Survival and growth of *Virola surinamensis* yearlings: Water augmentation in gap and understory

Brian L. Fisher[1], Henry F. Howe[2], and S. Joseph Wright[3]

[1] Department of Biology, University of Utah, Salt Lake City, UT 84112, USA
[2] Department of Biological Sciences (M/C 066), University of Illinois at Chicago, Box 4348 Chicago, IL 60680, USA
[3] Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama

Summary. Factors affecting seedling *Virola surinamensis* (Myristicaceae) survival and growth were investigated on Barro Colorado Island, Panama. Seedlings planted 3 months after germination were monitored in treefall gaps and understory using 2.25 ha irrigated and control plots through the first dry season. During the dry season, irrigated plants in gaps increased total leaf area significantly more than did irrigated plants in the shaded understory. Over the same dry season, control plants in gaps and in the shaded understory lost similar amounts of leaf area. Seedlings in understory were suppressed in stem height and biomass in both irrigated and control plots; these measures were greater in gaps and greatest in irrigated gaps (height). Roots were similar in length in all treatments, but greater in biomass in gaps than understory due to greater proliferation of secondary roots in control and irrigated gaps than in control and irrigated understory. This experiment demonstrates both water and light limitation during the first dry season after germination. *V. surinamensis* seedlings are capable of survival and modest growth of leaf area in the deep shade of the understory in moist locations; they are severely disadvantaged in shaded understory subject to drought, where most seeds fall and most seedlings establish. The broken canopy of a gap allows shoot and consequently root growth that permits seedlings to survive seasonal drought.

Key words: Tropical ecology – Panama – Gap dynamics – Seasonal drought – *Virola surinamensis*

Trees of tropical moist and wet forests may be shade-tolerant species that germinate and grow in the deep shade of the understory or shade-intolerant species that establish under the broken canopy of a treefall gap or other forest clearing (e.g. Whitmore 1988). Seeds of *Virola surinamensis* (Rol.) Warb. (Myristicaceae) germinate readily, without dormancy, in either gaps or understory,

a classic shade-tolerant 'persistent' tree of the Barro Colorado Island Forest, Panama. This species, however, presents a paradox on Barro Colorado Island because it is capable of persistence and even growth in the deep shade of the understory, but it rarely survives long there (Howe 1986). Seedlings of this species establish and survive as young juveniles during the wet months of the year in gap, edge, and understory, but experience disproportionate mortality in shaded understory during their first dry season (Howe 1990). In the highly seasonal forest of Barro Colorado Island, drought stress and mammalian herbivory interact to severely limit the persistence of this species in the habit to which it is thought to be adapted (Howe 1990). Under present conditions on Barro Colorado Island, this shade-tolerant species appears to be at a severe disadvantage through the first year unless it achieves accelerated growth in treefall gaps.

The objective of this study is to explore factors that influence survival of *Virola surinamensis* after weevil and rodent depredations on seeds and establishing seedlings pass, and without the complicating influences of mammalian herbivory which kills many seedlings during the first year of life (Howe 1990). The potential survival of seedlings of this species under different conditions of canopy cover and water availability is not yet understood. This paper concerns seedling response to canopy closure and water stress during the first dry season after germination and establishment. An irrigation experiment evaluates seedling survival and growth during seasonal drought in gaps and in understory in both wet and dry soils. We address the key questions presented by earlier work concerning the adequacy of shade-tolerant designation for this species: Can *Virola surinamensis* both persist and grow in shaded understory in the absence of seasonal drought? The answer is yes to both.

Study site and methods

79°51' W) during the wet season of 1986 and the dry season of 1987. The island harbors > 1,300 species of vascular plants, including > 400 species of trees (Croat 1978). A moist seasonal climate results in average annual precipitation of 2,600 m with 2,500 between April and December. Seasonal drought between December and April is potentially severe due to a drop in soil moisture at a depth of 5 cm drom > 45% to 27% by weight (Dietrich et al. 1982), corresponding to a drop in soil water potentials from 0.0 to −1.60 MPa (Wright and Cornejo 1991). Desiccation is a potential threat to tree seedlings, most of which germinate in the early wet season (Garwood 1983) and may or may not achieve significant growth by the onset of their first dry season. *Virola surinamensis* is, in this respect, a typical tree that germinates readily without dormancy within 1–3 weeks after fruit fall, which occurs from March through August with a population peak in June, July, or early August (Howe 1983). Seedlings exhaust parental endosperm within 12 weeks of germination (Howe et al. 1985), and are therefore independent of parental provisioning 4–28 weeks before the onset of their first dry season.

