Light and nutrient effects on growth and allocation of *Inga vera* (Leguminosae), a successional tree of Puerto Rico

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Abstract: With the aim of acquiring a better understanding of ecological growth and biomass allocation of Neotropical trees, I inoculated *Inga vera* Willd. (Leguminosae) plants from cuttings with *Rhizobium* spp. and arbuscular mycorrhizal fungi and grew them in a greenhouse for 8 months under varying light (L), phosphorus (P), and nitrogen (N) treatments. I obtained the following results: (1) L, P × N, and L × P × N treatments affected every response variable, but most increases occurred under full light; that is, light levels influenced growth of *Inga vera* to a greater extent than did P and N additions by themselves; (2) response variables showed a high degree of similarity in regard to which combination of treatment levels had the greatest positive response (full light – low N – high P) and which combination led to other significant increases (full light – low N – no P, full light – high N – no P); and (3) percent AM colonization was affected mainly by light, not P levels. I conclude that growth responses of *Inga vera* are primarily controlled by light availability, which can interact with nutrient addition to affect biomass allocation to both above- and below-ground structures.

Résumé : Dans le but de mieux comprendre l'écologie de l'allocation à la croissance et à la production de biomasse chez les arbres néotropicaux, des plants d'*Inga vera* Willd. (légumineuse) issus de boutures ont été inoculés avec *Rhizobium* spp. et des champignons mycorhiziens à arbuscules. Les plants ont été cultivés en serre pendant huit mois et soumis à différents niveaux de lumière (L), de phosphore (P) et d'azote (N). Les traitements L, P × N et L × P × N ont affecté toutes les variables dépendantes mais la pleine lumière a eu le plus d'effet; c'est-à-dire que les différentes intensités de lumière ont davantage influencé la croissance d'*I. vera* que l'ajout de P ou de N seulement. Les variables dépendantes ont démontré un fort degré de similitude quant à la combinaison de traitements qui a produit la plus forte réponse positive (pleine lumière – faible N – P élevé) et celles qui ont produit d'autres augmentations significatives (pleine lumière – faible N – aucun P, pleine lumière – N élevé – aucun P). Le pourcentage de colonisation par les champignons mycorhiziens a surtout été affecté par les différents niveaux de lumière mais les différents niveaux de P n'ont eu aucun effet. Les résultats indiquent que la croissance d'*I. vera* est surtout contrôlée par la disponibilité de la lumière qui interagit avec l'ajout de nutriments pour affecter l'allocation de biomasse vers les parties aériennes et souterraines.

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Introduction

The availability of light, nutrients, and water is often less than that needed for maximum plant growth, so plants display growth and allocation trade-offs (Grime 1979; Tilman 1988). Classic plant adaptations that illustrate such trade-offs include regulation of leaf stomatal conductance to maximize CO_2 uptake while minimizing water loss, and finely tuned allocation of photosynthates to shoots and roots for efficient uptake of nutrients and water (Smith and Huston 1989). In particular, successional plants may be adapted to points on temporal resource gradients of inversely proportional combinations of above- (e.g., light) and below-ground (e.g., nutrients, water) resources (Tilman 1988).

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Plant adaptations and evolutionary strategies are plastic in trade-off responses, which involve light, phosphorus (P), nitrogen (N), and arbuscular mycorrhizal (AM) fungi (Harley and Smith 1983; Bazzaz et al. 1987; Allen 1991) capable of increasing P uptake. AM fungi may also increase the uptake of water and nutrients as well as inhibit the formation of N-fixing nodules for some legumes on P-poor soils (Mabberley 1992), while increasing nodule size (Janos 1980), and inhibit nodulation and lower N-fixation rates in most other legume species (Hayman 1987; Franco and deFaria 1997). In addition, AM fungi may affect nodulation through competition both directly for host carbon and indirectly through resources that AM and nodulation supply independently to the host (Cluett and Boucher 1983). Furthermore, AM fungi may take up N themselves (Melin 1953; Siqueira et al. 1998), which can account for up to 43% of the annual throughput of N in an ecosystem (Mosse 1973).

