

## The Effect of Understory Palms and Cyclanths on the Growth and Survival of *Inga* Seedlings<sup>1</sup>

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### ABSTRACT

Seedlings of *Inga fagifolia* (L.) Willd. and *I. pezizifera* Benth. were planted into the understory of a Costa Rican rain forest to test whether the proximity of large-leaved dwarf palms and cyclanths affects seedling growth and survival and if so, whether that effect is primarily due to above or belowground processes. In two sites, seedlings were planted either near palms (or palm-like Cyclanthaceae) or nearby in sites with no overarching vegetation under 1.5 m. Half of the seedlings in each treatment were trenched to a depth of 30 cm by cutting all roots 25 cm from the seedling. The proximity of palms or cyclanths significantly affected growth and survival of both species. However, most of this effect could be attributed to loss of stem length due to herbivore or pathogen damage rather than to differences in growth rates. There was no significant effect of trenching on seedling growth. Vegetation data from ten widely distributed sites in the forest showed that seedling density was inversely correlated with the abundance of understory palms and cyclanths. Our data suggest that understory vegetation, especially broad-leaved palms and palm-like cyclanths, acts as a filter affecting the distribution and abundance of establishing seedlings.

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### RESUMEN

Plántulas de *Inga fagifolia* (L.) Willd. e *I. pezizifera* Benth. fueron plantadas en el sotobosque de un bosque lluvioso en Costa Rica para probar si la proximidad de palmas enanas o ciclantáceas afectaba el crecimiento y sobrevivencia de plántulas y si eso era así, probar si el efecto era primariamente debido a efectos arriba del suelo o a efectos en el suelo. Se tomaron 2 sitios y en cada sitio se hicieron 2 tratamientos: En un tratamiento se plantaron plántulas bajo palmas enanas o ciclantáceas y en el control se plantaron plántulas en sitios con no vegetación sobre ellas a un mínimo de 1.5 m. En cada grupo a la mitad de las plántulas se cortaron las raíces alrededor de cada plántula hasta una profundidad de 30 cm a una distancia de 25 cm de la plántula. La proximidad de palmas significativamente afectó el crecimiento y sobrevivencia de ambas especies. Sin embargo, la mayoría del efecto pudo ser atribuido a pérdida de crecimiento del tallo debido a herbivoría o daño de patógenos y no a diferencias en las tasas de crecimiento. No hubo efecto significativo del tratamiento de zanjas sobre el crecimiento de las plántulas. Datos sobre la vegetación de diez sitios bien distribuidos en el bosque mostraron que la densidad de plántulas fue negativamente relacionada con la abundancia de palmas y ciclantáceas. Nuestros datos sugieren que la vegetación de sotobosque, especialmente las palmas de hojas anchas actúan como filtros afectando la distribución y abundancia de plántulas.

IN THE UNDERSTORY OF NEOTROPICAL rain forests, establishing canopy tree seedlings compete with a well-developed and diverse community of shrubs, palms, herbs, and small trees. These understory species are well-adapted to the environmental conditions of the forest floor and are able not only to persist, but often to grow and reproduce under intact

forest canopy (Chazdon 1986, Levey 1988, Marquis 1988).

Although the seeds of many rain forest canopy trees are able to germinate in the forest understory (Garwood 1983), growth and survival rates of seedlings are often low, unless they occur in or near treefall gaps (Augsburger 1983, 1984; Denslow *et al.* 1990; D. A. Clark & D. B. Clark 1987). The few seedlings that do survive in the understory are very important in forest dynamics; suppressed seedlings and saplings are a major component of the regrowth that occurs in new treefall gaps (Brokaw

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1985, Uhl 1982, Uhl *et al.* 1988). Factors affecting the abundance, composition, and distribution of tree seedlings in the forest understory thus may affect forest dynamics and structure.

