

EFFECTS OF ABOVE- AND BELOWGROUND COMPETITION ON GROWTH AND SURVIVAL OF RAIN FOREST TREE SEEDLINGS

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Abstract. Because reducing aboveground competition for photosynthetically active radiation (PAR) increases growth and survival rates of tropical rain forest seedlings, belowground competition for nutrients is often assumed to be of little or no importance. We tested this assumption. We measured the growth, over one year, of seedlings of *Aspidosperma carapanauba* (shade tolerator) and *Dinizia excelsa* (light demander) transplanted into understory (high aboveground competition; 1% incoming photosynthetic photon flux density [PPFD]) and single treefall gap areas (lower aboveground competition; 6% PPFD in centers of gaps) without and with trenches cut around plots (high and low belowground competition). Over the wetter six months, location in gaps significantly increased relative height growth rates by 320% and 570%, and relative leaf production rates by 190% and 280%, while trenching significantly increased height by 330% and 520%, and leaf production by 170% and 260%, for *Aspidosperma* and *Dinizia*, respectively, with significant interactions between treatments. Trenching approximately doubled height growth in the understory. Leaf loss rates were unaffected by either treatment but were 3.7 times higher in *Dinizia* compared with *Aspidosperma*. *Aspidosperma* could persist in the understory, as leaf production and loss were balanced at 0.60% PPFD, whereas *Dinizia* could not, as it required 2.4% PPFD. Reducing either aboveground competition or belowground competition allowed *Dinizia* to persist as leaf production was increased above unchanging leaf loss rates. Gap and trenching treatments both significantly reduced mortality rates in *Dinizia*. Location in gaps significantly reduced mortality rates in *Aspidosperma*. Both species significantly increased allocation to leaves and significantly decreased allocation to roots in response to trenching. The increased growth in the wet season caused by trenching, and increased foliar nitrogen and phosphorus amount, showed that both species were probably competing with adult trees for nutrients as well as PAR. We deduced that phosphorus did not limit growth; however, we could not deduce which nutrient did limit growth. Given that 60–70% of the world's tropical rain forests occur on low-fertility oxisols, intense adult–juvenile competition both aboveground and belowground may be the norm, not the exception.

Key words: Amazonia; competition experiments; lowland tropical rain forest; nitrogen; nutrient availability; phosphorus; photosynthetically active radiation (PAR); root competition; seedling growth; tree fall gaps; trenching.

INTRODUCTION

Juvenile plants usually compete with the established vegetation within that community. In general, plants are likely to compete for three kinds of essential resources: photosynthetically active radiation (PAR), water, and essential nutrients. In tropical rain forests, competition for PAR is often assumed to be the important abiotic factor reducing juvenile plant growth and survivorship. Indeed, many studies have unequivocally established that increasing PAR (i.e., reducing aboveground competition) increases seedling growth and survival rates (e.g., Augspurger 1984, Popma and Bongers 1988, Uhl et al. 1988). However, an unproven secondary conclusion is that belowground adult–juvenile

competition is of little or no importance for seedling regeneration, a conclusion seemingly supported by the lack of effect of fertilizers on the growth of seedlings in the understory (e.g., Denslow et al. 1990). Three lines of evidence and one piece of theory suggest that release from belowground competition for nutrients may increase seedling growth and survival rates: field trenching experiments, pot experiments, field observations, and optimal foraging theory.

Reducing belowground competition in forests is most conveniently done by digging trenches around target plants, though the results of such studies are inconsistent. In three studies there was no effect of trenching on growth rates of target seedlings (Denslow et al. 1991, Ostertag 1998; P. J. Grubb, unpublished data), whereas three other studies showed approximately doubled height growth rates following trenching (Whitmore 1966, Fox 1973, Coomes and Grubb 1998).

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The studies that showed no effect were done on alfisols (La Selva, Costa Rica; Queensland, Australia), whereas the studies that showed significant effects were done on less fertile oxisols or psamments (Vanikoro, Solomon Islands; Sabah, Malaysia; La Esmeralda, Venezuela). This suggests that, on nutrient-poor soils, seedlings are competing with adult trees for nutrients as well as PAR. However, the strength of the conclusion that belowground competition is important on nutrient-poor soils but not on nutrient-rich soils is weakened by various deficiencies in some of the supporting studies. In the studies that showed no effects of trenching, Denslow et al. (1991) actually trenched control plots on one or two sides, and trenches were not lined, so roots grew into the trenched plots. Grubb's experiment was eventually abandoned due to excessive root ingrowth into the plots. In the studies that did show an effect, neither Fox nor Whitmore provided a statistical analysis. Only Coomes and Grubb's study in nutrient-starved Amazonian caatinga in Venezuela reported a rigorous trenching experiment that also measured the photosynthetic photon flux density (PPFD) seedlings received.

Pot experiments have shown that many plant species can increase growth rates with nutrient additions, but species differ as to the lowest PAR level at which they will respond to added nutrients (Peace and Grubb 1982, Latham 1992, Thompson et al. 1992a, Grubb et al. 1996). Experiments on tropical rain forest tree seedlings have shown that some species can respond to nutrient additions down to 0.5–3.0% PPFD in a nearby large clearing (Burslem et al. 1995, Burslem 1996, Burslem et al. 1996). In addition, glasshouse experiments using three rain forest species have shown that maximum rates of photosynthesis increased by an average of 30% and slopes of CO₂ fixation against PPFD increased in elevated nutrient treatments compared to controls when grown at ~2% of incoming PPFD (Thompson et al. 1988, Riddoch et al. 1991). If trenching increased nutrient availability, such increased slopes and maximum rates of photosynthesis would allow seedlings in trenched plots to increase carbon acquisition by taking greater advantage of sunflecks.

Field observations suggest that soils under central Amazonian terra firme forests are nutrient poor (Fearnside and Leal Filho, *in press*) and thus that understory plants might benefit from trenching if it increased nutrient availability. Gentry and Emmons (1987) reported numbers of fertile understory plants in 13 Neotropical rain forest sites and found that the highest densities of fertile understory plants were at sites with nutrient-rich soils and short/absent dry seasons. The area where we carried out the current experiment had the lowest density of fertile understory plants of any site studied (32 plants/ha), an order of magnitude less than sites with more nutrient-rich soils.

Optimal foraging theory suggests that because plants have morphological and physiological plasticity, they

can alter allocation patterns to stems, leaves, and roots to increase the acquisition of a resource that limits their growth. The theory suggests that plants should adjust allocation so as to be equally limited by all resources (Tilman 1988, Gleeson and Tilman 1992); hence they should be limited by belowground resources and respond to trenching if it increased belowground resources.

To test whether seedlings growing on nutrient-poor soils compete with adult trees for belowground resources as well as PAR, we transplanted seedlings of *Aspidosperma carapanauba* (shade tolerator) and *Dinizia excelsa* (light-demanding nonpioneer) into a two-factor factorial experiment. Factor one was trenching around plots (high vs. low belowground competition). Factor two was experimentally created treefall gaps (high vs. low aboveground competition). After transplanting at the start of the wet season, growth was measured six months later, toward the end of the wet season, and again one year after transplanting, after which plants were harvested and nutrient concentrations measured. The data were used to assess whether trenching and gaps did increase growth, and if trenching increased growth, whether it was due to increased nutrients and/or increased water availability.

