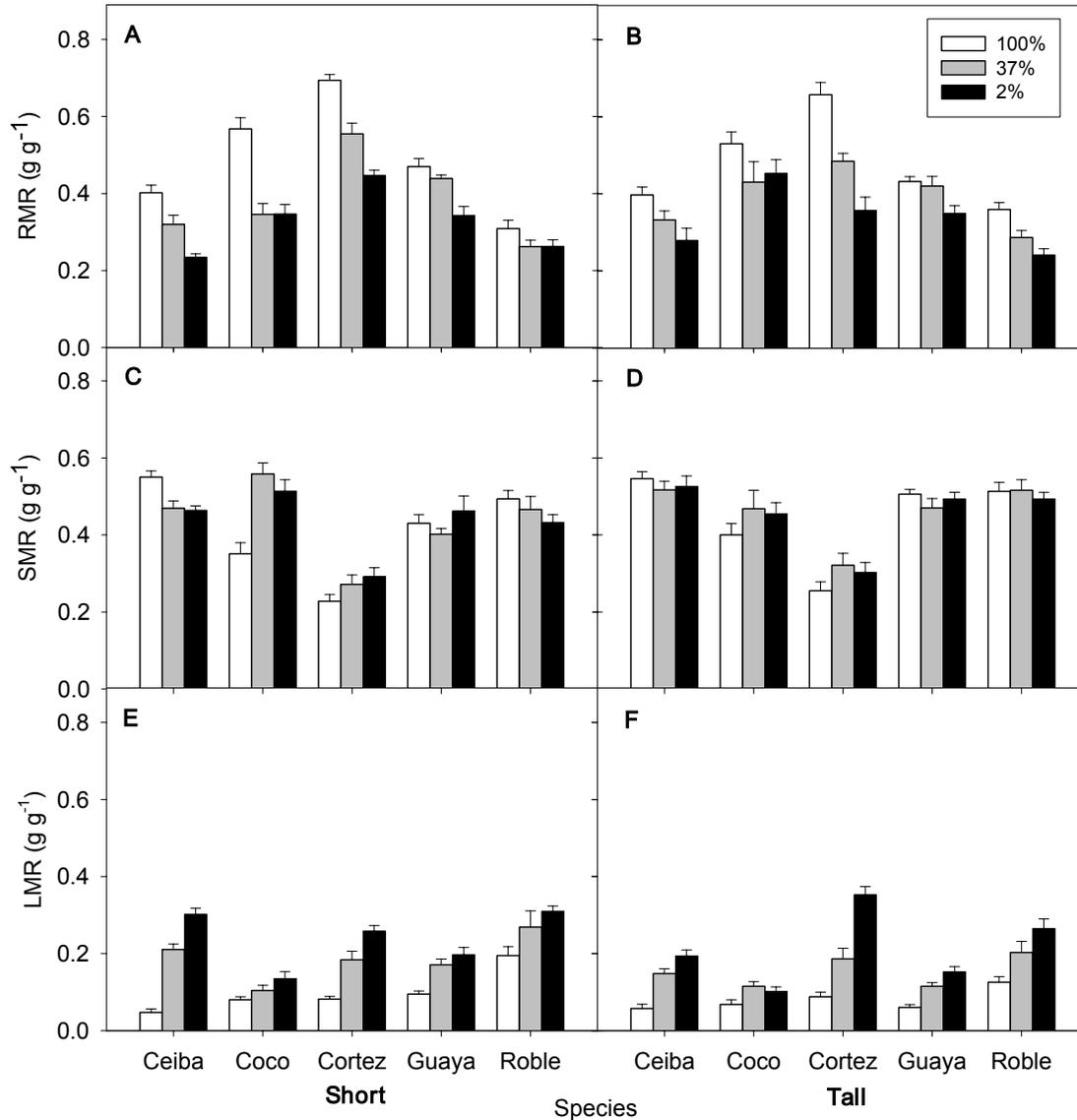


Figure 2-5. Growth variables: Root mass ratio (RMR), stem mass ratio (SMR) and leaf mass ratio (LMR) for each species grown under low (2%), medium (37%), and high (100%) light condition in each of the grass treatments, short and tall. A) Root mass ratio short grass. B) Root mass ratio tall grass. C) Stem mass ratio short grass. D) Stem mass ratio tall grass. E) Leaf mass ratio short grass. F) Leaf mass ratio tall grass. Mean values and standard error obtained from final harvest. See Table 2-1 for species coding.