Such strategies and trade-offs may be particularly important for determining Neotropical plant distribution, abundance, and composition (Edmisten 1970; Oberbauer 1983; Calderon-Gonzalez 1993; Franco and deFaria 1997). In addition, this information may be critical to restoration efforts

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in degraded lands in the tropics (Zangaro et al. 2003) because disturbance disrupts soil nutrients and AM fungi (Myster and Fernandez 1995; Zangaro et al. 2003). In fact, N, added to the system by *Inga* and other legumes, is a key factor in Neotropical succession and recovery after disturbance (Marrs et al. 1983; Myster and Fernández 1995).

To better understand light, P, N, and AM interactions, and how they affect the growth and biomass allocation patterns of Neotropical trees, I conducted a greenhouse experiment using *Inga vera* Willd. (Leguminosae), a common mid-successional tree found in Puerto Rico and elsewhere in the Neotropics (Little and Wadsworth 1989). *Inga vera* is an ideal test species both for light effects because it is an early-successional tree in tropical forests (Bazzaz and Pickett 1980) and for N and P interactions because it forms root nodules with the bacteria *Rhizobium* (with a high concentration of N in its tissues: Scatena et al. 1993; Myster 2002) and is facultatively mycorrhizal (Calderon-Gonzalez 1993), thus having a tripartite system, or double symbiosis, typical of plants in severely disturbed areas (Harley and Smith 1983; Myster and Walker 1997).

The main objective of this study was to understand how *I. vera* establishes in moderately disturbed habitats, and how its twin strategies of N_2-fixation and AM dependency help it grow under changing light and nutrient conditions. More specifically — and unlike previous tropical tree investigations — this study includes the interactive effects of light reduction and both N and P addition, separately and in combination, on the general growth of *I. vera* and on the allocation of biomass to N and to P uptake structures (e.g., root biomass, percent root infected by AM, nodule biomass). Although it may be hypothesized that increases in P and N should decrease allocation to AM and nodules, respectively, past studies have not completely examined the interactive effects of light and nutrients on these structures and on plant growth.

Methods

Study site

In early August 1995, stem cuttings a few centimetres tall were collected from a single tree of *I. vera* (Leguminosae), growing along the roadside in the Luquillo Experimental Forest (LEF), Puerto Rico. The LEF is a Long-Term Ecological Research (LTER) site of the National Science Foundation (Myster et al. 1997), and all the data used in this study can be found on the LTER Web site (http://luq.lternet.edu). The collection area is at 370 m of elevation and receives approximately 2.6 m of rainfall annually. Glasshouse facilities were supplied by the International Institute of Tropical Forestry US Forest Service and were located in Rio Piedras, Puerto Rico. The cuttings were grown in 1 L pots, filled with potting soil, until they were 10–12 cm tall, were nearly equal in basal diameters, and had developed suitably sized root system. This method of propagation was chosen over seeds and (or) cuttings from multiple individuals to minimize genetic variability and its effect on the responses measured. Although limiting the scope of inference, the approach led to increased robustness of the statistical results.

Experimental design

One hundred and thirty-five plants of similar height, chosen for the experiment, were transferred to 2.9 L pots that were filled with soil collected from the center of a single LEF landslide. To determine the P treatment levels, a preliminary experiment was performed on the soil (phosphorus-fixing clay with high iron concentrations: Myster and Fernandez 1995) by adding P (in the form of triple super phosphate (P_2O_5)) to soil samples until there was a saturation of the fixation sites. This occurred at 0.68 g/m^2 of pot surface area (0.00429 kg/m^2 of dry soil to 9 cm depth) with a large increase of extractable P (Olsen extraction procedure: Hunter 1974).

A 3 × 3 × 3 factorial set of treatments in a randomized complete-block design was used, representing three treatments with three levels each: light (full-light control; 50% light reduction with a black shade cloth; 80% light reduction with a black shade cloth), P (no P added; low P, 0.68 g/m^2 triple super phosphate added once at the start of the experiment; high P, 0.68 g/m^2 triple super phosphate added at the start of the experiment and after 3 and 6 months), and N (no N added; low N, monthly addition of 4.5 g/m^2 urea ($CO(NH_4)_2$) and 2.8 g/m^2 ammonium nitrate (NH_4NO_3); high N, monthly addition of 9.1 g/m^2 urea and 5.7 g/m^2 ammonium nitrate: see Fetcher et al. 1996). The low N treatment translated into 0.02838 kg/m^2 of dry soil to 9 cm depth of urea and 0.01766 kg/m^2 of dry soil to 9 cm depth of ammonium nitrate.

