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Fruit Fall in the Luquillo Experimental Forest, Puerto Rico[1]

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ABSTRACT

Fruit fall in the Luquillo Experimental Forest (LEF) varied with forest type but averaged 600 kg/ha/yr for the 11,000 ha forest. Within a given forest type, fruit fall varied spatially and seasonally. A palm (*Prestoea montana*) flood plain forest averaged 560 kg/ha/yr and individual palm fruit mass changed from season to season. Lower montane wet, or tabonuco (*Dacryodes excelsa*), forest had a low rate of fruit fall (332 kg/ha/yr) and strong seasonal pulses in both space and time. Fruit fall was higher in secondary forests (820 kg/ha/yr) and plantations (1418 kg/ha/yr) than in mature tabonuco forests that normally occur in those sites. Fruit fall in the upper montane, or palo colorado (*Cyrilla racemiflora*), forest averaged 263 kg/ha/yr. Somewhere in the LEF there always appears to be a stand at peak rate of fruit production. Fruit fall data are used to reduce a previous estimate of forest carrying capacity for the endangered Puerto Rican parrot, *Amazona vittata,* from 51,000 to 2000–38,000 birds.

RESÚMEN

La caída de frutos en el Bosque Experimental de Luquillo (BEL) varió con el tipo de rodal pero tuvo como promedio 600 kg/ha/año para las 11,000 ha del bosque. En cada tipo de bosque se observaron variaciones estacionales y espaciales en la caída de frutos. La caída de frutos en el bosque de palmeras (*Prestoea montana*) en planicies inundables fue de 560 kg/ha/año y la masa de frutos individuales varió a través de las estaciones. La caída de frutos en el bosque montano bajo muy húmedo localmente conocido como bosque de tabonuco (*Dacryodes excelsa*), fue de 332 kg/ha/año y se caracterizó por una estacionalidad marcada en tiempo y espacio. La caída de frutos fue más alta en bosques secundarios (820 kg/ha/año) y plantaciones (1418 kg/ha/año) que en los bosques maduros de tabonuco que normalmente predominan en esos sitios. En el bosque montano de palo colorado (*Cyrilla racemiflora*) la caída de frutos fue de 263 kg/ha/año. Observamos que durante cualquier mes del año algún rodal del BEL exhibe una caída máxima de frutos. Utilizamos la caída de frutos para estimar la capacidad que tiene el bosque para sostener poblaciones de la cotorra puertoriqueña (*Amazona vittata*), una especie en peligro de extinción. Encontramos que esta capacidad fluctúa entre 2000 y 38,000 animales. Anteriormente se había estimado una capacidad de alimentación para 51,000 cotorras.

Key words: Amazona vittata; *Caribbean forests; fruit fall; fruit production; Luquillo Experimental Forest; palm fruits; parrots; phenology; plantations; Puerto Rico; tropical trees.*

Management of tropical forests requires quantitative information of ecosystem processes. Unfortunately, much relevant ecological research fails to influence forest management because results are unavailable to managers, or because its relevance is not obvious. An example is fruit fall data, which are normally collected in ecological studies as part of litterfall measurements, but seldom used for purposes other than budget estimates of nutrients and biomass. Fruit fall data are not presented in Bray and Gorham's (1964) review of world litter production literature nor in Brown and Lugo's (1982) review of litter production in tropical forests. In fact, most studies of litterfall combine fruits with other miscellaneous components including flowers, bark, or seeds. Yet, fruit fall data is important for understanding geographic variation in reproductive output of tropical trees, and for estimating regenerative potential of these forests after disturbance (Terborgh 1990a). Animal activity is also influenced by fruit fall (Gautier-Hion 1990, Howe 1990).

Our objective is to review available fruit fall data for five forest ecosystems in the Luquillo Ex-

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TABLE 1. *Sources of information on fruit fall for the Luquillo Experimental Forest and methods used in the determination of fruit fall rates.*

Forest type and time interval of study	Area sampled (ha)	Number and area of baskets (m^2)	Frequency of sampling	Source
Tabonuco (lower montane) forest				
1964–1966	based on observations of 50 palms		monthly	Bannister 1970
1964–1966	2	50 (0.5)	monthly	Wiegert 1970
1967	?	55–?	monthly	Kline *et al.* 1967
1980–1981	4	80 (1.0)	bi-weekly	Patterson-Zucca, pers. comm.
1986–1987	10	60 (1.0)	monthly	Devoe 1989
Secondary forest				
1981–1982	0.8	80 (0.25)	bi-weekly	Lugo 1992
Plantations				
1981–1982	0.8	80 (0.25)	bi-weekly	Lugo 1992
1986–1987	0.4	60 (0.25)	bi-weekly	Cuevas and Lugo, pers. comm.
Palo colorado (upper montane) forest				
1981–1982	0.8	20 (0.25)	monthly	Weaver 1987
Palm flood plain forest				
1980–1981	0.25	20 (1.0)	bi-weekly	This study and Frangi and Lugo 1985

perimental Forest (LEF) as a necessary step to develop a data base useful to forest managers. As an illustration of the potential usefulness of fruit fall data to forest management, we review the estimate of parrot carrying capacity of Snyder *et al.* (1987).

We take advantage of an extensive data set on fruit fall available for the LEF (Table 1). Measurements began in the 1960s in the Rain Forest Radiation Project (Odum & Pigeon 1970) and have expanded to several forest types using the same methodology. We focus on three of the four forest environments in the LEF: lower montane (mature, secondary, and plantation stands) tabonuco (*Dacryodes excelsa*); sierra palm (*Prestoea montana* synonymous with *Euterpe globosa*); and palo colorado (*Cyrilla racemiflora*) forests. Because of high dominance by few species, the forest types of the LEF are usually designated by the common name of the dominant species. These ecosystems are described in detail in Brown *et al.* (1983). We lack fruit fall information for cloud forests which grow on mountain tops.

