

GAPS AND ROOT TRENCHING INCREASE TREE SEEDLING GROWTH IN PANAMANIAN SEMI-EVERGREEN FOREST

IGNACIO M. BARBERIS¹ AND EDMUND V. J. TANNER²

Department of Plant Sciences, University of Cambridge, Cambridge CB2 3EA, UK

Abstract. Although competition between plants is nearly universal in vegetation, we know relatively little about belowground competition and how it interacts with aboveground competition in tropical forests, and almost nothing about such interactions on soils of intermediate fertility in sites with a moderate dry season, despite the fact that such forests are extensive. We investigated this over one year in a Panamanian tropical semi-evergreen rain forest, using tree seedlings (*Simarouba amara*, *Gustavia superba*, *Tachigali versicolor*, and *Aspidosperma cruenta*; least to most shade tolerant), experimental gaps, and trenching. Gaps increased growth and decreased mortality; growth increases were: *Simarouba* 684% (increase in height relative growth rate), *Gustavia* 411%, *Aspidosperma* 364%, and *Tachigali* 324%. Trenching in gaps increased growth in three species (*Simarouba* 49%, *Gustavia* 63%, and *Aspidosperma* 38%) but had very small effects in the understory; trenching did not affect mortality. We infer that trenching caused increased growth due to increased nutrients in the wet season, and increased water and/or nutrients in the dry season. Thus, across the tropics, in all but the wettest sites with fertile soils, seedlings of many species will be limited by belowground competition, at least in gaps. This is similar to the pervasive importance of belowground competition in temperate forests.

Key words: Barro Colorado Nature Monument, Panama; belowground competition; lowland tropical semi-evergreen forest; nitrogen; nutrient availability; phosphorus; seedling growth; seedling mortality; tree-fall gaps; trenching.

INTRODUCTION

Competition between plants is nearly universal in vegetation. In temperate and tropical forests, seedlings mostly compete with mature vegetation (Coomes and Grubb 2000, Wright 2002), both aboveground (mainly for light) and belowground (for water and several mineral nutrients). The outcome of both forms of competition between seedlings and adult trees determines the composition of the advance regeneration and the relative size of the seedlings. These, in turn, strongly influence the outcome of competition to occupy small-to medium-sized canopy gaps (Hubbell et al. 1999), and ultimately species composition of the forest.

Treefalls that create gaps cause a reduction in aboveground competition for seedlings due to increased light, and may reduce belowground competition due to increases in water and/or nutrients, but these increases last only for several months (or a year or two) due to the rapid growth of plants both aboveground and belowground (Becker et al. 1988, Silver et al. 1996, Ostertag 1998). While there are good studies of the effects of gaps on seedling growth and mortality in quite a number of tropical forests (Denslow et al. 1998), there

are few studies of the combined effects of gaps and trenching (Coomes and Grubb 2000). The existing studies were done in forests which were dry (1500 mm/yr in Guanacaste, Costa Rica [Gerhardt 1996]), intermediate (2200 mm/yr in Manaus, Brazil [Lewis and Tanner 2000]), 2600 mm/yr in La Esmeralda, Venezuela [Coomes and Grubb 1998]), or wet (3900 mm/yr in La Selva, Costa Rica [Ostertag 1998]) and on soils that were fertile (entisols and less fertile ultisols in La Selva [Ostertag 1998]), infertile (oxisols north of Manaus, Brazil [Lewis and Tanner 2000]), or very infertile (arenosols at La Esmeralda [Coomes and Grubb 1998]). However, to our knowledge, there are no studies that have analyzed the effects of gaps and trenching in sites with intermediate drought and moderately fertile soils, despite the presence of huge areas of tropical forest with these characteristics (Cochrane et al. 1985, Salati 1985).

In a tropical dry forest in Costa Rica, where water supply severely limits growth, trenching increased seedling growth (Gerhardt 1996). In tropical forests on infertile soils, trenching increased seedling and sapling growth (Coomes and Grubb 1998, Lewis and Tanner 2000). In contrast, on fertile soils there was no effect of trenching on seedling growth (Denslow et al. 1991, Ostertag 1998), except for one experiment that showed a positive effect in one of three types of plantations (Gerwing 1995). In forests experiencing intermediate drought and on moderately fertile soils, we hypothesized that there would be an effect of trenching inter-

Manuscript received 19 April 2004; revised 13 July 2004; accepted 20 July 2004. Corresponding Editor: J. B. Yavitt.

¹ Present address: Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, C.C. 14, S2125ZAA Zavalla, Argentina.

² Corresponding author. E-mail: evt1@cam.ac.uk

mediate in magnitude between those in infertile and fertile sites, and those in dry and wet sites. Moreover, lack of studies in sites with such characteristics precludes analyzing whether the relative importance of aboveground and belowground competition changes along gradients of biomass productivity as suggested for grasslands (Cahill 1999).

