Leaf quality and herbivory responses to soil nutrient addition in secondary tropical dry forests of Yucatán, Mexico

Julio Campo[1] and Rodolfo Dirzo

Instituto de Ecología, Universidad Nacional Autónoma de México
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Abstract: Leaf quality (nutrient concentration) and herbivory were studied in a set of dominant tree species in regenerating, secondary tropical dry forests growing on limestone in the Yucatán Peninsula. The study's objective was to assess how variation in nutrient availability affects leaf nitrogen and phosphorus concentrations and herbivory. Our study included an area of young forest (10 y old), with phosphorus-poor soils, and an area of old forest (~60 y old), in which soil P was comparatively less limiting. The foliage of representative species of each site was studied, including *Acacia gaumeri*, *Leucaena leucocephala* and *Lysiloma latisiliquum* at the young forest site, and *A. gaumeri*, *Bursera simaruba* and *Pithecellobium dulce* at the old forest. Four independent plots (12 × 12 m) at each forest were either left intact (controls) or fertilized with N, with P, or with N plus P for three consecutive years. Relaxation of nutrient limitations at the young forest resulted in an increase in leaf phosphorus and herbivory in all species. In contrast, N and P fertilization at the old forest site did not consistently affect leaf nutrient concentration and leaf damage. In this site the main response to fertilization was an increase in leaf nitrogen only in *B. simaruba* and an increase in herbivory in *A. gaumeri*; leaf phosphorus was unaffected by soil fertilization. Overall, we observed that, subsequent to nutrient addition, leaf phosphorus concentration and herbivory in the leguminous species increased at the young site; leaf nitrogen concentration in the non-leguminous species increased at the old site while herbivory only increased in *A. gaumeri*, following a pattern similar to that observed in the young site. We conclude that the regulatory mechanisms of leaf quality and damage by herbivores will vary, depending on the details of the site's nutrient limitations and the identity of species.

Key Words: leaf nutrients, limestone, nitrogen, phosphorus, soil nutrient limitation

INTRODUCTION

Several aspects of the ecology and evolution of plants from tropical forests seem to have been shaped by spatio-temporal variation in resource availability (Mulkey *et al.* 1996) and by strong ecological interactions with their herbivores (see Coley & Barone 1996, Coley *et al.* 1985). For example, it has been postulated that resource allocation to anti-herbivore defences is greater in plants adapted to grow in habitats of limited resources than in those adapted to grow in resource-rich habitats (see Coley 1983, Coley *et al.* 1985). In addition to such fixed, presumably adaptive interspecific patterns of resource allocation to defence, leaf quality and herbivory may also be influenced by a species' phenotypic response to variations in nutrient availability leading to environmentally induced changes in foliar nutrient concentration.

In general, nutrient limitation for plant growth is correlated with low concentrations of the limiting nutrient in leaves. Recent reviews (Aerts & Chapin 2000) and fertilization experiments (Harrington *et al.* 2001) indicate that higher nutrient supplies generally lead to higher nutrient concentrations in leaves. Evidence that nutrient content in tropical forests influences the levels of herbivory has been obtained from studies of nitrogen concentration in leaves of rain-forest plants (Coley & Kursar 1996). Low leaf nitrogen is associated with reduced preference by insects due to reduction in nutritional value (Moran & Hamilton 1980); likewise, changes that reduce the nitrogen concentration in tropical rain-forest leaves reduce the rates of herbivory in the field (Kursar & Coley 1991).

Plant species from seasonally dry tropical forests exhibit considerable variation in herbivory, and such variation can be comparable with that of tropical rain-forest species (see Dirzo & Domínguez 1995). However, the influence of leaf nutrient quality on herbivory in plants from tropical dry forests has been poorly investigated (see reviews by Coley & Barone 1996 and Dirzo & Domínguez 1995).

