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Effects of nitrogen and phosphorus fertilization on the survival and recruitment of seedlings of dominant tree species in two abandoned tropical dry forests in Yucatán, Mexico

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Abstract

Seedling dynamics were studied in a set of dominant tree species in regenerating secondary tropical dry forests (TDF) growing on limestone in the Yucatán Peninsula. The objective of the study was to assess how variation in nutrient availability affects the recruitment and survival of individual species considering natural variations in light and bulk density in the topsoil. Our study included an area of young forest (10 years old), with phosphorus-poor soils, and an area of old forest ($\cong 60$ years old). We used 16 plots (12 m \times 12 m) per forest, in which we fertilized four plot replicates per treatment with nitrogen (N), phosphorus (P) and nitrogen plus phosphorus (NP). Another four replicates were kept as control. In four 1 m \times 1 m sub-plots set of each experimental plot, tree seedling dynamics were studied over 2 years. The species with the highest recruitment were *Acacia gaureri* and *Leucaena leucocephala* in the young forest, and *Bursera simaruba* and *Phyllostylon brasiliense* in the old forest. Recruitment of *A. gaureri* was affected more by light availability than fertilization, but its survival increased with N or with NP additions. *Leucaena leucocephala* benefited by fertilization (N, P, or NP) and the species regenerated on sites with lower light availability, but required high light conditions and N addition to increase its survival. The recruitment and survival of *B. simaruba* required low light availability, and the fertilization with P or with NP increased its regeneration. *Phyllostylon brasiliense* was recruited only in the old forest. The addition of P resulted in the highest recruitment and the lowest survival among fertilization treatments, leading to a negative final seedling density. Canonical analysis revealed that in the young forest, the most important variables that influenced species recruitment were bulk density in the topsoil, fertilization with P, fertilization with N, and light availability. In the old forest, the P and N fertilizations and bulk density in the topsoil appeared to be the most important variables; only light was not significant. Light requirement differences between forests suggest that a large number of opportunistic species in the young forest could exist there. Overall, our results suggest that the dynamic of understory vegetation in Yucatán Peninsula is strongly influenced by nutrient availability, especially P. The responses of seedling dominant species to nutrient addition will vary, depending on the details of the site's light availability and soil bulk density, and the identity of species.

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Keywords: *Acacia gaureri*; *Bursera simaruba*; Forest regeneration; *Leucaena leucocephala*; Light availability; *Phyllostylon brasiliense*; Seedling dynamic; Mexico

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1. Introduction

Most of the ecological studies of regeneration in tropical ecosystems have been carried out in tropical rain forests. These studies are mainly concerned with how gap dynamics modify light availability, nutrients and their impact on seed germination, recruitment, survival and plant growth (Augsburger, 1984a,b; Martínez-Ramos, 1985; Hubbel and Foster, 1986; Brokaw, 1987; Mulkey et al., 1996; Vázquez-Yanes and Orozco-Segovia, 1996). Tropical dry forests (TDF) have attracted less scientific attention than evergreen wet forests (Whitmore, 1996), and consequently, basic aspects of their ecology such as regeneration dynamics remain poorly understood (Mooney et al., 1995). Some authors have found evidence of differentiation in species' responses to light levels (Ray and Brown, 1995; Huante et al., 1998; Oliveira-Filho et al., 1998) and water availability (Swaine, 1996) in these ecosystems.

Evidence of low availability of mineral nutrients in TDF comes from studies of nutrient availability in mature forests (Agbenin and Tiessen, 1994) or from studies of changes in soil nutrient concentration during slash-and-burn agriculture (Kauffman et al., 1993; Maass, 1995; Giardina et al., 2000). Plant responses to different nutrient levels have been widely studied for temperate habitats (Grime, 1977; Chapin, 1980, 1988), but for TDF, information is rather limited (Rincón and Huante, 1994; Huante et al., 1995a; Khurana and Singh, 2001).

The TDF of the Yucatán Peninsula in Mexico have been used and managed for hundreds of years by the Mayan people. As a consequence, most TDF in the area are of a secondary nature today (Gómez-Pompa et al., 1987). Fertilization experiments and the biogeochemical characteristics of soils in Yucatán TDF indicated that forest regeneration has been limited by nutrient availability (Ceccon, 2001; Ceccon et al., 2002). This evidence suggests that phosphorus availability could be a key limiting resource for the seedling survival and plant growth (Ceccon et al., 2002; Campo and Dirzo, in press). These findings suggest that nutrients in interaction with light availability and bulk density in the topsoil may differentially influence the recovery of seedlings of secondary TDF. We studied the impact of nutrient addition on seedling dynamics of tree species with the highest

recruitment in two secondary forests with different ages of abandonment (10 years and $\cong 60$ years) after traditional Mayan slash-and-burn agriculture (maize and henequén, Flores, 1987). In particular, we evaluated the effect of fertilization with N and/or with P on the recruitment and survival of individual species over 2 years considering natural variations in light and bulk density in the topsoil. We expected differences among species in relation to their recruitment and survival in response to fertilization, light condition and bulk density in the topsoil. Because tropical forest ecosystems are considered largely to be P-limited (Vitousek, 1984), species' performance was expected to be better under P than under N addition or without nutrient addition. Moreover, in the early stage of regeneration a rapid colonization by resource-demanding species with fast-growth rates was expected. We predicted a higher response to fertilization in the early stage of regeneration (10-year-old forest) compared with the later regeneration stage ($\cong 60$ -year-old).

2. Methods

2.1. Study area

The experiment was carried out in the Dzibilchaltún National Park region, in the Northwest of the Yucatán Peninsula (21°06'N and 89°17'W), near Mérida City, Mexico. The whole of the area was previously used for henequén plantations (*Agave fourcroydes* Lem.) alley-cropped with corn slash-and-burn agriculture, known as "milpa" (Flores, 1987). One sector of this area was abandoned ~ 60 years ago (old secondary forest; see Lundell, 1934) and another sector was abandoned about 10 years ago (young secondary forest; F. Tum, personnel communication). The landscape is flat (with altitude below 10 m a.s.l.). The predominant lithology includes late Pliocene material with numerous areas of exposed limestone that are mainly shallow (<10 cm in depth) with frequent rock outcrops. In slightly undulating areas, the soil is deeper (<50 cm) with a high organic matter percentage (35%), and high pH (7.3; Campo and Vazquez-Yanes, submitted). Although both areas can be regarded as nutrient-poor, the old forest area has soils with higher availability of P. Most of the plots in the young forest occurred on soils where the total N varied from 0.7 to 1.7%

(average and S.E., $1.4 \pm 0.7\%$) and total P varied from 0.14 to 0.30% ($0.26 \pm 0.02\%$), respectively; available P was $10.0 \pm 0.7 \mu\text{g g}^{-1}$. In the old forest soils, the total N concentration range was 0.6–1.7% and does not differ from those of the young forest soils (Ceccon et al., 2002). However, total and available P concentrations are significantly greater than mean values in the young forest soils (1.5 and 1.9 times higher, respectively; Ceccon et al., 2002).