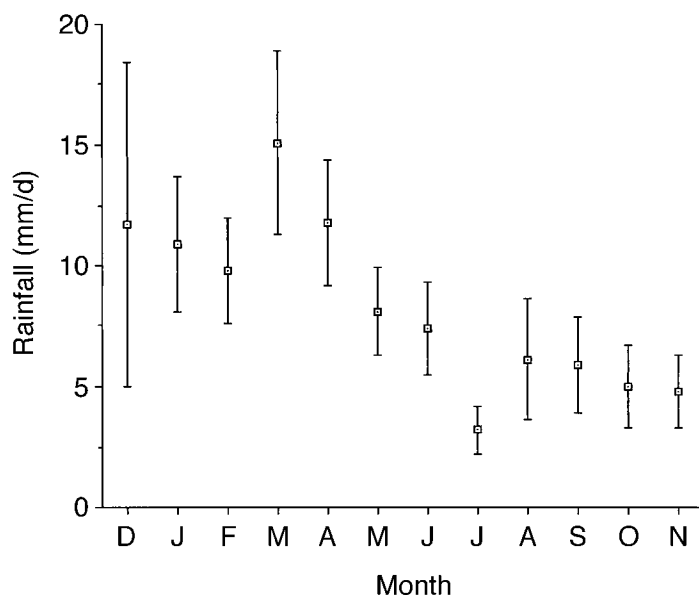
METHODS

Study area

The study area is ~80 km north of Manaus, Brazil, in central Amazonia (2°30'S, 60°W). The plots were located in continuous forests to the east and south of reserve 2303 of the joint Brazilian–U.S. Biological Dynamics of Forest Fragments Project (BDFFP; Lovejoy and Bierregaard 1990), and were 80–120 m above sea level. The 30-yr average rainfall for Manaus was 2186 mm (Anonymous 1978). On average the rainiest months are March and April (~300 mm each), and the driest July, August, and September (<100 mm each), thus giving a pronounced dry season; the climate is “tropical wet” with a perhumidity index of 10.5 (perhumidity index limits are –24 [driest] to +24 [wettest], Richards 1996). The rainfall for the year December 1995 through November 1996, the duration of the experiment, was 2838 mm at BDFFP reserve 1501, 45 km east from the study plots (Fig. 1). The canopy is 30–37 m tall with occasional emergents to 55 m. The basal area is 30.6 ± 3.5 m²/ha with 647 ± 51 stems/ha (>10 cm dbh); mean ± 1 SE; $n = 15$ one-ha plots; Rankin-de-Merona et al. 1990).

The soils in the plots are yellow latosols (Camargo 1979), or allic haplorthozes (USDA 1975), which are mildly to severely infertile in terms of agricultural potential. They are more fertile than the bleached white sand soils of Amazonian caatinga, but are less fertile than many soils under South American tropical rain forests, and especially infertile compared to the alfisols

FIG. 1. Daily rainfall per month (mean \pm 1 SE), from December 1995 to November 1996 at BDFFP reserve 1501, in central Amazonian rain forest. The larger SE value for December includes initial watering (see *Methods: species biology* ...).



of La Selva in Costa Rica where a trenching experiment showed no effects (Table 1).

Experimental design

We reduced aboveground competition by felling six large trees to create six single-treefall gaps, and reduced belowground competition by trenching. Thus there were four treatments: (1) untrenched subplots in understory areas (high aboveground, high belowground competition); (2) trenched subplots in understory areas (high aboveground, low belowground competition); (3) untrenched subplots in single treefall gaps (low aboveground, high belowground competition); and (4) trenched subplots in single treefall gaps (low aboveground, low belowground competition).

The replicates of the four treatments were half in

TABLE 1. Soil characteristics for various tropical rain forest sites, in order of increasing site fertility.

Soil characteristic	Caatinga, Venezuela ^a	This study (Brazil) ^b	S. American forests (n = 22) ^c	La Selva, Costa Rica ^d
pH	4.0 ^e	3.9	4.3	4.5
Total N (%)	0.03	0.16	0.15	0.42 ^f
Total P (mg/kg)	85	114	207	ND [†]
PO ₄ ³⁻ (cmol _c /kg)	0.3 [‡]	0.3 [§]	4.6	0.7 [¶]
K ⁺ (cmol _c /kg)	ND	0.6	0.88	2.9
Ca ²⁺ (cmol _c /kg)	ND	0.6	2.4	2.7
Mg ²⁺ (cmol _c /kg)	ND	0.8	1.7	2.7

Sources: These are indicated by lowercase superscript letters as follows: a, Coomes (1997); b, Fearnside and Leal Filho (*in press*); c, Thompson et al. (1992b); d, Sollins et al. (1994); e, Coomes (1995); f, Vitousek and Denslow (1986).

[†] ND = no data.

[‡] Resin exchangeable.

[§] Extractant 0.05 mol/L HCl + 0.025 mol/L H₂SO₄.

^{||} Dilute acid.

[¶] Acid fluoride extractant.

each of two areas of forest, ~3 km apart, which we call blocks. The two forest blocks were selected in an unbiased way being on the first "plateaus" encountered after 1 km along each of two new paths cut perpendicular to two continuous forest edges. In each block, six trees were selected that were on relatively flat ground, >0.35 m dbh. (mean diameter of chosen trees 0.41 m; SE = 0.09 m), not near any treefall gap or broken canopy and with an easily predictable direction of fall. The six trees were paired using their dbh. and one of each pair was randomly chosen and felled by chain saw on 16–17 May 1995; the other of each pair became an understory to which we assigned an area of 28 × 4 m. Each gap was stratified into base, trunk, and crown zones (base and crown zones were 4 × 4 m centered on the base or crown of the target tree, trunk zones were 20 m long × 4 m wide and connected base and crown zones); there were spatially equivalent subplots in the understory. In each zone of each plot, we randomly assigned two subplots (each 0.71 × 0.71 m), one trenched and one untrenched. Trenching consisted of removing a band of soil ~0.15 m wide and 0.5 m deep from the four sides of the plot to be trenched, lining the inside of the trench with heavy gauge plastic leaving a 0.05 m lip higher than the soil level (to prevent root ingrowth), and replacing the soil. Two seedlings of each of the two species were randomly assigned to each subplot and transplanted in a plot-by-plot order alternating between understory and gap plots, completing all transplanting in one block before starting the second (27 November and 12 December 1995). Thus there were four treatment combinations × six replicates (three in each block) × six seedlings per plot (three zones × two seedlings per subplot) = 144 seedlings transplanted for each species.

TABLE 2. Summaries of model fitting for relative height growth (R_H), leaf production (R_{LP}), and leaf loss (R_{LL}) rates for seedlings of *Aspidosperma carapanauba* and *Dinizia excelsa* transplanted into trenched and untrenched subplots in both understory areas and single treefall gaps in central Amazonian rain forest.

Factor	ss	df	F	P	r ²
<i>Aspidosperma</i> , height (R_H)†					
Trench	2.215	1	10.5	<0.01	0.227
Gap	1.963	1	9.31	<0.01	0.201
Trench × Gap	0.963	1	4.57	<0.05	0.099
Other terms	1.256	4	1.98	NS‡	0.129
Error	3.375	16			
<i>Dinizia</i> , height (R_H)†					
Trench	2.607	1	27.0	<0.001	0.219
Gap	4.403	1	45.5	<0.0001	0.371
Trench × Gap	2.609	1	27.0	<0.001	0.220
Other terms	0.715	4	1.85	NS	0.060
Error	1.547	16			
<i>Aspidosperma</i> , leaf production (R_{LP})					
Trench	1.131	1	14.2	<0.005	0.189
Gap	3.147	1	39.4	<0.0001	0.527
Trench × Gap	0.329	1	4.12	NS§	0.055
Other terms	0.086	4	0.27	NS	0.014
Error	1.277	16			
<i>Dinizia</i> , leaf production (R_{LP})†					
Trench	1.058	1	15.1	<0.005	0.189
Gap	2.726	1	38.9	<0.0001	0.484
Trench × Gap	0.371	1	5.29	<0.05	0.066
Other terms	0.353	4	1.26	NS	0.063
Error	1.122	16			
<i>Aspidosperma</i> , leaf loss (R_{LL})					
Trench	0.0017	1	0.02	NS	0.011
Gap	0.0913	1	1.35	NS	0.060
Trench × Gap	0.0864	1	1.27	NS	0.057
Other terms	0.2465	4	0.91	NS	0.163
Error	1.0852	16			
<i>Dinizia</i> , leaf loss (R_{LL})					
Trench	0.0022	1	0.02	NS	0.001
Gap	0.0630	1	1.35	NS	0.021
Trench × Gap	0.2795	1	1.27	NS	0.093
Other terms	0.7497	4	0.91	NS	0.250
Error	1.9086	16			

Note: The model has three two-level fixed factors: trench, gap, and block.