CHAPTER 3  
PHOTOSYNTHETIC RESPONSES OF TROPICAL TREE SEEDLINGS IN AN  
ABANDONED PASTURE UNDER GRASS COMPETITION AND VARIED LIGHT  
REGIMES

**Introduction**

The growth of tropical tree seedlings in particular light environments (Lambers et al., 1998), and their ability to adapt to changes, depends on the complex interaction of morphological and physiological attributes of each species (Garwood, 1996). Therefore, the ability of a species to acquire and utilize light is an important factor in their competitive ability (Chazdon et al., 1996). Learning more about their physiological demands will give us some insights as to when and how to introduce species into a pasture. For example, Loik and Holl (1999) experimented with several species of tree seedlings under remnant pasture trees and an open pasture in southern Costa Rica. They found higher levels of photosynthetic rates in open pastures than under remnants; however growth was higher under remnants.

In order to describe, in a quantitative fashion, how plants utilize light for carbon fixation, a light-response curve is often used. This curve is a non-linear function where net photosynthesis ( $A$ ) is the response variable and the estimated parameters allow representing key stages of photosynthesis, as follows: In dark; that is, in zero photosynthetic active radiation (PAR), there is net- $\text{CO}_2$  release due to respiration. As light intensity increases, net- $\text{CO}_2$  release is gradually reduced until the light compensation point (LCP) is attained, where net- $\text{CO}_2$  exchange is zero because photosynthetic  $\text{CO}_2$ -uptake increases until light saturation is reached. At this point, the rate of  $\text{CO}_2$  assimilation levels off. Any further increase in the amount of light striking the leaf does not cause an increase in the rate of photosynthesis-the amount of light is said to be 'saturating' for the photosynthetic process. This light-saturation point often is hard to determine precisely, because light saturation is approached gradually. Alternatively, the asymptote of net

assimilation at high light ( $A_{\max}$ ) is estimated. Finally, the slope of the nearly linear part of the curve below saturation gives the apparent quantum yield ( $A_{qe}$ : mol CO<sub>2</sub> per mol photons) of photosynthesis.

Understanding species photosynthesis and growth performances under different light scenarios will help us determine their optimal light requirements. Based on these findings, we can then suggest the ideal setting or sequence in which these species should be introduced in a restoration project.

The objectives of this study were (1) to estimate light response curve parameters: maximum net assimilation ( $A_{\max}$ ), apparent quantum yield ( $A_{qe}$ ), and light compensation point (LCP) under three different light environments and two levels of competition; (2) to determine relative growth rates (RGR) of seedlings under three different light environments and two levels of competition; and (3) to establish the sequence in which the native species should be planted in a pasture based on the previous characteristics.

We hypothesized that light response curve parameters will display the following relationship with seedlings light demand: the higher the seedlings light demand, the higher the maximum net assimilation ( $A_{\max}$ ), the higher the light compensation point (LCP), and the lower the apparent quantum yield ( $A_{qe}$ ). Also, seedling grown under Short-grass competition should all have maximum net assimilation ( $A_{\max}$ ) higher than under Tall-grass competition.

## **Materials and Methods**

### **Study Site**

This study was conducted in the pastures of the Santa Ana Conservation Center in Costa Rica, a protected spot in the outskirts of San Jose (9° 56'26.00" N 84° 11'44"10W), in the middle of the fastest urban expansion front in the country. According to the Holdridge Classification, the Santa Ana Conservation Center is located on a Premontane Wet Forest Life

Zone. The climate is seasonal, with a dry season that extends from early December to the end of April. The average annual rainfall is 2,467 mm and the average annual temperature is 23.4 °C. There are two rainfall peaks: one at the beginning of the rainy season, in May, and the second at the end of the rainy season between October and November. The average maximum temperatures occur during the dry season.

### **Experimental Design**

In the pastures of the Santa Ana Conservation Center, two grass competition regimes were selected by creating 18 (3.5 x 3.5 meter) plots in each of two areas: one dominated by *Hyparrhenia rufa* (Nees) Stapf (Tall-grass) and another dominated by *Cynodon mlenfluensis* Vanderyst (Short-grass), both of which had been hand machete once before planting to a height of about 15cm. These grasses are native to tropical Africa. *C. mlenfluensis* is a stoloniferous perennial without underground rhizomes, which can reach heights of 100 cm and *H. rufa*, also perennial, can reach heights that range from 60–240cm (Skerman and Riveros, 1990). In each area three light environments were created: low (2% light), medium (37% light) and high (100% light). Plots were separated by 3 meters to prevent neighbor shading. For the shaded treatments shade houses 2.5 meters tall were constructed to cover the entire plot using neutral shade-cloth (63% and 98% shade). Each light environment x grass competition treatment was replicated six times for a total of 36 plots. Therefore each plot was a sampling unit for this experiment.

