



Tree seedling dynamics in two abandoned tropical dry forests of differing successional status in Yucatán, Mexico: a field experiment with N and P fertilization

Eliane Ceccon^{1,3,*}, Salvador Sánchez² and Julio Campo¹

¹*Instituto de Ecología, AP 70-275 Ciudad Universitaria, UNAM 04510 Mexico, D.F;* ²*Instituto Politécnico Nacional. Prolongación Carpio y Plan Ayala, Col. Santo Tomás, 11340, Mexico, DF;* ³*Current address: Centro Regional de Investigaciones Multidisciplinarias. Av. Universidad s/n, Circuito 2 Colonia Chamilpa, Cuernavaca, 62210, Morelos, Mexico;* **Author for correspondence (e-mail: ececccon@miranda.ecologia.unam.mx)*

Received 9 October 2002; accepted in revised form 13 June 2003

Key words: Forest recovery, Nutrient limitation, Recruitment, Secondary tropical forests, Survival, Tree seedlings

Abstract

The effects of nitrogen (N) and phosphorus (P) fertilization on seedling survival, recruitment, species richness and diversity in two abandoned tropical dry forests (10-yr old, young forest, and *c.* 60-yr old, old forest) in Yucatán, Mexico, were studied over two years. The seedling dynamics in the control plots were found to be highly seasonal with highest recruitment and lowest death rates during the rainy season. A low percentage of seedlings were resprouts; this important mechanism for forest regeneration had a higher-than-expected survival when compared to seedlings regenerated from seeds. Nutrient addition had significant effects on seedling dynamics in both of the forest regeneration stages. In the young forest, N fertilization facilitated the increase of seedling density. In the old forest, the addition of P decreased seedling diversity, while it increased the recruitment of only a few species. In both forests, P fertilization increased the survival time of seedlings when interacting with light availability and bulk density on the topsoil layer. Results suggest that low nutrient availability combined with low light availability constrain forest succession in Yucatán, Mexico.

Introduction

Tropical dry forests (TDF) cover large areas in Africa, Australia, Central and South America, India and South-East Asia. They occupy *c.* 42% of the forested area of the tropics and have the highest rural human population density (Murphy and Lugo 1986). Dry forests are among the most exploited and endangered ecosystems of the world (Gerhardt 1993). In Central America, only 2% of the original area of TDF has remained in a more or less intact state and less than 0.1% has been protected under some kind of conser-

vation category (Janzen 1988). Compared to other tropical forest types, the status of TDF is critical.

In the Yucatán Peninsula, the Mayans have practiced slash-and-burn agriculture for over 2000 years (Gómez-Pompa et al. 1987), and thus the present TDF are almost entirely of secondary origin. Although slash-and-burn agriculture results in an increase in soil nutrient availability in the TDF (Giardina et al. 2000), the conversion of this forest into agro-ecosystems reduces soil fertility in the long term (Maass 1995). In addition, the important role that tropical secondary forests play in the conservation and maintenance of biodiversity and the factors influencing the

early success of colonization of trees after widespread human disturbance, have been largely unexplored (Janzen and Vázquez-Yanes 1991). Ceccon et al. (2002) have reported that tree species richness and stem density in both the adult and the seedling community components of the secondary forest in this area were correlated with nutrient availability, and suggested that mineral elements could be a key factor during forest regeneration. Also, the recruitment processes in TDFs are poorly known which constitutes a serious gap in our understanding of forest recovery processes (Campbell et al. 1990; Miller and Kauffman 1998). Knowledge of understory dynamics of secondary forests is not only important for our understanding of the community processes, but is also required for increasing the success and efficiency of restoration practices.

In the present study we fertilized the soil with nitrogen and phosphorus in order to test whether the seedling dynamics (recruitment and mortality rates) in secondary forests of Yucatán are affected by their supply. The original hypothesis was that, if natural supplies of N and/or P limit forest regeneration at the seedling level, then fertilizing the soil should result in an increased nutrient uptake by seedlings which would cause higher seedling survival and recruitment. This would be reflected in higher species richness and/or seedling density in fertilized plots. We also addressed a number of important questions about natural dynamics of seedlings, such as: (i) what are the effects of seasonality upon seedling germination and survival in different regeneration stages?; (ii) how does the regeneration-time affect the probability of tree recruitment?; and (iii) what is the role of seedling sprouting on forest regeneration?