† Specifying gamma errors.

‡ NS = not significant.

§ $P = 0.06$.

Species biology and seedling measurements

Aspidosperma carapanauba Pichon (Apocynaceae) is an emergent tree with a deeply fenestrated trunk. It has simple leaves and winged fruits ~60 mm diameter containing a single seed. As a seedling it is considered “shade-tolerant” because its seedlings have a low mortality in the shade. *Dinizia excelsa* Ducke (Mimosaceae) is also an emergent tree and is a major timber species. It has double compound leaves with many leaflets and a seed mass of 0.17 ± 0.005 g ($n = 10$; C. Dick, unpublished data). As a seedling it is considered a “light-demanding nonpioneer,” because it has few seedlings in the shade and seedlings planted into the shade have a high mortality.

Dinizia seeds were collected from beneath a single parent tree in the Ducke reserve north of Manaus (10 August 1994) and scarified and germinated in sand on 21–22 February 1995. *Aspidosperma* seedlings were collected from a “carpet” of identically aged, newly germinated seedlings from a single parent tree in reserve 1501 of the BDFFP on 8 June 1995. During 10–14 June 1995, both species were transferred to Root-trainer pots ($0.05 \times 0.05 \times 0.40$ m; Ronash, Kelso, Scotland, UK), filled with forest topsoil and placed in shade houses receiving 2–4% of photosynthetic photon flux density (PPFD) in a large clearing. Seedlings were watered daily. Between 27 November and 12 December 1995, two seedlings of each species were transplanted, with their soil, into each forest subplot; all other seedlings in the subplots were cut down to ground level. Each seedling was given 200 mL of water. All leaves of *Aspidosperma* and the oldest and youngest leaves of *Dinizia* were labeled with color-coded wire. Seedling heights (mm) and leaf (leaflet for *Dinizia*) numbers were recorded 2–7 d after transplanting, and after 6 mo (26 May–5 June 1996) and 12 mo (20–25 November 1996). The two intervals span the wetter 6 mo and the drier 6 mo of the year, respectively (Fig. 1). At the time of transplanting, 10 seedlings of each species were randomly selected and harvested. One year after transplanting (26 November to 16 December 1996), the largest of the two seedlings of each species from the trunk subplots was harvested, except in four subplots (two trenched, two untrenched) in the understory where both individuals had died and where the largest plant from the base or the crown zone subplot (chosen at random) was harvested instead. Hence 24 plants per species (six untrenched understory, six trenched understory, six untrenched gap, and six trenched gap) were harvested, complete with roots. The stems, roots, original leaves, and posttreatment-produced leaves of harvested plants were separated and dried at 60°C to constant mass.

As well as harvesting the transplanted seedling roots, in 16 trunk zones (four of the six replicates per treatment) $0.25 \times 0.25 \times 0.25$ m cubes of soil, centered on a transplanted seedling, were removed and all other roots, in addition to the target seedling roots, were washed out and dried to constant mass, which we call “competing roots.” The competing roots were separated into <5 mm and >5 mm diameter, classified as dead or alive by their external characteristics, and dried to constant mass at 60°C. No root ingrowth through the plastic lining of the trenched subplots was seen one year after trenching, but there was a small amount of competing root ingrowth over the top of the plastic.

To estimate the PPFD level at which a seedling's leaf losses were equaled by leaf production (light compensation point for leaf number, L), an estimate of the mass of leaves lost per plant per year was made. For *Aspidosperma* the mean leaf mass was calculated from the 10 plants harvested at the time of transplanting and multiplied by the mean number of leaves lost per plant

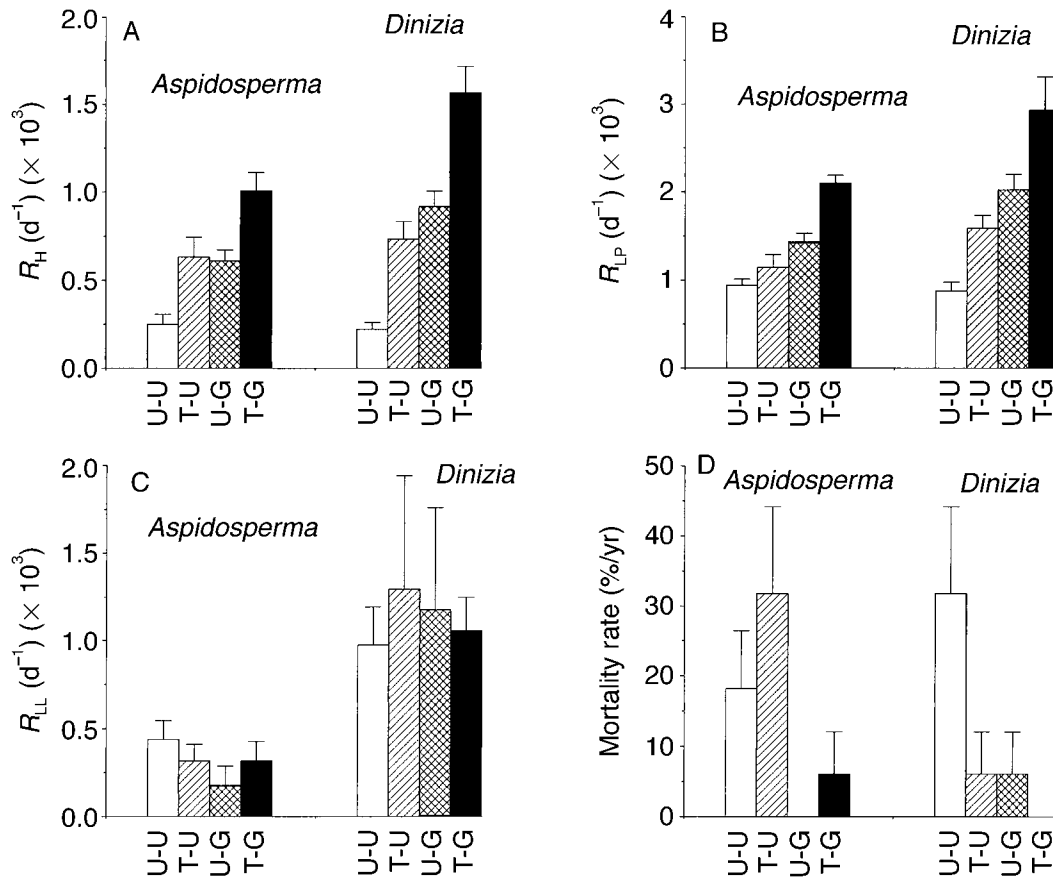


FIG. 2. The effects of reducing aboveground and belowground competition, in the wetter six months of a year, on relative growth rates (mean ± 1 SE) for (A) height, (B) leaf production, (C) leaf loss, and (D) percentage log annualized mortality rate, between transplanted seedlings of *Aspidosperma carapanauba* or *Dinizia excelsa* and the surrounding large trees in a central Amazonian rain forest ($n = 6$). Abbreviations for treatments are as follows: U-U = untrenched understory, T-U = trenched understory, U-G = untrenched gap, and T-G = trenched gap.

per year to obtain an estimate of the mass of leaves lost per plant per year. This method was not applicable to *Dinizia*, as we knew how many leaflets were lost but not how many primary and secondary rachises, and these constitute a large fraction of leaf mass. To estimate the leaf mass loss for *Dinizia*, relative leaf production rates were correlated with masses of leaves produced for the 24 harvested plants. We then assumed that relative leaf loss rates and masses of leaves lost showed the same relationship. Hence from the known mean relative leaf loss rate we estimated the mean mass of leaves lost.

