

# Survival and growth of dominant tree seedlings in seasonally tropical dry forests of Yucatan: site and fertilization effects

Luis Salinas-Peba<sup>1</sup>, Víctor Parra-Tabla<sup>1,\*</sup>, Julio Campo<sup>2</sup> and Miguel A. Munguía-Rosas<sup>3</sup>

<sup>1</sup> Departamento de Ecología Tropical, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Km. 15.5 Carretera Mérida-Xmatkuil, Yucatán 97000, México.

<sup>2</sup> Instituto de Ecología, Universidad Nacional Autónoma de México, A.p. 70–275, México D.F. 04510, México.

<sup>3</sup> Departamento de Ecología Humana, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (CINVESTAV), Km. 6 Antigua carretera a Progreso, Mérida 97310, México.

\*Correspondence address. Departamento de Ecología Tropical, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Km. 15.5 Carretera Mérida-Xmatkuil, Yucatán 97000, México. Tel: +999-942-32-06; Fax: +999-942-32-05; E-mail: [ptabla@uady.mx](mailto:ptabla@uady.mx)

## Abstract

### Aims

Seasonally tropical dry forests of the Yucatan Peninsula are typically found in sites with nutrient-poor soils because of the recent geological origin of the region. The landscape is dominated by extensive karstic plates that shape environments where vegetation regeneration through seed germination may be limited by the availability of suitable microsites. In this study, we documented the survival and growth of seedlings from three dominant tree species (*Bursera simaruba*, *Piscidia piscipula* and *Lysiloma latisiliquum*) in seasonally tropical dry forests in Yucatan. Specifically, we evaluated the effect of nutrient addition (N and P, separately and in combination) on seedling survival and growth across three sites with differing levels of precipitation.

### Methods

We conducted a nutrient addition experiment, whereby we established 12 plots of dimensions 10 × 10 m (100 m<sup>2</sup>) at each site, from which three plots were randomly selected to receive one of four treatments: N addition, P addition, N and P addition and no nutrient addition (controls). Prior to treatment application, in each plot,

we planted 10 seedlings of each species in October 2010 and subsequently conducted surveys of plant growth and survival every 20 days from November 2010 to April 2011.

### Important Findings

Overall, nutrient addition increased seedling survival and the magnitude of this effect was similar among sites. We did not observe an additive effect of the N + P treatment on survival. Similarly, we observed a positive effect of nutrient addition on seedling growth, but this effect was contingent upon site; regarding survival, the effects of N and P on seedling growth were not additive. These results suggest that seedling recruitment and growth in the three dominant species of trees in Yucatan are limited by nutrient availability but that the magnitude of this effect, particularly on seedling growth, is specific for species and site.

**Keywords:** growth, nitrogen, nutrient addition, phosphorus, seedling, survival, seasonally tropical dry forest

Received: 26 April 2013, Revised: 9 September 2013,

Accepted: 15 September 2013

## INTRODUCTION

Access to suitable sites for seed germination is a key factor shaping seed germination and seedling establishment (Bullock 1995; Schupp 1995). In tropical trees of seasonally dry forests (STDFs), multiple factors limit their seedling survival and establishment. For example, it has been shown that

water availability (Slot and Poorter 2007; Turner 1990), soil fertility (Ibañez and Schupp 2002; Murphy and Lugo 1986), vegetation canopy coverage and light availability (Callaway 1995; Poorter 2009; Rincón and Huante 1993) and herbivory (Gerhardt 1998; Howlett and Davidson, 2003) are all key factors influencing seedling survival and growth. In particular, soil nutrient availability may have a strong influence on

seedling establishment and survival in STDFs (Murphy and Lugo 1986; Vitousek 1984; Wright 1992). Soil nutrient availability is also influenced by water availability (Reich and Borchert, 1984) because low soil humidity constrains soil microbial activity (Singh *et al.* 1989), nutrient cycling dynamics (Ibañez and Schupp 2002) and, ultimately, nutrient availability (Murphy and Lugo 1986; Reich and Borchert 1984). For example, Reed *et al.* (2007) found that the rates of nutrient uptake by tropical plants are partially controlled by the availability of water during the rainy season.

STDFs are characterized by a marked seasonality in rainfall, where a dry season and a rainy season are clearly delimited (Bullock 1995; Murphy and Lugo 1986). Understanding how soil nutrient availability and its relationship with water availability influence patterns of vegetation regeneration in STDFs is of fundamental importance, given that these ecosystems are frequently found in nutrient-poor areas (Ceccon *et al.* 2006; Murphy and Lugo 1986; Vitousek 1984; Wright 1992).

STDFs of the Yucatan Peninsula are frequently found in soil-nutrient-poor areas because of the region's recent geological origin, where karstic substrate dominates the landscape (Bautista *et al.* 2011). As a result, exposed calcareous rock formations are evident throughout the region and there is a limited availability of microsites with nonshallow soils (depth < 20 cm; Duch 1988). In addition, these forests have been managed and used for centuries by Mayan communities and more recently by logging and agricultural activities, contributing to both a decrease in soil nutrient availability and modified patterns of vegetation regeneration (González-Iturbe *et al.* 2002; Kleinman *et al.* 1995; Wright 1992).

Another characteristic of STDFs in Yucatan is that they are found along a north–south gradient of increasing precipitation, with mean annual rainfall spanning from 600 mm near the coast to 1000 mm in the southern end of the state (García 1988). This precipitation gradient probably shapes the availability of soil nutrients (Roa-Fuentes *et al.* 2012) and, in turn, patterns of seedling survival and vegetation regeneration. Throughout the region, we observe several dominant species of deciduous tree species. However, we ignore the extent to which nutrient limitation varies along this gradient and whether it differentially shapes survival and growth of these tree species. Therefore, the present work has as its main goal evaluation of the effect of nutrient availability on the survival and growth of three dominant tree species of STDFs found along a precipitation gradient in Yucatan, Southeast Mexico. The study species were *Bursera simaruba*, *Piscidia piscipula* and *Lysiloma latisiliquum*, which are reported as dominant tree species in STDFs in Yucatan (González-Iturbe *et al.* 2002; Mizrahi *et al.* 1997) as they have a broad distribution within the region, are abundant and thus represent a large fraction of the seed bank in these communities (Marín 1997). In conducting a nutrient addition experiment, we sought to answer the following questions: (i) Does nutrient addition influence the survival and growth of seedlings? and (ii) Are seedling growth and survival responses to fertilization species and site specific?