Methods

Study area

The study site is located in the northwest region of the Yucatán Peninsula (21°06' N and 89°17', Dzibilchaltún National Park). The climate is hot and sub-humid. The mean annual temperature is 25.8 °C with less than 6 °C variation during the year. Total annual rainfall is 986 mm with summer seasonal rainfall (Trejo-Vázquez 1999). The topography consists of flat areas (with altitudes < 10 m). The bedrock under these forest sites is limestone (lithic rendolls), encompassing numerous areas with exposed rocks. Soils

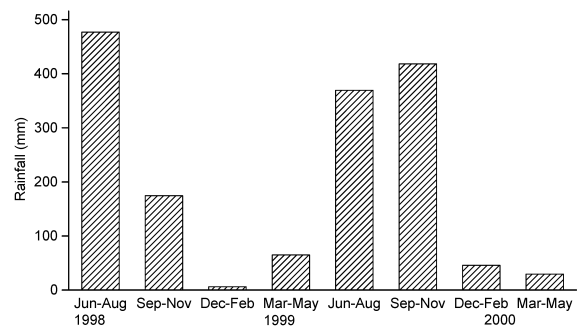


Figure 1. Accumulated rainfall in 3-mo periods prior to each seedling census in the 2-yr field fertilization experiment in Yucatán, Mexico.

are mainly shallow (< 10 cm in depth), organic rich (organic matter content > 20%), and with pH values that vary between 7.3 and 7.4 (J. Campo, unpubl. data). The predominant vegetation in the area is tropical deciduous forest with mean canopy height of 6 to 8 m (Miranda 1958). During the dry season, which extends from December to May (Figure 1) virtually all trees and shrubs lose their leaves (J. Campo, unpubl. data).

Experimental design

In 1997, sixteen 12-m×12-m plots with 8-m buffer zones between them were established at two sites within a secondary tropical dry forest. Both sites are 2 km apart and were previously used for slash-and-burn agriculture with henequén (*Agave fourcroydes* Lem.) plantations and were abandoned at different times. One site was abandoned c. 60 yr ago (old forest; Lundell 1934) and the other was abandoned 10 yr ago (young forest). Total soil nitrogen is similar between the forests (1.30% and 1.34%, for young and old forests, respectively) while the total phosphorus content is 0.22% in the young forest and 0.34% in its older counterpart (Ceccon et al. 2002). Tree density in old forest and young forests was 4015 ± 321 stem ha^{-1} and 4358 ± 282 stem ha^{-1} (mean \pm 1 S.E.), respectively (Ceccon et al. 2002).

The four treatments were control, added nitrogen (N), added phosphorus (P), added nitrogen and phosphorus (NP). Four replicates of each were allocated randomly in 16 plots at each site. In the 28 mo of the study (May-1998 to September-2000), fertilizers were added twice per year to give total N additions of 220 $kg\ ha^{-1}\ yr^{-1}$ and P additions of 75 $kg\ ha^{-1}\ yr^{-1}$. This scheme was chosen because of the strong effect of the

seasonality of rainfall on forest phenology (Holbrook et al. 1995) and nutrient availability (Singh et al. 1989; Campo et al. 1998) in TDF ecosystems. Dry fertilizers (urea and/or triple superphosphate) were applied manually as appropriate to each 12-m x 12-m plot at the end of the dry season (May) and in the middle of the rainy season (September) of each year.

Measurements

Assessment of seedling dynamics

In the central 6 m² of each plot, four subplots (1 m² each) were randomly established in which seedlings with a stem height \leq 1 m were identified, tagged and recorded; a series of 64 permanent sub-plots were used in each of the two forest sites. The seedling census was initiated in May (1998) and continued for a period of 27 mo. The effect of treatments on the final species richness, number of individuals and diversity, seedling survival and the total number of newly recruited individuals was assessed through censuses every 3 mo. Seedling species identity and origin (seed or sprout) were recorded by the observation method.

Light conditions

Light availability was measured by hemispherical photographs in September 2000. At each site, fish-eye (hemispherical) photographs (using a Minolta 7.5-mm lens) were taken two times over each subplot. The photographs were taken at heights of *c.* 1.0 m above the ground. The negatives were digitized using a computerized image analysis system, with a resolution of 512×512 pixels (CANOPY-SOLARCALC 4.0). A threshold gray level was determined for each negative to distinguish between visible sky and foliage. The same person took the photographs in order to minimize observer error. Analyses of the digitized images involved calculating the penetration of both diffuse and direct-beam radiation through the small but discrete openings visible between leaves. For the calculations, solar positions were determined at 2-min intervals for each day of the year using standard equations for solar geometry. This method limited the analysis to light quantity; it did not cater for light quality. The forest canopy effects on spectral quality of understorey light are fairly well known (e. g. Smith 1982). Only the annual averages of direct-beam radiation were used. Light percentage was used as a covariable to seedling recruitment and species survival.

