# HABITAT AND PREDATION EFFECTS ON SEEDLING SURVIVAL AND GROWTH IN SHADE-TOLERANT TROPICAL TREES

Jane Molofsky[1,2] and Brian L. Fisher[3]

The diversity of trees in the forest canopy depends on the successful recruitment of seedlings into the canopy. Tree species that become established as seedlings beneath an undisturbed canopy have been termed "shade-tolerant" (Canham 1989) or "climax" species (Swaine and Whitmore 1988). This is in contrast to "pioneer" species, which can germinate or establish only in the high light conditions of large canopy openings (Swaine and Whitmore 1988). In shade-tolerant species, survival may depend more on biotic factors than on abiotic factors. Therefore, susceptibility to predation can be more important than differences in habitat for determining the survival of these species.

In the present study we compare the survival of seedlings in tree-fall gaps and in closed forest understory sites for three shade-tolerant tropical tree species. We also assess the importance of mammalian predation and determine how it varies among species and among habitats. Finally, we analyze the relationship between seedling growth rates and their susceptibility to predation.

## Study Site and Methods

The study was conducted in the seasonal moist tropical forest of Barro Colorado Island, Panama (BCI; 9°10' N, 79°51' W). Extensive descriptions of the forest can be found in Croat (1978) and Leigh et al. (1982). The study species *Gustavia superba* (HBK.) Berg (Lecythidaceae), *Virola surinamensis* (Rol.) Warb. (Myristicaceae), and *Aspidospermum cruenta* Woods. (Apocynaceae) have been described as shade-tolerant because their seedlings grow and survive in the forest understory (Augspurger 1984, Howe et al. 1985, Sork 1987). *Gustavia* is a small understory tree that occurs commonly on BCI; of the three species, it produces the largest seeds (6.9 g; Molofsky and Augspurger 1992). *Virola* is a large canopy tree that most often occurs in

[1] Department of Plant Biology, University of Illinois, Urbana, Illinois 61801 USA.
[2] Present address: Botany Department, Duke University, Durham, North Carolina 27706 USA.
[3] Division of Insects, Field Museum of Natural History, Chicago, IL 60605 USA.

moist environments on BCI. It produces numerous large seeds (1.8 g; Molofsky and Augspurger 1992). *Aspidospermum* is a large canopy tree that is rare on BCI. It produces large seeds (0.7 g) that are wind dispersed (Molofsky and Augspurger 1992).

We conducted a multifactorial experiment with habitat (gap and understory), mammalian predation, and block as the main effects. Seeds of each species were planted in a growth house and grown for 3 mo prior to transplanting. Seedlings of each species were then planted into each of four gap and four understory sites. The gaps were 1–3 mo old and ranged from 50 to 150 m². Our gap sizes were comparable to the average gap size at a Costa Rican rain forest and gap sizes reported from Amazonia (Hartshorn 1978, Uhl et al. 1988). An understory site was haphazardly located within 10–15 m of each gap site to minimize soil differences. Canopy openness was characterized with high-contrast hemispherical canopy photographs taken with an 8-mm f 2.8 fisheye lens placed in one central location within each gap and understory site at seedling height on 11 November 1986, 3 mo after the seedlings were planted. Canopy openness was the proportion of the canopy open to the sky (presented as percentage of skylight) and was determined from the photographs using the automated computer program of Becker et al. (1989). Canopy openness ranged between 2.6 and 7.0% ($\bar{X} \pm$ 1 sd = 4.9 $\pm$ 1.77%, $n$ = 4) in the gaps and 0.2 and 0.7% (0.4 $\pm$ 0.2%, $n$ = 4) in the understory sites. Our canopy openness measurements for gap and understory sites were comparable to a similar study on BCI (Howe 1990).

