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ARE FIGS ALWAYS KEYSTONE RESOURCES FOR TROPICAL FRUGIVOROUS VERTEBRATES? A TEST IN GABON¹

ANNIE GAUTIER-HION

Station Biologique de Paimpont, CNRS UA 373, 35380 Plélan-le-Grand, France

AND

GEORGES MICHALOUD

Institut de Botanique, CNRS UA 327, Rue A. Broussonet, 64000 Montpellier, France

Abstract. This paper evaluates the suggestion of Terborgh (1986) that figs constitute “keystone plant resources” for frugivorous mammals and birds in African rain forests as they appear to do in South America and Asia. From studies of the diets of monkeys and other mammals and birds in Gabon, we show that figs are infrequently eaten by most species, and are always eaten in small amounts. Figs in Gabon occur at very low densities and have unpredictable fruiting patterns and relatively low crown production. Thus, fig fruits are not staple foods and cannot sustain most populations of frugivorous species during periods of low fruit availability. In Gabon, monkeys and large birds depend on the fruit of two species of Myristicaceae and of one species of Annonaceae. These regularly bear ripe fruit during the lean period and are abundantly consumed. Figs occur in such distant patches that they are mainly fed on by wide-ranging animals such as large frugivorous bats.

Key words: *Annonaceae; figs; frugivorous vertebrates; Gabon; keystone resources; Myristicaceae; rain forest monkeys.*

INTRODUCTION

Leighton and Leighton (1983) showed the importance of figs in a Bornean rain forest by identifying 30 species important to diurnal birds and monkeys. They stated that “the reproductive biology of figs makes them uniquely suited to play roles as keystone mutualists for many vertebrates.”

In a recent paper, Terborgh (1986) identified several plants that play a “key role” in the nutrition of frugivorous vertebrates during the period of fruit scarcity in the Manu tropical rain forest (Peru). Three species of palm nut and three figs were the most important of these resources. All were characterized by: a low interannual variation in fruit production, and/or by a regular timing of their fruiting period, and by a high rate of consumption by frugivorous animals. According to Terborgh, both palm nuts and figs are important for birds and mammals throughout the neotropics, while figs might play a prime role in Southeastern Asia and Africa. In the present paper, we evaluate Terborgh’s suggestion for frugivorous mammals and large birds living in northeastern Gabon.

SCOPE OF THE STUDY

To determine the existence and identity of key resources, we focus on the main foods consumed during the lean season, compared to those taken during the rest of the year. This comparison is based mainly on

cercopithecines, but additional evidence from other taxa is also considered. We then closely examine the case of figs and their use as foods. We further stress the features (density, patterns of distribution, fruiting phenology, and fruit production) that enable plant species to play a key role in sustaining frugivore populations. Finally, we discuss the applicability of our results to other tropical forests.

STUDY SITE AND ANIMAL COMMUNITY

All the observations reported below come from the tropical rain forest around Makokou, Gabon (0°04' N, ~500 m altitude), particularly the M’passa plateau. The climate of the area is characterized by an annual rainfall (10-yr mean) of 1621 mm, and by the following alternation of seasons: a minor dry season (December through February), a minor rainy season (March through May), a major dry season (June through August) and a major rainy season (September through November). During the major dry season, rains are almost absent.

The extent of frugivory in mammals and large birds of the Makokou Forest is well established (Gautier-Hion et al. 1980, Emmons et al. 1983, Gautier-Hion et al. 1985a, Brosset and Erard 1986). Detailed information has been published on the diets of forest rats (Duplantier 1982), squirrels (Emmons 1980), ruminants (Dubost 1984, Feer 1988) and monkeys (Gautier-Hion 1971, 1977, 1980, Quris 1975, Gautier-Hion and Gautier 1978, Gautier-Hion et al. 1981, Sourd 1983). Overall, fruit and seeds make up ~78% on av-

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erage of the diet of 85% of the 66 mammalian primary consumers.

PLANT COMMUNITY AND FRUITING PATTERNS

Fruiting in the Makokou Forest is seasonal (Emmons 1980, Gautier-Hion 1980, Gautier-Hion et al. 1981, 1985*b*). Despite interannual variations (in a 5-yr sampling), the mean number of fruiting species and fruiting individuals is greatest from October to February and lowest from June to August, i.e., during the major dry season, which represents the lean period for frugivorous vertebrates.