Our study was done in a tropical semi-evergreen forest on the Bohio peninsula of the Barro Colorado Nature Monument (BCNM), Panama. It has an annual rainfall of 2500 mm and a 4.5-month dry season. Its soils are moderately fertile alfisols (e.g., with half the levels of fluoride extractable phosphate compared to the fertile soils at La Selva [Sollins et al. 1994, Yavitt 2000]). We used a factorial experiment with seedlings of four tree species (*Aspidosperma cruenta*, *Tachigali versicolor*, *Gustavia superba*, and *Simarouba amara*) grown for one year in trenched and untrenched subplots within gaps and understories. The results were used to (1) assess the relative importance of aboveground and belowground competition; (2) infer whether nutrients, water, or both, limit seedling growth and mortality; and (3) contribute to a general model of the differences in aboveground and belowground competition along gradients of soil fertility and water availability in tropical forests.

MATERIALS AND METHODS

Study area

The study was carried out in a secondary, seasonally dry, tropical forest ~70 years old growing on montmorillonitic alfisols (Leigh 1999, Barberis 2001) on the Bohio Peninsula of the Barro Colorado Nature Monument (BCNM), Panama (9°10' N, 79°51' W). Annual rainfall averages 2600 mm with a pronounced dry season from January through April; during the study period, the dry season was shorter (101 days) than the average (135 days). Annual mean temperature is 27°C.

Experimental design

We chose eight sites in forest without gaps. In March–June 1999 in each site, we created one gap by felling to create ~10 × 10 m canopy opening (all aboveground plant material was removed), plus we set up one 10 × 10 m understory plot at least 10 m away from the gap edge. Each plot had 16 subplots with “trenching” and “subplot-size” treatments in a Latin square design. Eight subplots were trenched to 50 cm, lined with 6-mil plastic, and backfilled during May to July 1999; the others remained untrenched. Half of the subplots were large (80 × 80 cm) and half were small (40 × 40 cm). Four seedlings of one of the four tree species, were planted into each subplot in November 1999. Four shade-tolerant tree species were selected according to their shade tolerance (based on the index of Condit et al. [1996], which ranges from –2, which is most shade tolerant, to +8) and to the availability

of their seeds or seedlings in the forest. The shade indices for the four species were *Aspidosperma cruenta*, –1.167; *Tachigali versicolor*, 0.089; *Gustavia superba*, 0.493; and *Simarouba amara*, 1.195. In May and August 2000, gaps were weeded, roots that were growing over the surface into the trenched subplots were cut, and fallen branches removed.

Site measurements

The light environment (sky view factor, which ranges from 0 for darkness to 1.00 for unobscured sky) above the tallest seedling in each subplot was measured in March 2000 using a CI-110 Digital Plant Canopy Imager (CID, Vancouver, Washington, USA). Volumetric soil water content at 6 cm in each subplot was measured in March 2000 (at least one month into the dry season) and October 2000 (late wet season) with a ThetaProbe soil moisture sensor (Delta-T Devices, Cambridge, UK).

Seedling preparation and planting protocol

Gustavia and *Tachigali* seedlings were grown from seeds collected in May 1999, sown in 1200-cm³ pots with a 1:1 mix of Bohio forest soil and sand, and placed under screens (4% full daylight) on Barro Colorado Island, BCNM. *Simarouba* and *Aspidosperma* first-year bare-root seedlings were collected in August–September 1999 in BCNM, planted in pots with similar soil mix, and kept in the understory. Seedlings were watered during dry spells. From at least 550 healthy seedlings per species, we chose 352 individuals around the mean seedling size per species, and assigned them to the treatments in a stratified random way according to their heights, such that plants of all height classes were planted in all treatments, and planted them in October–November 1999. *Gustavia* subplots were fenced (1-m high with 1-cm² wire mesh) against predation by agouties (*Dasyprocta punctata*), which in a trial dug up freshly planted seedlings of (only) this species. The seedlings transplanted into gaps were covered by a thin layer of recently cut branches to allow acclimation.

Measurements of height, leaf area, growth, and mortality and biomass harvest

We measured seedling heights, lengths and breadths of each leaf (*Aspidosperma*, *Gustavia* and *Tachigali*), number of leaflets, and median leaflet length for each leaf (*Simarouba*), and recorded seedling mortality in November 1999, May 2000, and November 2000; leaf area was estimated using regression equations (coefficients of determination for the four species ranged from 0.92 to 0.98). We divided the study period into two halves, the “drier half” from November 1999 to May 2000, and the “wetter half” from May to November 2000. It is important to note that our ~180 day “drier half” included ~80 days of the wet seasons.

In November 2000, we randomly chose four sites and harvested the aboveground parts of the largest and

median-sized seedlings in each subplot. In two of these sites, the roots of the maximum-sized seedling from the large subplots were washed from the soil. Leaves, stems, and roots were dried at 70°C and weighed. In the two other sites, from each large subplot we removed a cube of soil 25 × 25 × 25 cm (centered on a seedling, but which did not always contain all the roots of the planted seedling because they were sometimes >25 cm long) from which roots of “competing” vegetation were washed out (we could not reliably distinguish living and dead roots in the many species present), and those <5 mm diameter were dried and weighed.