This study made use of an irrigation experiment in which water from Gatun Lake was pumped to a sprinkler system that augmented soil moisture in two 2.25 ha experimental plots (Wright and Cornejo 1991). The system of 160 sprinklers, distributed in a hexagonal array at 15.3 m intervals, delivered 675 metric tons of water to each plot per week during the dry season. *V. surinamensis* survival and growth in these plots were compared with those in the control plots. Water application maintained soil water potentials at or slightly above field capacity (−0.04 MPa), whereas soil water potentials dropped (−1.60 MPa) in adjacent plots. Water augmentation during the study period lasted from 15 December 1986 to 16 April 1987. The irrigation project is in forest thought to have been free from extensive human disturbance for a least 500 years (Piperno 1990).

Virola surinamensis seeds were collected from ten maternal parents on Barro Colorado Island, weighed, randomly mixed with respect to mother, and planted in forest soil in 15 cm peat pots in a screenhouse protected from insect seed predators and mammalian herbivores. On October 16, 3 months after germination, seedlings were planted into 12 treefall gaps and 12 randomly located sites in the shaded understory in each of the four plots. Only one seedling was planted in each gap and understory site. These 96 seedlings were planted in peat pots with the bottoms removed, and were protected from browsing mammals by 1.5 m tall cylinder of poultry mesh open at the top. Insect herbivory on plants more than 6 weeks old was negligible (< 1–5% of leaf area).

Treefall or branchfall gaps ranged from 7–216 m² (mean ± 95% confidence interval = 45 ± 13 m²). This is typical of gap sizes found in old forest on Barro Colorado Island (median = 47 m²; Brokaw 1982). Canopy closure was explicitly characterized with high-contrast hemispherical photographs taken with a 2.8 f 8 mm fisheye lens placed 1 m above the ground on 24 October 1986. Canopy openness was determined from the photographs using the automated computer program of Becker et al. (1990). Canopy openness was the proportion of the canopy open to the sky (presented as % skylight). Howe (1990) found that canopy openness measured 1 m above the ground provided a more accurate measure of light levels experienced by seedlings than just gap size: gap size was not significantly correlated with plant growth measurements because of ground level shading from regenerating vegetation.

The condition of each plant was evaluated at planting on 16 October 1986, at the end of the wet season on 17 December 1986, and near the end of the dry season on 18 April 1987. Plant height and the length of each leaf were measured to the nearest 0.5 cm. Regressions of leaf length on leaf area ($R^2 = 0.95$) were used to estimate the total leaf area for each seedling. The initial sample of 96 seedlings was reduced over time by branches or animals that dislodged cages, gaps that opened over seedlings that were originally shaded, and by mortality of caged seedlings. All seedlings that survived until 18 April 1987 ($n = 73$) were included in analyses of growth (height and leaf area).

On 21 May 1987, four randomly chosen seedlings from gaps and four from the understory were excavated from each plot. Shoot and root biomass were determined after oven drying to constant mass at 50° C.

Analyses were performed using SYSTAT (Wilkinson 1986). Logarithmic transformations made means independent of variances, and arcsine-square root transformations normalized binomial data. Where possible, dry season growth was analyzed by analyses of covariance, using December measurements as the covariate to factor in differences in growth due to canopy closure before the irrigation experiment began. Summary statistics are presented with untransformed means and 95% confidence intervals.

