

Density and growth rate of some tropical dry forest trees: Comparisons between successional forest types¹

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ABSTRACT

CHAPMAN, C. A. AND L. J. CHAPMAN (Dept. of Biology, McGill University, 1205 Dr. Penfield Ave., Montreal, Quebec, Canada, H3A 1B1). Density and growth rate of some tropical dry forest trees: comparisons between successional forest types. *Bull. Torrey Bot. Club* 117: 226–231. 1990.—During a 4-year study in northwestern Costa Rica, the density, phenology, and growth rate of 29 species of dry forest trees important in the diets of primates were documented in three habitat types: pristine semi-evergreen forest, old successional semi-deciduous forest, and young successional semi-deciduous forest. The overall density of adult trees for the species sampled was the lowest in the young successional forest (80 trees/ha) followed by the pristine semi-evergreen forest (140.3 trees/ha) and the older successional forest (154.8 trees/ha). However, the pristine semi-evergreen forest had a fairly constant level of food abundance, while both types of successional forest had more seasonally variable production. The average growth rate of trees in the semi-evergreen forest was slower than those documented in either of the successional forests.

Key words: tropical dry forest, successional forest, regeneration.

A growing body of literature on the ecology of tropical forests has focused on forest productivity (Golley 1983; Murphy and Lugo 1986), phenological cycles (Janzen 1967; Daubenmire 1972; Frankie *et al.* 1974; Koptur *et al.* 1988), secondary growth areas (Webb *et al.* 1972; Okali and Ola-Adams 1987), and forest composition and structure (Hubbell 1979; Lieberman and Lieberman 1987; Swaine *et al.* 1987). Recent studies have demonstrated a relationship between net primary productivity and forest type (Murphy and Lugo 1986). However, we know little concerning how floristic differences between forest types might affect particular groups of consumers, such as frugivores and folivores. Some types of forest may have such highly seasonal production that at some periods of the year they are unsuitable for many non-migratory consumers. Or some habitats may be highly pro-

ductive, but what is produced may be unsuitable for certain types of consumers. The construction of realistic conservation programs for endangered tropical animals requires that documented botanical differences between forest types be interpreted in light of the amount, type, and seasonality of production. Since many endangered animals are now living in altered environments, it is also necessary to evaluate differences between successional and pristine habitats.

This study examines the density, size, and growth rates of a set of dry forest trees in pristine semi-evergreen, old successional semi-deciduous, and young successional semi-deciduous forests. We chose species important in the diets of the primates in the area and examined seasonal differences in the abundance of food between these forest types. We use this information to evaluate how these different forest types might influence the distribution and feeding patterns of frugivores and folivores.

Methods. **STUDY SITE.** This study was conducted in Santa Rosa National Park which is situated in the northwestern corner of Costa Rica. Over the last 300 years, large sections of the upper plateaus in Santa Rosa have been cleared for cattle pastures. However, with the establishment of the park in 1971 and the removal of cattle in 1978, some of the grassland area has reverted to woody vegetation (Janzen 1986).

The climate of the area is characterized by two distinct seasons, the dry season, extending from

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early December to late May, and the wet season, encompassing the remainder of the year. Between 1980 and 1987, annual rainfall in the park has averaged 1527 mm/yr (range 914 mm to 2340 mm; Janzen 1988). On average, 98% of the rain falls from May to November (1980–1987, range 96.2%–99.2%; Janzen 1988). During the dry season the majority of the non-riparian trees in the successional areas lose their leaves.

Three sections of forest were studied: an area of pristine semi-evergreen forest, an area of old successional semi-deciduous forest, and younger successional area of semi-deciduous forest. The trees in the pristine semi-evergreen forest typically maintain their leaves throughout much of the year. This section of forest is relatively undisturbed, but it was selectively logged for trees such as mahogany (*Swietenia macrophylla*). The older successional area is between 75 and 100 years of age (Janzen personal communication), but when this area was cleared, a number of large trees were left standing. The younger section of successional semi-deciduous forest was extensively cleared for fence posts approximately 40 years ago (D. Janzen personal communication), leaving some large trees standing (e.g., *Mastichodendron capiri*, *Manilkara chicle*, and *Sloanea terniflora*).

SAMPLING PROCEDURES. This study was conducted between 1984 and 1988, during which time 3 years were spent in the park. Twenty-nine species of dry forest trees were selected to monitor the plant food resources of the three species of primates in the park (spider monkeys, *Ateles geoffroyi* howling monkeys, *Alouatta palliata*; white-faced capuchins, *Cebus capucinus*) (Table 1, Chapman 1988a, 1988b). Of the total time spent feeding on plants by spider monkeys, 90.2% was accounted for by the 29 species we selected for study. Equivalent values for capuchin and howling monkeys were 80.9% and 74.1%, respectively. We present the data in terms of seasonal abundance of food items, regardless of the type of plant part.

