

# Treefall gap size effects on above- and below-ground processes in a tropical wet forest

JULIE S. DENSLOW\*, AARON M. ELLISON† and  
ROBERT E. SANFORD‡

\*Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA; †Department of Biology, Mt Holyoke College, South Hadley, MA 01075, USA; and ‡Department of Biological Sciences, University of Denver, Denver, CO 80208, USA

## Summary

**1** We examined the effects of variation in gap size on above- and below-ground light and nutrient processes in a tropical wet forest in Costa Rica.

**2** Trees were felled to create canopy openings ranging in size from 65 to 611 m<sup>2</sup>. Following treefall, we measured initial litter mass in the crown zone of six gaps. During the subsequent year, we measured litter decomposition rate and light levels as well as NH<sub>4</sub>-N, NO<sub>3</sub>-N and PO<sub>4</sub>-P levels in surface soils, soil moisture and fine root mass. We also measured growth rates of fertilized and non-fertilized plants of four species of *Miconia* (Melastomataceae) to assess nutrient limitation to plant growth in large gaps.

**3** Light levels in the centres of gaps were significantly related to size of the canopy opening. After 1 year, light levels near the ground in larger openings (35–40% full sunlight immediately after treefall) declined to levels similar to those in smaller gaps (10–20%).

**4** Although canopy opening had only slight effects on soil NH<sub>4</sub>-N, NO<sub>3</sub>-N pools were significantly greater in gaps than in understorey at both sites. The effect was positively correlated with gap size. Extractable PO<sub>4</sub>-P was also greater in gaps than in adjacent understorey, although the difference did not vary as a function of gap size. In three of six gaps, fine root biomass was less in gaps than in adjacent understorey.

**5** Of four species of *Miconia*, only *M. affinis*, a small tree common in early secondary forests, grew significantly faster in fertilized than in non-fertilized treatments in three large gaps.

**6** Our data suggest that higher nutrient pools in surface soils of treefall gaps may result from decomposition and mineralization of the large mass of fresh litter from the fallen tree. While growth rates of shade-tolerant rain forest trees and shrubs are not much affected by the increased nutrient availability even at high light levels, growth rates of pioneer or high-light demanding species may be enhanced by increased above- and below-ground resources.

**Keywords:** Costa Rica, light, *Miconia*, nutrients, relative growth rate

*Journal of Ecology* (1998) **86**, 597–609

## Introduction

Canopy openings that result from treefalls are the predominant source of stand turnover in many mesic forests (e.g. Runkle 1985; Brokaw 1985; Veblen 1992).

Correspondence: Julie S. Denslow, Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA (fax 504 388 2597; e-mail jdenslo@unix1.sncc.lsu.edu).

In tropical rain forests, high light availability in gaps promotes growth and reproduction of seedlings of many, if not most, canopy trees as well as understorey species (reviewed in Denslow 1987). Patterns of plant growth and other ecological processes are thought to vary as a function of gap size, because gap size directly affects light levels and microclimates (Fetcher *et al.* 1985; Barton *et al.* 1989; Brown 1993; Denslow & Hartshorn 1994). Ricklefs (1977) and Denslow (1980) hypothesized that the complex environmental gradi-

ent that is associated with variation in gap size might promote the coexistence of tropical tree species through their differential responses to environmental variation at establishment sites. Subsequent studies have indicated that, when light gradients are considered, only two major resource-response groups are found, namely high-light demanding and shade-tolerant species (Swain & Whitmore 1988; Denslow *et al.* 1990; Brokaw 1985, 1987). However, gap size also may affect nutrient availability, and the consequences for plant growth along such gradients are not well understood (Whitmore 1996).

Previous studies have suggested that the environmental changes associated with treefalls are buffered by the surrounding trees, particularly in the small gaps typical of many tropical rain forests (Denslow 1987). In the centres of gaps smaller than 200 m<sup>2</sup> (76% of all openings at the La Selva Biological Station; Sanford *et al.* 1986), integrated light levels are less than 20% of full sunlight (Chazdon & Fetcher 1984; Denslow *et al.* 1990). Nutrient processes in the largely intact soils of these gaps also appear to differ little from those under closed canopy. Moisture levels of surface soils of gaps < 200 m<sup>2</sup> are often greater than under adjacent closed canopy (Vitousek & Denslow 1986; Uhl *et al.* 1988; Becker *et al.* 1988), but in a Costa Rican study, soil NH<sub>4</sub>-N, NO<sub>3</sub>-N, extractable PO<sub>4</sub>-P and N-mineralization rates measured a few months after gap formation did not differ appreciably from background levels (Vitousek & Denslow 1986). In contrast, NO<sub>3</sub>-N levels in soil and soil leachate increase following large-scale forest clearing (e.g. Parker 1985; Matson *et al.* 1987). These data suggest that many treefall gaps may be too small to produce detectable changes in soil nutrient processes, although microclimate (especially soil temperature and moisture), plant nutrient demand and litter inputs may all vary as a function of gap size and are therefore likely to affect nutrient availability.

Do nutrient pulses affect the growth of seedlings and saplings found in treefall gaps? While plant growth rates are generally higher in gaps than under forest canopy, the below-ground effects of treefall on plant growth have been less clearly demonstrated. Where plant growth is nutrient-limited, fine-root proliferation may closely follow pulsed nutrient enrichment, especially in fast-growing species (Crick & Grime 1987; Cuevas & Medina 1988; Campbell & Grime 1989; Jackson & Caldwell 1989; Pregitzer *et al.* 1993; Lodge *et al.* 1994; Ostertag, 1998). However, fertilization and trenching experiments of understorey plants in wet forest suggest that light availability may limit growth more strongly than nutrients at low to moderate light levels (Denslow *et al.* 1990, 1991; Ostertag, 1998).

This paper reports results of studies on nine experimental gaps ranging in size from 65 to 611 m<sup>2</sup>. We examined the effects of gap size on soil nutrient processes and tested the growth responses of four species

of *Miconia* (Melastomataceae) to experimentally increased nutrient availability in three large gaps.

## Materials and methods

### STUDY AREA

The study was conducted in premontane wet to very wet tropical forest (Hartshorn & Hammel 1994), Heredia Province, Costa Rica, on upland, well-drained sites at the La Selva Biological Station of the Organization for Tropical Studies and in a nearby fragment of lightly selectively logged forest above the Bijagual River. Vegetation composition and structure, soils, and climate of the two areas are similar (for a description of La Selva, see Hartshorn & Hammel 1994). La Selva receives approximately 4000 mm of rainfall annually with no month accumulating less than 100 mm (Sanford *et al.* 1994). The canopies of both sites are species-rich, but dominated by the legume *Pentaclethra macroloba* (Willd.) Kuntze (Mimosaceae) and several canopy palms (*Socratea durissima* (Oersted) H. A. Wendl., *Welfia georgii* H. A. Wendl. Ex Burret, and *Iriartea deltoidea* Ruiz & Pavón). *Vochisia hondurensis* Sprague (Vochisiaceae) is common at Bijagual, but not at La Selva. There was no indication of recent logging in the immediate vicinity of the study sites and neither soils nor canopies of the study sites showed any evidence of previous logging activity.

At La Selva, study areas were located on soils mapped as Jaguar ultisols (typic tropohumult, USDA Soil Taxonomy; Sancho & Mata 1987; Sollins *et al.* 1994). Bijagual soils were similar in colour, pH, and topographic position to the Jaguar and Matabuey ultisols of La Selva (J. S. Denslow, unpublished data). These soils have been weathered *in situ* from andesitic or andesitic/basaltic ash deposits; their chemical and structural characteristics are indistinguishable although they differ slightly in colour (Sollins *et al.* 1994). Both are poor in phosphorus but rich in organic matter and nitrogen supply (Vitousek & Denslow 1986; Sollins *et al.* 1994). Ultisols are widespread in the tropics, comprising about 28% of soils at lowland elevations (Vitousek & Sanford 1986).

