

## BELOWGROUND EFFECTS OF CANOPY GAPS IN A TROPICAL WET FOREST

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**Abstract.** Canopy gaps are a fairly well-studied phenomenon in tropical forests, but less well known are their belowground effects on patterns of root length and biomass and the consequences of such changes on regeneration and community structure. I examined canopy gaps and adjacent understory sites on two soil types of contrasting fertility in a lowland rain forest in Costa Rica to determine (1) whether canopy gaps create root gaps beneath the canopy opening, and (2) whether the effects of such root gaps on root ingrowth rates, root competition, and root responses to nutrient heterogeneity are related to soil type. Based on soil coring, canopy gaps had less fine (<2 mm) root length and biomass than comparable closed canopy sites. Reductions in root length and biomass were greater on the infertile (residual) soil type than the fertile (alluvial) type but were unrelated to gap size, age, or percentage canopy openness. Additionally, I measured root competition in a trenching experiment using the pioneer tree *Hampea appendiculata* as a bioassay species. Light appeared to be the only factor limiting relative growth rate, as seedlings grew faster in the canopy gaps than in the understory, regardless of soil type or trenching treatment (trench lined with root restriction cloth, trench open to colonization by neighboring roots, or no trench). The accumulation rate of live fine roots was unaffected by soil or light conditions. Finally, I altered nutrient heterogeneity of the gap and understory sites through the creation of fertilized microsites. Root proliferation into these microsites was enhanced only in the canopy gaps on the infertile soil. The differences between the two soil types in the amount of root length and biomass and in root proliferation responses suggest that the consequences of canopy gap formation may be dependent on background levels of soil fertility.

**Key words:** canopy gaps; disturbance; environmental heterogeneity; forest dynamics; nutrients; root competition; root gaps; root proliferation index; trenching.

### INTRODUCTION

Canopy gap formation, a frequent small-scale disturbance in many forests, has been hypothesized to be an important event in the structuring of many forest communities. Canopy gaps increase environmental heterogeneity (Brokaw 1985, Denslow 1987), by altering abundances and distributions of abiotic and biotic resources. Resources that have been demonstrated to change after gap formation are light (e.g., Chazdon and Fetcher 1984), soil moisture (e.g., Vitousek and Denslow 1986, Uhl et al. 1988), nutrients (e.g., Matson and Boone 1984, Vitousek and Denslow 1986, Mladenoff 1987, Uhl et al. 1988), fruit availability (e.g., Levey 1988), seed availability (e.g., Alvarez-Buylla and García-Barrios 1991), seed germination (e.g., Putz 1983, Murray 1988), and herbivores (e.g., Braker and Chazdon 1992). Such changes in the spatial and temporal heterogeneity of resources may affect forest dynamics by altering colonization success and competitive outcomes, thereby linking natural disturbances to the maintenance of plant species diversity (Ricklefs 1977, Denslow 1980, 1987, Connell 1989).

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Most studies of gap dynamics have emphasized aboveground patterns and processes (Denslow and Hartshorn 1994). Only recently have studies been undertaken that focus on belowground changes after canopy gap formation (Sanford 1989, 1990, Silver and Vogt 1993, Wilczynski and Pickett 1993, Parsons et al. 1994a, b, Ehrenfeld et al. 1995), and this information has yet to be incorporated into theories of forest dynamics or management practices based on gap dynamics models. Many studies on gap dynamics elucidate the effects of the disturbance without examining the disturbance in the context of the environmental conditions (e.g., soil nutrients, water relations, microclimate, and topography) in which it occurs. An understanding of how the consequences of gap formation vary in relation to background environmental conditions may be important for predicting patterns of recovery after natural disturbance and for understanding how such patterns might determine forest community structure.

I designed a series of experiments to address these issues by determining (1) the effects of canopy gap formation on root length and biomass and (2) whether or not the consequences of canopy gap formation are dependent on soil type. To answer these questions, I

identified canopy gaps on two soil types of contrasting fertility in a lowland tropical rain forest where canopy gap formation is frequent. Effects of canopy gap formation were determined by examining patterns of root biomass in gaps of various ages and sizes, while the consequences of canopy gap formation were investigated by measuring root competition, root ingrowth rates, and root responses to nutrient heterogeneity. In the first experiment I examined the belowground effects of gap formation by asking whether canopy gaps alter belowground resources through the formation of "root gaps." I defined root gaps as regions of lower root length and biomass compared to undisturbed forest. These root gaps can be formed by small- and large-scale disturbances that result in plant death, including animal burrowing, pathogen attacks (Eissenstat and Caldwell 1989), hurricanes (Parrotta and Lodge 1991, Silver and Vogt 1993), and treefalls (Sanford 1989, Silver and Vogt 1993, Wilczynski and Pickett 1993). Although root gap formation could have substantial effects on regeneration and forest structure by altering soil resource availability and consequently affecting competitive interactions and species composition, belowground gaps are not completely analogous to canopy openings. Canopy gaps are distinct holes in the forest canopy, while root gaps represent thinning of root biomass of various intensities. Additionally, the spatial distribution of canopy gaps and root gaps may vary; an opening overhead does not imply a root gap directly below or vice versa.