In the Yucatán Peninsula, Mexico, several Leguminosae dominate secondary tropical dry forest sites that differ widely in nutrient availability and successional stage

[1] Corresponding author. Postal address: A.P. 70-275, México D.F. 04510, México
Email: jcampo@miranda.ecologia.unam.mx and urania@ecologia.unam.mx

(Ceccon *et al.* 2002). Although soil nutrient availability varies with forest successional stage and spatial variation in species composition, the overall situation of regenerating, secondary forests of the Yucatán Peninsula is that soils are nutrient-limited (Ceccon *et al.* 2002). We speculate that such overall soil nutrient limitations and the spatial variation in soil fertility in these forests may affect leaf nutrient concentration, which may in turn affect leaf quality for herbivores. In the present study we conducted field fertilization experiments with nitrogen and phosphorus to test (1) whether soil nutrient content variability results in a concomitant variation in their concentration of these nutrients in leaves and (2) if this correlates with differences in levels of leaf damage by herbivores. Our hypothesis was that, if natural supplies of nitrogen and/ or phosphorus limit foliage quality, then soil fertilization would result in an increase in the nutrient content and herbivory levels in the foliage of representative species of these secondary forests.

STUDY SITE

As part of a study evaluating the consequences of nutrient limitation on forest ecosystem functioning (J. Campo, unpubl. data), fertilization experiments were established in two areas of secondary tropical dry forest in the Dzibilchaltún National Park region, in the north-west of the Yucatán Peninsula (21°06′N and 89°17′W). The whole of the area was previously used for *Agave fourcroydes* Lem. cultivation, and for slash-and-burn agriculture. One sector of this area was abandoned ∼60 y ago (old secondary forest area; see Lundell 1934) and another sector was abandoned 10 y ago (young secondary forest area; F. Tum, *pers. comm.*). Although both areas can be regarded as nutrient-poor, the old forest area has soils with higher availability of P. Soil total nitrogen and phosphorus in the young forest vary from 0.7 to 1.7% (average and SE, 1.4 ± 0.7%) and from 0.14 to 0.30% (0.26 ± 0.30%), respectively. Potential nitrogen mineralization is 5.58 ± 0.58 µg N g^{-1} d^{-1} and P availability (as determined by the method of Watanabe & Olsen 1965) is 10.0 ± 0.7 µg g^{-1}. In the old-forest soils, total nitrogen concentrations range from 0.6 to 1.7% and do not differ from those of the young-forest soils. However, total and available phosphorus concentrations are 1.5–1.9 times greater (Ceccon *et al.* 2002), and mineralization of nitrogen is 40% lower than mean values in the young-forest soils (J. Campo, unpubl. data). Soils (lithic rendolls) are mainly shallow (< 10 cm in depth; in slightly undulating areas they are deeper, < 50 cm), organic-rich (soil organic matter content 35%), and directly overlie weathering calcium carbonate. The soil pH is slightly basic (7.3; J. Campo, unpubl. data).

The climate in the area is hot and subhumid, with a small thermal oscillation during the year. Mean temperature is 25.8 °C, with less than a 6 °C difference between the coolest and warmest months. Annual rainfall during the last 3 years (1998–2000) averaged 741 ± 130 mm (mean ± SE), most of which falls between June and October. The landscape consists of flat areas (less than 10 m asl in elevation) and the predominant lithology includes late Pliocene material, with numerous areas of exposed limestone (Duch-Gary 1988).

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. The old site has slightly fewer trees (diameter at breast height, dbh ≥ 2.5 cm) per unit area than its younger counterpart (old site mean ± SE = 57.8 ± 4.6 trees per 144 m^2, young site mean ± SE = 62.8 ± 4.0 trees per 144 m^2); however, the basal area is 1.6 times greater than the mean values in the young forest (0.22 ± 0.02 m^2 per 144 m^2 vs. 0.14 ± 0.01 m^2 per 144 m^2) (Ceccon *et al.* 2002).

METHODS

In each forest area (i.e. young and old), sixteen 12 × 12-m plots with 8-m-width buffers between them were established during 1997. The plots were randomly assigned to one of four treatments (i.e. a completely randomized design): control, added nitrogen (N), added phosphorus (P) and added nitrogen plus phosphorus (N+P). Each of the plots was replicated four times. For three consecutive years (1998–2000) fertilizers were added in two pulses, at the end of the dry season (May, 60% of the total annual amount of added fertilizer), and in the middle of the rainy season (September, 40% of the total annual amount). In the N+P treatments a mixture was added using the same protocol as in the individual nutrient additions. 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 yield (trunk width increment) responses in a Venezuelan tropical forest (Tanner *et al.* 1992). Dry fertilizers (urea, consisting of $(NH_2)_2CO$, or triple super phosphate, consisting of $Ca(H_2PO_4)_2 \cdot H_2O$, or both) were applied by hand, as appropriate, to each of the plots.

