

Chapter 3

Patterns of fruit production.

Introduction.

Tropical forests are seasonal habitats exhibiting complex rhythms of plant production (see Sabatier, 1985). Phenology of flowering, fruiting and leaf production in tropical forests has been studied using three general techniques: direct observation of the respective plant parts *in situ*, assigning a score to represent the strength of production (e.g., Lieberman, 1982; Medway, 1972; Raemaekers *et al.*, 1980; Wheelwright, 1985); monitoring of the number of plants producing fruit in any one month (e.g., Gautier-Hion *et al.*, 1985a; Leighton & Leighton, 1983); or by collecting fallen plant parts in traps and counting and/or weighing sorted samples on a regular basis (e.g., Foster, 1982a; Hladik, 1978; Smythe, 1970; Terborgh, 1983). Chapman *et al.* (in press[a]) reviewed methods used in different studies to assess fruit abundance in tropical forests. All studies have revealed seasonal fluctuations in growth and production.

Frugivores are the dominant group of vertebrates in tropical forests (Emmons *et al.*, 1983; Fleming *et al.*, 1987; Gautier-Hion *et al.*, 1980, 1985b; Terborgh, 1983, 1986; Willis, 1980). In Gabon, 53% of mammals are primary consumers, and fruit and seeds are the staple diet of 85% of these species (Gautier-Hion *et al.*, 1985b). Close to Makokou, northeast Gabon, seven out of eleven ruminants (Dubost, 1984), eight out of nine squirrels (Emmons, 1980) and 13 diurnal primates (Hladik, 1973; Gautier-Hion, 1978; Tutin & Fernandez, 1985) rely principally on fruit foods. Therefore it is particularly interesting to study patterns of fruit production. Fruit availability has been shown to vary greatly over the course of the year in all major blocks of rain forest: Southeast Asia, (e.g., Leighton & Leighton, 1983; Medway, 1972; Raemaekers *et al.*, 1980); South and Central America, (e.g., Foster, 1982a; Terborgh, 1983); and Africa, (e.g., Gautier-Hion *et al.*, 1985a; Lieberman, 1982; Alexandre, 1980). In addition, long-term studies have demonstrated significant differences in fruit availability between years in the same site (Foster, 1982b; Leighton & Leighton, 1983; Tutin *et al.*, 1991a). Foster (1982b) demonstrated that failure of fruit crops, perhaps as a result of unusual weather conditions, can result in conditions of famine for

frugivores on Barro Colorado Island, Panama.

Community studies have shown that frugivorous species respond to periods of fruit scarcity by switches in the diet and/or changes in ranging patterns (Leighton & Leighton, 1983, Terborgh, 1983). During these periods of scarcity, plant species which do produce fruit become disproportionately important in the diet of frugivores. Species which provide a dependable resource during these times have been termed "keystone mutualists" (Gilbert, 1980). Keystone fruit producers play a vital role in the feeding ecology of rain forest frugivores, but species fulfilling this role vary between areas and for different animal species (Gautier-Hion & Michaloud, 1989; Leighton & Leighton, 1983, Terborgh, 1986; Tutin *et al.*, 1991a). This has serious implications for the management of tropical forests (Leighton & Leighton, 1983). Most tropical rain forests are likely to have been commercially logged within the next 25 years (Johns & Skorupa, 1987). If logging results in disproportionate damage to keystone plants, the effects on wildlife may be severe, even where levels of damage are low (Leighton & Leighton, 1983). In coastal Congo, forest exploitation is at low intensity, but concentrates on *Staudtia gabonensis* (Dowsett-Lemaire, 1991), a keystone species in northwest Gabon (Gautier-Hion & Michaloud, 1989).

It is therefore important that keystone plant species be identified in as many forest areas as possible. In addition, more data on the rhythms of production in tropical forests are necessary if the underlying mechanisms controlling these patterns are to be isolated. This study was undertaken to investigate seasonal patterns of fruit availability for frugivorous mammals, and to identify species that might fulfil the keystone role. Patterns of fruit production were monitored, from June 1990 to May 1991, by counting fallen fruit on the five transects.

Methods.

Between June 1990 to May 1991 the numbers of fallen ripe and unripe fruits of all species seen on a 1m strip along transects were counted (for fruits >1cm diameter) or estimated (for fruits <1cm diameter) (cf. Gautier-Hion *et al.*, 1985a). Counts were undertaken between the middle and end of each month (depending on site). Only fresh fruits were counted (i.e., fruits that were not rotten or dried up) and fruits were not removed because they would no longer have been fresh, even if seen in subsequent months. Fruits which had been partially

eaten, but were fresh, were also recorded (see below). Fruit-fall measures of phenology were used because: a) other workers at Lopé have been collecting phenology data using a method involving counts of fruits on plants since 1984 (see Williamson, 1988); b) data could be collected during dung and nest censuses (see Chapter 6); c) elephants were one of the focuses of the logging study, and they consume large amounts of fallen fruit (see Chapter 5).

Non-parametric statistics (Siegel & Castellan, 1988) were used to test for seasonal and inter-site differences in fruit production, and for correlations between fruit production and climatic variables.

Results.

A total of 195 species of fruit were found on transects, of which 150 species were recorded ripe and 121 unripe (76 species were only recorded unripe). It was possible to identify 156 (80%) to genus and 91% to family. At least 44 taxonomic families were represented. The majority (73%) of fruits came from trees, whilst the remainder were from lianes (17%), herbs (3%), shrubs (1%), epiphytes (1%), climbing palms (<1%) or of unknown origin (5%).

Each species was assigned to one of six fruit categories on the basis of morphological and dispersal characteristics (see Table 3.3 below - cf. Gautier-Hion *et al.*, 1985a):

1) Succulent - fruits with seed(s) embedded in a more or less succulent flesh. This is a relatively general category for fruits whose seeds are likely to be dispersed by animals. These fruits are generally drupes or berries, but vary in fruit and seed size, colour, and chemical composition of the flesh (cf. Rogers *et al.* 1990), in relation to the animal dispersers they are adapted to (cf. Gautier-Hion *et al.* 1985). Some are small, brightly coloured and have a high sugar content when ripe (e.g., *Antidesma laciniatum*, *Diospyros* spp., *Ganophyllum giganteum*). These attract bird and primate dispersers (cf. Gautier-Hion *et al.*, 1985). Others are larger, and generally dull, with fibrous flesh (e.g., *Klainedoxa gabonensis*, *Parinari excelsa*, *Duboscia macrocarpa*) and probably rely upon rodents, ungulates and elephants for dispersal (cf. Gautier-Hion *et al.*, 1985; see also Chapter 5).

2) Arillate - fruits whose seeds are surrounded (at least in part) by a brightly coloured aril, generally with two or more fleshy valves which open when

ripe to reveal arillate seeds (e.g., *Staudtia* spp., *Pycnanthus angloensis*, *Blighia welwitschii*), or in which carpels ripen into follicles which split down one side, again revealing the seeds (e.g., *Cnestis corniculata* other unidentified Connaraceae) These fruits attract bird and primate dispersers (cf. Gautier-Hion et al., 1985a; Pannell & Koziol, 1987)

3) Dehiscent - fruits which use abrupt dehiscence mechanisms to propel seeds away from the parent tree. The majority of these are Leguminosae and have lignified pericarps forming pods which recurve when ripe (dry) (e.g., *Pentaclethra* spp., *Paraberlinia bifoliolata*, *Augouardia letestui*).