To examine the consequences of root gaps on regeneration and community structure, I examined root competition by creating artificial root gaps. Competitive effects may become stronger after canopy opening if the increase in light levels is accompanied by a decrease in fine root biomass and a change in spatial and temporal distribution of available nutrients. Additionally, root growth may be limited under shaded conditions (Bilbrough and Caldwell 1995), but may be accelerated at higher light levels. Specifically, I investigated how the soil and light resources available affected the aboveground growth rate of seedlings of a pioneer (light-demanding) tree, and whether the growth rate of roots in the surrounding areas could explain variation in seedling performance.

Finally, I increased spatial heterogeneity of soil nutrients to test whether root responses, measured as length proliferation, are related to light levels and soil type. Belowground responses to fertilization may be more sensitive to nutrient availability than aboveground growth responses, which may be delayed until several years after fertilization (Tanner et al. 1990, 1992). Root proliferation into fertile microsites has been demonstrated (e.g., St. John 1983, Eissenstat and Caldwell 1989, Jackson and Caldwell 1989) and there is some evidence that plants can regulate the degree of root proliferation according to the fertility of these patches (e.g., Jackson and Caldwell 1989, Friend et al.

1990). Rapid root proliferation may be characteristic of successful competitors (Jackson and Caldwell 1989, Jackson et al. 1990), but it is unclear whether the benefits of employing this response depend on levels of available soil nutrients and the spatial and temporal patterning of these nutrients. I therefore hypothesized that root proliferation into fertile microsites would be influenced by both changes in resources after natural disturbance (comparison of canopy gap vs. forest understory) and by soil type.

## METHODS

### *Study area*

This study was conducted during portions of the wet (May–August 1993) and dry seasons (January–April 1994) at La Selva Biological Station, Costa Rica (10°26' N, 83°59' W). The forest is considered a tropical wet forest according to the Holdridge life-zone system (Hartshorn 1983). Average monthly temperature is 25.8°C and average rainfall is 3962 mm, with no month averaging <100 mm of rain (Sanford et al. 1994).

Gap formation is frequent in this forest, especially during the rainy season, and these canopy gaps are most commonly formed by uprooted trees (Hartshorn 1980). Estimates of average turnover time based on gap formation rates are 95 yr (Sanford et al. 1986) and  $118 \pm 27$  yr (Hartshorn 1980). Based on mortality rates of tagged trees, the average stand half-life of trees >10 cm dbh is 34 yr, but not all of these trees create canopy openings upon their death (Lieberman et al. 1985). About 75% of the gaps in this forest are <200 m<sup>2</sup> (Sanford et al. 1986), with mean gap size estimates ranging from 87 to 161 m<sup>2</sup> (Hartshorn 1980, Sanford et al. 1986).

Soils are derived from volcanic parent material and represent a range of fertilities, from relatively infertile Ultisols to more fertile Entisols and Inceptisols. The higher elevation areas have been extensively weathered to form "residual" Ultisols, while many of the lower elevation lava flows have been blanketed with more recent alluvial deposits. This alluvial material, which originated from the two main rivers that traverse the reserve, was deposited in several terraces, with the higher elevation sites containing older alluvial material than lower ones (Sollins et al. 1994).

I conducted this study on fertile (Holdridge consociation) and less fertile soil (Jaguar consociation) found in old-growth forest at La Selva. Although some plant species distributions are related to edaphic conditions (Clark et al. 1995), forest structure is similar between the two soil types, and many of the common species can occur on both alluvial and residual soil (R. Oosterag, *personal observation*). Both areas were dominated by *Pentaclethra maculosa* (Fabaceae) and *Welfia georgii* (Arecaceae). The Holdridge consociation is a middle terrace alluvial Andic Humitropept, consisting

TABLE 1. Characteristics of the 20 canopy gaps used for this study.

Gap size (m <sup>2</sup> )	Gap age (mo)	Canopy openness (%)	Apparent cause
Alluvial soil			
9	10–12	8.10	branchfall
18	12–18	4.94	snap
28	10–12	3.54	branchfall, snap
38	12–18	9.88	dead standing tree
38	2–3	8.34	snap
39	3–4	6.87	snap
75	12–18	6.12	partial uproot, snap
90	2–3	8.96	dead standing tree, branchfall
92	9–12	4.15	uproot
116	1–2	9.00	uproot, snap
Residual soil			
23	6–8	7.85	branchfall, snap
39	3–4	7.74	branchfall
45	2–3	7.40	snap, branchfall
58	3–4	6.52	snap, dead standing tree
84	6–8	9.39	uproot
86	2–3	9.35	dead standing tree, branchfall
88	2–4	6.70	snap, branchfall
94	3–4	9.25	snap
94	6–12	6.89	snap
154	2–3	5.30	partial uproot, snap

of an A horizon (0–22 cm) characterized by 28% clay, 4.7 pH in H<sub>2</sub>O, bulk density of 0.68 Mg/m<sup>3</sup>, and 8.91% organic matter (Sollins et al. 1994). Base saturation is 51.2%, effective cation exchange capacity (CEC) is 5.06 cmol<sub>c</sub>/kg, and acid-ammonium-fluoride-extractable P is 9.8 mg/kg (Sollins et al. 1994). In contrast, the Jaguar consociation is a residual, volcanically derived Typic Tropohumult with an A horizon (0–19 cm) with a similar bulk density (0.69 Mg/m<sup>3</sup>), and pH in H<sub>2</sub>O (4.5), but greater amounts of clay (40%), less organic matter (6.75%), and much lower base saturation (27.9%), effective CEC (4.85 cmol<sub>c</sub>/kg) and P (0.7 mg/kg) (Sollins et al. 1994). Due to high N mineralization rates, canopy dominance of a nitrogen-fixing legume (*P. maculosa*), and high adsorptive potential of both of these soils for P, it has been hypothesized that P rather than N is a limiting element in this forest (Vitousek and Denslow 1986, 1987).