### GAPS

Nine treefall clearings were created by felling one or two large trees and sufficient numbers of smaller trees to create substantial canopy openings. In all cases at least one of the gap makers was *Pentaclethra*. Felled trees were left in place. Six gaps were created at La Selva during August 1988. Three additional large gaps were created at Bijagual in July 1989.

### CROWN BIOMASS

We estimated the fine litter biomass of the fallen tree crowns immediately following treefall in the six La

Selva gaps. Transects, 0.5 m wide and randomly located within the crown zone, were cut from edge of the crown to the main trunk (two transects per gap). Fresh weights of all leaves and small stems (< 5 cm diameter) within these transects were measured in the field. Subsamples of fresh mass were oven dried at 80 °C to estimate percentage dry mass of each tissue type.

#### ESTIMATED LIGHT AVAILABILITY

The proportion of total annual incident sunlight received was estimated for all gaps using hemispherical canopy photographs, taken at 0.5 m above ground at fixed points on a transect through the centre of the long axis of the gap (three sampling points per gap). Photographs were taken within 1 month of treefall, then at intervals of 2.5–3.0 months for at least 1 year thereafter. We used CANOPY © software developed by Rich (1990) to interpret digitized images of the photographs. A description of the software and protocols used to minimize interpreter bias and maximize repeatability can be found in Denslow *et al.* (1991) and Bellingham *et al.* (1996). Incident light levels within the gaps were estimated as the weighted average of total annual incident direct and indirect radiation measured as proportion of sunlight reaching the tops of the canopies (0.45 direct site factor + 0.55 indirect site factor; Rich *et al.* 1993). We used these light levels as an index of effective gap size since light levels are more closely related to gap microclimates than the size of the canopy opening itself (Whitmore 1996).

#### FINE ROOT MASS

Dry mass of fine roots (< 2 mm diameter) was monitored for 1 year in the upper 10 cm of soil in three La Selva sites and three Bijagual sites. Five soil cores (6 cm diameter × 10 cm deep) were sampled monthly at random locations in forest understorey and crown zone of gaps. Roots were separated from the soil by washing the soil through a fine sieve. Live roots were sorted by diameter, oven dried at 80 °C, and weighed.

#### LITTER DECOMPOSITION

Decomposition rates of fresh *Pentaclethra* leaves in 2-mm mesh nylon bags were estimated using samples of 3.0 g fresh leaves taken from a single homogeneous mixed pool. Five sets of six bags were placed under the standing litter in contact with the soil surface at random locations in the centres of the crown zones and in the adjacent forest understorey immediately following treefall at three La Selva sites (SAL, GUA and HON). Bags were collected at biweekly (two collections) then monthly (three collections) intervals. The final dry mass of litter remaining after 140 days is reported here.

#### SOIL NUTRIENTS

La Selva gaps were sampled 15, 32, 61, 88, 115, 206, 263 and 319 days following treefall. Bijagual gaps were sampled 44 days prior to treefall, then at 0, 14, 42, 71, 98, 126, 154, 182, 238, 294 and 350 days following treefall. Six soil cores (6 cm diameter × 10 cm deep) were collected from random locations in the canopy zone of each gap and in the adjacent forest understorey at distances (> 15 m) sufficient to avoid effects of nearby canopy openings. Fresh soils were homogenized, subsampled and extracted with dilute acid fluoride within 24 h for PO<sub>4</sub>-P (Olsen & Sommers 1982) and with KCl for NH<sub>4</sub>-N and NO<sub>3</sub>-N (Keeney & Nelson 1982). Colorimetric analyses were performed on a Technicon Auto analyser following methods described by Vitousek & Denslow (1986).

#### PLANT GROWTH RESPONSE TO FERTILIZATION

We measured *in situ* growth responses to fertilization using rooted cuttings of four shrub and tree species. This experiment, conducted in the three large gaps at Bijagual, was similar in design to an earlier experiment on shrub growth response to fertilization in three small gaps at La Selva (Denslow *et al.* 1990).

Four species from the genus *Miconia* in the Melastomataceae, a species-rich family of tropical shrubs and small trees, were selected for study. Small size and slow early growth of *Miconia* seedlings precluded their use for these experiments. Single-leaf cuttings 3.5–13.0 cm long therefore were rooted in a sand-filled mist bench under 80% shade cloth. The species selected consisted of two trees (*Miconia affinis* DC and *M. multispicata* Naudin) and two shrubs (*M. gracilis* Triana and *M. nervosa* (J. E. Smith) Triana). Previous research (Denslow *et al.* 1990; Newell *et al.* 1993) and natural habitat distributions had shown that *M. affinis* and *M. nervosa* were relatively high-light demanding species, while *M. multispicata* and *M. gracilis* were more shade-tolerant. All four species are common in intact rain forest. Rooted cuttings were hardened off in a common garden under 80% shade, blocked by size, and planted into gaps. Transplanted cuttings dying within the first 2 weeks only were replaced.

Cuttings were planted at 0.5-m spacing in a randomized complete block design (4 species × 3 gaps × 2 treatments × 6 replicates). Plants were grown at two nutrient levels (added complete fertilizer and added distilled water). Half of the plantings were fertilized biweekly with 20 ml of complete fertilizer solution (66 mmol l<sup>-1</sup> NH<sub>4</sub>Cl; 32 mmol l<sup>-1</sup> KH<sub>2</sub>PO<sub>4</sub>; 5 mmol l<sup>-1</sup> CaCl<sub>2</sub>; 9 mmol l<sup>-1</sup> MgSO<sub>4</sub>; and micronutrients consisting of B, Zn, Cu, Fe and Mo). Control plants were watered with 20 ml of distilled water on the same schedule. Light environments of four randomly selected cuttings in each site were measured at the begin-

ning of the experiment using hemispherical canopy photographs and the protocol described above.

Growth was measured monthly for 11 months as the summed lengths of all stems and branches. After 1 year, all plants were harvested and separated into roots, stems, leaves and original cutting. Plants were oven dried at 80 °C and weighed.

Relative growth rates (Hunt 1978) were calculated by measurement interval as:

$$\text{RGR} = (\ln(\text{SL}_2) - \ln(\text{SL}_1)) / t$$

in which SL is the total cumulative stem length (in cm) measured on two different dates and  $t$  is the elapsed time in days between measurements.

#### STATISTICAL ANALYSES

Gap-understorey differences in fine root dry mass, soil moisture,  $\text{NH}_4\text{-N}$ ,  $\text{NO}_3\text{-N}$  and  $\text{PO}_4\text{-P}$  were tested using repeated-measures analysis of variance (PROC ANOVA, Ver. 6.11; SAS Institute 1996) for La Selva and Bijagual sites separately. Where  $\text{SITE} \times \text{GAP}$  interactions were significant gap-understorey differences were tested independently for each site.

### Results

#### GAP CHARACTERISTICS

A total of nine gaps were created at the two sites (Table 1). Gaps ranged in size from 65 to 611 m<sup>2</sup>, estimated by projecting the edges of crowns of bordering trees to the ground (Brokaw 1982). Crown areas (that part of the gap receiving the leaf and small wood litter from the fallen trees) varied between 38.5 and 189.0 m<sup>2</sup> (24–291% of gap area) in the six La Selva gaps in which it was measured (Table 1). Dry

mass of litter exclusive of large wood in the crown zones of these gaps varied between 1.4 and 12.0 kg m<sup>-2</sup> [mean (SD) 5.4 (3.8) kg m<sup>-2</sup>]. Estimated fine litter and small wood densities were significantly correlated with gap size ( $r^2 = 0.88$ ,  $n = 6$ ,  $P < 0.05$ ), although not with crown area.