## MATERIALS AND METHODS

### Study site

This study was conducted at three sites located along a precipitation gradient in Yucatan, Southeast Mexico. STDFs at these sites were previously managed and logged but have remained abandoned for a period >25 years (González-Iturbe *et al.* 2002; Mizrahi *et al.* 1997). Two of the sites (north and central site along gradient) are found in a region that has been traditionally used for cultivation of *henequen* (*Agave fourcroydes* Lem.) and both have been abandoned for a period >25 years (Mizrahi *et al.* 1997). The third site (at the southern end) is found in an area that was previously managed but has been abandoned for a period >30 years (Gauger-Araujo 2009). At all three sites, the dominant species of trees (*i.e.* the most frequent) are *B. simaruba* (L.) Sarg. (Burseraceae), *P. piscipula* (L.) Sarg. (Fabaceae) and *L. latisiliquum* (L.) Benth. (Fabaceae), representing 9.36–27.6% of the basal area of tree species at each site (González-Iturbe *et al.* 2002).

The selected sites in this study were Chicxulub (21°14'05.74"N–89°32'28.40"W), which is located toward the northern coast of Yucatan and has thorny deciduous forests. Climate at this site is semiarid, with a mean annual temperature of 26.3°C (maximum: 41.2°C) and mean annual precipitation ranging from 500 to 600 mm (Flores and Espejel 1994; García 1988). The second site (moving southward, away from the coast) is called Xmatkuil (20°52'07.44"N–89°36'51.64"W) and has a deciduous forest. Climate is warm subhumid, with a mean annual temperature of 26°C (maximum 36°C) and mean annual precipitation ranging from 728 to 1005 mm (Flores and Espejel 1994; García 1988). Finally, the southernmost site is called Hobonil (19°59'44.15"N–89°01'59.95"W) and has a subdeciduous forest, warm subhumid climate, with a mean annual temperature and precipitation of 25°C (maximum 35°C) and 1000–1200 mm, respectively (Flores and Espejel 1994; García 1988). The physiognomic characteristics of the vegetation at all three sites define these communities as tropical deciduous dry forests, with a marked climatic seasonality that results in a dry season and a rainy season (Murphy and Lugo 1986). The dry season spans from March to June and the rainy season from July to October, with a winter season having an intermediate level of precipitation (November to February), commonly known as “nortes” due to polar winds that result in temperature reduction (National Water Commission of Mexico or CONAGUA, 2011). Table 1 shows the main physical attributes of the soils at the study sites, and Fig. 1 shows historical climate data (60 years ago) for each site.

### Nutrient supplementation experiment

We conducted a factorial experiment manipulating nutrient addition (four levels) across all three sites. Nutrient supplementation consisted of the following treatments: fertilization with nitrogen (N), with phosphorus (P), with nitrogen plus phosphorus (N + P) or without supplementation (control).

**Table 1:** soil characteristics (0–10 cm in depth, mean  $\pm$  SE) at three STDF sites in Yucatan, Mexico

Soil attributes	Chicxulub	Xmatkuil	Hobonil
Soil texture (%)			
Sand	57.0 $\pm$ 8.2	27.8 $\pm$ 1.7	35.6 $\pm$ 1.5
Silt	5.6 $\pm$ 1.1	7.0 $\pm$ 0.8	4.1 $\pm$ 0.3
Clays	31.7 $\pm$ 6.1	58.2 $\pm$ 0.5	56.1 $\pm$ 1.5
Field capacity (% soil moisture)	65.6	43.0	33.1
Permanent wilting point (% soil moisture)	57.7	35.6	26.5
pH (H <sub>2</sub> O)	7.3 $\pm$ 0.1	6.8 $\pm$ 0.1	6.9 $\pm$ 0.1
Total N (%)	6.91 $\pm$ 0.13	3.79 $\pm$ 0.27	1.83 $\pm$ 0.13
Total P (%)	0.077 $\pm$ 0.05	0.066 $\pm$ 0.05	0.050 $\pm$ 0.04

Data taken from J. Campo (unpublished data); Roa-Fuentes *et al.* (2012).

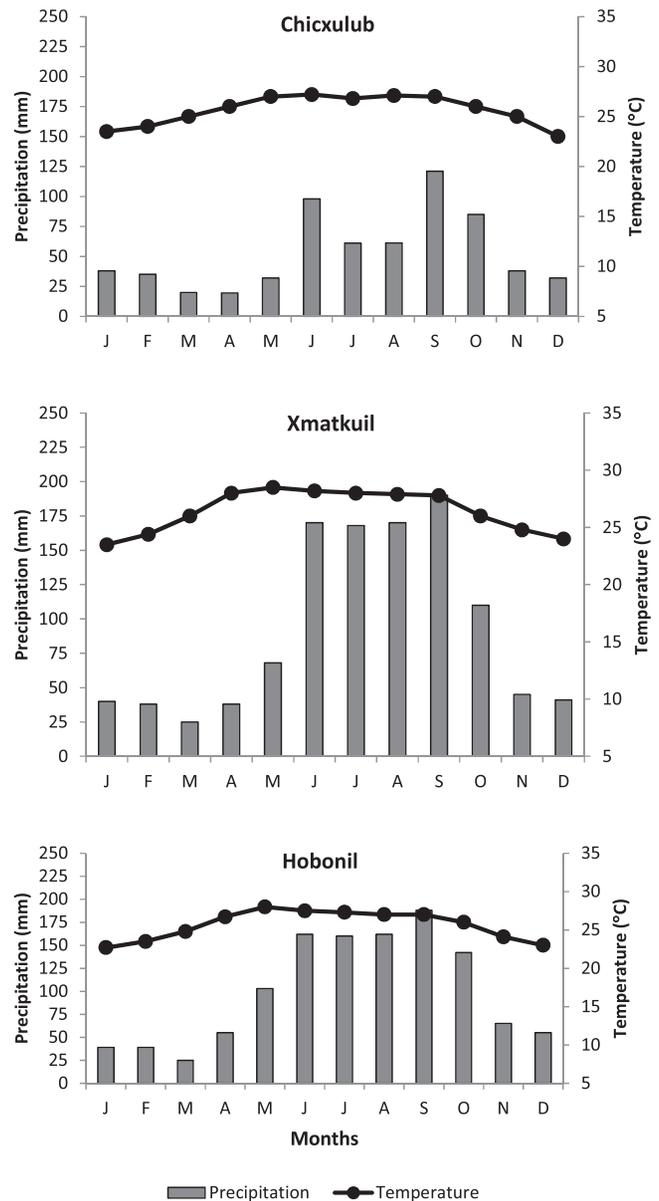
A total of 36 plots, 10 $\times$ 10 m (100 m<sup>2</sup>), were established, with 12 plots per site and a distance of 10 m between plots within each site to avoid spillover effects between treatments (Campo *et al.* 2007). Plots were established in the understory, with similar conditions of light availability. Fertilization treatments were randomly assigned to each plot.

N and P additions were applied manually following the methodology of Campo and Vázquez-Yanes (2004). Nutrient fertilization was performed during the rainy season (August 2010) by adding 12 g N/10 m<sup>2</sup> (as ammonium nitrate, NH<sub>4</sub>NO<sub>3</sub>) and 4.5 g P/10 m<sup>2</sup> (as triple superphosphate, H<sub>2</sub>PO<sub>4</sub>). The N + P treatment consisted of a mix of the previously described doses of N and P. These fertilization amounts fall within the range of fertilizer applications used in previous studies and have been shown to produce a significant effect on plant growth in tropical forests in general (Tanner *et al.* 1992), as well as in STDFs in particular (Campo and Vázquez-Yanes 2004; Campo *et al.* 2007; Ceccon *et al.* 2003, 2004).