METHODS OF ANALYSIS

The annual diets of frugivores were analyzed by two methods: (1) the study of stomach contents taken from animals shot by hunters (Gautier-Hion 1980); and (2) the percentage of a given fruit species relative to all fruit consumption events (one feeding event being recorded for each 15-min interval, over the daily activity cycle, Sourd and Gautier-Hion 1986). Fruit availability was estimated by: (1) the mean number of fruiting individuals found on a 6-km trail visited twice a month over a 1-yr period (Gautier-Hion et al. 1985*b*); and (2) the mean number of fruiting individuals per hectare encountered by visiting six different 1-ha plots weekly over one main dry season and the subsequent main rainy season. The number of fruits per tree was counted on felled trees (P. Heckestweiler, *personal communication*) and the fruit biomass calculated from the mean fruit mass. Plant species densities were obtained from mapping individuals over a surface area ranging from 7 to 100 ha depending on the species (for figs, see Michaloud and Michaloud-Pelletier 1987, Michaloud 1988).

RESULTS

The staple foods for monkeys

Analyses of 270 stomach contents and feeding observations were conducted on five species of guenons and two species of mangabeys. It has previously been shown (Gautier-Hion 1971, 1977, 1980, Quris 1975, Gautier-Hion and Gautier 1978, Gautier-Hion et al. 1981, Sourd 1983) that a large proportion of the monkeys' diet is made up of a small number of fruit species. This includes the fruits of *Cissus dinklagei* (Vitaceae), *Polyalthia suaveolens* (Annonaceae), and some members of the Apocynaceae and the Myristicaceae.

Staple foods outside the major dry season.—1. *Cissus dinklagei*.—Fruiting of this liana is bimodal, with maxima occurring during the rainy season (Fig. 1Aa, Ab). Fruits are succulent drupes that make up the major food of at least three monkey species. Fruit remains occurred in 62% of stomachs of *Cercopithecus pogonias*, 52% of *C. cephus*, and 38% of *C. nictitans* ($n = 214$) over the year. Consumption lasted over 11 mo,

and during four of the rainy months, >50% of all stomachs contained large amounts of *Cissus* seeds (Fig. 1Ac). During the major dry season, *Cissus* seeds were found in <10% of the stomachs. Similarly, the monthly percentage of sampling of *Cissus* fruit by a *C. cephus* troop had a yearly mean of 12.5%, with a minimum (0–4%) during the major dry season and a maximum (35%) during rainy months (Fig. 1Ad).

2. Apocynaceae.—Fruit of five apocynaceous lianas are commonly included in the monkeys' diets, the most frequent being those of *Dictyophleba stipulosa*, *Cylindropsis parvifolia*, and *Landolphia* sp. The overall fruiting pattern of these species is centered around the minor dry season (Fig. 1Ba). Fruits are large, brightly coloured polyspermous berries, covered by a thick, inedible husk enclosing a number of seeds embedded in a succulent pulp. Seeds occurred in an average of 15% of guenons' stomachs over the whole year. They reached 20% during a 4-mo period. No apocynaceous remains were found in stomachs during the major dry season (Fig. 1Bc). Similarly, these plants made up ~13% of the annual feeding records of a *C. cephus* troop and reached monthly averages around 20% from October to April (Fig. 1Bd).

In summary, together with fruits of *Cissus*, those of the Apocynaceae were present in >50% of stomachs and averaged 40% of the food items sampled by monkeys outside the major dry season.

Staple foods during the major dry season.—During the major dry season, fruit availability decreased and staple foods were no longer available. The diets of the monkeys changed significantly. A lower proportion of fruits was eaten and fewer species were sampled per day, while the consumption of insects and/or leaves increased (Gautier-Hion 1980). During this period, three fruit species were eaten most commonly: *Polyalthia suaveolens* and *Coelocaryon preussii*, followed at a lower rate by *Pycnanthus angolensis*.