Six species pertaining to different natural life histories were used; light demanding: *Pseudosamanea guachapele* (Kunth) Harms (Fabaceae), *Tabebuia impetiginosa* (Mart. Ex DC.) Standley (Bignoniaceae), *Ceiba pentandra* (L.) Gaertn. (Bombacaceae); shade tolerant: *Bombacopsis quinatum* (Jacq.) Dugand. (Bombacaceae), and intermediate: *Dalbergia retusa* Hemsl. (Fabaceae), *Tabebuia rosea* (Bertol.) DC. (Bignoniaceae) (See Table 2-1). Six

individuals of each species were directly planted into the ground in a row under each treatment (light environment and grass competition) for a total of 36 individuals per plot. Species were assigned a row by systematically rotating their position within the plot. Tree seedlings were provided by the Santa Ana Conservation Center nursery, located in the same area. All seedlings were grown under 40% shade in plastic bags (9cm x 18cm) for 11 months. They were planted during the first two weeks of the experiment starting the last week of May 2005 directly into the ground in holes of about 20cm in diameter. One week after planting, damaged seedlings were replaced.

### **Photosynthesis**

At least six individuals from each treatment (grass, light and species) were randomly selected and a photosynthetic light-response curve was determined for the third most fully developed leaf from the apical meristem of each individual in the sample. If the leaf was missing or damaged, the second most fully developed leaf was used. *B. quinatum* was not taken into consideration, due to the fact that in some of the treatments individuals had lost all their leaves at the time of measurements. Measurements were done during the period of December 2005 and January 2006 using an open-mode portable photosynthesis system (*Li-6400*, *Li-Cor*, Inc. Lincoln, Nebraska, USA). Using a light-emitting diode (LED) light source, ten light (Photosynthetically Active Radiation, PAR) intensities were set: 0, 25, 50, 100, 200, 500, 800, 1,000, 1,500, and 2,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , starting from the lowest and then increasing every 2 minutes. The leaf chamber was controlled to a  $\text{CO}_2$  concentration of 380  $\mu\text{mol mol}^{-1}$ , the temperature of the block chamber was set at 26 °C, and air flow was maintained at 500  $\mu\text{mol s}^{-1}$ .

### **Growth**

The relative growth rate (RGR) was calculated following the “classical” method

$$\frac{(\overline{\ln M_f} - \overline{\ln M_i})}{(T)}$$

over the growth period (Hunt et al., 2002). Where M is total dry mass of seedling (g) and T is time (weeks). Subscripts refer to initial (i) final (f) harvest. (Table 2-2).

## Analysis

### Model Fitting

A nonlinear mixed model was used in our analysis. Nonlinear mixed models allow both fixed (treatments) and random (experimental unit) effects to have a nonlinear relationship to the response variable (Wolfinger, 2000). In addition, fitting an appropriate nonlinear model lends biological meaning to estimated parameters (Peek, Russek-Cohen, Wait, and Forseth, 2002). For our experiment, our fixed effect treatment design was a 2x3 factorial with two grass competitions (short and tall) and three light levels (100%, 37% and 2%), for each species separately. We took repeated measurements of net photosynthesis on the same leaf at different light levels, which requires the incorporation of a random effect for each individual. For each treatment a light-response curve was fitted to a nonlinear Mitscherlich model equation (Peek et al., 2002).

$$A = A_{\max} \left[ 1 - e^{-\frac{A}{A_{\text{qe}}} (PAR - LCP)} \right]$$

Where  $A_{\max}$  is the asymptote of photosynthesis at high light,  $A_{\text{qe}}$  is the apparent quantum yield,  $LCP$  is light compensation point,  $PAR$  is the photosynthetic active radiation and  $A$  is net photosynthesis, the response variable. We used a nonlinear mixed models procedure (NLMIXED) (SAS Institute Inc., Cary, North Carolina USA) to fit curves to photosynthetic data from each plant. Initial values of parameters to start the model iterations were obtained from the NLIN procedure of SAS, ignoring random effects. The mean for the three parameters ( $A_{\max}$ ,  $A_{\text{qe}}$

and *LCP*) for each treatment by species was compared using a multiple comparison procedure of contrasts.