### Seedling survival and growth

Previously, from June to August 2010, we collected seeds from 30 adult trees of each species at each site. Subsequently, seeds were germinated in plastic trays using a 4:1 mix of sterile soil and sand. After an initial 2-month growing period, we selected 360 seedlings of each species and transplanted them to their site of origin in early October, such that 10 seedlings of each species were present in each plot, randomly interspersed with seedlings of the other species. Although October is the last month of the rainy season in the study area, precipitation continues until the end of the year, before the dry season (Fig. 1); furthermore, to reduce physiological stress incurred during transplantation, seedlings were watered during the first month (biweekly). Distance between seedlings within each plot was 1 m.

We surveyed seedling survival and growth every 20 days from November 2010 to April 2011. During each survey, we documented the number of surviving seedlings and seedling



**Figure 1:** historical data (60 years) of mean monthly precipitation and temperature for the three study sites located in Yucatan, Mexico (CONAGUA 2011).

coverage. Plant coverage was estimated by calculating the area of an ellipse using the formula:  $\pi \times D1 \times D2 / 4$ , where D1 was the largest diameter of the plant (from tip to tip of the largest pair of leaves) and D2 was the smaller diameter (perpendicular to D1; Ortegón-Campos *et al.* 2009).

### Statistical analyses

As an initial exploration of effects of site and nutrient addition on seedling survival, we used a nonparametric survival analysis with the statistical package SYSTAT version 10.0 (SYSTAT 1996), which estimates the Kaplan–Meier probabilities of survival of each period of time (Pyke and Thompson 1986,

SYSTAT 1996); initial plant coverage was used as a covariate in this model. However, because we were particularly interested in testing the interactive effects of site and nutrients (i.e. Site  $\times$  Nutrient treatment term), we also used a generalized linear model assuming a Poisson error distribution and a log link function in Proc GENMOD in SAS version 9.1 (SAS 2002, Cary, NC). This model included site (Chicxulub, Xmatkuil and Hobonil) and nutrient treatment (control, N, P and N + P) as main effects, as well as their interaction, and was tested separately for each species. The response variable was the number of surveys during which a given plant remained alive throughout the study season (see Ortégón-Campos *et al.* 2009). In the case of seedling growth (measured as plot coverage), we performed a repeated-measures analysis of variance in SAS, which included time (number of surveys performed), site, nutrient treatment and all two-way interactions. We also included initial plant coverage as a covariate in this model. Significant differences between treatment levels and sites were set at  $P \leq 0.05$  and preplanned contrasts were performed to compare means for significant main effects.

## RESULTS

### Effect of nutrient supplementation on seedling survival

Forty days after transplantation, we observed a mean percentage survival  $<20\%$  across all species, which was consistent among sites (Fig. 2). The analysis of survival curves showed no effect of site on survival of *P. piscipula* or *B. simaruba* ( $\chi^2 = 0.98$  and  $\chi^2 = 1.59$ , respectively;  $P > 0.05$  in both cases) but did show a significant effect of nutrient treatment ( $\chi^2 = 7.61$  and  $\chi^2 = 11.25$ , respectively;  $P \leq 0.05$  in both cases). For *L. latisiliquum*, however, we observed significant effects of both site ( $\chi^2 = 13.72$ ,  $P = 0.003$ ) and nutrient treatment ( $\chi^2 = 15.9$ ,  $P < 0.001$ ). Overall, during the sampling periods for the three species, there was an overlap in survival confidence intervals (upper and lower survival probabilities) between control, P addition and N + P addition treatment levels, in addition to a greater (nonoverlapping) probability of survival under the N addition (data not shown, but see Fig. 2). In *L. latisiliquum*, an overlap between the Xmatkuil and Chicxulub sites was observed for all sampling periods, whereas at Hobonil, the survival probabilities were always higher relative to the previous two sites (data not shown, but see Fig. 2).

Overall, across species and sites, we found that nutrient addition caused  $\sim 5\%$  mean increase in survival during each survey compared with the control treatment (Fig. 2). Results from the generalized linear model, which evaluated the number of surveys during which a given plant remained alive, showed that *P. piscipula* and *B. simaruba* showed significant differences among nutrient treatment levels, whereas *L. latisiliquum* showed significant differences in survival based on both site and nutrient treatment (Table 2). We did not find a significant Treatment  $\times$  Site interaction on seedling survival for any of the species (Table 2).

Preplanned contrasts for *P. piscipula* showed that N addition treatment differed significantly from the control treatment ( $\chi^2 = 14.32$ ,  $P < 0.01$ ) and the P addition treatment ( $\chi^2 = 5.24$ ,  $P = 0.02$ ). Seedlings subjected to N fertilization survived 13 days more on average ( $\sim 20\%$ ) relative to control seedlings and eight days more ( $\sim 12\%$ ) compared with those experiencing P addition. We found that survival from P and N + P addition treatments did not differ from that of controls ( $\chi^2 = 2.27$ ,  $P = 0.13$  and  $\chi^2 = 0.40$ ,  $P = 0.52$ , respectively; Fig. 3a).

In the case of *B. simaruba*, we found that seedlings subjected to N addition survived 11 days more ( $\sim 18\%$ ) on average relative to control seedlings ( $\chi^2 = 8.79$ ,  $P = 0.003$ ). Nonetheless, survival of seedlings from the N addition treatment did not differ significantly from survival under the P ( $\chi^2 = 1.78$ ,  $P = 0.18$ ) or N + P ( $\chi^2 = 0.89$ ,  $P = 0.34$ ) treatments. Survival under the N + P treatment did differ significantly from that under the control treatment ( $\chi^2 = 4.12$ ,  $P = 0.04$ ; Fig. 3b). Seedlings subjected to the N + P treatment remained alive 8 days more ( $\sim 13\%$ ) on average relative to control seedlings. Survival for the P addition treatment did not differ from that under the N + P treatment ( $\chi^2 = 0.15$ ,  $P = 0.69$ ) or that of the control ( $\chi^2 = 2.69$ ,  $P = 0.10$ ; Fig. 3b).

