

Non-calling males were not measured in this study, but their effect on the mating success of calling males is probably small. Non-calling males might sneak into another male's territory and mate with local females. No non-calling males were found within 16 cm of a focal male, so this sneak-mating appears to be uncommon.

Future studies should investigate the importance of perches as a potentially limiting resource. Males in habitats with few high perches might have generally lower reproductive success than males in habitats with many high perches. Perch

availability may, therefore, limit the range of habitats in which *D. pumilio* can successfully reproduce.

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A COMPARISON OF PRIMARY AND SECONDARY FOREST GAPS IN A LOWLAND TROPICAL RAINFOREST

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Abstract. Gaps in the forest canopy caused by treefalls are an important process for regeneration in tropical forests. Because physical conditions as well as tree sizes and species are very different between secondary and primary forests, we hypothesized that gaps in secondary and primary forests would differ in structure, and that the soil in the two types of gap would differ in pH and soil moisture from the surrounding forest and between gaps. We found that at Estacion Biologica La Selva, gaps showed a greater range in size and number of fallen trees in the primary forest than in the secondary forest. We also found that soil pH and the proportion of moisture in the soil increased significantly with gap size. In the primary forest, gaps had a significantly lower pH and proportion of moisture in the soil than the surrounding forest, while secondary forest gaps did not show these differences. These results may have implications for nutrient cycling and forest regeneration differences in primary and secondary forest.

INTRODUCTION

The structure of primary tropical rain forests is greatly affected by treefalls and gap formation. At La Selva, Denslow and Hartshorn (1994) estimated that 75% of the 105 canopy tree species require gaps for regeneration. In order to understand the effects that gaps have upon forest communities it is important to understand the environmental conditions within a gap. These conditions are extremely different from the surrounding forest in terms of soil moisture, decomposition rates, and light levels.

Treefalls and their attendant gaps have been well studied within primary forests (Balsler et al. 1992, Denslow and Hartshorn 1994). However, the relative importance of treefalls and gap formation in secondary forests has received less attention. We predicted that size of the gaps, density of the gaps, and other physical characteristics would vary between primary and secondary forests. We also hypothesized that gap formation in primary and secondary forests would significantly affect soil moisture and pH level, because the nutrient cycling and forest structure may be different between these two forests. If these hypothesis are supported, this may suggest that species

regeneration is less in secondary forest than in primary forest due to a decrease in frequency and size of gaps.

METHODS

We conducted our study at the Organization for Tropical Studies Estacion Biologica La Selva. We sampled in primary and secondary forest along the Sendero Holdridge, and Lindero Occidental on 12 and 14 February 1995.

We sampled along 50 m transects, to a distance of 15 m on each side of the trail. To control for variations in topography, we eliminated low-lying riparian and steeply sloped sections of the trail. We surveyed all gaps in 45 transects, 23 in primary and 22 in secondary along approximately 9 km of trail.

We defined a treefall gap to be an area in the forest in which there was no canopy cover, a clearly identifiable fallen tree, and understory sapling growth no higher than 3 m. Through prior observations made on successional plots of known age, this sapling height was thought to be representative of vegetation < 2 years old.

For each gap, we took measurements of (1) length (through the center of the gap along the fallen tree or "gap-maker"), (2) width (perpendicular to the bole of the

gap-maker), (3) DBH of gap-maker, (4) total number of fallen trees (brought down by the gap-maker), and (5) number of uproots and snapped trunks. We sampled soils in the six gaps closest to the station, three in primary and three in secondary. For each gap we sampled from the center of the gap and from the surrounding forest, two gap radii from the first. At each point we took two grab samples after removing leaf-litter, 1 m apart.

Soil samples were later analyzed in the lab for pH and percent moisture content. pH was measured with a 2:1 water to soil solution, each sample was tested three times with a pH meter accurate to two decimal places and an average value was used for analysis. Soil samples were weighed, oven-dried for two hours 45 minutes, and re-weighed to calculate percent moisture content.

RESULTS

Gaps in the primary forest were larger than in secondary forests (Fig. 1) but the difference was not significant (U-statistic=3.00, $n_1, n_2=5, 3$, $p=0.180$). However, had we removed one non-representative outlier from the primary forest sample (38 m²), this difference would have been significant. We saw a similar trend for number of treefalls per gap with more treefalls per gap in the primary forest (Fig. 2), though this difference was not

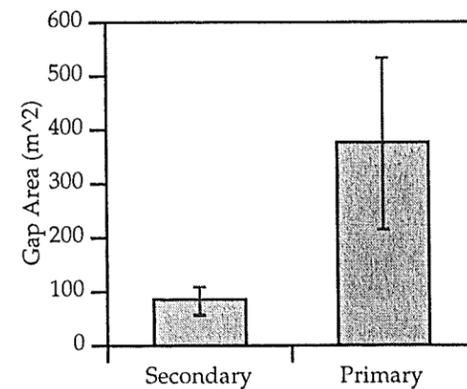


FIG. 1. Average gap area in secondary (n=3) and primary forests (n=5). Differences were not significant.

significant (U-statistic=2.50, $n_1, n_2=5, 3$, $P=0.195$). We found mostly uprooted trees in primary forest gaps (12 uproots, 5 snaps), whereas in secondary forest gaps were formed exclusively by four snaps.