Species differed significantly in height at the beginning of the experiment (Barberis 2001); hence, we estimated relative growth rates in height (RGR_h) as $(\ln H_1 - \ln H_0)/(t_1 - t_0)$, where H_0 and H_1 were the initial and final height (in centimeters) and $t_1 - t_0$ was the elapsed time (in days). A similar equation was used to estimate RGR in leaf area (in square centimeters).

Nutrient analyses

At the Waite Analytical Services, University of Adelaide, Australia, oven-dried leaf samples from harvested plants were digested with nitric acid, finished with hydrochloric acid, and analyzed by inductively coupled plasma optical emission spectrometry (IC-POES) to obtain P, Ca, K, and Mg concentrations. Nitrogen was analyzed by combustion technique using a Carlo Erba instrument (NA1500, series 2, Carlo Erba, Milan, Italy). Accuracy was checked using subsamples of a large homogenized sample, which had been analyzed by independent international laboratories.

Statistical analyses

The effects of habitat (gaps and understories), trenching, species, and subplot size on environmental variables (light, soil moisture, and competing roots), seedling growth (RGR in height and leaf area), size (height, leaf area, and biomass), and nutrient concentrations and contents were analyzed using a generalized linear model with PROC MIXED of SAS version 8.0 (Littell et al. 1996, SAS Institute 1999). We used a split-plot design with habitat as the main-plot effect and trenching, species, and subplot size as the split-plot effects. All effects were nested within replicated sites. Treatment effects (habitat, species, trenching, and subplot size) were assumed to be fixed effects, whereas sites were considered random. For RGR in height and leaf area, we analyzed the effect of seasons (i.e., drier vs. wetter season) by repeated measures design with PROC MIXED using compound symmetry as a covariance structure (Littell et al. 1996).

All variables were log₁₀-transformed prior to each analysis to reduce heteroscedasticity and improve normality. For analyses of RGR in height and leaf area, we added 1 plus a value a bit higher than the smallest RGR recorded to allow inclusion of zeroes and negative values. Analyses were performed on the means of the

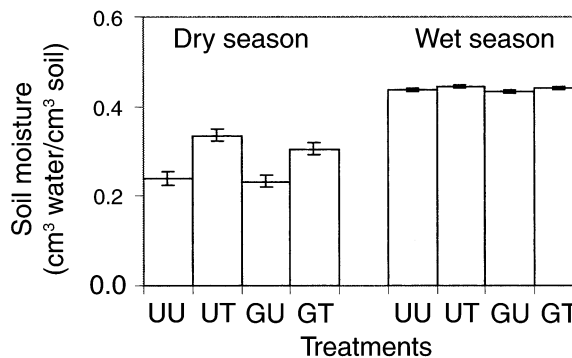


FIG. 1. Volumetric soil moisture concentration (mean ± 1 SE) for the dry and wet seasons in a Panamanian forest. Abbreviations for the treatments are as follows: UU, understory untrenched; UT, understory trenched; GU, gap untrenched; and GT, gap trenched.

surviving seedlings in each subplot. As there was no significant effect of subplot size or its interactions with the other terms, this term was discarded from the model. The interaction of species with habitat and trenching were significant in almost all analyses, so each species was analyzed separately.

The effects of habitat, trenching, and their interaction on annual seedling mortality were analyzed separately for each species using the GLIMMIX macro in PROC MIXED of SAS 8.0 (Littell et al. 1996, SAS Institute 1999). That macro allows the use of binomially distributed data in the split-plot design (Littell et al. 1996). *Gustavia* was not included in the analyses because its seedling mortality was almost nil.

All differences discussed in the *Results* section were significant at the 5% level unless otherwise stated.

RESULTS

Light was higher in gaps than understories (Sky-view factors 0.126 and 0.043; $F_{1,7} = 49.03$, $P < 0.0005$), but similar in trenched and untrenched subplots in both gaps and understories (trench, $F_{1,226} = 0.09$, $P > 0.75$; habitat × trench, $F_{1,226} = 0.03$, $P > 0.85$), and did not differ between subplots with different species. Soil water concentration was similar in gaps and understories even in the dry season ($F_{1,7} = 1.62$, $P > 0.20$), but trenching increased soil water concentration in both gaps and understories by 40% in the dry season ($F_{1,226} = 183$, $P < 0.0001$; Fig. 1) and by 2% in the wet season ($F_{1,226} = 133$, $P < 0.0001$; Fig. 1). There were no differences in soil water concentration among subplots with different species either in the dry or wet season (dry, $F_{3,226} = 1.41$, $P > 0.20$; wet, $F_{3,226} = 0.75$, $P > 0.50$). The biomass of the competing roots (<5 mm diameter) was similar in gaps and understories ($F_{1,1} = 1.58$, $P > 0.40$), but trenching reduced competing root biomass in both gaps and understories (13.0 g root <5 mm diameter in 0.016 m³ of soil in trenched and 26.2 g in untrenched; many of the roots in the trenched