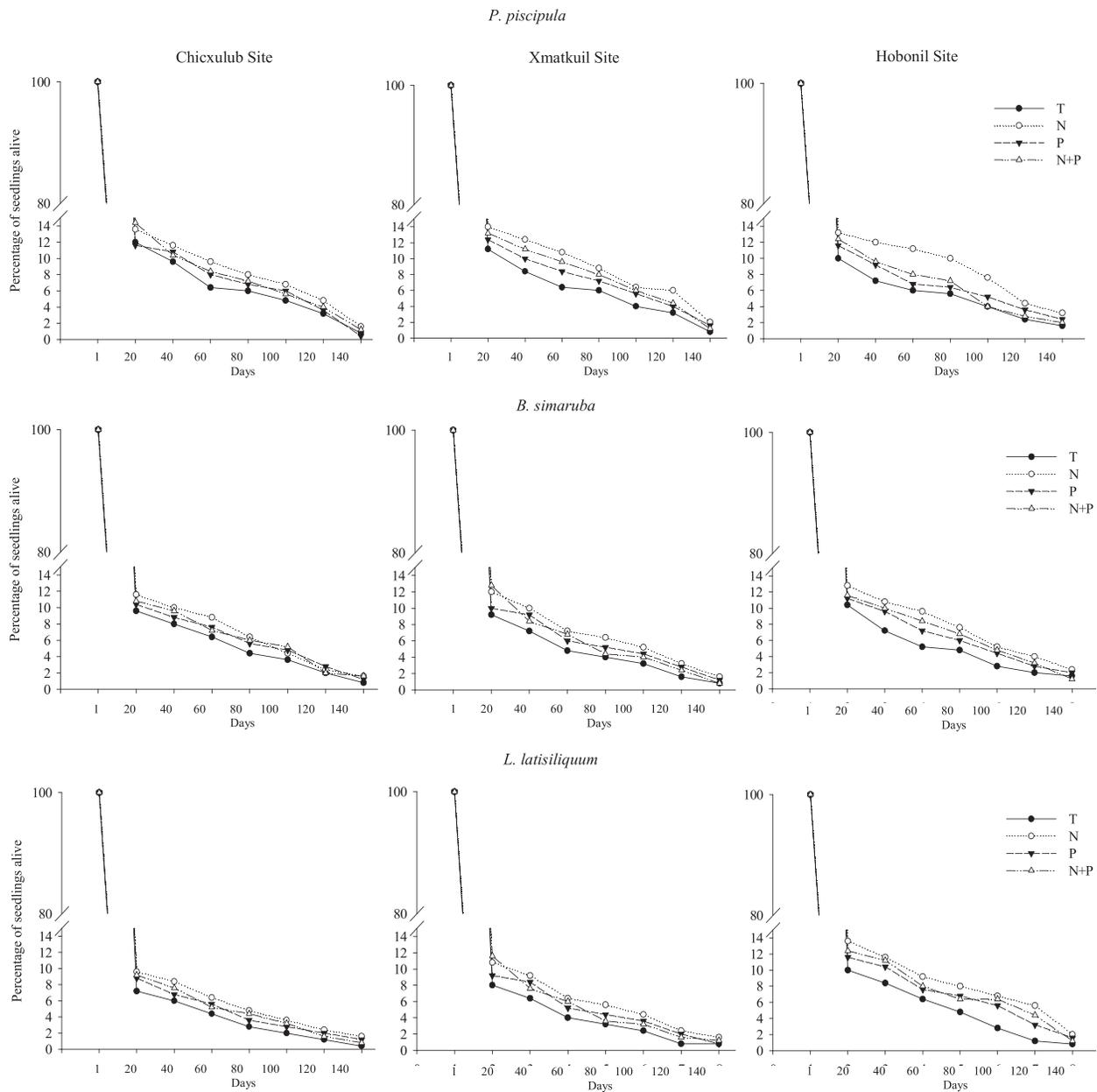
For *L. latisiliquum*, we observed a similar pattern relative to *B. simaruba*. Survival under the N addition treatment differed significantly compared with survival of control seedlings ( $\chi^2 = 11.30$ ,  $P < 0.01$ ); seedlings of the former treatment remained alive 13 days more ( $\sim 20\%$ ) on average relative to controls. However, N addition did not cause a significant change in survival compared with P ( $\chi^2 = 2.24$ ,  $P = 0.13$ ) or N + P ( $\chi^2 = 1.13$ ,  $P = 0.28$ ) additions. The results from the that N + P addition treatment differed significantly from that of the controls ( $\chi^2 = 5.31$ ,  $P = 0.02$ ; Fig. 3c), with seedlings from the former treatment remaining alive  $\sim 9$  days more ( $\sim 15\%$ ) on average relative to control seedlings. The P addition treatment did not differ from either the N + P ( $\chi^2 = 0.19$ ,  $P = 0.66$ ) or the control ( $\chi^2 = 3.51$ ,  $P = 0.06$ ) treatments (Fig. 3c).

Site comparisons showed that *L. latisiliquum* seedling survival was significantly different among the sites Hobonil, Chicxulub and Xmatkuil ( $\chi^2 = 14.21$ ,  $P < 0.01$  and  $\chi^2 = 9.83$ ,  $P = 0.001$ , respectively). At Hobonil, seedlings of this species remained alive  $\sim 12$  days more (19%) on average relative to those in Chicxulub and 10 days more ( $\sim 16\%$ ) on average relative to those in Xmatkuil.

For all three species, we observed a nonsignificant effect of initial plant cover on seedling survival ( $F \leq 2.08$ ,  $P \geq 0.14$  in all cases).

### Effect of nutrient supplementation on seedling growth

For *P. piscipula*, we observed a significant Nutrient  $\times$  Site interaction on seedling growth after the fourth survey ( $F_{6,34} = 2.95$ ,  $P = 0.02$ ; Fig. 4a). Specifically, the effects of N



**Figure 2:** percentage survival of seedlings of three dominant species under four treatments of soil nutrient addition at the three study sites in seasonally tropical dry forests in Yucatan, Mexico. C: control; N: nitrogen supplementation; P: phosphorus supplementation; N+P: nitrogen plus phosphorus supplementation (note scale change on Y-axis).

addition on seedling growth varied across sites ( $P < 0.05$  in all cases), being greatest at Hobonil ( $15.24 \pm 0.41 \text{ cm}^2$ ) and comparatively lower at Xmatkuil ( $14.85 \pm 0.19 \text{ cm}^2$ ) and Chicxulub ( $14.47 \pm 0.03 \text{ cm}^2$ ). In contrast, the effects of P addition on seedling survival did not differ among sites ( $P > 0.05$  in all cases). The N + P addition treatment resulted in significant differences in mean growth for Chicxulub ( $14.56 \pm 0.08 \text{ cm}^2$ ) relative to Xmatkuil ( $14.78 \pm 0.15 \text{ cm}^2$ ) and Hobonil ( $14.80 \pm 0.26 \text{ cm}^2$ ), which themselves did not differ ( $P < 0.05$  in both cases, Fig. 4a). We did not find

significant differences in growth among sites for control plants ( $P > 0.05$ ).

