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Trenching increased growth, and irrigation increased survival of tree seedlings in the understorey of a semi-evergreen rain forest in Panama

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Abstract: Seedlings in tropical forests are ultimately the source of canopy trees, thus factors controlling their composition and growth potentially influence the composition of the forest. Seedlings are primarily limited by above-ground competition with trees, but below-ground competition is potentially also important. Over 4 y we experimentally reduced below-ground competition by trenching to 50 cm and reduced drought stress by irrigating in the dry seasons (6 cm every 2 d) in the understorey of a semi-evergreen rain forest in Panama. There were four irrigated plots and four unirrigated, in each plot there were eight subplots (four trenched, four untrenched); 32 seedlings (two per subplot) of each of four tree species were equally allocated to the four treaments; the four species were: *Aspidosperma cruenta*; *Gustavia superba*; *Simarouba amara* and *Tachigali versicolor*. Over all species together, trenching increased seedling height by 41% and leaf area by 140% over 4 y. The cause was likely to be increased nutrient supply, because the amounts of N, K and Ca were higher in trenched plants, though concentrations were not higher. Irrigation had no significant effect on growth. Irrigation, but not trenching, reduced seedling mortality. We conclude that below-ground competition was a major limitation for seedling growth for at least some common species (*Gustavia* and *Tachigali* in this experiment). More experiments are necessary to determine whether below-ground competition is also important in other tropical rain forests on fairly fertile soils.

Key Words: *Aspidosperma cruenta*, below-ground competition, *Gustavia superba*, irrigation, *Simarouba amara*, *Tachigali versicolor*, tree seedlings, trenching, tropical semi-evergreen forest

INTRODUCTION

In most tropical evergreen and semi-evergreen forests, the formation of canopy gaps promotes seedling growth from the seedling bank (Whitmore 1984). Hence, the factors limiting the survival and growth of tree seedlings are of great importance in determining the species present, their density and their relative size, which in turn can be crucial in determining success in the competition to fill a canopy gap (Tanner *et al.* 2005).

It is well established that above-ground competition for light is usually the most important factor limiting tree seedling growth; however, below-ground factors are also important (Casper & Jackson 1997). Furthermore, in tropical forests with either very infertile soils but sufficient water supply or with long dry seasons (i.e. at least 6 mo), trenching (i.e. digging trenches around a block of soil to cut roots) greatly increases seedling growth and survival in the understorey (Coomes & Grubb 2000). More recently in a semi-evergreen rain forest in Barro Colorado Nature Monument (BCNM) in Panama, on more fertile soil and with a moderate dry season (*c.* 4 mo), we have shown that trenching to reduce below-ground competition also increased tree seedling growth, but mostly in gaps rather than in the understorey (Barberis & Tanner 2005). The latter study lasted only 1 y, but even so was beginning to show small effects of trenching in the understorey. As tree seedlings in tropical forests may persist for decades in the shaded understorey (De Steven 1994), a much longer-term study of trenching in understorey conditions might detect a larger effect. In addition to the trenching treatment, we also carried out an irrigation treatment because we expected the dry season to limit seedling survival and growth. Thus, the study we present here investigated the extent and cause of below-ground competition in the shaded understorey at a site with moderately fertile soils and a moderate dry season.

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We tested the following four hypotheses. First, we hypothesized that trenching in the understorey, if measured for several years, would increase seedling growth. This is based on an earlier study of two species (Haines 1971); reinforced during our study by a small effect measured over 1 y in a parallel experiment investigating the effects of gaps in a nearby forest (Barberis & Tanner 2005). Second, we hypothesized that trenching will decrease seedling mortality, due to increased water in soils in trenched plots. Third, we hypothesized that irrigation in the understorey would increase seedling growth; as was found for *Virola surinamensis* in nearby forest (Fisher *et al.* 1991) and in 25 of 28 species in another experiment in nearby forest (Engelbrecht & Kursar 2003). It should be noted that subsequent to our fieldwork Bunker & Carson (2005) showed no effect of irrigation on seedling growth over 1 y, in a large experiment with many species in forest on Barro Colorado Island itself (BCI, part of BCNM). Fourth, we hypothesized that irrigation will decrease seedling mortality, based on field irrigation experiments in the understorey of nearby tropical semi-evergreen forest in BCNM (Engelbrecht & Kursar 2003, Engelbrecht *et al.* 2005, Fisher *et al.* 1991, Mulkey *et al.* 1991); however, after our field work, Bunker & Carson (2005) showed no effect of irrigation on mortality of naturally occurring (as opposed to planted in) seedlings over 1 y on BCNM.

METHODS

Study area

The study was carried out in a tropical semi-evergreen forest in BCNM, Panama (9°10′N, 79°51′W). Rainfall on the study area averages 2643 ± 445 mm y^{-1} (1925–2005) with a pronounced dry season from January to April of average length 135 d. Actually, the length of the ‘dry season’ is a complicated metric based on 11 variables, only one of which is rainfall (STRI Environmental Sciences Program; http://striweb.si.edu/esp/). During the 4-y study in 2000–2003, annual rainfall and length of the dry season were close to the average (2544 mm with a dry season of 114 d in 2000; 2302 mm and 136 d in 2001; 2301 mm and 123 d in 2002; 2891 mm and 148 d in 2003). Although 2003, which was an El Niño year, had a moderate drought, its dry season was only the 11th longest in 30 y. Mean annual temperature is 26 °C and mean monthly temperatures vary by just 1 °C through the year (Windsor 1990).

The plots were located in the Buena Vista peninsula (about 35 m asl), an area of secondary forest *c.* 40 y old, contiguous with Soberanía National Park (Denslow & Guzmán 2000) with uneven canopy about 10–30 m tall. Soils are montmorillonitic (alfisols), derived from the calcareous Caimito marine facies (Leigh 1999, Yavitt 2000). The soil (0–15 cm) in the plots is of average fertility (pH 4.8, total N 0.36%, total P 336 mg kg^{-1}, Bray’s P < 1.0 mg kg^{-1}, exchangeable ions (all in mg kg^{-1}) Ca 1591, K 75, Mg 729). Compared to 43 soils from 13 sites in lowland rain forests in the Neotropics, the N and K are near the average, the Ca and Mg are high (O. Phillips, J. Lloyd & S. Lewis pers. comm.); the total P is the same as the median total P for 16 tropical soils in Silver (1994). Despite the very low Bray’s P it is likely that P is in sufficient supply to the canopy trees because in a nearby site, Gigante, which has similar Bray’s P, phosphorus in litterfall is 6 kg ha^{-1} y^{-1} (Sayer *et al.* 2006), which is among the highest for lowland tropical forests with similar annual rainfall (Vitousek 1984).