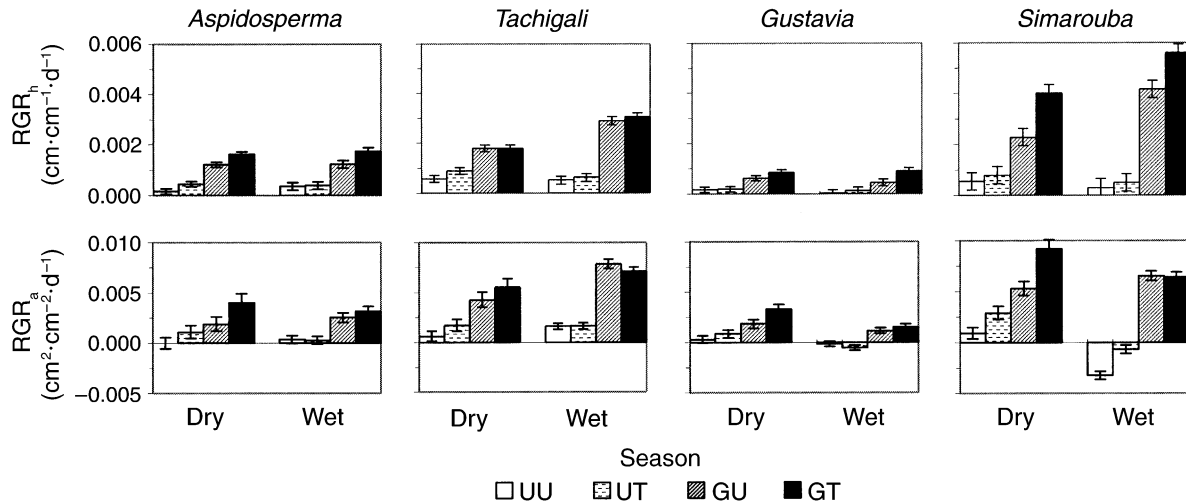


FIG. 2. Relative growth rate in height (RGR_h) and leaf area (RGR_a ; mean \pm 1 SE) of seedlings of four species during the drier and the wetter seasons in trenched and untrenched subplots in gaps and the understory. Treatment abbreviations are: UU, understory untrenched; UT, understory trenched; GU, gap untrenched; and GT, gap trenched. Species are presented from higher (*Aspidosperma*) to lower shade tolerance according to Condit et al. (1996).

subplots were dead; trench, $F_{1,26} = 14.3$, $P = 0.0008$; habitat \times trench, $F_{1,26} = 1.44$, $P = 0.24$).

Gaps increased growth in height and leaf area (RGR_h and RGR_a) in all species, but the effect varied according to the season (Fig. 2 and Table 1). Growth increases due to gaps were greater during the wet season for *Tachigali* (RGR_h and RGR_a) and *Simarouba* (RGR_h), but similar in both seasons for *Aspidosperma* and *Gustavia*. Trenching increased growth, but much less than gaps; three of four species (*Aspidosperma*, *Gustavia*, and *Simarouba*, but not *Tachigali*) showed increased growth in trenched plots. There was an interaction between gaps and trenching for *Gustavia* (RGR_h and RGR_a) and *Simarouba* (RGR_h): trenching increased growth only in gaps, whereas for *Aspidosperma* (RGR_h and RGR_a) and *Simarouba* (RGR_a), the small but significant trenching effects were similar in both habitats. The increased leaf area growth due to trenching was similar in both seasons for *Aspidosperma* and *Simarouba*, but greater during the dry season for *Tachigali* and *Gustavia*.

The increased growth in height and leaf area in gaps resulted in taller plants with more leaf area in all species (Fig. 3), and in higher biomass for *Simarouba* ($F_{1,1} = 282.47$, $P = 0.0378$). Similarly, increased growth due to trenching resulted in taller plants with more leaf area for *Aspidosperma* in both habitats, and for *Gustavia* and *Simarouba* in gaps. Trenching also increased *Simarouba* biomass, but only in gaps (trench, $F_{1,10} = 18.92$, $P = 0.0014$; habitat \times trench, $F_{1,10} = 5.17$, $P = 0.0463$).

The increase in RGR_h due to gaps (plants grown in gaps compared to those grown in the understories for untrenched subplots) differed among species: *Simarouba* (684%) > *Gustavia* (411%) > *Aspidosperma*

(364%) > *Tachigali* (324%). Likewise, species differed in their increase in RGR_h due to trenching (plants grown in trenched compared to those grown in untrenched subplots in gaps): *Gustavia* (63%) > *Simarouba* (49%) > *Aspidosperma* (38%) > *Tachigali* (4%). Increases in RGR_h due to gaps were much higher than the relative increases due to trenching.