The climate in this area is hot and sub-humid with a small thermal oscillation during the year (less than 6°C of difference between the coolest and the warmest months). The mean annual temperature is 25.8°C and the total annual rainfall is 986 mm, most of which falls between June and October (Trejo-Vázquez, 1999). The predominant vegetation in the area is tropical deciduous forest (Miranda, 1958), in which mean canopy height is 6–8 m. Floristically, Leguminosae are the most important family in both forest areas (Ceccon et al., 2002).

2.2. The study design

In each forest (i.e. young and old), 16, $12\text{ m} \times 12\text{ m}$ plots with 8 m width buffers between them were established during 1997. Three treatments and one control with four replicates of each were randomly allocated in each forest as follows: added nitrogen (N), added phosphorus (P), added nitrogen plus phosphorus (NP), and control (no fertilizer). For two consecutive years (1998–1999), fertilizers were added in two pulses. Sixty percent of the total annual amount was added at the end of the dry season (May) and the remainder (40% of the total annual amount) was added in the middle of the rainy season (September). Average precipitation for the 2 years of the study in the dry and rainy seasons was 47.2 and 123.7 mm, respectively (J. Espinoza personnel communication, INEGI). Due to the strong effect of rainfall seasonality on forest phenology (Holbrook et al., 1995) and nutrient availability (Singh et al., 1989; Campo et al., 1998) in dry forest ecosystems this scheme of fertilization distribution was preferred. These treatments gave total yearly N additions of 220 kg ha^{-1} and P additions of 75 kg ha^{-1} . Such nutrient additions are similar to the range of applications found to produce significant growth responses in a Venezuelan tropical forest (Tanner et al., 1992). Dry fertilizers (urea, consisting of $(\text{NH}_2)_2\text{CO}$, or triple

superphosphate, consisting of $\text{Ca}(\text{H}_2\text{PO}_4)_2 \cdot \text{H}_2\text{O}$, or both) were applied manually and each experimental plot was divided in to 36 sub-plots ($1\text{ m} \times 4\text{ m}$), in order to guarantee precision in the application.

2.3. Light availability

Hemispherical photographs (Minolta 7.5 mm lens) were used to measure understory light availability (percentage of canopy openness); we took two photos on each sub-plot during the rainy period (September 2001), when vegetation grows, plants produce leaves and the forest regeneration occurs. The photographs were taken at 1.0 m above the ground in the center of each sub-plot. The camera was positioned horizontally in relation to the forest floor, and a mark within the field of view lets us to determine the true north. The photos were taken either early or late in the day or under overcast conditions to minimize glare from direct sunlight (ter Steege, 1993). The negatives were digitized using a CANOPY-SOLARCALC 4.0 program. The effects of forest canopies on spectral quality of understory light are well known (e.g. Smith, 1982). We obtained the annual average direct radiation and we calculated from these data the light percentage (canopy openness) per sub-plot. We measured light percentage in order to use it as a covariable, which could provide information about the effects of its interaction with fertilization on the seedling recruitment and species survival. Differences in light percentage between young and old forests were tested using a *t*-test on normalized data.

2.4. Evaluation of bulk density in the topsoil

In the study area, it was not easy to measure soil depth because soils are mainly shallow (<10 cm in depth) with many exposed rocks. To solve problems with the rocky nature of the soil we decided to use the bulk density as the weight of soil at each experimental plot. For the analysis of bulk density, litter material was cleaned from the soil surface and a volume of soil, approximately $10\text{ cm} \times 10\text{ cm} \times 10\text{ cm}$ from the upper profile was excavated (Elliot et al., 1999). A total of 32 samples of soil were randomly collected in each $12\text{ m} \times 12\text{ m}$ plot. Generally (in 87% of samples) soils were very shallow (<10 cm in depth) and the average depth was $\sim 5\text{ cm}$. All soil collected was

sieved through a 2 mm mesh, coarse roots and rock materials were removed and the remaining fraction of the soil was saved, oven-dried at 105 °C overnight, and weighed. Frequent rock outcrops limited our capacity to determine the volume of soil excavated, therefore, the results are reported as kilogram of soil by square meter. The average bulk density in the top soil per plot was used as a covariable, which could give us information about the effects of its interaction with fertilization and light availability on the recruitment of seedling species. Differences in bulk density between young and old forests were tested using a *t*-test on normalized data.

2.5. Seedling census

A subset of four 1 m × 1 m sub-plots were randomly established in the central 6 m² of each experimental plot (12 m × 12 m) resulting in a total of 64 permanent sub-plots. Within these sub-plots, all tree seedlings of <1 m height were tagged, identified and recorded quarterly. All seedlings regenerated by seeds and by sprouts were registered. The seedling census was initiated in May 1998 and continued for a period of 27 months. However, the evaluation of changes in seedling density, recruitment and survival spanned 24 months.

2.6. Seedling analysis

To evaluate changes in seedling density per species during 24 months, we calculated the difference in density between the beginning (before the fertilization, May 1998) and the end of the study (24 months later, May 2000) for each treatment per forest. We compared the percentage of species which increased between the young and old forest using a *t*-test on normalized data.

In order to examine the effects of the fertilizer treatments on seedling survival during the 24 months period, a Generalized Linear Model was fitted separately for each forest (GLIM program version 4.0). In this model, the survival (in days) of each individual seedling was regarded as the response variable, for which a Weibull error distribution was assumed (Crawley, 1993). The response variable was modeled as a function of N and P fertilizations, and light percentage of the sub-plot. The fitted parameters obtained with the Weibull model were used to estimate mean days of seedling survival in each treatment.

However, only two species in each forest had enough individuals recruited in all treatments, to make it possible to conduct a Weibull analysis per species: *Acacia gaumeri* (186 individuals) and *Leucaena leucocephala* (115 individuals) in the young forest, and *Bursera simaruba* (229 individuals) and *Phyllostylon brasiliense* (450 individuals) in the old forest. Fertilization was used as a categorical variable. The days of survival of each plant were recorded (from 90 up to 720 days) and were considered as a response variable for the Weibull model. The seedlings that survived up to the last census (720 days) were recorded as being alive (to do this, the censoring indicator was $w = 0$), and the seedlings which had died on the previous census received the censoring indicator $w = 1$. The significance of each parameter on the Weibull model was estimated after dividing the estimated parameter by the standard error and their significance was determined using a *t*-test.