#### Site selection and experimental layout

I located 10 canopy gaps per soil type in old-growth forest. Eight of these 20 gaps were chosen (four on each soil type) in 1993, while the others were located and sampled in 1994. I defined gaps and measured gap size based on the criteria of Brokaw (1982), in which a gap is considered a hole in the forest canopy extending down to an average height of 2 m. I chose only gaps that I estimated to be 2–18 mo old at the time of sampling, based on observations of resprouting, new seedling establishment, and decomposition of woody debris. Subsequently, I observed regular gap formation over a period of several years, and found my estimates based on forest recovery to be consistent with gaps of

known age. The selected gaps were formed in several different manners (i.e., by uprooted trees, snapped trees, or large branchfalls; Table 1). I paired each gap site with a closed canopy understory site, located ~40–50 m from an edge of the treefall gap. I defined understory areas whenever canopy closure was ≥94% on average (range, 93–99%) as measured by a spherical densiometer (Lemon 1956) over the designated plot center. Hemispherical photographs were subsequently taken at 50 cm above the center of each gap and understory site and analyzed using Solarcalc 6.03 (Chazdon and Field 1987). Percentage canopy openness was  $7.31 \pm 1.82$  in gaps (mean  $\pm 1$  SD) and  $3.90 \pm 1.62$  in the understory.

#### Root gap presence

I tested for the presence of root gaps by estimating root length density (measured in centimeters of root per cubic centimeter of soil) and root biomass (grams of root per square meter of soil) in canopy gaps and understory sites on both soil types. Three soil cores, 8 cm in diameter and 20 cm deep, were taken in each gap and understory site. Cores taken in 1993 were part of a root ingrowth experiment (see *Ingrowth cores* below), but were located in the gap center within a 2 m diameter area that was relatively free of fallen logs and large tree roots. In 1994, cores were taken at three random locations (azimuth and distance) within a 5 m radius of the gap center. In both cases, samples were taken in the gap center and corresponded to the bole zone of a canopy gap (sensu Oriens 1982). Understory cores were taken in the same manner, with an area

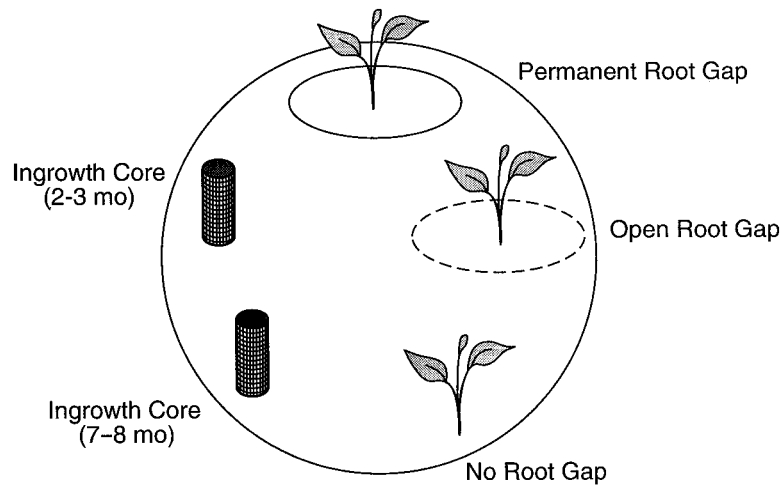


FIG. 1. Experimental setup for the root competition and root ingrowth experiments, conducted in four gap and understory sites on each soil type.

relatively free of debris being designated as the “center” and cores taken randomly within that area.

Soil samples were frozen until they could be processed. I washed soil samples for 17–22 min with a hydropneumatic root elutriator (Gillison’s Variety Fabrication Incorporated, Benzonia, Michigan, USA; Smucker et al. 1982) using 0.76-mm mesh filters; I then hand-picked roots out of the remaining organic debris. I separated live and dead roots based primarily on texture and secondarily on color; all data reported are for live roots. I measured root length density of four diameter classes (<1 mm, 1 to <2 mm, 2 to <5 mm, and  $\geq 5$  mm) using the line-intercept method (Newman 1966, Tennant 1975). Compared to root biomass, root length is considered to be a more direct estimate of the nutrient and water uptake functions of fine roots (Nye and Tinker 1977). Roots were dried at 80°C for 48 h to correlate root length and biomass.

#### Soil moisture

I measured soil moisture in gaps and understory sites using time-domain reflectometry (TDR) (TDR 6050X1, Soil Moisture Trace Corporation, Santa Barbara, California, USA). In late January 1994, after a 21-d dry period (27 mm precipitation as measured by an automatic rain gauge; La Selva weather records), soil moisture to 20 cm depth was sampled (Topp et al. 1980, 1982) in five random locations in 18 gap and 18 adjacent understory sites using a buriable TDR waveguide. Soil moisture, as a percentage of volume, was recorded and averaged over the five locations within each gap or understory site at which the waveguide was buried.

#### Root competition bioassay

I examined root competition in the four canopy gaps per soil type located in May 1993. Within each gap and understory site, I chose five treatment areas within

a 2 m diameter area that were relatively free of woody debris and large tree roots and were fairly homogeneous in litter depth (Fig. 1). Three of these treatment areas were used for the competition experiment, and the remaining two were used for ingrowth core measurements. I took spherical densitometer readings at 1 m above each treatment, and at each site I measured the diameter at 1.3 m above the ground (dbh) of all trees, lianas, and palms in a 5 m radius from the circle’s center.