Three 4-hectare grids, one in each of the different forest areas, were used to determine the density of these trees. Two of the grids were 200 m and 200 m, and the third was 400 m by 100 m. Each grid was divided into 400 cells that were 10 m by 10 m in size. Corners of the cells were marked with individually labelled steel posts. In each grid cell all individuals of the 29 species of trees with stems 5 cm in diameter at breast height (DBH) or greater were monitored. For *Acacia*

collinsii all trees 1 m in height or greater were included. Trees were measured in January 1985 and again in January 1988. To determine the phenology of each of these species, we examined each tree in all grids approximately once every 3 weeks, and recorded the stage of leaf development (no leaves, leaf buds, young leaves, mature leaves) and the presence or absence of fruit and flowers. We use the taxonomic nomenclature suggested by Janzen and Liesner (1980).

Results. DENSITY AND PHENOLOGY OF SOME DRY FOREST TREES. The density of the trees of the species sampled was the lowest in the young successional semi-deciduous forest (80.4 trees/ha), and highest in the older successional forest (154.8 trees/ha, Table I). Density was intermediate in the pristine semi-evergreen forest (140.3 trees/ha). Forest types differed widely in the densities of particular tree species. The average absolute difference in the density of each enumerated tree species was greatest between the pristine and old successional forests (8.7 trees/ha \pm 2.61 SE). The equivalent difference between the pristine forest and young successional forest was 6.9 trees/ha \pm 2.41 SE. The smallest difference in the density of individual species was observed between the young and old successional forests (4.39 trees/ha \pm 1.66 SE).

Of the species sampled, *Spondias mombin* (31.0 trees/ha) and *Bursera simaruba* (19.3 trees/ha) were also the most common in the young successional forest. While these two tree species were also abundant in the older successional area (*Spondias mombin* 18.9 trees/ha, *Bursera simaruba* 35.3 trees/ha), *Luehea speciosa* (41.5 trees/ha) was the most common of the species examined. In the pristine semi-evergreen forest, none of the tree species considered reached as high a density as in the successional forest sites. In this grid, *Manilkara chicle* was the most common tree of those enumerated (24 trees/ha). The pristine semi-evergreen forest contained 26 of the 29 species sampled, while the old successional forest contained 20 of the species, and the younger successional area contained 19 of the species.

A number of studies have shown a relationship between some measure of the size of tropical trees and the quantity of fruit they produce (Leighton and Leighton 1982; Peters *et al.* 1988). Since the sizes (DBH) of the trees in the sample grids were known, a measure of overall food abundance of the tree species examined was cal-

Table 1. The density and size of 29 species of trees studied in Santa Rosa National Park, Costa Rica (density = number of trees/ha; DBH = average diameter at breast height in cm).

Plant	Semi-deciduous (young)		Semi-deciduous (old)		Semi-evergreen	
	Density	DBH	Density	DBH	Density	DBH
Anacardiaceae						
<i>Spondias mombin</i>	31.0	25.1	18.8	38.1	8.5	24.7
<i>Spondias purpurea</i>	1.0	24.3	1.0	10.0	—	—
Araliaceae						
<i>Sciadodendron excelsum</i>	1.3	38.0	0.3	64.0	0.5	45.0
Burseraceae						
<i>Bursera simaruba</i>	19.3	20.5	35.3	20.4	8.0	22.3
Caesalpiniaceae						
<i>Swartzia cubensis</i>	—	—	—	—	0.3	73.0
Chrysobalanaceae						
<i>Licania arborea</i>	0.5	31.5	3.0	38.0	0.5	61.5
Elaeocarpaceae						
<i>Muntingia calabura</i>	—	—	0.3	27.0	0.8	15.3
<i>Sloanea terniflora</i>	0.5	79.3	—	—	6.5	36.2
Fagaceae						
<i>Quercus oleoides</i>	—	—	—	—	16.5	57.3
Flacourtiaceae						
<i>Zuelania guidonia</i>	—	—	—	—	2.3	27.6
Guttiferae						
<i>Rheedia edulis</i>	—	—	—	—	0.5	10.8
Lauraceae						
<i>Ocotea veraguensis</i>	0.3	50.0	7.0	11.6	14.0	16.3
Mimosaceae						
<i>Acacia collinsii</i>	5.0	3.6	31.8	3.7	3.8	2.9
<i>Inga vera</i>	0.3	17.0	0.3	28.0	—	—
<i>Pithecellobium saman</i>	0.8	44.5	1.3	53.0	0.3	31.0
Moraceae						
<i>Brosimum alicastrum</i>	—	—	—	—	2.3	30.0
<i>Castilla elastica</i>	1.8	13.6	0.5	19.5	10.0	22.1
<i>Chlorophora tinctoria</i>	0.8	27.3	5.3	28.3	0.5	35.0
<i>Cecropia peltata</i>	8.3	23.0	1.0	31.0	13.8	19.0
<i>Ficus</i> spp.	—	—	0.3	104.0	1.5	112.0
<i>Trophis racemosa</i>	0.3	20.0	0.3	10.0	0.3	37.0
Rubiaceae						
<i>Genipa americana</i>	2.3	20.7	—	—	—	—
<i>Randia echinocarpa</i>	0.3	20.0	3.5	7.1	1.0	18.5
Sapindaceae						
<i>Dipterodendron costaricensis</i>	—	—	—	—	7.5	17.5
Sapotaceae						
<i>Manilkara chicle</i>	3.3	30.1	2.0	40.8	24.0	28.3
<i>Mastichodendron capiri</i>	0.8	75.0	0.3	76.0	0.5	70.5
Simaroubaceae						
<i>Simarouba glauca</i>	—	—	1.0	10.3	0.3	29.0
Sterculiaceae						
<i>Sterculia apetala</i>	—	—	—	—	0.3	61.0
Tiliaceae						
<i>Luehea speciosa</i>	2.5	37.0	41.5	27.1	15.8	25.1