1. *Polyalthia suaveolens*.—This species shows two fruiting peaks, which occurred during the two dry seasons (Fig. 1Ca, Cb). The fruits are berries, which were rarely identified in monkeys' stomachs, because only the pulp is usually swallowed. Direct observations, however, showed that these fruits constituted >25% of the monthly feeding records of *C. cephus* in June and July (Fig. 1Cd), and 15–20% for *C. nictitans* and *C. pogonias*.

2. *Coelocaryon preussii* and *Pycnanthus angolensis*.—These two species of Myristicaceae bear dehiscent monospermous drupes with arils surrounding the seeds. Fruits ripen during the major dry season: *Coelocaryon* is in fruit mainly from June to August, while the fruiting period of *Pycnanthus* extends into the following rainy season (Fig. 1Da, Db). In the main dry season, arils with or without seeds were present in 80, 75, 69, and 45% of the stomachs of *Cercocebus albigena*, *Cercopithecus pogonias*, *C. nictitans*, and *C. cephus*, respectively. In August, 100% of the stomachs analyzed

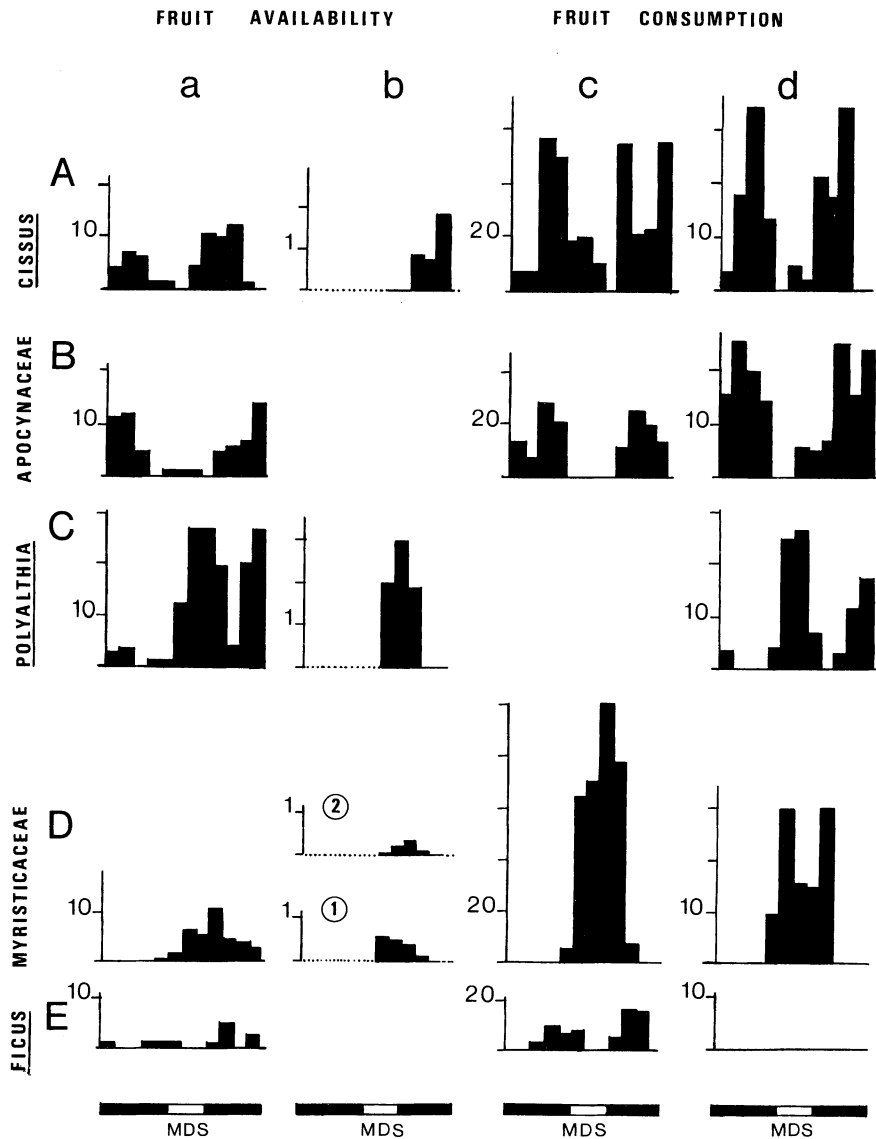


FIG. 1. Fruit availability (ripe fruit) and fruit consumption over the annual cycle from January through December. Left to right: (a) mean number of fruiting individuals found per 100 m; (b) mean number of fruiting trees per hectare; (c) percentage of guenon stomachs including fruit remains; (d) percentage of feeding records by a *C. cephus* troop. Top to bottom: (A) *Cissus dinklagei*; (B) Apocynaceae (*Dictyophleba stipulosa*, *Cylindropsis parvifolia*, *Landolphia* sp.); (C) *Polyalthia suaveolens*; (D) Myristicaceae: *Coelocaryon preussii* (1), *Pycnanthus angolensis* (2); (E) *Ficus* spp. MDS = major dry season.

contained one or both species (Fig. 1Dc). Both species made up 20% per month, on average, of the feeding records of *C. cephus* during the main dry season (Fig. 1Dd) and up to 30% for *C. pogonias*.

To sum up, berries of *Polyalthia* and arils of *Coelocaryon* and *Pycnanthus* accounted for ~50% of the food items sampled by monkeys from June through August and constituted major resources during the lean period.

Polyalthia suaveolens and the Myristicaceae in the diets of other mammals and large birds

Among 32 species of frugivorous mammals and large birds for which lists of consumed food items are avail-