In all plots, species identity, density, frequency and basal area (derived from dbh measurements) of individuals were used to calculate Curtis & McIntosh's (1950) Importance Value (IV) (see Ceccon *et al.* 2002). Such IVs were used to select the three most important species with dbh ≥ 5 cm at each forest area. The species selected were *Acacia gaumeri* Blake, *Leucaena leucocephala* Wit and *Lysiloma latisiliquum* (L.) Benth. at the young forest area and *A. gaumeri* Blake, *Pithecellobium dulce* (Roxb.) Benth. and *Bursera simaruba* (L.) Sarg. at the old forest; with the exception of *B. simaruba* (Burseraceae) all species are members of the Leguminosae.

Four healthy (one per plot), mature individuals of each

selected species were randomly chosen for leaf sampling. Mature leaves from ten twigs (haphazardly retrieved from all parts of the crown to ensure that all zones of the canopy were represented) of each individual were obtained in September 2000, 3 mo after the onset of the rainy season. For each forest site the three selected species were represented in all nutrient treatments, except *A. gaumeri* in N-fertilized plots of the old forest where this species was absent. Leaf samples were immediately brought to the laboratory in polythene bags. The sampled leaves of each individual tree belonging to each of the species were mixed and, from this stock, two subsamples were drawn; one was used to analyse nutrient concentration and the other was used to measure herbivory.

All of the subsamples for nutrient analysis (leaf laminae) were oven dried (60 °C for 48 h) and ground (40 µm mesh size). From these, two 0.5-g samples were chosen from each plant. Nitrogen and phosphorus content were determined by Kjeldahl digestion; the samples were digested with 7 ml of concentrated H_2SO_4, 1.1 g of digest mixture (K_2SO_4 and Cu_2SO_4, 9:1), and 3 ml of H_2O_2. Extracts and standards were analysed colorimetrically using an Auto Analyser II (Bayer, Germany).

Herbivory was measured on the basis of standing leaf area damaged (see Filip *et al*. 1995). For all legumes with small leaflets (*A. gaumeri*, *L. leucocephala* and *L. latisiliquum*) we estimated herbivory as follows. All the leaves from each selected plant were detached from the twigs and individually numbered. From these, a random sample of 20 was selected and per cent leaf area damage was estimated as the number of partly or completely eaten leaflets divided by the total number of leaflets per leaf × 100. This value, averaged for the 20 leaves, gave an estimate of per cent herbivory per tree. For the other two species (*B. simaruba* and *P. dulce*) the procedure was the same, except that leaf damage was estimated by measuring the leaf area eaten using a LI COR leaf area meter.

Statistical analyses for leaf quality were performed using SYSTAT (SYSTAT, Evanson, IL, USA); all statistical tests involved analysis of variance (ANOVA) by site. Where necessary, data were log-transformed. A significance level of P = 0.05 was used in all these tests. For the analysis of herbivory independent ANOVAs were carried out for each of the two forest types. Per cent herbivory data were analysed after arcsine transformation (Zar 1996).

RESULTS

Young forest

Leaf nitrogen and phosphorus concentrations in unfertilized plots differed considerably among species (by 40% in the case of nitrogen, and by a factor of 2 in the case of

Table 1. Leaf nitrogen and phosphorus concentration of dominant tree species under four treatments of nutrient addition in a young and an old secondary tropical dry forests of Yucatán, Mexico. Values for each species are means ± SE of four plots.