To investigate the relationship between the relative number of individuals recruited for each species in each sub-plot (number of individuals × 4 m⁻²/total of individuals in each forest × 100) and the environmental variables (fertilization with N, with P, with NP, and control, light percentage and bulk density in the topsoil), we used a canonical correspondence analysis, CCA (ter Braak, 1994; JMP-SAS program, Version 4). Only species with relative recruitment density >4% in each forest, were included in the matrix for analysis. The matrix of environmental variables per sub-plot included fertilization as a dummy variable (presence 1 or absence 0, of P and N additions). Light (%) and soil bulk density (kg m⁻²) values were standardized. Because there were dummy variables, we used the discriminant function to determine what environmental variables were the best predictors of species' recruitment and the significance tests used were: Wilk's Lambda, Pillai's Trace, Hotteling-Lawley, Roy's Max Root test (JMP-SAS program, Version 4).

3. Results

3.1. Light availability and soil bulk density in the topsoil

Light availability was significantly higher in the young than in the old forest ($t = 2.86$, $P \leq 0.05$,

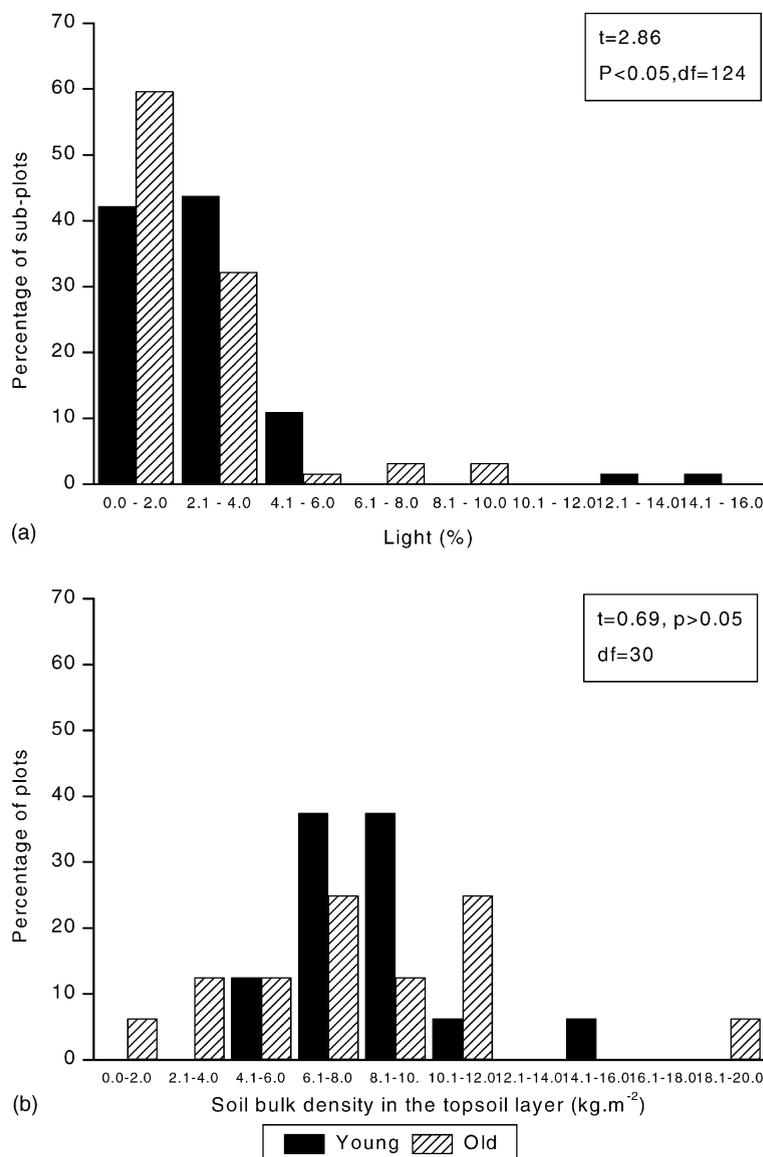


Fig. 1. (a) Frequency distribution of light amounts and (b) soil bulk densities in a young and an old secondary forests of the Yucatán Peninsula.

d.f. = 124). In the old forest, 60% of the sub-plots were ≤ 2 and 8% of sub-plots had more than 4% of light, while in the young forest, 42% of the sub-plots were ≤ 2 and 14% of the sub-plots had more than 4% of light (Fig. 1a). There was lower variability in soil bulk density in the young forest (range from 4.74 to 14.84 kg m⁻²; mean and S.E., 7.97 ± 0.58 kg m⁻²) than in the old forest (range from 0.68 to 19.27 kg m⁻²; 8.16 ± 1.1 kg m⁻², Fig. 1b), but the average

value was not significantly different between forests ($t = 0.69$, $P > 0.05$, d.f. = 30).

3.2. Changes in the density of species between 1998 and 2000

A total of 828 seedlings of 50 species in the young forest and 976 individuals of 48 species in the old forest were recruited during the 24 months of this study.

After 2 years, 63 and 20% of the species increased their density in the young and in the old forest, respectively. The percentage of species that increased in density was significantly different between sites ($t = 8.33$, $P = 0.006$, d.f. = 16).

In the young forest, in the control plots, 69% of total species increased their seedling density (in some cases greatly as in the case of *Acacia gaumeri*), and 10% of species decreased their abundance (Appendix A). In N addition plots, 60% of total species increased seedling density (mainly *Neea choriophylla* with a change of 76% compared to a reduction in the control plots by 43%), and 25% of species reduced their abundance (e.g. *Randia aculeata* density decreased by 73%). Interestingly, *A. gaumeri* which increased four-fold in control plots, changed slightly under N addition. Generally (70% of the total number of species), the species showed a higher seedling density after 2 years of P addition, and only 1 of 23 species in this treatment diminished its abundance. With the addition of NP most of the species increased in seedling abundance (60% of the total number of species; especially *Gymnopodium floribundum* and *Samyda yucatanensis* which showed the largest increases in density, ~20 times, Appendix A);

in contrast, the application of NP fertilizers reduced the seedling abundance of 36% of species. *Acacia riparia*, which was not present in the fertilized plots at the beginning of the experiment, appeared in all fertilized treatments at the end of the study in this forest.

In the old forest, in the control plots, a similar and low proportion (~20%) of species increased or decreased their abundance (Appendix B). Generally, fertilization treatments had no effects on final seedling density of individual species. A strong effect of fertilization on final seedling density was only observed with *A. gaumeri* under N addition, but the effect was not confirmed with NP treatment.

Among the species listed in Appendices A and B *Acacia gaumeri* and *Leucaena leucocephala* for the young forest, and *Bursera simaruba* and *Phyllostylon brasiliense* for the old forest were selected for a detailed analysis because they presented the highest recruitment. *Acacia gaumeri* decreased its abundance under N and NP fertilizations regarding control plots; *L. leucocephala* increased its density after N and NP additions; *B. simaruba* and *P. brasiliense* had slight changes in density under nutrient addition (Appendices A and B; Fig. 2).