We compared the pH of soils in secondary and primary forest gaps and forest under full canopy (Table 1). Of these comparisons, we found that soil under the primary forest canopy had a significantly higher pH than in primary forest gaps ($t=-2.95$, $df=5$, $P=0.032$, Fig. 3). We also found that as gap area increased, soil pH within these gaps also increased (Fig. 4). This relationship was significant ($R^2=0.492$, $df=1, 11$, $P=0.008$). All secondary soil (gap and surrounding forest samples combined) had a significantly higher pH than all primary forest soil sampled ($t=2.66$, $df=22$, $P=0.014$, Fig. 5).

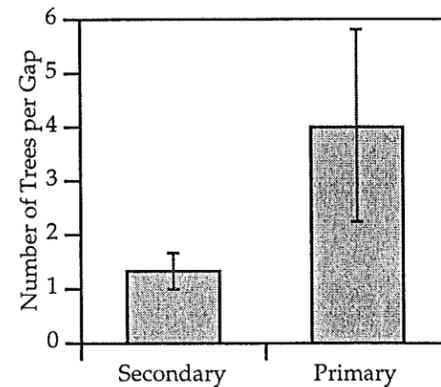


FIG. 2. Average number of trees per gap in secondary (n=3) and primary forests (n=5). Differences were not significant.

TABLE 1: Results of statistical comparisons of soil pH in gaps (G) and surrounding forest (F), in secondary (S) and primary (P) forests. Data are summarized - Figs. 3 and 5. * indicates significant difference

	t	df	P - value
SG v. SF	-0.40	5	0.722
PG v. PF	-2.95	5	0.032 *
SG v. PG	2.19	10	0.054
SF v. PF	1.58	10	0.144
G v. F	-1.96	11	0.075
S v. P	2.66	22	0.014 *

TABLE 2: Results of statistical comparisons of soil moisture in gaps (G) and surrounding forest (F), in secondary (S) and primary (P) forests. Data is summarized - Fig. 6.

	t	df	P - value
SG v. SF	-0.08	5	0.455
PG v. PF	-3.73	5	0.014 *
SG v. PG	2.11	10	0.061
SF v. PF	-0.28	10	0.784
G v. F	1.91	11	0.083
S v. P	0.94	22	0.358

* indicates significant difference

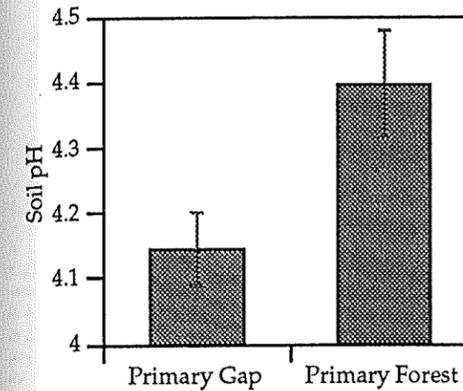


FIG. 3. Average soil pH in primary gaps (n=6) and the surrounding forest (n=6). Difference was significant (P=0.032).

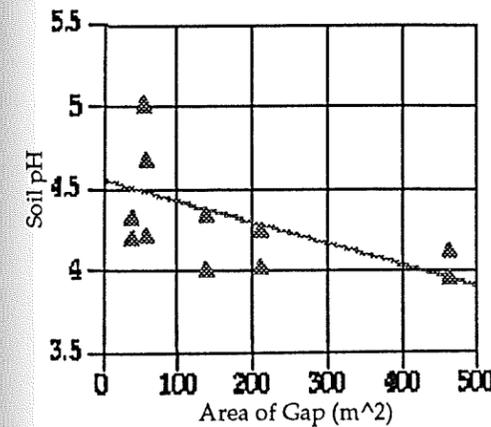


FIG. 4. Soil pH vs. gap area for primary and secondary forests combined ($R^2=0.49$, $n=12$, $P=0.008$).

We compared the proportion (arcsine transformed) of moisture in the soil of secondary and primary forest gaps and with that in intact forests (Table 2). Of these comparisons, we found that primary forest had a significantly higher moisture level in the soil than primary forest gap soil ($t=-3.73$, $df=5$, $P=0.014$, Fig. 6). We also found that as gap size increased, the

proportion of moisture in the soil also increased significantly ($R^2=0.517$, $df=1, 11$, $P=0.006$, Fig. 7). We found no significant difference in soil moisture level between all secondary and all primary forest samples.

