

Phenology of neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae)

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To relate differences in phenological strategies of a group of closely related plants to biotic (pollinators, dispersers) and abiotic (water, light) factors, we studied leafing, flowering, and fruiting phenology of 12 species of *Piper* (Piperaceae) in a neotropical lowland forest in Panama for 28 months. We asked how *Piper* may partition time and vertebrate frugivores to minimize possible competition for dispersal agents. Based on habitat preferences and physiological characteristics we discriminate between forest *Piper* species (eight species) and gap *Piper* species (four species). Forest *Piper* species flowered synchronously mostly at the end of the dry season. Gap *Piper* species had broader or multiple flowering peaks distributed throughout the year with a trend towards the wet season. Both groups of *Piper* species showed continuous fruit production. Fruiting peaks of forest *Piper* species were short and staggered. Gap *Piper* species had extended fruiting seasons with multiple or broad peaks. Both groups of *Piper* species also differed in their time of ripening and disperser spectrum. Forest *Piper* species ripened in late afternoon and had a narrow spectrum consisting mainly of two species of frugivorous bats: *Carollia perspicillata* and *C. castanea* (Phyllostomidae). Fruits of gap *Piper* species, in contrast, ripened early in the morning and were eaten by a broader range of diurnal and nocturnal visitors, including bats, birds, and ants. We conclude that the differences in flowering phenology of forest and gap *Piper* species are primarily caused by abiotic factors, particularly the availability of water and light, whereas differences in fruiting patterns are mostly influenced by biotic factors. The staggered fruiting pattern of forest *Piper* species may reflect competition for a limited spectrum of dispersers. The long and overlapping fruiting periods of gap *Piper* species are associated with a larger spectrum of dispersers and may be a strategy to overcome the difficulty of seed dispersal into spatially unpredictable germination sites with suitable light conditions.

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The many species of pantropical pepper plants (*Piper*, Piperaceae) are important food resources for frugivorous insects and vertebrates (Gilbert 1980, Fleming 1985), especially during seasonal scarcity of other fruits. Crops of individual *Piper* plants are small with a few fruits ripening in predictable time intervals over a period of several weeks or months, a steady-state pheno-

logical strategy. Fruits are harvested by a limited group of dispersers, mainly bats, in some cases also birds and ants (Fleming 1981, 1985, O'Donnell 1989). Patterns of fruit production and disperser spectrum of *Piper* contrast strongly with those of “big-bang” plants such as Neotropical figs (Moraceae: *Ficus*). Figs produce huge fruit crops and attract a wide range of diurnal and

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nocturnal dispersers (Janzen 1979, Milton et al. 1982, Terborgh 1983, 1986, Charles-Dominique 1993, Kalko et al. 1996b, Korine et al. 2000).

Neotropical *Piper* species occur in a variety of habitats (Croat 1969, Fleming 1985, Fleming and Maguire 1988, Greig 1991, Laska 1997). Members of this genus are well-known as pioneer plants that colonize gaps, clearings, and forest edges and are thus involved in regeneration processes and maintenance of plant diversity. Some *Piper* species also grow in closed forest. Denslow et al. (1990) and Greig (1991) separated shade tolerant or late successional "forest" species from shade intolerant or early successional "gap" species. In spite of their importance for frugivores and their crucial role in regeneration processes, little is known about the flowering, fruiting, and leafing pattern of most *Piper* species in local plant communities (Fleming 1981, 1985, Marquis 1988, Marinho-Filho 1991) and even less about the relationship between their fruiting phenology and their main dispersers (Fleming 1981, 1985). The temporal pattern of fruiting of animal-dispersed plants is not only vital for the successful dispersal of fruits and seeds and the establishment of seedlings, but also strongly influences the reproductive activity (Bonaccorso 1979, Wheelwright 1983, Dinerstein 1986, Levey 1988, Worthington 1990, Sosa and Soriano 1996) and seasonal movements (Janzen 1967, Snow 1971, Heithaus et al. 1975, Karr 1976, Thompson and Willson 1979, Stiles 1980, Pyke 1983, Wheelwright 1983) of the dispersers that depend on them.

We studied the leafing, flowering, and fruiting phenology of 12 common *Piper* species in a tropical lowland forest on Barro Colorado Island (BCI) in Panama over a 28-month period. On BCI, a total of 22 species of *Piper* co-occurs. They form a distinctive group of understory plants that are insect-pollinated. Two frugivorous leaf-nosed bats (Phyllostomidae: *Carollia perspicillata* and *C. castanea*) that are common on BCI and whose diet contains large portions of *Piper*, are the main dispersers of their seeds (Bonaccorso 1979, Kalko et al. 1996a). The main objective of our study was to determine whether and how flowering, fruiting, and leafing differ among *Piper* species on BCI and to which extent abiotic (i.e. climatic) and biotic factors (i.e. pollinators, dispersers) may contribute to this pattern. Furthermore, we examine the role of *Piper* in the diet of its main dispersers, short-tailed fruit-bats (*Carollia* sp.), and assess the degree of specialization in the interaction between *Piper* and the two species of bats.

Material and Methods

Study site and climate

This study was conducted between February 1994 and December 1997 on Barro Colorado Island (9°09'N,

79°51'W), the field station of the Smithsonian Tropical Research Institute in Panama. The island (15.6 km²) is covered with tropical moist, semi-deciduous forest of several successional stages (Foster and Brokaw 1990). To the northeast, about half of the island consists of secondary forest of about 100 to 200 years. Old forest of about 300 to 400 years covers most of the southwestern part of BCI and a small strip of old forest near the laboratory area. The laboratory area is cleared and is composed of early successional vegetation with pioneer plants, mainly *Cecropia*, *Ochroma*, *Solanum*, *Piper*, and *Trema*.