The bioassay species was *Hampea appendiculata* Donn. Sm. (Malvaceae), a dioecious early successional tree (Croat 1978). I chose this species because it has fast-growing seedlings (Huston 1982) that are capable of germinating and surviving for short-time periods in both canopy gap and understory sites (R. Ostertag, *personal observation*). It also responds to nutrient addition under high-light conditions by increasing growth rates (Huston 1982), suggesting that this species might be limited by nutrients.

In January 1993 I collected and mixed together fruit from seven *H. appendiculata* mother trees. Seedlings were grown in a nursery in alluvial soil that was inoculated with mycorrhizal symbionts. Seedlings were planted in the field in June 1993. In one treatment area a seedling was planted in otherwise undisturbed soil (control). In the other two treatment areas I planted a seedling in the center of an experimentally created root gap or trench (Fig. 1). One trench was lined with a double layer of root restriction cloth (permanent root gap) while the other trench did not have this cloth and was therefore subject to root ingrowth (open root gap). I created these 20 cm diameter  $\times$  25 cm deep circular trenches by using a shovel to cut through roots, but some sub-soil was overturned in the process.

The height and basal diameter of each seedling was monitored at 2, 7, and 12 mo after planting to compare

relative growth rates between the three root-gap treatments and between light and soil fertility levels. Relative growth rates were calculated as  $(\ln[\text{height}_1] - \ln[\text{height}_0]) / (\text{time}_1 - \text{time}_0)$ . Basal diameter did not change much over this period and these data were therefore not analyzed. After 12 mo, surviving seedlings were excavated to determine root:shoot ratios. Plant parts were dried until constant mass at 80°C for biomass measurements.

#### *Ingrowth cores*

I estimated root growth by measuring root production into root-free areas of soil using ingrowth cores in two of the treatment areas (see Fig. 1). I created ingrowth cores by removing a core 8 cm diameter by 20 cm deep and placing an ingrowth bag, made of fiberglass window screening (1.5 mm<sup>2</sup> mesh) in the resulting hole. Bags were filled with hand-sieved (1 mm mesh) root-free soil taken from a nearby location; care was taken to pack the soil in the bags to bulk densities similar to original levels. One set of bags ( $n = 15$ ) was harvested in August 1993 (72–90 d later); the other set of bags ( $n = 14$ ) was harvested in January 1994 (223–241 d). I processed ingrowth samples similarly to the root-gap cores, but measured only root length and not biomass.

#### *Root proliferation in response to nutrient-rich patches*

Within 5 m radius of the center of the 40 gap and understory sites, I located 6 debris-free areas, each separated by at least 1 m. Half of these experimental locations were fertilized with a 50-mL solution of fertilizer (Peters' complete fertilizer, 20% N, 20% P<sub>2</sub>O<sub>5</sub>, 20% K<sub>2</sub>O by mass) and half were treated with 50 mL of deionized water (controls). Treatments were randomly assigned and were applied to a 10 cm diameter circle of soil. Fertilizer was added at a concentration of 1000 kg/ha (equivalent to 200 mg/kg N, 87 mg/kg P, and 142 mg/kg K). Such high concentrations were necessary to ensure that a lack of root proliferation would indicate no effect of the fertilizer, rather than the confounding effect of the nutrient levels being too low to elicit a plant response. The fertilizer and water solutions were sprayed as a fine mist directly on top of the soil with a spray bottle at a steady, slow rate to saturate the soil pores but avoid too rapid infiltration. To minimize post-treatment leaching by rain, each treatment was covered with a 15 cm diameter circle of plastic window sheeting, elevated 1–2 cm above the manipulated area.

Thirty days after fertilization, a 2 cm diameter × 20 cm deep core was taken at each experimental location. Roots were washed for 8–10 min and measured as described above. Few dead roots were found in these cores and therefore only live roots are reported. Roots were originally separated into diameter classes, but al-

most all were <2 mm, so I combined all diameter classes together as total root length.

To analyze the data I created a root proliferation index (RPI) to account for site differences between replicates (gap or understory sites). For each site I calculated the RPI as the mean root length density of the three fertilized cores divided by the mean root length density of three unfertilized control cores. An RPI of 1, therefore, corresponds to equal root length density under fertilized and unfertilized conditions. These RPIs were then used after log transformation in an ANOVA model (see *Statistical analysis*) to test the hypotheses that (1) root length density in fertilized patches is greater than root length density in unfertilized patches (i.e., RPI > 1), (2) the average RPI is greater on less fertile soils than on more fertile soils, and (3) the average RPI is greater in canopy gaps than in the understory.

To demonstrate that the fertilized soil had increased nutrient levels, I prepared one extra fertilized and one extra control treatment area at half of the sites (randomly chosen for both soil types). Set-up of the fertilized and control patches followed the same procedures as above. Soil cores (2 cm diameter × 20 cm deep) were taken 24 h after treatment to ensure that all of the added nutrients had not been leached or taken up by plants. Each sample was analyzed for NO<sub>3</sub>-N and NH<sub>4</sub>-N by extracting 10 g of wet soil with 100 mL of 1 mol/L KCl and then analyzing the two duplicate samples of the supernatant with a Technicon Auto-analyzer (Scientific Instruments Corporation, Hawthorne, New York, USA). Plant-available PO<sub>4</sub>-P was estimated using sodium bicarbonate as an extractant; each 2.5 g of wet soil was extracted with 50 mL of 0.5 mol/L, pH 8.5 sodium bicarbonate (Watanabe and Olsen 1965, Anderson and Ingram 1993). Absorption was determined colorimetrically at 880 nm using spectrophotometry (Perkin-Elmer Lambda 3A UV/VIS Spectrophotometer). Soil not used for nutrient analysis was oven-dried at 105°C for 48 h to determine water content.