Forests/Species	Treatment	N (%)	P (%)
Young forest			
Acacia gaumeri	Control	2.64 ± 0.35	0.08 ± 0.02
	N	2.88 ± 0.25	0.14 ± 0.03
	P	2.32 ± 0.17	0.10 ± 0.01
	N + P	2.50 ± 0.34	0.15 ± 0.01
	Significance		NP**
Leucaena leucocephala	Control	2.49 ± 0.30	0.10 ± 0.02
	N	3.27 ± 0.25	0.18 ± 0.02
	P	2.83 ± 0.43	0.16 ± 0.03
	N + P	3.13 ± 0.27	0.17 ± 0.02
	Significance		N**, NP**
Lysiloma latisiliquum	Control	1.88 ± 0.08	0.05 ± 0.01
	N	1.99 ± 0.22	0.08 ± 0.01
	P	2.04 ± 0.25	0.08 ± 0.02
	N + P	2.34 ± 0.27	0.09 ± 0.01
	Significance		N*, NP**
Old forest			
Acacia gaumeri	Control	2.34 ± 0.20	0.17 ± 0.03
	N	nd	nd
	P	2.42 ± 0.22	0.22 ± 0.04
	N + P	2.57 ± 0.16	0.23 ± 0.03
Bursera simaruba	Control	1.41 ± 0.15	0.15 ± 0.03
	N	1.83 ± 0.13	0.15 ± 0.02
	P	1.83 ± 0.18	0.18 ± 0.03
	N + P	1.81 ± 0.13	0.21 ± 0.03
	Significance	N*, P*, NP*	
Pithecellobium dulce	Control	2.04 ± 0.14	0.14 ± 0.01
	N	2.62 ± 0.27	0.14 ± 0.02
	P	2.62 ± 0.24	0.16 ± 0.04
	N + P	2.55 ± 0.28	0.20 ± 0.04

nd, non-available data.
Significance of main effect: *P < 0.05, **P < 0.01.

phosphorus) (Table 1). Addition of N plus P consistently increased leaf phosphorus concentration in all three species relative to control. In addition, the effect of N enrichment significantly increased foliar phosphorus concentration in *Leucaena leucocephala* and *Lysiloma latisiliquum*. In contrast, application of fertilizers did not have a significant effect on leaf nitrogen concentration in any of the species.

Levels of herbivory were very consistent across species within each of the fertilization treatments. The range of variation across species was only 1% in controls and 3% in all three fertilization treatments. An analysis of variance of herbivory among the three species indicated that interspecific variation was statistically indistinguishable (F = 2.66, P > 0.07). Therefore, we combined the results of these three legumine species, and only report the effects of fertilization. We found an increasing gradient of herbivory in the direction of Control < P < N < N+P (Figure 1a). The corresponding ANOVA indicated that this gradient is highly significant (F = 28.6, P < 0.0001) and paired comparisons using the Tukey–Kramer HSD test shows that plants of the control plots consistently sustained lower levels of damage (P < 0.05 in all cases), while plants in N+P treatment were the most heavily damaged

(P < 0.05 in all cases). Plants of the N and P treatments constituted an intermediate, statistically homogeneous group (P > 0.05). These results are consistent with the higher concentration of P in the foliage of the plants in the N+P plots in comparison with those of the control plots (see Table 1).

Old forest

Leaf nitrogen concentration in control plots differed among species by a factor of 1.7, largely reflecting differences in N requirements between leguminous trees and *Bursera simaruba* (Table 1). In contrast, differences in leaf phosphorus among species in control plots were low and non-significant. Addition of nutrients increased leaf nitrogen concentration in *B. simaruba*, in comparison to the other species, by ~30% (Table 1). However, fertilization did not affect the concentration of foliar nitrogen of the leguminous trees. Although the addition of P or P plus N increased the concentration of phosphorus in the foliage of the three species by about 30% with respect to the controls, this tendency was not significant (Table 1). Thus, although the interaction N+P was not significant (P > 0.05), leaf phosphorus in *B. simaruba* and *P. dulce* increased by 14% and 20%, respectively, in comparison with the P treatment alone.

The gradient of herbivory across treatments detected in the plants of the young-forest plots was not observed in the old forest (Figure 1b). In this forest, two of the species, *B. simaruba* and *P. dulce*, showed a similar response, while *A. gaumeri* consistently had the lowest levels of herbivory among this set of species. Furthermore, while *B. simaruba* and *P. dulce* did not exhibit significant variation in herbivory across treatments (F = 1.39, P = 0.27 and F = 0.715, P = 0.56, respectively), *A. gaumeri* in this site showed significant variation (F = 4.11, P = 0.039), with a comparable response to that it exhibited at the young forest: plants of *A. gaumeri* in the N+P fertilization had significantly higher levels of herbivory than in the other treatments (Tukey–Kramer HSD, P < 0.05). The homogeneous response of the plants of *B. simaruba* and *P. dulce* in this site is consistent with the lack of a significant pattern of phosphorus concentration in their foliage, as well as nitrogen in the case of the latter species. However, the lack of response of *B. simaruba* is inconsistent with the observed variation in nitrogen concentration in its foliage. The significant increase in herbivory of *A. gaumeri* in the N+P treatment is consistent with the higher concentration of both nitrogen and phosphorus in leaves in the N+P fertilized plots (Table 1), even though such variation is not statistically significant.