Results

Physical variables

Hemispherical photographs indicated canopy openness of 1.5–5.7% (2.9 ± 0.4%) skylight in gaps and 0.1–1.3% (0.4 ± 0.1%) skylight in understory. Canopy openness values for gap and understory sites did not overlap. Gap and understory designations explained 74% of the variance in canopy openness indices. Therefore, analyses of dry season growth were simplified by using the categorical variable of canopy closure, gap and understory, without a great loss of detail. Soil remained saturated in irrigation plots with soil water potential above −0.04 MPa, but was dry and cracked in control plots (soil water potential −1.60 MPa). Dry season gravimetric soil water content averaged 42.5 ± 2.4% in irrigated and 27.7 ± 1.0% in control plots (unpublished data).

Survival

Canopy closure and irrigation were important factors in survival. More than 90% of the seedlings in irrigated and non-irrigated gaps and in irrigated understory survived as seedlings through the dry season; 67% survived in non-irrigated understory (Table 1). Drought during the first dry season made a difference in the understory, but not in the gaps. Because so few irrigated or gap plants died, expected cell values are too small for multiway contingency analysis.

Growth

Seed weight, height, and total leaf area did not differ significantly among sites or treatments at planting. By mid December 1986, before the onset of the dry season,

Table 1. Survival of *Virola surinamensis* seedlings planted at 3 months of age in October 1986 and counted at the end of the dry season

Habitat	Treatment	Alive	Dead
Gap	Irrigated	18	1
	Control	20	2
Understory	Irrigated	19	2
	Control	16	8

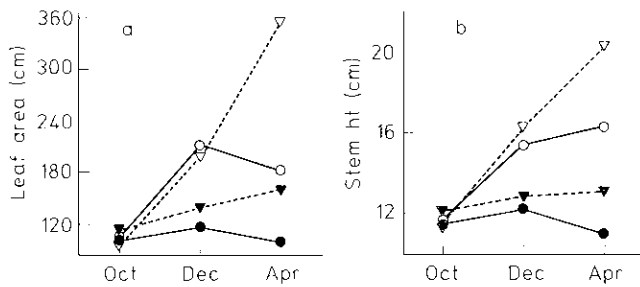Fig. 1a, b. Mean total leaf area a and mean stem height b of irrigated-gap (▽), control-gap (○), irrigated-understory (▼), and control-understory (●), plants. Measurements were taken: at the time of transplanting, 16 October 1987; at the end of the wet season, 17 December 1987; and at the end of the dry season, 18 April 1987. Irrigation began on December 15 at the start of the dry season

37 seedlings alive in gaps exceeded 42 plants in the shade in leaf area (Fig. 1a; 205.0 ± 20 cm^2 versus 126.9 ± 11.0 cm^2; $t = 6.71$, $P < 0.001$) and in height (Fig. 1b; 15.7 ± 1.0 cm versus 12.5 ± 0.6 cm; $t = 5.42$, $P < 0.001$). This corresponds to a 61% increase in leaf area and a 26% increase in height between October and December for seedlings planted in gaps.

Leaf area measured in April showed by far the most rapid gain in irrigated gaps (Fig. 1a). Total leaf areas increased over mid December measurements in both irrigated-understory and irrigated-gap sites and decreased in size in control-gap and control-understory sites. Dry season growth in leaf area was analyzed by analysis of covariance with the logarithm of total leaf area in December as the covariate. The homogeneity of slopes assumption of the ANCOVA was valid ($P > 0.5$), and the analysis of covariance model was tested with the covariate, the main effects (canopy closure and water status) and their interaction, and the nested plot effect as predictors. The nested plot effect was not significant ($P > 0.25$). Therefore, the mean square error for the nested plot effect was pooled with the overall experimental error (Sokal and Rohlf 1981, pp. 285 286).

The main effects, canopy closure and water status, are difficult to interpret because there is a significant interaction of canopy closure and water status on dry season seedling growth (Table 2). A posteriori analyses were used to test the null hypothesis that canopy closure did not affect dry season growth for each level of water status. The null hypothesis could not be rejected for the control treatment
($F_{1,62} = 0.24$, $P = 0.63$). The null hypothesis was rejected for the irrigated treatment ($F_{1,62} = 21.77$, $P < 0.0005$). Therefore, during the dry season, canopy closure does affect total leaf area within the irrigated plots but canopy closure does not affect total leaf area within the control plots. Overall, irrigated plants in gaps increased total leaf area significantly more than did irrigated plants in the shaded understory. Over the same dry season, control plants in gaps and in the shaded understory lost similar amounts of leaf area (Fig. 1a).