At each gap and understory site, two adjacent 5 × 5 m plots were set up. Five seedlings of each species were transplanted into the plots. Within each plot the species were intermixed at random to control for possible edge effects. At each site one plot was surrounded by a 1 m high wall of hardware cloth (mesh size: 6.25 cm²) with the top left open. The exclosures were dug 6 cm into the ground and they remained intact throughout the experiment. The exclosure design allowed access to the seedlings by insects, but minimized herbivory by medium and large-sized mammals. Common mammal predators on BCI include agoutis (*Dasyprocta punctata*), pacas (*Agouti paca*), collared peccaries (*Tayassu tajacu*), coatis (*Nasua narica*), and deer (*Odocoileus virginiana* and *Mazama americana*). Smaller and more agile mammal predators may be capable of climbing the 1 m high exclosure, such as red-tailed squirrels (*Sciurus granatensis*) and spiny rats (*Proechimys centralis*). The open-topped exclosures did not provide protection from falling debris, known to be an important mortality agent (Clark and Clark 1989). In the gap sites, seedlings were planted in the most open area so that they had no shrub or sapling canopies over

**NOTES AND COMMENTS**

them. Seedling mortality within 1 wk of transplanting was considered to be due to transplanting, and such seedlings were replaced. Mortality after this point was considered a treatment effect. An estimate of insect damage to the seedlings was determined by recording the number of seedlings that exhibited damaged or missing parts of leaves. This results in an underestimate of insect damage because seedlings that were completely defoliated or removed were not included in our estimate of insect damage.

Height, leaf length, and leaf number were recorded for each seedling at the start of the experiment. Seedling height, leaf length, and leaf number were recorded at 9 mo. For each species, four leaves taken from each of five seedlings were measured with a leaf-area meter. Regressions of leaf area × leaf length were significant for all three species ($r^2 = 0.74$, $r^2 = 0.92$, and $r^2 = 0.81$ for *Gustavia*, *Virola*, and *Aspidospermum*, respectively). These regressions were used for nondestructive estimates of the total leaf area for each plant from leaf lengths measured in the field.

We monitored survivorship at 3-mo intervals over the course of the 12-mo study. This allowed us to distinguish between mortality that was caused by falling debris and mortality that was caused by predation. If falling debris caused mortality, we expected that signs of the debris would be present. During the 12-mo study we found no evidence of seedlings dying as a result of fallen debris. The number of seedlings that survived for 12 mo was analyzed using a log-linear model (SAS 1987) in which the number of seedlings surviving was analyzed as a function of the species, habitat, protection, and block treatments. Planned contrasts were performed to determine significant differences in species response to the protection treatment (SAS 1987). To determine if protection changed the relative survival among species, we performed pairwise interspecific comparisons using planned-contrast statements within each protection treatment (SAS 1987). Because of the low survival in unprotected plots, growth was analyzed only for the protected plots. We performed an analysis of variance on final stem height and final estimated leaf area using initial height and leaf area as covariates.

### Results

*Survival.* Natural levels of survival differed among the three species. The survival results are pooled from gap and understory sites because survival did not differ between habitats (Table 1). Seventy-eight percent of the *Aspidospermum* seedlings survived, compared to 30% and only 3% for *Gustavia* and *Virola*, respectively (Fig. 1).

In both habitats, exclosures significantly increased survival of *Gustavia* seedlings ($x^2 = 9.0$, df = 1, $P = .0027$) and *Virola* seedlings ($x^2 = 17.7$, df = 1, $P =$

TABLE 1. Maximum likelihood analysis of variance for the seedling survival data of three shade-tolerant tree species in Panama, showing the main effects and two- and three-way interactions.*

| Effect | df | $x^2$ | $P$ |
|---|---|---|---|
| Species | 2 | 24.8 | .00001 |
| Habitat | 1 | 2.3 | NS |
| Protection | 1 | 20.2 | .00001 |
| Block | 3 | 4.5 | NS |
| Sp. × Habitat | 2 | 0.3 | NS |
| Sp. × Protection | 2 | 1.7 | NS |
| Sp. × Block | 6 | 12.4 | .0586 |
| Hab. × Protection | 1 | 0.1 | NS |
| Hab. × Block | 3 | 3.8 | NS |
| Sp. × Hab. × Prot. | 2 | 2.3 | NS |
| Sp. × Prot. × Blk. | 6 | 5.6 | NS |
| Sp. × Hab. × Blk. | 6 | 7.3 | NS |
| Hab. × Prot. × Blk. | 3 | 0.6 | NS |
| Likelihood ratio | 9 | 3.5 | .9421 |