METHODS

The methods consisted of random placement of baskets on the forest floor of each type of forest, periodic collection of material that fell on baskets, separation of material by litter component in the laboratory, drying to constant weight, and weighing. Because the area of the basket is known as well as the time interval between collections, it is possible to arrive at a quantitative estimate of fruit fall for the whole ecosystem (Table 1). Most fruit production studies count fruits on or below individual trees (*e.g.*, Foster 1990) or estimate fruit abundance qualitatively (*e.g.*, Milton 1991). The method used here provides a quantitative area-based estimate of falling fruits. Our method does not measure fruit production rates because it does not account for fruit consumption prior to fruit fall. The single estimate of sierra palm fruit production that we have for the LEF was 14 times that of the measured fruit fall for the species (Bannister 1970).

The absolute fruit fall of various sectors of the LEF was estimated using stand fruit fall data and information on forest area reported in Brown *et al.* (1983). Palm flood plain forest fruit fall per unit area data were multiplied by the area of palm brake forest to arrive at an estimate of fruit fall in palm forests. This assumes that trees in the flood plain are as productive as those in the steep slopes that characterize the palm brake. We believe the assumption overestimates fruit fall as flood plains appear to be more productive than palm brakes (Frangi & Lugo 1985, Lugo & Rivera Batlle 1987, Lugo *et al.* in press).

From the outset we had an interest in sierra palm fruits because they are the preferred and sometimes the single food source of the endangered Puer-

TABLE 2. *Sierra palm* (Prestoea montana) *fruit mass and density data for the Luquillo Experimental Forest. Standard error and number of fruits (in parentheses) are shown.*

Forest type and species	Parameter	Value	Source
Palm flood plain			
Prestoea montana	Fruit weight (g)		
	Green	1.08 ± 0.03 (37)	This study
	All in litter fall	0.81 ± 0.03 (1706)	This study
	All April–Sept. 1980	0.86 ± 0.05 (1632)	This study
	Damaged	0.59 ± 0.04 (75)	This study
	Fruit density on ground (#/m^2)	42 ± 86 (100 plots)	This study
Tabonuco (lower montane) forest			
Prestoea montana	Fruit weight (g)		
		0.07 (seed)	Bannister 1970
		0.59 (seed)	Devoe 1989
		0.52	Patterson-Zucca, pers. comm.
	Fruit density on ground (#/m^2)		
		37.7–55 (below palms)	Bannister 1970
		1.41 (whole forest)	
		0.06–4.3	Odum 1965

to Rican parrot (*Amazona vittata* or higüaca). Moreover, the sierra palm tree is one of the most abundant tree species in the wet and rain forests of the Caribbean (Lugo *et al.* 1992). We therefore supplemented the data set with additional measurements on this species using ecosystem-level information. Palm fruits falling on randomly located traps in a flood plain forest were classified according to their appearance (fresh [green] or old [damaged] fruits), counted, dried to constant weight at 60°C, and weighed individually. In addition, we had access to unpublished information based on monthly observations of 23 sierra palm trees growing in two of the traditional forest feeding sites of the higüaca (Institute of Tropical Forestry files).

We dissected 37 sierra palm fruits to separate the pericarp eaten by parrots (Snyder *et al.* 1987) from the rest of the fruit. This portion was dried and weighed separately. Chemical analysis for this part of the fruit was reported in Snyder *et al.* (1987). We multiplied mass by nutrient concentration to estimate total nutrient content of the tissue consumed by parrots. To estimate the amount of sierra palm food available to parrots, we multiplied fruit fall by the fraction that was pericarp. This is an underestimate because it ignores the amount of fruit that is eaten before fall but by using flood plain fruit fall data, we may overestimate fruit fall.

Sierra palm fruit fall was also compared with total fruit fall in other forest types in the LEF. For these comparisons we used data in Odum (1965), Kline *et al.* (1967), Bannister (1970), Wiegert (1970), Weaver (1987), Weaver and Murphy (1990), Lugo (1992), and unpublished information of Patterson-Zucca, Cuevas and Lugo, and in the files of the Institute of Tropical Forestry (Table 1).

RESULTS

SIERRA PALM FOREST FRUIT FALL.—Peak fruit fall in flood plain forests during 1980 occurred between May and August (Fig. 1) when 75 percent of the collection baskets ($N = 20$) had palm fruits. In 1981 fruit fall decreased dramatically. The variability of fruit fall was much higher in 1980 than in 1981. The mass of individual palm fruits varied seasonally and also by condition *i.e.,* green fresh fruits > damaged old fruits (Fig. 2a; Table 2). The average mass of individual fruits in the flood plain forest was higher in 1980, a year of high fruit fall, than in 1981, a year of low fruit fall (Fig. 2a). The proportion of green fruits that was available to parrots (the pericarp) was 12 percent; the rest of the fruit is not consumed by the higüaca (Snyder *et al.* 1987). We don't know if the weight of pericarp changes seasonally or annually.

In the traditional feeding grounds of the higüaca, palm trees had peak values of ripe fruits during February 1987 and December to February in 1988 (Fig. 3). The same pattern was observed in the number of inflorescences bearing fruits per tree.