4) Fleshy pods - species with indehiscent pods in which seeds are surrounded by fleshy pulp (e.g., *Parkia bicolor*, *Tetrapleura tetraptera*, *Swartzia fistuloides*) which often attracts elephants (Chapter 5).

5) Wind-dispersed - species either with pods which open down one side to release samaras, small seeds enveloped in papery wings (e.g., *Fillaeopsis discorphora*, *Piptadeniastrum africanum*), dry drupes surrounded by a wing (e.g., *Debordesia glaucescens* or with a persistent calyx which acts as a membranous wing (e.g., *Lophira alata* *Marquesia excelsa*) for air-borne dispersal.

6) Others - Species which do not fit into any of the above categories and which show no apparent adaptation for dispersal, including dry drupes (e.g., *Marathes glabra*) and achenes, (some may be aimed at rodents which hoard seeds in underground stores, many of which are forgotten e.g., *Maranthes glabra*)

Table 3.1 shows the number of species of each fruit class recorded on each of the five transects. There were differences in the number of species recorded fruiting in the five sites (see below). Table 3.2 shows that only about 15% of species were recorded on at least four of the five transects, with almost 50% present in only one site. Figure 3.1 shows the distribution of the 195 fruit species found on transects in each fruit category. Succulent fruit were the dominant class, accounting for 60.5% of all species encountered. About three-quarters of all species had fruits characteristic of those dispersed by animals (i.e., succulent, arillate or fleshy pods).

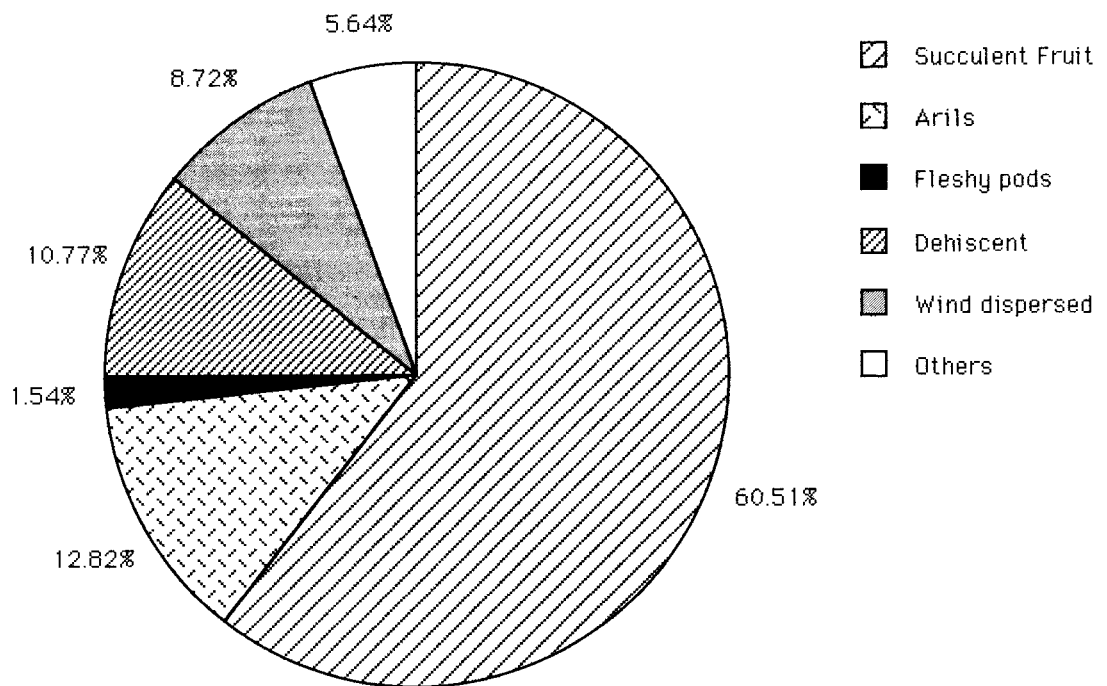
Table 3.1: Number of species in each fruit category / study site.

Fruit type	Ripe fruit					Unripe Fruit					All fruit				
	Study Site														
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Arils	6	12	9	11	10	5	2	2	4	5	8	13	9	14	11
Dehiscent	3	5	5	5	5	4	6	5	4	4	6	9	9	9	6
Fleshy Pods	2	0	1	1	2	1	0	0	0	2	2	0	1	1	3
Others	3	5	7	8	5	1	0	1	3	0	3	5	7	8	5
Succulent (Fleshy)	20	30	41	32	35	24	28	34	31	26	32	41	53	46	45
Wind Dispersed	6	4	7	7	6	3	4	5	4	4	7	7	9	9	7
Totals	40	56	70	64	63	38	40	47	46	41	58	75	88	87	77

Table 3.2: Overlap of fruit species between sites.

Number of sites in which species detected:	5	4	3	2	1
Number of Species	12	18	25	42	95
% of Total	6.3	9.4	13.0	21.9	49.5

Figure 3.1: Pie chart showing relative frequencies of fruit categories.



To check for any differences in the number of species recorded between sites, monthly data for the total number of ripe fruit species detected each month on each transect (two values were missing for July so this month was excluded

from the analysis) were tested using a Friedman two-way analysis of variance corrected for ties. There was a significant difference between sites ($P < 0.05$). Multiple comparisons showed significant differences between site one and site three ($P < 0.002$) and site one and site five ($P < 0.05$). The number of species of trees > 10 cm diameter at breast height in a 2.5 Ha sample along each transect (see Chapter 2) was tested against number of species of ripe fruit and total number of fruit species recorded on each transect, to see if the number of species detected on phenology transects was correlated with plant diversity (as measured by tree diversity). There was a positive correlation in both cases between tree species diversity and the number of fruit species detected (Spearman rank-order correlation coefficient, $r_s = 0.9$, $P < 0.05$ - one tailed).

There was a marked seasonal pattern to fruit production. Figures 3.2 & 3.3 show the number of species of ripe and unripe fruit respectively for each fruit class found on transects each month (data for all transects lumped). The number of species producing ripe fruit was greatest in January, whilst the peak for unripe fruit was one month earlier. There were fewest species fruiting during May-September, throughout the major dry season. Data for the abundance of the different fruit classes each month were compared to see if there were statistically significant seasonal differences. As is to be expected from the figures, there was a significant difference in the number of species of ripe and unripe fruit detected between months (Friedman two-way analysis of variance corrected for ties, $P < 0.001$ in each case). Multiple comparisons for ripe fruit showed that the number of species present in January differed significantly from eight of the other months (i.e., January had significantly more fruit than the eight months with lowest numbers of fruiting species, as illustrated in figure 3.2), February from four months, March from three, November and December from two and September from one ($P < 0.05$, two tailed). A similar pattern was observed for unripe fruits, with November, December, January and March being significantly different (higher) than four, five, five and three months respectively.

The total number of ripe and unripe fruits counted on each transect each month was tested for differences in overall productivity between sites (Friedman two-way analysis of variance corrected for ties, NS for ripe fruit, $P < 0.01$ for unripe fruit). Therefore, abundance of ripe fruit did not differ significantly between sites, but for unripe fruit there was a difference - site four differed significantly from sites one and three ($P < 0.05$). If site four was excluded from

Figure 3.2: Number of species detected with ripe fruit each month.