The levels of the light, N, and P in the glasshouse treatments were similar to light, N, and P conditions in LEF successional areas where *I. vera* is commonly found, e.g., landslides (Myster and Walker 1995), and landslide soil was used in the treatments. For example, *I. vera* grows in the lower debris areas of landslides under the following ranges: 4%–31% of full light, 0.05–0.20 kg/m^2 to 9 cm depth of N, and 0.003–0.015 kg/m^2 to 9 cm depth of P (Myster and Fernández 1995; Fernández and Myster 1995). Similar levels of N and P were used in another Puerto Rican greenhouse experiment on successional trees (Fetcher et al. 1996). Light levels in the greenhouse were within 85%–90% of full sunlight (full sunlight provides a photosynthetic photon flux density of approximately 40 mol·m^{-2}·day^{-1}: D. Schaefer, personal communication; Myster and Fernandez 1995). There were five replicates of each treatment combination. Shading treatments were achieved with sleeves sown from the shade cloth and then fit over the entire pot and tightly secured.

All propagation and growth pots were inoculated with 50 g of *Guarea* sp. root fragments that were collected from under a single *Guarea* tree in the field, leading to infection with the bacteria *Rhizobium* spp. and AM fungi that infect *Inga* and many other tree species (Calderon-Gonzalez 1993; N. Fetcher, personal communication). This was done to minimize the possibility that treatment differences in root mass could affect the percentage of root colonized by AM. Past studies have shown that the AM colonization found in a greenhouse is a reliable tool for estimating AM colonization in the field for native tropical trees (Zangaro et al. 2000). Although addition of N could potentially alter P availability through modification of soil pH (Schlesinger 1991), similar experiments on LEF landslide soil have suggested that this

Table 1. ANCOVA summary table of response variables with their *F* values and *P* values (in parentheses).

Source	Final height	Leaf biomass	Primary root biomass	Secondary root biomass	Stem biomass	Root nodule biomass	Percent AM	Total biomass
L	6.85 (0.001)	17.36 (0.001)	13.40 (0.001)	13.47 (0.001)	13.37 (0.001)	5.55 (0.005)	4.12 (0.020)	16.21 (0.001)
P	1.41 (0.249)	0.14 (0.867)	0.48 (0.621)	0.31 (0.730)	0.64 (0.529)	1.01 (0.370)	0.34 (0.714)	0.25 (0.778)
N	0.92 (0.401)	0.63 (0.536)	0.15 (0.858)	0.18 (0.839)	0.11 (0.894)	0.46 (0.634)	0.42 (0.656)	0.32 (0.725)
L × P	1.14 (0.346)	0.12 (0.973)	0.29 (0.884)	0.06 (0.993)	0.47 (0.758)	0.29 (0.882)	1.58 (0.189)	0.18 (0.949)
L × N	1.44 (0.227)	1.17 (0.332)	1.71 (0.151)	1.36 (0.255)	0.77 (0.550)	1.87 (0.124)	0.76 (0.551)	1.20 (0.319)
P × N	6.88 (0.001)	3.57 (0.041)	4.46 (0.002)	4.37 (0.003)	3.10 (0.020)	3.54 (0.036)	0.20 (0.939)	3.79 (0.007)
L × P × N	3.86 (0.021)	4.52 (0.011)	4.03 (0.015)	4.64 (0.007)	3.42 (0.033)	2.85 (0.046)	1.01 (0.443)	4.42 (0.017)

Note: *P* values less than 0.05 were considered significant. L, light; P, phosphorus; N, nitrogen.

should not be a concern (Fetcher et al. 1996). The temperature and relative humidity were monitored inside the glasshouse where a daily watering regime was maintained. Under glasshouse conditions, the mean daily temperature was 30 °C, with a range of 25–35 °C, and the mean humidity was 80%, with a daytime maximum of 55% and a nighttime maximum of 95%.