### **Growth and photosynthesis**

Relative growth rate (RGR) mean values over the growth period and net photosynthetic rate ( $A_{\max}$ ) for each treatment (grass, light and species) were compared using a correlation analysis to determine relationships between the two variables. A nonparametric Spearman's rank correlation coefficients ( $r_s$ ) were used because it is robust to sample distribution problems.

## **Results**

### **Photosynthesis**

Based on the estimated parameters obtained for the model, *C. pentandra* had the highest  $A_{\max}$  in the Short 37%, Tall 100% and Tall 37% treatments, but was significantly lower for the Short 100%, Short 2% and Tall 2% (Table 3-1 and Figure 3-2). *D. retusa* had the highest  $A_{\max}$  in the Short 100%, Short 37%, Tall 37%, and the lowest values in the Tall 100%, Tall 2% and Short 2% (Table 3-1 and Figure 3-1). *P. guachapele* had the highest  $A_{\max}$  in Short 37% and 100% and the lowest at the Tall 2% and Tall 100% (Table 3-1 and Figure 3-1). *T. impetiginosa* and *T. rosea* did not differ at any of the treatments.

Regarding the parameters  $A_{qe}$  and *LCP*, for all species they did not differ significantly between treatments.

### **Growth and Photosynthesis**

Overall there was a positive relationship ( $r_s=0.49$ ;  $p=0.007$ ) between relative growth rate and  $A_{\max}$  when all species were combined (Figure 3-3). However when each species was analyzed individually, there was a positive significant relationship for *T. impetiginosa* ( $r_s=0.83$ ;

p=0.04), *P. guachapele* ( $r_s=0.83$ ; p=0.04), and *T. rosea* ( $r_s=0.89$ ; p=0.02) and no trend was observed for *C. pentandra* and *D. retusa*.

## Discussion

### Photosynthesis

There are tradeoffs between persistence in low light and adaptations for exploiting high light environments. Species in general do well in one environment and not in both. However there are some species that can do well in both such as *C. pentandra* (Bazzaz, 1996). Studies of photosynthetic responses of tropical species have shown that pioneer species show a larger acclimation to light conditions than shade tolerant (Davidson, Mauffette, and Gagnon, 2002; Holscher, Leuschner, Bohman, Juhrbant, and Tjitrosemito, 2004; Tinoco-Ojanguren and Pearcy, 1995)  $A_{max}$  of pioneers in low light conditions is about 4-6  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and at high light 11-22  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and for their shade tolerant species at low light ranges 2-4  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and at high light 2-6  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .

Photosynthetic performances of our species were not as expected. Light demanding species *T. impetiginosa* (Cortez) and intermediate species *T. rosea* (Roble) did not vary with respect to all photosynthetic parameters for each treatment (Table 3-1). This could be due to the fact that initial seedling height (Table 2-1) was not sufficient to overcome the aboveground competition. Therefore, seedlings experienced low light levels regardless of light treatment. Holl (2002) measured light levels under grass canopies and found that light can be as low as 5  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  and was most likely the factor which contributed to low growth of their seedlings.

Seedlings with taller initial heights did show a response to light treatment. Light demanding species *C. pentandra*, *P. guachapele* and intermediate species *D. retusa* had highest  $A_{max}$  in high light (100%) and intermediate light (37%). The potential maximum photosynthetic

capacity ( $A_{max}$ ) often is not obtained due to limiting resources such as water, nutrients, herbivore damage and internal feedback mechanisms (Bazzaz, 1996).

The parameters apparent quantum yield ( $A_{qe}$ ) and light compensation point ( $LCP$ ) for all species did not differ significantly between treatments. However this only represents leaf level traits and does not take into account other plant tissues physiological activities that influence whole plant carbon economy (Givnish, 1988).

### **Growth and Photosynthesis**

Photosynthesis parameters have been correlated with growth parameters (Zipperlen and Press, 1996). In this study the only varying photosynthetic parameter was  $A_{max}$  for *C. pentandra*, *P. guachapele* and *D. retusa*. When relating  $A_{max}$  to relative growth rate we found that there was no relationship for *D. retusa* and *C. pentandra*. However, *P. guachapele*, *T. impetiginosa* and *T. rosea* exhibited significant relationships between  $A_{max}$  and RGR. It must be recalled though, that correlation simply shows how the parameters move when observed together; it does not represent a cause-effect relationship. The way they move together may be determined by other factors. In fact, photosynthetic measurements are not the only determinant of dry matter gain. Biomass partitioning, and factors which control assimilate distribution may therefore be more diagnostic of the ecological status of a species than its rate of carbon dioxide fixation per unit area of leaf (Press, Brown, Baker, and Zipperlen, 1996; Zipperlen and Press, 1996).