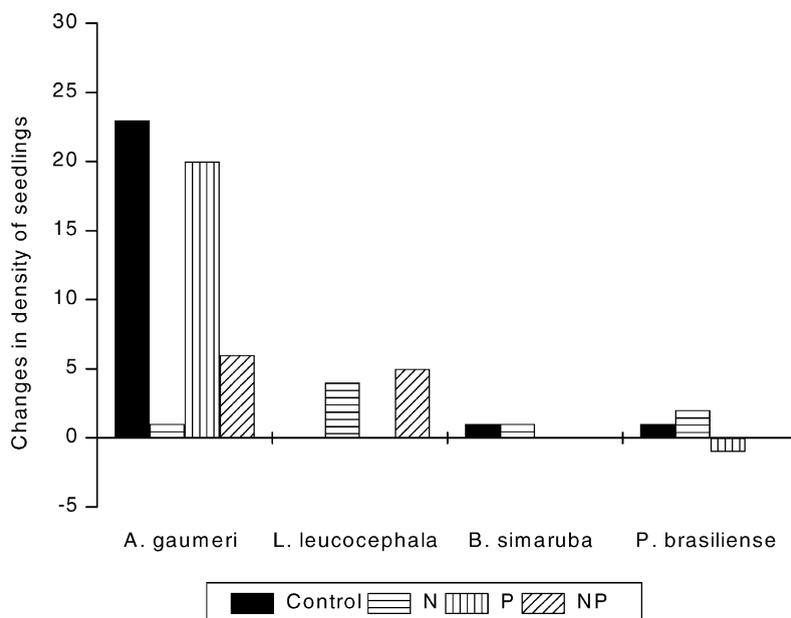


Fig. 2. Changes in density of seedlings recruited (May 1998 to May 2000) per specie under four treatments of soil nutrient addition in a young and an old secondary forest of the Yucatán Peninsula. The data corresponds to the two dominant species in the young forest (*A. gaumeri* and *L. leucocephala*), and in the old forest (*B. simaruba* and *P. brasiliense*).

3.3. Survival of species with the highest recruitment

The four species studied in detail had a shape parameter (α) of the Weibull distribution >1 , which indicates that the risk of death of these species increases with age (*A. gaumeri*: $\alpha = 1.4865$, d.f. = 180; *L. leucocephala*: $\alpha = 2.2435$, d.f. = 107; *B. simaruba*: $\alpha = 1.5254$, d.f. = 221; *P. brasiliense*: $\alpha = 1.5731$, d.f. = 441).

In the young forest, results of the Weibull survival model for *A. gaumeri* denoted significant effects of light ($P < 0.05$), N fertilization ($P < 0.001$), and of light

percentage \times N fertilization interaction ($P < 0.05$). The survival of *A. gaumeri* increased under N or NP additions at high light percentage (Fig. 3a). The survival model for *L. leucocephala* showed significant effects of P addition, light availability, and of the interaction of light availability with P and N treatments ($P < 0.001$). In control plots, the survival of *L. leucocephala* was negatively influenced by high light availability (Fig. 3b). However, the NP treatment showed the opposite response compared with the control, and in NP plots the highest survival at high light and the lowest at low

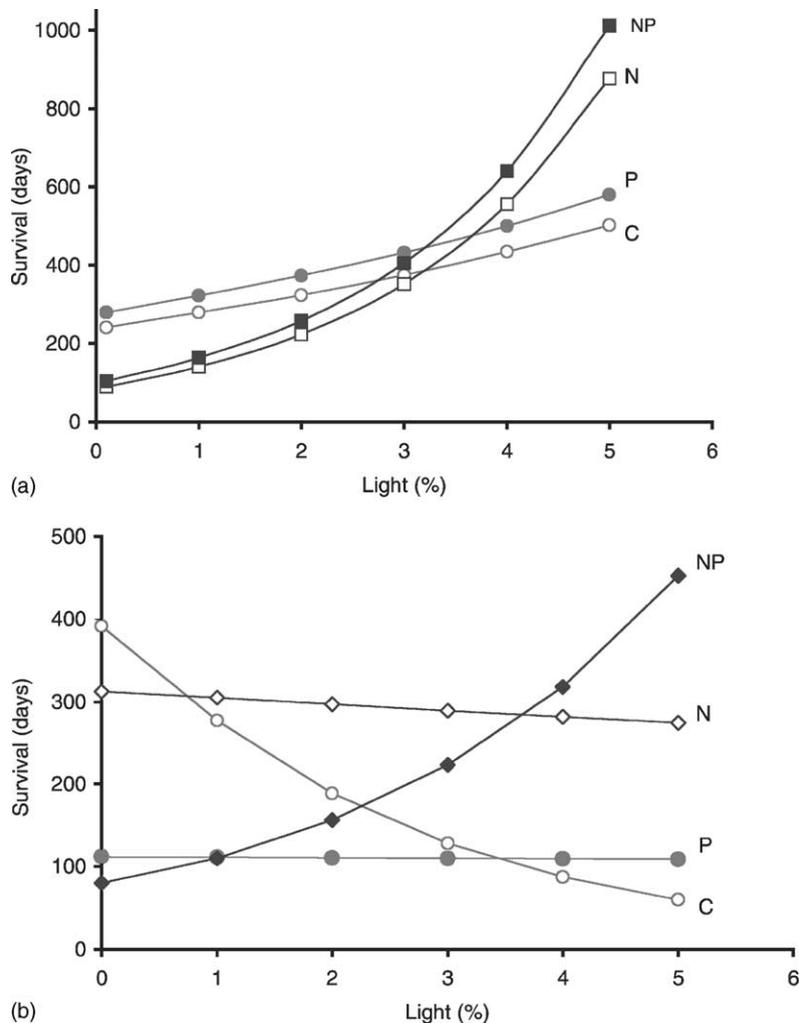


Fig. 3. Fitted lines from GLIM model showing the effect of N, P, or NP additions on seedling survival at different light level in a young and an old secondary forests of the Yucatán Peninsula. Control plots (C) without fertilization. The data corresponds to the dominant species in the young forest (a) *A. gaumeri*, and (b) *L. leucocephala*, and in the old forest (c) *B. simaruba*, and (d) *P. brasiliense*.