Statistical analysis

After 2 months of growth, the experiment started on 1 October 1995 when plants that were at least 10 cm tall were measured for initial height. Eight months later, final height was measured, plants were harvested, and a fine-root sample was taken for AM analysis. Fine roots were cleared with alternating hot KOH and cold H_2O_2 with NH_4OH and HCL. The roots were then acidified with 5 drops of HCL, stained with acid fuchsin, and mounted on microscope slides with glycerin. The density of AM was estimated by placing the slide on a 5 mm grid and noting the proportion of roots intersecting with the grid that were mycorrhizal (Myster and Fernandez 1995). It was observed that the pots had adequate room for plant growth. Each plant was dried at 65 °C for 48 h, then divided into stem, leaf, and root (primary, secondary, nodules) subsamples and weighed. During this process, root samples were examined under a dissecting microscope. Variables measured were final height, stem biomass, leaf biomass, primary root biomass, secondary root biomass, root nodule biomass, percentage of fine roots colonized by AM, and total biomass.

Treatment effects were investigated with a three-way (L, P, N) analysis of covariance (ANCOVA; SAS Institute Inc. 1985) for each of the response variables separately, using initial height as the covariate. Homogeneity of variances was checked in all cases, and normality was assured. Pots were arranged randomly in the greenhouse, and there were no significant block effects due to pot location within the greenhouse. The Ryan–Einot–Gabriel–Welsch multiple range test (SAS Institute Inc. 1985) was used to investigate significant differences among treatments. The sequential Bonferroni test (Rice 1989) was employed to investigate whether any significant effects should be viewed with suspicion, because of the large number of ANCOVA performed.

Results

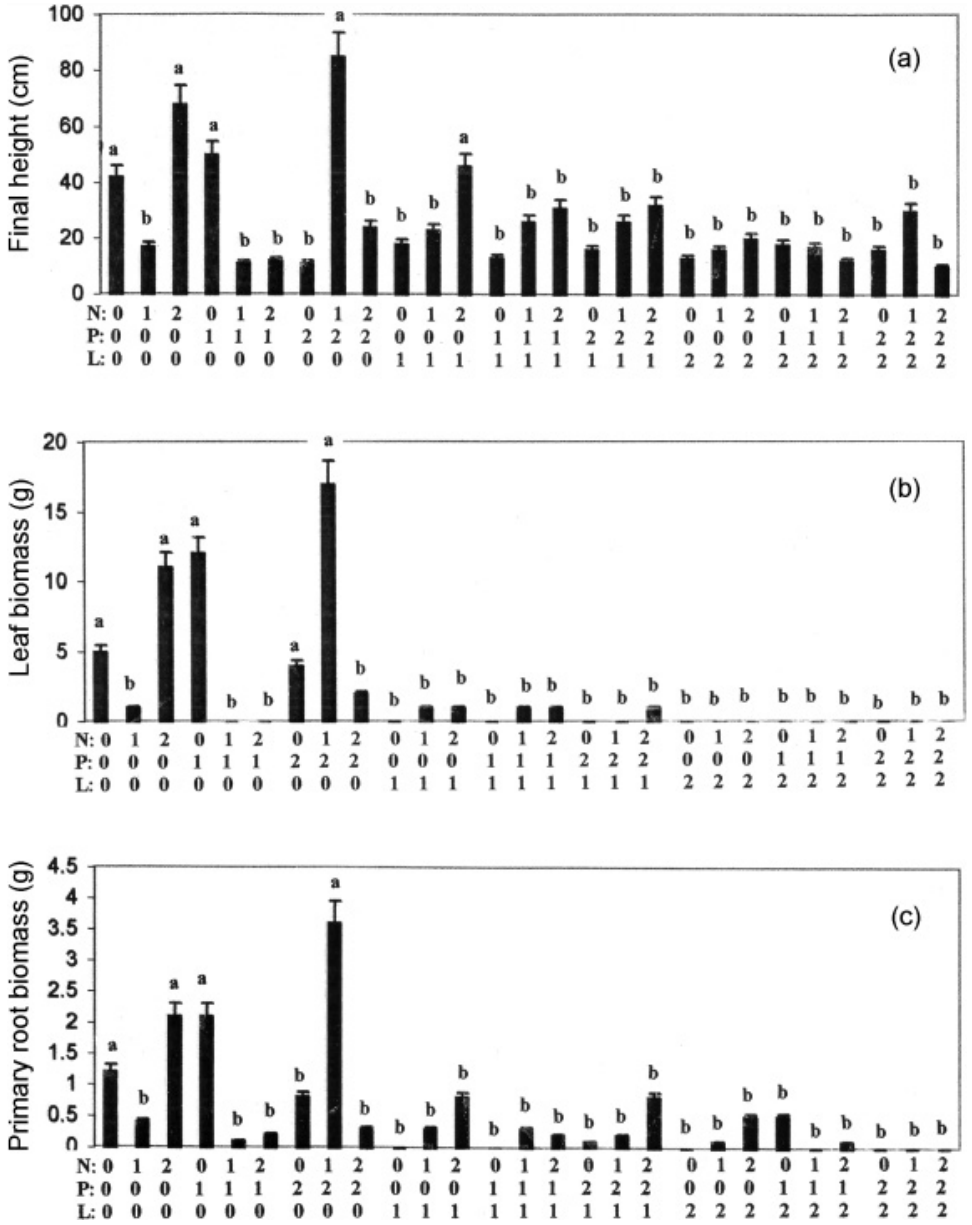
For full-light control plants, mean total biomass was 11.2 g and survival rate was 100%. For plants under the 50% light reduction treatment, mean total biomass was 9.8 g and survival rate was 100%, and for plants under the 80% light reduction treatment, in combination with all other treatment levels, mean total biomass was 8.2 g and survival rate was 65%. The three-way ANCOVA showed that the only significant main effect was the light treatment, which had an effect on all response variables, and the only significant interaction effects were the two-way P × N interaction and three-way L × P × N interaction, which also had an effect on all response variables except percent AM colonization (Table 1). Consequently, for all response variables (except percent AM), the L × P × N interaction effects are presented as the best way to interpret all effects.