In this study, we investigated effects of competition on the survival and growth of tree seedlings in the rain forest understory. Specifically, we asked whether growth and survival of two species of canopy trees, *Inga fagifolia* and *I. pezizifera*, are affected by nearby large-leaved understory vegetation such as small palms or palm-like cyclanths and, if so, whether that effect is primarily due to aboveground or belowground interactions between the seedlings and the existing understory vegetation. We predicted that proximity to a large-leaved understory plant would hinder the growth and survival of these canopy tree seedlings through aboveground competition for light and through belowground competition for water and nutrients.

## METHODS

**SITE DESCRIPTION.**—Field experiments were conducted in the premontane wet–very wet tropical forest (Holdridge *et al.* 1971) of the La Selva Biological Station of the Organization for Tropical Studies in Heredia Province, Costa Rica. La Selva receives approximately 4200 mm of rain annually, distributed between a dry season (generally January–April) and a wet season (May–December). The length and severity of the dry season is variable; during the 2 years of this study, the first dry season was relatively mild (only 1 month receiving less than 100 mm of rain). During the second dry season there were 3 consecutive dry months, 2 receiving less than 100 mm of rain.

The two study sites were located on well-drained upland residual soils (ultisols, Jaguar Consocios; Sancho & Mata 1987, Sollins *et al.*, in press). These soils are strongly acid (pH (H<sub>2</sub>O) *ca* 4.5), highly leached, rich in organic matter, and with low (*ca* 30%) base saturation (Sancho & Mata 1987, Sollins *et al.*, in press), low extractable phosphorus (acid ammonium fluoride extraction, 2.6  $\mu\text{g/g}$ ; Vitousek & Denslow 1987, Sancho & Mata 1987) and high N mineralization rates (50–80  $\mu\text{g/g/mo}$ ; Vitousek & Denslow 1986). Both sites were in old growth forests without nearby canopy gaps. The understory of the two sites was typical of that of much of the old growth forest at La Selva. In addition to large-leaved herbs and palm-like plants (Palmae, Cyclanthaceae), shrubs and small trees in the families Melastomataceae, Piperaceae, and Rubiaceae were common.

**EXPERIMENTAL DESIGN.**—Seedlings of *Inga fagifolia* (L.) Willd. and *Inga pezizifera* Benth. (Mimosaceae) were established from seed in a 50:50 soil:sand plotting mixture under shade cloth at 20 percent full sunlight in April 1987. Both species are relatively common shade tolerant canopy trees at La Selva (Denslow and Chaverri, unpub. data, Lieberman *et al.* 1985). During the rainy season (June 1987) 160 two-month-old seedlings of each species were planted bare root into the forest understory in a 3  $\times$  2 factorial design (blocked by seedling size).

To test the importance of aboveground interactions, 80 seedlings of each species were planted under palms or cyclanths (*e.g.*, Palmae: *Asterogyne martiana* Wendl. ex Burret, *Geonoma cuneata* Wendl. ex Spruce; Cyclanthaceae: *Asplundia uncinata* Harling) and another 80 seedlings were planted in spots with no overarching vegetation under 1.5 m. To test the importance of belowground interactions, half of the seedlings were trenched.

Seedlings were planted in groups of four with one plant at each corner of a quadrat measuring 50 cm on a side. The quadrats were either centered beneath understory palms or cyclanths or placed nearby where overarching vegetation under 1.5 m, if present, had been removed. Two seedlings in each group of four were trenched with a tiling shovel to a depth of 40 cm at a distance of 25 cm from the seedling. Trenches were recut with machetes to a depth of 30 cm at bimonthly intervals. The experimental design was replicated at two sites designated by their trail locations: Sendero Jaguar (JAG) and Lindero Occidental (LOC).