### **Conclusions**

*P. guachapele* was the best performer with the highest  $A_{max}$  and relative growth rates. We recommend planting this species as an initial step in reforesting pastures. As for the other species, it is hard to determine their performance solely based on their  $A_{max}$  and relative growth rates. Further research is needed to understand why species performances varied and what are

the factors controlling this variation other than the photosynthetic capacities. Also it will be important to see how *P. guachapele* shade and competition will affect grasses and other seedlings once it establishes a canopy. Seedling height may also be a factor one should consider when planting in a pasture and should be examined for each species.

Table 3-1. Estimated parameters of photosynthesis model: light saturated point ( $A_{max}$ ), apparent quantum yield ( $A_{qe}$ ), and light compensation point (LCP). Means and standard errors. See Table 2-1 for species coding.

Treatment	$A_{max}$	$A_{qe}$	LCP
-----Ceiba-----			
Tall 100%	7.91±2.35ab	0.0021±0.0011a	-12.42±50.03a
Tall 37%	9.50±2.71a	0.0026±0.0015a	2.69±55.77a
Tall 2%	5.21±2.74b	0.0070±0.0051a	-7.26±59.18a
Short 100%	4.87±3.24b	0.0017±0.0023a	3.56±93.63a
Short 37%	10.45±2.84a	0.0039±0.0016a	19.77±51.79a
Short 2%	5.46±2.69b	0.0064±0.0045a	-5.15±59.01a
-----Coco-----			
Tall 100%	4.49±1.70ab	0.0018±0.0021a	-50.67±121.30a
Tall 37%	6.15±2.07ab	0.0071±0.0037a	17.30±121.99a
Tall 2%	4.29±2.18b	0.0080±0.0061a	5.25±123.50a
Short 100%	9.24±2.08a	0.0051±0.0026a	20.52±121.88a
Short 37%	7.33±2.19ab	0.0075±0.0034a	11.00±121.98a
Short 2%	3.68±2.19b	0.0079±0.0076a	0.36±125.17a
-----Cortez-----			
Tall 100%	5.25±1.53a	0.0021±0.0018a	-13.58±59.69a
Tall 37%	4.83±2.02a	0.0049±0.0041a	10.84±66.89a
Tall 2%	3.81±2.20a	0.0032±0.0054a	-31.01±124.86a
Short 100%	5.45±1.91a	0.0049±0.0034a	19.62±63.31a
Short 37%	6.97±2.00a	0.0060±0.0031a	14.84±61.69a
Short 2%	3.88±2.14a	0.0042±0.0066a	-12.62±100.23a
-----Guaya-----			
Tall 100%	5.41±1.29cd	0.0027±0.0014a	30.82±24.93a
Tall 37%	9.18±1.51bc	0.0039±0.0022a	14.03±31.56a
Tall 2%	5.07±1.91d	0.0030±0.0036a	-33.30±87.38a
Short 100%	12.61±1.86ab	0.0028±0.0015a	24.67±29.31a
Short 37%	14.18±1.85a	0.0042±0.0017a	23.99±26.95a
Short 2%	7.44±1.91cd	0.0039±0.0029a	-10.14±44.80a
-----Roble-----			
Tall 100%	7.36±1.52a	0.0023±0.0011a	14.37±34.73a
Tall 37%	7.74±2.08a	0.0050±0.0027a	9.23±39.71a
Tall 2%	4.99±1.82a	0.0062±0.0041a	-6.96±45.48a
Short 100%	8.83±2.23a	0.0035±0.0020a	7.83±42.50a
Short 37%	8.39±2.31a	0.0059±0.0022a	13.19±37.18a
Short 2%	4.60±2.30a	0.0032±0.0065a	-42.59±163.74a

Note: Different superscript letters assigned to means in the same column designate statistically significant differences at the 0.05 level; the same letters indicate that no statistically significant differences exist.