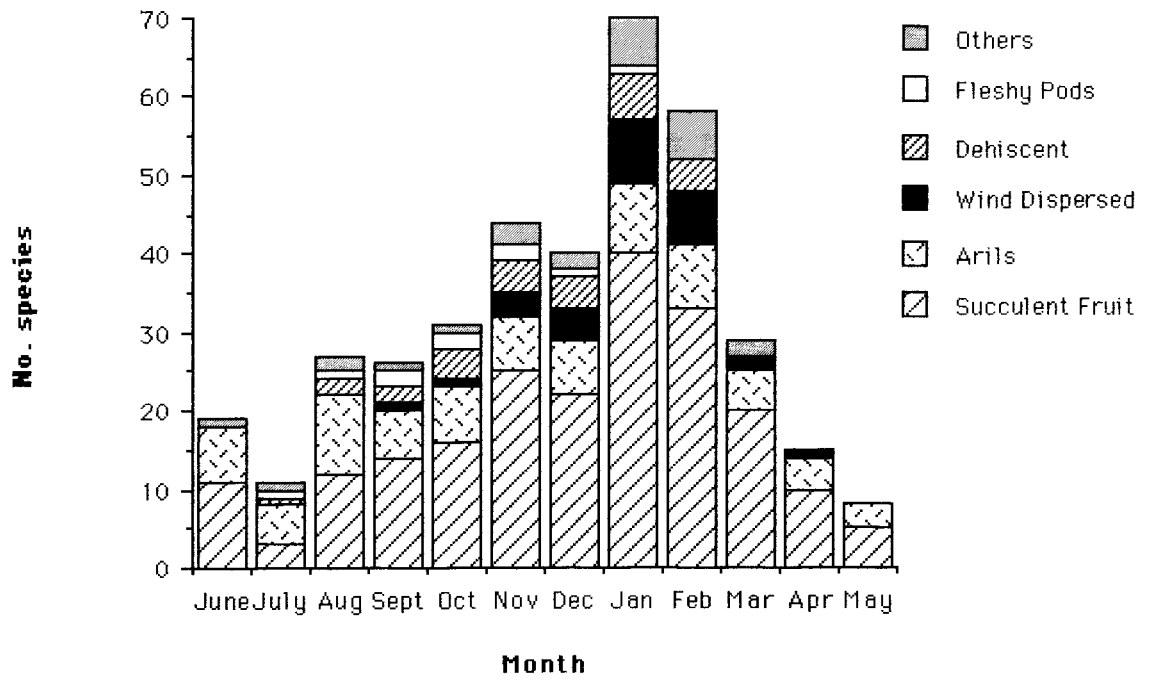
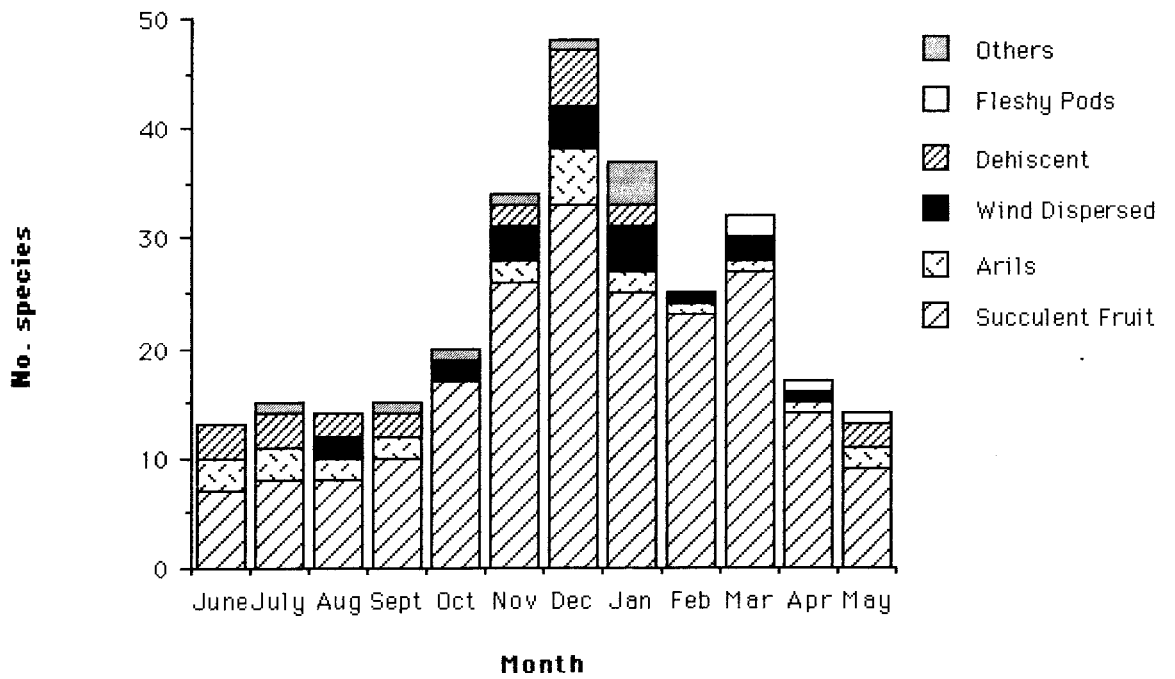


Figure 3.3: Number of species detected with unripe fruit each month.



the analysis for unripe fruit there was no significant difference between the remaining four sites, so data from site four was not used when testing for inter-monthly variation in unripe fruit production (below).

Figures 3.4 & 3.5 show the average numbers of ripe and unripe fruits respectively of each fruit class counted each month (data for all transects pooled). These show that the seasonal pattern of fruit production is similar to that for the number of species fruiting, but the peaks in production were more marked. Again there were significant differences in availability of all ripe ($P < 0.001$) and unripe fruit ($P < 0.05$, only four sites tested) between months, with January and February respectively showing the greatest number of statistical differences from other months.

Data for all species encountered on transects are summarised in Table 3.3. Species encountered ripe in June (the first month for which there were data) are listed first, then July, and so on. Figure 3.6 shows that 75% of species produced fruit during three months or less, and Table 3.4 lists those species whose fruiting period extended over at least 4 months. Of 77 species recorded ripe in at least two study areas, 71 (92%) fruited in the same, or successive months in the different sites.

Of 37 species found producing ripe fruit in the major dry season (June, July, August - see Table 3.3) 21 were only recorded in one month on one of the transects. Table 3.5 lists the 16 species present in at least two sites, or during at least two of the three dry season months. *Cissus dinklagei* is a yellow drupe about 2cm long when ripe, with a sugary mesocarp. Other species had fatty arils or drupes with high crude lipid content (*Elaeis guineensis*) (cf., Rogers et al., 1990) or were large fruits, generally with large, well protected seeds. All these species except *Coelocaryon preussi* and *Cissus dinklagei* were recorded producing ripe fruit during at least four months of the study.

Figure 3.4: Number of ripe fruit counted / month.

