

## Delimiting the gap phase in the growth cycle of a Panamanian forest

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**ABSTRACT.** Despite the importance of treefall gaps in tropical forest dynamics, few studies have followed gap-phase processes for more than 2 y. We monitored, for five years, the growth and survival of many seedlings of *Tetragastris panamensis* (Engler) O. Kuntze, *Protium panamense* (Rose) I. M. Johnston, and *Desmopsis panamensis* (Rob.) Saff. (three common tree species of the Panamanian tropical moist forest) in artificially created treefall gaps and under intact-canopy control plots. On these same plots, we also monitored light levels using hemispherical photographs taken over an 8-y period. Seedling height growth was faster in gaps than under intact canopies during the first 42 mo of regrowth, then declined to rates similar to those under intact canopies. Light levels in gaps similarly rose and fell, returning to pre-gap levels by month 48. Only *Tetragastris panamensis* showed higher survival in gaps, contrary to the general assumption that seedling survival is enhanced by gap creation. Our results document important transition points that mark the conclusion of the gap phase, suggesting an estimate of 4y for the duration of the gap phase in this tropical forest.

**KEY WORDS:** average daily global radiation, *Desmopsis*, gap phase regeneration, Panama, *Protium*, *Tetragastris*, treefall gap, tropical forest

### INTRODUCTION

Whitmore (1975) describes the tropical forest growth cycle as consisting of three phases: gap, building, and mature. Similarly, Oldeman (1978) describes ‘chablis’ (treefall) and ‘sylvigenesis’ (forest development) in the tropics. Both

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models postulate a dynamic, initial gap phase of rapid colonization and growth after a treefall. During the gap phase plants display rapid growth (e.g., Burton & Mueller-Dombois 1984, Denslow *et al.* 1990, Popma & Bongers 1988, Turner 1990), enhanced survival (e.g., Augspurger 1984, Brown & Whitmore 1992, Howe, 1990, Turner 1990, but see Schupp *et al.* 1989), and increased fruit production (Levey 1988, Smith 1987), thereby increasing their fitness. But for how long after gap creation do these benefits persist?

Answering this question of course requires relatively long-term studies. In spite of the vaunted importance of the gap phase (Hartshorn 1978, Whitmore 1975), surprisingly few studies have followed gap-phase processes in tropical forests for more than 2 y (exceptions are Brokaw 1985, 1987; Brown & Whitmore 1992, De Steven 1988, Kennedy & Swaine 1992, Uhl *et al.* 1988, van der Meer & Bongers 1996, Whitmore & Brown 1996). In this paper we describe the first 5 y of seedling growth and survival of three common tree species during the gap phase in a Panamanian forest. We acknowledge that even a 5-y study of three species is not adequate to the full task of understanding regrowth in gaps, yet our study does record a major transition in seedling growth in this period, and we also document a profound change in the gap light environment as regrowth proceeds. Our work documents important transition points that mark the conclusion of the gap phase. Thus we estimate that the gap phase occupies the first 4 y of the forest development cycle in this forest.

#### METHODS

The study was conducted on the Gigante Peninsula, Panama (9°N, 80°W), part of the Barro Colorado Nature Monument, administered by the Smithsonian Tropical Research Institute. Climate and soils are similar to those on Barro Colorado Island (BCI), 1 km to the north. Mean annual rainfall on BCI is 2616 mm, with a dry season from December to April (Rand & Rand 1982). BCI soils are mostly well-weathered oxisols, low in nitrogen, potassium and phosphorus (Leigh & Wright 1990). The Peninsula supports semi-evergreen tropical moist forest.

The three study species were selected because they are abundant representatives of the canopy (adults 20 m tall), midstorey (10–20 m), and understorey (4–10 m) tree growth forms, respectively (Welden *et al.* 1991). *Tetragastris panamensis* (Engler) O. Kuntze (Burseraceae) was the canopy tree, *Protium panamense* (Rose) I. M. Johnston (Burseraceae) the midstorey tree, and *Desmopsis panamensis* (Rob.) Saff. (Annonaceae) the understorey tree. The species are all in the non-pioneer (Swaine & Whitmore 1988) or shade-tolerant guild (juveniles commonly found under intact canopy). We refer to these species by their generic names.