Photosynthetic photon flux density measurements

The PPFD that plots received was measured using two quantum sensors (model QS1, Delta-T Devices, Cambridge, UK) attached to data loggers (model DL2, Delta-T Devices), one in a large clearing (~ 1 km²), the other in an experimental plot. The data logger recorded PPFD every 30 seconds, and averaged every 10 min. We recorded PPFD for at least one day in each trunk zone subplot before gap creation; PPFD (as a percent-

age of that in the large clearing) was not significantly different between trunk zones of future understory plots (mean 1.0%; SE = 0.16; $n = 6$) and trunk zones of future gap plots (mean = 0.95%; SE = 0.14; $n = 6$; $F_{1,8} = 0.108$; $P = \text{NS}$). Prior to harvest, we recorded PPFD above each plant to be harvested. A single day's data were collected with the sensor 10 mm above the apex of each of the 24 plants of each species to be harvested. The correlation between PPFD and seedling mass was poor, probably because PPFD was only measured for one day. Short-term PPFD measurements are poorly correlated with longer term measurements due to the presence/absence of sunflecks, degree of cloud cover, and solar position of the sun on the day of measurement. This is a problem for PPFD measurements especially in small gaps: for example, Barton et al. (1989) calculated that PPFD ranged from 3.9% to 9.6% of that in a nearby clearing for a single point over seven consecutive days. To account for this, we estimated the long-term incoming PPFD immediately above the seedlings by taking into account sunflecks and variability in the relation of diffuse/total PPFD. To do this we

TABLE 3. Summaries of model fitting for the proportion of seedlings dying within 6 mo of being transplanted, using binomial errors on untransformed proportions.

Factor	df	χ^2	<i>P</i>	<i>r</i> ²
<i>Aspidosperma</i> †				
Trench	1	1.13	NS	0.052
Gap	1	6.61	<0.05	0.303
Trench × Gap	1	1.79	NS	0.082
Other terms	4	2.93	NS	0.134
<i>Dinizia</i> †				
Trench	1	4.31	<0.05	0.204
Gap	1	4.22	<0.05	0.200
Trench × Gap	1	0.00	NS	0.000
Other terms	4	3.84	NS	0.182

Notes: All values are approximate except degrees of freedom. Species, treatments, and model terms are as for Table 2.

† Error df = 16.

used 41 d data from both understory and gap areas (not including any data for seedlings to be harvested) spanning a wide range of weather conditions. We plotted the indirect site factor (ISF), which we took as the mean of the lowest 10-min average PPFD for each hour from 1000 to 1400 ($n = 4$ hours), against the total incoming PPFD (ISF plus sunflecks), both expressed as a proportion of that in the large clearing. This gave us the average relationship, for the continuum from understories to gaps, of ISF plus sunflecks, to ISF alone. We then calculated the ISF for each seedling to be harvested, multiplied it by the proportion of ISF plus sunflecks, and multiplied that by the mean PPFD in a large clearing ($52.3 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) to obtain an estimate of the total incoming PPFD above each harvested seedling in moles per square meter per day.

Nutrient analyses

Nitrogen (N) and phosphorus (P) concentrations were measured in oven-dried leaves produced following transplantation. Approximately 20 mg of leaf material from each of the 24 harvested plants for each species was weighed and then digested for 8–10 h in hot concentrated sulfuric acid and hydrogen peroxide using mercuric oxide as a catalyst (Allen et al. 1974). This was followed by N and P determination using an autoanalyzer (Chemlab Instruments, Great Dunmow, Essex, UK). Accuracy was checked by analyzing subsamples of a large homogenized sample, which had been analyzed by independent international laboratories.

Statistical analysis

The design was a two-factor factorial randomized block, with six replicates and two sites (blocks), each with three plots of each treatment combination. We used generalized linear modeling using GLIM software for the statistical analyses (Baker 1987). We constructed “minimum adequate models,” the simplest adequate description of the data (Crawley 1993). We analyzed

various residual plots (not shown) of each model for normality of distribution, homogeneity of variance, and adequate representation of the data over the full range of the data set. Often the variance increased with the mean, usually with a constant coefficient of variance, hence gamma errors were specified (Taylor 1961, Crawley 1993). For brevity *F* ratios and degrees of freedom are given for main terms and important interactions only, along with sums of squares and *r*² values (proportion of deviance explained by the term) if these are important.

Terms used in analyses were (1) reduced below-ground competition (trench), a two-level fixed factor, (2) reduced aboveground competition (gap) as either a two-level fixed factor or continuous explanatory variable (covariate), and (3) block (site) as a two-level fixed factor. Seedling height data were converted to relative growth rates for height (R_H) using the standard logarithmic model (Evans 1972) and means for each plot of each treatment combination obtained as millimeter per millimeter per day $\times 1000$. Analogous logarithmic models for relative leaf production (R_{LP}) and losses (R_{LL}) and mortality rates (Swaine and Lieberman 1987) were used. Only seedlings alive at the final enumeration were included in calculations. Analysis was conducted on means of relative growth rates from each plot (means of six seedlings per plot, two from each subplot) of each treatment combination, or untransformed masses for harvested seedlings, where each seedling is a replicate. As results from the wetter and drier halves of the year are not statistically independent, we calculated the growth in the wetter half of the year as a proportion of the growth over the full year for R_{LP} and R_{LL} , which are probably sensitive to low water potentials. This allows the detection of changes in R_{LP} and R_{LL} , between the two halves of the year, which allows the partitioning of effects of trenching on relieving nutrient and/or water shortages, without compromising statistical independence. All differences discussed are significant to at least $P < 0.05$.

TABLE 4. *F* ratios from model fitting for leaf, stem, and root mass ratios for transplanted seedlings.

Factor	df	Root	Stem	Leaf
<i>Aspidosperma</i> †				
Trench	1	11.8**	1.86	12.8**
Gap	1	2.87	0.02	1.72
Trench × Gap	1	1.37	0.06	0.38
Other terms	4	3.87	1.50	2.42
<i>Dinizia</i> †				
Trench	1	27.3***	0.55	25.7***
Gap	1	0.22	3.22	3.03
Trench × Gap	1	0.99	0.05	0.48
Other terms	4	0.98	0.62	0.60

Note: Species, treatments, and model terms are as for Table 2.

** $P < 0.01$, *** $P < 0.001$.

† Error df = 16.

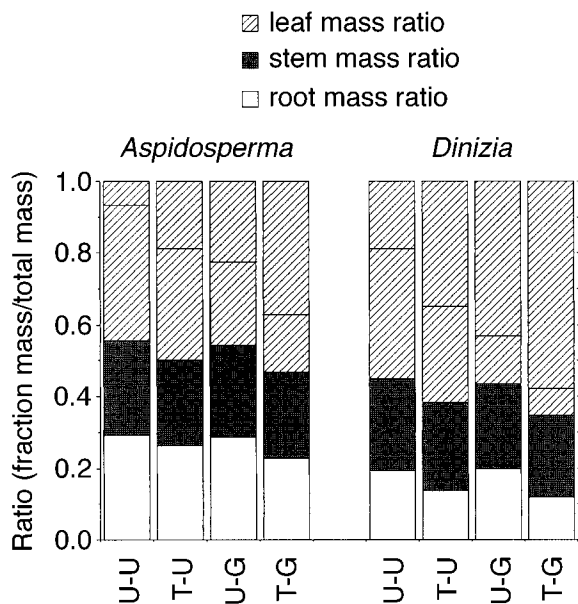


FIG. 3. Leaf, stem, and root mass ratios for seedlings of *Aspidosperma carapanauba* and *Dinizia excelsa* transplanted into trenched and untrenched subplots in both understory areas and single treefall gaps in central Amazonian rain forest ($n = 6$). The solid line shows the divide between leaves produced since transplanting and those remaining from before transplanting. Abbreviations are defined in Fig. 2.