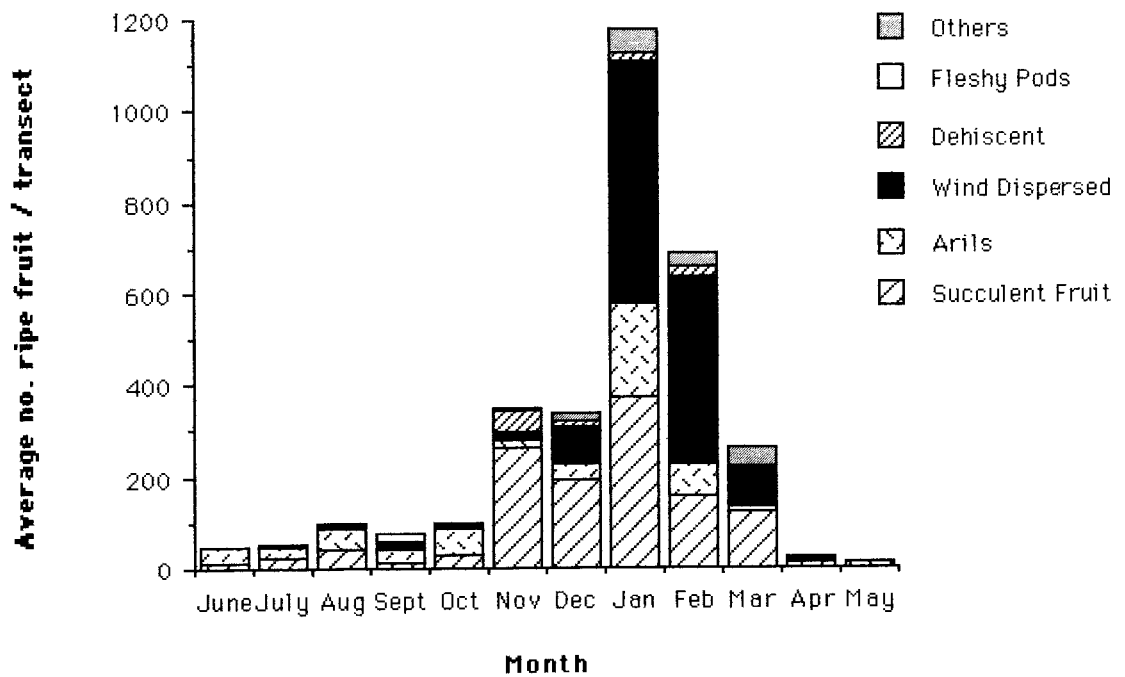


Figure 3.5: Number of unripe fruit counted / month.

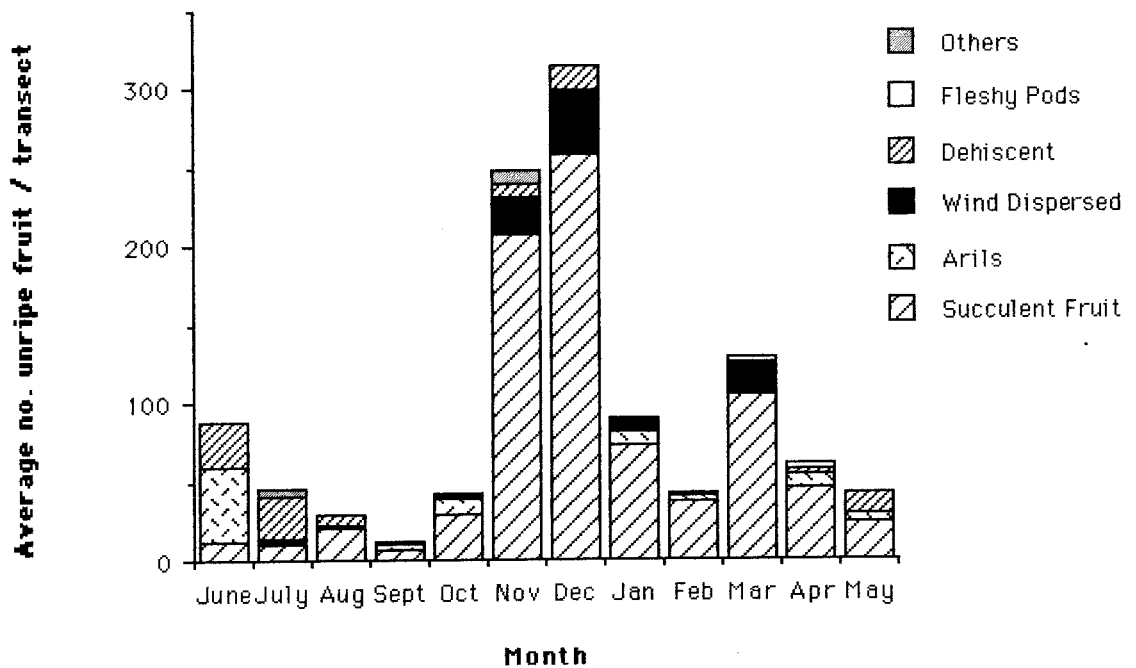
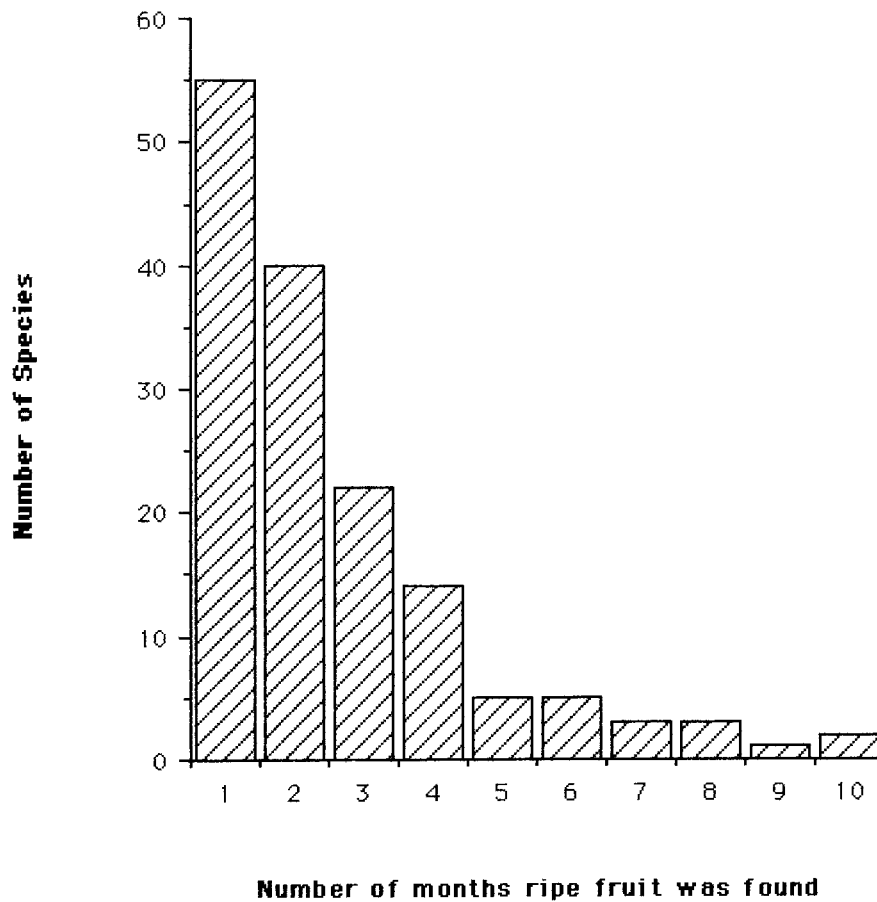


Figure 3.6: The number of months during which species produced ripe fruit.



Rainfall, and average monthly humidities and maximum and minimum temperatures for the study period (Chapter 2) did not differ from the average annual patterns observed at Lopé (SEGC, unpublished data). There were no simple correlations between fruit production and any of these environmental parameters. Insolation was not measured at Lopé, but figures were available for Libreville (1961–1965), Franceville (1951–1970) and Makokou (1961–1980). There were positive correlations between the number of species, and the total number of ripe fruit, and insolation data for the previous month for Libreville (Spearman rank-order correlation coefficient, 1-tailed test, $p < 0.005$ and 0.001 respectively) and Franceville ($p < 0.01$ in both cases), whilst for data from Makokou the relationship was less convincing ($p < 0.05$ and 0.1 respectively).