#### LIGHT LEVELS

Estimated total annual light levels in the centres of the nine experimental gaps varied between approximately 11% and 40% full sunlight at the time of treefall (Table 1). Gap size explained 53% of the variation in light level ( $P < 0.023$ ,  $n = 9$ ). In addition to size, gap shape and orientation as well as height of surrounding forest affect the duration of direct sunlight striking the gap floor. For example, initial light levels of gaps differing in size by a factor of 3 (STRY 483 m<sup>2</sup> and GUA 158 m<sup>2</sup>) were nevertheless similar (27% and 28% full sunlight, respectively).

Patterns of change in light availability near the ground also varied as a function of gap size (Fig. 1). Light levels changed little during the year following treefall in three smaller gaps (initial light levels 10–20%), whereas in four out of six larger gaps (initial light levels 35–40%) light levels declined by about 50% to <20% full sunlight. Light availability in one gap (HON) increased somewhat during the course of the study due to fall of trees on the edge of the gap. One year following treefall, light levels at seedling heights in all gaps remained 5–10 times the reported understorey light levels in these forests of 1.5–2% full sunlight (Denslow *et al.* 1987).

#### FINE ROOTS

In three sites (TERM, VOCH and HON), fine root dry mass in the upper 10 cm of soil was significantly

**Table 1** Characteristics of experimental gaps at La Selva and Bijagual, ordered by size

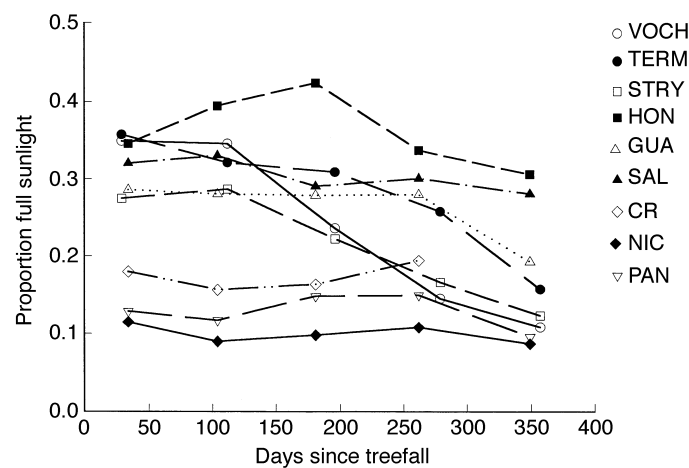
Gap code	Site*	Date	Gap makers	Area† (m <sup>2</sup> )	Light‡ (%)	Litter bags	Crown area (m <sup>2</sup> )	Litter mass§ (kg m <sup>-2</sup> )
VOCH	BIJ	6-89	<i>Pentaclethra macroloba</i>	611	0.35 (0.03)	X		
TERM	BIJ	6-89	Unknown Sapindaceae	550	0.36 (0.03)	X		
			<i>Terminalia oblonga</i>					
			<i>P. macroloba</i>					
STRY	BIJ	6-89	<i>P. macroloba</i>	483	0.27 (0.01)	X		
			<i>Stryphnodendron excelsum</i>					
HON	LS	7-88	<i>P. macroloba</i>	444	0.34 (0.03)	X	108.5	12.0
GUA	LS	7-88	<i>P. macroloba</i>	158	0.28 (0.01)	X	38.5	6.7
SAL	LS	7-88	<i>P. macroloba</i>	129	0.34 (0.06)	X	58.2	6.0
CR	LS	7-88	<i>P. macroloba</i>	126	0.18 (0.01)		62.5	3.4
NIC	LS	7-88	<i>P. macroloba</i>	76	0.11 (0.02)		84.8	1.4
PAN	LS	7-88	<i>P. macroloba</i>	65	0.13 (0.02)		189.0	2.6

\* LS = La Selva; BIJ = Rio Bijagual.

† Gap area measured to edge of crowns projected onto forest floor.

‡ Proportion full sunlight in gap centres at treefall [mean (SE)].

§ Dry mass of leaf and fine stem litter in crown zone.



**Fig. 1** Changes in light levels during the first year following treefall in nine gaps. Light levels in the centres of the gaps are estimated from hemispherical photographs and reported as the proportion of total annual incident radiation. Gaps are ordered by area.

lower in gaps than in the adjacent understorey (Fig. 2 and Table 2). Gap understorey differences were not consistent or significant in two of the remaining sites (GUA and STRY). At SAL, fine root dry mass was significantly greater in the gap samples than in the understorey.

#### NUTRIENT PROCESSES

Canopy opening had no significant effect on the decomposition rates of fresh *Pentaclethra* litter as estimated by litter mass remaining after 140 days in the field ( $F = 0.77$ ,  $n = 6$ , NS).

Soil levels of  $\text{NH}_4\text{-N}$  were only weakly affected by gap processes (Table 2). At La Selva,  $\text{NH}_4\text{-N}$  levels varied significantly among sites;  $\text{NH}_4\text{-N}$  levels were significantly higher in gaps than in the understorey at SAL and PAN, but not at the other four sites, accounting for a significant  $\text{SITE} \times \text{GAP}$  ANOVA interaction term. Among the Bijagual sites, soil  $\text{NH}_4\text{-N}$  did not differ significantly among sites or as a function of canopy opening.

In contrast, soil  $\text{NO}_3\text{-N}$  pools in the period following gap formation were significantly different among sites and, with one exception, significantly greater in gaps than in understorey samples at both La Selva and Bijagual areas (Table 2 and Fig. 3). A significant  $\text{SITE} \times \text{GAP}$  interaction term for La Selva soils was due to a similar gap and understorey  $\text{NO}_3\text{-N}$  levels in one of the smallest gaps (NIC). In most sites, except the three smallest (CR, PAN and NIC), gap soil  $\text{NO}_3\text{-N}$  levels peaked 40–60 days after treefall and, in all sites,  $\text{NO}_3\text{-N}$  levels in gap soils approached those in soils under closed canopy within a year following treefall. The magnitude of the gap effect on soil  $\text{NO}_3\text{-N}$  levels (measured as the log of the difference between gap and understorey measurements) increased with gap size as measured by light levels near the floor in the gap centres (Fig. 4;  $r^2 = 0.61$ ,

$P < 0.05$ ,  $n = 9$ ) or as a projection of the canopy opening ( $r^2 = 0.72$ ,  $P < 0.05$ ,  $n = 9$ ).

Treefall and canopy opening had a significant although smaller transient effect on extractable  $\text{PO}_4\text{-P}$ . In seven of the nine sites, extractable  $\text{PO}_4\text{-P}$  levels in the soil were higher in gaps than in adjacent understorey (Fig. 5 and Table 2). In contrast to the  $\text{NO}_3\text{-N}$  pattern, gap understorey differences in P remained relatively constant during the first year following treefall, although in most cases the gap effect had largely disappeared after a year. There was no correlation between levels of extractable P in gap surface soils and gap size, litter mass  $\text{m}^{-2}$  or gap light levels.