RESULTS

Effects of gaps and trenching in the wetter six months

Gap trunk zones had higher PPFD ($6.0\% \pm 1.3\%$; $n = 6$; mean ± 1 SE) than understory trunk zones ($1.0\% \pm 0.16\%$; $F_{1,8} = 46.7$; $P < 0.001$). Gaps (reduced aboveground competition) increased relative growth rates for height (R_H) and leaf(let) production (R_{LP}) for seedlings of both *Aspidosperma* and *Dinizia*, but there was no significant effect on relative leaf loss rates (R_{LL}) for either species (Fig. 2, Table 2). Mortality was lower in gaps for both species (Fig. 2, Table 3). The mortality rate for *Dinizia* in the untrenched understory plots was 42% higher than in *Aspidosperma*, suggesting that *Dinizia* was more light-demanding as a seedling (Fig. 2). Neither species altered allocation patterns in response to location in gaps (Fig. 3, Table 4).

Trenching (reduction of belowground competition) increased R_H and R_{LP} for seedlings of both species, but there was no significant effect on R_{LL} for either species (Fig. 2, Table 2). Mortality was decreased by trenching in *Dinizia* only (Fig. 2, Table 3). Seedlings of both species increased allocation of mass to leaves and decreased allocation to roots in trenched plots (Fig. 3, Table 4). *Dinizia* was more plastic in its allocation of mass than *Aspidosperma* (Fig. 3, Table 4). For competing roots (roots in subplots, excluding transplanted seedling roots) < 5 mm diameter, both total and live mass was lower in trenched plots, as the act of trenching

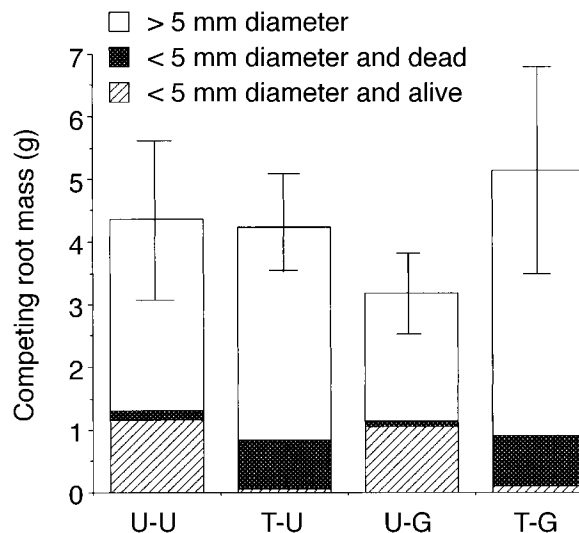


FIG. 4. Three fractions of "competing root" (see *Methods: Species biology* . . .) dry mass (mean ± 1 SE): > 5 mm diameter, < 5 mm diameter, and < 5 mm diameter and alive, for 0.25 m^3 cubes of soil from central Amazonian rain forest ($n = 6$). The standard errors are not shown where < 0.2 g. $n = 4$. Abbreviations are as in Fig. 2.

killed them (Fig. 4, Table 5). For roots of all diameters combined, trenching had no significant effect on total competing root mass, but this was due to most of the mass being in large roots that had not decomposed in the year following trenching (Fig. 4, Table 5).

For R_H and R_{LP} there was a positive interaction between reductions in aboveground and belowground competition; however this effect was weaker than the main treatment effects, and only $P = 0.06$ for R_{LP} in *Aspidosperma* (Fig. 2, Table 2). *Dinizia* was more responsive to both location in gaps and trenching and gap \times trench interaction than *Aspidosperma* (Fig. 2). There were no significant interaction effects on R_{LL} (Fig. 2, Table 2), mortality (Fig. 2, Table 3), or allocation patterns (Fig. 3, Table 4) for either species.

Comparisons of the wetter and drier halves of the year

Mean daily rainfall was 10 mm/d (11 mm/d including initial watering) in the wetter half of the year (Decem-

TABLE 5. F ratios from model fitting for various classifications of "competing root" mass (see *Methods: Species biology* . . .).

Factor	df	Total dry mass	< 5 mm diameter	Alive and < 5 mm
Trench	1	0.0693	10.8*	340***
Gap	1	0.0133	0.159	0.548
Trench \times Gap	1	1.33	1.31	2.38
Other terms	4	0.977	0.666	2.93
Error	8			

Note: Species, treatments, and model terms are as in Table 2.

* $P < 0.05$, *** $P < 0.001$.

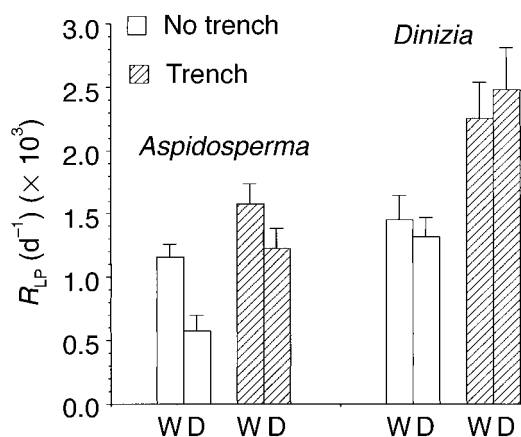


FIG. 5. Relative leaf production rates (mean \pm 1 SE) in the wetter (W) and drier (D) six months of a year in trenched and untrenched subplots for seedlings of *Aspidosperma carapanauba* and *Dinizia excelsa* transplanted into a central Amazonian rain forest; $n = 12$ (understory and gap plots pooled).

ber 1995 to May 1996 inclusive) and 5.4 mm/d in the drier half of the year (June 1996 to November 1996 inclusive; Fig. 1). There were 33 rainless days in the wetter half of the year, with two rainless periods that exceeded two consecutive days: one for three days, the other for six days. The drier half of the year had 65 rainless days with seven rainless periods that exceeded two days, and a maximum length of six days.

In *Dinizia*, gap and trenching treatments increased R_{LP} in both halves of the year similarly (Fig. 5). Relative leaf production and R_{LL} in the wetter half of the year, as a proportion of R_{LP} or R_{LL} over the full year, showed no significant differences between treatments (data not shown). We conclude that, for *Dinizia*, whatever was causing the trenching effect did not differ between the wetter and drier halves of the year and was therefore nutrients and not water. *Aspidosperma*, unlike *Dinizia*, showed possible seasonality in R_{LP} , as untrenched plots produced more leaves in the wetter (first) half of the year (70% of total year's R_{LP}), compared to trenched plots (57% of total year's R_{LP} ; trench term in analysis: $F_{1,16} = 5.91$; $P < 0.05$; $r^2 = 0.20$). This difference is in addition to the significant increases in R_{LP} in trenched plots in the wetter half of the year as the test compares differences in proportions (wetter/drier halves of the year) and not absolute levels. *Aspidosperma* had such low R_{LL} that many of the pro-

portions were 0 or 1, thus meaningful analysis was not possible.

Effects of gaps and trenching on the balance of leaf production and loss

Dry mass from harvested plants 1 yr after transplanting showed qualitatively similar trends to results from the wetter 6 mo on R_H R_{LP} (Table 6). Dry mass of leaves produced over 1 yr was increased by higher PPFD, trenching, and their interaction, for both *Aspidosperma* and *Dinizia* (Fig. 6, Table 7). *Dinizia* was more responsive to both PPFD and trenching than *Aspidosperma*, by 40% and 60%, respectively. The minimum adequate model lines for untrenched and trenched seedlings were not parallel for either species, which implies that the absolute impact of trenching depends on the PPFD level, i.e., the higher the PPFD, the greater the absolute impact of belowground competition.