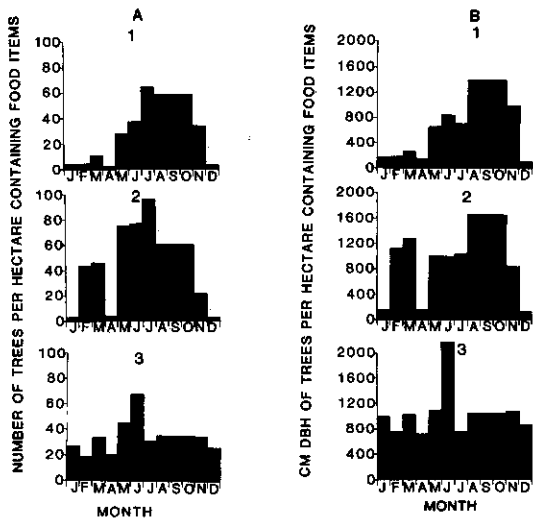


Fig. 1. A) A monthly estimate of the number of trees per hectare with food items in (1) young successional semi-deciduous forest, (2) old successional semi-deciduous forest, and (3) pristine semi-evergreen forest in Santa Rosa National Park, Costa Rica.

B) A monthly estimate of the cumulative size (cm DBH) per hectare of trees containing food items in (1) young successional semi-deciduous forest, (2) old successional semi-deciduous forest, and (3) pristine semi-evergreen forest in Santa Rosa National Park, Costa Rica.

culated by weighting the density of trees of a given species by the average size of that species. Using this measure, the young successional semi-deciduous forest had less food available (1925 cm DBH/ha), than either the older successional forest (3353 cm DBH/ha), or the pristine semi-evergreen forest (4010 cm DBH/ha).

Since the species sampled bear food items for different lengths of time and at different times of the year, density alone will not adequately represent what is available to a consumer. Figure 1 depicts the density and the weighted density of trees that produced food items in each month of the year. These data illustrate that for much of the year the successional forests had more trees per hectare and higher cm DBH per hectare bearing food than the pristine semi-evergreen forest. However, the pristine semi-evergreen forest had more constant food production than the successional forest areas.

SIZE CLASS STRUCTURE AND GROWTH RATE.

The mean size of trees differed between the three forest types. The mean DBH of trees in the pristine semi-evergreen forest ($\bar{x} = 29.6 \text{ cm} \pm 0.83 \text{ SE}$) was larger than the trees found in either the old successional forest ($\bar{x} = 26.4 \text{ cm} \pm 0.84 \text{ SE}$)