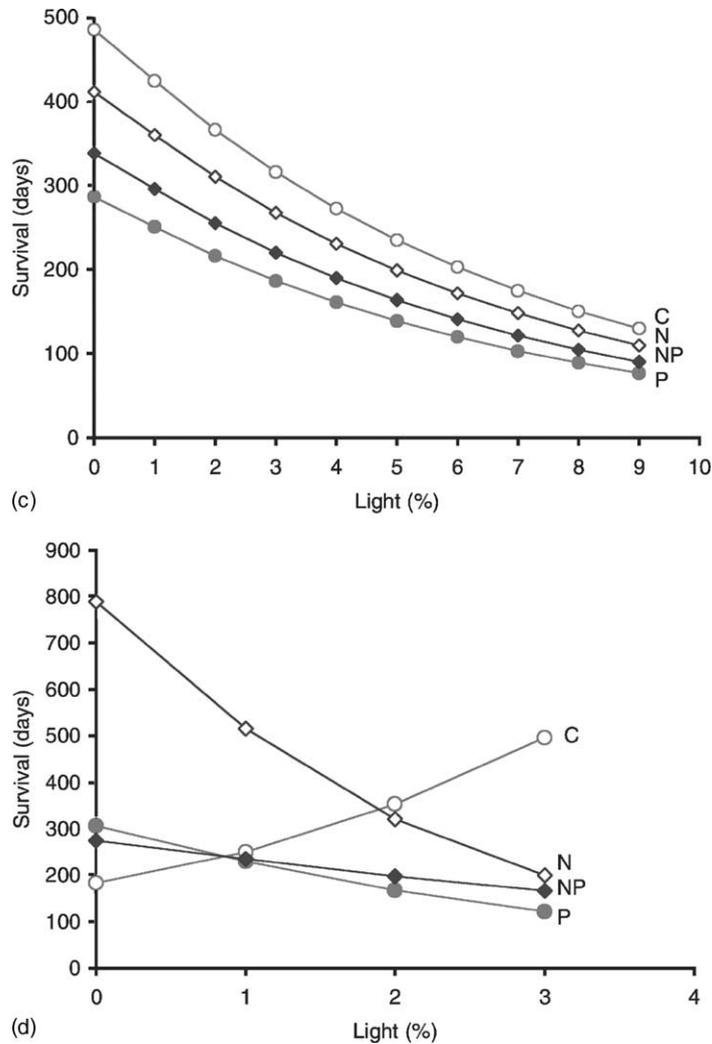


Fig. 3. (Continued).

light percentage was observed. In contrast, no response to light percentage was exhibited by *L. leucocephala* when N or P was applied separately (Fig. 3b).

In the old forest, the survival model for *B. simaruba* showed significant effects for fertilization ($P < 0.05$) and light ($P < 0.001$), but there was no significant interaction between them. In the control plots the highest survival followed by a decreasing gradient of survival in the direction of $N > NP > P$ was observed (Fig. 3c). Survival decreased as the light percentage increased in both control and fertilization treatments. In the survival model for *P. Brasiliense*, all parameters

used and their interactions were significant (N addition, $P < 0.001$; P addition, $P < 0.01$; light, $P < 0.01$; light \times P addition, $P < 0.001$; light \times N addition, $P < 0.001$; light \times P addition \times N addition, $P < 0.001$). Survival in control plots increased with light percentage (Fig. 3d). However, under fertilization, seedling survival had the opposite response. The most contrasting response was for N fertilization, which had the highest survival with low light. Under fertilizations with P or NP there was a very slight response to light. *Phyllostylon brasiliense* recruited well in a very narrow range of light percentage (0.01–3%; Fig. 3d).

3.4. Recruitment of dominant species

Most of the *A. gaumeri* individuals were recruited at light percentages between 1.0 and 4.5% (Fig. 4a). The

highest number of seedlings recruited was in control plots, where recruitment occurred at light percentages even higher than 4.5%. Among fertilization treatments, the P addition plots had the highest recruitment.

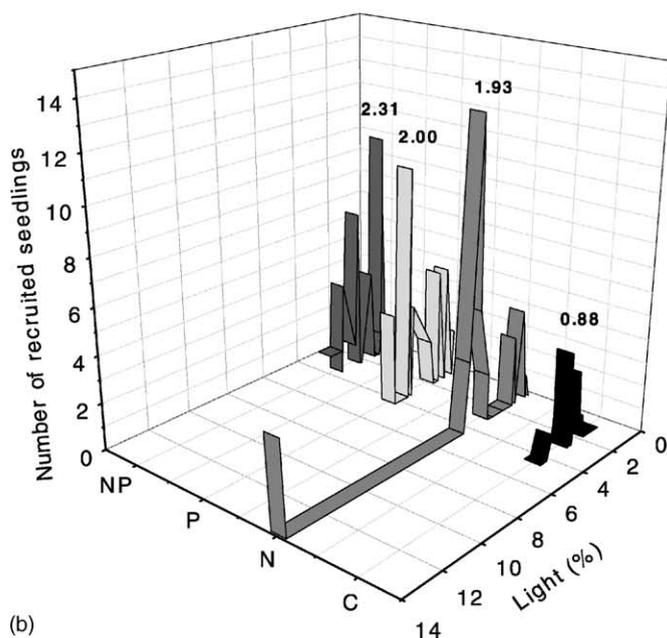
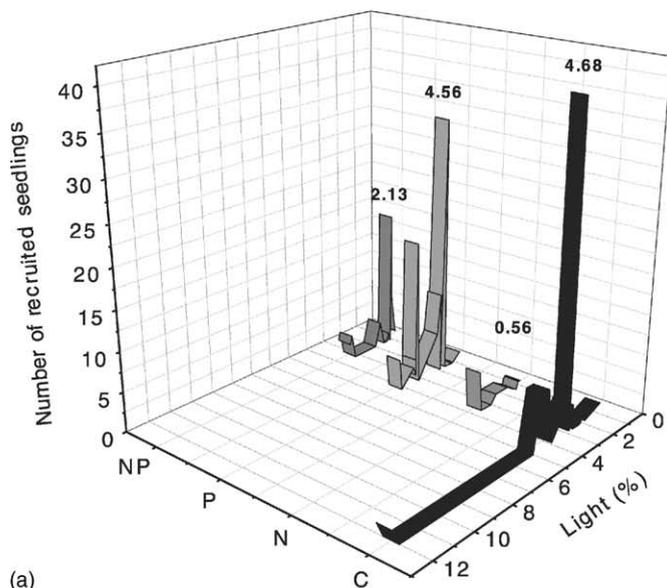


Fig. 4. Number of recruited seedlings per specie under four treatments of soil nutrient addition in a young and an old secondary forests of the Yucatán Peninsula. The data above each ribbon show the average recruitment in each treatment and corresponds to the dominant species in the young forest (a) *A. gaumeri*, and (b) *L. leucocephala*, and in the old forest (c) *B. simaruba*, and (d) *P. brasiliense*.