Hemispherical canopy photographs were taken above seedlings to determine the effect of our palm treatment on the amount of light available to seedlings. Direct and indirect radiation received by the seedlings were estimated as proportions of total annual incident direct and indirect radiation, respectively. Black and white photographs were taken at seedling height with a Minolta f7.5 mm fisheye lens over six palm and six nonpalm seedlings selected at random at each site. Photographs were interpreted for percent total direct radiation and percent total indirect radiation (reflected skylight) using the public domain computer program CANOPY(c) developed by P. Rich (1989, in press). This technique weights the proportion of canopy openness under the track of the sun to calculate percent total direct radiation and under the azimuth to calculate percent reflected skylight. A strict protocol was developed for interpreting the photographs to minimize the introduction of user bias. Selection of the gray level

TABLE 1. *Light environments of Inga seedlings at time of harvest as estimated using canopy photographs. Direct radiation and indirect radiation (reflected skylight) as a percentage of estimated total incident radiation above the forest ( $\bar{x} \pm SE$ ). Values were arcsin transformed for analysis of variance.*

	With palm	Without palm	F
Indirect radiation	1.3 (0.1)	2.9 (0.6)	6.656 df = 1,20, $P < .05$
Direct radiation	1.2 (0.2)	1.8 (0.4)	2.150 df = 1,20, NS

threshold for distinguishing foliage from canopy openings was determined twice independently. If the difference between the two estimates of canopy openness was not less than 0.2 percent, the entire analysis was repeated. Similar techniques developed elsewhere have shown strong correspondence between photographic estimates and actual light levels as measured by PAR sensors (*e.g.*, Chazdon & Field 1987).

Root biomass was sampled at planting (July 1987) and again at harvest (June 1989) in trenched and nontrenched plots to assess the effect of trenching on the number of potentially competing roots. Fine (<2 mm diameter) and coarse (>2 mm diameter) root biomass was sampled in 6.5 cm diameter cores at three soil depths (0–10 cm, 10–20 cm, and 20–30 cm) from 10 palm and 10 nonpalm plots in each site. These plots, which contained no seedlings, were established at the time of planting and maintained on the same trenching schedule as the plots containing seedlings. Soil cores were washed through a 2 mm mesh sieve. Roots were sorted by hand, oven dried at 90°C, and weighed.

Seedling responses to treatments were estimated through periodic nondestructive measurements of growth and through measurements of biomass and leaf area at harvest. Number of leaves and total stem length of each surviving seedling was measured monthly. Survival time was estimated as the number of days the seedling survived following out-planting. Seedlings were also scored monthly for the absence of damage or presence thereof, manifested as missing leaf area or as stem damage. Reported here are data on growth and incidence on insect damage taken approximately 6 mos (196 days) following planting. After 6 mos, reduced sample sizes, due to seedling mortality, diminished the power of the test to distinguish treatment effects. Stem loss and growth increments were calculated from monthly measurements to ages of 6 mos. Surviving plants were harvested after 697 days (23 mos); total leaf area (LiCor Model 3100 area meter) and biomass (oven dry mass) of roots and shoots were determined.

Data were analyzed using analysis of variance (SPSS/PC+; Norûsis 1986), chi-square, and Kruskal-Wallis statistics (Sokal & Rohlf 1981).

SEEDLING DISTRIBUTION.—Seedling densities were sampled at ten sites in old growth forest distributed across La Selva. All sites were located on level topography and distributed among the major alluvial and residual soil consociations described for La Selva (Sancho & Mata 1987; Arboleda—2 sites, Holdridge—1, Experimental—1, Jaguar—3, Mata-buey—3). At each site woody seedlings less than 0.5 m tall were counted in 20 1-m<sup>2</sup> quadrats randomly located in larger (25 m<sup>2</sup>) quadrats established for a study of the distribution and composition of understory vegetation (Denslow, pers. obs. and Chaverri, pers. comm.). For each site the Importance Value (Curtis & McIntosh 1951) of palms and cyclanths was calculated as the sum of relative frequency and relative density of plants in the 20 larger quadrats. Mean density of seedlings (plants/m<sup>2</sup>) was regressed on the combined IV of palms and cyclanths for the ten sites.