Bulk density on the topsoil layer

To characterize indirectly the general availability of nutrients and water for plants (Jha and Singh 1990; Oliveira-Filho et al. 1998) soil bulk density in the topsoil layer was measured instead of the soil depth because the soils were mainly shallow (< 10 cm in depth). For the analysis of bulk density, 10-cm×10-cm×10-cm soil cubes from the upper profile were excavated (Elliot et al. 1999). A total of 32 samples of soil were randomly collected in each 12-m×12-m plot. All soil collected was sieved through a 2-mm mesh, and coarse roots and rock materials were removed. The remaining fraction of the soil was saved and oven-dried at 105 °C.

Data analysis

To test the effects of different fertilization treatments over 2 yr on the structure of the seedling community, final diversity (evaluated by Shannon's diversity index), final total number of individuals and final species richness per plot were analyzed by means of a two-way covariance analysis, separately for the two sites (i.e. young and old forests). For these analyses, N and P were regarded as factors and the initial values of diversity, total seedling density and species richness as covariates. The response variables (e.g., final seedling diversity, density and species richness) were logarithmically transformed in order to meet the assumptions of the normality. To test the effect of fertilization on recruitment, two-way (General Linear Model, GLM) covariance analysis was also used. Nitrogen and P fertilization were factors and light percentage, bulk density on the topsoil layer and initial values of seedling density were used as covariates. The response variables were again logarithmically transformed. Significance for the tests was determined at the 5 % level. The program used was STATISTICA (version 5.0).

To evaluate the effects of fertilization treatments over 2 yr on the survival of newly recruited tree seedlings, a Generalized Linear Model was fitted separately for each site. In this model, survival (in days) of each individual 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 fertilization. Seedlings that survived or died up to the 720th day were recorded and coded as dummy variables. Seedling origin (from seed or sprout) was coded as a dummy variable, light percentage in each subplot, and bulk

Table 1. Seedling diversity, species richness and number of individuals per 4 m², in the young and the old secondary forests of Yucatán, Mexico, after 2 yr of a field fertilization experiment. Fertilization treatments were N, nitrogen; P, phosphorus; NP, nitrogen plus phosphorus, and control (without fertilization). The data show the average of the four plots and standard errors are given in parentheses.

Parameter	Young forest			Old forest	
	Treatment	May 1998	May 2000	May 1998	May 2000
Diversity (H')					
	Control	0.782 (0.152)	0.802 (0.108)	1.043 (0.074)	1.093 (0.176)
	N	0.696 (0.252)	0.624 (0.246)	0.804 (0.040)	0.813 (0.144)
	P	0.896 (0.174)	0.884 (0.055)	0.936 (0.105)	0.709 (0.123)
	NP	0.742 (0.189)	0.867 (0.208)	0.953 (0.082)	0.759 (0.219)
Species richness					
	Control	9.00 (1.25)	9.75 (0.99)	5.52 (2.92)	8.00 (1.7)
	N	7.75 (1.79)	7.25 (1.19)	4.50 (1.8)	0.25 (3.9)
	P	10.25 (1.72)	10.51 (1.80)	5.51 (2.13)	8.75 (1.96)
	NP	10.75 (2.23)	11.50 (3.07)	4.75 (1.44)	9.00 (3.13)
Number of individuals					
	Control	10.75 (6.71)	30.75 (17.84)	18.25 (2.76)	12.02 (4.27)
	N	7.00 (2.71)	35.22 (6.45)	21.00 (13.19)	25.53 (19.47)
	P	8.75 (4.58)	24.00 (11.5)	30.5 (7.68)	48.01 (8.73)
	NP	9.00 (3.16)	22.25 (3.41)	26.25 (8.41)	38.25 (17.62)

density on the topsoil layer (g m⁻²) in each plot were recorded as covariates. The Weibull model's fitted parameters were then used to estimate the mean survival time (days) of seedlings in each treatment. To test the significance of each parameter in the model, a *t*-test according to Crawley (1993) was used. The program used was GLIM (version 4.0).

Results

Seedling community in control plots

Fifty species of seedlings were recorded in the young forest site and 48 species in the old forest. In each site the area sampled was 2304 m². The species with the highest recruitment rates over the 2-yr period in control plots were *Acacia gaumeri* and *Pisonia aculeata* in the young forest, and *Bursera simaruba* and *Phyllostylon brasiliense* in the old forest (Appendices 1 and 2).