* Model is run with all two-way and three-way interactions. Likelihood ratio is nonsignificant indicating that the model is a good fit to the data.

.0001) but did not significantly affect *Aspidospermum* seedlings although they followed the same trend (Fig. 1). In protected plots 90% of the *Aspidospermum* seedlings survived, compared to 80% of the protected *Gus-*
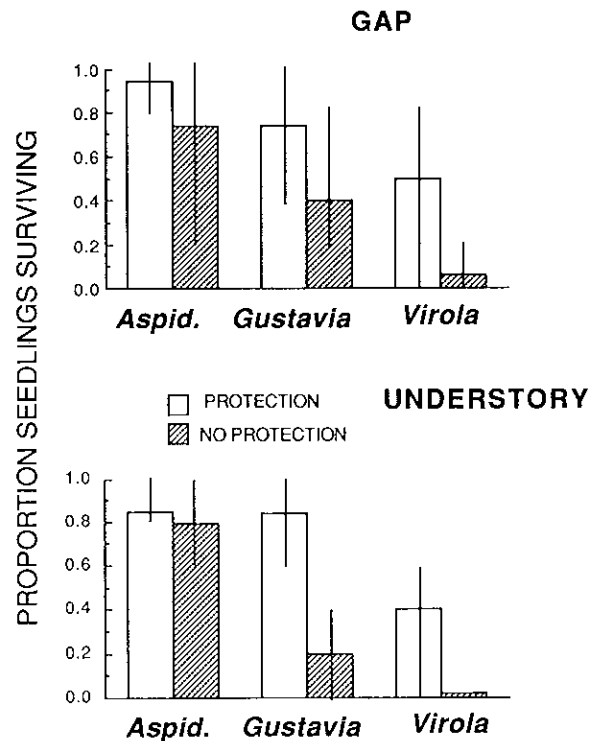


FIG. 1. Proportion of seedlings surviving (out of 20 initial seedlings) for each of three shade-tolerant tree species over 12 mo, with and without exclosures, in gap and understory sites at Barro Colorado Island, Panama. Vertical lines indicate the maximum and minimum values for each block within a treatment. *Aspid.* = *Aspidospermum*.
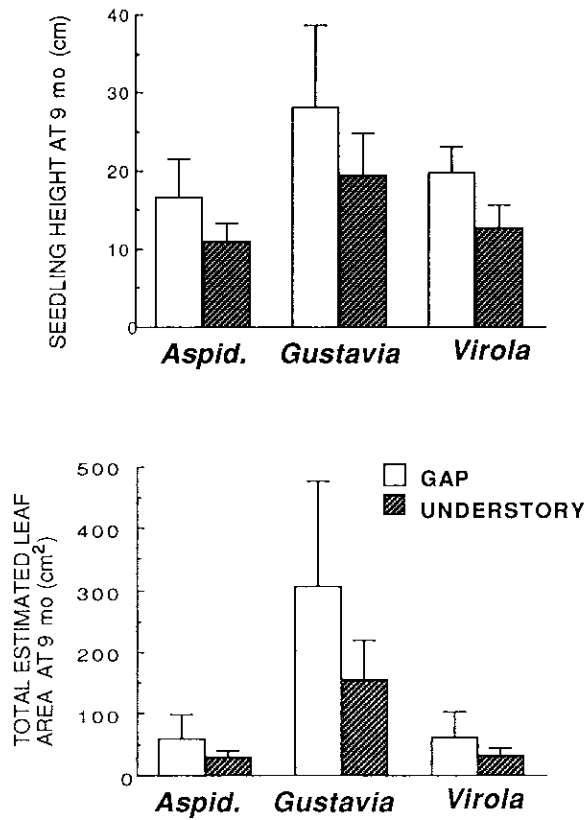
FIG. 2. (top) Final seedling height for each tropical tree species at 9 mo after planting. (bottom) Estimated total leaf area for each species at 9 mo after planting. Data show mean and 1 SD. *Aspid.* = *Aspidospermum*.