## RESULTS

Light levels in the forest understory were low, ranging from 1 to 3 percent full sunlight in the two sites studied. The presence of understory palms in the vicinity of the seedlings significantly lowered the estimated availability of indirect radiation but not direct radiation (Table 1).

The biomass of fine roots in the upper 30 cm of soil was significantly reduced by trenching ( $F = 4.751$ ,  $P < 0.05$ ,  $df = 1,32$ ), but was not significantly affected by proximity to a palm or cyclanth (Table 2). During the two years between planting and harvest the biomass of fine roots in nontrenched plots decreased ( $t$ -test for unequal variances:  $t = 4.022$ ,  $P < 0.001$ ,  $df = 19$ ), but not to the extent observed in the trenched plots. Fine roots were more abundant at the Jaguar site at planting ( $F = 4.140$ ,

TABLE 2. Total fine (<2 mm diameter) and coarse (>2 mm diameter) root biomass (g) at 0–30 cm soil depth ( $\bar{x} \pm SE$ ).

	Site		Palm		Trench	
	JAG	LOC	+	-	+	-
<b>Planting</b>						
Fine roots	2.778 (0.266)	2.158 (0.151)	2.311 (0.211)	2.625 (0.238)		
<i>P</i>	< 0.05		NS			
Coarse roots	4.794 (1.170)	5.824 (1.849)	4.406 (1.781)	6.213 (1.248)		
<i>P</i>	NS		NS			
<b>Harvest</b>						
Fine roots	1.524 (0.412)	1.334 (0.118)	1.376 (0.136)	1.482 (0.178)	1.191 (0.174)	1.666 (0.120)
<i>P</i>	NS		NS		< 0.05	
Coarse roots	1.843 (0.560)	1.730 (0.729)	1.417 (0.430)	2.156 (0.804)	1.407 (0.810)	2.166 (0.419)
<i>P</i>	NS		NS		< 0.05	

$P < 0.05$ ,  $df = 1,36$ ), but not at harvest. The biomass of coarse roots in the upper 30 cm of soil was similarly affected by the treatments. By the time of harvest, coarse root biomass was significantly decreased by trenching ( $\chi^2 = 10.16$ ,  $P < 0.005$ ,  $df = 1$ ), but it did not differ between palm and nonpalm plots nor between sites. Results were similar in upper, middle, and lower 10 cm soil layers (not reported).

Although survival was relatively high for these seedlings during the 23 months of study (*I. fagifolia* 44%, *I. pezizifera* 77%), growth rates overall were extremely low (Table 3). After almost two years, plants were still small (*I. fagifolia* ( $\bar{x} \pm SE$ ): 16.1  $\pm$  0.58 cm,  $N = 70$ ; *I. pezizifera*: 11.6  $\pm$  0.42 cm,  $N = 129$ ). Leaf number had remained the same or decreased by the time of harvest (*I. fagifolia*, planting: 2.94  $\pm$  0.04; harvest: 2.96  $\pm$  0.14, Stu-

TABLE 3. Above and belowground effects of palms on growth of Inga seedlings ( $\bar{x} \pm SE$ ).

	Palm		Trench	
	+	-	+	-
<i>I. fagifolia</i>				
Stem length at 6 mos (cm)	10.9 (0.5)	11.2 (0.4)	11.1 (0.5)	11.0 (0.4)
<i>N</i>	49	63	56	56
Dry mass (g)	0.45 (0.06)	0.48 (0.04)	0.52 (0.04)	0.43 (0.04)
<i>N</i>	25	45	32	38
Leaf area (cm <sup>2</sup> )	39.6 (5.4)	37.4 (3.4)	41.0 (4.1)	35.6 (4.1)
<i>N</i>	25	45	32	38
<i>I. pezizifera</i>				
Stem length at 6 mos (cm)	13.2 (0.5)	15.7 (0.4)	14.7 (0.5)	14.2 (0.5)
<i>N</i>	74	79	79	74
Dry mass (g)	0.69 (0.06)	1.13 (0.11)	0.95 (0.10)	0.94 (0.10)
<i>N</i>	51	72	64	59
Leaf area (cm <sup>2</sup> )	55.0 (6.5)	83.2 (10.5)	73.8 (9.7)	69.0 (9.6)
<i>N</i>	51	72	64	59