able, 65% are known to eat *Coelocaryon* and/or *Pycnanthus* fruits. These included: 4 out of 7 frugivorous small terrestrial rats (Duplantier 1982), the 2 large terrestrial rodents, 4 out of 8 squirrels (L. Emmons 1980 and *personal communication*), 6 out of 7 ruminants (Dubost 1984), all 4 hornbills and 1 out of 3 turacos (C. Erard, *personal communication*). A similarly large assemblage has been observed to eat *Polyalthia* fruits (6 small rats and 2 large rodents, 2 squirrels, 7 ruminants, 3 turacos, and at least 3 hornbills). In addition, both *Polyalthia* fruit and arils of Myristicaceae were eaten by blackbirds, bulbuls, and some other small birds (Brosset and Erard 1986; C. Erard, *personal communication*).

The amount of these food species in the diets of these animals has not been estimated in all cases. However, *Polyalthia* was noted as one of the species most frequently consumed by *Cephalophus dorsalis* and *C. calipygus* (Feer 1988). Similarly, its fruits were present in large amounts in 64% of the 19 turaco and hornbill gizzards analyzed by J-P. Decoux and C. Erard (*personal communication*) from June to July. At this period, fruiting trees in the Myristicaceae were the most important feeding places for hornbills, blackbirds, and other birds, as they were for cercopithecines. Agonistic interactions among species were observed: monkeys displaced hornbills and the latter displaced smaller birds. Nocturnal and diurnal terrestrial mammals were also observed there. Therefore, Myristicaceae and *Polyalthia* fruits likely play a key role for a large community of mammals and birds.

Figs in the diets of mammals and large birds

For all fig species combined (namely 20 hemi-epiphytic species, Michaloud and Michaloud-Pelletier 1987), figs were so rare along the 6-km trail censused that no seasonal fruiting pattern could be detected (Fig. 1Ea).

Fig use by monkeys.—Figs are included in the list of food species of all mainland forest-dwelling monkeys studied (Gautier-Hion 1977, 1980). However, fig seeds were found in <8% of the stomachs of *Cercocebus albigena*, *Cercopithecus nictitans*, *C. pogonias*, and *C. cephus*, and were not included in their diets in July and August (Fig. 1Ec). Further, the number of figs eaten was always very low. Direct observations showed that monkeys did not actively search for fig trees, but fed on them opportunistically. The best evidence came from the fact that figs were not included in the fruit species sampled by a *C. cephus* troop followed during five consecutive months covering the major dry season and the subsequent rainy season (Gautier-Hion et al. 1981). Figs were not included in the diet of a neighboring troop followed over 1 yr (Sourd and Gautier-Hion 1986, Fig. 1Ed).