For *Aspidosperma* the estimated mass of lost leaves (see *Methods: Species biology* ...) was 0.023 g per plant per year; thus in untrenched plots the minimum PPFD required to balance leaf gains and losses (light compensation point for leaf number, L), was 0.32 mol·m⁻²·d⁻¹ (95% CI: 0.18–0.43), equivalent to 0.60% (0.34–0.83%) of PPFD in a nearby large clearing (Fig. 6). Persistence in the untrenched understory is therefore expected for *Aspidosperma*, as PPFD is typically 0.5–2.5% of that in a large clearing. Trenching decreased L to 0.10 (0.09–0.13) mol·m⁻²·d⁻¹ or 0.20% (0.17–0.25%) PPFD (Fig. 6). For *Dinizia* the estimated mass of lost leaves was 0.16 g·plant⁻¹·yr⁻¹, thus in untrenched plots L was 1.3 (0.91–2.1) mol·m⁻²·d⁻¹ or 2.4% (1.7–4.0%) PPFD (Fig. 6). *Dinizia* is therefore not expected to persist in understory areas with 0.5–2.5% PPFD, as leaf losses would exceed leaf gains. Trenching decreased L to 0.33 (0.26–0.38) mol·m⁻²·d⁻¹, or 0.63% (0.50–0.73%) PPFD (Fig. 6). Thus, decreasing either aboveground competition or belowground competition would theoretically allow persistence (see mortality results, Fig. 2). The almost fourfold higher L in *Dinizia* compared to *Aspidosperma* is mostly determined by *Dinizia*'s much higher R_{LL} , which was 1.13 (SE = 0.071, $n = 24$) leaves lost, leaf⁻¹ d⁻¹ \times 1000, compared to 0.308 (SE = 0.053, $n = 24$) for *Aspidosperma* (Fig. 2, Table 2). Estimates of L should be treated with caution as the intercepts are extrapolations below all measured values (except untrenched *Dinizia*

TABLE 6. Per-plant mean dry mass (g; 1 SE in parentheses) for roots, stems, and leaves combined from plants harvested one year after transplanting.

Species	Untrenched understory	Trenched understory	Untrenched gap	Trenched gap
<i>Aspidosperma</i>	0.412 (0.039)	0.680 (0.070)	0.985 (0.097)	1.45 (0.13)
<i>Dinizia</i>	0.499 (0.082)	0.810 (0.13)	0.872 (0.079)	2.06 (0.30)

Note: $n = 6$.

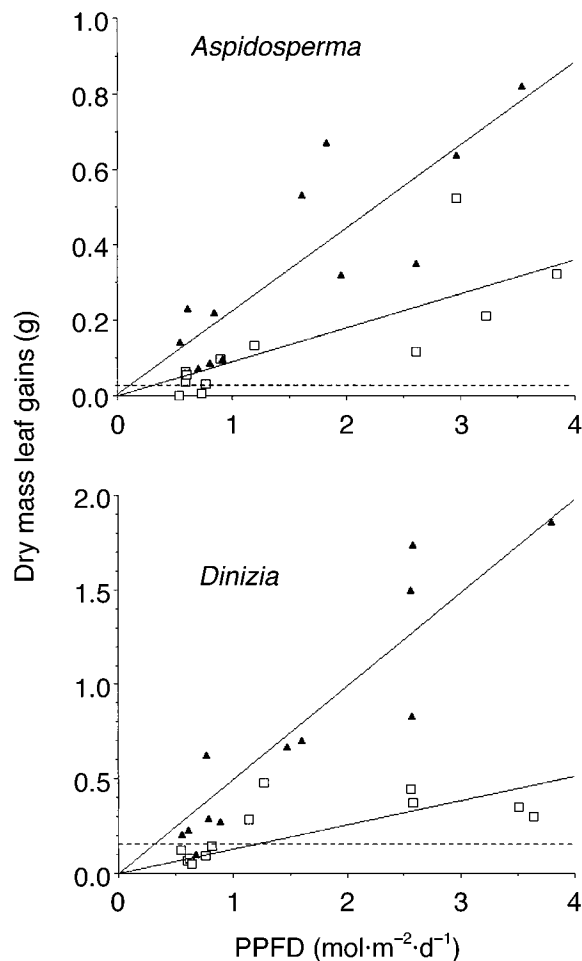


FIG. 6. Estimated long-term incoming photosynthetic photon flux density (PPFD) plotted against dry masses of leaves produced following transplanting into subplots without trenches (squares) and with trenches (triangles) to eliminate belowground competition, for seedlings of (top) *Aspidosperma carapanauba*, and (below) *Dinizia excelsa*, grown for one year, in a central Amazonian rain forest. The solid lines, forced at zero (using GLIM), are: *Aspidosperma*, untrenched, $y = 0.0912x$; *Aspidosperma*, trenched, $y = 0.219x$; *Dinizia*, untrenched, $y = 0.129x$; *Dinizia*, trenched, $y = 0.496x$. The dashed lines are estimated leaf loss mass, per plant per year (mean of all treatments; treatments not significantly different).

estimates). However, the large differences between the two species are probably robust.

Effects of gaps and trenching on foliar nitrogen and phosphorus

Both gaps and trenching treatments increased the absolute amount of foliar nitrogen (N) and phosphorus (P) in leaves produced after transplanting (Fig. 7, Table 8). For *Dinizia*, there was a positive interaction between gaps and trenching for amounts of N and P (Fig. 7, Table 8). Nitrogen concentrations in leaves produced after transplanting did not differ significantly with lo-

cation in gaps or trenching for either species (Fig. 7, Table 8). In *Aspidosperma*, P concentrations in leaves produced after transplanting were decreased by trenching, but not by location in gaps (Fig. 7, Table 8). In *Dinizia*, the opposite was seen: trenching had no significant effect on P concentrations, while location in gaps decreased foliar P concentrations (Fig. 7, Table 8). The amounts of N and P in posttreatment produced leaves, per gram of root at harvest, were higher in trenched plants of both species (Fig. 7, Table 8). This suggests that for a given quantity of root, roots in trenched plots took up more N and P than the same quantity of roots in untrenched plots, and hence that N and P were easier to obtain for plants in trenched plots. *Dinizia* was more efficient at taking up both N and P, per gram of root at harvest, than *Aspidosperma* (Fig. 7).

DISCUSSION

Experimental limitations

The study has some limitations that should be considered when interpreting the results: (1) all seedlings came from one parent tree for each species, which may not have been representative of that species as a whole, (2) creating treefall gaps causes multiple effects in addition to reducing aboveground competition for PPFD, and (3) making trenches around plants causes multiple effects in addition to reducing belowground competition for nutrients. In addition, as only two species were studied in one location generalizations should be made with caution.

Using treefall gaps to increase PPFD levels allows other factors to covary. Treefall gaps have increased maximum air temperatures, decreased relative humidity, and increased red:far red light ratios (Brown 1993), while soil moisture levels may increase or decrease (Bruijnzeel 1990). Extractable soil nutrients sometimes

TABLE 7. Summaries of model fitting for post-transplanting annual production of leaf dry mass.

Factor	ss	df	F	P	r ²
<i>Aspidosperma</i>					
Trench	0.2799	1	29.6	<0.001	0.221
PPFD	0.4910	1	52.0	<0.0001	0.388
Trench × PPFD	0.0697	1	7.38	<0.05	0.055
Initial leaf mass	0.0031	1	0.33	NS	0.002
Other terms	0.0844	4	2.23	NS	0.067
Error	0.1418	15			
<i>Dinizia</i>					
Trench	1.620	1	46.2	<0.0001	0.264
PPFD	2.395	1	68.3	<0.0001	0.391
Trench × PPFD	1.302	1	37.1	<0.001	0.213
Initial leaf mass	0.029	1	0.84	NS	0.005
Other terms	0.085	4	0.61	NS	0.014
Error	0.526	15			

Notes: Species and treatments are as in Table 2. The model contained two two-level fixed factors (trench and block) and two explanatory variables (PPFD and dry mass of initial leaves surviving to harvest).