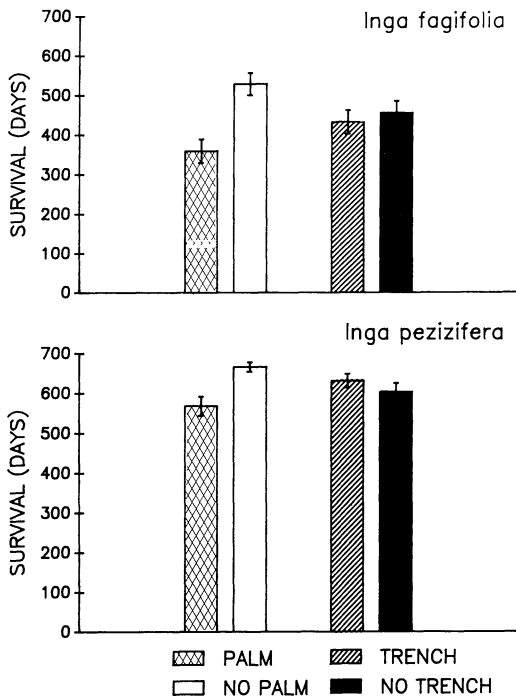


FIGURE 1. Survival of *Inga* seedlings following out-planting (means with standard error bars). All surviving plants were harvested at 697 days. Sample sizes were 80 plants in each treatment.

dent's  $t = 0.183$ , NS; *I. pezizifera*, planting:  $3.12 \pm 0.05$ , harvest:  $2.84 \pm 0.10$ ,  $t = 2.569$ ,  $P < 0.05$ ).

Proximity of palms had a highly significant effect on survival time in both species (Fig. 1, Table 4). Mean survival times were shorter in plants growing near palms than in those growing in the more open forest understory. Trenching did not significantly affect survival times.

Proximity of palms also had a significant effect on the gain and loss of stem length (Fig. 2, Table 4). Although data on mean stem length suggest there was very little change in stem length over six months, the monthly measurements of stem length reveal a more dynamic picture. Both species suffered frequent loss of growing tips from both insects and pathogens. In both species, the presence of palms significantly increased the amount of stem length lost (Kruskal-Wallis: *I. fagifolia*:  $H_{K-W} = 2.885$ ,  $N = 111$ ,  $P < 0.01$ ; *I. pezizifera*:  $H_{K-W} = 16.757$ ,  $N = 153$ ,  $P < 0.001$ ). The production of new stem tissue was not significantly affected by palms. As a result of the effect of palms and cyclanths on stem loss, net changes in stem length during the

first 6 mos of growth were significantly less under palms (*I. fagifolia*:  $H_{K-W} = 6.6196$ ,  $N = 111$ ,  $P < 0.05$ ; *I. pezizifera*:  $H_{K-W} = 23.558$ ,  $N = 153$ ,  $P < 0.001$ ).

We expected belowground effects on seedling growth would be particularly high during the dry season when soil moisture content is low in the understory (Vitousek & Denslow 1986). Growth rates, as measured by changes in stem length, were low during the first (9 February–2 May 1988) and second (6 February–1 May 1989) dry seasons for both species (*I. fagifolia*: Dry Season I:  $\bar{x}$  (SE) =  $-0.12$  (0.13) cm,  $N = 99$ ; Dry Season II:  $0.74$  (0.20) cm,  $N = 74$ ; *I. pezizifera*: Dry Season I:  $1.11$  (0.16) cm,  $N = 141$ ; Dry Season II:  $0.11$  (0.28) cm,  $N = 125$ ), but not affected significantly by the presence of either palms or trenches.