Within the study area on the Peninsula, we located 56 canopy trees (of any species) that were accessible from trails and not near a treefall gap. From this pool of trees, we randomly selected five that would be felled to create gaps (our

'gap plots') and six that would serve as control plots (our 'intact-canopy plots'). We created the gap plots in July 1982, with no further treatment. Gap plot area was defined as the opening in the forest canopy, free of vegetation down to *c.* 2 m or less from the forest floor. Gap plots ranged in size from 138 to 368 m<sup>2</sup>, with a median size of 204 m<sup>2</sup>. The intact-canopy plots were each 12 m × 24 m (288 m<sup>2</sup>).

Just before gap creation, we uniquely tagged and measured the height of all seedlings (stems to 1 m tall) of the three species within each plot, excluding individuals in the cotyledon stage. We defined height as the vertical distance from the ground to the uppermost apical meristem. To re-find individual seedlings, we established a grid of 2 m × 2 m 'cells' within each plot. Data were collected from all cells within the plots, with two exceptions: (1) cells on the border of gap plots were excluded, and (2) in two intact-canopy plots with high densities of seedlings, 50% of the cells were selected in a stratified random manner for sub-sampling of the plots.

We revisited the plots four times (July 1983, July 1984, January 1986 and November 1987) over the next 64 mo to record height and survivorship of those trees initially tagged in July 1982, just prior to gap creation. When re-censusing, if we could not locate a particular tree, but its tag was found, we recorded it as dead. If we could not locate a tree nor its tag for two consecutive sampling dates, we recorded it as dead.

We used 180° hemispherical photographs of the forest canopy to estimate light availability in the plots. Photographs were taken over a 96-mo period, the first being taken in July, 1982 (the wet season), just prior to gap creation. Subsequent photographs were taken at various times during the wet seasons of 1983, 1984, 1986 and 1990. For purposes of graphing and analysis, all wet-season photographs were considered to have been taken in July. Photographs were taken at 0.6 m above the forest floor in 12 to 65 randomly-selected cells in each plot. We processed the photographs with the SYLVA program to determine an estimated average daily global radiation (ADGR) for each photograph (Becker *et al.* 1989). Although the use of ADGR may be inappropriate for studies of ecophysiology (*cf.* Whitmore *et al.* 1993), it is appropriate for comparisons of light levels among sites (Becker *et al.* 1989).

### *Analysis*

For each species, seedling growth in gaps was compared to growth under intact canopies by a Mann-Whitney test based on incremental growth (final minus initial height). Preliminary plots of the seedling height data in gaps showed a reduced rate of growth for all three species after month 42. The significance of this trend was tested for each species by comparing incremental growth (expressed as height increase per month) during the final sampling interval (months 42 to 64) to that of the two previous sampling intervals (months 12 to 42) by a Wilcoxon sign-rank test, with data paired by individual seedlings. This method produced a simple approximation of the inflection point

in the growth curves – that point at which the initial rapid growth began to decline.

To examine trends in light levels in gap plots, we used a repeated-measures ANOVA (SAS Institute Inc. 1989), which contrasted pre-gap with post-gap light levels. ADGR (the response light-level variable) values were log-transformed prior to analysis. The light data were not directly linked to the seedling data for analyses because light data were collected on dates different from seedling data, and, by month 42, most seedlings had grown above the height (0.6 m) at which the photographs were taken, making the light data less applicable to seedling growth.

We addressed seedling survival by two questions: (1) did the same proportion of seedlings survive until month 64 in gap and intact-canopy plots, and (2) did the shapes of the survivorship curves differ between gap and intact-canopy plots? Answering these questions required that the data be pooled across plots (all gap plots combined, all intact-canopy plots combined), and that each species be analyzed separately. The first question was answered with a two-way contingency table (dead vs. living and gap vs. intact canopy); the second question was answered with a log-rank test (Pyke & Thompson 1986; LIFETEST procedure, SAS Institute Inc. 1989).