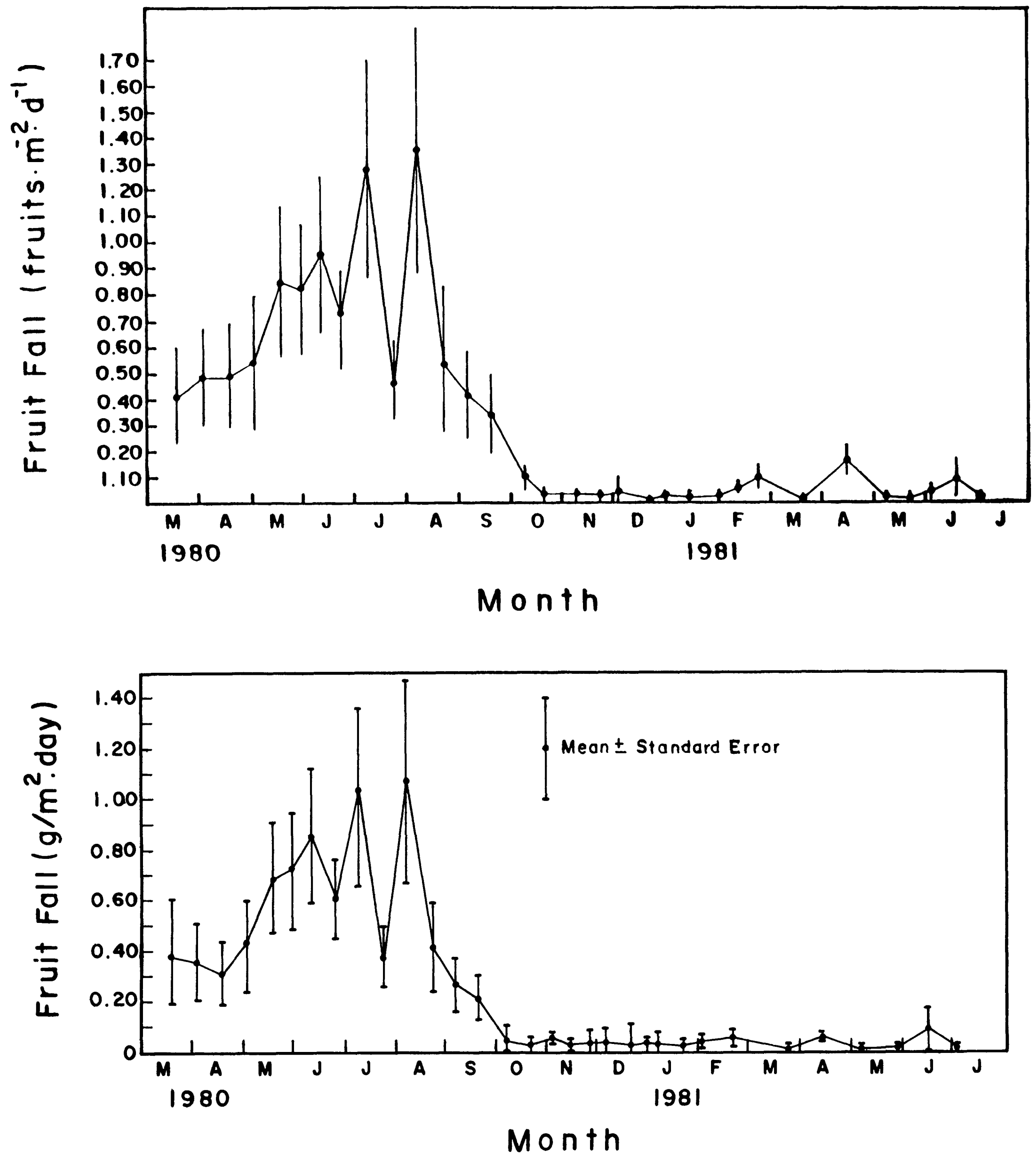

FIGURE 1. Rate of fruit fall in a flood plain forest in the Luquillo Experimental Forest. Fruit fall was measured in (a) number and (b) biomass of *Prestoea montana* fruits which dominated fruit fall in this forest. Standard error bars are based on 20 values per sampling period.

Tabonuco forest fruit fall.—Mature tabonuco forest produced a low but steady supply of fruits year-round, although at anytime different species exhibited pulses of production (Fig. 4; Estrada Pinto 1970, Odum 1970, Devoe 1989, Lugo 1992, C. Patterson-Zucca, pers. comm.). During 1964 to 1966 the forest had a peak of flower production between June and December. Peaks of fruit fall occurred between October and December (Odum 1970). Devoe (1989) reported low fruit fall rates in May and June 1987, and peak rates in July and August 1987. Figure 4 shows peaks of fruit fall in April and October of 1981.

On an annual basis fruit fall in the mature tabonuco forest varied widely from one stand to another (Wiegert 1970, Devoe 1989, C. Patterson-Zucca, pers. comm.). For example, 1981 fruit fall in four adjacent 1-ha plots studied by Patterson-Zucca was 207, 24.2, 16.4, and 9.6 kg/ha. Individual seed mass also changes seasonally in this