When plants were harvested after 697 days total stem length, biomass, and total leaf area measurements of *I. pezizifera* but not *I. fagifolia* also showed a significant effect of the presence of palms on the growth of surviving seedlings (Tables 3 and 4). Trenching, however, had no significant effect on any measures of seedling growth and survival (Tables 3 and 4), nor were there any significant interactions among main factors.

By several measurements (but not change in stem length during the first six months), *Inga pezizifera* grew better than *I. fagifolia* (survival times:  $F = 45.331$ ,  $P < 0.001$ ,  $df = 1, 318$ ; biomass:  $F = 26.412$ ,  $P < 0.001$ ,  $df = 1, 182$ ; leaf area:  $F = 12.794$ ,  $P < 0.001$ ,  $df = 1, 182$ ), although it was also more likely to suffer leaf area loss or stem tip damage ( $\chi^2 = 7.36$ ,  $df = 1$ ,  $P < 0.01$ ). In general there were no site effects, although the mean survival time and total stem length of *I. fagifolia* was significantly greater at LOC than at JAG.

Seedling density was significantly correlated negatively with the abundance of understory palms and cyclanths in vegetation samples from 10 different sites (Fig. 3;  $r^2 = 0.50$ ,  $P = 0.022$ ,  $N = 10$ ).

## DISCUSSION

Neotropical rain forests are characterized in part by a well-developed community of understory trees, shrubs, and large herbs. Although growth is slow in this light-limited environment, species diversity is high. At La Selva, several plant families and genera are represented by numerous species largely restricted to forest understory environments: Piperaceae (*Piper*: 47 species), Melastomataceae (*Miconia*: 26 spp), Rubiaceae (*Psychotria*: 33 spp),

TABLE 4. *The effects of palms on Inga seedling survival and growth. ANOVA tables. No interaction terms were significant.*

Source of variation	df	MS	F	P
<i>I. fagifolia</i>				
Survival				
Site	1	400,100	5.872	0.017
Palm	1	1,151,753	16.903	0.000
Trench	1	20,318	0.298	0.586
Residual	152	68,137		
Stem length (196 days)				
Site	1	65.287	4.927	0.029
Palm	1	2.350	0.177	0.675
Trench	1	2.267	0.171	0.680
Residual	104	13.250		
Dry mass				
Site	1	0.011	0.170	0.681
Palm	1	0.007	0.105	0.747
Trench	1	0.144	2.174	0.145
Residual	63	0.066		
Leaf area				
Site	1	65.107	0.105	0.747
Palm	1	92.745	0.150	0.700
Trench	1	579.689	0.936	0.337
Residual	63	619.134		
<i>I. peizifera</i>				
Survival				
Site	1	33,931	1.204	0.274
Palm	1	377,524	13.393	0.000
Trench	1	31,416	1.115	0.293
Residual	152	28,187		
Stem length				
Site	1	11.695	0.749	0.388
Palm	1	245.705	15.733	<0.001
Trench	1	10.991	0.704	0.403
Residual	145	15.617		
Dry mass				
Site	1	0.135	0.227	0.634
Palm	1	5.825	9.791	0.002
Trench	1	0.038	0.065	0.800
Residual	116	0.595		
Leaf area				
Site	1	12,345	2.209	0.140
Palm	1	28,187	5.043	0.027
Trench	1	1,169	0.209	0.648
Residual	116	5,589		

Cyclanthaceae (*Asplundia*: 8 spp), Araceae (*Diefenbachia*: 7 spp). The data from this study suggest that at least some of the large-leaved species are important competitors with the seedlings of canopy trees and may, through their effect on the composition of the seedling pool, ultimately influence forest structure and dynamics.