#### RESULTS AND DISCUSSION

All three species grew faster in gap plots than in intact canopy plots (Figure 1;  $P = 0.0001$  for all species; *Tetragastris*  $n = 183$  in gaps and 566 in intact canopies; *Protium*  $n = 30$  and 56; *Desmopsis*  $n = 29$  and 87), a widely reported result (references above). This faster growth was no doubt related to the five-fold increase in ADGR 12 mo after gap creation (Figure 2). Growth in gap plots during the first interval was apparently not as rapid as in some later intervals (Figure 1), a lag due perhaps to necessary acclimatization (Oberbauer & Strain 1985) or to a severe El Niño drought in that period (Leigh *et al.* 1990).

*Protium* clearly grew faster than the other study species (Figure 1). Brokaw (1985) reported that *Protium* grows exceptionally fast in gaps for a species that is typically found under the intact canopy, and Welden *et al.* (1991) found that *Protium*'s diameter growth is greater than that of our other two study species.

The growth of the three species and light levels increased dramatically after gap creation. However, between 42 and 64 mo after gap creation, growth rates had levelled off to values similar to those under intact canopy (Figure 1). For all three species, incremental growth during the final sampling interval (months 42 to 64) was significantly less than that of the previous two intervals (Figure 1;  $P = 0.0001$  for all species), indicating that the rapid growth rate resulting from gap creation diminished after month 42. Diminishing ADGR in the gap plots (Figure 2) may explain the diminished growth rates: after 48 mo light levels at 0.6 m above ground had returned to values resembling those before gap creation (Figure 2; contrasts of pre-gap ADGR to months 12 and 24,