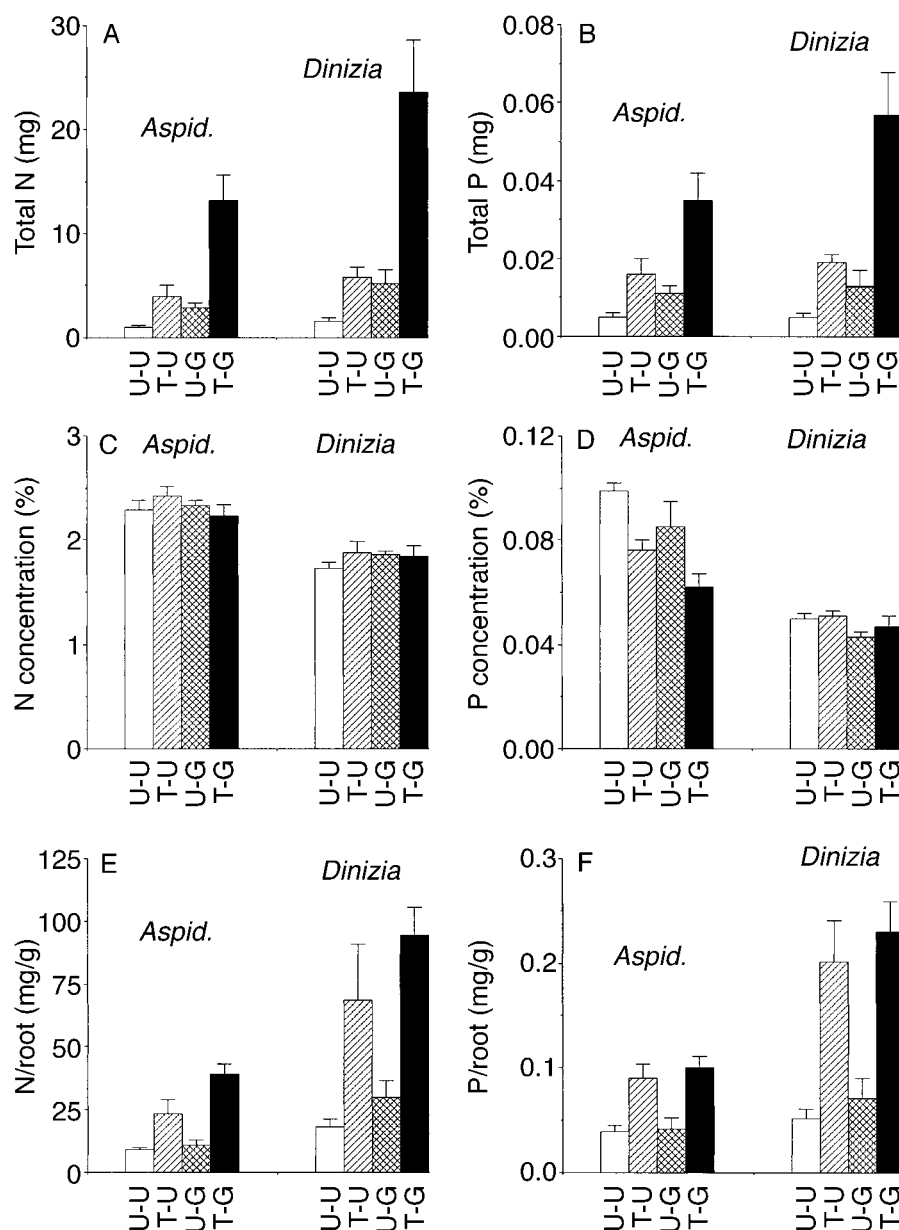


FIG. 7. Mean (± 1 SE) of (A) total nitrogen (N) amount, (B) total phosphorus (P) amount, (C) concentration of N, (D) concentration of P, (E) amount of N as mg N/g roots, and (F) amount of P as mg P/g roots, for leaves produced after transplanting for seedlings of *Aspidosperma carapanauba* and *Dinizia excelsa* transplanted into trenched and untrenched subplots in both understory areas and single treefall gaps in central Amazonian rain forest ($n = 6$, except untrenched understory plots for *Aspidosperma* where $n = 4$). Abbreviations are as in Fig. 2.

increase when gaps form, though the effects differ depending on the site and nutrient under study (Vitousek and Denslow 1986, Uhl et al. 1988, Denslow et al. 1998, Luizão et al. 1998). Nutrient availability to plants is affected by the amount of plant-available nutrient and the competition from other roots; fine root biomass may be higher (Sanford 1990) or lower in gaps (Sanford 1989). Thus it is impossible to make a generalization about whether seedlings growing in gaps will experi-

ence higher nutrient availability than seedlings in understories. The biggest difference between single treefall gaps and understories is the increased PPFD, but it is likely that other covarying factors may have influenced seedling growth in gaps.

Trenching increases nutrient mineralization rates (Vitousek et al. 1982). However, digging trenches around target plants also alters factors other than the belowground isolation of target plants from the sur-

TABLE 8. *F* ratios from model fitting for the total amount, percentage concentration, and nutrient amount per gram root for nitrogen (N) and phosphorus (P) in post-transplanting produced leaves.

Factor	df	Total amount		Concentration		Amount/gram root	
		N	P	N†	P†	N†	P†
<i>Aspidosperma</i> ‡							
Trench	1	33.9***	24.3***	2.19	11.0**	56.3***	14.5**
Gap	1	9.28**	9.16**	0.71	3.61	1.68	0.31
Trench × Gap	1	3.45	2.47	0.04	0.01	0.16	0.00
Other terms	4	0.48	0.62	0.59	1.28	1.74	0.49
<i>Dinizia</i> §							
Trench	1	47.3***	46.3***	2.15	0.57	46.3***	40.8***
Gap	1	29.1***	21.9***	0.38	4.81*	1.73	0.73
Trench × Gap	1	7.85**	5.97*	0.30	0.39	2.14	0.85
Other terms	4	3.63*	2.72	1.39	1.10	1.45	0.71

Note: Species, treatments, and model terms are as in Table 2.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Specifying gamma errors.

‡ Error df = 14 due to missing values (two seedlings produced no new leaves).

§ Error df = 16.

rounding vegetation. The use of plastic to line trenches may affect the lateral movement of mobile ions and water. Also trenching inevitably severs all roots entering a plot which then decompose, possibly producing a pulse of nutrients. Thus results from trenching experiments may overemphasize the magnitude of belowground competition for nutrients due to the “extra” nutrient input from severed roots, but if results of trenching are positive, as ours are nutrient and/or water limitation is still demonstrated.

Effects of gaps, trenching, and their interaction

The greater growth of seedlings in gaps was expected, having been shown by numerous other studies. The greater response of *Dinizia* as compared to *Aspidosperma*, was also expected, because previous studies suggested that *Dinizia* was light demanding. Trenching in the understory approximately doubled height growth, a response similar to that from other trenching studies in tropical lowland rain forests on nutrient poor soils (Whitmore 1966, Fox 1973, Coomes and Grubb 1998). In addition, Coomes and Grubb's study in Amazonian caatinga showed a greater effect of trenching than of gap creation (trenching explained 44% of the deviance in their height data set, whereas the gaps explained only 6%, for all species combined). In contrast, gaps explained more (29%) of the deviance in the height data in the present Brazilian study, whereas trenching explained less (22%; for both species combined). Hence when moving from exceptionally nutrient-starved Amazonian caatinga forest growing on white sand soils to central Amazonian forest growing on slightly more fertile oxisols, competition has switched from the dominance of belowground competition to dominance of aboveground while belowground competition remains important (Fig. 2). Indeed, aboveground competition is probably more important relative to belowground competition in our central Am-

azonian oxisols because the relative treatments were unequal: belowground competition was mostly eliminated, but aboveground competition was not because PPFD in the trunk zones of gaps was only increased to ~6% of that in a nearby large clearing. With even higher PPFD (as found in larger gaps) growth rates of seedlings would probably have been much greater, making the effects of trenching look less important. Other studies have shown that tropical rain forest tree seedlings increase growth when PPFD is higher than 6% of full PPFD; for example, Veenendaal et al. (1996) reported that 14 of 15 Ghanaian forest tree species had highest R_H 's at a PPFD of at least 16% full daylight.