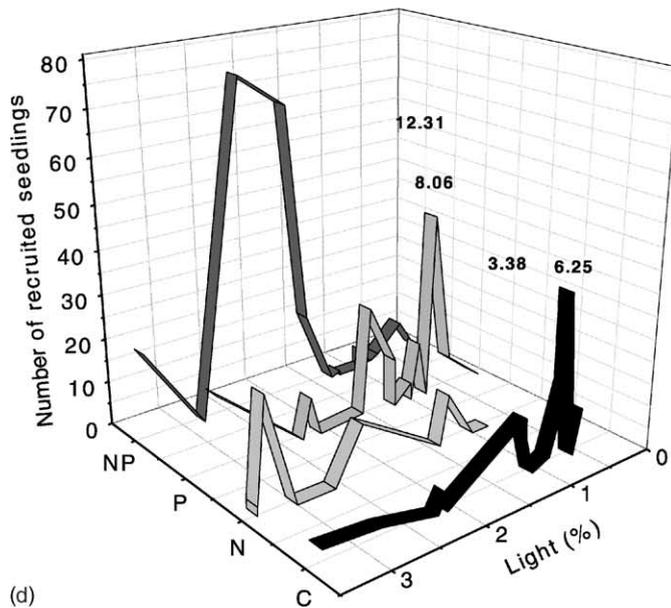
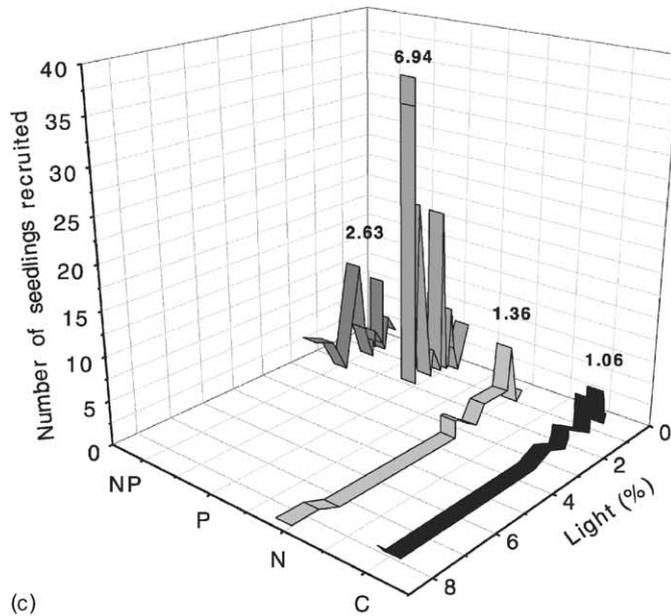


Fig. 4. (Continued).

In both the P and NP treatments the highest recruitment occurred with the lowest light, while in the N treatment no variation in recruitment was observed in response to differences in light. Most of the *A. gaumeri* individuals (90%) were recruited in plots with more than 9 kg m^{-2} of bulk density in the topsoil. Almost all

of these individuals (98%) regenerated from seed rather than from vegetative reproduction.

The average number of *L. leucocephala* seedlings recruited per plot was lower in the control plots (0.88 seedlings per 4 m^2) than in the fertilization treatments and similar among the fertilized plots (in the N plots

1.93 seedlings per 4 m², in the P plots 2.00 seedlings per 4 m², in the NP plots 2.31 seedlings per 4 m²) (Fig. 4b). Recruitment with N and P was higher at light percentages between 3 and 4.5%. The N treatment had a recruitment of five seedlings at the extreme light percentage of 14%. Seedling recruitment was not affected by bulk density in the topsoil. Only 1.7% of *L. leucocephala* seedlings regenerated by sprout.

The highest recruitment of *B. simaruba* was between light percentages of 1–3% (Fig. 4c). Compared with the control, fertilization with P and NP increased seedling recruitment; the highest for P plots. The control and N fertilization plots exhibited a similar recruitment pattern, but N fertilization had the lowest recruitment among fertilized plots. Most of the recruited seedlings of *B. simaruba* were associated with bulk density in the topsoil (5 and 9 kg m⁻²). All the seedlings regenerated by seeds.

Among the four species analyzed in detail, the recruitment of *P. brasiliense* occurred at the lowest light percentages (0.1–3.5%). Fertilization with P and NP increased seedling recruitment compared with the control (Fig. 4d). This increase was the highest for the NP treatment at 2–3% of light, while for the P treatment the highest recruitment was at low light. At least 93% of the *P. brasiliense* seedlings occurred with bulk density in the topsoil lower than 8 kg m⁻² and, within this percentage, 28% regenerated in bulk density in the topsoil lower than 3 kg m⁻². Only 1.1% of seedlings regenerated by sprouting.

3.5. Species ordination

The canonical correspondence analysis revealed that species recruitment in both forests was related to N and P fertilization and to the bulk density in the topsoil (Tables 1 and 2). Light percentage was significant only in the young forest. The relationship between environmental variables and the axis that resulted from the CCA are shown in Table 1 and Fig. 5a and b for the young and the old forests, respectively. The species ordination by CCA had large eigenvalues for the environmental variables (Table 2). In the analysis, 12/23 species from the young forest and 8/23 from the old forest had a significant correlation with at least one of the environmental variables considered (MANOVA analysis and Wilk's Lambda, Pillai's Trace, Hotteling-Lawley and Roy's Max Root tests with $P < 0.05$).

Table 1

Canonical correspondence analysis for the tree seedling community and the environmental variables (N and P fertilizations, light availability, and bulk density in the top soil) in a young and an old secondary forest of the Yucatán Peninsula

	Axis 1	Axis 2	Axis 3	Axis 4
Young forest				
Eigenvalues	1.5408	0.5027	0.3652	0.1758
Species–environmental correlation	0.7787	0.5783	0.5121	0.3867
Old forest				
Eigenvalues	1.1787	0.4252	0.1858	0.038
Species–environmental correlation	0.7355	0.5462	0.3958	0.1915

In the young forest, all environmental variables were significant (Table 2). The first canonical axis was best correlated with bulk density in the topsoil, followed to a lesser extent by N fertilization and correlated negatively with P fertilization and light. The second canonical axis was best correlated with P fertilization and light. Most of the species recruited in the young forest were correlated with NP fertilization, high to intermediate light percentage and low bulk density in the topsoil (Fig. 5a). This group included *Neea choriophylla*, *Croton glabellus*, *Neomilspaughia emarginata*, *Chiococca alba* and *Bursera simaruba*. A second group of species recruited was correlated positively with N fertilization and high bulk density in the topsoil and negatively with P fertilization. This second group included *Leucaena leucocephala*, *Thouinia paucidentata*, *Dyospiros verae-crucis* and

Table 2

Canonical correspondence coefficients in the first two ordination axes

	Axis 1	Axis 2	P-value
Young forest			
Light	-0.1164	0.0671	<0.05
Phosphorus	-0.1285	0.1347	<0.01
Nitrogen	0.1239	-0.010	<0.01
Bulk density in the top soil	0.2498	-0.041	<0.01
Old forest			
Light	0.0018	0.0052	n.s. ^a
Phosphorus	0.1971	0.0860	<0.01
Nitrogen	-0.080	-0.1251	<0.05
Bulk density in the top soil	0.0300	0.1863	<0.05

^a Non significant.