*tavia* seedlings and only 45% of the protected *Virola* seedlings.

The species × protection interaction was not significant (Table 1). Irrespective of treatment, survival of seedlings was highest in *Aspidospermum* and lowest in *Virola*. There was no interaction between habitat and protection (Table 1). There was a significant species × block interaction that was due to *Aspidospermum* having higher mortality in one of the blocks (Table 1, Fig. 1).

Interspecific comparisons done separately for the protected and unprotected plots indicate whether the protection treatment changed the relative success of the different species. Both *Aspidospermum* and *Gustavia* had a higher proportion of seedlings surviving than *Virola* in both the protected and unprotected plots ($\chi^2 = 10.9$, df = 1, $P = .0009$ and $\chi^2 = 17.3$, df = 1, $P = .00001$ for the comparison of *Aspidospermum* vs. *Virola* for the protected plots and the unprotected plots, respectively, and $\chi^2 = 8.1$, df = 1, $P = .0045$ and $\chi^2 = 5.6$, df = 1, $P = .0185$ for the comparison of *Gustavia*

vs. *Virola* for the protected plots and the unprotected plots, respectively). Protection changed the relative success of *Aspidospermum* and *Gustavia*. In the protected plots there was no significant difference in seedling survival between *Aspidospermum* and *Gustavia* seedlings; however, in the unprotected plots *Aspidospermum* survival was significantly higher than *Gustavia* ($\chi^2 = 7.1$, df = 1, $P = .0076$). In addition, 12% of *Gustavia* seedlings were damaged by mammalian predators, but resprouted. Survivorship differences among species in the protected and unprotected plots allow us to assess the importance of mammalian predation relative to other forms of mortality for these three species. Mammalian predation accounted for an increase in mortality of 10%, 58%, and 45% for *Aspidospermum*, *Gustavia* and *Virola*, respectively.

Insect damage differed significantly among species (ANOVA, $F = 5.1$, df = 2,40, $P = .0120$), primarily because damage was lower in *Aspidospermum* (17%) than in either *Gustavia* (58%) or *Virola* (60%). The proportion of insect-damaged plants did not differ between habitats and treatments or among different blocks.

*Growth.* Habitat significantly affected height of the three species at 9 mo (ANOVA, $F = 10.8$, df = 1,80, $P = .0001$). Seedlings of all species were on average 30% taller in the light gaps than in the understory (Fig. 2). The covariate, initial seedling height, explained a significant amount of the variation in the final seedling height (ANOVA, $F = 101.8$, df = 1,80, $P = .0001$).

Habitat also affected the amount of leaf area produced (ANOVA, $F = 20.9$, df = 1,78, $P = .0001$). Gap-grown plants produced more leaf area than understory plants (Fig. 2). Species differences were not significant, but the species × habitat interaction was significant (ANOVA, $F = 6.1$, df = 2,78, $P = .0036$). *Aspidospermum* (ANOVA, $F = 10.6$, df = 1,78, $P = .0030$) and *Gustavia* (ANOVA, $F = 17.4$, df = 1,78, $P = .0002$) produced significantly more leaf area in gaps, but the difference was not significant in *Virola* because of the smaller sample size caused by the overall higher mortality. The high variability in leaf area in gaps caused a significant habitat × block interaction (ANOVA, $F = 4.8$, df = 3,78, $P = .0040$), but no one gap consistently produced greater leaf area than the others. The covariate, initial differences in leaf area for the three, removed a significant amount of the variation among the species (ANOVA, $F = 50.8$, df = 1,78, $P = .0001$).