Figure 1*a* shows that seedlings under full light (low N – high P) had the greatest final height, and that all other significant increases of the response variables also occurred under full light (no N – no P, high N – no P, no N – low P), except for one, which occurred under 50% light reduction (high N – no P). Figure 1*b* shows that all significant increases of leaf mass were under full light (no N – no P, high N – no P, no N – low P, no N – high P), with the greatest increase with low N – high P. Figure 1*c* shows that all significant primary root biomass increases occurred under full light (no N – no P, high N – no P, no N – low P), with the greatest again under low N – high P.

Figure 2*a* shows that secondary root biomass had significant increases only with the exact same treatment combinations that produced significant increases in primary root biomass, with the greatest increases again occurring at low N – high P. Figure 2*b* shows that stem biomass also significantly increased with the exact same treatment combinations that produced significant increases in primary root biomass, with the greatest increases again occurring at low N – high P, but with an increase under no N – high P in full light as well. Figure 2*c* shows that all significant increases of responses variables were under full light (high N – no P, no N – low P, no N – high P, low N – high P), except for one, which occurred under 80% light reduction (high N – low P).

Figure 3*a* shows that all significant total biomass increases occurred under full light (no N – no P, high N – no P, no N – low P, no N – high P), with the greatest increases occurring under low N – high P. Figure 3*b* shows a significant increase in percent AM colonization under both 50% and 80% light reduction, with the most colonization at 80% light reduction. As suggested by the Bonferroni test and because of the low number of significant effects compared with the number of tests performed, no results warranted re-evaluation.

Fig. 1. Response of *Inga vera* (A) final height, (B) leaf biomass, and (C) primary root biomass for the significant L × P × N interactions seen in Table 1. Levels of the L treatments are full light (L = 0), 50% light reduction (L = 1), and 80% light reduction (L = 2), the P treatment levels are no P addition (P = 0), low P addition (P = 1), and high P addition (P = 2), and the N treatment levels are no N addition (N = 0), low N addition (N = 1), and high N addition (N = 2). Means and standard error bars are presented. Means with the same letters are not significantly different according to the Ryan–Einot–Gabriel–Welsch multiple range test.