Numbers of individuals at the end of the study were 30.7 ± 17.8 and 12.0 ± 4.3 stems per 4 m² for the young and old forests respectively. Species richness per 4 m² was 9.8 ± 1.0 for the young forest and 8.0 ± 1.7 for the old forest. Diversity per 4 m² was 0.8 ± 0.1 and 1.1 ± 0.2 for young and old forests, respectively. In both forest sites, the number of individuals, species richness and diversity (16 m²) did not change over 2 yr (Table 1).

Seedling recruitment and mortality in control plots

Over the 2 yr of the study, a total of 15.3 and 11.1 seedlings m⁻² were recorded as newly recruited for the young and the old forests, respectively. Annual rainfall for 1998, 1999 and 2000 was 789, 898 and 537 mm respectively, most of which fell between June and October (J. Espinosa, pers. comm.; Figure 1). Recruitment was highly seasonal and increased progressively during the rainy season, reaching a peak during August-November in both forests (Figure 2a). Although c. 35% of species showed an ability to regenerate by sprouting, most species regenerated from seed; 80 and 86% in the young and old forests, respectively.

Total percentage mortality of the recruited seedlings (excluding those present at the beginning of the study) after 24 mo, were 63% and 54%, for the young and old forests, respectively. During the 2-yr period, seedling mortality was lowest during the first half of the rainy season (i.e., from June to August; Figure 1, Figure 2b).

Effects of fertilization on seedling recruitment

In the young forest, there were no noticeable effects of the nutrient additions on the recruitment over 2 yr. However, in the old forest the addition of P increased the seedling recruitment compared to the control (*P* < 0.05, Figure 3). Light availability, bulk density on

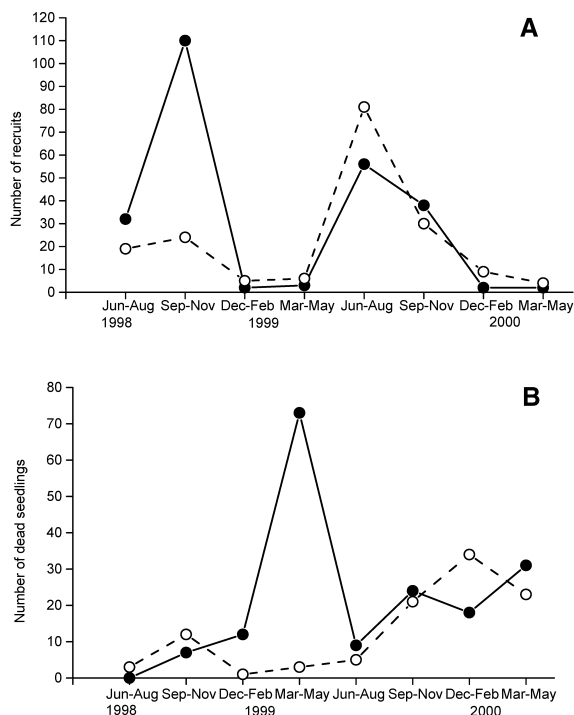


Figure 2. Dynamic of seedlings in the control plots in a young (dashed line, open curves) and an old (solid line, closed curves) secondary forests in the 2-yr fertilization experiment in Yucatán, Mexico: (a) number of recruits, (b) number of deaths, between censuses.

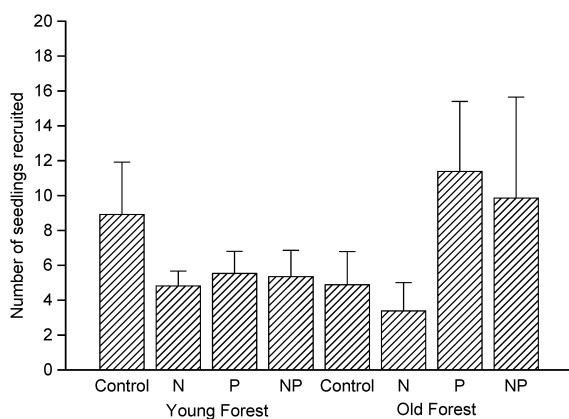


Figure 3. Number of seedlings recruited after 2 yr in control plots and plots fertilized with nitrogen (N), phosphorus (P) or nitrogen plus phosphorus (NP) in a young and an old secondary forest of Yucatán, Mexico.

the topsoil layer and initial individual number had no significant effect on recruitment either alone or through interaction ($P > 0.05$).