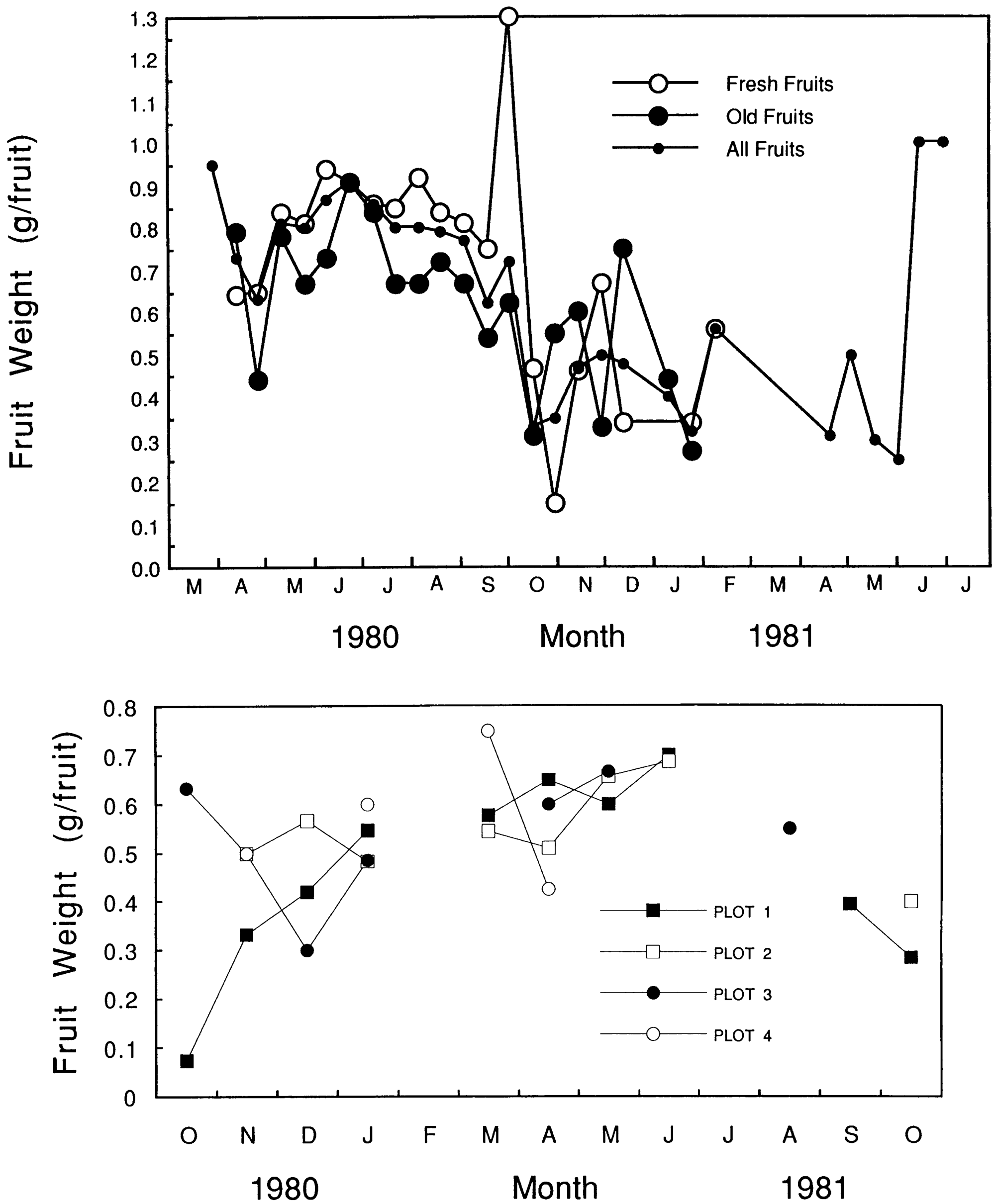

FIGURE 2. Variation in the dry weight of *Prestoea montana* fruits falling in (a) the flood plain forest, and (b) in tabonuco (*Dacryodes excelsa*) forest in the Luquillo Experimental Forest. Tabonuco forest data are from C. Patterson-Zucca (pers. comm.).

forest (Devoe 1989). In addition, fruit fall varied from year to year (Fig. 5).

Bannister (1970) observed sierra palms inside tabonuco forests at peak fruit production in October to February, and at maximum fruit fall between February and April. She observed palms bearing fruit all year long, but more than 50 percent of them had fruits between November and February. She reported large year to year variation in these patterns.

Sierra palm fruit mass also varied seasonally inside tabonuco forest (Fig. 2b). The average individual fruit mass of sierra palm in tabonuco forest is lower than that in the flood plain forest (Table 2; Fig. 2). The low value reported by Bannister (1970) has not been confirmed by subsequent stud-