Although fig trees are more numerous in riparian than in mainland forest (46.5 and 1.5 individuals/ha, respectively), the importance of figs is not different for the three monkey species living in riparian forests. Figs were observed taken occasionally by *Miopithecus talapoin* in only 5 mo (all out of the main dry season); only 1 of 19 stomachs analyzed included fig seeds (Gautier-Hion 1971). Fig seeds occurred in 2 of 9 stomachs of *Cercopithecus neglectus* examined, and two direct observations of fig consumption were made during a 4-mo study (Gautier-Hion and Gautier 1978). Infrequent consumption of figs by *Cercocebus galeritus* was also reported by Quris (1975).

Fig use by other mammals and birds.—Figs were noted in the diet of only two squirrel species (Emmons 1980) and one ruminant (Dubost 1984). When examining 19 hornbill and turaco gizzards in June and

July, C. Erard and J-P. Decoux (*personal communication*) found fig seeds in only one *Tauraco macro-rhynchus* gizzard. Like monkeys, these large, canopy birds are opportunistic fig-eaters which do not actively monitor fig trees (C. Erard, *personal communication*). Among the smaller frugivorous birds, Brosset and Erard (1986) observed that figs were eaten by 6 of 15 species of Pycnonotidae, by 2 of 4 Sturnidae, and 3 of 8 species of Columbidae. However, these authors mentioned figs as important resources for only one columbid and one pycnonotid.

Six frugivorous bats occur in Makokou forest. Bradbury (1977, 1981) found that figs constituted a large amount of the diets of the two large species: *Hypsignathus monstrosus* and *Epomops franqueti*. Eighty-eight percent of the 133 oral swabs and fecal samples of *H. monstrosus* analyzed from May to October contained seeds of *Ficus*.

To conclude, figs cannot be considered as a staple food for monkeys at Makokou, nor as a major resource when fruit availability is low. Further, they do not appear to be important for large birds of the canopy, for most mammals, or for many birds of smaller size. In fact, they appear to be major food only for bats.

Key resources and foraging

Table 1 summarizes some characteristics of the biology of the three species identified as major plant foods in the major dry season. *Polyalthia* ranks sixth among the most abundant species on M'passa plateau (Caballé 1986), while *Coelocaryon* (ranked 20th) and *Pycnanthus* occur at lower densities (17.57, 1.12, and 0.44 individuals/ha, respectively, Table 1). In all three species, fruiting peaks occur in the main dry season, without significant interannual variations and with a high intraspecific synchrony (Gautier-Hion et al. 1985b). In July, a mean of 2.22 *Polyalthia*, 0.65 *Coelocaryon*, and 0.04 *Pycnanthus* trees/ha were found simultaneously bearing fruit. In August, these figures reached 2.92, 0.66, and 0.08 trees/ha (Table 1). Fruit crops are relatively large. The average biomass of fruit per individual plant for *Polyalthia*, *Coelocaryon*, and *Pycnanthus* are 14, 50, and 140 kg, respectively, when the whole fruit mass is considered, or 7, 3, and 10 kg, respectively, when only the pulp or arils are taken into account (Table 1). These arils are especially rich in lipids, and they also contain high levels of proteins (Sourd and Gautier-Hion 1986). Thus, these three plant species are well-distributed, highly predictable, abundant, and rich foods. They are particularly well suited to play a key role for frugivores during a season of fruit scarcity.

Ficus species display quite opposite characteristics. Species density is very low, ranging from 0.1 to a maximum of 0.32 individuals/ha on the M'passa plateau, with a mean overall density of 1.5 individuals/ha for all 20 species grouped (Michaloud and Michaloud-Pel-

TABLE 1. Some features of the reproductive biology of three key resources for frugivores during the lean fruit period.