Effects of fertilization on diversity, number of individuals and species richness

In the young forest, the addition of N increased the final number of individuals with respect to the initial number (Table 1, Table 2). However, this treatment had no effect on seedling species richness and diversity. In the old forest, the addition of P reduced the seedling diversity, but did not change significantly the number of individuals or the richness of species (Table 1). The initial diversity was the only covariate that had statistical significance; it showed an interaction with P (Table 2). During the study period species richness tended to increase in all treatments in the old forest; however, in its younger counterpart it tended to decrease or did not change at all.

Effects of fertilization on seedling survival

Significant differences among treatments were observed in the survival times of seedlings in both forests (Figure 4a, Figure 4b). The addition of P increased seedling survival. Although the survival time of seedlings in control plots did not show any differences between forests, the response of seedlings to P addition seems greater in the young than in the old forest. Estimated sprout survival was 3 and 10 times ($\leq 6\%$ of light level) higher than survival from seeds (i.e., 1315 and 408 days, respectively, in the control plots of the young forest; 3615 and 353 days, respectively, for those in the old forest). However, the percentage of total recruited individuals regenerated by sprouting was low in both forests (12.2 and 12.7% for the young and the old forests, respectively).

Seedling survival was significantly affected by fertilization, light percentage and bulk density on the top soil layer (Table 3, Table 4). In the young forest, significant interactions were found between P fertilization with N fertilization, light availability and soil bulk density. Nitrogen fertilization had a significant effect but only without interaction with other environmental variables. Also, in the old forest significant interactions between P fertilization with light availability and soil bulk density were observed. In this forest, the survival of sprouts was affected by N addition and percentage light; the old forest was significantly less illuminated than the young forest ($t = 2.86$, $df = 124$, $P < 0.05$).

Table 2. Analysis of covariance (GLM) of final number of seedlings in a young forest and final diversity of seedlings in an old forest, after 2 yr field fertilization experiment in Yucatán, Mexico; N, nitrogen; P, phosphorus. The initial number of seedlings and the initial diversity of seedlings were used as covariates for the young and old forests, respectively.

Source	df	Final number of seedlings (Young forest)		Final diversity of seedlings (Old forest)	
		F	P	F	P
Covariate	1	11.0	< 0.05	0.116	n.s.
N	1	10.5	< 0.05	0.082	n.s.
P	1	0.383	n.s.	12.1	< 0.01
N.P	1	0.363	n.s.	1.138	n.s.
N. Covariate	1	15.2	< 0.01	0.395	n.s.
P. Covariate	1	0.180	n.s.	11.1	< 0.01
P. N. Covariate	1	0.405	n.s.	1.207	n.s.
Error	8				

n.s., non-significant ($P > 0.05$)

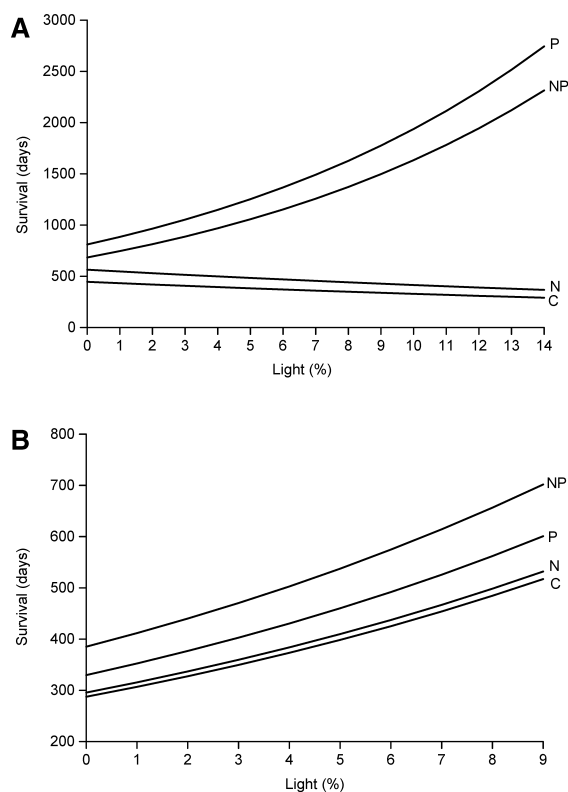


Figure 4. Seedling survival (as fitted curves) after 2 yr in control plots and plots fertilized with nitrogen (N), phosphorus (P) or nitrogen plus phosphorus (NP) as a response to percentage light in (a) young and (b) old secondary forest of Yucatán, Mexico.