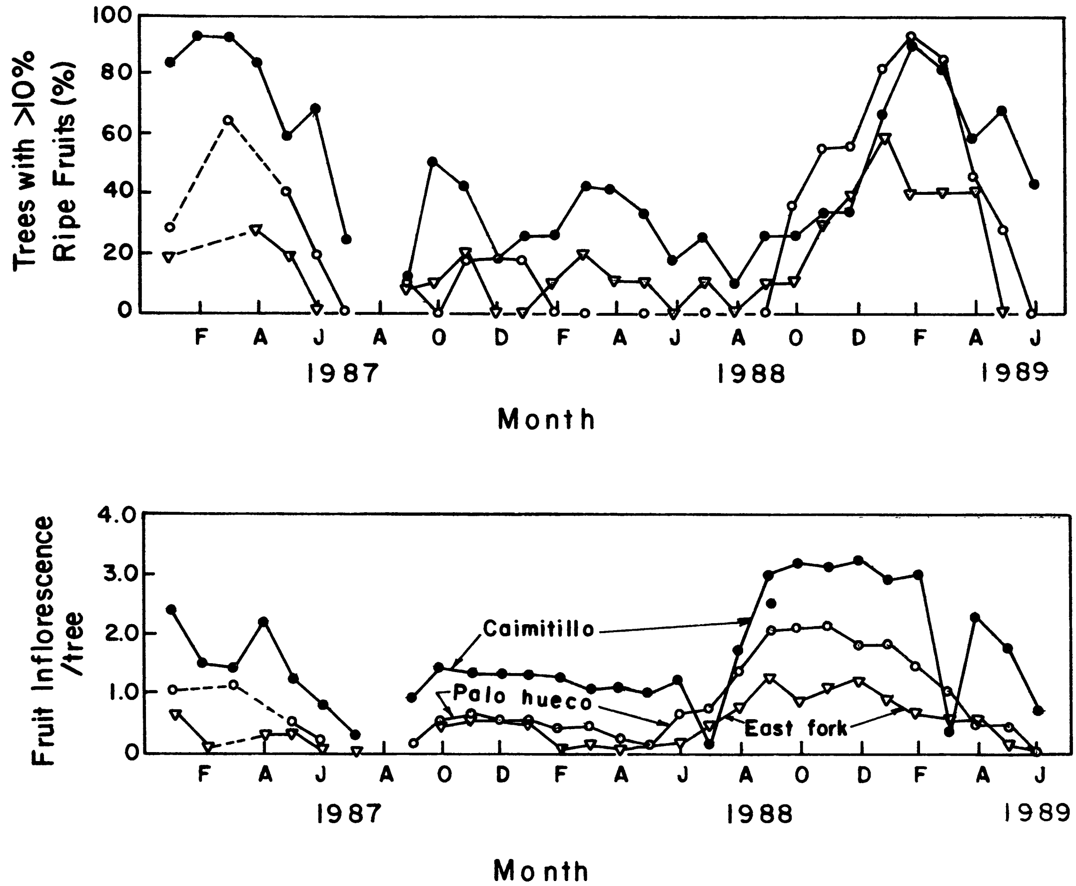

FIGURE 3. Phenology of 23 *Prestoea montana* trees in the Luquillo Experimental Forest. Trees were growing in a traditional foraging area of the Puerto Rican parrot, *Amazona vittata*. Data are from the files of the Institute of Tropical Forestry.

ies. Fruit density on the forest floor appears to be a function of distance from source trees (Table 2).

Secondary forests in the tabonuco forest zone ranged widely in annual fruit fall, probably due to age differences and species composition (Lugo 1992; Fig. 5). The seasonal fruit fall variation in these forests was similar to that in mature stands in the sense that peaks and valleys can occur at any time of the year (Fig. 6). This phenological behavior could also be a function of species composition.

Plantation forests growing in the tabonuco forest zone had the broadest range of fruit fall among all forest types in the LEF (Fig. 5). Values ranged from no fruit fall or a low fruit fall in a 4 yr old pine (*Pinus caribaea*) plantation (Guzmán in Fig. 6) and an 18 yr old mahogany (*Swietenia macrophylla*) plantation (Sabana in Fig. 6) to about 3700 kg/ha/yr in a 26 yr old *Eucalyptus patentinervis* plantation (Cuevas and Lugo, pers. comm.). An older pine plantation (Cubuy in Fig. 6) had multiple peaks of fruit fall while an old mahogany plantation (El Verde in Fig. 6) had a single, but high, peak of fruit fall during 1981 and 1982. Ten plantation species of the same age, growing adjacent to each other in the LEF arboretum, exhibited different seasonal rates and patterns of fruit fall (Cuevas and Lugo, pers. comm.). For example, five species had periods of peak fruit fall between December and April (*P. elliottii, S. macrophylla, P. caribaea, Terminalia ivorensis,* and *Khaya nyasica*). Three species had no marked peaks of fruit fall during the year of study (*Hibiscus elatus, E. patentinervis,* and *Anthocephalus chinensis*).

PALO COLORADO FOREST FRUIT FALL.—Fruit fall in the palo colorado forest studied by Weaver (1987) was 276 and 250 kg/ha/yr in 1981 and 1982, respectively. With the exception of certain planta-

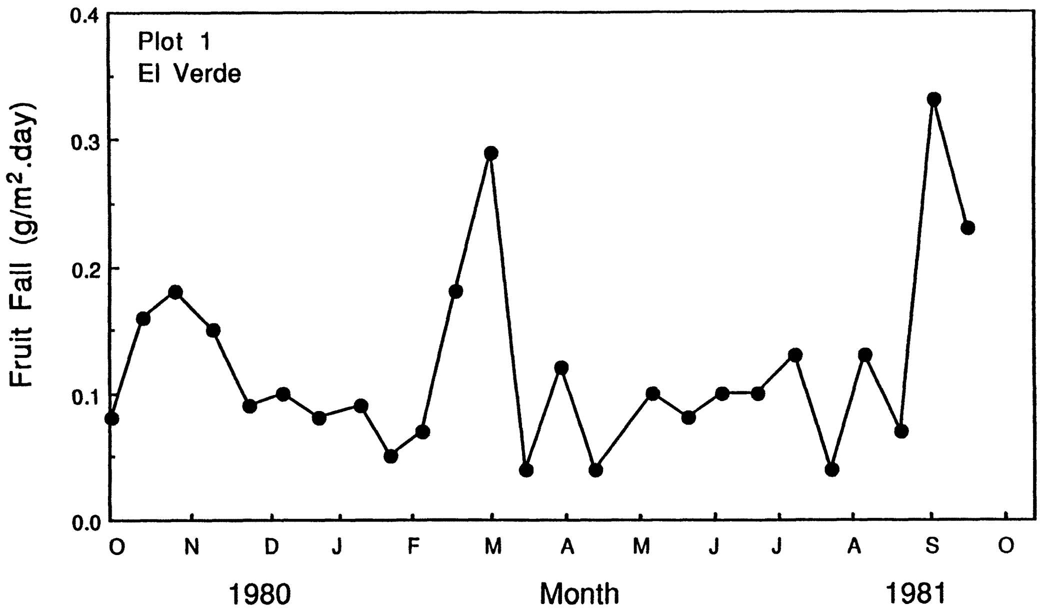

FIGURE 4. Fruit fall in tabonuco (*Dacryodes excelsa*) forest at El Verde, Luquillo Experimental Forest. These are data from one of four replicate 1-ha sites studied by C. Patterson-Zucca (pers. comm.). Table 1 summarizes methods used.