	Species		
	<i>Polyalthia</i>	<i>Coelocaryon</i>	<i>Pycnanthus</i>
Density (no. individuals/ha)			
$\bar{X} \pm \text{SD}$	17.57 \pm 7.46	1.12 \pm 1.36	0.44 \pm 0.05
Range	8–30	0–6	0–3
Sample	7 ha	25 ha	25 ha
Fruiting timing			
Peaks	two dry seasons	main dry season	main dry season
Interannual variations	low	low	low
Intraspecific synchrony	high	high	high
No. fruiting trees/ha:			
July			
$\bar{X} \pm \text{SD}$	2.22 \pm 1.91	0.65 \pm 0.77	0.043 \pm 0.21
Range	0–5	0–3	0–1
Sample	23 ha	23 ha	23 ha
August			
$\bar{X} \pm \text{SD}$	2.92 \pm 1.91	0.66 \pm 0.96	0.083 \pm 0.28
Range	0–7	0–3	0–2
Sample	24 ha	24 ha	24 ha
No. of fruits/tree*			
$\bar{X} \pm \text{SD}$	5790 \pm 5133	3045 \pm 2680	8443 \pm 3779
Sample	7 trees	4 trees	4 trees
Fruit biomass (kg/individual)			
Whole fruit	14	55	140
Pulp or aril	7.2	3	10

* P. Heckestweiler, *personal communication*.

letier 1987). This low density is accompanied by a lack of fruiting peaks.

We monitored 67 trees in 1977–1978 and 150 in 1980. For four sampling days (in July, August, October, and February), the percentage of trees bearing fruit varied from 1.5% to a maximum of 9%. When only ripe fruits were considered, this percentage varied from 0 to 3.3%. In both cases, the minimum was observed during the main dry season (namely 1.5% in July and 4.2% in August for the whole fruit, and 0% in July and 1.4% in August for ripe fruits).

Similarly, from May to October, Bradbury (1977) found a maximum of 7% of trees fruiting during any single month (35 trees over 19 ha). During his 1st yr of observation, he observed only two fruiting trees in July, one in August, none in June, and no fruiting at all over the same 3 mo during the second year.

In addition to this interspecific asynchrony of fruiting, we found that fruiting among fig trees of any single species was highly asynchronous while fruiting within each tree was synchronous, the whole crop ripening in a short period of 5–10 d. Furthermore, the individual crop production was usually low (a few hundred to a few thousand fruits on a single tree) except for successful stranglers, which were able to give huge crops due to their ability to reach a larger crown development. Only 5 out of the 20 fig species (39 of the 150 trees) found at M'passa, *Ficus burretiana*, *F. macrosperma*, *F. wildemaniana*, *F. cyathistipuloïdes*, and *F. elasticoides*, have the ability to strangle. Only 7 out of

these 39 individuals did strangle their hosts (C. Berg and G. Michaloud, *unpublished manuscript*) and only three of these were successful stranglers that gave huge crops (> 10 000 fruits) at fruiting intervals ranging from 1 to 3 yr.

Figs are thus an unpredictable resource, always produced by a few trees that are widely scattered. The combined effects of low density, low individual production, and small number of simultaneously fruiting individuals make figs unsuitable to sustain populations of sedentary animals.

To illustrate the situation, we have plotted on Fig. 2 the *Polyalthia*, *Coelocaryon*, and *Pycnanthus* trees simultaneously bearing ripe fruits during two daily surveys covering 6 ha each, and the fruiting *Ficus* recorded among the 150 trees monitored in 1 d on 100 ha. It can be seen that randomly foraging animals, even those with small foraging ranges, can expect to encounter a significant number of *Polyalthia*, *Coelocaryon*, and even *Pycnanthus* fruiting trees on a given day. On the contrary, only wide-ranging animals could expect to visit a significant number of patches when relying on figs. Indeed, only nine trees bearing fruit including only five trees with ripe fruit occurred on 100 ha (Fig. 2).

DISCUSSION

This study provides evidence that figs in the Makokou Forest are infrequently and opportunistically eaten in small amounts by frugivorous birds and mammals except for large bats. Reliance on such food patches

requires that a species be able to forage very widely. This is obviously the case for *H. monstruosus* or *E. franguetti*, two bats that are able to visit quite distant figs in a single night (Bradbury 1981). The importance of wide-ranging abilities for species living on figs is supported by the sex-related differences found both in fig consumption and in foraging distances. *H. monstruosus* females forage at smaller distances than males (1–4 km vs. 10 km), and figs make up a much smaller fraction of their diet than that of wider ranging males (36 vs. 58%). One can therefore expect figs to be important only for a few “nomadic” species, as may be the case for the bulbul (*Ixonotus gustatus*), whose flocks increased their foraging areas during the major dry season (C. Erard, *personal communication*).