#### *Statistical analysis*

Data were analyzed using SAS 6.03 (SAS Institute 1988). Whenever comparisons were made between gap and understory sites on the two soil types, data were analyzed using a nested and crossed analysis of variance model. Sites (gap and understory replicates) were nested within a soil type because the two soil types were not juxtaposed in space and because gaps and their understory controls could not be chosen randomly within each soil type. This basic model was expanded for the bioassay experiment, where a split-plot design was performed within the nested/factorial framework (Fig. 1). Due to the mortality of some seedlings, the design is unbalanced. Other data sets were analyzed with the appropriate parametric and nonparametric paired tests. Data were log transformed where necessary, and multiple comparisons were done using orthogonal contrasts (see Montgomery 1991). To deal

TABLE 2. Mean ( $\pm 1$  SD) fine root length density (centimeters of roots per cubic centimeter of soil) for the gap and understory sites on the alluvial (more fertile) and residual (less fertile) soils.

Site	Root diameter class				Total roots $\ddagger$
	<1 mm	1-<2 mm $\dagger$	2-<5 mm	$\geq 5$ mm	
Alluvial soil					
Gaps	0.359 $\pm$ 0.132	0.025 $\pm$ 0.010	0.009 $\pm$ 0.003	0.004 $\pm$ 0.005	0.397 $\pm$ 0.111
Understory	0.449 $\pm$ 0.059	0.028 $\pm$ 0.020	0.010 $\pm$ 0.008	0.002 $\pm$ 0.001	0.489 $\pm$ 0.045
Residual soil					
Gaps	0.371 $\pm$ 0.128	0.038 $\pm$ 0.015	0.019 $\pm$ 0.009	0.007 $\pm$ 0.008	0.435 $\pm$ 0.087
Understory	0.610 $\pm$ 0.151	0.070 $\pm$ 0.050	0.022 $\pm$ 0.018	0.006 $\pm$ 0.005	0.708 $\pm$ 0.095

$\dagger$  For fine roots <2 mm,  $F_{1,18} = 9.49$ ,  $P < 0.01$  for soil type;  $F_{1,18} = 29.78$ ,  $P < 0.0002$  for site; and  $F_{1,18} = 7.11$ ,  $P < 0.02$  for soil  $\times$  site interaction.

$\ddagger$  For all root diameters combined,  $F_{1,18} = 11.33$ ,  $P < 0.004$  for soil type;  $F_{1,18} = 31.50$ ,  $P < 0.0002$  for site; and  $F_{1,18} = 7.71$ ,  $P < 0.02$  for interaction.

with problems of non-normality and heteroscedascity in the root : shoot ratios and the root biomass data (but not in the length data), data were analyzed parametrically using a rank transformation procedure (Potvin and Roff 1993).

## RESULTS

### *Root gap presence and soil moisture*

Fine (<2 mm) root length density (Table 2) and biomass (Table 3) were lower under canopy gaps. Soil type also affected fine root length density and biomass, with both measures being greater on the more infertile residual soil. Understory sites on the residual soil had much greater root length density than any of the other three treatments ( $F_{1,18} = 18.50$ ,  $P < 0.01$ ), which is responsible for the significant interaction between canopy gaps and soil type. Gap size, percentage canopy openness, and median gap age were poor predictors of fine and total root length and biomass (linear regressions using each soil core, rather than the site average, as an independent sample:  $n = 59$ ,  $r^2 < 0.12$  in all cases).

Patterns of total root length were similar to fine root length (Table 2), although for total biomass, only the soil type effect was significant (Table 3). The difference in the fine and total root biomass is due to the fact that only 31.8% of total root biomass was made up of fine roots <2 mm, while 96.0% of total root length com-

prised fine roots. For all four diameter classes, biomass and length were positively correlated (Table 4). Although many root studies measure biomass instead of root length, the length measurements showed stronger patterns in this study.

Surface soils (0–20 cm) in canopy gaps were significantly wetter than adjacent understory sites (paired  $t$  test on log-transformed data,  $t = 3.2$ ,  $P < 0.005$ ,  $n = 18$ ). Back-transformed means and standard deviations for percentage soil moisture in canopy gaps were  $40.54 \pm 1.19\%$  and  $33.90 \pm 1.14\%$  for the forest understory.

### *Root competition bioassay*

No effect of root competition was demonstrated in this experiment. After 2 mo, seedlings growing in the canopy gaps had faster relative growth rates (RGR) than those in the understory ( $F_{1,5} = 21.10$ ,  $P < 0.006$ ), but there was no difference in RGR between the two soil types or the three trenching treatments (Fig. 2). Seedlings in the open root gaps tended to grow slower than those in the other two treatments, but this effect was not significant ( $P < 0.07$ ). Similar results were obtained after the 7-mo and 12-mo measurements; only the main effect of light was significant. On a finer scale, RGR was not correlated to percentage canopy openness. Because there was no difference between the root-gap treatments, root : shoot ratios of the surviving seed-

TABLE 3. Mean ( $\pm 1$  SD) fine root biomass (grams of roots per square meter of soil) for the gap and understory sites on the alluvial (more fertile) and residual (less fertile) soils.