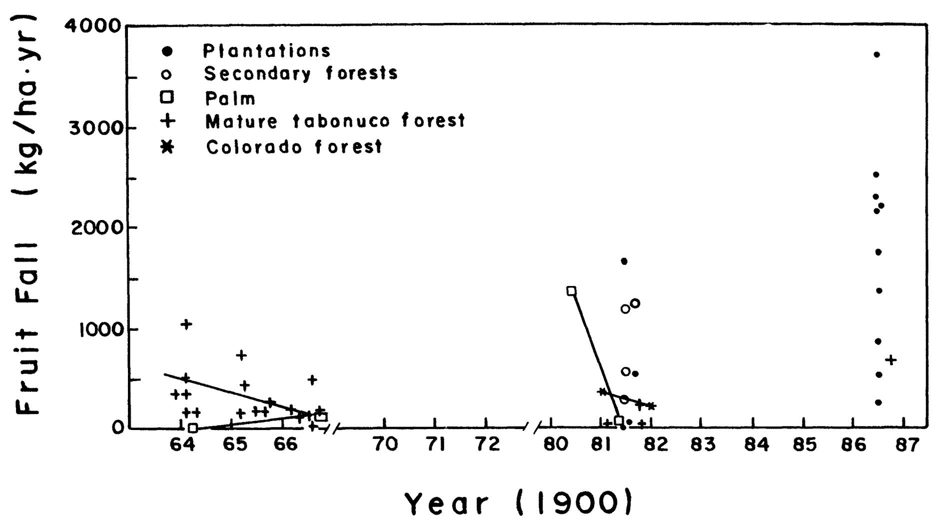

FIGURE 5. Annual rate of fruit fall in several forest types in the Luquillo Experimental Forest. Plantation and secondary forest data for 1981–1982 are from Lugo (1992). Plantation data for 1986–1987 correspond to ten different plantation stands in the Arboretum (Cuevas & Lugo, pers. comm.). Lugo *et al.* (1990) describe these plantations and methods are summarized in Table 1. Palm data are from this study, but the 1964, 1967, and 1986–1987 data were based on information in Bannister (1970), Kline et al. (1967) and Devoe (1989), respectively. These data correspond to palm trees (*Prestoea montana*). Mature tabonuco forest data are from Wiegert (1970) for the 1964–1967 data, C. Patterson-Zucca (pers. comm.) for 1981 data, and Devoe (1989) for 1986–1987 data. Palo colorado forest data are from Weaver (1987).