The interaction between canopy closure and water status is also demonstrated by plotting the residuals

Table 2. Analysis of covariance for *Virola surinamensis* leaf area April as a function of leaf area in December, canopy status (gap or understory) and water status (irrigated or control). Leaf area measurements were analyzed with logarithm transformations

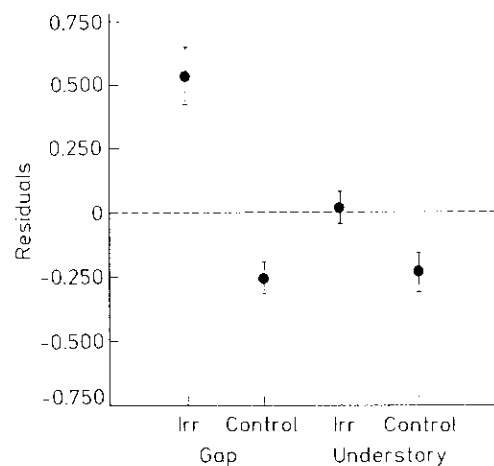| Source	R^2	SS	DF	MS	F
Total leaf area in December	0.76	6.06	1	6.06	55.12***
Canopy status		1.28	1	1.28	11.66***
Water status		4.70	1	4.70	42.76***
Plot		0.06	2	0.03	0.30
Canopy status × water status		1.12	1	1.13	10.29**
Canopy status × water status × plot		0.30	2	0.15	1.37
Error		6.91	62	0.11	

$** = P < 0.01$; $*** = P < 0.001$

Fig. 2. Residuals ($\pm$ standard error) from regression of the log of total leaf area in April and log of total leaf area in December in irrigated and control plots in gaps and understory. There is an across treatment effect of water status but not of canopy closure

from the regression of the log of total leaf area in April on the log of total leaf area in December in irrigated and control plots in gaps and in understory sites (Fig. 2). Irrigated plots have larger residuals than do control plots. There is an effect of water status across all treatments, but there is no global effect of canopy closure. During the first dry season, gaps have a positive effect on seedling growth only when irrigated (Fig. 2).

Stem height taken in April indicated substantial growth in irrigated and control gaps, as well as in deep shade of irrigated plots (Fig. 1b, Table 3). Stem heights increased over planting heights (11.7 ± 0.4 cm) in all but dry understory, where a decrease was recorded. Dry season growth in stem height was analyzed by analysis of covariance using the logarithm of stem height in December as the covariate. The homogeneity of slopes assumptions of the ANCOVA was valid ($P > 0.5$). Habitat significantly affected stem height of seedlings ($P < 0.001$;

Table 3. Analysis of covariance for *Virola surinamensis* stem height in April as a function of stem height in December, canopy status (gap and understory) and water status (irrigated and control). Stem heights were analyzed with logarithm transformations

Source	R²	SS	DF	MS	F
Stem height in December	0.86	1.73	1	1.72	116.20***
Canopy status		0.61	1	0.61	41.14***
Water status		0.35	1	0.35	4.37
Plot		0.16	2	0.08	5.4**
Canopy status × water status		0.06	1	0.06	0.99
Canopy status × water status × plot		0.12	2	0.06	3.83*
Error		0.92	62	0.02	

$* = P < 0.05$; $** = P < 0.01$; $*** = P < 0.001$

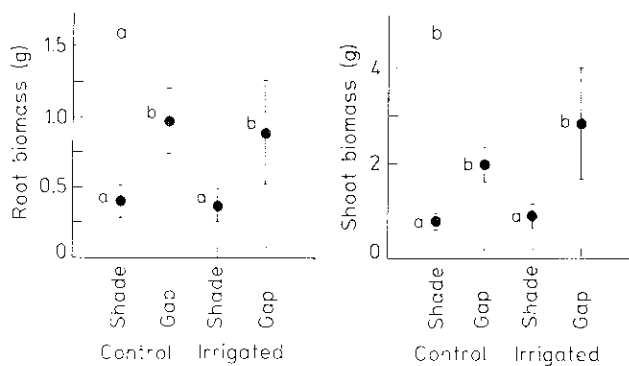**Fig. 3a, b.** Root a and shoot b biomasses at the end of the first dry season for young *Virola surinamensis* seedlings planted in irrigated and control plots in gaps and understory. Post-hoc Tukey tests show significantly different means ($P < 0.05$). as indicated by different superscripts. See Table 3 for analyses of variance. Each sample size is 8