Experimental design and implementation

In August 1999 in the SW of the Buena Vista peninsula close to Gatun Lake we selected four sites (a minimum of 20 m apart at the closest point). In each site we located two plots (7.4 m × 6.1 m each) a minimum of 10 m apart at the closest point; one of each pair was randomly selected and an irrigation system installed. The irrigation system consisted of a water pump connected to system of PVC tubes. Within each irrigated plot, eight PVC tubes (6.1 m long and 2.5 cm in diameter) were placed in parallel, separated by 1.1 m and their ends were connected by PVC tubes of the same diameter. Small holes (about 1 mm) were drilled in the parallel tubes every 20 cm that caused jets of water up to 1 m high. Water was drawn from Gatun Lake where nutrient concentrations are lower than in rainwater collected on Barro Colorado Island (Wright 1991, Wright & Cornejo 1990). During the dry seasons (i.e. from January to April 2000, 2001, 2002 and 2003) the irrigated plots were watered every other day with *c.* 6 cm of water over 30–40 min, after which there was surface runoff (which did not run towards the unirrigated plots).

Within each plot, eight subplots (57 cm × 57 cm) were located on the four non-contiguous strips delimited by the PVC tubes. Half of the subplots were randomly selected and trenched, the others remained untrenched. Soil within trenched plots was undisturbed during trenching. Trenches were 0.5 m deep and the inner side was lined with a polyethylene sheeting (black 6 mil B0620, Carlisle Plastics Inc., Minneapolis, MN 55431) to prevent root ingrowth from adult trees; trenches were then refilled with soil. The upper part of the plastic emerged from the soil to prevent the entrance of surface roots. We frequently cut the roots growing over the surface into the trenched subplots and checked that there were no fallen branches or palm leaves on the subplots. As most roots in nearby forest were located in the upper 25 cm of soil (Cavelier

1992), this trenching depth was considered enough to prevent most root competition.

Seedling preparation and allocation to different treatments

We used four tree species that spanned half (–1.2 to 1.2) of the shade tolerance range (–2 to 3) that included most species (Condit *et al.* 1996). From the most shade tolerant they were: *Aspidosperma cruenta* Woodson (shade tolerance = –1.17), *Tachigali versicolor* Standl. & L.O. Williams (tolerance = 0.09), *Gustavia superba* Berg. (tolerance = 0.49) and *Simarouba amara* Aubl. (tolerance = 1.20). Hereafter species are referred to in the text by their generic names. *Gustavia* and *Tachigali* seedlings were raised from seeds collected on BCNM and Soberanía National Park, Panama in May 1999, sown in 1200-cm^3 pots with a 1:1 mix of *c.* 0–15 cm forest soil from the Bohio Peninsula BCNM and lake sand, and placed under mesh screens (4% full daylight) on BCI until transplanting. Newly germinated bare-root seedlings of *Aspidosperma* and *Simarouba* were collected from the Gigante Peninsula (BCNM) in August and September 1999, transplanted into similar pots with similar soils and kept in the understorey of the Gigante Peninsula until their allocation to the experiment. Seedlings were watered during dry spells and shaded during transport to the Buena Vista Peninsula to avoid photo-inhibition.

The studied seedlings were planted in the 64 subplots, where all pre-existing seedlings and small saplings were cut off at ground level; there were no other saplings or trees in the subplots. There were four sites each with two plots (i.e. one irrigated and one unirrigated); each plot had eight subplots (i.e. four trenched and four untrenched; two for each species, one trenched and one untrenched); and each subplot had two seedlings of one species. Thus there were 64 subplots in total, 16 irrigated and trenched, 16 irrigated and untrenched, 16 unirrigated and trenched, 16 unirrigated and untrenched (i.e. controls). Of the 64 subplots, 16 had two seedlings of *Aspidosperma*, 16 had two seedlings of *Gustavia*, 16 had two seedlings of *Simarouba*, 16 had two seedlings of *Tachigali*. Thus, there were 4 sites × 2 water treatments × 2 trenching treatments × 2 plants per subplot for each species; and the per species per treatment replication was four. Seedlings, around the mean height for each species, were assigned using a stratified random procedure (stratified by height and treatment) such that there were no significant differences in seedling heights within a species between the four treatments at the beginning of the experiment ($P > 0.15$). Our removal of the largest and smallest seedlings from our pool of available seedlings and the stratification means that we can detect significant differences between treatments with relatively small sample sizes. All seedlings were transplanted on 27 October 1999. Seedling density was 6.2 individuals m^{-2}, a quarter of the 23 individuals m^{-2} reported by Bunker & Carson (2005) for their control plots on BCI, but as competition among tree seedlings is assumed to be negligible (Wright 2002) the difference is probably not important. Moreover, we found no differences in growth over 1 y, between seedlings grown at 25 individuals m^{-2} and 6 individuals m^{-2}, in a parallel experiment with the same species (Barberis & Tanner 2005). All *Gustavia* subplots were fenced with 1-m-tall wire mesh (1 cm^2) to prevent predation by agouties (*Dasyprocta punctata* Gray) which in a trial dug up freshly planted seedlings of only this species.

Measurement of seedling growth and record of seedling mortality

The experiment lasted for 4 y, from November 1999 to December 2003. At the time of transplanting in October 1999, we measured seedling height and length and width of each leaf(-let). For each species, we derived leaf area by using a regression relationship obtained from a subset of 16 seedlings harvested at the beginning of the experiment (Average r^2: 0.95; range: 0.91–0.98; Barberis 2001). We remeasured surviving seedlings and recorded mortality in February, May, August and November 2000, August 2002, January, April and December 2003. In December 2003 we harvested the above- and below-ground biomass of the largest surviving seedling, of the initial two in each subplot.