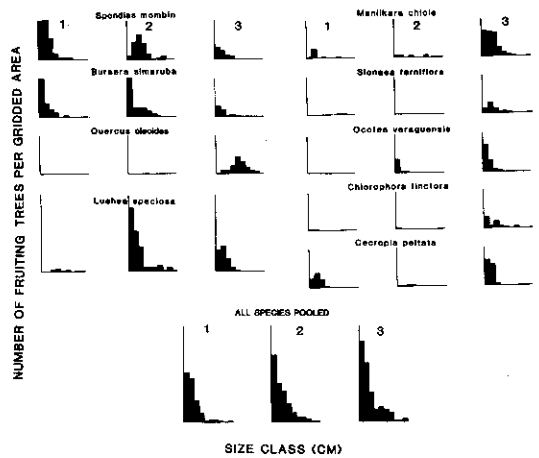


Fig. 2. Size frequency distribution of trees for each of 10 selected species and for all 29 sampled species in (1) young successional semi-deciduous, (2) old successional semi-deciduous, and (3) pristine semi-evergreen forests in Santa Rosa National Park, Costa Rica.

or the young successional forest ($\bar{x} = 25.7 \text{ cm} \pm 0.88 \text{ SE}$; $F = 6.03$, $P = 0.003$, Scheffé $P < 0.05$).

Figure 2 depicts the size frequency distribution for specific tree species and for all tree species combined in each of the forest types. Although in general the pristine forest had slightly more large trees, the size distributions of the three forest types were similar. In contrast, the size frequency distribution of particular species varied considerably between the forest types (Fig. 2). For instance, *Spondias mombin* was common in the young successional forest; however most of the trees were small. In contrast, in the older successional forest, large *S. mombin* (trees $> 30 \text{ cm DBH}$) were common, and few small trees were found. This suggests that recruitment of *S. mombin* trees declines as the successional forest matures. *Cecropia peltata*, a tree often considered to quickly invade disturbed areas (Charles-Dominique 1986), was common in both the young successional forest and the pristine forest (Fig. 2), but in the older successional forest there were only a few large *Cecropia* trees. In the successional forest, this tree had probably colonized areas that were recently pasture, while in the pristine semi-evergreen forest this tree species seemed to be primarily found in old tree fall gaps.

The trees were measured in January 1985 and again in January 1988. The growth rate of trees over this 3-year period was lower in the semi-evergreen forest ($\bar{x} = 0.84 \pm 0.08 \text{ SE}$) than in either the old successional forest ($\bar{x} = 1.50 \pm 0.22 \text{ SE}$) or the young successional forest ($\bar{x} =$

Table 2. The annual growth rate in mm DBH and standard error, measured from plant species found in Santa Rosa National Park, Costa Rica.

Plant species	Semi-evergreen	Semi-deciduous (young)	Semi-deciduous (old)	# of trees sampled
<i>Bursera simaruba</i>	3.1 ± 0.55	5.8 ± 0.87	5.1 ± 0.34	182
<i>Spondias mombin</i>	4.6 ± 1.32	6.9 ± 0.59	4.3 ± 0.53	160
<i>Manilkara chicle</i>	2.6 ± 0.39	4.8 ± 1.92	6.4 ± 1.32	97
<i>Cecropia peltata</i>	3.5 ± 0.73	4.6 ± 0.75	3.9 ± 1.25	59
<i>Quercus oleoides</i>	3.5 ± 0.78	—	—	51
<i>Castilla elastica</i>	3.1 ± 0.58	7.8 ± 1.92	—	38
<i>Sloanea terniflora</i>	6.9 ± 0.58	—	—	24

1.95 ± 0.18; $F = 10.78$, $P < 0.001$; Scheffé $P < 0.05$). No estimates of the mortality of trees in the different forests are available.

The grids were too small to include sufficient numbers of most individual species for us to examine growth on a per species basis; however, sample size was adequate (>20 trees) for 7 species (Table 2). Growth rates of particular species varied among forest types. For example *Manilkara chicle* grew 2.5 times faster in the old successional semi-deciduous forest than in the pristine semi-evergreen forest.

Discussion. The documentation of differences in the size and density of the enumerated tree species and the monitoring of the seasonal cycle of food abundance in three forest types illustrates the degree of spatial and temporal variability in food resources that can be experienced by an animal consumer. We documented that the month to month variability in food abundance was not synchronized between forest types. These findings concur with previous studies in tropical forests which have demonstrated high degrees of spatial and temporal variability in food abundance (Terborgh 1986a, 1986b; Leighton and Leighton 1983; Foster 1982).

Animals must develop strategies for coping with periods of food scarcity. The use of alternative food resources has been proposed as one option used by animals during such periods (Terborgh 1986a; Leighton and Leighton 1983). Our study demonstrates that in some instances, there may be sufficient variability among habitats that animals may be able to take advantage of spatial differences in food abundance to cope with local food shortages. Thus, instead of exploiting alternative resources when food is scarce, animals may exploit different habitats.