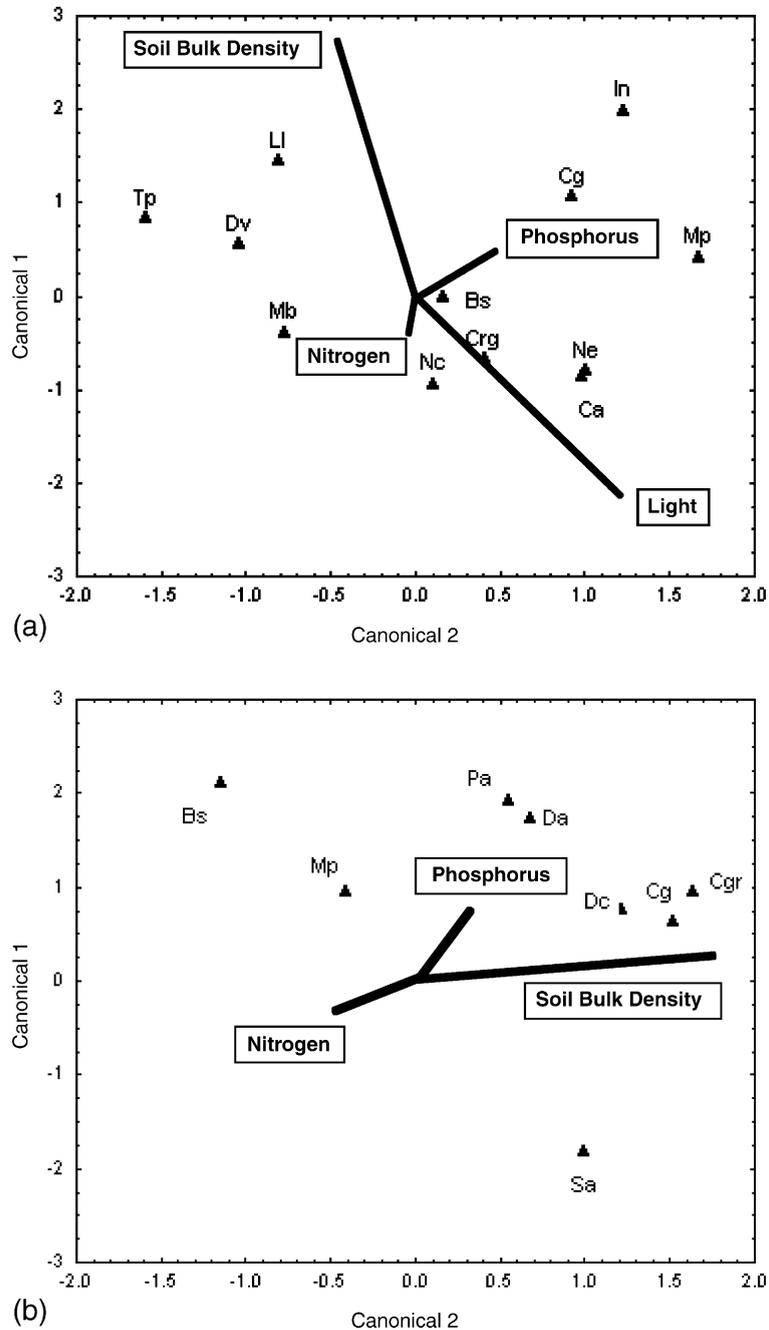


Fig. 5. Canonical correspondence ordination showing distribution of species (a) in a young and (b) an old secondary forests of the Yucatán Peninsula, in the first two ordination axis. Significant explanatory variables are indicated by lines. Species names are abbreviated as follows: Bs, *Bursera simaruba*; Ca, *Chiococca alba*; Cg, *Colubrina greggii*; Cgl, *Croton glabellus*; Da, *Diospyros anisandra*; Dc, *Diospyros cuneata*; Dv, *Diospyros verae-crucis*; In, *Indigofera* sp.; Ll, *Leucaena leucocephala*; Mb, *Mimosa bahamensis*; Mp, *Malpighia puniceifolia*; Nc, *Neea choriophylla*; Ne, *Neomillspaughia emarginata*; Pa, *Pisonia aculeate*; Sa, *Senna atomaria*; and Tp, *Thouinia paucidentata*. Environmental variables are given as arrows.

Mimosa bahamensis. A third group was correlated positively with P fertilization at intermediate light percentages (*Colubrina greggii* and *Malpighia puniceifolia*) or at low light environments (*Indigofera* sp.). Species ordination with respect to light percentages regardless of fertilization can be distinguished in three groups: (i) recruitment at high light percentage: *N. choriophylla*, *C. glabellus*, *M. puniceifolia*, *N. emarginata* and *C. alba*; (ii) at intermediate light percentage: *M. bahamensis*, *B. simaruba* and *C. greggii*; and (iii) at low light percentage: *L. leucocephala*, *T. paucidentata*, *D. verae-crucis* and *Indigofera* sp.

In the old forest, light percentage was the only environmental variable not significantly correlated with the species recruitment (Table 2). The first canonical axis was best correlated with P fertilization. The second canonical axis was best correlated with bulk density in the topsoil, but correlated negatively with N fertilization. Two groups of species were clearly distinguished: the first group included *Phyllanthus acuminatus*, *Dyospiros anisandra*, *Dyospiros cuneata*, *Colubrina greggii* and *Croton glabellus* which correlated positively with P addition and bulk density in the topsoil, and the second group included *Bursera simaruba* and *Malpighia puniceifolia* which showed a positive correlation with NP fertilization and a negative correlation with bulk density in the topsoil.

4. Discussion

4.1. Seedling species dynamic

The different percentage of species which increased in density in both secondary forests was possibly due to the higher light availability in the young forest than in the old forest, even though in the young forest only small gaps (<14% of light) were found. These results suggest that light was an important resource for the successful recruitment of many species. Indeed, possibly there was a higher number of shade-intolerant species in the young than in the old forest (Whitmore, 1975).