Table 3.3: Species which were detected with ripe fruit each month (continued).

Species	Family	Fruit type ¹	Plant form ²	Month								
				June Jul ³	Aug Sept	Oct Nov	Dec Jan	Feb Mar	Apr May			
<i>Coelocaryon preussi</i>	MYRISTICACEAE	A	T		*	*						
<i>Cnestis corniculata</i>	CONNARACEAE	A	L		*				*	*		
<i>Diospyros melocarpa</i>	EBENACEAE	S	T		*							
<i>Diospyros viridicans</i>	EBENACEAE	S	T		*							
<i>Eriacaelum macrocarpum</i>	SAPINDACEAE	D	T		*	*	*	*	*	*		
<i>Loranthus</i> sp.	LORANTHACEAE	S	Ep		*	*						
<i>Massularia acuminata</i>	RUBIACEAE	S	T		*	*	*	*	*	*	*	*
<i>Pentaclethra eetveldeana</i>	MIMOSACEAE	D	T		*		*					
<i>Polyalthia suaveolens</i>	ANNONACEAE	S	T		*			*				
<i>Swartzia fistuloides</i>	CAESALPINIACEAE	FP	T		*	*	*	*	*			
<i>Symphonia globulifera</i>	GUTTIFERAE	S	T		*					*	*	
<i>Uvaria</i> sp.	ANNONACEAE	S	L		*							
<i>Vitex</i> sp.	VITACEAE	S	T		*							
<i>Xylocarpus aethiopicus</i>	ANNONACEAE	A	T		*	*			*	*		
LJTW 131		O	T		*							
U/K 4	CONNARACEAE	A	L		*							
U/K 27		S			*							
U/K 26	ANNONACEAE	S			*							
<i>Antracaryon klaineana</i>	ANACARDIACEAE	S	T			*						
<i>Coryanthe mayumbensis</i>	RUBIACEAE	D	T			*						
<i>Desbordesia glaucescens</i>	IRVINGIACEAE	W	T		*	*	*	*	*			
<i>Gambeya africana</i>	SAPOTACEAE	S	T		*	*						
<i>Garcinia afzeli</i>	GUTTIFERAE	S	T		*		*	*	*	*		

Table 3.3: Species which were detected with ripe fruit each month (continued).

Species	Family	Fruit type ¹	Plant form ²	Month							
				June Jul ³	Aug Sept	Oct Nov	Dec Jan	Feb Mar	Apr May		
<i>Plagiostyles africana</i>	EUPHORBIACEAE	S	T		*	*					
<i>Syzigium</i> sp.	MYRTACEAE	S	T		*	*					
U/K 5		S	?		*						
<i>Conceveiba africana</i>	EUPHORBIACEAE	D	T			*	*	*			
<i>Coula edulis</i>	OLACACEAE	S	T			*	*	*	*	*	*
<i>Dacryodes igaganga</i>	BURSERACEAE	S	T			*			*		
101 <i>Dacryodes normandii</i>	BURSERACEAE	S	T			*	*	*			
<i>Enantia chlorantha</i>	ANNONACEAE	S	T			*	*	*			
<i>Hexalobus crispiflorus</i>	ANNONACEAE	S	T			*		*			*
<i>Landolphia cf. heudelotii</i>	APOCYNACEAE	S	L			*	*		*		
<i>Farinaria chrysophylla</i>	CHRYSOBALANACEAE	S	T			*	*				
<i>Pentaclethra macrophylla</i>	MIMOSACEAE	D	T			*					
<i>Uapaca heudelotii</i>	EUPHORBIACEAE	S	T			*					*
LJTW 0327	CONNARACEAE	A	L			*	*		*	*	
U/K 7	CONNARACEAE	A	L			*					
<i>Augouardia letestui</i>	CAESALPINIACEAE	D	T				*	*	*	*	
<i>Barteria fistulosa</i>	PASSIFLORACEAE	S	T				*		*		
<i>Caloncoba glauca</i>	FLACOURTIACEAE	S	T				*		*	*	
<i>Canarium schweinfurthii</i>	BURSERACEAE	S	T				*				
<i>Dichapetalum</i> sp.	DICHAPETALACEAE	S	L				*				*
<i>Eriocaelum</i> sp.	SAPINDACEAE	D	T				*				
<i>Garcinia</i> sp.	GUTTIFERAE	S	T				*			*	
<i>Hylodendron gabunense</i>	CAESALPINIACEAE	W	T				*				

Table 3.3: Species which were detected with ripe fruit each month (continued).

Species	Family	Fruit type ¹	Plant form ²	Month							
				June Jul ³	Aug Sept	Oct Nov	Dec Jan	Feb Mar	Apr May		
<i>Irvingia gabonensis</i>	IRVINGIACEAE	S	T				*	*	*		
<i>Jalldora duperquetiana</i>	CONNARACEAE	S	S/T				*	*	*	*	
<i>Lingelshemia</i> sp.	EUPHORBIACEAE	O	T				*				
<i>Macaranga barteri</i>	EUPHORBIACEAE	S	T				*	*	*		
<i>Macaranga manandra</i>	EUPHORBIACEAE	S	T				*	*			
<i>Pentadesma africana</i>	GUTTIFERAE	S	T				*	*		*	
<i>Petersianthus macrocarpus</i>	LECYTHIDACEAE	W	T				*	*	*		
<i>Poga oleosa</i>	RHIZOPHORACEAE	S	T				*	*	*		
<i>Trichoschypa patens</i>	ANACARDIACEAE	S	T				*				
LJTW 0360	?PASSIFLORACEAE	O	L				*		*	*	*
LJTW 0436	CONNARACEAE	A	L				*			*	*
LJTW 425	SAPOTACEAE	S	T				*				
<i>Aucoumea klaineana</i>	BURSERACEAE	W	T					*			
<i>Cala lizae</i>	STERCULIACEAE	S	T					*	*	*	*
<i>Combretum</i> sp.	COMBRETACEAE	W	L					*	*	*	
<i>Daniellia klaineana</i>	CAESALPINIACEAE	D	T					*			
<i>Heisteria parvifolia</i>	OLACACEAE	S	T					*	*	*	
<i>Klaineanthus gabonise</i>	EUPHORBIACEAE	A	T					*	*		
<i>Maprounea membrenaceae</i>	EUPHORBIACEAE	O	T					*		*	
<i>Quratea</i> sp.	OCHNACEAE	A	T					*			
<i>Salacia mayumbensis</i>	HIPPOCRATACEAE	S	L					*			
<i>Santiria trimera</i>	BURSERACEAE	S	T					*			
<i>Scyphacephalum achacae</i>	MYRISTICACEAE	S	T					*	*	*	*

Table 3.3: Species which were detected with ripe fruit each month (continued).