With respect to the 29 species of trees we examined, the old successional forest had a higher density than either pristine semi-evergreen forest or the younger successional forest. However, the

pristine semi-evergreen forest exhibited more constant food production than the successional forests. We cannot provide sufficient evidence to suggest that frugivore and folivore populations originally inhabiting pristine semi-evergreen forest could be sustained in successional semi-deciduous forest. However, we suggest that if the forest is allowed to regenerate around patches of pristine semi-evergreen or perhaps riverine forest, these populations could be supported by relying on the high food abundance of successional forests during certain times of the year, and exploiting the more constant food production of the pristine semi-evergreen forest during times of food scarcity in the successional forest.

Literature Cited

- CHAPMAN, C. 1988a. Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. *Behaviour* 105: 99-106.
- . 1988b. Patterns of foraging and range use by three species of neotropical primates. *Primates* 29: 177-194.
- CHARLES-DOMINIQUE, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guyana, pp. 119-135. In A. Estrada and T. H. Fleming [eds.], *Frugivores and seed dispersal*. Dr. W. Junk Publishers, Dordrecht.
- DAUBENMIRE, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in northwestern Costa Rica. *J. Ecol.* 60: 147-170.
- FOSTER, R. 1982. The seasonal rhythm of fruitfall on Barro Colorado Island, pp. 151-172. In E. G. Leigh, A. S. Rand, and D. M. Windsor [eds.], *The ecology of a tropical forest: Seasonal rhythms and long-term changes*. Smithsonian Instn. Press, Washington.
- FRANKIE, G. W., H. G. BAKER AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forest in the lowlands of Costa Rica. *J. Ecol.* 62: 881-919.
- GOLLEY, F. B. (ed.). 1983. *Tropical rain forest ecosystems: Structure and function*. Elsevier, New York. 381 p.
- HUBBELL, S. P. 1979. Tree dispersion, abundance, and diversity in tropical dry forest. *Science* 203: 1299-1309.

- JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* 21: 620-637.
- . 1986. Guanacaste National Park: Tropical, ecological, and cultural restoration. Editorial Univ. Estatal a Distancia. San Jose.
- . 1988. Temperature and rainfall records for Santa Rosa National Park, Guanacaste, Costa Rica. Unpublished report.
- AND R. LIESNER. 1980. Annotated check-list of plants of lowland Guanacaste Province, Costa Rica, exclusive of grasses and nonvascular cryptogams. *Brenesia* 18: 15-90.
- KOPTUR, S., W. A. HABER, G. W. FRANKIE AND H. G. BAKER. 1988. Phenological studies of shrubs and treelets in tropical cloud forests of Costa Rica. *J. Trop. Ecol.* 4: 323-346.
- LEIGHTON, M. AND D. R. LEIGHTON. 1982. The relationship of size of feeding aggregate to size of food patch: Howler monkeys feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. *Biotropica* 14: 81-90.
- AND ———. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest, pp. 181-196. *In* S. L. Sutton, T. C. Whitmore and A. C. Chadwick [eds.], *Tropical rain forest: Ecology and management*. Blackwell, London.
- LIEBERMAN, D. AND M. LIEBERMAN. 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982). *J. Trop. Ecol.* 3: 347-358.
- MURPHY, P. G. AND A. E. LUGO. 1986. Ecology of tropical dry forest. *Annu. Rev. Ecol. Syst.* 17: 67-88.
- OKALI, D. AND B. A. OLA-ADAMS. 1987. Tree population change in treated rain forest at Omo Forest Reserve, southwestern Nigeria. *J. Trop. Ecol.* 3: 291-313.
- PETERS, R. H., S. CLOUTIER, D. DUBE, A. EVANS, P. HASTINGS, H. KAISER, D. KOHN AND B. SARWER-FONER. 1988. The ecology of the weight of fruit on trees and shrubs in Barbados. *Oecologia* 74: 612-616.
- SWAINE, M. D., D. LIEBERMAN AND F. E. PUTZ. 1987. The dynamics of tree populations in tropical forest: A review. *J. Trop. Ecol.* 3: 359-366.
- TERBORGH, J. 1986a. Community aspects of frugivory in tropical forests, pp. 371-384. *In* A. Estrada and T. H. Fleming [eds.], *Frugivores and seed dispersal*. Dr. W. Junk Publishers, Dordrecht.
- . 1986b. Keystone plant resources in the tropical forest, pp. 330-344. *In* M. E. Soule [ed.], *Conservation biology: The science of scarcity and diversity*. Sinauer Associates, Inc. Sunderland, MA.
- WEBB, L. J., J. G. TRACEY, AND W. T. WILLIAMS. 1972. Regeneration and pattern in a subtropical rain-forest. *Ecology* 60: 675-696.