Discussion

Seedling regeneration

The number of newly recruited seedlings recorded in this study (15 and 11 seedlings m^{-2} for the young and the old forests, respectively) in a 2-yr period, was similar to that reported in a primary TDF in Ghana for a similar period of study time (13 to 19 seedlings m^{-2} ; Lieberman and Li 1992). The dynamic of seedlings in Yucatán forests was highly seasonal. Germination reached a peak in the middle of the rainy season, while mortality was the lowest in this period. A similar seasonality in the mortality patterns has been reported for seedlings of undisturbed TDF (Lieberman and Lieberman 1984; Lieberman et al. 1990; Lieberman and Li 1992). These germination and mortality patterns indicate that the favorable growth period in the dry tropics is restricted to the short rainy season. The mortality rate in the Yucatán secondary forests was similar to those reported for mature TDF in other sites (e.g. > 60% in Costa Rica, by Lieberman et al. 1990; 62% in Ghana, by Swaine et al. 1990). These results suggest that seedling dynamics in TDF may be more sensitive to seasonality than successional status.

Studies on adult trees indicate that species with the ability to regenerate either by root suckers or basal sprouts tend to dominate TDF ecosystems (Swaine et al. 1990; Rico-Gray and García-Franco 1992; Miller and Kauffman 1998). Although studies on tree seedlings indicate that a high number of species show sprouting capacity, in the TDFs of Yucatán seeders are more abundant than sprouters in the understorey community (Mizrahi et al. 1997; Ceccon et al. 2002).

Table 3. Parameters of seedling survival, regenerating by sprouts or by seeds, in a 2-yr field fertilization experiment in a young secondary forest of Yucatán, Mexico (Weibull shape parameter $\alpha = 1.1652$, $df = 802$): N, nitrogen; P, phosphorus.

Parameter	Estimate	S.E.	t test	P
Constant	- 8.479	0.330		
N	- 0.272	0.141	1.93	< 0.05
P	- 0.696	0.503	1.30	n.s.
Sprout	1.364	0.214	6.39	< 0.0001
Light	3.568	2.896	1.23	n.s.
Bulk density of top soil	0.006	0.031	0.16	n.s.
N.P	0.471	0.207	2.27	< 0.05
P.Light	13.72	7.72	1.77	< 0.05
P.Bulk density of top soil	0.114	0.059	1.93	< 0.05

n.s., non-significant ($P > 0.05$)

Table 4. Parameters of seedling survival regenerating by sprouts or by seeds, in a 2-yr field fertilization experiment in an old secondary forest of Yucatán, Mexico (Weibull shape parameter $\alpha = 1.2808$, $df = 972$): N, nitrogen; P, phosphorus.

Parameter	Estimate	S.E.	t test	P
Constant	- 8.603	0.477		
N	1.181	0.344	3.42	< 0.001
P	- 0.176	0.221	0.79	n.s.
Sprout	1.388	0.318	4.36	< 0.0001
Light	- 50.00	18.16	2.75	< 0.01
Bulk density of top soil	- 0.036	0.034	1.04	n.s.
N.Sprout	- 1.217	0.357	3.55	< 0.001
Sprout.Light	41.33	15.72	2.63	< 0.01
Light.Bulk density of top soil	0.310	1.079	0.29	n.s.
P.Light.Bulk density of top soil	4.931	1.712	2.88	< 0.01

n.s., non-significant ($P > 0.05$)

Our results indicated that the estimated survival time of seedlings regenerated by sprouts is much higher than those regenerated from seeds in Yucatán secondary forests. Sprouting seems to be advantageous to many species including those that regenerate frequently by seeds, presumably because vegetative shoots may take advantage of the extensive root system and the substantial storage of metabolites in the remaining parts of the parent plant (Negrelle 1995). The below-ground carbohydrate storage could improve survival at the expense of growth (Kobe 1997). In this sense, data of secondary forests in Yucatán suggest that sprouts dominate in the disturbed TDF due to their high survivorship during the seedling phase rather than due to a high frequency in the understorey community.

Effects of fertilization

The number of individuals increased with N addition at the end of the study in the younger site. It is possible that urea fertilization stimulated the germination

in this site. In general, chemical factors that stimulate germination are also beneficial for survival and seedling growth (Karsen and Hilhorst 1992).