We removed a cube of soil of side 25 cm (centred on a planted seedling) from which the target seedling roots and the 'competing' roots were washed through sieves and separated in three size classes (< 2 mm, 2–5 mm and > 5 mm diameter), they were not sorted into living and dead. After 4 y, roots had grown underneath the 50-cm plastic barrier back into the trenched subplots, thus the measured root densities underestimate the initial conditions. When large roots of target seedlings exceeded the 25-cm cube they were excavated. Smaller roots of the target seedlings probably exceeded the 25-cm cube (Becker & Castillo 1990), they are physiologically significant but probably a small fraction of total root mass. Leaves, stems and roots were dried at 70 °C to constant weight.

Relative growth rates in height (RGR_h) were calculated with the following equation: $(\ln H_1 - \ln H_0)/(t_1 - t_0)$, where H_0 and H_1 are the initial (October 1999) and final height (December 2003) in cm, and t_1-t_0 is the elapsed time (y) between measurements. A similar equation was used to estimate RGR in leaf area (RGR_a). From the biomass data, we derived root mass fraction, stem mass fraction and leaf mass fraction.

Plant element analyses

Element concentrations were measured in oven-dried composite samples from seedlings harvested in December 2003. The whole seedling harvested from each subplot was ground to pass a 1-mm mesh. For each species and treatment a composite sample was made by combining subsamples from the four replicates (three replicates in 7 of 64 cases where both individuals in a subplot had died) in proportion to their masses, resulting in 16 composite samples (2 (irrigated/unirrigated) × 2 (trenched/untrenched) × 4 species). In addition, for the unirrigated subplots only, we analysed leaf material from the tallest individuals in each subplot (i.e. separate individuals not composite samples). These samples were analysed by the Waite Analytical Services, University of Adelaide, Australia, where they were digested with nitric acid, finished with hydrochloric acid, and analysed by inductively coupled plasma emission spectrophotometry (ICPOES) to obtain P, K, Ca, Mg, Fe, Mn, Co and Al. Nitrogen was analysed by combustion technique using a Carlo Erba instrument (NA1500, series, 2, Carlo Erba, Milan, Italy). Accuracy was checked by comparing analyses of standard samples analysed by independent international laboratories.

Abiotic measurements

The light environment of each subplot was quantified by hemispherical photographs taken above the tallest seedling in March 2000. Photographs were taken under overcast sky conditions, using a CI-110 Digital Plant Canopy Imager (CID Inc., Vancouver, USA). The software provided calculates the diffuse radiation transmission coefficients (the sky view factor).

Volumetric soil water concentration (SWC) in the top 6 cm of soil of each subplot was measured monthly from January to October 2000 with a ThetaProbe soil moisture sensor, which was calibrated for these soils (Delta-T Devices, Cambridge, England). Three measurements were made in each subplot, just before watering the plots. We used the filter-paper technique (Deka *et al.* 1995) to construct a soil moisture characteristic curve for these soils. Then, we used that curve to plot a line for –1.5 MPa on our soil water graph. We do not attach great importance to precisely –1.5 MPa, but it is a useful guide to when water becomes difficult to obtain for plants (little water is available below – 1.5 MPa, see caption to Figure 1).

Data analyses

The effects of irrigation, trenching and species on environmental variables (light, soil moisture and competing roots), relative growth rates (RGR in height and leaf area), size (height, leaf area, and biomass), and biomass allocation (root, shoot and leaf mass fractions: RMF, SMF, and LMF) were analysed using generalized linear mixed models (the GLIMMIX macro and PROC MIXED from SAS version 8.0 (SAS Institute Inc.). We used split-plot design with irrigation as the main-plot effect and trenching and species as the split-plot effects. All effects were nested within replicated sites. Treatment effects (irrigation, species and trenching) were assumed to be fixed, whereas sites were considered random.

Generalized linear mixed models use quasi-likelihood to accommodate random effects. For the environmental, RGR and size variables we assumed a gamma probability distribution and reciprocal link function, whereas for allocation variables we assumed a binomial probability distribution and logit link function (Littell *et al.* 1996). Light measured at each subplot was incorporated into the model as a covariate for all analyses. The models with the covariate explained significantly more scaled deviance in all analyses ($P < 0.001$). Analyses were performed on the means of the surviving seedlings in each subplot.

For height and leaf area through the study period, we analysed the effect of censuses by repeated-measures design with PROC MIXED using compound symmetry as a covariance structure; we assumed a normal probability distribution and identity link function (Littell *et al.* 1996). Height and leaf area data were log-transformed to improved normality and homogeneity of variance. As in the previous analyses, light measured at each subplot was incorporated into the model as a covariate. The models with the covariate explained significantly more scaled deviance only for *Simarouba* ($P < 0.001$).

Element concentrations and amounts per plant were compared between treatments (i.e. trenched vs. untrenched and irrigated vs. unirrigated) by paired t-tests (i.e. treatments were paired by species). Similar analyses were run for leaf element concentrations and amounts.

We examined the probability of mortality (P_m) for each seedling with respect to irrigation, species, and trenching for the whole experiment using logistic regression. We first used the GLIMMIX macro and PROC MIXED of SAS (Littell *et al.* 1996) using binomial error distribution and logit link function. As 'site' and 'site × irrigation' variance component estimates were zero, we dropped them from the analysis, and used the PROC LOGISTIC of SAS 8.0 (Littell *et al.* 1996). We assessed the effect of irrigation on seedling survival at the end of the experiment by using two indices proposed by Engelbrecht *et al.* (2006). We calculated the species drought sensitivity index (DS), a measure of species susceptibility to drought, defined as the reduction in survival in the unirrigated compared with the irrigated treatment relative to the survival in the irrigated treatment: $DS = (S_{irrigated} - S_{unirrigated})/S_{irrigated}$ where $S_{irrigated}$ and $S_{unirrigated}$ are the % survival (S) in the irrigated and unirrigated treatment, respectively. Then,