Annual seedling mortality was significantly reduced by gaps for *Simarouba* ($F_{1,14} = 23.32$, $P = 0.0003$; Fig. 4), and almost significantly for *Tachigali* ($F_{1,14} = 4.52$, $P = 0.0518$; Fig. 4). Trenching did not affect annual seedling mortality for any species (all $P > 0.35$).

Species differed in their leaf nutrient concentrations (Fig. 5). Concentrations for all nutrients were higher for *Gustavia*, intermediate for *Aspidosperma* and *Simarouba*, and lower for *Tachigali* (except N). Nutrient concentrations in leaves of plants grown in gaps were higher in trenched plants than untrenched plants for P and K in *Gustavia*; there were no differences in N, Mg, and Ca concentrations for any species. Higher growth in trenched plants resulted in higher nutrient amounts (total in the leaf mass) for N, P, K, Mg, and Ca in *Simarouba*, and for N, P, and K in *Gustavia*.

DISCUSSION

The effects of gaps and trenching on seedling growth and mortality

In our experiment, gaps increased growth and decreased mortality, much more than trenching, but trenching had significant effects on growth. Gaps increased growth in all four species, whereas trenching increased growth in three of four species (*Aspidosperma*, *Gustavia*, and *Simarouba*, but not *Tachigali*), and the effect was mainly observed in gaps. Gaps reduced

TABLE 1. The effects of habitat (gap or understory), trenching (trenched or untrenched), and season (drier or wetter) on height growth (RGR_h) and leaf area growth (RGR_a) for seedlings of *Aspidosperma*, *Tachigali*, *Gustavia*, and *Simarouba*.

Effect	RGR _h			RGR _a		
	df	F	P	df	F	P
<i>Aspidosperma</i>						
Habitat (H)	1, 7	90.64	<0.0001	1, 7	59.07	<0.0001
Trench (T)	1, 106	13.07	0.0005	1, 106	5.92	0.0167
Season (S)	1, 106	0.82	0.3685	1, 106	0.59	0.4450
H × T	1, 106	3.14	0.0793	1, 106	0.81	0.3709
H × S	1, 106	0.00	0.9647	1, 106	0.00	0.9806
T × S	1, 106	0.25	0.6192	1, 106	2.50	0.1169
H × T × S	1, 106	1.51	0.2218	1, 106	0.02	0.8828
<i>Tachigali</i>						
Habitat (H)	1, 7	146.28	<0.0001	1, 7	147.47	<0.0001
Trench (T)	1, 104	2.26	0.1359	1, 104	2.73	0.1015
Season (S)	1, 104	38.28	<0.0001	1, 104	14.87	0.0002
H × T	1, 104	0.44	0.5109	1, 104	0.52	0.4707
H × S	1, 104	66.08	<0.0001	1, 104	5.81	0.0177
T × S	1, 104	0.01	0.9075	1, 104	4.69	0.0327
H × T × S	1, 104	1.27	0.2615	1, 104	0.05	0.8273
<i>Gustavia</i>						
Habitat (H)	1, 7	17.53	0.0041	1, 7	38.11	0.0005
Trench (T)	1, 106	10.39	0.0017	1, 106	7.32	0.0080
Season (S)	1, 106	3.17	0.0780	1, 106	34.51	<0.0001
H × T	1, 106	4.94	0.0283	1, 106	5.42	0.0218
H × S	1, 106	0.11	0.7361	1, 106	0.20	0.6518
T × S	1, 106	2.70	0.1030	1, 106	6.63	0.0114
H × T × S	1, 106	0.49	0.4865	1, 106	0.00	0.9751
<i>Simarouba</i>						
Habitat (H)	1, 7	117.58	<0.0001	1, 7	56.69	<0.0001
Trench (T)	1, 102	24.21	<0.0001	1, 100	6.80	0.0105
Season (S)	1, 102	16.40	<0.0001	1, 100	10.79	0.0014
H × T	1, 102	13.17	0.0004	1, 100	0.73	0.3941
H × S	1, 102	31.54	<0.0001	1, 100	6.83	0.0103
T × S	1, 102	0.18	0.6696	1, 100	0.19	0.6606
H × T × S	1, 102	0.16	0.6935	1, 100	2.04	0.1568

Notes: Species are presented from higher to lower shade tolerance according to Condit et al. (1996). F tests considered Type III sums of squares. Values in boldface denote significant differences.