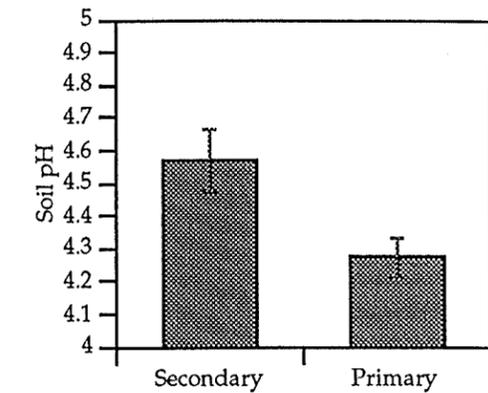


FIG. 5. Average soil pH in secondary (n=12) and primary (n=12) forest habitats (gap and surrounding forest combined). Difference was significant (P=0.014)

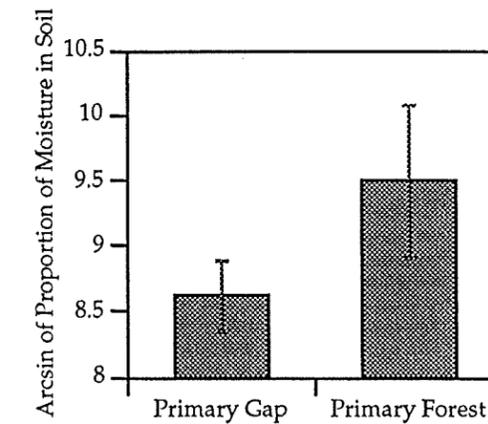


FIG. 6. Average of arcsines of the proportion of moisture found in soils of primary gaps (n=6) and the surrounding forest (n=6). Difference was significant (P=0.014).

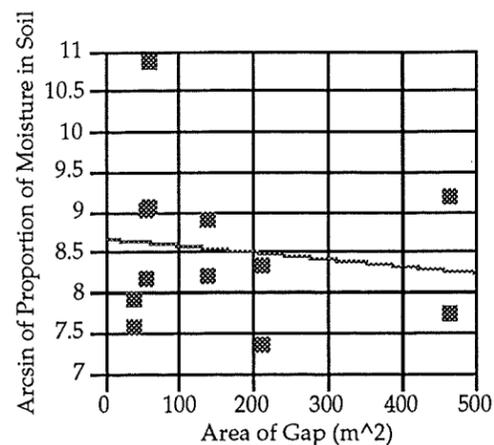


FIG. 7. Arcsines of the proportion of moisture in soil vs. the area of the gap in which the sample was taken ($R^2=0.517$, $n=12$, $P=0.006$).

DISCUSSION

Our results indicate that gaps in primary and secondary forests were different in both physical and chemical characteristics. The most obvious physical characteristic of a gap is its area. We found much larger gaps in primary than in secondary forest and gaps in primary forest generally had a larger number of treefalls. Gap size in primary forest ranged from small (38 m²), caused by only one tree, to large (952 m²), caused by greater than 10 treefalls. Secondary forests had a much smaller variation in area (range of 58 - 137 m²) and fewer numbers of treefalls. Although our sample size was not large enough to show this statistically, our observations also supported the idea that the number of gaps in primary forests was greater than in secondary forests.

The dynamics of treefalls in both forests also appeared to be different. Weaker wood, perhaps as a result of more fast-growing, early successional tree species, may have caused a greater proportion of snaps in secondary forest. Smaller secondary forest gaps generally appeared to have more canopy overhanging the gap than primary gaps of similar size and age.

Chemically, gaps in both forests were also very different. pH variation in soils may be caused by high nutrient uptake by roots, high decomposition rates, increased

exposure to sunlight, differing moisture inputs or a combination of these factors. The trend of lower pH of soils in gaps versus soils under the surrounding canopy in primary forest might be due to higher nutrient uptake in the gap. A high concentration of fast-growing pioneer trees may take up many more nutrients than trees in the surrounding forest. The trend of decreasing pH versus area in gaps of both forests supports this, as a larger gap in either forest would provide a better environment for these fast-growing trees. Larger gaps in primary forest had lower pH. These differences in pH levels therefore, are larger between primary forest and primary forest gaps than between secondary forest and secondary forest gaps. Potentially reduced levels of soil nutrients caused by past disturbance in secondary areas may cause higher pH levels.

We also found that primary forest gaps had less moisture than the surrounding forest, and larger gaps generally had less moisture than smaller gaps. Because we sampled surface soil, this could be due to greater evaporation rates caused by more direct sun exposure. Because high moisture content decreases decomposition rates by making the soils anoxic, this may in turn raise pH levels.

We found a higher density of gaps and larger differences between gaps and the surrounding forest in primary forests. These differences may allow primary gaps to be more important for regeneration than secondary forest gaps. Species that require gaps for regeneration will find few opportunities for recruitment in secondary forests after the initial large disturbance. These species therefore will recruit only in the initial stages of secondary succession and then again in the large gaps of the climax old growth or primary forest. Further quantification of the effects of gaps on soil quality and forest regeneration in both habitats would be useful. Additional study could also clearly quantify the effects of large-scale forest disturbances on pH and nutrient uptake.

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