For *B. simaruba*, we also observed a significant Site  $\times$  Nutrient treatment interaction on seedling growth after the fourth survey ( $F_{6,29} = 3.51$ ,  $P = 0.009$ ). However, this effect was largely due to site differences in the magnitude of the effect of N addition (Fig. 4b). The N treatment showed significant mean differences in growth for Chicxulub ( $13.02 \pm 0.09 \text{ cm}^2$ ) relative to Xmatkuil ( $13.36 \pm 0.71 \text{ cm}^2$ ) and Hobonil ( $13.13 \pm 0.60 \text{ cm}^2$ ), which themselves did not differ

**Table 2:** results from a generalized linear model showing the effects of nutrients, study site and their interaction on the survival of seedlings of three species of dominant trees in STDFs in Yucatan, Mexico

Factor	<i>P. piscipula</i>			<i>B. simaruba</i>			<i>L. latifolium</i>		
	df	$\chi^2$	<i>P</i>	df	$\chi^2$	<i>P</i>	df	$\chi^2$	<i>P</i>
Site	2/468	1.24	0.537	2/468	1.13	0.569	2/468	16.54	<0.001
Nutrient addition	3/468	14.85	<b>0.002</b>	3/468	9.19	<b>0.027</b>	3/468	11.82	<b>0.008</b>
Site × Nutrient addition	6/468	1.37	0.967	6/468	0.40	0.998	6/468	0.41	0.998

df = degrees of freedom. Significant effects are in bold.

( $P < 0.05$  in both cases). Furthermore, P, N + P or control treatments showed significant differences between sites ( $P > 0.05$  in all cases). For *L. latifolium*, we also observed a significant Site × Nutrient addition interaction on seedling growth ( $F_{6,22} = 4.63$ ,  $P = 0.003$ ). For *B. simaruba*, this interaction term was due to differences among sites in the effect of N addition (Fig. 4c). The N addition treatment showed significant differences in growth for Hobonil ( $18.32 \pm 1.65 \text{ cm}^2$ ) compared with that for Chicxulub ( $17.02 \pm 0.14 \text{ cm}^2$ ) and Xmatkuil ( $17.45 \pm 0.61 \text{ cm}^2$ ), which themselves did not differ significantly ( $P < 0.05$  in each case). The means for P, N + P and controls did not differ among sites ( $P > 0.05$  in all cases).

For all three species, we observed a significant effect of initial plant coverage on plant growth ( $P < 0.001$  in all cases).

## DISCUSSION

### Effect of nutrient supplementation on seedling survival

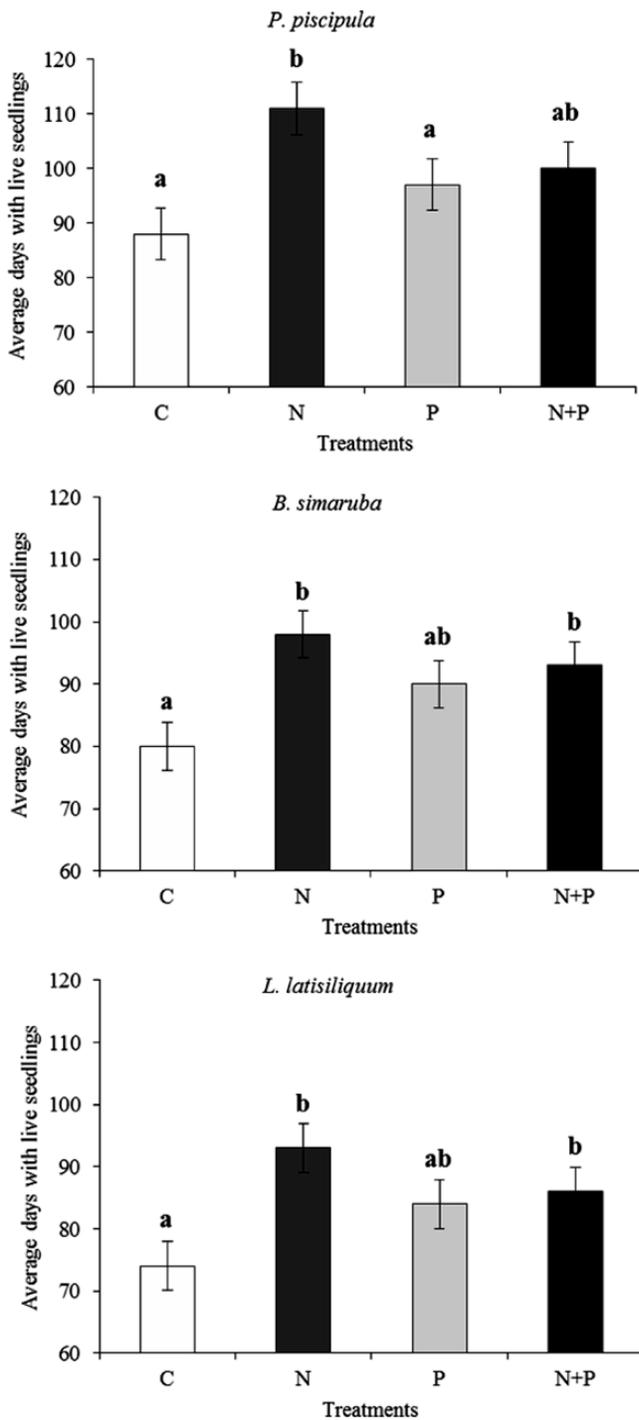
Seedlings of all three studied tree species exhibited a high mortality (>80%) after the first 40 days of the experiment, which subsequently leveled off between 80 and 120 days after initiation of the experiment. This temporal pattern of mortality is similar, although overall higher, relative to that reported for other species of tropical trees in Costa Rica (Lieberman *et al.* 1990), Ghana (Swaine *et al.* 1990) and Yucatán (Ceccon *et al.* 2004), where mortality reached 55–70%. The higher mortality observed in our study could be because seedling transplantation was conducted toward the last third of the rainy season, which decreased seedling survival rates (even though seedlings were watered during the first month). In spite of these differences in overall survival, the survival curves in our study are characteristic of species exhibiting high mortality during the initial life stages (i.e. type III survival curve, *sensu* Pearl 1928) and are characteristic of tropical trees (Sarukhan 1980). The survival rates observed for species in this study support this view and further suggest that such pattern remains relatively constant across sites despite marked differences in rainfall.

Our findings show that independently of the specific nutrient added (or combination) and the plant species, fertilization can lead to an overall increase in seedling survival (ranging

from 12 to 20%) compared with control plants. For STDFs, it has been suggested that nutrient availability is one of the key factors influencing seedling survival (Ceccon *et al.* 2006). Overall, N and P availability in this study appears to be limiting seedling survival to a similar extent across all sites. We also found that these macronutrients did not have additive effects on survival for any of the species, as survival of seedlings with both N and P did not differ relative to that observed under the N and P treatments individually. This finding is similar to that reported by Cleveland and Townsend (2006), who did not find differences between the individual and combined effects of N and P addition on the production of fine root biomass in a tropical forest of Costa Rica. Such a pattern may be due to seedlings having different requirements for each nutrient and the interactions between these nutrients being important only when their availability is low. In this way, the increase in abundance of one nutrient stimulates plant growth, which may induce a deficiency in the other nutrient (Clarkson and Hanson 1980).