## Discussion

Canopy gaps are known to be important for the growth and reproduction of many tropical trees (Hartshorn 1978, Brokaw 1985). Higher light levels and soil moisture (Chazdon and Fetcher 1984, Vitousek and

Denslow 1986) enhance growth in gaps (Fetcher et al. 1983, Uhl et al. 1988). In this study, gap-grown plants grew taller and produced more leaf area than did their understory counterparts. Enhanced growth, however, did not translate into increased seedling survivorship—at least through the first year of life. High levels of post-germination seedling predation was a more important determinant of seedling survivorship than was light level. A previous study of *Gustavia* seedlings on BCI showed that mammalian predation on seedlings was more important than light conditions in determining seedling density (Sork 1987). Earlier studies on seedlings of *Virola* and *Dipteryx panamensis,* another large-seeded tree species, found seedling survival was greater in gaps than in the understory (De Steven and Putz 1984, Howe 1990). For *Virola,* increased survival in gaps was attributed to faster growth rates, which resulted in greater root growth and thus reduced the vulnerability to desiccation during the dry season (Fisher et al. 1991). Survivorship of *Virola* seedlings was correlated to small differences in canopy openness (Howe 1990). Although we found no difference in *Virola* survival among gaps, small differences in canopy openness within gaps may affect survival of the *Virola* seedlings. Longer-term studies are needed to determine whether gaps confer an advantage in survival for these species after the first year of life.

Our study was designed to monitor seedling survival after seed predation and early seedling predation had occurred. Both *Gustavia* and *Virola* are known to suffer high predation levels at the seed and early seedling stage (Howe et al. 1985, Sork 1987). Even at a later stage, predation was an important component of mortality during the first year of seedling life for *Gustavia* and *Virola* but not for *Aspidospermum.* The high level of mortality for established seedlings experienced by unprotected *Gustavia* and *Virola* seedlings is consistent with levels found for other studies of *Gustavia* and *Virola* (Sork 1987, Howe 1990). Mammalian predation levels on BCI may be higher than other seasonal tropical forests because the extinction of the large felids on BCI has resulted in an abundance of herbivorous mammals (Glanz 1990). Levels of seed-eating predators, such as agoutis, paca, and coatis, are more than 10 times greater on BCI than on a similar area of forest at Cocha Cashu, Peru, a forest located at a similar latitude and experiencing similar levels of annual rainfall (Terborgh 1988). These high levels of seed and seedling predators may have significant effects on the abundance of large-seeded tree species in the forest. Two large-seeded tree species, *Gustavia superba* and *Dipteryx panamensis,* were shown to suffer higher seed and seedling predation rates on BCI than on the adjacent mainland peninsula (De Steven and Putz 1984, Sork 1987). Top carnivores are still present on the mainland and thus the mainland is assumed to have lower densities of seed- and seedling-eating predators. Predation levels on BCI appeared uniformly distributed among habitats and locations. The three species experienced similar predation levels in both habitats. Important differences are likely to exist among species, especially if different predators are specializing on different species. Seeds and early seedling predation was higher in gaps than in the understory for *Welfii georgii* seeds (Schupp and Frost 1989) and for seeds and 2-wk-old seedlings of *Faramea occidentalis* (Schupp 1988). Lower survival in light gaps was attributed to a higher concentration of rodent activity within tree-fall gaps (Schupp 1988).