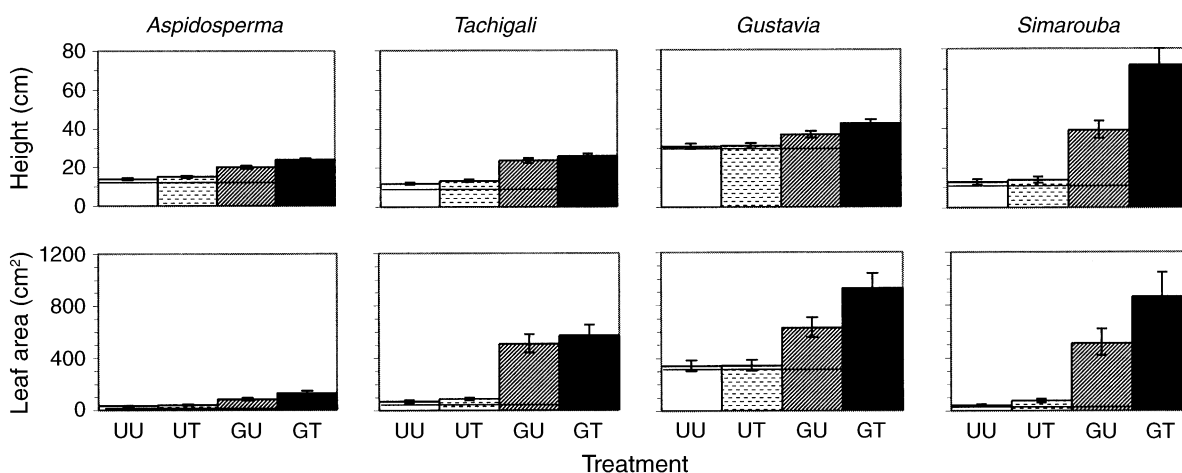


FIG. 3. Height and leaf area (mean ± 1 SE) for seedlings of four species after one year's growth in trenched and untrenched subplots in gaps and understories. The line across the bars denotes the initial height or leaf area in November 1999. Treatment abbreviations are as in Fig. 1. Species are presented from higher (*Aspidosperma*) to lower shade tolerance according to Condit et al. (1996).

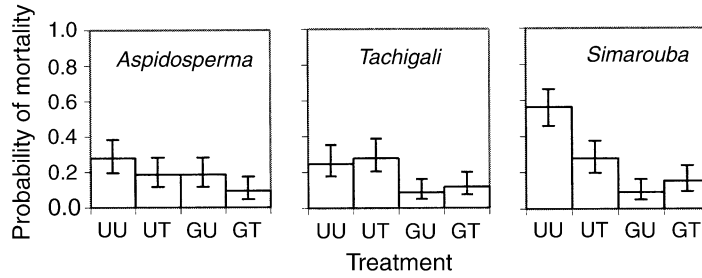


FIG. 4. Effects of habitat and trenching (mean ± 1 SE) on mortality of *Aspidosperma*, *Tachigali*, and *Simarouba* seedlings after one year, as described by a three-parameter logistic regression for each species. Probability of mortality = $e^{\logit(p)} / (1 + e^{\logit(p)})$. Treatment abbreviations are as in Fig. 1.

mortality in *Simarouba* and marginally in *Tachigali*, but trenching did not affect mortality. The greater effect of trenching in gaps was mostly due to seedlings being so limited by the very low light levels in the understory that they were hardly limited by nutrient availability,

but there may have been a small secondary effect in that root density was $\sim 15\%$ lower in gaps (not significant); root density is sometimes reduced by gaps because of tree death (Ostertag 1998). When compared with similar experiments in sites in Central and South America, a pattern emerges of a decreasing trenching effect in the understory as seedlings become less limited by nutrients and water; our intermediate site shows intermediate effects of trenching. On very infertile arenosols in rain forest in Venezuela (Coomes and Grubb 1998), trenching increased seedling height growth by 52% and effects were similar in understories and gaps. On infertile oxisols north of Manaus in Brazil (Lewis and Tanner 2000), trenching increased seedling growth by 128% and again effects were similar in understories and gaps. On the more fertile alfisols in Panama, we found that trenching increased seedling growth by only 35%, and effects were mostly observed in gaps. Whereas on the fertile entisols and ultisols in Costa Rica (Denslow et al. 1991, Ostertag 1998), no trenching effect on seedling growth was observed, either in understories or gaps. Likewise, trenching increased seedling growth and survival in Guanacaste, Costa Rica (Gerhardt 1996), which has a six-month dry season, whereas in BCNM, Panama, with a four-month dry season, trenching only increased growth, and did not increase survival (Barberis 2001), and finally in La Selva, Costa Rica, which has no dry season, trenching had no effects (Ostertag 1998). Therefore, we can generalize that the importance of belowground competition in limiting the growth of tropical tree seedlings decreases as soil fertility increases and decreases as drought decreases. We can also generalize that the increases in growth due to gaps are greater than increases due to trenching in wetter and more fertile sites.