The positive interaction between trenching and gaps was expected; however, the interaction was weaker than the effects of the main terms. The interaction explained 11% of the deviance compared to 21% and 40% for the trenching and gap treatments, respectively (both R_H and R_{LP} of both species combined, Table 2). As PPFD increased, growth was probably becoming increasingly nutrient limited, hence the greater than additive effects of both gaps and trenching treatments. However, the only other study in tropical rain forests to study effects of gaps and trenching, and to test for an interaction, did not find one (Coomes and Grubb 1998). Coomes and Grubb explained their lack of interaction between trenching and PPFD increases by proposing, (1) with small increases in PPFD or increases in nutrients at low PPFD, seedlings increase their growth by increasing their leaf area ratio (LAR) only, and (2) at higher PPFD seedlings increase their growth by increasing LAR and increasing unit leaf rate (ULR). They argued that it was the interaction of increase in LAR and ULR that causes the PPFD–nutrient interaction in response, and that the lack of interaction in their study was due to their experiment only considering a narrow range of PPFD levels. We studied a greater sixfold PPFD range (1–6%) compared to Coomes and Grubb's threefold range

(1.7–5.5%), but Coomes and Grubb's mechanism does not apply to our study because we found no significant difference in LAR between gap and understory plants. A further complication with Coomes and Grubb's mechanism is that pot experiments have shown increased maximum CO_2 assimilation rates (A_{sat}), with higher nutrient additions, at ~2% PPFD (Thompson et al. 1988, Riddoch et al. 1991), suggesting that, with increased nutrient supply at low PPFD, seedlings could increase carbon gains by being better able to exploit high PPFD sunflecks.

While some pot experiments and some trenching experiments have shown increased growth of tropical rain forest seedlings due to higher nutrient availability, the very few field experiments where fertilizer has been added to seedlings in forest understories have either shown no effects (Denslow et al. 1990, Turner et al. 1993) or detrimental effects (Dalling and Tanner 1995). Most interestingly, fertilization of seven species of *Miconia* and *Piper* in pots of forest soil (at 20% of PPFD in a large clearing) resulted in increases in growth, but the same species planted directly into gaps and understories in the forest showed no effects of fertilizers (Denslow et al. 1990). Dalling and Tanner (1995) suggested that the lack of, or negative, response in the forest understory in their study resulted from increased competition for the available nutrients with the surrounding adult trees. If this was generally true, nutrient additions would need to be large enough to satiate both the roots of large trees, and possibly microorganisms, before seedlings would show an effect. This is true for herbs competing with trees in temperate forests: low levels of nutrient additions show no effect, but large additions do (summarized in Grubb 1994). Thus lack of increased growth in fertilized seedlings growing in tropical rain forests may actually demonstrate the importance of belowground competition for nutrients, rather than its absence.

Dinizia responded more than *Aspidosperma* to trenching and location in gaps, which is consistent with *Dinizia* seedlings being more light demanding. The greater responsiveness of *Dinizia* to both reduced belowground and reduced aboveground competition is also consistent with other studies of tropical trees. Four Australian rain forest species had the same rank order for responsiveness to increased PPFD and nutrient additions (Thompson et al. 1992a), and in Amazonian caatinga forest saplings of tree species that were highly responsive to increased PPFD were generally highly responsive to trenching (Coomes 1995). The hypothesis that responsiveness to increased PPFD is correlated with responsiveness to increased nutrient availability deserves more study.

Seedlings of *Dinizia* persist in the understory for less time than *Aspidosperma* (mortality 32% and 23% per year, respectively, Lewis 1998) due to the twin impacts of intense aboveground and belowground competition. On average, in *Dinizia* leaf losses exceeded leaf pro-

duction in the untrenched understory. An increase in the availability of either aboveground or belowground resources reverses this situation by increasing R_{LP} above the unchanging R_{LL} (Fig. 2). In contrast *Aspidosperma* has a positive leaf balance down to 0.6% of the PPFD in a large clearing because of its low R_{LL} . However, R_{H} and R_{LP} are similar in *Dinizia* and *Aspidosperma* in the untrenched understory. *Dinizia* has a high R_{LL} because its leaflets have a relatively short leaf life span, 7.2 months, as compared to 27 months for leaves of *Aspidosperma*. The importance of leaf life spans was shown in a Costa Rican lowland rain forest where life spans of leaves on saplings ranged from 4.4 months for the pioneer *Cecropia obtusifolia* to an average of 12 months for light demanding nonpioneers, and to an average of 30 months for shade-tolerant species (King 1994).

Belowground competition for nutrients or water?

In *Dinizia* trenching increased R_{H} and R_{LP} in the wetter six months (when rainfall was 10 mm/d and potential evapotranspiration 3.5 mm/d; Camargo and Kapos 1995). In *Dinizia* R_{LP} and R_{LL} were apparently not affected by any potential water shortage in the drier half of the year (5.4 mm/d) because there was equal leaf production and leaf loss in the wetter and drier halves of the year. Thus the increase in growth in *Dinizia* in trenched plots was most likely due to increased nutrient availability alone.

Aspidosperma also showed increased R_{H} and R_{LP} in trenched plots in the wetter half of the year, which shows that they were responding to increased nutrients. Unlike *Dinizia*, *Aspidosperma* showed possible seasonality in R_{LP} as in untrenched plots seedlings produced more of their leaves in the wetter half of the year. Thus *Aspidosperma* increased growth due to trenching as a result of increased nutrients in the wetter half of the year, and may have been responding to increased water in the drier half of the year.

Seedlings of both species took up more N and P in trenched plots. As both species increased growth while decreasing P concentrations (*Aspidosperma* in trenched plots, *Dinizia* in gaps, Fig. 7, Table 8) extra growth in trenched plots was probably not due to extra P; more likely it was due to extra N or an unmeasured nutrient. Nitrogen concentrations in leaves produced after trenching in the understory tended to be higher than those in untrenched understory plants, which suggests that increased growth following trenching may have been due to increased N. The lack of increased N concentration in leaves in trenched plots in the gaps could be a result of the extra growth (above that produced by trenching alone) resulting in a higher N demand, which resulted in a large increase in mass with an unchanged N concentration. Other studies of tropical plants have similarly shown an increase in growth due to increased N availability, but no increase in N concentration (Healey 1989). Our interpretation that in-

creased growth due to trenching was not due to an increase in P availability is counter to the hypothesis that tropical lowland rain forests are generally P limited (Tanner et al. 1998). It is also specifically counter to the evidence from litterfall nutrient content for this site: N and P concentrations in freshly fallen litter were 15 and 0.3 mg/g, respectively and total litterfall 8.3×10^3 kg·ha⁻¹·yr⁻¹ (Sizer et al. 2000), which when compared with values for other tropical lowland forests (Tanner et al. 1998) suggests that P is much more limiting than N. Perhaps the canopy trees are limited by P and the seedlings not by P, but by some other nutrient. Our study is not alone in providing evidence that P may not be limiting the growth of seedlings. Burslem et al. (1995) working in Singapore showed that P was not limiting for seedlings of four species grown in pots of forest soil with and without P additions. Reviewing the literature, Burslem et al. (1995) claim that P limitation of seedlings is the exception, not the norm, in tropical rain forests, and our results support this. In our study area K, Ca, and Mg are all at low levels in the soils (Fearnside and Leal Filho, *in press*), leaves, and litterfall (Vitousek and Sanford 1986); thus increases in these nutrients may have caused the increased growth in trenched plants.

To conclude, we have demonstrated experimentally that for seedlings growing in the understory of central Amazonian rain forest on nutrient-poor oxisols, trenching increased growth due to increased nutrient availability and possibly increased N, not increased P. Given that 60–70% of the world's tropical forests grow on low-fertility oxisols (Vitousek and Sanford 1986), intense juvenile–adult competition both aboveground and belowground may be the norm, and not the exception, as is often assumed.

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