Site	Root diameter class				Total roots $\ddagger$
	<1 mm	1-<2 mm $\dagger$	2-<5 mm	$\geq 5$ mm	
Alluvial soil					
Gaps	80.410 $\pm$ 30.309	35.994 $\pm$ 13.933	63.608 $\pm$ 39.973	138.555 $\pm$ 147.512	318.567 $\pm$ 207.779
Understory	81.687 $\pm$ 11.493	37.803 $\pm$ 18.115	53.403 $\pm$ 37.508	97.239 $\pm$ 112.955	270.132 $\pm$ 131.863
Residual soil					
Gaps	86.484 $\pm$ 27.279	54.740 $\pm$ 21.171	125.830 $\pm$ 63.668	394.346 $\pm$ 409.118	661.40 $\pm$ 416.973
Understory	138.987 $\pm$ 46.536	111.167 $\pm$ 61.989	133.045 $\pm$ 123.658	373.099 $\pm$ 444.257	756.298 $\pm$ 523.359

$\dagger$  For fine roots <2 mm diameter,  $F_{1,18} = 16.88$ ,  $P < 0.0008$  for soil type;  $F_{1,18} = 5.72$ ,  $P < 0.03$  for site.

$\ddagger$  For all root diameters combined, only the soil type effect is significant ( $F_{1,18} = 13.28$ ,  $P < 0.002$ ).

TABLE 4. Correlation of root length (cm) and root biomass (g);  $n$  = number of soil cores containing roots of each size class. Data were log transformed for normality.

Root diameter class	$r^2$	$P$	$n$
$\geq 5$ mm	66.5%	<0.001	54
2–<5 mm	78.1%	<0.001	95
1–<2 mm	72.2%	<0.001	113
<1 mm	53.8%	<0.001	116

lings ( $n = 32$ ) were analyzed without considering the effects of trenching. Seedlings growing in canopy gaps and understory sites had similar root:shoot ratios, but those on the alluvial soil tended to have lower ratios ( $F_{1,6} = 4.43$ ,  $P < 0.08$ ).

#### Ingrowth cores

After 2–3 mo there was no difference in accumulation of live or dead fine roots (<2 mm) between soil or light-gap treatments (Table 5). Accumulation of live roots in the ingrowth bags averaged  $28 \pm 18.9\%$  (range, 9–73%) of the length in the soil before the ingrowth core was created. For the cores left in the soil for 7–8 mo, the ingrowth cores had an average of  $39 \pm 29\%$  (range, 12–130%) of the initial root length. Canopy gaps, however, had significantly fewer dead roots ( $F_{1,6} = 10.01$ ,  $P < 0.05$ ), with a trend toward more dead roots accumulating in the understory on the residual soil ( $F_{1,6} = 5.69$ ,  $P < 0.08$ ).

Basal area of surrounding trees, palms, and lianas within a 5 m radius had little effect on root ingrowth rate. Basal area of lianas was weakly related to the accumulation of live roots after 2–3 mo ( $r^2 = 0.35$ ,  $P < 0.02$ ), but had no effect on root growth rate after 7–8 mo. Similarly, the basal area of neighboring trees and palms within a 5 m radius could not be used to predict root ingrowth rate at either time period.

#### Root proliferation in response to nutrient-rich patches

Levels of  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$ , and  $\text{PO}_4\text{-P}$  were elevated over distilled water controls (Wilcoxon signed rank test,  $P < 0.0001$  for all three nutrients). The root proliferation index (RPI) was greater on the residual soil ( $F_{1,18} = 4.92$ ,  $P < 0.04$ ) and tended toward a lower value under canopy gaps ( $F_{1,18} = 3.73$ ,  $P < 0.07$ ; nested and factorial ANOVA on log-transformed data). RPI, however, was only greater than a value of 1 (no proliferation response) on the residual soil in canopy gaps (one-tailed  $t$  test on log-transformed data,  $t = 2.19$ ,  $P < 0.05$ ). On the alluvial soil, under both canopy gaps and in the understory, as well as in the understory on the residual soil, the RPI was not significantly different than 1 (Fig. 3).

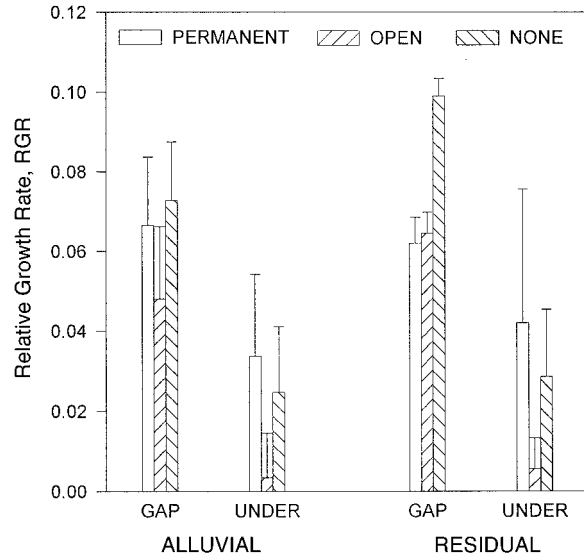


FIG. 2. Relative growth rates (means + 1 SE) of *Hampea appendiculata* 2 mo after planting in gaps and understory sites on both alluvial and residual soil types. The permanent-root-gap treatment was a trench lined with root restriction cloth, the open-root-gap treatment was a trench with no lining, and the no-root-gap treatment was a seedling planted in undisturbed soil. Relative growth rates were calculated as  $(\ln[\text{height}_1] - \ln[\text{height}_0]) / (\text{time}_1 - \text{time}_0)$ , where height was measured in millimeters and time in days.