Table 4. Analysis of variance for *Virola surinamensis* root and shoot biomass as functions of canopy status (gap or understory) and water status (irrigated or control). Biomass measurements were analyzed with logarithm transformations

Source	Shoot biomass				Root biomass			
	R²	DF	MS	F	r²	DF	MS	F
Canopy status	0.68	1	2.75	56.69**	0.57	1	0.83	36.43**
Water status		1	0.16	3.24		1	0.01	0.51
Canopy × water		1	0.04	0.80		1	0.00	0.12
Error		28	0.05			28	0.02	

$** = P < 0.01$

Table 5. Analysis of variance for *Virola surinamensis* root/shoot biomass ratios as functions of canopy status (gap or understory) and water status (irrigated or control). Root-to-shoot ratios were analyzed with arcsine square root transformations

Source	R²	SS	df	MS	F
Canopy status	0.54	0.02	1	0.02	2.07
Water status		0.12	1	0.12	15.56**
Plot		0.01	2	0.07	0.81
Canopy status × water status		0.02	1	0.02	0.98
Canopy status × water status × plot		0.04	2	0.02	2.56*
Error		0.18	23	0.01	

$* = P < 0.05$ $** = P < 0.001$

Table 6. Number of secondary roots and length of primary roots of *Virola surinamensis* seedlings planted at 3 months of age in October 1986 and measured at the end of the first dry season in May 1987. Means are accompanied by 95% confidence intervals for sample of 8 in each treatment

Treatment	Secondary roots (N)	Root length (cm)
Irrigated in gaps	32.0 ± 4.6[a]	17.1 ± 2.1[a]
Irrigated in understory	18.1 ± 3.6[b]	13.9 ± 1.9[a]
Not irrigated in gaps	26.8 ± 3.8[a]	16.5 ± 2.3[a]
Not irrigated in understory	16.6 ± 3.1[b]	14.4 ± 3.4[a]

[a] Means in a column that bear different superscripts are significantly different at the $P < 0.05$ level as determined by the post-hoc Tukey test

Table 3). Because the nested plot effect is significant, the associated main effect, water status, was evaluated against the nested plot effect and was found not to be significant (Table 3). The test for the interactions of canopy closure and water status lacks power because the nested effect of plot was substantial (Table 3). The nested plot effect seems to be due to irrigated-understory plants in one plot with stem heights indistinguishable to control plot heights.

Measures of shoot and root biomass showed significant differences between gap and understory treatments, but not between water treatments (Fig. 3). Shoots and roots in gaps are clearly heavier than those in understory, regardless of water treatment (Table 4). Because a covariate of root and stem biomass in December is impossible, the analysis is biased toward the canopy closure effects which affected plant for a longer period of time than the water status experiment.

Measures of root-to-shoot biomass ratios were analyzed by analysis of variance where the response variable was the angular transformation of the root-to-shoot ratio. Root-to-shoot ratios were affected by water status but not by canopy closure (Table 5). Irrigated plants had significantly lower root-to-shoot ratios than did control plants. The test for the canopy closure-water status interaction lacks power because the nested effect of plot was substantial (Table 5). The nested plot effect is due to 4 irrigated-shade plants in one plot with root-to-shoot ratios indistinguishable to control plot ratios.

Excavation revealed obvious morphological differences among roots in gap and understory sites. Primary root lengths did not differ significantly among treatments, but roots in gaps had significantly greater numbers of secondary roots than those in understory (Table 6).