Total incident radiation in the understory of neotropical rain forests is frequently measured at 1–

2 percent of full sunlight (Chazdon & Fetcher 1984, Denslow *et al.* 1990), received as short duration sun flecks (10–78 percent of total photon flux, reviewed in Chazdon 1988) or diffuse radiation. At seedling heights (<0.5 m), the presence of understory herbs and shrubs, including acaulescent or short stemmed palms and palm-like Cyclanthaceae also affect the spatial distribution of light. Although the absolute change in incident light levels under

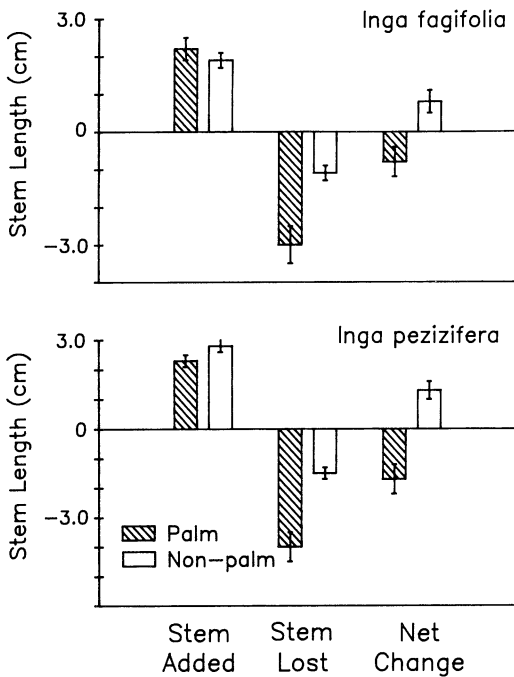


FIGURE 2. Analysis of change in stem length of *Inga* seedlings during the first 196 days of growth following outplanting (means with standard error bars). Results of statistical analyses in the text.

these plants is small (less than 1.5% of potential indirect radiation), it represents approximately 50 percent of the light available to establishing seedlings in the forest understory.

Single leaf photosynthetic responses to measured photon flux densities in forest understory are complex functions of the duration and distribution of sun flecks, background levels of diffuse radiation, leaf water potentials, leaf temperatures, and photoinhibition (Chazdon 1988). They are hence not easily predictable from estimates of total incident radiation. However, on a whole plant basis, current evidence suggests that plant growth approximates a linear function of available light for levels less than 20 percent full sunlight (Chazdon 1988). Most species studied have shown greater vegetative growth and reproduction in gaps or at gap edges than under intact canopy (Piñero & Sarukhan 1982, Chazdon 1986, D. B. Clark & D. A. Clark 1987, Denslow 1987, Denslow *et al.* 1990, Smith 1987). We expected, therefore that small differences in total incident light may also have a strong effect on both seedling growth and survival for plants growing at light levels near their compensation points.

Although our study does confirm the hypothesis

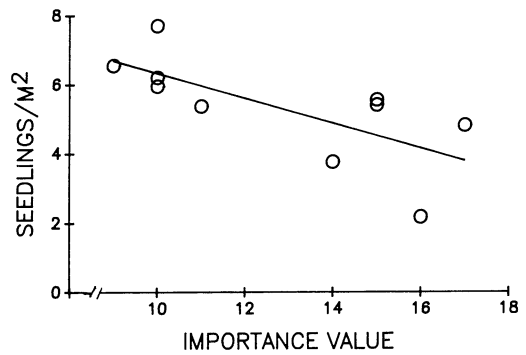


FIGURE 3. Regression of mean seedling density on Importance Value of understory palms and cyclanths at 10 sites across La Selva ( $y = -0.36x + 9.95$ ,  $N = 10$ ,  $P = 0.022$ ).

that proximity of dwarf palms negatively affects seedling growth and survival, it is apparent that a large component of that effect is due to insect and pathogen damage. Higher rates of stem loss among seedlings growing under palms largely accounted for observed differences in stem length and likely contributed to significant differences in survival, dry mass accumulation, and total leaf area as well. Growing tip damage has been previously noted as an important source of mortality among seedlings growing in tropical forest understory (Janzen 1971, Denslow 1980, Becker 1983, Clark & Clark 1985). In some cases the manifestation of damage is characteristic of that caused by damping off fungi (Augsburger 1983, 1984), although this was not true in the present study.