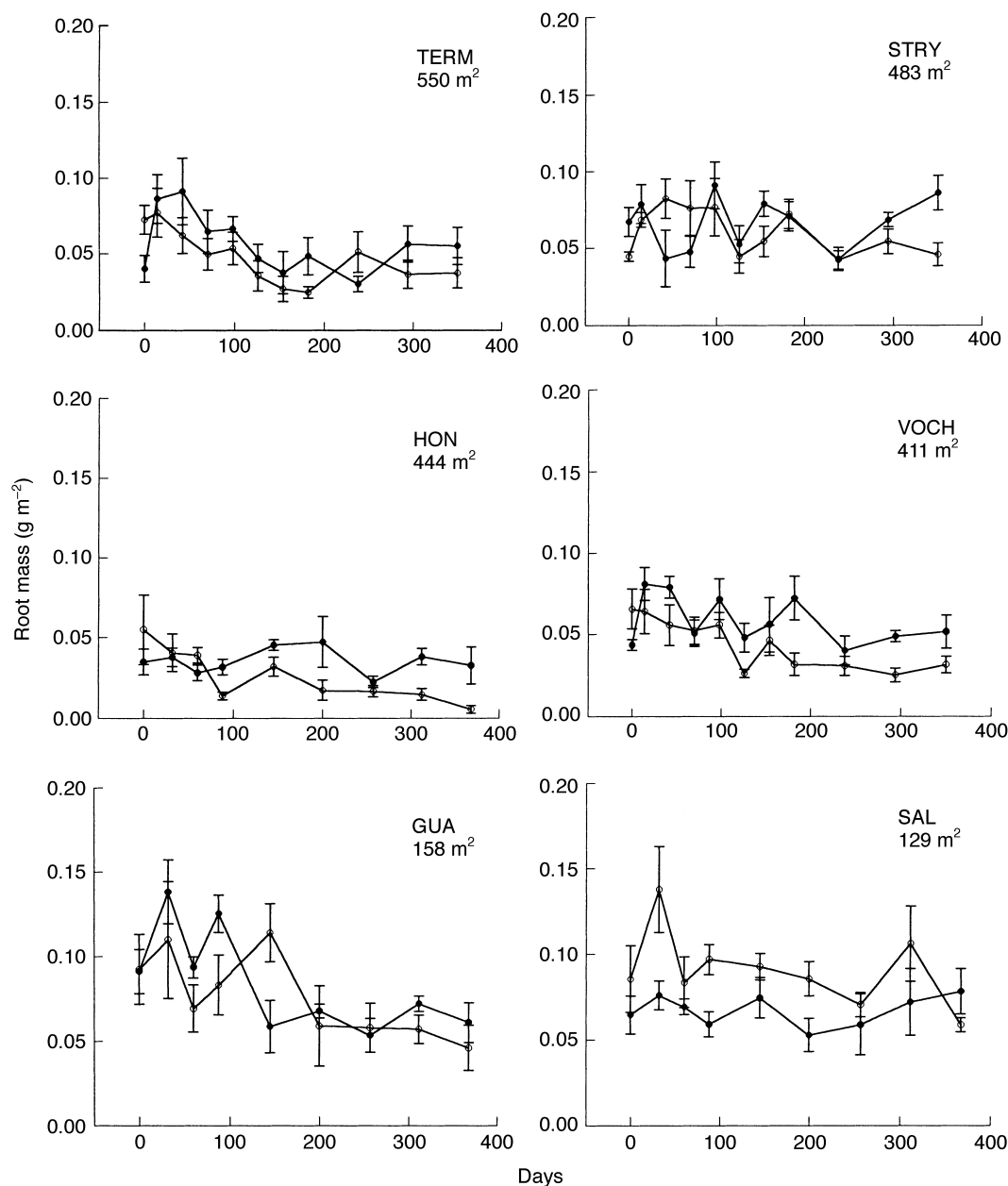
The proportion of moisture in the surface soils of gaps was significantly higher than in soils under closed canopy in seven of nine sites (Fig. 6 and Table 2). Moisture content of surface soils was not significantly correlated with either gap size or initial gap light levels.

#### MICONIA GROWTH EXPERIMENT

Incident light levels estimated from hemispherical photographs taken over four randomly selected, experimental plants in each gap at Bijagual confirmed that the plantings were exposed to light levels typical of large gaps [mean (SD): VOCH, 43 (1)%; TERM, 48 (1)%; STRY, 31 (1)%]. Of the four species of *Miconia* tested, only *M. affinis*, a small tree common in early secondary forests, grew significantly faster in fertilized than in non-fertilized treatments [ANOVA (between subjects, repeated measures design): d.f. = 1,16;  $F = 13.01$ ;  $P = 0.002$ ; Fig. 7]. Fertilization did not affect biomass allocation to roots in any of the four species.

#### Discussion

The size of the opening produced by the fall of canopy trees has several implications for subsequent eco-



**Fig. 2** Changes in root mass ( $\text{g cm}^{-2}$ ) in gaps and adjacent understorey areas during the first year following treefall. Open circles = gaps; filled circles = understorey samples.

logical processes. Above-ground, the size of the canopy opening has a direct effect on light levels, in turn affecting vegetation growth rates (Barton *et al.* 1989; Denslow & Hartshorn 1994). In large gaps, growth of existing and newly established shrubs, lianas and large herbs rapidly reduces light availability at seedling levels. In small gaps, light levels may change little during the first year, unless subsequent treefalls enlarge the original canopy opening (e.g. Young & Hubbell 1991). In these smaller gaps, initial light levels are not sufficient to promote high growth rates or the establishment of high-light demanding liana and herbaceous species. As a result, across a range of gap sizes, light levels near the ground converge within a year.

Surface soil temperatures (Fetcher *et al.* 1985) and moisture content are generally higher in gaps than in the adjacent understorey (Vitousek & Denslow 1986; Uhl *et al.* 1988; Becker *et al.* 1988; this study). Increased gap soil moisture levels are probably due to both higher throughfall and lower evapotranspiration loads. The reduction in fine root mass observed following treefall in this and in other studies (Sanford 1989, 1990; Silver & Vogt 1993; Ostertag, 1998) is consistent with a hypothesis of reduced transpiration loads on gap soils.

The fall of living trees deposits a large mass of fresh litter under the fallen crown. Extrapolating from our estimates of the mass of fresh leaf and small-branch litter deposited in the crown zones of treefall gaps,

**Table 2** Analysis of variance (between subjects, repeated measures design) results for gap effects on soil characteristics at La Selva and Bijagual sites. (F (d.f.); \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ ). One-way ANOVA results are provided for GAP effects at sites in which SITE  $\times$  GAP interaction terms are significant

	Root dry mass	Soil moisture	NH <sub>4</sub> -N	NO <sub>3</sub> -N	PO <sub>4</sub> -P
La Selva					
SITE	88.35 (2)***	21.34 (5)***	4.21 (5)***	9.18 (5)***	26.23 (5)***
GAP	0.12 (1)	62.59 (1)***	4.01 (1)*	69.30 (1)***	74.09 (1)***
SITE $\times$ GAP	9.58 (2)***	3.73 (5)**	4.90 (5)***	9.55 (5)***	7.98 (5)***
CR		6.20 (1)*	4.27 (1)	11.38 (1)**	13.35 (1)**
GUA	1.62 (1)	33.42 (1)***	3.48 (1)	20.81 (1)**	7.41 (1)*
HON	7.96 (1)*	9.69 (1)*	3.43 (1)	28.11 (1)***	5.75 (1)
NIC		10.37 (1)**	1.26 (1)	0.02 (1)	27.46 (1)***
PAN		22.68 (1)**	9.67 (1)*	11.81 (1)**	41.71 (1)***
SAL	11.57 (1)**	0.00 (1)	5.51 (1)*	39.24 (1)***	8.03 (1)*
Bijagual					
SITE	6.14 (2)**	0.51 (2)	0.21 (2)	6.35 (2)**	5.82 (2)**
GAP	9.36 (1)**	45.07 (1)***	3.39 (1)	50.52 (1)***	12.10 (1)**
SITE $\times$ *GAP	1.12 (2)	7.20 (2)**	0.86 (2)	1.66 (2)	0.73 (2)
VOCH		24.93 (1)***			
TERM		17.19 (1)**			
STRY		1.20 (1)			