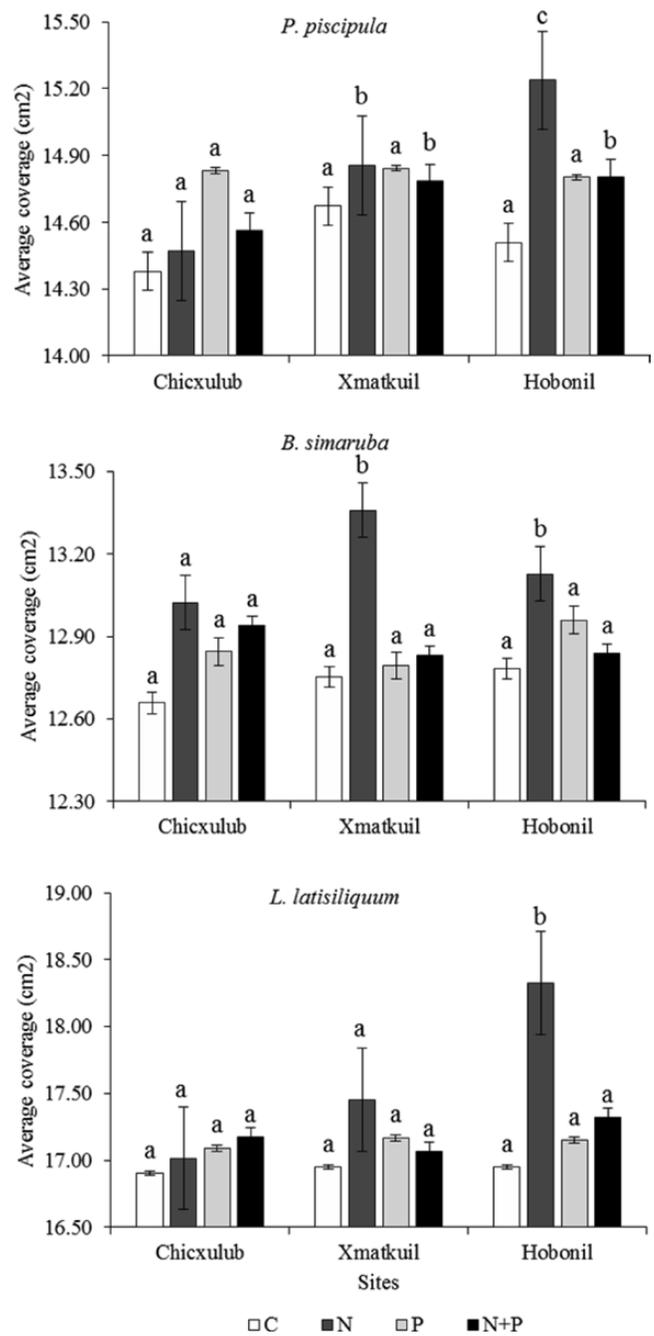
Authors have previously suggested that tree growth and survival in STDFs of the northern Yucatan Peninsula are strongly P limited (Campo and Vázquez-Yanes 2004; Ceccon *et al.* 2003). Moreover, P may be limiting in these areas regardless of conservation status or successional stage (Campo and Vázquez-Yanes 2004; Campo *et al.* 2007). It has also been suggested that throughout the succession of tropical forests, the mechanisms that regulate the processes of decomposition and the mineralization and immobilization of nutrients between the leaf litter and the soil vary across sites (Campo *et al.* 2007). Such differences may in turn explain observed differences in nutrient effects on survival relative to seedling growth. In our study, although we observed an overall positive effect of nutrient addition on survival, which was similar across sites, nutrient effects on seedling growth did vary in magnitude across sites (see the following text).

Although N and P had a significant effect on the number of surveys through which seedlings remained alive, it should also be noted that the difference between these treatment levels and control plants were not large. This suggests that other factors may be influencing plant survival and that their relative importance may be species specific. For *P. piscipula* and *B. simaruba*, we observed that the effect



**Figure 3:** mean ( $\pm$  SE) of the number of days that seedlings of three dominant tree species remained alive under four treatments of soil nutrient addition, at the three study sites in seasonally tropical dry forests in Yucatan, Mexico. C: control; N: nitrogen supplementation; P: phosphorus supplementation; N+P: nitrogen plus phosphorus supplementation. Different letters indicate significant differences ( $P < 0.05$ ) among fertilization treatment level means.

of nutrient addition on seedling survival was independent of the site, whereas for *L. latisiliquum*, we found that the effect of nutrient addition was greatest at the site with



**Figure 4:** mean ( $\pm$  SE) values of plant growth (coverage) for seedlings of three dominant species under four treatments of soil nutrient addition at the three study sites in seasonally tropical dry forests in Yucatan, Mexico. C: control; N: nitrogen supplementation; P: phosphorus supplementation; N+P: nitrogen plus phosphorus supplementation. Different letters indicate significant differences ( $P < 0.05$ ) among treatment level means.

highest rainfall (Hobonil), with seedlings remaining alive for a greater number of surveys relative to the other two sites. It is probable that such response is due to this species having a greater nutrient uptake performance at sites with higher soil humidity, which promotes increased nutrient

mineralization, as well as the establishment of underground mutualistic interactions as reported for other species of legumes (Allen *et al.* 2005).

Similarly, light and water availability have been suggested as other relevant forces influencing seedling survival and growth in tropical forests (Poorter 2009; Rincón and Huante 1993; Slot and Poorter 2007; Turner 1990). However, our results suggest that site differences in water availability did not explain the difference in seedling survival between the drier sites and the wettest one.

With reference to light availability, our experiment was designed to minimize variation due to this factor by selecting sites with homogeneous canopy conditions. However, it is clear that in order to fully evaluate this condition, future work that carefully documents variation in light availability at each site is necessary. Finally, herbivores could be another important factor limiting seedling growth and survival in both dry and wet tropical forests (Dirzo and Domínguez 1995; Janzen 1981). However, during the course of this experiment, we observed very low levels of aboveground damage.

Our results suggest that the effects of nutrient addition on seedling survival are species specific but appear to be independent of site. Due to the recent geological origin of the Yucatán Peninsula, the landscape is dominated by extensive rock outcrops and the soil layers are considerably thin. Such outcrops and soil conditions are especially prevalent in the northern portion of the Yucatán Peninsula, where suitable sites for seed germination and seedling establishment are relatively rare (Bautista *et al.* 2011). Our nutrient addition treatment can be viewed as a simulation of an environmental effect (or component of the environment) that determines whether a site is 'safe or unsafe' (*sensu* Harper *et al.* 1965). Hence, although seedling responses to soil nutrient conditions appear to be species specific, our findings illustrate that nutrient availability can be a key factor for seedling establishment of tree species in the STDFs of Yucatán. Yet, seedling establishment could be related not only to the availability of microhabitat conditions but also to larger-scale climatic events such as hurricanes and fires, which are relatively frequent in this region (e.g. Sánchez-Sánchez and Islebe 1999; Mizrahi *et al.* 1997; Walker *et al.* 2003; Whigham *et al.* 2010).