Do such conclusions apply to other African forests? Comparisons can be made between guenon communities of Gabon and Uganda. *Cercopithecus mitis* of Kibale Forest is a close relative of *C. nictitans*. Rudran (1978) found that its fruit diet included up to 21.4% figs in one month. T. Butynski (*personal communication*) observed that *Ficus exasperata* was the most frequent species eaten for one of his *C. mitis* study groups, totalling 30.8% of its food in a year. Similarly, in Kakamega Forest (Kenya), three *Ficus* species accounted for 17.6% of the fruit diet of *C. mitis* and for 15.9% of that of *C. ascanius* (Cords 1987). In fact, *F. exasperata* was the 19th most common plant species in Kibale Forest and the 18th most common in Kakamega Forest, where it reached greater densities (1.6 trees/ha) than the overall density of all Makokou fig species combined. This suggests that the small role played by figs at Makokou primarily results from their poor representation at this site. On the other hand, this site offers to frugivores a much larger fruit spectrum than East African sites, due to a greater plant species richness and a greater number of trees per hectare (Gautier-Hion 1983).

But how can we explain the poor representation of figs in some tropical rain forests? Indeed, as early as 1940, Corner, dealing with forests of Malaya, wondered “why strangling figs do not occur on most big trees . . . considering how vigorous they are and how easily their seeds are distributed.” In the rain forest of Makokou as well as in the Taï Forest (Ivory Coast), large terrestrial figs that germinate on the ground are found mostly in secondary growth, by the forest edge, or in open forest swampy areas. Conversely, in primary mainland habitat, figs are almost exclusively hemi-epiphytic forms that germinate on trees. Their densities always remain much lower than those of both terrestrial and hemi-epiphytic figs dwelling in open habitats. For example, only 1.5 hemi-epiphytic figs/ha were found on M’passa plateau, whereas 46.5 individuals/ha were found by the forest edge along a river, a few hundred metres away. The same was true in Taï Forest, with only 4.7 hemi-epiphytic trees/ha (Michaloud and Michaloud-Pelletier 1987) vs. 51.3 terrestrial figs/ha