Discussion

Forest dynamic studies have stressed the role of gaps as a determinant in population dynamics and forest structure. Whitmore (1988) proposed the dichotomous pioneer/climax paradigm based on light requirements to distinguish species with different average life histories. Studies on Barro Colorado Island support this framework; gaps influence distributions of pioneer, shade tolerant and generalist tree species (Brokaw 1985a, b; Brokaw and Scheiner 1989; Hubbell and Foster 1986a, b). Studies on gaps are becoming more refined, incorporating the idea that "forests are not just swiss cheese" (Lieberman et al. 1989), yet few studies have combined the influence of gaps with other abiotic and biotic factors that influence success of a seedling in the forest. Both water status and canopy closure are investigated in this field experiment with *Virola surinamensis* seedlings.

This irrigation experiment demonstrates that *Virola surinamensis* seedlings are capable of persistence and even modest growth in wet soils in deep shade. This is consistent with the view that the species is, as expected (Croat 1978; see Whitmore 1988), a shade-tolerant member of late successional or primary forest. Most intriguing is the interaction between canopy closure and water status. During the dry season, we show growth advantage to seedlings in gaps only when irrigated. Measures of height, leaf area, shoot and root biomass, and root morphology clearly indicate that yearlings of this species are water-limited as well as light limited in the seasonal forest of Barro Colorado Island. Seasonal drought interacts with canopy cover to place young seedlings of this species at a disadvantage in shaded understory.

Light gap studies usually omit the effects of canopy closure on root growth. This study revealed that root structure may be critical to the survival of a seedling during its first year of growth. Roots in gaps have a greater biomass and a greater number of lateral roots. Greater fine root biomass under light gap openings in old forest is predicted on the basis of greater nutrient availability in recently formed gaps (Collins et al. 1985), but in one case not demonstrated (Sanford 1989). Our results, however, suggest that the greater number of fine roots may result from a higher demand for water in gaps coupled with a faster rate of growth in gaps during moist conditions. Irrigated plants had a lower root-to-shoot ratio than non-irrigated plants. Figure 1a suggests that this is from a loss of leaf area in non-irrigated plants. Control plants lost shoot biomass during the dry season due to desiccation. Water stress and the resulting reduction in leaf area may be critical to the survival of the seedlings, especially for non-irrigated understory seedlings which lost equal amount of leaf area as non-irrigated gap seedlings and experienced the lowest survival of all treatments (Table 1). These results explain the high drought mortality of defoliated *Virola surinamensis* seedlings reported by Howe (1990). Howe (1990) found that size of *Virola surinamensis* seedlings is important to root development. Therefore, first year seedlings that experience defoliation from herbivory may have suppressed root development and a greater chance of death from desiccation during the dry season.

Evidence reported here indicates that *Virola surinamensis* yearlings are vulnerable to seasonal drought unless situated in a treefall gap. As a shade-tolerant tree capable of germination and modest growth in deep shade of moist understory, a gap advantage for this species is really an establishment advantage that permits seedlings to grow large enough – and develop root systems extensive enough – to survive the first dry season. More water may also be available in larger gaps than in understory soils (Becker et al. 1988), but this effect is not likely in gaps as small as those used here. As suggested by Howe (1990), the advantage in size of seedlings in gaps permits these plants to survive when smaller conspecifics in the shaded understory cannot. This study indicates that drought stress may be most critical in seedlings and merits future research.

These results suggest why this species is historically more common on hillsides and in steep ravines on Barro Colorado Island than in the dryer soils of flat tableland; *Virola surinamensis* occurs in an average density of 4.8 stems > dbh/ha in forest on level ground (Hubbell and Foster 1983; pers. comm.) and 15.2/ha on hillsides and ravine slopes (Howe and Fisher, unpublished). Recent studies have shown that soils on steep slopes maintain higher water potentials than those of flat land on Barro Colorado Island, due to greater shading and drainage from the tableland itself (Becker et al. 1988). Other things being equal, it is clear that seedlings of this species should fare better in seasonal forest if they establish in rare new gaps (1–3% of forest area; Brokaw 1982; Hubbell and Foster 1986a) or in moist soils of hillsides and ravines.