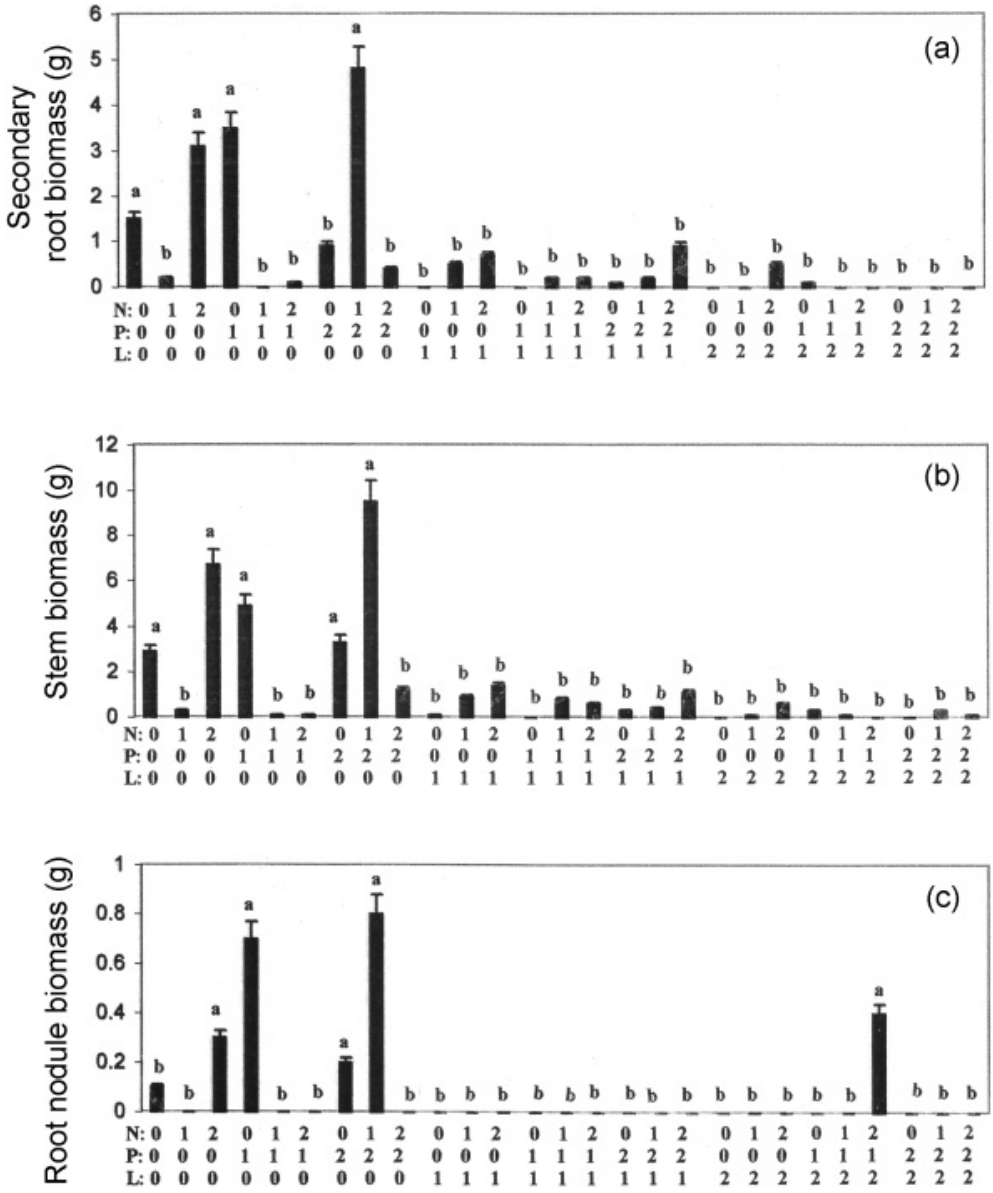


Discussion

The main conclusion that can be drawn from the glasshouse experiment described here is that light levels influence growth of *I. vera* to a greater extent than P and N additions by themselves because almost all significant increases were under full light. Not surprisingly then, seedlings of this tropical tree grew less under low light intensity (Gehring 2003). This finding relates well with the ecology of this species because *I. vera* grows in mid-successional stages of recovery, where light is reduced and because light availability is likely to be the resource that most frequently limits growth, survival, and reproduction in the tropics (Bazazz and Pickett 1980; Fetcher et al. 1994; Kitajima 1996). Response variables showed a high degree of similarity as to which combination of treatments had the greatest response (full light – low N – high P) and which combination led to other significant increases (full light – no N – no P, full light – high N – no P, full light – no N – low P). Results show a greater response to P addition than to N addition (Kitajima 1996). *Inga vera* could be exposed to high light levels after tree-fall gap formation.