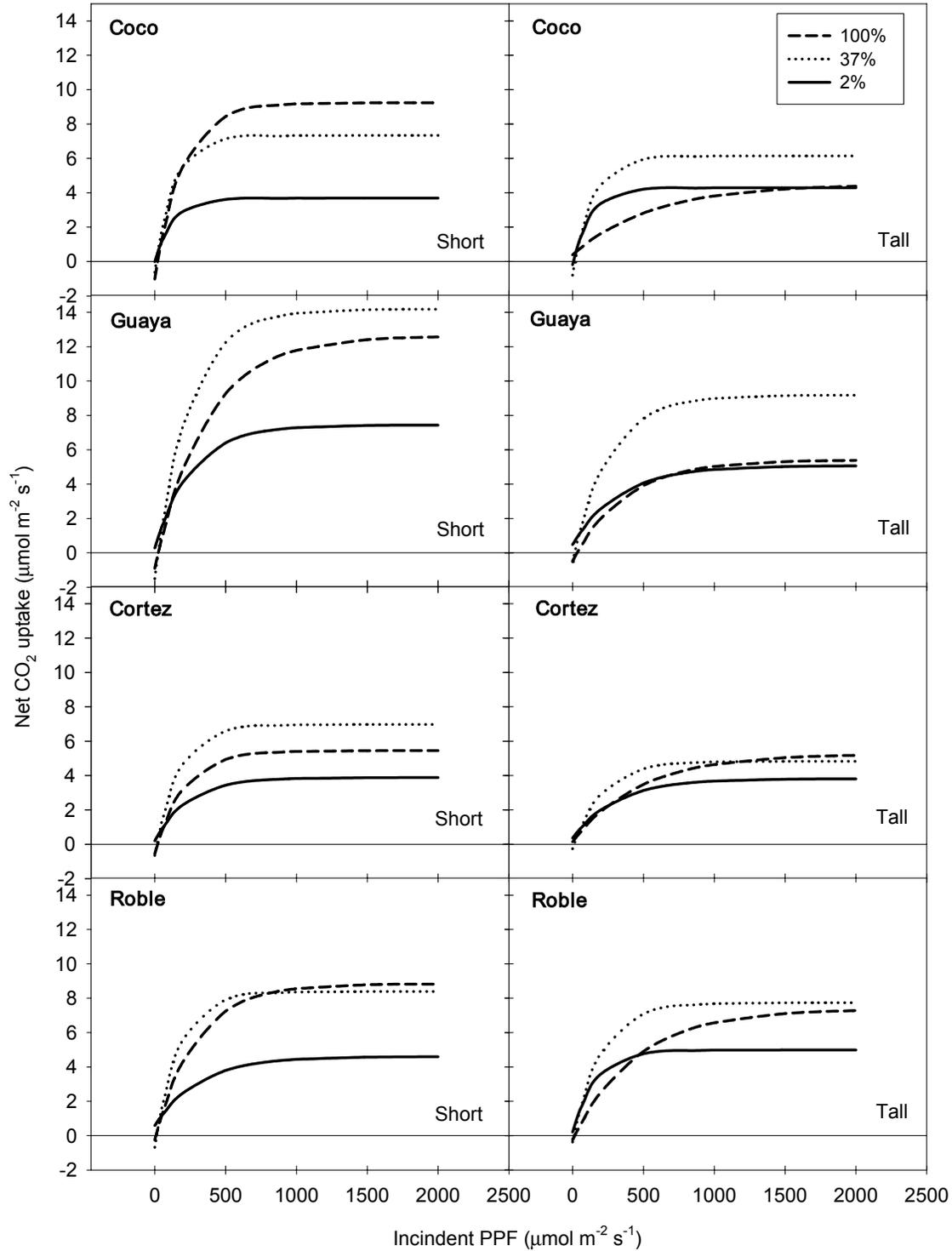


Figure 3-1. Light response curves fitted with nonlinear Mitscherlich model equations from parameter estimates obtained from nonlinear mixed models analysis using SAS. See Table 2-1 for species coding.