In both forests studied, fertilizers applied in two growing seasons did not change species richness. However, we found a negative effect of P addition on species diversity in the old forest. This reduction in the species diversity was not a result of a loss of species, but of an increase in dominance by a few species (*Bursera simaruba* and *Phyllostylon brasiliense*) after an increase of P supply. Both species (i.e. *B. simaruba* and *P. brasiliense*) represented 81% and 68%, respectively, of total number of seedlings recorded in the P fertilized plots of the old forest at the end of the study. Additionally, the significant response to P fertilization in recruitment rate in the old forest was mainly due to the high number of *B. simaruba* and *P. brasiliense* seedlings. On the other hand, these species showed a high mortality rate, suggesting the existence of a density-dependence process in their population (Ceccon et al. 2003), and therefore, they did not significantly influence the increase of the

final number of individuals. Greenhouse experiments indicate that seedling responses to nutrient addition in TDF species are sensitive to light availability (Huante et al. 1998). Also, previous studies in these sites in Yucatán, indicated that the higher light availability in the young forest compared to the old forest, caused a large number of species to increase their abundance in response to changes in the nutrient level, in the early regeneration stage (Ceccon et al. 2003).

A recent review of the effects of soil nutrients in TDF suggests that N and P application increased the growth of seedlings of woody species (Khurana and Singh 2001). However, there are no references available about the effects of fertilization on seedling survival time. In our study, P addition over two growing seasons led to increased seedling survival time in both secondary forests. Additionally, we found a positive interaction between P supply and bulk density in the topsoil layer on seedling survival in both forests. This suggests that higher levels of light and a greater amount of soil may be enhancing the seedling responses to nutrient inputs.

In conclusion, the results of this study support the hypothesis that P supply limits forest recovery in disturbed TDF in Yucatán on limestone soils. This is in agreement with the general view of Vitousek (1984), that P limits tree growth in many tropical forests. Other factors such as light and soil potentially limit the regeneration of TDF as well. Our study did not directly address the physiological basis for the change in seedling dynamics; but identified which nutrients are limiting to forest recovery. These observations should be useful to restoration managers.

The appendices about the recruitment of seedling species (≥ 5 individuals) between August 1998 and May 2000 after N, P, and NP fertilizations in the young and old secondary TDF of Yucatán, México, can be found in the following web-page: http://scifunam.fisica.unam.mx/mir/el/append_pe.pdf

Acknowledgements

We are grateful to C. Siebe and T. Valverde for valuable suggestions on earlier drafts of this paper; E. J. F. Tanner, D. M. Newbery and one anonymous referee provided critical reviews on drafts of this paper. We also, wish to thank Guadalupe Chuc Puc and Pastor Gómez Xequé for their field assistance with the field work. We also acknowledge the Instituto Nacional de Antropología e Historia for access to the field

sites and the Centro de Investigación Científica de Yucatán for its support in the fieldwork. E. Ceccon is grateful to CAPES-Brazil for the fellowship and Instituto de Ecología-UNAM for support during the final phase of the study. This research was supported by CONACyT grants (G0011 and 31954).

References

- Campbell B.M., Lynam T. and Hatton J.C. 1990. Small-scale in the recruitment of forest species during succession in tropical dry forest, Mozambique. *Vegetatio* 87: 51–57.
- Campo J., Jaramillo V.J. and Maass J.M. 1998. Pulses of soil phosphorus availability in a Mexican tropical dry forest: effects of seasonality and level of wetting. *Oecologia* 115: 167–172.
- Ceccon E., Olmsted I., Vázquez-Yanes C. and Campo-Alves J. 2002. Vegetation and soil properties in two tropical dry forests of differing regeneration status in Yucatán. *Agrociencia* 36: 621–631.
- Ceccon E., Huante P. and Campo J. 2003. 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. *Forest Ecology & Management* 182: 387–402.
- Crawley M.J. 1993. *GLIM for ecologists*. Blackwell Scientific Publications, London.
- Elliot E.T., Heil J.W., Kelly E.F. and Monger H.C. 1999. Soil structural and other physical properties. In: Robertson G.P., Coleman D.C., Bledsoe C.S. and Sollins P. (eds), *Standard soil methods for long-term ecological research*. Oxford University Press, New York, pp. 74–85.
- Gerhardt K. 1993. Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica. *Journal of Vegetation Science* 4: 95–102.
- Giardina C.P., Sanford R.L., Dockersmith I.C. and Jaramillo V.J. 2000. The effects of slash and burning on ecosystem nutrients during the land preparation phase of shifting cultivation. *Plant & Soil* 220: 247–260.
- Gómez-Pompa A., Flores J.S. and Sosa V. 1987. The 'pet kot': a man-made tropical forest of the Maya. *Interciencia* 12: 10–15.
- Holbrook N.M., Whitbeck J.L. and Mooney H.A. 1995. Drought responses of neotropical dry forest trees. In: Bullock S.H., Mooney H.A. and Medina E. (eds), *Seasonally dry tropical forests*. Cambridge University Press, Cambridge, pp. 243–276.
- Huante P., Rincón E. and Chapin F.S. 1998. Foraging for nutrients, responses to changes in light, and competition in tropical deciduous tree seedlings. *Oecologia* 117: 209–216.
- Janzen D.H. 1988. Tropical dry forests: the most endangered major ecosystem. In: Wilson E.O. (ed.), *Biodiversity*. Academic Press, Washington, pp. 130–137.
- Janzen D.H. and Vázquez-Yanes C. 1991. Aspects of seed ecology of relevance to management of tropical forested wildlands. In: Gómez-Pompa A., Whitmore T.C. and Hadley M. (eds), *Rain forest regeneration and management*. MAB, vol. 6. UNESCO, Paris, pp. 137–154.
- Jha C.S. and Singh J.S. 1990. Composition and dynamics of dry tropical forest in relation to soil texture. *Journal of Vegetation Science* 1: 609–614.