DISCUSSION

Soil nutrient additions generated plant responses in terms of leaf nutrient concentrations that suggest nutrient limita-
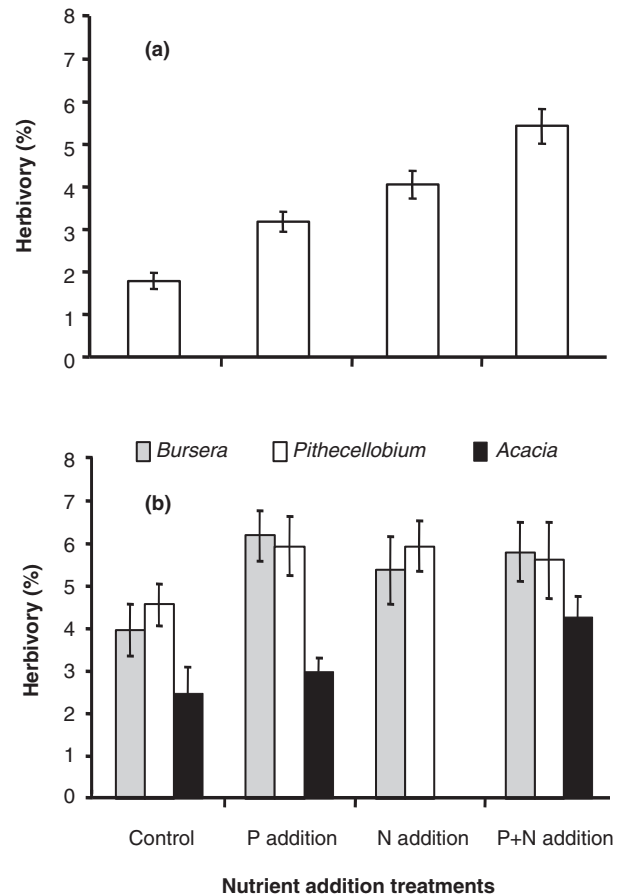

Figure 1. Levels of herbivory (mean ± SE per cent leaf area eaten) per plant under four treatments of soil nutrient addition in a young and an old secondary forest of the Yucatán Peninsula. The data correspond to the three dominant species (a) in the young forest (*Acacia gaumeri*, *Leucaena leucocephala*, *Lysiloma latisiliquum* combined) and (b) in the old forest (*Bursera simaruba*, *Pithecellobium dulce*, *Acacia gaumeri*).

tion in young forests of the Yucatán Peninsula. The mean N:P mass ratio in leaves from plants of young-forest plots without fertilization was greater than 16 (range 25 to 38). This value has been suggested to be indicative of P-limited ecosystems (Koerselman & Meuleman 1996). However, in the old forest the N:P mass ratio only ranged from 9 to 14, suggesting a lack of P-limitation. Interestingly, the leaf phosphorus concentrations of *Acacia gaumeri*, the only species present in both sites, suggest that there is an accumulation of P within plant tissues with regeneration time. In accordance, P is higher in old-forest soils than in young-forest soils. This finding is consistent with the argument that the young forests of the Yucatán Peninsula are P-limited ecosystems and that such limitation decreases with regeneration time (Ceccon *et al.* 2002). This hypothesis could be verified with a study of primary production at the ecosystem level, analysing the way in which P-limited forests respond to a release of such limitation (see Harrington *et al.* 2001).