Species	Family	Fruit type ¹	Plant form ²	Month						
				June Jul ³	Aug Sept	Oct Nov	Dec Jan	Feb Mar	Apr May	
<i>Trichilia monadelpha</i>	MELIACEAE	A	T				*			
LJTW 0283		S	L				*			
LJTW 0309	EUPHORBIACEAE	O	L				*	*	*	
U/K 10		S	?				*			
<i>Aframomum</i> sp. ?nov	ZINGIBERACEAE	S	H				*	*	*	
<i>Agave impressa</i>	FABACEAE	W	L				*			
<i>Antidesma laciniatum</i>	EUPHORBIACEAE	S	T				*	*		
<i>Berlinia bracteosa</i>	CAESALPINIACEAE	D	T				*	*		
<i>Compastyles mannii</i>	FLACOURTIACEAE	S	T				*	*		
<i>Coccoloba barteri</i>	FLACOURTIACEAE	S	T				*	*	*	
<i>Centropogon glaucinus</i>	PANDACEAE	A	T				*	*		
<i>Dioclea zenkeri</i>	OLACACEAE	S	T				*	*		
<i>Diospyros abyssinica</i>	EBENACEAE	S	T				*	*		
<i>Diospyros zenkeri</i>	EBENACEAE	S	T				*	*		
<i>Eremus patha</i>	PALMAE	S	CP				*	*		
<i>Eriosema exsul</i>	VOCHYSIACEAE	W	T				*	*		
<i>Gambeya subnuda</i>	SAPOTACEAE	S	T				*	*		
<i>Hypodaphnis zenkeri</i>	LAURACEAE	S	T				*			
<i>Julbernardia brieyi</i>	CAESALPINIACEAE	D	T				*	*		
<i>Landolphia</i> sp. LJTW 0323	APOCYNACEAE	S	T				*	*		
<i>Lophira alata</i>	OCHNACEAE	W	T				*	*		
<i>Marquesia excelsa</i>	DIPTEROCARPACEAE	W	T				*			
<i>Myrianthus arborea</i>	MELIACEAE	S	T				*			

Table 3.3: Species which were detected with ripe fruit each month (continued).

Species	Family	Fruit type ¹	Plant form ²	Month						
				June Jul ³	Aug Sept	Oct Nov	Dec Jan	Feb Mar	Apr May	
<i>Neachevalierodendron stephannii</i>	CAESALPINIACEAE	D	T				*			
<i>Paraberlinia bifoliolata</i>	CAESALPINIACEAE	D	T				*	*		
<i>Parinari excelsa</i>	CHRYSOBALANACEAE	S	T				*			
<i>Pentadesma</i> sp. ?nov	GUTTIFERAE	S	T				*			
<i>Pterocarpus sayauxii</i>	PAPILIONACEAE	W	T				*	*		
<i>Scatellia coriacea</i>	FLACOURTACEAE	A	T				*	*	*	*
104 <i>Strambasia pustulata</i>	OLACACEAE	S	T				*			
<i>Strambasiopsis</i> sp. ?nov	OLACACEAE	S	T				*	*		
<i>Strychnos</i> sp.	LOGANIACEAE	S	L				*	*		
<i>Treculia abavoidea</i>	MORACEAE	S	T				*			
<i>Trichaschypha acuminata</i>	ANACARDIACEAE	S	T				*			
LJTW 467	?MELIACEAE	O	T				*			
U/K 13	CONNARACEAE	O	L				*	*		
U/K 14	ANNONACEAE	S	?				*			
U/K 16		O	L				*	*		
<i>Diospyras polystemon</i>	EBENACEAE	S	T					*	*	*
<i>Garcinia smeathmannii</i>	GUTTIFERAE	S	T					*		
<i>Haumania dinklagei</i>	MARANTACEAE	O	H					*		
<i>Megaphrynium gabonense</i>	MARANTACEAE	A	H					*	*	*
<i>Newtonia leucocarpa</i>	MIMOSACEAE	W	T					*		
<i>Piptadeniastrum africanum</i>	MIMOSACEAE	W	T					*	*	
<i>Ptychopetalum petiolatum</i>	OLACACEAE	S	T					*	*	
<i>Liopaca vanhouttei</i>	EUPHORBIACEAE	S	T					*		

Table 3.3: Species which were detected with ripe fruit each month (continued).

Species	Family	Fruit type ¹	Plant form ²	Month											
				June Jul ³	Aug Sept	Oct Nov	Dec Jan	Feb Mar	Apr May						
U/K 19		S	L						*						
U/K 20		S	S/T						*						
U/K 22		W	?						*						
<i>Aframomum ?leptolepis</i>	ZINGIBERACEAE	S	H							*					
<i>Dialium dinklagei</i>	CAESALPINIACEAE	S	T							*					
<i>Dialium pachyphyllum</i>	CAESALPINIACEAE	S	T							*					
<i>Scytocetalum klaineianum</i>	SCYTOPETALACEAE	S	T							*					
LJTW 0369	COMBRETACEAE	W	T							*					
LJTW 0402		S	Ep							*	*				
<i>Diaspyras denda</i>	EBENACEAE	S	T								* *				
<i>Diaspyras piscataria</i>	EBENACEAE	S	T								*				
<i>Fillaeopsis discophora</i>	MIMOSACEAE	W	T								*				
Total number of fruiting species:				19	11	29	26	31	44	40	70	59	29	15	8

¹ - S = succulent, A = arillate, D = dehiscent, FP = fleshy pod, W = wind dispersed, O = others.

² - T = tree, H = herb, S = shrub, L = liane, CP = climbing palm, S/T = shrub/tree, Ep = epiphyte, ? = unknown.

³ - no data for sites 2 & 3.

Table 3.4: Plant species producing fruit during at least four months.

Species	Family ¹	Fruit type ²	No. months with ripe fruit					
			Study Site					
			All	1	2	3	4	5
<i>Duboscia macrocarpa</i>	TILIAC.	S	10			4	6	
<i>Massularia acuminata</i>	RUBIAC.	S	10		4	6		5
<i>Sacoglottis gabonensis</i>	HUMIR.	S	9		9			
<i>Klainedoxa gabonensis</i>	IRVING.	S	8	6				6
<i>Staudtia gabonensis</i>	MYRIST.	A	8		5	6	7	
<i>Xylocarpus hypolempus</i>	ANNON.	A	8	8				
<i>Elaeis guineensis</i>	PALMAE.	S	7					5
<i>Klainedoxa trilesii</i>	IRVING.	S	7		6	4		
<i>Pycnanthus angolensis</i>	MYRIST.	A	6			4	3	5
<i>Coula edulis</i>	OLAC.	S	6		5	4	4	
<i>Eriocaulum macrocarpum</i>	SAPIND.	D	6	5		5		5
<i>Maranthes glabra</i>	CHRYS.	O	6				4	
<i>Swartzia fistuloides</i>	CAES.	FP	6	1		3	1	1
<i>Xylocarpus quintasii</i>	ANNON.	A	6					4
<i>Desbordesia glaucescens</i>	IRVING.	W	5				4	
<i>Garcinia afzelii</i>	GUTT.	S	5					
<i>Panda oleosa</i>	PAND.	S	5					
<i>Staudtia kamerunensis</i>	MYRIST.	A	5			5		
<i>Strombosiaopsis tetrandra</i>	OLAC.	S	5		4		4	
<i>Augouardia tetestui</i>	CAES.	D	4					
<i>Cnestis corniculata</i>	CONN.	A	4					
<i>Cala lizae</i>	STERC.	S	4	4				
<i>Jalilydora duparquetiana</i>	CONN.	O	4				4	
<i>Scatellia coriacea</i>	FLAC.	A	4					4
<i>Scyphacephalum achacae</i>	MYRIST.	S	4					
<i>Scytopetalum</i> sp.	SCYTO.	S	4					
<i>Strombosia ?zenkeri</i>	OLAC.	S	4				4	
<i>Tetrapleura tetraptera</i>	MIMOS.	FP	4					
<i>Xylocarpus aethiopicus</i>	ANNON.	A	4					
LJTW 0092	CONN.	A	4				4	
LJTW 0327	CONN.	A	4			4		
LJTW 0360	?PASSIF.	O	4				4	
LJTW 0436	CONN.	A	4					

¹ - see Table 3.3 for unabbreviated Family name, ² - see Table 3.3 for fruit types.