### Effects of nutrient supplementation on seedling growth

Our results revealed that although seedling growth of all three species responded positively to nutrient addition, this effect was contingent on site. Regarding survival, however, we found that N and P effects on seedling growth were not additive, which appears to be a common condition in tropical forests (Bustamante *et al.* 2012; Cleveland and Townsend 2006).

It has been shown for STDFs that P is a limiting nutrient for both seedling growth and adult growth and reproduction (e.g. Ceccon *et al.* 2002, Parra-Tabla and Bullock

1998). For example, Ceccon *et al.* (2003) reported that P fertilization increased growth of *B. simaruba* seedlings in an STDFs site in northern Yucatan, Mexico. Our results show that for STDFs of the Yucatan Peninsula, not only is P limiting, but also N, although in a site- and species-specific manner. We expected that plant nutrient supplementation would have the greatest effect at Hobonil, the site with the greatest rainfall. However, we found that nutrient input contributed to plant growth differentially across sites. In particular, N addition caused a greater increase in seedling growth for *P. piscipula* and *L. Latisiliquum* at Hobonil, although this pattern was not observed for *B. simaruba*. As mentioned earlier, it is probable that the nutrient effects varied across sites due to differences in nutrient mineralization rates. It has been proposed that the residence time and movement of nutrients in soils are determined by immobilization and release during decomposition, both of which are controlled by environmental conditions (e.g. temperature, soil humidity) and chemical traits of the leaf litter (Juárez *et al.* 2006), which ultimately lead to differences across sites in plant nutrient uptake and growth (Roa-Fuentes *et al.* 2012).

It is probable that the relative importance of N at our study sites is attributable to the long dry season observed in the region (up to 5 months), which may lead to low levels of leaching, limiting the nutrient uptake. Similarly, it is possible that the importance of N resides in its effects on soil microbial activity, which is responsible for increasing nutrient availability for seedlings during their initial growth stages (O'Connell 1990; Singh *et al.* 1989). Hence, differences across sites and among species in soil microbial activity and composition may represent an important source of variation to be addressed in future work.

The strong seasonality in rainfall observed for STDFs of the Yucatan Peninsula probably generates contrasting biotic and abiotic conditions (e.g. of greater or lesser microbial activity), making soil nutrient availability a driver of tree species seedling survival and growth (Ceccon *et al.* 2006; Slot and Poorter 2007; Turner 1990).

In conclusion, our results suggest that nutrient availability appears to be an important factor controlling tree seedling survival and growth in STDFs in the Yucatan Peninsula. However, we also show that the effects of nutrient addition vary across species and sites. Therefore, we suggest future work should address physiological plant responses to nutrient uptake, different levels of soil microbial activity and the long-term role of both processes in the establishment of tree seedlings in STDFs.

### FUNDING

Consejo Nacional de Ciencia y Tecnología of México (PhD to L.S.P., 128856 to V.P.T.).

## ACKNOWLEDGEMENTS

We thank field and laboratory assistance provided by Nicolás Salinas, Enrique Bojórquez and Ana del Carmen Pérez. The authors also acknowledge Mr Luis Salinas Bustamante for help with seedling germination and maintenance. Luis Abdala- Roberts, Juan Tun Garrido, José Ramos, Bernhard Schmid Patricia Balvanera and two anonymous reviewers provided useful comments.

*Conflict of interest statement.* None declared.