Processes leading to these patterns of insect and pathogen damage are likely to be complex. Microsite differences in light, humidity, temperature, and air movement likely affect not only the dispersion of pathogens and behavior of insects but also the vulnerability of seedlings due to differences in capacity for resistance or compensatory growth (Vaartaja 1962, Grime 1966). Augspurger (1983, 1984) and Augspurger and Kelly (1984) documented lower mortality attributable to damping off fungi among seedlings growing in light gaps than among those growing in the forest understory. High seedling mortality rates are often associated with high seedling density and proximity to conspecific adults (reviewed in Clark & Clark 1984). With respect to the distribution of safe sites for seedling establishment, the forest understory presents a coarse grained, heterogeneous environment which reflects the influences of both abiotic (Bratton 1976, Schneider & Sharitz 1988, but see Marquis *et al.* 1986)

and biotic (Augsburger & Kelly 1984, Connell *et al.* 1984, Clark & Clark 1984) factors.

Results from previous studies gave us reason to suspect that root competition might also influence the growth and survival of tree seedlings. Soil moisture levels in the upper 10 cm of soil in the forest understory are significantly lower than in nearby gaps, presumably due to higher evapotranspiration loads on the understory soils (Vitousek & Denslow 1986) and understory vegetation at La Selva often shows moisture stress during severe dry seasons (D. A. Clark & D. B. Clark, pers. comm.). However, the data from this study suggest that the negative effect of palms on seedling establishment is primarily due to aboveground processes. Trenching had no effect on seedling growth or survival during the two years of this study or during the two dry seasons when growth was most likely limited by soil moisture availability. Our results are consistent with prior results from fertilization experiments which showed no significant effect of increased nutrient availability on the growth of rooted cuttings planted in rain forest understory or in small gaps where light levels were generally below 20 percent full sunlight (Denslow *et al.* 1990).

Although trenching significantly decreased both fine and coarse root biomass in the treatment plots in comparison to controls, trenching may have also reduced fine root biomass in the control plots over the pretreatment levels. However, the magnitude of difference in fine root biomass measured in our study (*ca* 30%) was well within the range of monthly variation measured by Sanford (1990) on a nearby site (*ca* 50%). Our data suggest nevertheless that root competition is not an important component of the effect of palms on establishing seedlings because fine and coarse root biomass did not differ significantly between palm and nonpalm plots.

It is apparent from these results that dwarf palms and cyclanths act as a filter for establishing seedlings, significantly affecting not only the length of time that seedlings survive in the understory, but

the abundance and distribution of seedlings as well. Similar effects of understory herbs on tree seedlings have been observed in North American broad-leaved and evergreen forests (Shirley 1945, Maguire & Forman 1983). These surviving seedlings in turn play an important role in gap dynamic processes. Data from several sites suggest that a large portion of sapling recruitment to the abundant small gaps in Neotropical forests is from seedlings previously established and surviving in the forest understory (Brokaw 1985, Brokaw & Scheiner 1989, Uhl *et al.* 1988).

The abundance and composition of the seedling size class is also important for the development of sustained yield logging practices (Troup 1952). For example, it has been suggested that the success of polycyclic timber management for mixed species tropical hardwoods in the Far East is largely due to the abundance of tree seedlings and saplings in the understories of the Southeast Asian forests (Whitmore 1984). In the Neotropics the understory is often dominated by shrubs, palms, and small trees and the demography of some canopy trees may be characterized by the scarcity of sapling size classes (*e.g.*, Knight 1975; Hubbell & Foster 1987; D. A. Clark, in press). Our data present evidence that in some forests palms and palm-like plants may contribute to this pattern of low seedling abundance.

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