Percent AM colonization was affected by light, not by P levels (Daft and Nicolson 1966; Pairunam et al. 1980), and there is experimental evidence for both a positive and a negative relationship between AM colonization and light levels

Fig. 2. Response of *Inga vera* (A) secondary root biomass, (B) stem biomass, and (C) root nodule biomass for the significant L × P × N interactions seen in Table 1. Levels of the L treatments are full light (L = 0), 50% light reduction (L = 1), and 80% light reduction (L = 2), the P treatment levels are no P addition (P = 0), low P addition (P = 1), and high P addition (P = 2), and the N treatment levels are no N addition (N = 0), low N addition (N = 1), and high N addition (N = 2). Means and standard error bars are presented. Means with the same letters are not significantly different according to the Ryan–Einot–Gabriel–Welsch multiple range test.

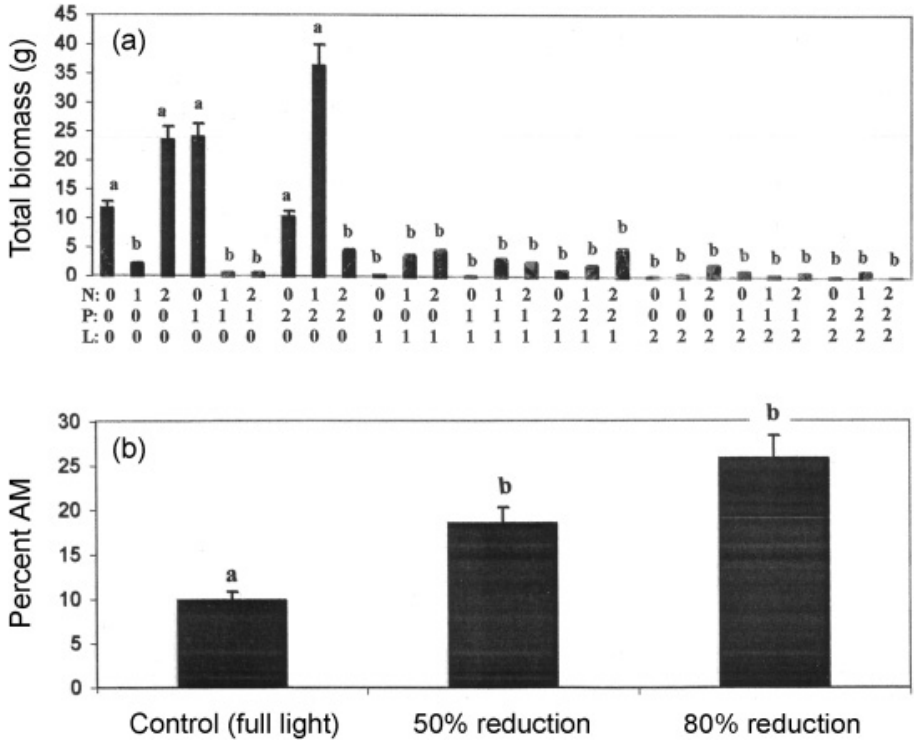


(Gehring 2003). These relationships, however, could not depend on seed reserves, since seedlings came from cuttings. Percent AM colonization for other *Inga* sp. raised in a greenhouse experiment was in a similar range of 17%–31% (Zangaro et al. 2003).

Effects of P and N additions from full light treatments showed that no N or low N addition treatments interacted at a greater significance with P treatments than did the high N addition treatment. Perhaps because *Inga* has the double symbiosis (R.W. Myster, unpublished data), the lowest N levels resulted in the most root nodulation (energy cost–benefit trade-offs: Van Kessel and Roskoski 1983). Results were consistent with another study that showed that leaf biomass was affected by the same resource levels as nodule biomass (Van Kessel and Roskoski 1981), but that study did not show whether legumes required AM infection for nodulation (Oberbauer 1983). The biomass increase under high N addition may reflect limiting P levels in landslide soils (Myster and Fernandez 1995; Fetcher et al. 1996). Finally, possible explanations for the greater responses at low N rather than high N for many of the response variables may include (1) specific *I. vera* biology, (2) pathogen infestation, or (3) treatment toxicity.