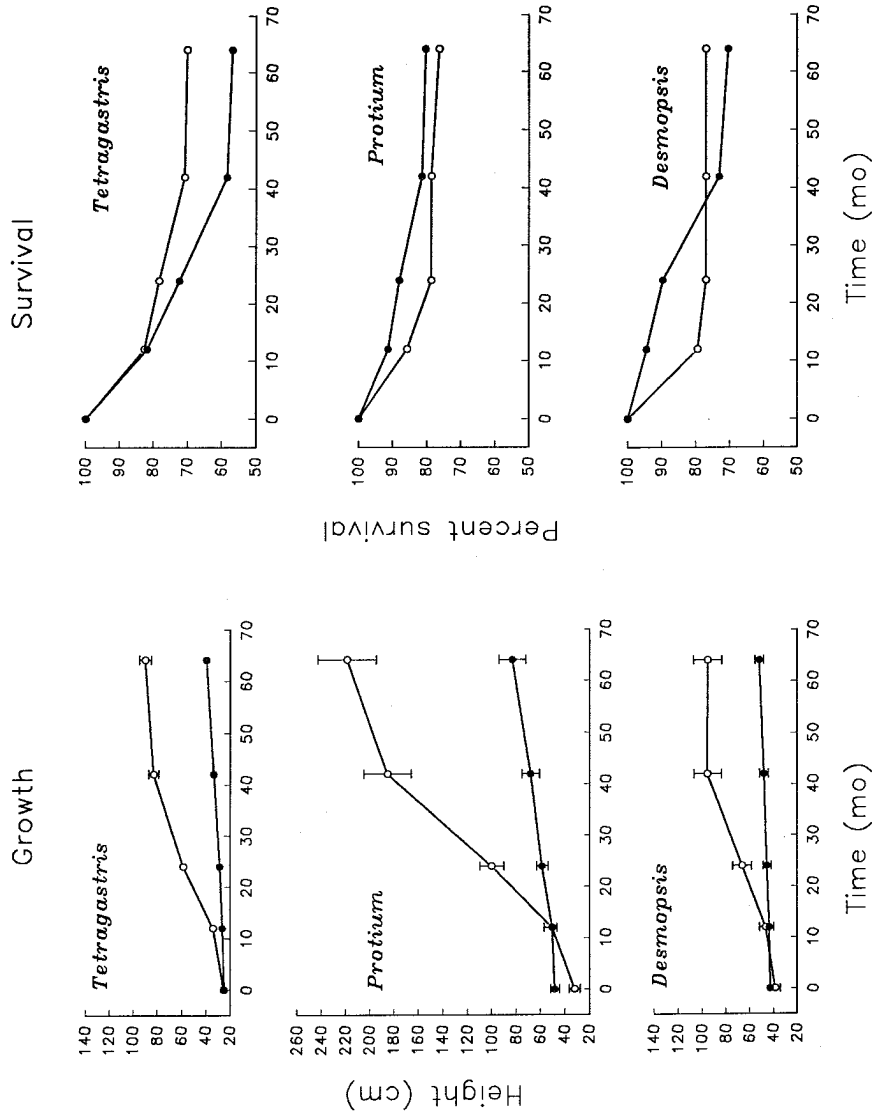


Figure 1. Growth and survival for seedlings of the three species in treefall gap (○) and intact-canopy (●) plots over a 64-mo period in a Panamanian forest. Survival percentages are from data pooled across all gap and all intact-canopy plots. All three species grew significantly faster in gap plots; *Tetragastris* was the only species to show a significant difference in survival between gap and intact-canopy plots. Error bars represent  $\pm$  SE; some error bars were too small to display.

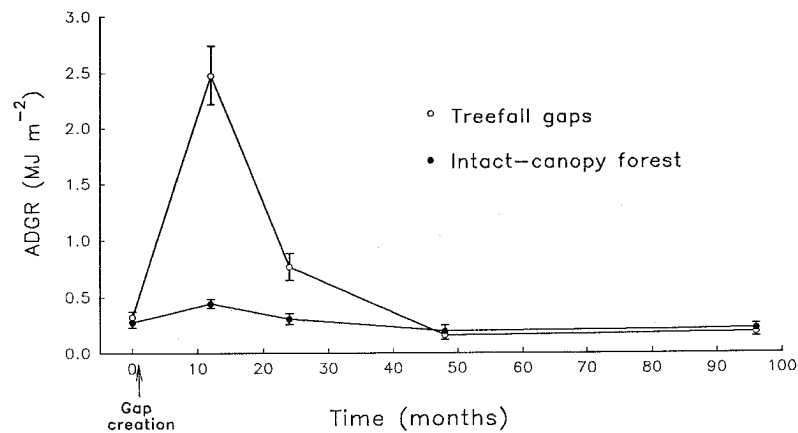


Figure 2. Changes in average daily global radiation (ADGR expressed in MJ m<sup>-2</sup>) in treefall gap and intact-canopy plots over a 96-mo period in a > Panamanian forest. Gap creation caused a > five-fold increase in ADGR at month 12. The elevated ADGR at month 12 in intact-canopy plots is likely the result of an El Niño drought at that time. Error bars represent  $\pm 2$  SE.

$P = 0.0001$ ; to months 48 and 96,  $P \gg 0.05$ ). Declining ADGR at this height is likely the result of the vertical regrowth of seedlings and saplings, as well as the lateral ingrowth of surrounding trees (Denslow & Hartshorn 1994).

After 64 mo a higher proportion of *Tetragastris* seedlings had survived in gap plots (70.1%) than in intact canopy plots (56.8%;  $\chi^2 = 16.68$ ,  $df = 1$ ,  $P = 0.001$ ,  $n = 1428$ ), and the shapes of its survivorship curves differed significantly between gap and intact canopy plots (log-rank test,  $\chi^2 = 14.20$ ,  $df = 1$ ,  $P = 0.0002$ ; Figure 1), also indicating higher survival in gaps. Neither of the other species showed significant differences in proportions surviving in gap vs. intact-canopy plots (*Desmopsis*, 76.9 vs. 71.1%;  $\chi^2 = 0.51$ ,  $df = 1$ ,  $P = 0.48$ ,  $n = 167$ ; *Protium*, 76.2 vs. 80.3%;  $\chi^2 = 0.27$ ,  $df = 1$ ,  $P = 0.60$ ,  $n = 123$ ), or differences in the shapes of their survivorship curves between plot types (log-rank test, *Desmopsis*  $\chi^2 = 0.85$ ,  $df = 1$ ,  $P = 0.36$ ; *Protium*  $\chi^2 = 0.48$ ,  $df = 1$ ,  $P = 0.49$ ; Figure 1).