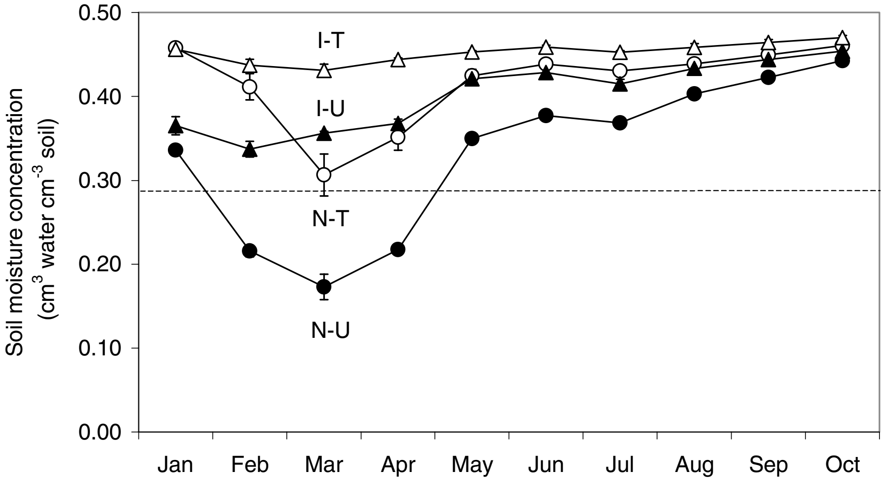

Figure 1. Annual course of volumetric soil moisture concentration in 2000 for trenched and untrenched subplots in irrigated and unirrigated plots on the Buena Vista peninsula, Panama. Treatment codes: N-U = unirrigated untrenched, N-T = unirrigated trenched, I-U = irrigated untrenched, I-T = irrigated trenched. The dashed line shows the –1.5 MPa value estimated for the forest soil (at –1.5 MPa soil moisture content is 0.29 cm^3 water cm^{-3} soil; at –2.5 MPa it is 0.27; at –4.0 MPa it is 0.25). Data are mean ± 1 SE.

we calculated species drought importance index (DI), a measure of the proportion of mortality in the unirrigated treatment that is directly attributable to drought, as opposed to other factors responsible for mortality in both treatments: $\text{DI} = (S_{\text{irrigated}} - S_{\text{unirrigated}})/(100\text{-}S_{\text{unirrigated}})$.

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

RESULTS

Light, water availability and competing roots

Light was similar in irrigated and unirrigated plots ($F_{1,3} = 0.09$, $P = 0.780$), but trenched subplots received a little more light than the untrenched ones ($F_{1,42} = 4.70$, $P = 0.036$); Skye View factors (which range from 0.00 for darkness to 1.00 for unobscured sky): unirrigated untrenched 0.034 ± 0.003 (mean ± SE); unirrigated trenched 0.035 ± 0.003; irrigated untrenched 0.032 ± 0.002; irrigated trenched 0.039 ± 0.003. The soil water concentration followed the rainfall pattern and in 2000 varied from 0.18 cm^3 water cm^{-3} soil in the dry season to 0.44 cm^3 water cm^{-3} soil in the wet season (Figure 1). Irrigation increased soil water concentration even in the wet season, when the plots were not irrigated (Dry season: $F_{1,3} = 54.7$, $P = 0.005$; Wet season: $F_{1,3} = 27.7$, $P = 0.013$) (Figure 1). Trenching increased soil water concentration in both irrigated and unirrigated plots in both seasons; even in the wet season trenched subplots had higher water than untrenched subplots ($F_{\text{Dry }1,42} = 106$, $P < 0.001$; $F_{\text{Wet }1,42} = 48.8$, $P < 0.001$). At the end of the dry season (March) the soil water concentration increase due to trenching was about 77% in the unirrigated plots and 21% in the irrigated plots ($F_{\text{Irrigat} \times \text{Trench }1,42} = 47.4$, $P < 0.001$) (Figure 1). In the wet season, trenching increased soil water concentration about 5% in both irrigation treatments ($F_{\text{Irrigat} \times \text{Trench }1,42} = 1.39$, $P = 0.245$) (Figure 1). At the end of the experiment, the biomass of the competing roots (< 2 mm diameter) was similar in irrigated and unirrigated plots ($F_{1,3} = 0.07$, $P > 0.809$), but subplots trenched 4 y previously still had lower competing root biomass in both irrigated and unirrigated plots (9.54 g root < 2 mm diameter (in 0.016 m^3 of soil) in trenched and 14.2 g in untrenched; $F_{\text{Trench }1,42} = 18.7$, $P < 0.001$; $F_{\text{Irrigat} \times \text{Trench }1,42} = 0.81$, $P = 0.373$).

Trenching and irrigation effects on seedling growth, element concentrations and mortality

Trenching increased seedling height growth (RGR_h) and was close ($P = 0.08$) to increasing leaf area growth, when evaluated across all species (RGR_a; Figure 2; Table 1), and therefore seedlings were taller and larger in trenched than in untrenched subplots (Figure 3; Table 1). In contrast, irrigation had no significant effect on seedling growth over 4 y either in height (RGR_h) or leaf area (RGR_a), and thus no effect on seedling size (Figures 2 and 3; Table 1). Biomass allocation to root, stem, or leaves was not affected by trenching or irrigation (all $P > 0.45$).

Species differed markedly in their RGR in height and leaf area (Table 1), and in their responses to trenching and irrigation (Table 2). *Simarouba* and *Tachigali* showed the fastest growth in height and leaf area followed by *Aspidosperma* and finally *Gustavia* (Figure 3). At the end of the experiment *Aspidosperma* and *Tachigali* seedlings were

Table 1. Results of mixed model ANOVA for relative growth rate in height (RGR_h) and leaf area (RGR_a), height, leaf area, height, and biomass with irrigation and trenching as fixed effects and sites as random effect for seedlings planted in trenched and untrenched subplots in irrigated and unirrigated plots. Light was used as a covariate. Numerator and denominator degrees of freedom, F-values and significance are shown. Bold values denote significant differences.