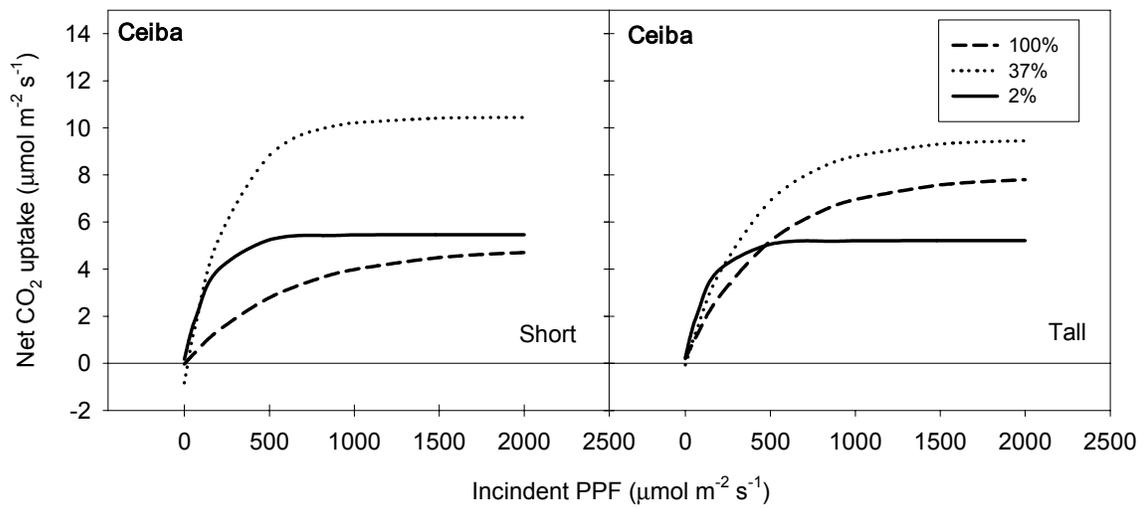


Figure 3-2. Light response curves fitted with nonlinear Mitscherlich model equations from parameter estimates obtained from nonlinear mixed models analysis. See Table 2-1 for species coding.

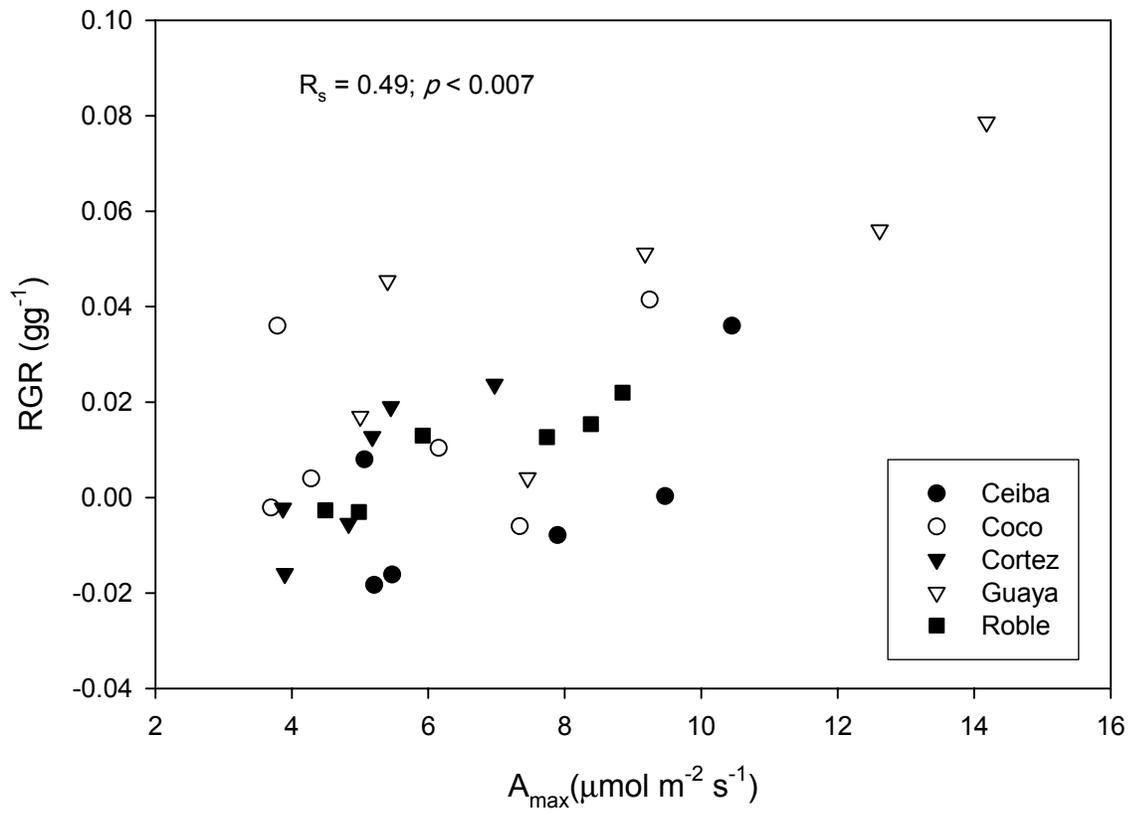


Figure 3-3. Relationship between net photosynthesis and relative growth rate for all species.