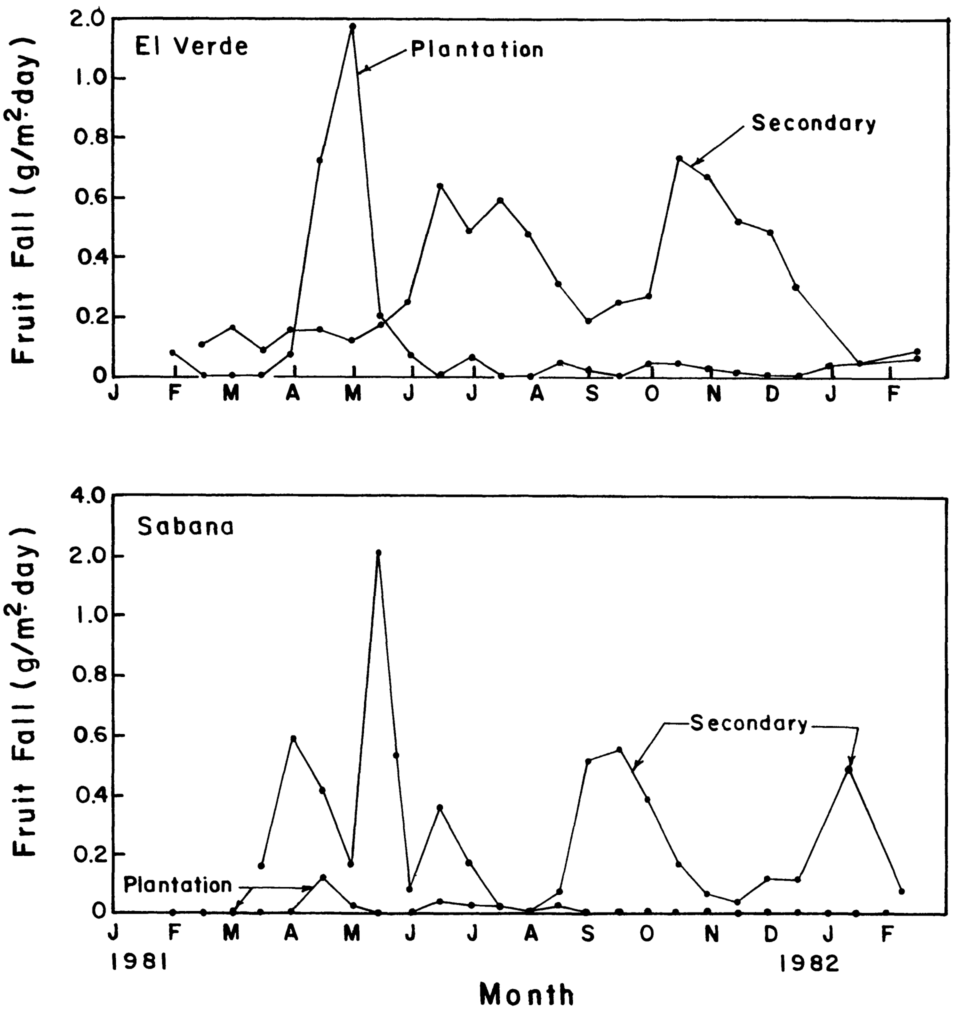

FIGURE 6. Seasonal pattern of fruit fall in plantations and paired secondary forests in the tabonuco forest zone of the Luquillo Experimental Forest. Sites are described in Lugo (1992). Data are from the files of the Institute of Tropical Forestry.

tions, these were the lowest rates observed in the LEF. Weaver reported peak fruit fall between April and August. The pattern occurred two years in a row (1981 and 1982). He reported more wind in stands during periods of peak fruit fall.

DISCUSSION

TEMPORAL AND SPATIAL VARIATION IN FRUIT FALL.— Results show strong seasonal (Figs. 1, 3, and 6) and annual (Fig. 5) variation in fruit fall in all forest types of the LEF. Similar temporal variation in fruit fall has been described in other tropical forests (Wheelwright 1986, Dunham 1990, Foster 1990, Terborgh 1990b). When periods of peak fruit fall of all forest types are considered together, there is no month in the year when one of the forest types is not at peak fruit fall. However, sierra palm and secondary forests appear to have the longest periods of peak fruit fall, while plantations and mature tabonuco forests have the shortest. The variation from year to year is evident if one compares fruit fall in tabonuco forests in the 1960s with the 1980s; colorado forest in 1981 and 1982, and sierra palm forest in 1980 with 1981 (Fig. 5).

Fruit production is also variable in space even within the same forest type. This is evident if one compares the phenology of three palm populations

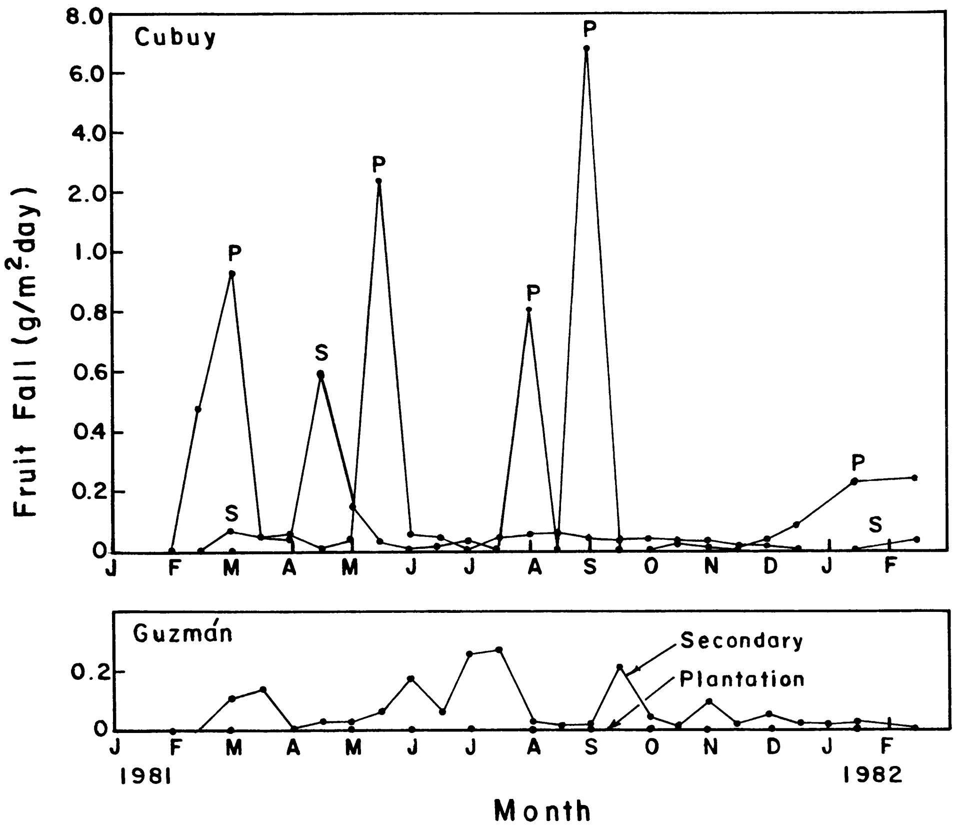

FIGURE 6. Continued.

in the late 1980s (Fig. 3), the fruit fall of mature tabonuco forest in three geographic locations in the 1960s (Wiegert 1970), or the variation of fruit fall for 1986 in plantations inside the arboretum (Fig. 5). Wheelwright (1986), Foster (1990), and Milton (1991) described similar spatial variation in other tropical forests.