		RGRh		RGRa		Height		Leaf area		Biomass	
Effect	df	F	P	F	P	F	P	F	P	F	P
Light	1,34	1.70	0.200	1.25	0.272	7.40	**0.010**	7.77	**0.009**	3.36	0.076
Irrigation	1,3	0.00	0.995	0.38	0.583	0.00	0.955	0.25	0.649	2.08	0.245
Trenching	1,34	9.67	**0.004**	3.37	0.075	5.90	**0.021**	4.16	**0.049**	7.13	**0.012**
Irrigation × Trenching	1,34	0.36	0.552	0.12	0.731	3.73	0.062	4.07	0.052	6.19	**0.018**
Species	3,34	20.4	< **0.001**	14.3	< **0.001**	31.0	< **0.001**	8.03	< **0.001**	21.2	< **0.001**
Irrigation × Species	3,34	0.88	0.460	0.27	0.850	0.56	0.644	0.43	0.731	0.89	0.457
Trenching × Species	3,34	1.67	0.192	1.15	0.343	3.21	**0.035**	0.46	0.713	3.22	**0.035**
Irrigation × Trenching × Species	3,34	1.91	0.147	0.02	0.995	2.57	0.071	0.88	0.460	2.38	0.087

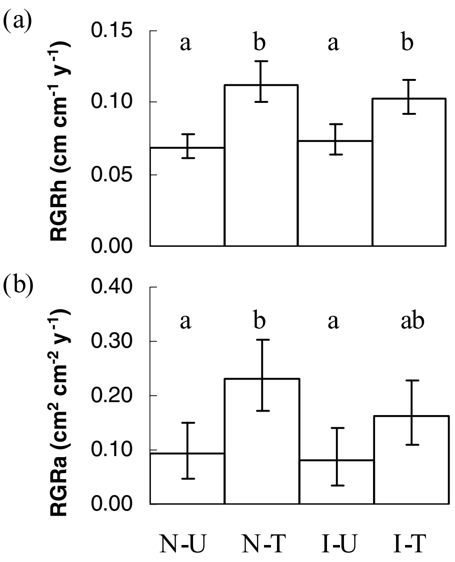

Figure 2. Relative growth rate in (a) height (RGRh) and (b) leaf area (RGRa) (mean ± 1 SE) for the 84 surviving seedlings (*Aspidosperma* 17 seedlings, *Gustavia* 31, *Simarouba* 16, and *Tachigali* 20) grown through 4 y in trenched and untrenched subplots in irrigated and unirrigated understorey plots. Treatment codes: N-U = unirrigated untrenched, N-T = unirrigated trenched, I-U = irrigated untrenched, I-T = irrigated trenched. Light was used as a covariate. Different letters within a panel indicate significant differences.

still increasing their leaf area, whereas *Simarouba* seemed to have reached a plateau and *Gustavia* leaf area was decreasing (Figure 3). Trenching increased seedling size in *Gustavia* (leaf area) and *Tachigali* (height and leaf area), but not in *Aspidosperma* or *Simarouba* (Figure 3; Table 2). In contrast, irrigation had no significant effect on seedling size (either leaf area or height) for any species.

A negative irrigation × trenching interaction was observed for *Simarouba* seedlings (height and leaf area) – trenched seedlings in irrigated plots were smaller than trenched seedlings in unirrigated plots. Trenching effects on seedling leaf area and height increased through the 4-y study period (Figure 3; Table 2). Across all species, trenching effects on height became significant sometime between 14 ($P = 0.08$) and 35 mo ($P = 0.02$) and for leaf area after 8 mo ($P = 0.01$); for *Gustavia* (RGR_h and RGR_a) they were significant after the first year (Barberis 2001).

Element concentrations in whole plants were mostly unaffected by trenching, but irrigation caused plants to have significantly higher concentrations of Fe, Mn, Co, S and Al (Table 3). Element concentrations in leaves were unaffected by trenching (data not shown). Amounts of element per whole plant were larger for seven elements (N, K, Ca, Fe, Al, Mn and Co) in trenched plants compared with untrenched plants (data not shown), because trenched plants were larger.

Seedling mortality differed among species (*Aspidosperma* = 47%, *Gustavia* = 3%, *Simarouba* = 50%, *Tachigali* = 38%; Wald $\chi^2_{3\,df} = 11.1$, $P = 0.011$). Trenching had no significant effect on seedling mortality (untrenched = 33%, trenched = 36%; Wald $\chi^2_{1\,df} = 0.17$, $P = 0.680$), whereas irrigation reduced seedling mortality (unirrigated = 42%, irrigated = 27%; Wald $\chi^2_{1\,d.f.} = 4.03$, $P = 0.045$). *Aspidosperma* and *Tachigali* were more sensitive to drought, whereas *Gustavia* and *Simarouba* were almost insensitive (Table 4). The importance of drought on seedling mortality was higher for *Gustavia*, intermediate for *Aspidosperma* and *Tachigali* and nil for *Simarouba* (Table 4).

DISCUSSION

Irrigation and trenching both increased soil water concentration, but even 6 cm of irrigation every 2 d was not sufficient to keep the surface soils near field capacity 2 d after irrigation. Subplots that were both trenched and irrigated had water concentrations that hardly varied throughout the year and were thus probably at field capacity. We think that waterlogging was not a problem even in irrigated trenched subplots because leaf growth in *Aspidosperma* was not reduced in those