## REFERENCES

- Allen MF, Allen EB, Gómez-Pompa A (2005) Effects of mycorrhizae and nontarget organisms on restoration of a seasonal tropical forest in Quintana Roo, Mexico: factors limiting tree establishment. *Restor Ecol* **13**:325–33.
- Bautista F, Palacio-Aponte G, Quintana P, et al. (2011) Spatial distribution and development of soils in tropical karst areas from the Peninsula of Yucatan, Mexico. *Geomorphology* **135**:308–21.
- Bullock SH (1995) Plant reproduction in neotropical dry forest. In Bullock SH, Mooney HA, Medina E (eds). *Seasonally Dry Tropical Forest*. Cambridge, UK: Cambridge University Press, 277–303.
- Bustamante C, de Brito D, Kozovits A, et al. (2012) Effects of nutrient additions on plant biomass and diversity of the herbaceous-subshrub layer of a Brazilian savanna (Cerrado). *Plant Ecol* **213**:795–808.
- Callaway RM (1995) Positive interactions among plants. *Bot Rev* **61**:306–49.
- Campo J, Solís E, Valencia M (2007) Litter N and P dynamics in two secondary tropical dry forests after relaxation of nutrient availability constraints. *For Ecol Manage* **252**:33–40.
- Campo J, Vázquez-Yanes C (2004) Effects of nutrient limitation on aboveground carbon dynamics during tropical dry forest regeneration in Yucatan, Mexico. *Ecosystems* **7**:311–19.
- Ceccon E, Huante P, 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 Yucatan, Mexico. *For Ecol Manage* **182**:387–402.
- Ceccon E, Huante P, Rincón E (2006) Abiotic factors influencing tropical dry forest regeneration. *Brazil Arch Biol Technol* **49**:305–12.
- Ceccon E, Omstead I, Vázquez-Yanes C, et al. (2002) Vegetation and soil properties in two tropical dry forests of differing regeneration status in Yucatán. *Agrociencia* **36**:621–31.
- Ceccon E, Sánchez S, Campo J (2004) Tree seedling dynamics in two abandoned tropical dry forest of differing successional status in Yucatan, Mexico: a field experiment with N and P fertilization. *Plant Ecol* **170**:277–83.
- Clarkson DT, Hanson JB (1980) The mineral nutrition of higher plants. *Ann Rev Plant Physiol* **31**:239–98.
- Cleveland CC, Townsend AR (2006) Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. *Proc Natl Acad Sci U S A* **103**:10316–21.
- CONAGUA (2011) *Base de datos mensuales climatológicos correspondientes a las estaciones Chicxulub, Mérida y Tzucacab, Yucatán. Subgerencia Técnica, Jefatura de Aguas Superficiales*. Mérida, Yucatán: Comisión Nacional del Agua, Gerencia Regional Península de Yucatán.
- Dirzo R, Domínguez C (1995) Plant-herbivore interactions in Mesoamerican tropical dry forest. In Bullock SH, Mooney HA, Medina E (eds) *Seasonally Dry Tropical Forest*. Cambridge, UK: Cambridge University Press, 304–25.
- Duch G (1988) *La conformación territorial del estado de Yucatán*. Chapingo, México: Universidad Autónoma de Chapingo.
- Flores JS, Espejel I (1994) *Tipos de la vegetación de la Península de Yucatán. Etnoflora Yucatanense Fascículo.3*. Yucatan, México: Universidad Autónoma de Yucatán.
- García E (1988) *Modificaciones al sistema de clasificación climática de Köppen*, 3rd edn. Mexico City, México: Instituto de Geografía, UNAM.
- Gaumer-Araujo R (2009) Estructura, composición y potencial maderables de la vegetación secundaria con diferente uso de suelo en el rancho Hobonil, Yucatán, México. Tesis de Licenciatura. Universidad Autónoma de Yucatán.
- Gerhardt K (1998) Leaf defoliation of tropical dry forest tree seedlings-implications for survival and growth. *Trees* **13**:88–95.
- González-Iturbe JA, Olmsted I, Tun-Dzul F (2002) Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico. *For Ecol Manage* **167**:67–82.
- Harper JL, Williams JT, Sagar GR (1965) The behaviour of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *J Ecol* **53**:273–86.
- Howlett BE, Davidson DW (2003) Effects of seed availability, site conditions, and herbivory on pioneer recruitment after logging in Sabah, Malaysia. *For Ecol Manage* **184**:369–83.
- Ibañez I, Schupp EW (2002) Effects of litter, soil surface conditions, and microhabitat on *Cercocarpus ledifolius* Nutt. seedling emergence and establishment. *J Arid Environ* **52**:209–21.
- Janzen DH (1981) Patterns of herbivory in a tropical deciduous forest. *Biotropica* **13**:271–82.
- Juárez M, Sánchez J, Sánchez A (2006) *Química del suelo y medio ambiente*. Alicante, España: Publicaciones Universidad de Alicante.
- Kleinman P, Pimentel D, Bryant R (1995) The ecological sustainability of slash-and-burn agriculture. *Agri Ecosyst Environ* **52**:235–49.
- Lieberman D, Hartshorn GS, Lieberman M, et al. (1990) Forest dynamics at La Selva Biological Station, 1969–1985. In Gentry AH (ed) *Four Neotropical Rain Forests*. New Haven, CT: Yale University Press, 509–21.
- Marín J (1997) Composición y estructura de la vegetación y sus relaciones con el banco de semillas en tres sitios de selva baja caducifolia de la Península de Yucatán. Tesis de Maestría. Universidad Autónoma de Yucatán.
- Mizrahi A, Ramos Prado JM, Jiménez-Osornio JJ (1997) Composition, structure and management potencial of secondary dry tropical vegetation in two abandoned henequén plantations of Yucatan, Mexico. *For Ecol Manage* **96**:273–82.
- Murphy P, Lugo A (1986) Ecology of tropical dry forest. *Ann Rev Ecol Systemat* **17**:67–88.
- O’Connell AM (1990) Microbial decomposition (respiration) of litter in Eucalypt forest of south-western Australia: an empirical model base on laboratory incubations. *Soil Biol Biochem* **22**:153–60.
- Ortegón-Campos I, Parra-Tabla V, Abdala-Roberts L, et al. (2009) Local adaptation of *Ruellia nudiflora* (Acanthaceae) to biotic counterparts: complex scenarios revealed when two herbivore guilds are considered. *J Evol Biol* **22**:2288–97.

- Parra-Tabla V, Bullock SH (1998) Factors limiting fecundity of tropical tree *Ipomea wolcottiana* (Convolvulaceae) in a Mexican tropical dry forest. *J Trop Ecol* **14**:615–27.
- Pearl R (1928) *The Rate of Living*. New York, NY: Knopf & Borzoi Books.
- Pyke DA, Thompson JN (1986) Statistical analysis of survival and removal rate experiments. *Ecology* **67**:240–5.
- Poorter L (2009) Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. *New Phytol* **181**:890–900.
- Reed SC, Cleveland CC, Townsend AR (2007) Controls over leaf litter and soil nitrogen fixation in two lowland tropical rain forests. *Biotropica* **39**:585–92.
- Reich PB, Borchert R (1984) Water stress and tree phenology in tropical dry forest in the lowlands of Costa Rica. *J Ecol* **72**:61–4.
- Rincón E, Huante P (1993) Growth responses of tropical deciduous tree seedlings to contrasting light conditions. *Trees Struct Funct* **7**:202–7.
- Roa-Fuentes L, Campo J, Parra-Tabla V (2012) Plant biomass allocation across a precipitation gradient: an approach to seasonally dry tropical forest at Yucatan, Mexico. *Ecosystems* **8**:1234–44.
- Sánchez-Sánchez O, Islebe GA (1999) Hurricane Gilbert and structural changes in a tropical forest. *Glob Ecol Biogeog* **8**:29–38.
- Sarukhan J (1980) Mecanismos de regulación de poblaciones vegetales. In Rabinovitch Hy (eds) *Tópicos Selectos de Ecología Contemporánea*. México City, México: CECSA.
- SAS (2002) *SAS, Versión 9.1*. Cary, NC: SAS Institute Inc.
- Schupp EW (1995) Seed-seedling conflicts, habitat choice and patterns of plant recruitment. *Am J Bot* **82**:399–409.
- Singh JS, Raghubanshi AS, Singh RS, *et al.* (1989) Microbial biomass acts as a source of plants nutrients in dry forest and savanna. *Nature* **338**:499–500.
- Slot M, Poorter L (2007) Diversity of seedling responses to drought. *Biotropica* **39**:683–90.
- Swaine MD, Lieberman D, Hall JB (1990) Structure and dynamics of a tropical dry forest in Ghana. *Vegetatio* **88**:31–51.
- SYSTAT (1996) *SYSTAT Version 10.0*. Chicago, IL: SPSS Inc.
- Tanner EV, Kapos V, Franco W (1992) Nitrogen and phosphorus fertilization effect on Venezuela montane forest trunk growth and litterfall. *Ecology* **73**:78–86.
- Turner IM (1990) The seedling survivorship and growth of three *Shorea* species in a Malaysian tropical rain forest. *J Trop Ecol* **6**:469–78.
- Vitousek P (1984) Litterfall, nutrient cycling and nutrient limitation in tropical forests. *Ecology* **65**:285–98.
- Walker LR, Lodge DJ, Guzmán-Grajales S, *et al.* (2003) Species-specific seedling responses to hurricane disturbance in Puerto Rican rain forest. *Biotropica* **35**:472–85.
- Whigham DF, Olmsted I, Cabrera Cano E, *et al.* (2010) Impacts of hurricanes on the forests of Quintana Roo, Yucatán Peninsula, Mexico. In Scott FJ, Gomez-Pompa A (eds) *The Lowland Maya Area: Three Millennia at the Human-Wildland Interface*. Binghamton, NY: Food Products Press, 193–216.
- Wright SJ (1992) Seasonal drought, soil fertility and the species density of tropical forest plant communities. *Trends Ecol Evol* **7**:260–3.