We had predicted that high survivorship would have been maintained in gap plots for some time after gap creation, later dropping off as the canopy closed. This predicted drop-off, analogous to the inflection point in the growth curves, would mark the conclusion of the gap phase. For example, Brokaw (1985) found that sapling densities began to decrease (reflecting mortality) 3–6 y after gap formation. Contrary to our prediction, the survivorship curves showed no such trend (Figure 1), nor was survival enhanced by gap creation for two of the species under study. Our results for these two species contradict the general assumption that seedling survival is initially enhanced in treefall gaps (references above). The especially high mortality just after gap creation may have been caused by exposure, exacerbated by the El Niño drought. It was not the result of seedlings being crushed by the felled tree, as only 1% of the seedlings in gap plots died from crushing.

The diminished growth that began for all three species at month 42, coupled

with the return of ADGR values to pre-gap levels by month 48, suggests a gap longevity of roughly 4 y. We recognize that this estimate is based on growth data from only three species and light data collected from only one height (0.6 m). Rapid growth rates of pioneer species, for instance, might persist longer than those of the shade-tolerant species studied here, and estimates of the time required for light levels to return to their pre-gap levels might have been longer if photographs had been taken at higher than 0.6 m. (However, we feel that it is informative to focus on the lower strata of the forest, as many of the important effects of gap creation – rapid seedling growth, recruitment, and herbaceous plant dynamics – are manifest there.) Also, gap closure rate is no doubt a function of gap area, meaning that our estimate may apply only to gaps similar in size to those studied here (median of 204 m<sup>2</sup>). Further, we recognize that the gap phase does not end at one discrete point – its effects likely diminish asymptotically over time as the gap closes.

With these limitations in mind, we will point out that our estimate of gap longevity generally corroborates previous studies that addressed – either implicitly or explicitly – canopy closure in tropical forests. Brokaw (1987) showed that recruitment by pioneer trees in large gaps on BCI generally ends by 5 y after gap creation, and sapling densities start to decline at 3–6 y. De Steven (1988) and Kennedy & Swaine (1992) reported rapid growth increases of seedlings in gaps, followed by decline at 55 mo and 24 mo, respectively. Using our same gap plots and sampling periods, Smith *et al.* (1992) found that the number of flowering or fruiting herbaceous plants increased steadily for 2 y after gap formation, then dropped. Van der Meer & Bongers (1996) explicitly address canopy gap closure, and suggest that small canopy gaps in French Guiana close 5–6 y after creation, based on canopy openness determined from hemispherical photographs. Yavitt *et al.* (1995) found that gaps closed from ingrowth by 31 mo after gap creation, although the gaps they studied (89–159 m<sup>2</sup>) were much smaller than ours.

Several studies in the tropics (Jans *et al.* 1993, Van der Meer & Bongers 1996, see reviews in Denslow 1987, Hartshorn 1990) have estimated that each year roughly 1% of forest area is converted to treefall gaps, suggesting a 100-year forest turnover time (years required for gaps to have formed throughout a given area). Using a 1% gap-creation rate and our process-based, 4-y estimate of gap longevity, one would predict that at any given time, 4% of a forest area would be occupied by gaps, an estimate only slightly less than actual measurements of 4.3% (Yavitt *et al.* 1995), 5% (Uhl *et al.* 1988), 5.1% (Hartshorn 1978), 6.3% (Sanford *et al.* 1986), and 7.3% (Lang & Knight 1983) in the tropics. The percent of forest occupied by gaps is of course sensitive to one's definition of gap (Brokaw 1982, Popma *et al.* 1988), making a direct comparison of these percentages difficult.

### Conclusions

This paper describes one of the few longitudinal studies of gap-phase processes in a tropical forest. The principal results were: (1) height growth of

seedlings of three common tree species was faster in gaps than under intact canopy during the first 42 mo of regrowth, then declined to rates similar to those under intact canopy; (2) ADGR values at 0.6 m above ground in gaps similarly rose and fell, returning to pre-gap levels by month 48; and (3) only the canopy tree *Tetragastris* showed higher survival in gaps, and survival curves revealed little about gap longevity.

Our results and those stated or implied in previous studies of gaps similar in size to ours seem to converge on an estimate of 4–6 y for the duration of the gap phase in tropical forests. The gap phase is characterized by increased seedling growth, recruitment, fruit production, and, in some cases, survival. Thus the fitness conferred on individuals exposed to a gap increases substantially as the result of a relatively brief and ephemeral episode. In this sense, the brevity of the gap phase belies its importance in the overall forest growth cycle.

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