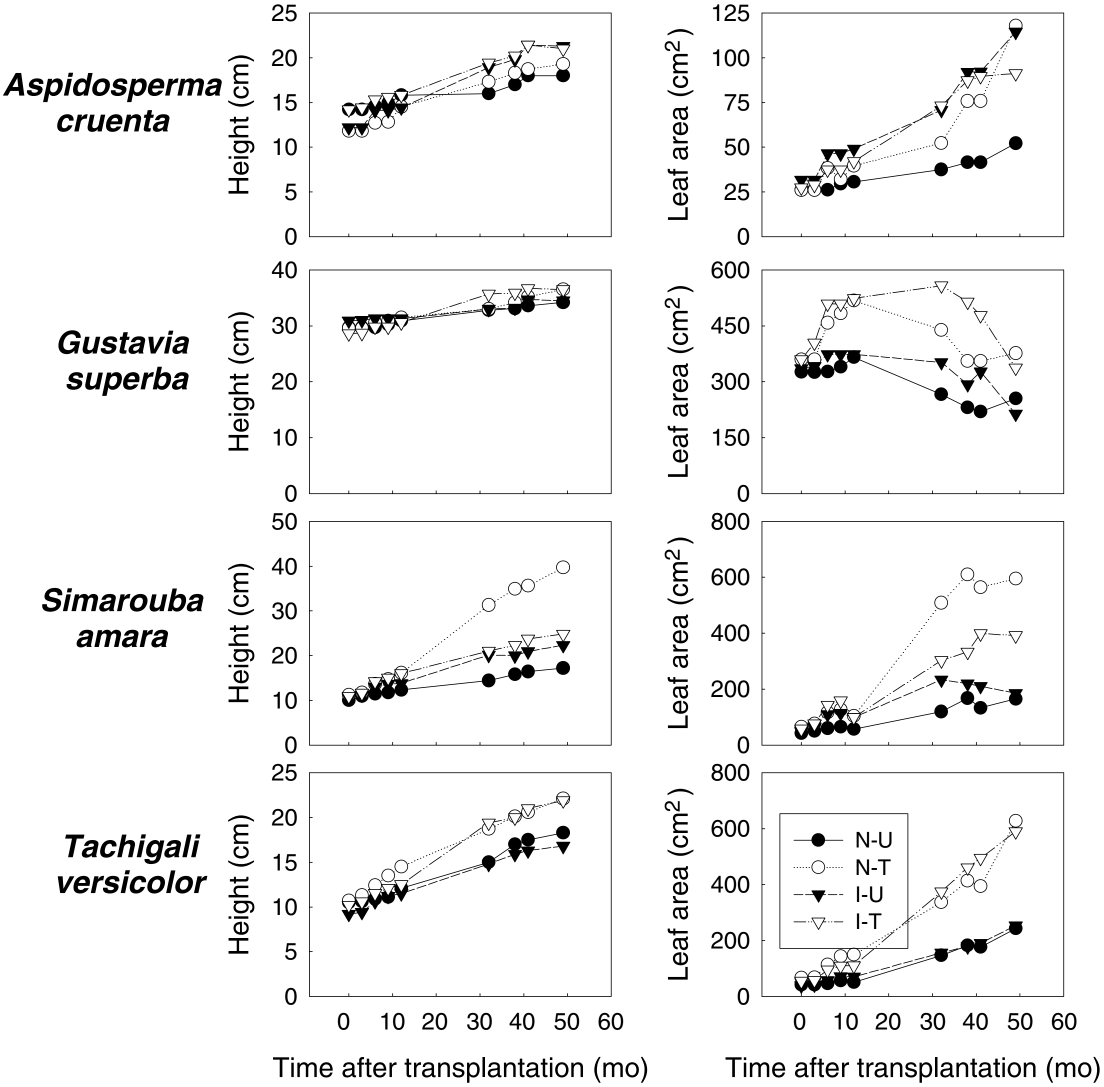

Figure 3. Mean height and leaf area for *Aspidosperma*, *Gustavia*, *Simarouba* and *Tachigali* surviving seedlings grown over 4 y in trenched and untrenched subplots in irrigated and unirrigated plots in the understorey. Treatment codes: N-U = unirrigated untrenched, N-T = unirrigated trenched, I-U = irrigated untrenched, I-T = irrigated trenched. For *Simarouba*, light was used as a covariate. Note different scales among graphs.

subplots; leaf production in *Aspidosperma* was very much reduced by waterlogging in an experiment by López & Kursar (2003). However, it is possible that the reduced growth of *Simarouba* in irrigated and trenched subplots was due to excess water; *Simarouba* was not studied by López & Kursar.

Effects of irrigation on seedling growth and mortality

Seedling growth was not affected by irrigation, despite the fact that one of our study years was a mild El Niño year, as judged by growth over 4 y of surviving seedlings in our experiment. An evaluation of our species using distributions of individuals in the 50-ha plot on BCI showed no strong patterns with respect to habitats, which differ in water availability in the dry season, and in that respect our species are representative of most species on the 50-ha plot on BCI (Harms *et al.* 2001). Our lack of effect of irrigation agrees with that from a large field experiment on nearby BCI, in which naturally occurring seedlings of 10 common species did not grow more when irrigated as compared with unirrigated controls over 1 y (Bunker & Carson 2005); although increased growth was found in irrigated plants in the dry season itself. The year of their study, 1998, was an El Niño year with a long 'dry season' of 171 d, but a relatively short continuous dry period (only 24 continuous days with < 5 mm of rain). Poorter & Hayashida-Oliver (2000) also reported an earlier leaf flush, but no increased growth over nearly 1 y, in an irrigation experiment with one species in the understorey in a semi-evergreen forest in Bolivia. A different drought

Table 2. Results of mixed model ANOVA for height and leaf area with irrigation, trenching and censuses as fixed effects and sites as random effect for seedlings planted in trenched and untrenched subplots in irrigated and unirrigated plots in the understorey of Buena Vista Peninsula (Panama). For Simarouba light was used as a covariate. Numerator and denominator degrees of freedom, F-values and significance are shown. Bold values denote significant differences.