Table 3.5: Species producing fruit in the major dry season (June–August).

Species	Family	Fruit Type ¹	Months present	Sites present
<i>Xylocopa quintasii</i>	ANNONACEAE	A	3	3
LJTW 0092	CONNARACEAE	A	3	2
<i>Pycnanthus angolensis</i>	MYRISTICACEAE	A	2	3
<i>Staudtia gabonensis</i>	MYRISTICACEAE	A	2	3
<i>Cissus dinklagei</i>	VITACEAE	S	2	2
<i>Duboscia macrocarpa</i>	TILIACEAE	S	2	2
<i>Elæis guineensis</i>	PALMAE	S	2	2
<i>Klainedoxa gabonensis</i>	IRVINGIACEAE	S	2	2
<i>Sacoglottis gabonensis</i>	HUMIRIACEAE	S	2	2
<i>Panda oleosa</i>	PANDACEAE	S	2	1
<i>Staudtia kamerunensis</i>	MYRISTICACEAE	A	2	1
<i>Xylocopa hypoleuca</i>	ANNONACEAE	A	2	1
<i>Strombosiaopsis tetrandra</i>	OLACACEAE	S	1	3
<i>Coelocaryon preussi</i>	MYRISTICACEAE	A	1	2
<i>Eriocaelum macrocarpum</i>	SAPINDACEAE	D	1	2
<i>Maranthes glabra</i>	CHRYSOBALANACEAE	D	1	2

¹– see Table 3.3 for fruit types.

Discussion.

Fruit-fall measures of phenology employed in this study have been used elsewhere in Gabon (Feer, 1989; Gautier-Hion *et al.*, 1985a) and may be considered as a modification of the fruit trap method used commonly in South America (e.g., Foster, 1982a; Smythe, 1970; Terborgh, 1983). This method has the limitation that it relies on fruit falling from the canopy. Fruit fall may be natural, or a result of arboreal animals feeding activities, and fruit consumed in the canopy will obviously not be recorded (Chapman *et al.*, in press[a]; Terborgh, 1983). This will have led to an under-representation of fruits that are consumed by vertebrates. Counting fresh fruit remains will have compensated somewhat for this, as many vertebrate frugivores in Gabon drop part of the fruits they feed upon (Gautier-Hion *et al.*, 1985a; personal observation). For some species it is difficult to assess fruit numbers on the tree since they are concealed amongst

foliage (e.g., fruit counts on *Ganophyllum giganteum* at SEGC underestimated fruit crop by a factor of 10, compared to counts of fruit remains on the floor - B. Voysey & K. McDonald, unpublished data). Sampling in this study was of low intensity (in terms of area censused) and was only conducted once monthly, so was unlikely to provide good quantitative data for rare species. Fresh fruits that are fed upon by terrestrial animals may have been removed before they were counted (which is not a problem with conventional fruit traps - Foster, 1982a) so the method may have underestimated availability of favoured species, especially if they were rare. Chapman et al. (in press[a]) found fruit-fall traps gave different results to methods which recorded fruit *in situ*. However, they based this conclusion on traps with a combined surface area of 24m², whilst 5000m² were monitored on transects in this study.

Since counts were undertaken only once-monthly, and only fruit that was not rotten or dry was counted, some species with short highly synchronised fruiting patterns were not recorded ripe, even though they were relatively common and unripe fruits were seen (e.g., the entire fruit crop of *Ganophyllum giganteum*, a common large tree in two sites, ripened and disappeared between the December and January samples). The length of time fruits remained fresh (i.e., in a state in which they would be counted if seen on the transect - 'residence time') was not monitored, but any fruit considered unlikely to change in appearance (e.g., dry achenes) were removed, so it is unlikely that a fruit would have been counted in successive months. Without residence data it is not possible to estimate the total productivity as have other workers (Foster, 1982a; Smythe, 1970; Terborgh, 1983), and it is possible that residence time varied between months, as is the case for dung deposits (see Chapter 6). However, the total number of fruits in each class counted per month can be considered as a rough index of productivity, although it would have been better to have measured the weight of fallen fruit, as this would dampen the effect of some species producing large numbers of small fruits (e.g., *Centropogon glaucinus*, *Macaranga* spp.).

The large number of species found on transects, and the low overlap of species found fruiting on the five transects (Table 3.2) reflects the high plant species diversity of tropical rain forest at Lope. Just over 60% of species of fruit were succulent and almost 13% were arillate. These fruit types generally rely upon mammals and birds for dispersal (Gautier-Hion et al., 1985a; Pannell & Koziol, 1987), suggesting that animals disperse about three-quarters of all plant

species in the forest at Lope (fleshy pods also rely upon animal dispersers). Other species were dispersed by explosive dehiscence (11%) or by the wind (9%). This agrees closely with other data collected at Lope, where Williamson (1988) found that 74% of fruits were adapted for dispersal by animals, 19% were wind dispersed and 8% were dehiscent. Other studies show that strong reliance upon animal dispersers is characteristic of tropical rain forests: Alexandre (1980) found that 76% of plants in the Tai forest, Ivory Coast, relied upon animal dispersers whilst 18 and 6% respectively relied on wind and auto-dispersal; Foster (1982a) found that 72% of fruits on Barro Colorado Island were animal dispersed, whilst 25% relied upon the wind, 2% were dehiscent and for 1% the dispersal mechanism could not be determined; in Guyana Sabatier (1985) found 83.4% relied upon animals with 6.8, 4.9 and 4.9% dependent on wind, auto-dispersal and 'other' means respectively; Raemaekers *et al* (1980) found that at least 73% of species in Kuala Lompat, Peninsular Malaysia, were dispersed by animals; and Frankie *et al* (1974) found over 90% of fruit in Costa Rica were fleshy, and hence probably animal dispersed.

The number of species of fruit found in the five study sites was, as might be expected, proportional to the plant diversity as measured by the diversity of trees > 10 cm dbh, but there was no statistical difference in the total number of ripe fruits found on the five transects. Total numbers of unripe fruit unexpectedly showed a statistical difference between sites, due to consistently high counts along transect four. Data for unripe fruit might be expected to show some anomalies when fruit-fall monitoring is chosen as the method for data collection, since these fruits must have either aborted (and abscised) or have been physically displaced, whilst many ripe fruits will fall naturally once ripe.

Fruit production patterns were obviously related to climate at Lopé, but no simple correlations were detected between fruit availability and any of the environmental variables measured in this study. The positive correlations of fruit production and diversity with insolation data from three weather stations in Gabon suggest that this may well be an important factor. Data from northeastern Gabon have shown similar low fruit productivity in the long dry season (Feer, 1989; Gautier-Hion *et al.*, 1985b; Hladik, 1978; Sourd & Gautier-Hion, 1986) and suggest peaks in fruit production in September, November and January–March. Elsewhere in Africa, Lieberman (1982) recorded peak fruiting of fleshy fruits in the wet season in dry tropical forest in Ghana, but noted that dry fruited species

ripened in the dry season, and in Ivory Coast, Alexandre (1980) recorded peak fruiting in the November–March dry season. In this site there was a positive correlation between fruit production and rainfall three months previously. On Tiwai Island, Sierra Leone, peak fruiting is in the dry season, but most fruits are dehiscent (G. Dasilva, personal communication).