Species differed in their susceptibility to mammalian predation. *Virola* seedlings experienced the highest level of mortality overall, but were equally affected by mammalian predation and other forms of mortality such as insect damage. *Gustavia* was the most susceptible to mammalian predation. Several characteristics may make *Gustavia* seedlings more likely to be eaten. *Gustavia* has the largest seed, and produced the tallest seedlings and the most leaf area. Its leaves are thinner than the other two species (J. Molofsky, *personal observation*). *Aspidospermum* seedlings had the highest survival rates and were particularly resistant to mammalian mortality and insect damage. Leaves of *Aspidospermum* saplings produce tough leaves that contain relatively high levels of secondary defensive compounds (Coley 1983).

Early differences in seedling removal by predation can affect species' relative abundances within the forest. In the absence of predation the proportion of *Gustavia* and *Aspidospermum* seedlings surviving did not differ significantly. However, in the presence of predation more *Aspidospermum* seedlings survived than did *Gustavia.* Differences in the abundance of mammalian seed and seedling predators may result in a change in the species composition of similar forests. The fragmentation of forests into "islands" too small to support populations of carnivorous mammals may result in forests of different areas having very different floristic compositions (Terborgh 1988).

*Literature Cited*

Augspurger, C. K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. Journal of Ecology 72:777–795.

Becker, P., D. W. Erhart, and A. P. Smith. 1989. Analysis of forest light environments. Part I. Computerized estimation of solar radiation from hemispherical canopy photographs. Agricultural and Forest Meteorology 44:217–232.

Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. Ecology 66:682–687.

Canham, C. D. 1989. Different responses to gaps among shade-tolerant tree species. Ecology 70:548–550.

Chazdon, R. L., and N. Fetcher. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. Journal of Ecology 72:553–564.

Clark, D. B., and D. A. Clark. 1989. The role of physical damage in the seedling mortality regime of a neotropical rainforest. Oikos 55:225–230.

Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecological Monographs 53:209–233.

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, California, USA.

De Steven, D., and F. E. Putz. 1984. Impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis*, in Panama. Oikos 43:207–216.

Fetcher, N., B. R. Strain, and S. F. Oberbauer. 1983. Effects of light regimes on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. Oecologia (Berlin) 58:314–319.

Fisher, B. L., H. F. Howe, and S. J. Wright. 1991. Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understory. Oecologia (Berlin) 86:292–297.

Glanz, W. E. 1990. Neotropical mammal densities: How unusual is the community on Barro Colorado Island, Panama? Pages 287–313 *in* A. H. Gentry, editor. Four neotropical rainforests. Yale University Press, New Haven, Connecticut, USA.

Hartshorn, G. S. 1978. Tree falls and tropical forest dynam-

ics. Pages 617–632 *in* P. B. Tomlinson and M. H. Zimmerman, editors. Tropical trees as living systems. Cambridge University Press, London, England.

Howe, H. F. 1990. Survival and growth of juvenile *Virola surinamensis* in Panama: effects of herbivory and canopy closure. Journal of Tropical Ecology 6:259–280.

Howe, H. F., E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). Ecology 66:781–791.

Leigh, E. G., Jr., A. S. Rand, and D. M. Windsor, editors. 1982. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C., USA.

Molofsky, J., and C. K. Augspurger. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73:68–77.

SAS. 1987. SAS/STAT guide for personal computers. Version 4 edition. SAS Institute, Cary, North Carolina, USA.

Schupp, E. W. 1988. Seed and early seedling predation in the forest understory and treefall gaps. Oikos 51:71–78.

Schupp, E. W., and E. J. Frost. 1989. Differential predation of *Welfia georgii* seeds in treefall gaps and the forest understory. Biotropica 21:200–203.

Sork, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. Ecology 68:1341–1350.

Swaine, M. D., and T. C. Whitmore. 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75:81–86.

Terborgh, J. 1988. The big things that run the world—a sequel to E.O. Wilson. Conservation Biology 2:402–403.

Uhl, C., K. Clark, N. Dezzeo, and P. Maquirrino. 1988. Vegetation dynamics in Amazonian treefall gaps. Ecology 69:751–763.

Vitousek, P. M., and J. S. Denslow. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical forest. Journal of Ecology 74:1167–1178.