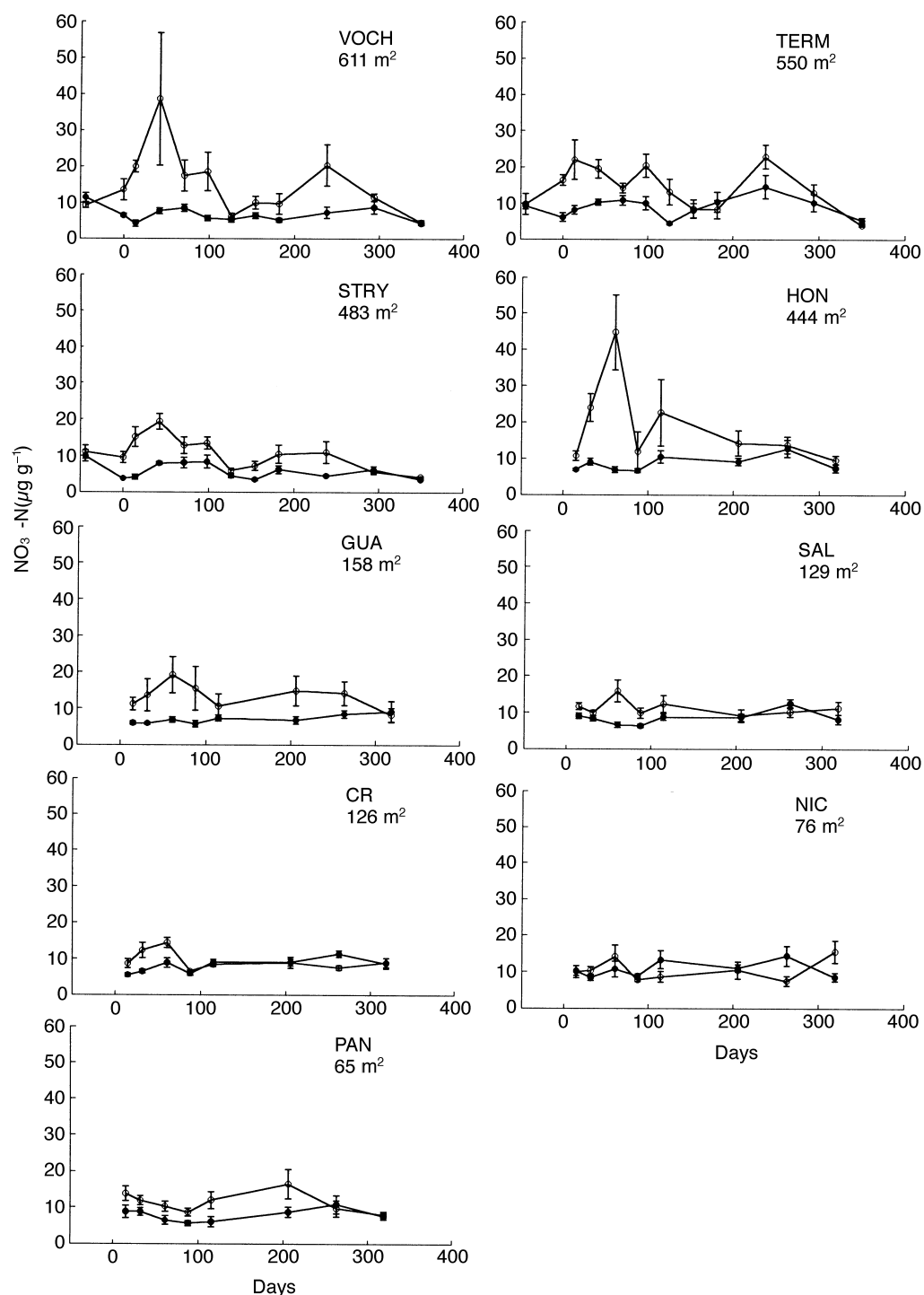
from published measurements of foliar and branch nutrient contents in forests on ultisols and oxisols (Vitousek & Sanford 1986; Scatena *et al.* 1993), and from estimated canopy turnover time of 118 years for La Selva (Hartshorn 1978), we calculated annual inputs of N and P due to treefalls at 3.7 kg ha<sup>-1</sup> year<sup>-1</sup> and 0.2 kg ha<sup>-1</sup> year<sup>-1</sup>, respectively. Assuming annual N (108 kg ha<sup>-1</sup>) and P (3.1 kg ha<sup>-1</sup>) inputs from litter fall measured in forests on similar soils (Vitousek & Sanford 1986), we estimated that treefalls contribute 3% of annual N and 6% of annual P inputs per hectare. N and P input to the crown zone of gaps was approximately four and eight times annual background levels from litter fall.

Vitousek & Denslow (1986) found no difference in P and N pool sizes or in N-mineralization rates in six small, natural gaps 2–12 months old at La Selva. They speculated that high background N-mineralization rates and high P adsorption on variable-charge clays may have masked an effect of the high litter inputs, and that an early, ephemeral peak in N pools would have been missed in their study. Our data from newly created gaps document this early peak in soil NO<sub>3</sub>-N levels. While pool sizes of both NO<sub>3</sub>-N and PO<sub>4</sub>-P were higher in our gaps during the first year following treefall, the effect on NO<sub>3</sub>-N was strongest approximately 2 months following treefall. Moreover the magnitude of the effect on NO<sub>3</sub>-N concentration is a function of gap size. Within the range of gap sizes used in this study, we found no evidence of a threshold effect (e.g. Parker 1985; Parsons *et al.* 1994). Soil concentrations of both NO<sub>3</sub>-N and extractable P return to background levels within a year of treefall or canopy disturbance (this study; Silver *et al.* 1996).

Higher NO<sub>3</sub>-N and extractable P concentrations in

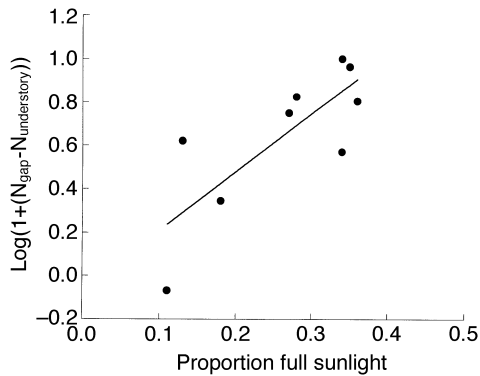
gap surface soils are likely to be due to both reduced uptake by vegetation and an input pulse due to decomposition of both leaf and fine root litter associated with tree mortality (Silver & Vogt 1993; Lodge *et al.* 1994). The gap size effects observed here are likely to be due primarily to greater litter densities in larger gaps. Although gap formation significantly reduced root densities and increased soil moisture, the effect of treefall on fine root densities was highly variable and not significantly related to gap size. Neither litter decomposition rates (this study) nor mineralization rates (Vitousek & Denslow 1986; Marrs *et al.* 1991) appear to be affected by canopy opening. Increases in NO<sub>3</sub>-N may contribute to cation leaching (Silver & Vogt 1993), so gap formation may not represent increased availability of all nutrients.

Does an increase in N and P availability affect plant growth in large gaps? Productivity of most lowland tropical moist forests is thought to be limited more by P than by N availability (Vitousek 1984; Silver 1994). However, while complete nutrient fertilization often has a significant effect on plant growth in pots (Denslow *et al.* 1987; Turner 1991; Burslem *et al.* 1994, 1995; Gunatilleke *et al.* 1997), nutrient limitation is not often shown *in situ* (Denslow *et al.* 1990; Turner *et al.* 1993). Similarly, trenching of seedlings planted in the understorey (Denslow *et al.* 1991) and in small gaps (Ostertag 1998) did not affect growth or survival on ultisols. Low light levels in small gaps and forest understorey are more likely to limit plant growth in most rain forest habitats than soil moisture or nutrient availability. However, several temperate and tropical studies suggest that the above-ground response to lower root competition or increased nutrient availability may be slower than the below-ground response