The results of this study show a striking contrast in the consequences of addition of N+P in an ecosystem with low supply of P, such as the young forest, in comparison with an ecosystem with higher nutrient supply, such as the old forest. Fertilization of low-supply systems with N+P leads to a very high increase in foliar phosphorus, much higher than in the site where P is less limiting (as might be expected if simple passive uptake was involved). This effect is much greater than that observed for foliar nitrogen in both forests. Studies of young eucalyptus plantations in Australia (Bennet *et al.* 1996, Judd *et al.* 1996) and *Metrosideros polymorpha* in Hawaiian sites (Cordell *et al.* 2001, Vitousek 1998) also have reported a large increase in leaf phosphorus concentration following P and/or N+P additions, and a lesser increase in leaf nitrogen following the addition of N alone or together with P. When results of *Acacia gaumeri* in both sites are considered, we observed that trees with low leaf phosphorus concentration (i.e. controls from young forest) showed responses to nutrient additions but not those with high leaf phosphorus (i.e. controls from old forest). Thus, our study also suggests that the response of leaf phosphorus concentration to fertilization depends on the initial foliar nutrient status of the plants which is an index of site fertility.

The overall levels of herbivory we observed in these plants are lower than the average for plants from primary seasonally dry tropical forests of Mexico (6.7–9.2% in three consecutive years; see Dirzo & Domínguez 1995). However, no data are available to assess if our levels of herbivory are related to the type of soils (limestone), or the regenerating nature of our sites, or the fact that no data are available for legumes with small leaflets, as is our case. Clearly, this is an aspect that warrants further investigation. Nevertheless, even within the low levels of herbivory in our study site, we detected significant variation among forest types and species. Leaf damage shown by N+P-fertilized trees in the P-limited young site was significantly higher than in unfertilized plots. We cannot determine whether such increase in herbivory resulted from the observed increased concentration of P itself (thus relaxing a possible direct nutrient limitation to herbivores), or whether it reflects decreased defences in leaves (an indirect consequence of increase in nutrient supply) (cf. Cunningham *et al.* 1999), or both. Again, fertilization with N+P had no comparable effects on leaf N concentration. Although the relation between leaf N and palatability to herbivores is well established (see Coley & Barone 1996), the relation between leaf P and herbivory is less clear.

Soil P availability in the old forest lies at the lower end of the range reported for tropical dry forest soils (Ceccon *et al.* 2002). In this site, fertilization did not affect P concentration in leaves as would be expected. However, the leaf N concentration in the N+P-fertilized *Bursera simaruba* trees increased with respect to unfertilized plots, suggesting a luxury consumption of N beyond its functional requirements. The lack of a concomitant response in terms of increased herbivory is surprising, as increased N concentration in leaves has been found to increase herbivory rates in rain-forest plants (Coley & Barone 1996, Coley & Kursar 1996). Thus, although we observed a clear relationship between leaf nutrient concentration and herbivory in all three legumes in the young forest, the response of two of the species in the old forest site was unclear and only the legume *A. gaumeri* yielded a similar response to that showed at the young forest site. An understanding of the lack of responses to nutrient addition in the tree species of the old site will need to consider differences in specific resource requirements and lags in species responses. In any case, our results show that, in addition to the inter-specific variation in resource allocation to defence, leading to predictable patterns of herbivory in tropical forest plants (Coley *et al.* 1985, Coley & Barone 1996), an environmentally induced, phenotypic response, may be also determinant of the levels of herbivory.

From an ecosystem perspective, if the increased rates of damage by herbivores we observed in leaves from fertilized plots continue, our results suggest that the young forest site could exhibit a positive feedback due to enhanced P availability resulting from a more rapid return of nutrients to the soil and due to high amounts of P mineralization from high-quality litter. The mechanisms underlying this plant effect could be more complex than a simple increase in P return to soil because it has been observed that fertilization significantly enhanced both P availability and potential N mineralization in the young-forest soils (E. Solís, *pers. comm.*). Additionally, a possible negative feedback for P availability by nutrient export from the ecosystem by insects could be balanced by an increase of litterfall production with respect to unfertilized plots, such as that observed after 3 y of fertilization in our study sites (J. Campo, unpubl. data).

Aside from these short- and long-term scenarios, our study on the consequences of the spatio-temporal variation in nutrient supply in limestone soils of the Yucatán Peninsula, allows us to conclude that the regulatory mechanisms of leaf quality and damage by herbivores in these ecosystems will vary, depending on the details of the site's nutrient limitations and the identity of species. Given the potential for tropical forest regeneration subsequent to the massive impact of land use on tropical ecosystems (Dirzo 2001), the topic of the present study warrants subsequent investigation.

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