## DISCUSSION

### Root gaps and nutrient cycling

On both fertile and infertile soil types, canopy gaps had significantly greater soil moisture and lower fine root length, suggesting that belowground changes accompanied changes in light resources after canopy opening. The decreased root biomass corroborates pre-

TABLE 5. Accumulation rate ( $10^{-4} \times$  centimeters of roots per cubic centimeter of soil per day) of live and dead roots <2 mm diameter into ingrowth bags left in the soil for 2–3 mo or 7–8 mo. Data are presented as means  $\pm$  1 SE.

Root and site type	Duration of accumulation	
	2–3 mo†	7–8 mo
Live roots		
Alluvial soil		
Gap	14.37 $\pm$ 1.01	7.06 $\pm$ 2.28
Understory	17.62 $\pm$ 1.03	11.09 $\pm$ 3.58
Residual soil		
Gap	18.42 $\pm$ 0.91	9.53 $\pm$ 2.42
Understory	26.27 $\pm$ 0.89	12.57 $\pm$ 3.10
Dead roots		
Alluvial soil		
Gap	4.51 $\pm$ 0.85	6.81 $\pm$ 2.57
Understory	8.72 $\pm$ 1.25	6.01 $\pm$ 2.78
Residual soil		
Gap	11.25 $\pm$ 0.80	10.10 $\pm$ 2.49
Understory	6.56 $\pm$ 1.18	16.40 $\pm$ 5.12

† Back-transformed means after log transformation.

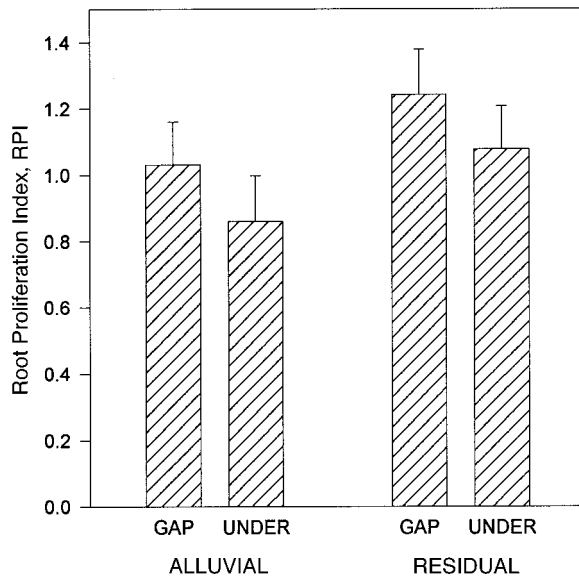


FIG. 3. Back-transformed means (means + 1 SD) of the root proliferation index (RPI, mean root length density in fertilized patches divided by root length density in unfertilized patches) in gaps and understory sites on the two soil types. The only RPI value significantly greater than 1 was on the residual soil under canopy gaps. Actual nontransformed means (+1 SD) for RPI values are  $1.06 + 0.27$  for canopy gaps, alluvial soil;  $0.90 + 0.33$  for understory, alluvial soil;  $1.30 + 0.42$  for canopy gaps, residual soil; and  $1.11 + 0.28$  for understory, residual soil.

vious investigations of root gaps in this forest (Sanford 1989) and in other temperate and tropical forests (Sanford 1990, Silver and Vogt 1993, Wilczynski and Pickett 1993, Parsons 1994b, Ehrenfeld et al. 1995, Cavelier et al. 1996).

Although soil moisture was only measured on one sampling date, soils in gaps have been found to be wetter at La Selva (Vitousek and Denslow 1986) and in other neotropical forests (Becker et al. 1988, Uhl et al. 1988). Besides the obvious effects on plant water use, soil moisture may also interact with nutrient cycling by altering decomposition (e.g., Silver and Vogt 1993) or nutrient loss rates. The loss of root biomass in canopy gaps may depress water and nutrient uptake by plants, leading to increased leaching, especially of mobile elements—an effect that may be exacerbated by nutrient pulses (Lodge et al. 1994). For example, in a Puerto Rican forest, increased root mortality due to trenching led to increased concentrations of  $\text{NO}_3\text{-N}$  within 2 mo, along with a subsequent decrease in cations (exchangeable Ca and Mg), presumably by leaching (Silver and Vogt 1993). Similarly, in a Rocky Mountain coniferous forest,  $\text{NO}_x\text{-N}$  was higher in gaps created by tree felling (Parsons et al. 1994a), coupled with a decrease in active ectomycorrhizal root tip densities (Parsons et al. 1994b).