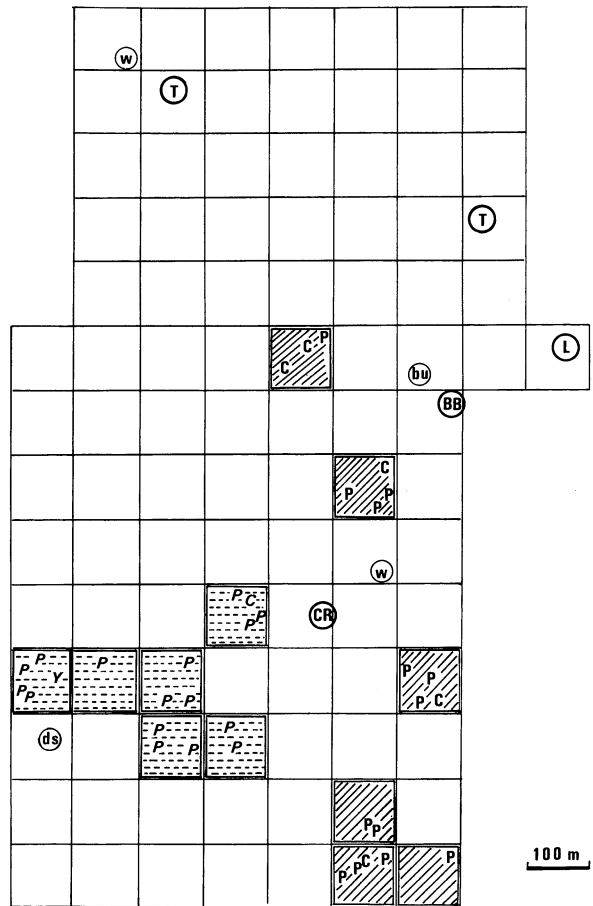


FIG. 2. *Polyalthia suaveolens* (P), *Coelocaryon preussii* (C) and *Pycnanthus angolensis* (Y) trees bearing ripe fruit on a given day within six sampled hectares on the M’passa plateau (12 July 1977: hatched area; 24 August 1977: stippled area); and fruiting figs (circled letters) found from the sampling of the entire 100 ha (10 November 1980; 150 individuals monitored). w = *Ficus wildemania*, T = *F. toninghii*, L = *F. lingua*, bu = *F. burretiana*, BB = *F. bubu*, CR = *F. cratereostoma*, D = *F. densistipulata* (uppercase letters indicate ripe fruit; lowercase indicate unripe fruit).

in an open area ~200 km away in the same region (Thomas 1982). Again, in a “typical second-growth neotropical lowland forest” of Barro Colorado, Milton et al. (1982) found only terrestrial figs; their density was “five to nine times as high as in older sections of the forest”; 83.3% of these species were *Ficus yoponensis* and *F. insipida* (Morrison 1978), species that are not recruited into old second-growth or primary forest, except in light gaps or along riverbanks (Milton et al. 1982).

Michaloud and Michaloud-Pelletier (1987), analyzing the structural characteristics of trees colonized by hemi-epiphytic figs in Taï Forest, suggested that access to light was the most important parameter determining successful fig settlement. Since only 20.6% of the 160 species of trees had individuals colonized by figs, the authors concluded that the low density of fig trees found

there (4.69 trees/ha, with none of 19 species reaching 1 tree/ha) was the result of a lack of hosts offering suitable light conditions for settlement of figs. It is likely that similar explanations could apply to Makokou Forest, whose floristic composition is close to that of Taï Forest.

From these data, one can foresee that any rain forest evolving from second-growth stage to older stages (1) will not have its population of terrestrial figs renewed, (2) will have room only for hemi-epiphytic figs to settle, (3) and therefore will undergo a severe decrease in fig density and fruit production. The latter decrease results from both the decrease in density and in individual crop size. As a consequence, figs may constitute a staple food for frugivores, in a given rain forest at a given successional stage, but will no longer represent a staple food when the forest reaches the subsequent stages of maturation. However, the decrease in crop size will depend on the relative abundance of fig trees belonging to species that can grow to stranglers. It is possible that rain forests growing on highly productive soils harbor higher densities of such species than Makokou forest. In such a case, the decrease in crop size would be less important, since hemi-epiphytic stranglers can produce as big a fruit crop as terrestrial figs do (up to 40 000 fruits in Barro Colorado, Hladik and Hladik 1969).

It would be useful to learn how, in a given rain forest, a community of frugivores would adapt itself to a change in availability of its staple food resources through maturation of the forest. Would the diversity of potential food species be a factor determining whether consumers could remain, feeding on substitutes, or whether they would have to move to other habitats? In the latter case, it is actually a question of a "keystone" resource, since animals have to move to search for the same food species elsewhere. In the former case, one can speak only of key resources, in so far as frugivores are able to switch their diet onto substitutes.

These considerations stress the difficulty of generalizing, not only between continents but within a single country, where forests are made up of a mosaic of different seral stages. Incidentally, this points out the need for moderating generalizations drawn from studies conducted in more or less disturbed or small-sized forests such as those in East Africa, at the extreme limit of the tropical rain forest.

CONCLUSION

In periods of low fruit availability, the frugivores of Makokou, as well as those of other tropical rain forests (e.g., the Kutai Nature Reserve in Indonesia, Leighton and Leighton 1983; and the Manu site in Peru, Terborgh 1986), rely on a few plant species characterized by high density, high rates of fruit production, and/or highly predictable fruiting periods. But these key species do not necessarily belong to the same taxonomic groups on all continents, or at every maturational stage within a single forest. At Makokou, *Polyalthia suaveolens* and

Myristicaceae are, at the present time, the species most suited to play this role, whereas figs are mainly food for bats. An improved knowledge of such key resources might have profound implications for the management and conservation of tropical rain forest ecosystems.

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