The effects of aboveground and belowground competition were not independent, for *Gustavia* and *Simarouba* trenching increased growth more in gaps than in the understories. Attempts to make generalizations about the interaction between aboveground and belowground competition have been made by Cahill (1999) based on experiments in grasslands; however, these predict the opposite interaction to that which we ob-

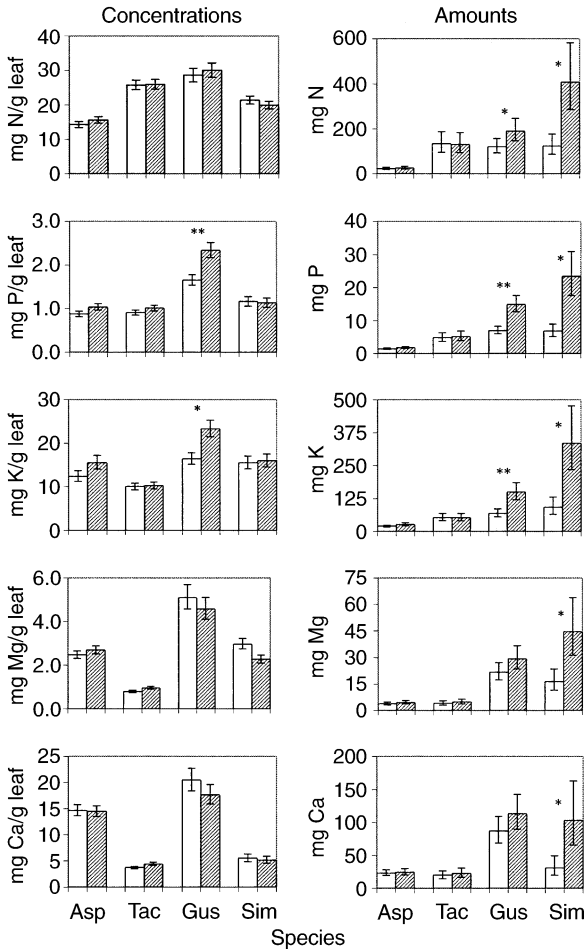


FIG. 5. Concentrations and amounts of nutrients (mean ± 1 SE) in leaves of seedlings of *Aspidosperma* (Asp), *Tachigali* (Tac), *Gustavia* (Gus), and *Simarouba* (Sim) in untrenched (open bars) and trenched (hatched bars) subplots in gaps. * $P < 0.05$; ** $P < 0.01$.

served in our site with intermediate soil fertility. Thus, separate models may be needed for forests and grasslands.

*What caused the trenching effect:
water, nutrients, or both?*

We infer that water (and/or nutrients) limited seedling growth in the drier season, because seedlings of all species produced more leaf area in trenched subplots (which had higher soil water concentrations) than in untrenched subplots. Even *Tachigali*, which on an annual scale did not show a trenching effect, seems to be limited by water during the drier season. Our inference, together with increased growth due to trenching in the much drier forest (six-month dry season) in Guanacaste, Costa Rica (Gerhardt 1996), suggests that we may generalize that, in dry sites, increased growth due to trenches is caused, at least in part, by increased water availability. The relative importance of water, as compared to nutrients, warrants further study by experimental irrigation and fertilization.

We infer that nutrients limited seedling growth of three species in gaps (RGR_h *Gustavia* > *Simarouba* = *Aspidosperma*, with no effect on *Tachigali*) in the wetter half of the year, because trenched seedlings were larger and had more nutrients. For *Gustavia*, we infer that seedling growth was increased by P and/or K, because concentrations of both nutrients, as well as their amounts, were higher in leaves in trenched compared to untrenched plants in gaps. For *Simarouba*, N may have been limiting, because the amount of N in leaves was higher in trenched compared to untrenched plants in gaps. It has been shown that plants may increase growth as a result of added N without showing an increase in N concentration; the extra N is used to produce more mass with the same N concentration (Healey 1989). It is also interesting that *Tachigali*, which fixes its own N, did not respond to trenching in gaps and was therefore not limited by any nutrient. Two other studies of tropical tree seedlings have concluded that N was likely to be more limiting growth than P (Lewis and Tanner 2000, Metcalfe et al. 2002). Thus, it seems that seedlings in the Panama site were limited by P and/or K and sometimes N, depending on the species. These conclusions differ somewhat from the usual interpretation that in tropical lowland rain forests P is more limiting than N (Tanner et al. 1998), but agree with two more recent fertilization studies in lowland rain forest, which do not support the idea that P is limiting (Mirmanto et al. 1999, Newbery et al. 2002). Fertilization experiments are necessary to discover specifically which nutrients are limiting seedling growth in the Panamanian forest.

A global perspective

With our result that belowground competition is significant in a site with a moderate dry season and intermediately fertile soils, it is now clear that below-

ground competition is an important factor throughout tropical forests; it is present wherever it has been looked for, except in the ever-wet, fertile soils at La Selva. The importance of belowground competition in tropical forests matches its pervasive importance in temperate forests where it has been better studied (Coomes and Grubb 2000).

ACKNOWLEDGMENTS

This study was supported by an external doctoral studentship from FOMECA, UNR, Argentina. The whole study was carried out at the Smithsonian Tropical Research Institute in Panama, to whom we are extremely grateful. The following people helped with field work: Edmundo Ayarza, Javier Ballesteros, Jennie Bee, Lucinda Hayes, Erick Manzané, Yaxelis Mendoza, Arturo Morris, Melva Olmos, Simon Queenborough, Rebecca Upson, Maria Vorontsova. The following loaned equipment: David Burslem, Matthew Daws, Joe Wright. The following provided useful discussion during the fieldwork and writing up: David Coomes, Roberto Cordero, Jim Dalling, Peter Grubb, Omar López, Jens Svenning, Joe Wright. Valerie Kapos and four anonymous reviewers made useful suggestions that improved the manuscript.