		Height		Leaf area	
Effect	df	F	P	F	P
Aspidosperma cruenta					
Irrigation	1,3	1.65	0.289	2.98	0.183
Trenching	1,4	0.07	0.810	3.44	0.137
Irrigation × Trenching	1,4	2.77	0.171	13.4	**0.022**
Census	8,80	49.3	< **0.001**	13.2	< **0.001**
Irrigation × Census	8,80	1.48	0.178	1.08	0.385
Trenching × Census	8,80	0.43	0.899	0.11	0.999
Irrigation × Trenching × Census	8,80	3.37	**0.002**	0.42	0.907
Gustavia superba					
Irrigation	1,3	0.15	0.726	0.26	0.64
Trenching	1,6	0.17	0.694	38.0	< **0.001**
Irrigation × Trenching	1,6	0.12	0.742	0.00	0.960
Census	8,96	57.4	< **0.001**	7.20	< **0.001**
Irrigation × Census	8,96	0.78	0.624	1.92	0.066
Trenching × Census	8,96	4.82	< **0.001**	2.23	**0.032**
Irrigation × Trenching × Census	8,96	2.37	**0.023**	0.15	0.996
Simarouba amara					
Light	1,72	16.2	< **0.001**	16.0	< **0.001**
Irrigation	1,2	0.15	0.736	0.58	0.527
Trenching	1,2	0.17	0.721	0.95	0.432
Irrigation × Trenching	1,2	13.8	0.066	7.90	0.107
Census	8,72	124	< **0.001**	54.0	< **0.001**
Irrigation × Census	8,72	1.40	0.212	0.83	0.581
Trenching × Census	8,72	8.83	< **0.001**	1.86	0.079
Irrigation × Trenching × Census	8,72	5.36	< **0.001**	0.54	0.823
Tachigali versicolor					
Irrigation	1,2	0.06	0.830	0.30	0.637
Trenching	1,5	6.78	**0.048**	8.69	**0.032**
Irrigation × Trenching	1,5	0.03	0.871	0.79	0.415
Census	8,80	114	< **0.001**	61.3	< **0.001**
Irrigation × Census	8,80	0.40	0.918	0.29	0.967
Trenching × Census	8,80	1.45	0.190	0.74	0.653
Irrigation × Trenching × Census	8,80	0.73	0.666	0.79	0.612

Table 3. Element concentrations of whole seedlings (leaves plus stems plus roots). Treat. = treatment: UI = unirrigated; I = irrigated; UT = untrenched; T = trenched; *Asp* = *Aspidosperma*; *Gus* = *Gustavia*; *Sim* = *Simarouba*; *Tac* = *Tachigali*.

		($mg\ g^{-1}$)							($mg\ kg^{-1}$)	
Treat.	Species	N	P	K	Ca	Mg	Fe	Al	Mn	Co
UI/UT	*Asp*	13.0	1.40	10.2	10.8	3.20	1.27	1.45	146	1.00
UI/UT	*Gus*	10.4	0.75	7.60	6.20	1.26	0.40	0.54	69.0	0.61
UI/UT	*Sim*	14.5	0.89	11.6	5.50	2.50	1.49	1.82	127	0.79
UI/UT	*Tac*	19.5	0.54	4.30	3.40	1.23	0.69	0.88	99.0	1.09
UI/T	*Asp*	12.2	0.78	9.00	9.50	2.60	1.54	1.63	200	1.34
UI/T	*Gus*	11.7	0.62	8.50	8.00	1.27	0.47	0.63	76.0	0.52
UI/T	*Sim*	17.5	0.76	9.80	6.00	2.10	0.80	0.89	95.0	0.67
UI/T	*Tac*	24.0	0.52	4.40	3.60	1.18	0.90	1.19	102	0.63
I/UT	*Asp*	12.3	0.75	8.20	14.3	3.50	2.40	2.60	210	1.35
I/UT	*Gus*	11.9	0.87	10.4	8.30	1.86	0.93	1.13	101	0.69
I/UT	*Sim*	16.8	0.84	9.30	5.10	2.20	3.10	3.10	137	1.66
I/UT	*Tac*	17.5	0.47	4.40	4.90	1.51	1.33	1.52	117	1.06
I/T	*Asp*	13.3	0.98	9.40	12.5	3.40	3.20	3.40	240	1.56
I/T	*Gus*	14.4	0.69	10.5	7.70	1.18	0.72	0.76	107	0.71
I/T	*Sim*	15.7	0.76	9.00	5.60	2.40	1.38	1.66	99.0	0.87
I/T	*Tac*	16.7	0.59	5.50	3.80	1.43	2.00	2.10	134	1.35

Table 4. Seedling survival (%) to the end of the experiment in irrigated ($S_{irrigated}$) and unirrigated ($S_{unirrigated}$) plots, drought sensitivity (DS) and the importance of drought for their total mortality (DI) for four shade-tolerant species in the understorey of Buena Vista Peninsula (Panama).

	$S_{irrigated}$	$S_{unirrigated}$	DS	DI
Aspidosperma cruenta	69	37	0.45	0.50
Gustavia superba	100	94	0.06	1.00
Simarouba amara	50	50	0.00	0.00
Tachigali versicolor	75	50	0.33	0.50
All species	73	58	0.21	0.37

experiment on Buena Vista in Panama (i.e. the site of the current experiment) also reported higher leaf area in irrigated compared with droughted plots by the beginning of the wet season, but did not have data for a whole year (Engelbrecht & Kursar 2003). We think that the explanation for this pattern, increased growth by the beginning of the wet season but no increase by the end of the wet season, is that irrigation brings forward the time of leaf and stem growth early in the wet season but the 'droughted' plants catch up by the end of the wet season.

Survival was higher in our irrigated plants, and this agrees with the finding of greater survival in one of two large understorey marantaceous herbs (Mulkey *et al.* 1991) in irrigated compared with unirrigated understorey plots on BCI. Similarly, in a drought experiment done on the Buena Vista peninsula, 16 of 28 species had significantly higher seedling survival in irrigated plots (Engelbrecht & Kursar 2003, Engelbrecht *et al.* 2005). In contrast, Bunker & Carson (2005) found no effect of irrigation on mortality in their experiment on BCI. These differences are likely to result from various differences in treatments between experiments, including severity of drought/intensity of irrigation, but also the use of naturally occurring seedlings (Bunker & Carson 2005, Mulkey *et al.* 1991) versus planted seedlings (Engelbrecht & Kursar 2003, our study). Naturally occurring seedlings probably have deeper roots providing a better water supply, whereas planted seedlings may have shallower root systems and are acclimated to a frequent watering regime of a nursery, and are thus more susceptible to drought especially in their first year. In conclusion, it seems likely that first-year seedlings of many species are differentially susceptible to drought and thus the severity of the dry season can affect species composition of the seedling flora and hence, eventually, potentially affect the species composition of the mature trees; this would be a mechanism for climate change to affect the species composition of seasonally moist forests, as pointed out by Engelbrecht *et al.* (2005).