Elsewhere there seems to be a general trend for low fruiting in periods of low rainfall, with one or more peaks of production in wetter months (e.g., Foster, 1982a; Terborgh, 1983) or in minor dry seasons (e.g., Frankie *et al.*, 1974), although individual species or fruit classes as a whole often vary from the general community trend: wind dispersed species often fruit in seasons with high winds (e.g., Foster, 1982a; Terborgh 1983); and dehiscent species sometimes ripen in major dry seasons when humidity levels fall (e.g., Lieberman, 1982; G. Dasilva, personal communication). Long term studies of phenology, environmental variables, and means of seed dispersal are required if we are to understand the patterns and variability of fruiting within tropical rain forests.

Succulent fruits were the most abundant class at Lopé, and so had greatest influence on the pattern of overall fruit availability. Figure 3.2 indicated that diversity of ripe fruit increased in August, immediately after the long dry season, but 1989–1990 was a 'good' fruit year (Tutin *et al.*, 1991a), and consequently there was a relatively high figure for June 1990. Figure 3.4 showed that there was a lag of three months until November before the numbers of succulent fruits on transects increased, showing that measures of the number of species with ripe fruit may not always be a true reflection of food availability. This may be due to differences in reproductive strategies of species fruiting at different times of the year. Species fruiting in the wet season were generally highly synchronised, perhaps either to swamp seed predators (cf. Janzen, 1969), or encourage large bodied seed dispersers to concentrate their foraging time on those species. Some of these species occasionally failed to set fruit despite flowering, perhaps because of disease (e.g., *Celtis tessmannii*) or fruit was lost when eaten unripe during atypical periods of fruit scarcity (e.g., *Dialium* sp. ?nov - C. E. G. Tutin, personal communication). Species fruiting during, and shortly after, the major dry season tended to produce fruit over longer periods, and individuals often fruited asynchronously (see below), perhaps because environmental conditions limited the number of fruit that could ripen at any given time (cf. Gautier-Hion *et al.*, 1985b), or to avoid losing the whole crop to unusual events. From figure 3.4 it is clear

that the November–March period is the most favourable for frugivores.

Arillate fruits seemed to be more constant in production than the other classes, and the large peak in production in January (Figure 3.4) was due mostly to large counts of small *Centroplacus glaucinas* fruits. Arillate species generally produced fruits during several months, often including the dry season. It is possible that this fruit type is adapted to enable ripening during periods of water stress and low insolation (cf. Fautier-Hion et al., 1985b), since their thin arils would require little water, and they have low sugar content (Rogers et al., 1990). By fruiting in the dry season, they would avoid competition for animal dispersers from species with sugar-rich fruits (cf. Snow, 1966). Wind dispersed fruits began to ripen in August, but peaks in diversity and numbers were both in January/February (high total counts were caused principally by large crops of *Lophira alata* and *Desbordesia glaucescens*). Dehiscent fruit species were equally represented from August to February, although there seemed to be a peak in numbers in November. It might be expected that these species should ripen in the dry season (Lieberman, 1982; G. Dasilva, personal communication), but Gabon is unusual in that humidity does not fall during this period (Chapter 2), so desiccation would not be facilitated.

Williamson (1988) monitored a sample of up to 344 trees of 83 species, monthly at SEGC from August 1984 to May 1985, by scoring plant parts *in situ* on a 0–4 scale. The sample showed peaks in succulent fruit production in October, January and May and a peak in dry fruit production in November. This might reflect a difference in sampling techniques (fruit on the plant, versus fruit-fall in this study), but 1984–85 exhibited uncharacteristic climatic conditions which affected phenology patterns (Williamson, 1988) and it is not a good period for comparison. Tutin et al., (1991a) presented data on the average number of species with ripe fruit amongst a sample of 600 individuals of 60 species (mostly succulent fruits which are consumed by apes) monitored over a five-year period at SEGC from 1986, which showed that fruit diversity increased either side of the long dry season. Their pattern is similar to that for succulent fruit in Figure 5, although number of fruiting species was equally high from November–February.

Species which fruited in the major dry season are potential keystone foods for frugivores. Those for which ripe fruits were recorded in several sites during more than one of the dry season months are more likely to fulfil this role. Of 16 species which produced ripe fruit in at least two of the three dry season months,

or in at least two sites during the dry season (Table 3.4), 14 were extended fruiterers. *Cissus dinklagei* was an exception, as it was only recorded in two months, and also because it was a small, sugary drupe. However, levels of water soluble carbohydrates were lower than for many species that fruit in the wet season (cf. Rogers *et al.*, 1990). Other succulent species were large and fibrous and three of these, *Panda oleosa*, *Klainedoxagabonensis*, *Sacoglottis gabonensis* were adapted for dispersal by elephants (Chapter 5). *Sacoglottis gabonensis* fruiting peaked in November/December and only a few individuals produced fruit in the dry season.

Leighton & Leighton (1983) identified tree species of the Meliaceae and Myristicaceae, which exhibited temporally staggered fruiting, as keystone resources for territorial hornbills in periods of overall fruit scarcity in a Bornean lowland tropical rain forest. Trees of the Annonaceae were important for primates at this time, and common climbing and strangling *Ficus* species (Moraceae), showed fruiting asynchrony and frequent crop production, and provided a relatively continuous supply of fruits for frugivores throughout the year. Terborgh (1986) working in Cocha Cashu, Peru, confirmed the vital role played by figs in periods of scarcity and found that nectar from three species was important for most arboreal mammals and birds and that palm nuts were also important for some species. In northeast Gabon, Gautier-Hion & Michaloud (1989) found that figs were uncommon and were not important keystone resources, but that two species of arillate Myristicaceae (*Coelocaryon preussi* and *Pycnanthus angolensis*) and one succulent Annonaceae (*Polyalthia suaveolens*) were keystone resources for the frugivore community in the long dry season.

Pycnanthus angolensis, *Coelocaryon preussi* and *Polyalthia suaveolens* all occur in Lope, but they fruit from August onwards, with peak production in September–November, not during the height of the dry season when fruit availability is at a minimum (C.E.G. Tutin, personal communication; this study). They do not therefore represent keystone resources throughout Gabon. This emphasises the fact that one cannot make generalisations about phenology patterns in tropical rain forest areas, even if they are close geographically. Those species listed in Table 3.5 are the best candidates for the role of keystone fruiterers in Lope, and as in other areas, many produce arillate fruits (cf., Gautier-Hion & Michaloud, 1989; Leighton & Leighton, 1983). Tutin *et al.* (1991a) found that two of these were indeed keystone species for chimpanzees (*Duboscia macrocarpa* and *Elaenis*

guineensis) and that gorillas consumed one (*Duboscia macrocarpa*) in the major dry season, in addition to vegetative parts of aquatic Marantaceae and bark of the tree, *Milicia excelsa*, which they ignored at other times of the year. However, there are large inter-annual differences in fruiting patterns at Lope (C. E. G. Tutin, personal communication), and it will be necessary to undertake long-term studies of fruiting and frugivores to identify keystone species with confidence. Further studies are to be recommended, especially in areas where tropical forests are to be managed for timber exploitation, as this may disrupt the precarious balance between fruit availability and frugivores during periods of low fruit production, especially if keystone resources are likely to be adversely affected. Foster (1982b) working on Barro Colorado Island, recorded a period of famine when many frugivorous animals died, and suggested that such crises were relatively frequent in this area. If the same is true of other rain forest areas, any interference with keystone resources may have disproportionately large negative effects on vertebrate frugivores (Leighton & Leighton, 1983), and it is important that these species are identified in more rain forest areas.