LITERATURE CITED

- Barberis, I. M. 2001. Above- and belowground competition for seedlings in a Panamanian moist forest. Dissertation. University of Cambridge, Cambridge, UK.
- Becker, P., P. E. Rabenold, J. R. Idol, and A. P. Smith. 1988. Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology* 4:173–184.
- Cahill, J. F. J. 1999. Fertilization effects on interactions between above- and belowground competition in an old field. *Ecology* 80:466–480.
- Cochrane, T. T., L. G. Sánchez, L. G. d. Azevedo, J. A. Porras, and C. L. Garver. 1985. Land in tropical America. Centro Internacional de Agricultura Tropical de Colombia and Empresa Brasileira de Pesquisa Agropecuária do Brasil, Cali, Colombia and Planaltina, Brasil.
- Condit, R., S. P. Hubbell, and R. B. Foster. 1996. Assessing the response of plant functional types to climatic change in tropical forests. *Journal of Vegetation Science* 7:405–416.
- Coomes, D. A., and P. J. Grubb. 1998. Responses of juvenile trees to above- and belowground competition in nutrient-starved Amazonian rain forest. *Ecology* 79:768–782.
- Coomes, D. A., and P. J. Grubb. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs* 70:171–207.
- Denslow, J. S., A. M. Ellison, and R. E. Sanford. 1998. Tree-fall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology* 86:597–609.
- Denslow, J. S., E. A. Newell, and A. M. Ellison. 1991. The effect of understory palms and cyclanths on the growth and survival of *Inga* seedlings. *Biotropica* 23:225–234.
- Gerhardt, K. 1996. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management* 82:33–48.
- Gerwing, J. J. 1995. Competitive effects of three tropical tree species on two species of *Piper*. *Biotropica* 27:47–56.
- Healey, J. R. 1989. A bioassay study of soils in the Blue Mountains of Jamaica. Pages 273–287 in J. Proctor, editor. *Mineral nutrients in tropical forest and savannah ecosystems*. Blackwell Scientific, Oxford, UK.
- Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999.

- Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* **283**:554–557.
- Leigh, E. G. J. 1999. *Tropical forest ecology. A view from Barro Colorado Island*. Oxford University Press, New York, New York, USA.
- Lewis, S. L., and E. V. J. Tanner. 2000. Effects of above- and belowground competition on growth and survival of rain forest tree seedlings. *Ecology* **81**:2525–2538.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. *SAS system for mixed models*. SAS Institute, Cary, North Carolina, USA.
- Metcalfe, D. J., P. J. Grubb, and S. S. Metcalfe. 2002. Soil dilution as a surrogate for root competition: effects on growth of seedlings of Australian tropical rainforest trees. *Functional Ecology* **16**:223–231.
- Mirmanto, E., J. Proctor, J. Green, L. Nagy, and Suriantata. 1999. Effects of nitrogen and phosphorus fertilization in a lowland evergreen rainforest. *Philosophical Transactions of the Royal Society of London, Series B* **354**:1825–1829.
- Newbery, D. M., G. B. Chuyong, J. J. Green, N. C. Songwe, F. Tchuenteu, and L. Zimmerman. 2002. Does low phosphorus supply limit seedling establishment and tree growth in groves of ectomycorrhizal trees in central African rainforest? *New Phytologist* **156**:297–311.
- Ostertag, R. 1998. Belowground effects of canopy gaps in a tropical wet forest. *Ecology* **79**:1294–1304.
- Salati, E. 1985. The climatology and hydrology of Amazonia. Pages 18–48 *in* G. T. Prance and T. E. Lovejoy, editors. *Amazonia*. Pergamon Press, Oxford, UK.
- SAS Institute. 1999. *SAS system, version 8*. SAS Institute, Cary, North Carolina, USA.
- Silver, W. L., F. N. Scatena, A. H. Johnson, T. G. Siccama, and F. Watt. 1996. At what temporal scales does disturbance affect belowground nutrient pools? *Biotropica* **28**:441–457.
- Sollins, P., F. Sancho, M. R. Mata Ch., and R. L. Sanford, Jr. 1994. Soils and soil process research. Pages 34–53 *in* L. A. McDade, K. S. Bawa, H. A. Hespenhide, and G. S. Hartshorn, editors. *La Selva: ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago, Illinois, USA.
- Tanner, E. V. J., P. M. Vitousek, and E. Cuevas. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* **79**:10–22.
- Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**:1–14.
- Yavitt, J. B. 2000. Nutrient dynamics of soil derived from different parent material on Barro Colorado Island, Panama. *Biotropica* **32**:198–207.