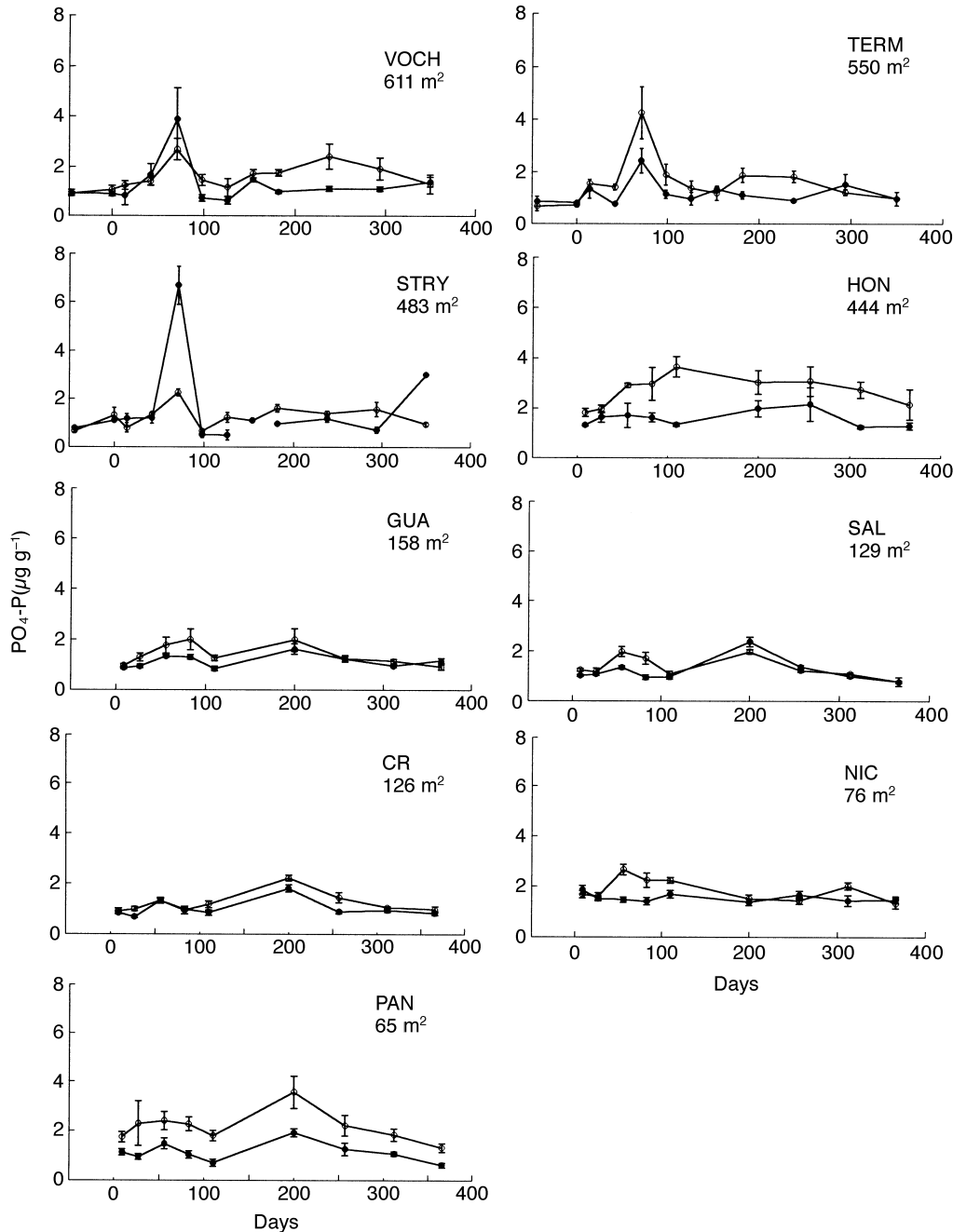


**Fig. 3** Changes in concentrations of  $\text{NO}_3\text{-N}$  in surface soils of gaps and adjacent understorey areas during the first year following treefall. Open circles = gaps; filled circles = understorey.

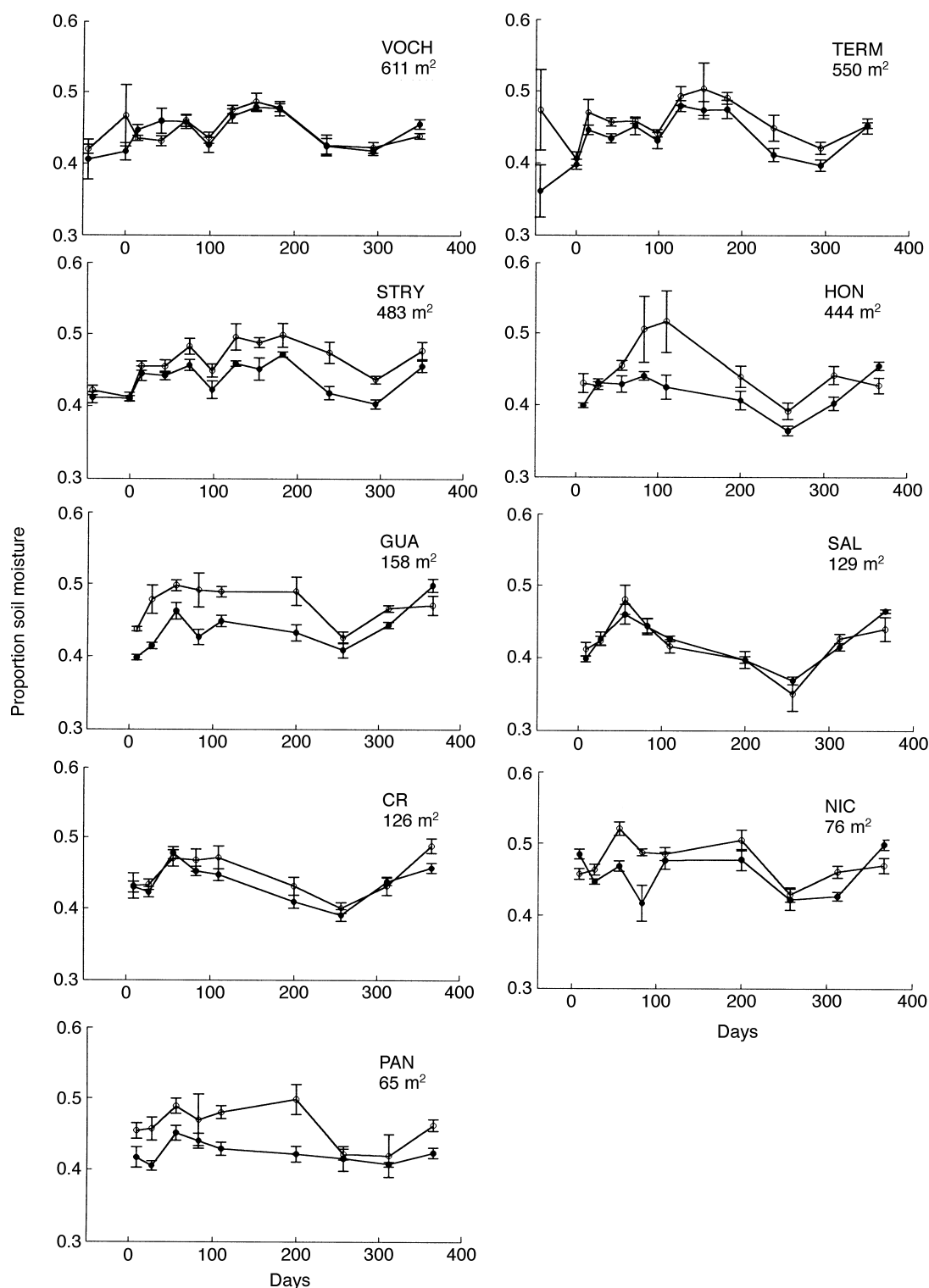




**Fig. 4** Effects of size of canopy opening (measured as percentage annual incident radiation at treefall) on soil NO<sub>3</sub>-N concentrations ( $r^2 = 0.61$ ;  $n = 9$ ;  $P < 0.05$ ).



**Fig. 5** Changes in levels of extractable PO<sub>4</sub>-P in surface soils of gaps and adjacent understorey areas during the first year following treefall. Open circles = gaps; filled circles = understorey.