This study was motivated by the importance in the Neotropics of both interactions among L, P, and N and the plant strategies of AM association and N fixation (Edmisten 1970; Calderon-Gonzalez 1993), where P and N limit productivity (Waide et al. 1998). One advantage of the study

Fig. 3. Response of *Inga vera* (A) total biomass for the significant L × P × N interactions seen in Table 1, and (B) percent arbuscular mycorrhizae (AM) for the significant light main effect seen in Table 1. For total biomass, levels of the L treatments are full light (L = 0), 50% light reduction (L = 1), and 80% light reduction (L = 2), the P treatment levels are no P addition (P = 0), low P addition (P = 1), and high P addition (P = 2), and the N treatment levels are no N addition (N = 0), low N addition (N = 1), and high N addition (N = 2). For percent AM, light treatments are indicated directly. Means and standard error bars are presented. Means with the same letters are not significantly different according to the Ryan–Einot–Gabriel–Welsch multiple range test.



design was the possibility of examining light–nutrient interactions, allocation trade-offs (Thompson et al. 1988, 1992; Denslow et al. 1990; Riddoch et al. 1991; Turner 1991; Fetcher et al. 1996), and symbiotic relationships (Allen 1991; Calderon-Gonzalez 1993). Another important Neotropical issue is how resource interactions and AM colonization affect successional plants (Janos 1980, 1984; Myster and Fernandez 1995; Fetcher et al. 1996; Siqueira et al. 1998). Disturbance may break up and (or) remove enough roots to make AM limiting because AM generally live only on and between roots and not freely in the soil (Janos 1994). Consequently, on low fertility tropical soils facultative-mycorrhizal trees like *I. vera* may have difficulty establishing after severe disturbances. In a Puerto Rican landslide, for example, increased light and N × P interaction led to increased growth for the pioneer species *Cecropia schreberiana*, and N addition alone led to increased growth both for the mid-successional species *Palicourea riparia* and for the climax species *Manilkara bidentata* (Fetcher et al. 1996). Because the AM strategy and biology of these species are largely unknown (Siquerira et al. 1998) and none of them contain nodules that fix N, further interpretation is not possible

Results of this study relate well with experiments on other tropical trees. Riddoch et al. (1991) found that rates of tree growth increased after addition of nutrients and in response to a significant light–nutrient interaction, especially in the pioneer tree species *Nauclea diderrichii*. Thompson et al. (1988) showed that *Flindersia brayleyana* was unable to respond to high light when growing under a low nutrient treatment. Thompson et al. (1992) showed that the pioneer species *Toona australis* had a greater total biomass response than some climax species and that this response greatly increased after nutrient addition, but only under high light. Finally, two studies at La Selva Costa Rica used *Pentaclethra macroloba*, a tree species that also has a double symbiosis of mycorrhizae and N-fixing bacteria: Carpenter and Allen (1988) found that N increased leaf and total biomass both under full light and under 80% light reduction, but not under 98% light reduction, and that there was a significant P × N effect on leaf, root, and total biomass only in full sun, while Oberbauer (1983) found that N decreased nodulation both in full sun and at 80% light reduction, with no nodulation at 98% light reduction.

In conclusion, a complete understanding of tropical tree life histories should include not only the traditional traits of seed size, shade tolerance, and growth rate (Bazzaz and Pickett 1980) but also traits that are related to AM formation and N_2 fixation (Allen 1991). This study supports the findings of other studies on tropical trees: (1) at high light levels, successional species respond more to added P than to added N, particularly compared with primary canopy species (Huston 1982; Dalling and Tanner 1995; Fetcher et al. 1996); (2) at low light levels, there is little or no response to fertilization (Denslow et al. 1990); (3) light levels are critical because mortality is much greater under 80% light reduc-

tion; and (4) complex interactive effects of N and P, which are so important to Neotropical rain-forest regeneration and dynamics, are most apparent at high light.

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