Variation within a species.—The occurrence of the sierra palm in tabonuco and palm flood plain forests allows us to compare the behavior of this species in two contrasting communities. Fruit production by palms, measured in terms of the numbers of fruits that fell (Fig. 1a), was almost a hundred times higher in the flood plain forest in 1980 than in the tabonuco forest in the early 1960s (based on Bannister 1970). If data are expressed in mass units (Figs. 1b, 5), the difference is greater because of differences among individual fruits. Palm fruits in the flood plain forest are heavier than palm fruits in the tabonuco forest (Table 2; Figs. 2a and b, 5). However, in 1981 the flood plain forest produced a similar quantity of palm fruits as did the tabonuco forest. Differences in fruit fall influence the number of fruits on the forest floor (Table 2) *i.e.*, more fruits on the flood plain forest floor than on the tabonuco forest floor, and must also influence the life history of palm populations in these forests.

Estimating total fruit fall.—On a total area basis, most of the fruit fall in the LEF occurs in secondary forests, followed by sierra palm forests (Table 3). Fruit fall among mature forests peaks in the flood plain forest (750 m elev.) with lower values at lower (tabonuco) and higher (palo colorado) elevations (Table 3). Secondary forests had higher fruit fall than mature stands within the tabonuco forest type. Moreover, fruit fall increases within certain plantations relative to the tabonuco stand that they replaced (Table 3).

On an average year in the LEF, fruit fall in mature tabonuco forests is relatively low. Sierra palm fruits constitute about 12 percent of the total fruit fall in the LEF. Sierra palm fruit fall is highest in

TABLE 3. *Estimates of palm (*Prestoea montana*) and total fruit fall by forests in the Luquillo Experimental Forest.*

Forest type	Area[a] (ha)	Palm fruits: Unit area mean fall (kg/ha/yr)	Palm fruits: Total fall (Mg/yr) Low	Mean	High	All fruits: Unit area mean fall (kg/ha/yr)	All fruits: Total fall (Mg/yr) Low	Mean	High
Tabonuco									
Mature	1132	35	6	40	118	332	57	376	1189
Secondary	3593	86[b]	111	309	467	820	1056	2946	4449
Plantations	378	0	0	0		1418	0	536	1397
Palo colorado	2083	0	0	0		263	520	548	575
Palm	2024	560	146	1133	2732	560	146	1133	2732
Total	9210	161[c]	263	1482	3317	600[c]	1779	5539	10,342

[a] From Brown *et al.* (1983); areas are approximate, cloud forest and deforested land not included.
[b] Used same proportion to total fall as in mature tabonuco forest.
[c] Area weighted average.

the palm flood plain forest, no matter the unit of measurement (on a unit area or total area basis; Table 3). Within tabonuco forests, sierra palm fruit fall is about 10 percent of the total fruit fall.

Area-weighted fruit fall in the LEF (600 kg/ha/yr) is low compared to the values reported by Terborgh (1986, 1990b) for a Peruvian rain forest at Cocha Cashu (~2737 kg/ha/yr) or by Singh *et al.* (1990) for central Himalayan oak forests at (2500–3500 kg/ha/yr). However, individual stands in the LEF reach the higher values reported elsewhere. Our results are higher than those of Morellato (1992) for subtropical moist altitudinal and semideciduous forests in southeastern Brazil (160 and 400 kg/ha/yr, respectively) and those of Dunham (1990) for riverine woodlands in Zimbabwe (7 to 559 kg/ha/yr).

REVISING THE ESTIMATE OF SNYDER *ET AL.* (1987).— Fruit production data were considered for the development of a management plan for the endangered Puerto Rican parrot. Snyder *et al.* (1987) estimated that over 1.5 million sierra palms produced over 7.5 billion fruits per year, or an amount capable of supporting some 51,000 higüacas. This estimate and other analyses of the parrot's natural history supported the assumption that food was not limiting to the bird. As a result, a long-term effort to rescue the species from extinction has focused on nesting sites and reproductive success rather than food availability (Snyder *et al.* 1987).

The large difference between high and low years of fruit fall greatly affect the food carrying capacity of the forest. Using the same food demand given by Snyder *et al.* (1987) for the parrot (87.6 kg/parrot/yr), and sierra palm fruit fall data in Table 3, we estimated a carrying capacity of 3000 to 38,000 parrots. The wide range in the estimate reflects the range of fruit fall between high and low years. The calculation uses only one source of food but is based on fruit fall, not production. We don't know the ratio of fruit production to fruit fall in the various forest types and during different seasons. Therefore, our estimate is conservative and much

TABLE 4. *Sierra palm (*Prestoea montana*) food availability (kg/yr) to the parrot* Amazona vittata *in the Luquillo Experimental Forest.*

Seasonal value[a]	Mass[b]	Protein[c]	Fat[c]	Fiber[c]	Ca[c]	Carbohydrates[c,d]
Maximum	398,040	20,379	57,676	124,228	2607	153,683
Minimum	31,560	1616	4573	9850	207	12,185
Average	177,840	9105	25,769	55,503	1165	68,664

[a] Based on fruit fall data in Table 3.
[b] 12% of fruit fall is pericarp.
[c] Average concentration value from Snyder *et al.* (1987).
[d] Water soluble.

lower than the estimate of 51,000 of Snyder *et al.* (1987).

The estimate can be further constrained if carrying capacity is based not on total sierra palm fruit fall but on food available in fruits by multiplying total palm fruit fall by the nutritional quality of pericarp (in Snyder *et al.* 1987) and the percentage of the fruit (the pericarp) actually consumed by the bird (12%). With these data (Table 4), the carrying capacity for the higüaca is reduced to an average of about 2000 birds. Even if this value is multiplied by 14 (to account for the difference between fruit production and fruit fall [Bannister 1970]) it results in a low carrying capacity for parrots. The assumption that food was not limiting to parrots when populations were much larger than today may have to be revised and perhaps even the recovery strategy of today's program requires revision because it has not considered food availability per unit area of habitat as potentially limiting to the current population.

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