- Karszen C.M. and Hilhorst H.W.M. 1992. Effect of chemical environment on seed germination. In: Fenner M. (ed.), *Seeds: the ecology of regeneration in plant communities*. CAB International, Wallingford, pp. 327–348.
- Kobe R.K. 1997. Carbohydrate allocations to storage as a basis of interspecific variation in sapling survivorship and growth. *Oikos* 80: 226–233.
- Khurana E. and Singh J.S. 2001. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. *Environmental Conservation* 28: 39–52.
- Lieberman D. and Lieberman M. 1984. The causes and consequences of synchronous flushing in a dry tropical forest. *Biotropica* 16: 193–201.
- Lieberman D., Hartshorn G.S., Lieberman M. and Peralta R. 1990. Forest dynamics at La Selva Biological Station, 1969–1985. In: Gentry A.H. (ed.), *Four neotropical rain forests*. Yale University Press, New Haven, pp. 509–521.
- Lieberman D. and Li M. 1992. Seedling recruitment patterns in a tropical dry forest in Ghana. *Journal of Vegetation Science* 3: 375–382.
- Lundell C.L. 1934. Preliminary sketch of the phytogeography of the Yucatan Peninsula. Publication N° 436, Contribution N° 12. Carnegie Institution of Washington, Washington.
- Maass J.M. 1995. Conversion of tropical dry forest to pasture and agriculture. In: Bullock S.H., Mooney H.A. and Medina E. (eds), *Seasonally dry tropical forests*. Cambridge University Press, Cambridge, pp. 399–422.
- Miller P.M. and Kauffman J.B. 1998. Seedling and sprout response to slash-and-burn agriculture in a tropical deciduous forest. *Biotropica* 30: 538–546.
- Miranda F. 1958. Estudios de la vegetación. In: Beltran E. (ed.), *Los recursos naturales del sureste y su aprovechamiento*, Part 2. Instituto Mexicano de Recursos Naturales Renovables, Mexico, pp. 215–271.
- Mizrahi A.P., Ramos J.M.P. and Jimenez-Osornio J.J. 1997. Composition, structure and management potential of secondary dry tropical vegetation in two abandoned henequen plantations of Yucatan, Mexico. *Forest Ecology & Management* 94: 79–88.
- Murphy P.G. and Lugo A.E. 1986. Ecology of tropical dry forest. *Annual Review of Ecology Systematics* 17: 67–88.
- Negrelle R. 1995. Sprouting after uprooting of canopy trees in the Atlantic rain forest of Brazil. *Biotropica* 27: 448–454.
- Oliveira-Filho A.T., Curi N., Vilela E.A. and Carvalho D.A. 1998. Effects of canopy gaps, topography, and soils on the distribution of woody species in a Central Brazilian deciduous dry forest. *Biotropica* 30: 362–375.
- Rico-Gray V. and García-Franco J. 1992. The maya and the vegetation of the Yucatan Peninsula. *Journal of Ethnobiology* 11: 135–142.
- Singh J.S., Raghubashi A.S., Singh R.S. and Srivastava S.C. 1989. Microbial biomass acts as a source of plant nutrients in dry tropical forest and savanna. *Nature* 338: 499–500.
- Smith H. 1982. Light quality, photoperception, and plant strategy. *Annual Review of Plant Physiology* 33: 481–518.
- Swaine M.D., Lieberman D. and Hall J.B. 1990. Structure and dynamics of a tropical dry forest in Ghana. *Vegetatio* 88: 31–51.
- Trejo-Vázquez I. 1999. El clima de la selva baja caducifolia en México. *Investigaciones Geográficas* 39: 40–52.
- Vitousek P.M. 1984. Litterfall, nutrient cycling and nutrient limitation in tropical forests. *Ecology* 65: 285–298.