## CHAPTER 4 SUMMARY AND CONCLUSION

One of the main factors influencing the successional trajectory of abandoned pastures into forest communities is seed dispersal. Since pastures have little or no woody vegetation, the majority of woody species that colonizes abandoned pastures are wind-dispersed (Finegan and Delgado, 2000; Holl, 2002; Holl et al., 2000; Toh et al., 1999; Zimmerman et al., 2000). Those species that eventually colonize have to undergo seed predation, unfavorable conditions for germination, and intense competition once they germinate (Camargo et al., 2002; Holl and Lulow, 1997; Holl et al., 2000; Wijdeven and Kuzee, 2000).

In order to aid the restoration of abandoned tropical pastures into forested ecosystems, we must overcome some of these barriers through manipulative efforts. In doing so, we need to learn more about the performance of native tree species in these extreme environments.

The present study was designed to characterize the light requirements of six native tree species under contrasting light environments and grass competition. Understanding their early establishment requirements could be used in selecting proper light and competition regimen for the success of restoring a pasture after abandonment.

Based on our morphological and physiological findings, overall, *Pseudosamanea guachapele* was the best performer under open pasture conditions. We recommend planting this species as an initial step in reforesting pastures. Once this species is established the canopy may produce enough shade to reduce grass cover. Possibly under this scenario, *Tabebuia rosea*, *Tabebuia impetiginosa* and *Ceiba pentandra* can be planted as a second step in the restoration process. However, *C. pentandra* may be affected by competition with grasses and/or *P. guachapele* presence.

Further research is needed to understand why species performances varied and what are the factors controlling this variation other than light. It is also important to examine how *P. guachapele* canopy shade and competition will affect grasses and other seedlings once it established. It seems that seedling height may also become an important factor needed to overcome pasture competition and should be more closely examined by each species.

APPENDIX  
SOIL NUTRIENTS

Table A-1. Soil nutrient levels.

pH/ water	K	Ca	Mg	P	Fe	Cu	Zn	Mn
	-----cmol+/L-----				-----ppm-----			
5.5	0.17	15.7	8.65	4.7	67	15	2.6	21

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## BIOGRAPHICAL SKETCH

Gerardo Celis was born in Costa Rica. At the age of four, his entire family moved to the US where his father was to pursue his graduate studies in Resource Economics. When they returned to Costa Rica, eight years later, he was fascinated by the rainforests and began to develop an interest for the environment and for understanding the impact of humans on it. This motivated him to pursue a career in this area.

As a first step, upon conclusion of High School, he initiated a program in Environmental Studies at the University of British Columbia in Vancouver. After one year there, he then returned to Costa Rica, where he completed his undergraduate studies in Biology at Universidad Latina. His undergraduate research, entitled: “Seed germination of two sympatric palm species: *Chamaedorea tepejilote* Liebm. and *Chamaedorea Costaricana* Oerst (Arecaceae) in natural conditions and in a nursery,” was the result of a pro bono collaboration with the National Museum.

After concluding his undergraduate studies he taught Biostatistics at the same university and was awarded a scholarship by the Organization for Tropical Studies (OTS) to participate in the program Research Experiences for Undergraduates (REU) at La Selva Biological Station. The research conducted was entitled: “Do patterns of seed germination and seedling biomass allocation reflect a shade tolerance syndrome in *Gnetum leybodianum* Tul. (GNETACEAE)?” Later on, he became TA, under Professor Luis Diego Gómez, for OTS’ course “Plantains, Iguanas and Shamans: An Introduction to Field Ethnobiology.”

At this point in his career, he felt that he needed to develop a broader understanding of environmental processes by incorporating the interdisciplinary dimension; in particular, how humans could help restore the environment. Thus, he decided to pursue a master’s in interdisciplinary ecology at the University of Florida (UF). In 2004, he obtained a 9-credits out-

of-state tuition exemption from the Florida-Costa Rica Linkage Institute (FLORICA). For the second year he was awarded a fellowship by UF's Tropical Conservation and Development Program (TCD) within the Center for Latin American Studies. His master's thesis was entitled: "Restoring abandoned pasture land with native tree species in Costa Rica: An ecophysiological approach to species selection" funded by the Compton's fellowship.

Upon completion of his master's degree he enrolled in a PhD in Urban restoration ecology at the University of Florida. He plans to continue research in the area of urban restoration ecology, teach courses at universities, become part of teams performing environmental impact assessments and designing policy reforms, and develop community level activities. With the information generated from his research, he wants to create programs that will help to establish a better interpretation of the environmental impacts of urban expansions and to give a solid basis for urban planning and policy design.