A higher response to nutrient addition in interaction with light availability is expected for fast growing tropical species (Whitmore, 1975; Rincón and Huante, 1994; Huante et al., 1998). In our study, some fast growing species were recruited only in the young forest such as *L. leucocephala*, or reduced their density

in the old forest, such as *A. gaumeri*. The seedling density of *A. gaumeri*, in the young forest increased regardless of fertilization, but N fertilization reduced its density. Seedling survival of *A. gaumeri*, in the young forest was favored by N fertilization under high light. At lower light levels, fertilization did not result in any measurable effect on survival. Hence, we may conclude that the success of *A. gaumeri* was affected more by light availability than fertilization. However, regeneration of this species only occurred in fertilized plots and high light environments. Consequently, this species is better considered as a facultative light demanding, a characteristic that may account for its wide distribution in the study area.

The success of fast growing species with high levels of soil nutrients (Huante et al., 1995b) is not evident when plants grow in the shade (Huante et al., 1998). Shelton and Brewbaker (1994) proposed that *L. leucocephala* has a moderate shade tolerance because it can regenerate under its own canopy. Our study shows that in its natural environment, the survival of *L. leucocephala* was higher in low light environments (as shown by the control), and increased under nutrient addition (NP) when light availability was higher. We cannot determine whether such increase in survival in high light environments resulted from a release in nutrient constraints by combined fertilization, or whether the difference in species' response to light between our study and others reflects different environmental conditions (our data were obtained in a native forest, and the other published studies were conducted in silvicultural plantations with more homogeneous environmental conditions), or both. In any case, our results show that, *L. leucocephala* benefits from fertilized habitats, and may regenerate in sites with lower light availability but requires high light conditions and nutrient addition for better survival. These requirements may limit the survival of this species in shaded environments of the young forests.

Species with slower growth rates such as *P. brasiliense* were present only in the old forest, or had the highest recruitment in this forest, such as *B. simaruba*. Fertilization with P increased the recruitment of *B. simaruba* but reduced its survival. This response may be caused by "compensatory mortality" when there is a large recruitment (the correlation between individuals recruited and death was very high, $R^2 = 91.8\%$, $P < 0.0001$). As in the present case, some

studies have reported dependence between seedling performance and seedling density (Condit et al., 1992; Webb and Peart, 1999). High mortality affected the success of *B. simaruba* in the old forest. Low light availability favored its recruitment and survival. These results agree with Ray and Brown (1995) and Birdsall et al. (2000), who showed that *B. simaruba* colonize young forests in all environments but seems to be limited by high light exposure. Thus, it appears that survival and recruitment of *B. simaruba* requires environments with low light, and benefited by P fertilization.

Several studies have documented that slow growing tree species are more common on P deficient soils and have a low P dependency (Ashton and Hall, 1992; Huante et al., 1995b). In the case of *P. brasiliense*, which was recruited only in the old forest, the addition of P increased its recruitment and reduced its survival, producing a negative final seedling density. The low survival of *P. brasiliense* after P addition suggests, as in the case of *B. simaruba*, a density-dependence phenomenon (the correlation between number of individuals recruited and mortality was $R^2 = 99.8\%$, $P < 0.0001$). In our study, *P. brasiliense* occurred only on low light environments of the old forest and was absent in the young forest where it would receive more light, suggesting that it may be shade-tolerant as the some other late successional and slow growing species (Whitmore, 1975; Denslow, 1980; Givnish, 1988; Bazzaz, 1991).

4.2. Canonical correspondence analysis

The floristic gradient resulting from the CCA showed that only a subset of species displayed differences in recruitment among treatments. Species without significant differences among them may respond to other factors not evaluated in this study. It has been suggested that light is less important for species differentiation in TDF than in tropical rain forests (Murphy and Lugo, 1986; Swaine et al., 1990). However, in our young forest site, the most important variables influencing species recruitment were bulk density in the topsoil, fertilization with P and/or N, and light. In the old forest, all environmental variables except light percentage were significant. It is possible that the absence of gaps in the old forest, during the time of this study, produced a low heterogeneity in the light environment, which may have caused a lack of recruitment differences among species.

Tropical dry forests are ecosystems with water limitation for plant function. The woody species in these forests normally have different strategies dealing with water economy, which influence their distribution (Olivares and Medina, 1992; Swaine, 1996). The species' distribution in TDF has been associated with variations in the ground water regime based on measurements of soil depth (Jha and Singh, 1990; Oliveira-Filho et al., 1998). Our data indicate that bulk density in the topsoil was a highly important variable for understanding species distribution in both forest ages. However, the young forest had fewer species associated with high bulk density in the topsoil than the old forest. These differences between forests were possibly due to the lower variation in bulk density in the topsoil and hence in water content in the young forest than in the old forest.

The TDF has a characteristic seasonal pattern of rain, causing periods of leaf production and shedding, which causes changes in light availability at the soil surface. Seed dispersal generally occurs during the dry season (Bullock and Solis-Magallanes, 1990), and the seeds remain in seed banks until the rainy season when environmental conditions are more favorable for regeneration. Thus, at least the first stages of regeneration occur during the period of tree leaf production and hence during changes in light conditions (Huante et al., 1998). In this sense, light-related factors may have strong effects on species differentiation. In the young forest, we can identify two groups: (i) strict light-demanding species, such as *N. choriophylla*, *C. glabellus* and *C. alba*, which were found only at high and intermediate light levels; (ii) understory specialist species such as *T. paucidentata* and *D. verae-crucis*, associated with sites that have low light. Also, at least for some species (*A. gaumeri*, *L. leucocephala*, *B. simaruba* and *P. brasiliense*), light availability was very important for seedling survival.

Previous studies with tropical deciduous woody species have documented a positive response to P fertilization in early successional species and a lower (or null) response to P fertilization in late successional species (Huante et al., 1995b). Also, a nutrient cycling study for a mature TDF of Mexico reported P accumulation at the ecosystem level and did not find evidence of P limitation for forest function (Campo et al., 2001). However, results of this study showed positive responses to P fertilization of the dominant

species in both young and old forests, which may be related to a P limitation on these forest soils. The P dependence of seedlings in the young and in the old forest indicates strongly that this nutrient is a key limiting factor for the regeneration phase of the secondary TDF in Yucatán.

Our study on the consequences of the spatio-temporal variation in nutrient supply, soils and light environments in Yucatán Peninsula, allows us to conclude that the dynamic of understory vegetation in Yucatán Peninsula is strongly influenced by the nutrient availability, especially P. The responses of seedling dominant species to nutrient addition will vary, depending on the details of the site's light availability and soil bulk density, and the identity of species. Given the potential practical application for tropical forest regeneration, the topic of the present study warrants future researches.

The appendices with the information on changes in the density of seedling species (individuals per 4 m²) with relative abundance >4%, between August 1998 and May 2000 after N, P, and NP fertilizations in the young and the old secondary TDF of Yucatán, Mexico, can be found in the following web-page: <http://scifunam.fisica.unam.mx/mir/el/appendix.pdf>.

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