References

Becker P, Rabenold PE, Idol JR, Smith AP (1988) Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. J Ecol 52:27–41

Becker P, Erhart D, Smith AP (1990) Analysis of forest light environments I. Computerized estimation of solar radiation from hemispherical canopy photographs. Ag For Met (in press)

Brokaw N (1982) Treefalls: frequency, timing, and consequences. In: Leigh EG, Rand AS, Windsor DM (eds) The ecology of

a tropical forest: season rhythms and long-term changes. Smithsonian Institution Press, Washington, pp 101 108

Brokaw N (1985a) Gap-phase regeneration in a tropical forest. Ecology 66:682–687

Brokaw N (1985b) Treefalls, regrowth, and community structure in tropical forest. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp 53–69

Brokaw N, Schiener SM (1989) Species composition in gaps and structure of a tropical forest. Ecology 70:538 541

Collins BS, Dunne KP, Pickett STA (1985) Responses of forest herbs to canopy gaps. In: Pickett STA, White PS. The ecology of natural disturbance and patch dynamic. Academic Press, New York

Croat TB (1978) Flora of Barro Colorado Island Stanford University Press, Stanford

Dietrich WE, Windsor DM, Dunn T (1982) Geology, climate, and hydrology of Barro Colorado Island. In: Leigh EG, Rand AS, Windsor DM (eds) The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, pp 21–46

Garwood NC (1983) Seed germination in a season tropical forest in Panama: a community study. Ecol Mon 53:158–181

Howe HF (1983) Annual variation in a neotropical seed dispersal system. In: Sutton SL, Whitmore TC, Chadwick AC (eds) Tropical rain forest: ecology and management. Blackwell Scientific Publications, Oxford, pp 211–217

Howe HF (1986) Consequences of seed dispersal by birds: a case study from Central America. J Bombay Nat Hist Soc [S] 83:19–42

Howe HF (1990) Survival and growth of juvenile *Virola surinamensis* in Planama: effects of herbivory and canopy closure. J Trop Ecol 6:259 280

Howe HF, Schupp EW, Westley LC (1985) Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). Ecology 66:781–791

Hubbell SP, Foster RB (1983) Diversity of canopy trees in a neotropical forest and implications for conservation. In: Sutton SL, Whitmore TC, Chadwick AC (eds) Tropical rain forest: ecology and management. Blackwell Scientific Publications, Oxford, pp 25–41

Hubbell Sp, Foster RB (1986a) Canopy gaps and the dynamics of a tropical forest. In: Crowley MJ (ed) Plant Ecology: 77–96. Blackwell Scientific Publications, Oxford

Hubbell SP, Foster RB (1986b) Biology, chance, and history and the structure of tropical rain forest tree communities. In: Diamond J, Case TJ (eds) Harper & Row, New York Community Ecology, pp:314–329

Lieberman M, Lieberman D, Peralta R (1989) Forests are not just swiss cheese: canopy stereogeometry of non-gaps in tropical forests. Ecology 73:550 552

Piperno DR (1990) Fitolitos, arqueología y cambios prehistóricos de la vegetación en un lote de cincuenta hectáreas de la isla de Barro Colorado. In: Leigh EG, Rand AS, Windsor DM (eds) Ecología de un bosque tropical. Smithsonian Institution Press, Washington, pp 153–156

Rand AS, Rand WM (1982) Variation in rainfall on Barro Colorado island. In: Leigh EG, Rand AS, Windsor DM (eds) The ecology of a tropical forest: seasonal rhythms and long-term changes: 47–62. Smithsonian Institution Press, Washington

Sanford RL Jr (1989) Fine root biomass under a tropical forest light gap opening in Costa Rica. J Trop Ecol 5:251–256

Sokal RR, Rohlf FJ (1981) Biometry. WH Freeman, San Francisco, California, USA

Whitmore TC (1988) The influence of tree population dynamics on forest species composition. In: Davy AJ, Hutchings MJ, Watkinson AR (eds) Plant population ecology. Blackwell Scientific Publications, Oxford, pp 271 292

Wilkinson L (1986) The system for statistics. Evanston, Illinois. Systat, Inc.

Wright SJ, Cornejo FH (1991) Seasonal drought and the timing of flowering and leaf fall in a Neotropical forest. In: Bawa KS, Hadley M (eds) Reproductive ecology of tropical forest plants. UNESCO/MAB (in press)