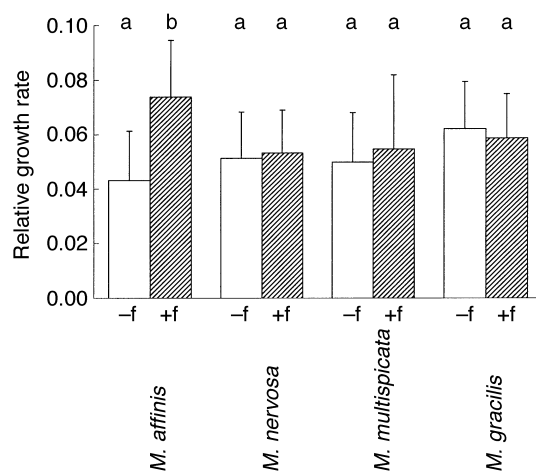


**Fig. 6** Changes in moisture content of surface soils from gaps and adjacent understorey areas during the first year following treefall. Open circles = gaps; filled circles = understorey.

(St John 1983; Campbell & Grime 1989; Jackson & Caldwell 1989; Tanner *et al.* 1990, 1992; Pregitzer *et al.* 1993; Ostertag 1998).

Of the four *Miconia* species we tested, only *M. affinis*, a fast-growing tree typical of early secondary forests, was significantly affected by fertilization. Growth of the two shade-tolerant species, in particu-

lar, was not likely to be light-limited in these large gaps (Denslow *et al.* 1990; Newell *et al.* 1993) but nevertheless showed no response to nutrient addition. Growth of stress-adapted species appears to be less plastic in response to increased resource availability than growth of species adapted to high resource levels (Chapin 1980; Bloom *et al.* 1985). Where light avail-



**Fig. 7** Growth responses of four *Miconia* species to fertilization (f). Relative growth rates (cm cm<sup>-1</sup> day<sup>-1</sup>). Within a species, treatments designated by different letters are significantly different ( $P < 0.05$ ).

ability is the primary limitation to growth in tropical moist forest, the species most likely to be able to take advantage of pulses in both light and nutrient availability are pioneer, high-light demanding species. In tropical as well as temperate studies, invasive or pioneer species respond more strongly in fertilization experiments than stress-adapted species (Harcombe 1977; Crick & Grime 1987; Denslow *et al.* 1987; Jackson & Caldwell 1989). Growth of high-light demanding species in large natural gaps is thus likely to be enhanced in comparison to shade-tolerant species both by increased light and by increased nutrient availability. For these species, large gaps are thus a rare and ephemeral but critical resource. High dispersal rates (Silman 1996), persistence of seed in the soil (Alvarez-Buylla & Garcia-Barrios 1991; Dalling *et al.* 1997) and highly plastic growth responses (Brokaw 1987; Denslow *et al.* 1990; Kitajima 1996) all contribute to the persistence of these species in tropical forests characterized by frequent, small canopy openings.

### Acknowledgements

We are grateful for assistance in the field by G. Chaverri, J. Alvarado and D. Brenes, and in the laboratory by D. Turner and G. Flattman. G. Xu helped with data analyses. The manuscript was improved by suggestions from S. DeWalt and A. J. Tabanez. We are grateful for the support of the US National Science Foundation (BSR 83-06923 and 86-05106).

### References

- Alvarez-Buylla, E.R. & Garcia-Barrios, R. (1991) Seed and forest dynamics: a theoretical framework and an example from the neotropics. *American Naturalist*, **137**, 133–154.
- Barton, A.M., Fetcher, N. & Redhead, S. (1989) The

relationship between treefall gap size and light flux in a Neotropical rain forest in Costa Rica. *Journal of Tropical Ecology*, **5**, 437–439.

- Becker, P., Rabenold, P.E., Idol, J.R. & Smith, A.P. (1988) Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology*, **4**, 173–184.
- Bellingham, P.J., Tanner, E.V.J., Rich, P.M. & Goodland, T.C.R. (1996) Changes in light below the canopy of a Jamaican montane rainforest after a hurricane. *Journal of Tropical Ecology*, **12**, 699–722.
- Bloom, A.J., Chapin, F.S. III & Mooney, H.A. (1985) Resource limitation in plants – An economic analogy. *Annual Review of Ecology and Systematics*, **16**, 363–392.
- Brokaw, N.V.L. (1982) The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica*, **14**, 158–160.
- Brokaw, N.V.L. (1985) Gap-phase regeneration in a tropical forest. *Ecology*, **66**, 682–687.
- Brokaw, N.V.L. (1987) Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology*, **75**, 9–20.
- Brown, N. (1993) The implications of climate and gap microclimate for seedling growth in a Bornean lowland rain forest. *Journal of Tropical Ecology*, **9**, 153–168.
- Burslem, D.F.R.P., Grubb, P.J. & Turner, I.M. (1995) Responses to nutrient addition among shade-tolerant tree seedlings of lowland tropical rain forest in Singapore. *Journal of Ecology*, **83**, 113–122.
- Burslem, D.F.R.P., Turner, I.M. & Grubb, P.J. (1994) Mineral nutrient status of coastal hill dipterocarp forest and adinandra belukar in Singapore: bioassays of nutrient limitation. *Journal of Tropical Ecology*, **10**, 579–599.
- Campbell, B.D. & Grime, J.P. (1989) A comparative study of plant responsiveness to the duration of episodes of mineral enrichment. *New Phytologist*, **112**, 261–267.
- Chapin, F.S. III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233–260.
- Chazdon, R.L. & Fetcher, N. (1984) Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology*, **72**, 553–564.
- Crick, J.C. & Grime, J.P. (1987) Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. *New Phytologist*, **107**, 403–414.
- Cuevas, E. & Medina, E. (1988) Nutrient dynamics within Amazonian forests. II. Fine root growth, nutrient availability and leaf litter decomposition. *Oecologia*, **76**, 222–235.
- Dalling, J.W., Swaine, M.D. & Garwood, N.C. (1997) Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama. *Journal of Tropical Ecology*, **13**, 659–680.
- Denslow, J.S. (1980) Gap partitioning among tropical rainforest trees. *Biotropica*, **12**, 47–55.
- Denslow, J.S. (1987) Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics*, **18**, 431–451.
- Denslow, J.S. & Hartshorn, G.S. (1994) Treefall gap environments and forest dynamic processes. *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (eds L.A. McDade, K. Bawa, H. Hespeneide & G.S. Hartshorn), pp. 120–127. University of Chicago Press, Chicago.
- Denslow, J.S., Newell, E.A. & Ellison, A.M. (1991) The effect of palms on growth and survival of tree seedlings in a rain forest understory. *Biotropica*, **23**, 225–234.
- Denslow, J.S., Schultz, J.C., Vitousek, P.M. & Strain, B.R. (1990) Growth response of tropical shrubs to treefall gap environments. *Ecology*, **71**, 165–179.
- Denslow, J.S., Vitousek, P.M. & Schultz, J.C. (1987) Bio-