The reason for the more pronounced root gaps on the residual soil is not obvious, because even though

the chosen gaps on the residual soil tended to be larger and younger (Table 1), there was no relationship between canopy gap characteristics and root length or biomass measurements. There was also no difference in net growth rates of live roots into ingrowth bags between the two soils or between gap and understory sites. On the residual soil, however, root mortality is reportedly faster than on alluvial soils (R. L. Sanford, *personal communication*), and this differential mortality rate may partly account for greater loss of root biomass. Root mortality could also have an effect on nutrient cycling because given the similar N and P concentrations of root litter between the two soil types (Parker 1994), decay of a larger quantity of dead roots would lead to greater cycling of these elements on the residual soils. It is still unclear whether the larger root gaps and potential differences in nutrient-cycling patterns between the two soil types may affect plant performance and competitive interactions of species regenerating in canopy gaps.

#### Root competition

Although changes in belowground environments after natural disturbances have been demonstrated to decrease competition intensity (Wilson and Tilman 1993), decreased root competition in canopy gaps was not evident on either soil type. Light, rather than nutrients, seemed to be the primary limiting factor of aboveground growth of the bioassay species, *Hampea appendiculata*, despite previous indications that this pioneer species may be limited by nutrients (Huston 1982). This result was supported by the similar ingrowth rates of live roots (all species) on both soil types. Alternatively, trenching may have had little effect in canopy gaps due to the already lowered fine root length density and biomass caused by the canopy gap formation. Trenching was not done in areas of higher light that lacked root gaps, allowing for the possibility that the lower root biomass in canopy gaps may have contributed to enhanced seedling growth. Furthermore, the added nutrients that should be available after trenching may not have been made more available in these high P-fixing soils (Sollins et al. 1994), especially if the trench size was inadequate or if mycorrhizal connections were not completely severed.

The apparent lack of root competition found in this study agrees with studies on dipterocarp seedlings (Turner et al. 1993) and two previous studies conducted in this forest on the residual soil, in which neither fertilized shrub seedlings in treefall gaps (Denslow et al. 1990) nor trenched understory tree seedlings (Denslow et al. 1991) experienced growth increases. Phosphorus concentrations in leaves of the fertilized species, however, were increased (Denslow et al. 1990), and root competition between trees and underplanted shrubs has been demonstrated on a plantation growing on alluvial soils of this forest (Gerwing 1995).

The results found in this study therefore may be ex-



plained by the choice of species (see also Denslow et al. 1987) or by the practice of measuring aboveground growth when studying root competition rather than measuring root parameters. For example, even though no changes in stem height of the bioassay species were detected after trenching, roots of the entire community growing on the residual soil responded to nutrient-enriched patches by proliferating. Delays in trunk growth after fertilizer additions have been noted in other tropical forests (Tanner et al. 1990, 1992), suggesting that conclusions about the nutrient limitation of a site based on plant bioassays may be premature if both above- and belowground components are not considered at appropriate temporal scales.

*Nutrient heterogeneity: effects on gap dynamics*

Nutrient pulses may be common after disturbances due to changes in the spatial scale of above- and belowground biomass distribution after disturbances. Short-term temporal pulses in  $\text{NO}_3\text{-N}$  have been noted after treefalls (Uhl et al. 1988, Denslow and Hartshorn 1994), as well as after trenching or hurricanes (Silver and Vogt 1993). Root proliferation into fertile microsites appears to be dependent upon the nutrient concentration of the patches (Jackson and Caldwell 1989), the ion involved (Drew 1975), duration and timing of the nutrient pulse (Crick and Grime 1987, Campbell and Grime 1989, Pregitzer et al. 1993), prior nutrient status of the responding plants (Friend et al. 1990), and, as some results from this study demonstrate, soil conditions of the nonpatch areas. The differential root proliferation response on the two contrasting soil types, with similar community composition and structure, suggests that the consequences of gap formation may depend on background levels of soil fertility. On the more fertile site, heterogeneity in soil resources resulting from or associated with canopy gap formation apparently does not elicit a root growth response. On the more infertile site, this heterogeneity may be important in determining the success of species that regenerate in the gap; similar root proliferation responses into fertilized microsites have been reported in other nutrient-limited ecosystems (Cuevas and Medina 1988, Raich et al. 1994, Riley and Vitousek 1994). What cannot be determined conclusively, however, is whether the increased root proliferation index in canopy gaps on the residual soil was due also to the presence of root gaps that were created after canopy opening.

Nutrient heterogeneity between zones of a canopy gap (i.e., bole zone, crown zone, and root throw zone) has been hypothesized to be important in allowing differential colonization success of species and thereby maintaining diversity (Orrians 1982, Brandani et al. 1988). Differences in physical conditions between gaps may be a more appropriate scale for use in determining patterns of root biomass, root foraging, and subsequent regeneration, especially because differences in fine root biomass between gaps are greater than those within

gaps (Sanford 1990). Although this study demonstrates the pattern of root gap formation after canopy opening, the consequences of these root gaps appear to be dependent on site characteristics as well as the response variables measured. Under conditions of reduced competition or increased nutrient availability, neither root proliferation nor aboveground growth of the indicator species increased on the more fertile soil, but root growth was stimulated by fertilization on the infertile soil. Additionally, the larger root gaps on the residual soil irrespective of gap size or age suggest that the size of root gaps created after canopy opening may be related more to site conditions than to gap characteristics (see also Ehrenfeld et al. 1995). It is therefore unlikely that a natural disturbance will have the same effect on both soil types. If nutrient addition does not affect plant growth on the more fertile soil, hypothesized mechanisms of niche partitioning along interacting soil and light gradients to promote maintenance of species diversity (Ricklefs 1977, Denslow 1980) may not be useful for explaining patterns of high diversity on very fertile sites.

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