Our species showed marked differences in their sensitivity of mortality to drought. *Aspidosperma* and *Tachigali* were sensitive to drought, whereas *Gustavia* and *Simarouba* were not. The two latter species showed different patterns. *Simarouba* seedlings had the same survival in the irrigated and in the unirrigated plots and the importance of drought as a mortality factor was nil, possibly because it is the most light-demanding of the analysed species. In contrast, *Gustavia* seedlings had a very high survival, probably due to their large size, but the few seedlings that died were probably killed by drought (*pers. obs.*).

Trenching effects on seedling growth and survival

Trenching increased growth in seedling height and leaf area in two of our four species (*Gustavia* and *Tachigali*) in the understorey of our tropical semi-evergreen forest. Root mass of plants, other than those of the planted-in seedlings, was lower in the trenched subplots 4 y after trenching; even though competing roots had grown under the 50-cm-deep plastic lining. An earlier study also showed increased growth of the shrub *Aphelandra* sp., but not 'bejuco' (which in Spanish means vine) in trenched plots in the understorey on BCI (Haines 1971). The cause of the increased growth in our trenched plants was likely to be increased nutrients. We think that it was not the increased water available in trenched subplots, because irrigated plants did not grow more. Our interpretation that trenching increased plant growth due to an increased nutrient supply has a parallel in the finding that fertilization increased seedling growth in two experiments in the understorey on BCNM (Hättenschwiler 2002 and S. J. Wright *pers. comm.*). In our current experiment we expected to find an increase in nutrient concentrations in the plants from trenched plots because we conclude that trenching increased nutrient supplies (based on the finding that fertilization experiments normally cause an increase in nutrient concentrations). However, it may be that the much smaller (compared with fertilization), and much more realistic increases in nutrient availability caused by trenching do not cause increases in leaf nutrient concentrations. Two other trenching experiments have also found increases in growth attributed to increases in nutrients, despite the fact that the trenched plants did not have higher nutrient concentrations (Kueffer *et al.* 2007, Lewis & Tanner 2000).

It is not clear which nutrient(s) was limiting our seedlings. Nitrogen limitation does not seem likely because N/P mass ratios in the leaves of the control plants of the three non-legume species were 15 (*Aspidosperma*), 17 (*Gustavia*) and 28 (*Simarouba*), which are near or above the ratio of 16 where N might in general limit growth (Sterner & Elser 2002). Furthermore the legume *Tachigali*, which had an N/P ratio of 36, and was unlikely to be N limited, showed a strong trenching effect. Phosphorus limitation is a possibility, even though P concentrations were not higher in the larger trenched plants (increased growth in P-fertilized plants in P-limited soils usually results in increased plant P concentration). Easily extractable soil P is low in Buena Vista (Phillips, O., Lloyd, J., Lewis, S. *pers. comm.*) and on BCI (Powers *et al.* 2005) though there is a substantial amount of P cycling in litterfall in nearby forest (Sayer *et al.* 2006); thus adult trees can acquire sufficient P, but seedlings might still be P limited. Calcium and K were unlikely to limit seedling growth, even though amounts of Ca and K were higher in trenched plants, because exchangeable cations were in high concentrations in the soil in unirrigated plots and there were large quantities in litterfall. The higher concentrations of Fe and Mn in the irrigated plants could be due to more reducing conditions in the inner part of soil crumbs due to excess water; however such conditions would also tend to increase pH and make Al and Co less available (Kirk 2004). The increased amounts (as opposed to concentrations) of nutrients in trenched plants, interpreted by us as a result of increased nutrient supply caused by trenching, could be a result of the reduction, by trenching, of some 'other limitation' on seedling growth, in which case the resulting larger plants simply took up more of the sufficiently available nutrients. However, we do not know what the 'other limitation' might be – possibilities include allelochemicals derived from living roots; or herbivores; or pathogens. Whatever the mechanism, trenching had a strong effect.

Relative limitations of water and nutrients

Drought clearly increases seedling mortality (though this conclusion is mostly based on planted-in seedlings) and does so differentially between species, and thus potentially affects mature tree composition (Engelbrecht & Kursar 2003, Engelbrecht *et al.* 2005, 2006), but drought might not have much effect on the *growth* of surviving seedlings in the understorey in most years for at least two reasons. Firstly, at least one species, *Psychotria marginata*, continues to photosynthesize in the understorey in the dry season (Mulkey *et al.* 1992) perhaps because it has access to water at depth; seedlings of other species do have access to such water (Becker & Castillo 1990, Poorter & Hayashida-Oliver 2000). Secondly, drought at BCNM might limit seedling growth for only a month or two per year (but see Engelbrecht *et al.* 2006 for very small seedlings of pioneer species in gaps), and even then, it might be partly offset by higher light in the understorey for some of the time (a vine on BCI, *Connarus turczaninowii*, showed more growth in years with longer dry seasons; Aide & Zimmerman 1990). In contrast, mineral supply can limit growth for much longer, 10–11 mo per year (i.e. when water is sufficient). If trenching increased mineral supply, it is perhaps not surprising that it should have a much greater effect than irrigation, because it has so long to act relative to irrigation. We do not mean to dismiss the limitation caused by drought of seedling growth and survival at BCNM, but we think that drought has potentially much stronger effects on mortality than on seedling growth.

Below-ground competition limits seedling growth in most tropical forests

Our finding of increased seedling growth following trenching in the shade of the understorey, in a site with a moderate dry season and moderately fertile soils (as judged by the relatively high productivity of the forest (Leigh 1999) and relatively large amounts of potentially limiting nutrients cycling in litterfall), potentially greatly extends the area of tropical forest where seedlings have been shown to suffer root competition (Coomes & Grubb 1998, Lewis & Tanner 2000). Only in a tropical forest on fertile soils in a site with abundant rainfall was a trenching effect not found (but this was based on only one species, Ostertag 1998). New experiments in other tropical lowland forests in fairly fertile soils should be done to discover whether our new result is generalizable and whether seedling growth is affected by below-ground competition in tropical forests growing on a very wide range of soil fertilities and in a wide range of rainfalls.

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