- assays of nutrient limitation in a tropical rain forest soil. *Oecologia*, **74**, 370–376.
- Fetcher, N., Oberbauer, S.F. & Strain, B.R. (1985) Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *International Journal of Biometeorology*, **29**, 145–155.
- Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., Perera, G.A.D., Burslem, D.F.R.P., Ashton, P.M.S. & Ashton, P.S. (1997) Responses to nutrient addition among seedlings of eight closely related species of *Shorea* in Sri Lanka. *Journal of Ecology*, **85**, 301–311.
- Harcombe, P.A. (1977) The influence of fertilization on some aspects of succession in a humid tropical forest. *Ecology*, **58**, 1375–1383.
- Hartshorn, G.S. (1978) Tree falls and tropical forest dynamics. *Tropical Trees as Living Systems* (eds P.B. Tomlinson & M.H. Zimmerman), pp. 617–638. Cambridge University Press, Cambridge.
- Hartshorn, G.S. & Hammel, B.E. (1994) Vegetation types and floristic patterns. *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (eds L.A. McDade, K.S. Bawa, H.A. Hespenheide & G.S. Hartshorn), pp. 73–89. University of Chicago, Chicago.
- Hunt, R. (1978) *Plant Growth Analysis*. Arnold, London.
- Jackson, R.B. & Caldwell, M.M. (1989) The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials. *Oecologia*, **81**, 149–153.
- Keeney, D.R. & Nelson, D.W. (1982) Nitrogen – inorganic forms. *Methods of Soil Analysis Part 2. Chemical and Microbiological Properties* (eds A.L. Page, R.H. Miller & D.R. Keeney), pp. 643–698. American Society of Agronomy Inc., Madison.
- Kitajima, K. (1996) Cotyledon functional morphology, patterns of seed reserve utilization and regeneration niches of tropical tree seedlings. *Ecology of Tropical Forest Tree Seedlings* (ed. M.D. Swaine), pp. 245–266. Parthenon, Paris.
- Lodge, D.J., McDowell, W.H. & McSwiney, C.P. (1994) The importance of nutrient pulses in tropical forests. *Trends in Ecology and Evolution*, **9**, 384–387.
- Marrs, R.H., Thompson, J., Scott, D. & Proctor, J. (1991) Nitrogen mineralization and nitrification in terra firme forest and savanna soils on Ilha de Maraca, Roraima, Brazil. *Journal of Tropical Ecology*, **7**, 123–137.
- Matson, P.A., Vitousek, P.M., Ewel, J.J., Mazzarino, M.J. & Robertson, G.P. (1987) Nitrogen transformations following tropical forest felling and burning on a volcanic soil. *Ecology*, **68**, 491–502.
- Newell, E.A., McDonald, E.P., Strain, B.R. & Denslow, J.S. (1993) Photosynthetic responses of *Miconia* species to canopy openings in a lowland tropical rainforest. *Oecologia*, **94**, 49–56.
- Olsen, S.R. & Sommers, L.E. (1982) Phosphorus. *Methods of Soil Analysis Part 2. Chemical and Microbiological Properties* (eds A.L. Page, R.H. Miller & D.R. Keeney), pp. 403–430. American Society of Agronomy Inc., Madison.
- Ostertag, R. (1998) Belowground effects of canopy gaps in a tropical wet forest. *Ecology*, **79**, 1294–1304.
- Parker, G.G. (1985) *The effect of disturbance on water and solute budgets of hillslope tropical rainforest in north-eastern Costa Rica*. PhD thesis, University of Georgia, Athens, Georgia.
- Parsons, W.F.J., Knight, D.H. & Miller, S.L. (1994) Root gap dynamics in lodgepole pine forest: nitrogen transformations in gaps of different size. *Ecological Applications*, **4**, 354–362.
- Pregitzer, K.S., Hendrick, R.L. & Fogel, R. (1993) The demography of fine roots in response to patches of water and nitrogen. *New Phytologist*, **125**, 575–580.
- Rich, P.M. (1990) Characterizing plant canopies with hemispherical photographs. *Remote Sensing Reviews*, **5**, 13–29.
- Rich, P.M., Clark, D.B., Clark, D.A. & Oberbauer, S.F. (1993) Long-term study of solar radiation regimes in a tropical wet forest using quantum sensors and hemispherical photography. *Agricultural and Forest Meteorology*, **65**, 107–127.
- Ricklefs, R.E. (1977) Environmental heterogeneity and plant species diversity: a hypothesis. *American Naturalist*, **111**, 376–381.
- Runkle, J.R. (1985) Disturbance regimes in temperate forests. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White), pp. 17–34. Academic Press, Orlando.
- Sancho, M.F. & Mata, Ch.R. (1987) *Estudio detallado de suelos. Estacion Biologica 'La Selva'*. Organization for Tropical Studies, San Jose, Costa Rica.
- Sanford, R.L. Jr (1989) Fine root biomass under a tropical forest light gap opening in Costa Rica. *Journal of Tropical Ecology*, **5**, 251–256.
- Sanford, R.L. Jr (1990) Fine root biomass under light gap openings in an Amazon rain forest. *Oecologia*, **83**, 541–545.
- Sanford, R.L. Jr, Braker, H.E. & Hartshorn, G.S. (1986) Canopy openings in a primary neotropical lowland forest. *Journal of Tropical Ecology*, **2**, 277–282.
- Sanford, R.L. Jr, Paaby, P., Luvall, J.C. & Phillips, E. (1994) Climate, geomorphology, and aquatic systems. *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (eds L.A. McDade, K.S. Bawa, H.A. Hespenheide & G.S. Hartshorn), pp. 19–33. University of Chicago, Chicago.
- SAS Institute Inc. (1996) *The SAS System for Windows. Version 6.11*. SAS Institute Inc., Cary, NC.
- Scatena, F.N., Silver, W.L., Siccama, T., Johnson, A. & Sanchez, M.J. (1993) Biomass and nutrient content of the Bisley experimental watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. *Biotropica*, **25**, 15–27.
- Silman, M.R. (1996) *Regeneration from seed in a neotropical rain forest*. PhD thesis, Duke University, Durham, NC.
- Silver, W.L. (1994) Is nutrient availability related to plant nutrient use in humid tropical forests? *Oecologia*, **98**, 336–343.
- Silver, W.L., Scatena, F.N., Johnson, A.H., Siccama, T.G. & Watt, F. (1996) At what temporal scales does disturbance affect belowground nutrient pools? *Biotropica*, **28**, 441–457.
- Silver, W.L. & Vogt, K.A. (1993) Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. *Journal of Ecology*, **81**, 729–738.
- Sollins, P., Sancho, M.F., Mata, Ch. R. & Sanford, R.L. Jr (1994) Soils and soil process research. *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (eds L.A. McDade, K.S. Bawa, H.A. Hespenheide & G.S. Hartshorn), pp. 34–53. University of Chicago, Chicago.
- St John, T.V. (1983) Response of tree roots to decomposing organic matter in two lowland Amazonian rain forests. *Canadian Journal of Forest Research*, **13**, 346–349.
- Swaine, M.D. & Whitmore, T.C. (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio*, **75**, 81–86.
- Tanner, E.V.J., Kapos, V. & Franco, W. (1992) Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. *Ecology*, **73**, 78–86.
- Tanner, E.V.J., Kapos, V., Freskos, S., Healey, J.R. & Theobald, A.M. (1990) Nitrogen and phosphorus fertilization of Jamaican montane forest trees. *Journal of Tropical Ecology*, **6**, 213–238.
- Turner, I.M. (1991) Effects of shade and fertilizer addition

- on the seedlings of two tropical woody pioneer species. *Tropical Ecology*, **32**, 24–29.
- Turner, I.M., Brown, N.D. & Newton, A.C. (1993) The effect of fertilizer application on dipterocarp seedling growth and mycorrhizal infection. *Forest Ecology and Management*, **57**, 329–337.
- Uhl, C., Clark, K., Dezzio, N. & Maquirino, P. (1988) Vegetation dynamics in Amazonian treefall gaps. *Ecology*, **69**, 751–763.
- Veblen, T.T. (1992) Regeneration dynamics. *Plant Succession: Theory and Prediction* (eds D.C. Glenn-Lewin, R.K. Peet & T.T. Veblen), pp. 152–187. Chapman and Hall, London.
- Vitousek, P.M. (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, **65**, 285–298.
- Vitousek, P.M. & Denslow, J.S. (1986) Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *Journal of Ecology*, **74**, 1167–1178.
- Vitousek, P.M. & Sanford, R.L. Jr (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics*, **17**, 137–167.
- Whitmore, T.C. (1996) A review of some aspects of tropical rain forest seedling ecology with suggestions for further enquiry. *The Ecology of Tropical Forest Tree Seedlings* (ed. M.D. Swaine), pp. 3–39. UNESCO and Parthenon Publishing, New York.
- Young, T.P. & Hubbell, S.P. (1991) Crown asymmetry, tree-falls, and repeat disturbance of broad-leaved forest gaps. *Ecology*, **72**, 1464–1471.

Received 24 July 1997

revision accepted 8 January 1998