Rainfall is seasonal, with a dry period between the end of December and the end of April and a wet period between May and most of December. Total annual rainfall is 2650 mm (Windsor et al. 1990, Paton 1996). In the wet season, an average of 300 mm of rain falls per month, with a short, slightly drier period between August and September.

Fruit availability and removal rate

Fruit availability was determined for six *Piper* species (*P. aequale*, *P. grande*, *P. culebranum*, *P. reticulatum*, *P. dilatatum*, and *P. marginatum*) by counting nightly production of ripe fruits. Removal rates of ripe fruits were determined for three *Piper* species (*P. aequale*, *P. grande*, and *P. dilatatum*) by marking ripe fruits and counting the fruits remaining the next morning shortly after sunrise.

Diet composition of *C. perspicillata* and *C. castanea* on BCI

To determine the importance of *Piper* in the diet of their two main dispersers, we collected feces from 229 bats (79 fecal samples of *C. perspicillata* and 150 fecal samples of *C. castanea*) concurrently with the phenological study. Bats were caught in mist nets set over trails and streams at 15 localities on BCI. As some fecal samples of the bats contained more than one type of seed, we extracted a total of 271 seed samples from 229 fecal samples (84 seed samples from *C. perspicillata* and 187 seed samples from *C. castanea*). Seeds were identified by comparing them with the seed collection of the BCI herbarium and with our identification key. Further details of capture data of the bats and of seasonal variation in diet composition will be given elsewhere.

Phenological patterns of *Piper*

We tagged adult individuals (characterized by several stems or one main stem of more than 1 cm diameter at 20 cm above ground) of 12 *Piper* species along small

trails in a strip of old forest near the laboratory clearing and in the adjacent secondary forest, covering a total area of about 24 ha. Except for *P. reticulatum*, which is a small tree 3 to 7 m in height, all *Piper* species are shrubs with heights of 1 to 3 m. For each of the seven abundant species (*P. aequale*, *P. carilloanum*, *P. cordulatum*, *P. dilatatum*, *P. grande*, *P. marginatum*, and *P. reticulatum*), 15 individuals were tagged; for the five less common species (*P. arboreum*, *P. culebranum*, *P. darienense*, *P. perlasense*, and *P. hispidum*), we tagged as many adults as could be found along the trails (6 to 11 individuals). This resulted in a total of 143 marked individuals and an average of 12 individuals per species (Table 1). Individuals that were lost due to falling branches or trees were replaced by nearby individuals of the same species. Tebbs (1990) regards *P. perlasense* as synonymous with *P. aequale*. Due to clear differences in morphology and phenology on BCI (Croat 1978), we treat both as separate species.

Table 1. Spearman rank correlation coefficients (r_s) for the consistency of flowering and fruiting periods of gap and forest *Piper* species on BCI between the years 1994/95 ($n = 7$ months), 1994/96 ($n = 5$) and 1995/96 ($n = 8$). $p < 0.05$ (*); $p < 0.02$ (**); $p < 0.01$ (***)¹. Numbers in parentheses indicate the numbers of individual plants monitored per species.

Species	Year	Flowering	Fruiting
<i>Forest Piper species</i>			
<i>P. aequale</i> (15)	94/95	0.64	0.79 *
	94/96	0.88	1.00 *
	95/96	0.70	0.88 **
<i>P. arboreum</i> (10)		0.69	0.71
		0.90	0.38
		0.60	0.42
<i>P. carilloanum</i> (15)		0.54	1.00 ***
		-0.03	1.00 *
		0.61	0.81 *
<i>P. cordulatum</i> (15)		0.16	0.91 **
		0.13	0.68
		0.93 ***	0.51
<i>P. darienense</i> (11)		0.88 *	0.81 *
		0.85	0.53
		1.00 ***	0.78 *
<i>P. grande</i> (15)		0.91 **	0.78
		0.78	0.78
		0.69	1.00 ***
<i>P. perlasense</i> (6)		0.35	1.00 ***
		0.6	1.00 *
		0.83 *	1.00 ***
<i>P. culebranum</i> (8)	95/96	0.83 *	0.62
<i>Gap Piper species</i>			
<i>P. dilatatum</i> (15)	94/95	0.61	0.71
	94/96	0.70	0.40
	95/96	0.98 ***	0.78 *
<i>P. hispidum</i> (8)		-0.62	0.38
		-0.03	0.25
		0.44	0.91 ***
<i>P. marginatum</i> (15)		0.91 **	0.79 *
		0.98	0.78
		0.73	0.96 ***
<i>P. reticulatum</i> (15)		0.04	0.14
		0.13	0.08
		0.33	0.59

We recorded the phenological data at bi-weekly intervals. During the 28-month study, February to April and June were monitored three times, the rest of the months were monitored twice. *Piper culebranum* was added in 1995. Numbers of immature and flowering inflorescences as well as immature and mature infructescences (hereafter called fruits) were classified into predetermined categories. To obtain an estimate of medium crop size of *Piper* species, the fruits of 150 randomly chosen adults of *P. aequale* were counted shortly before ripening. *Piper aequale* is one of the most common *Piper* species on BCI and its average fruit number (11.7 ± 14.6 fruits/plant) is within the range of the other monitored species. Based on this result, we classified the number of immature and flowering inflorescences as well as immature and mature fruits into the categories "none" (no inflorescences, no fruits), "few" (1–10), and "many" (> 10). For new leaves, we distinguished only between "present" and "absent". We choose these criteria because *Piper* in general has only few leaves and flushes them at very low rates. For data analysis the categories "none", "few", and "many" for flowers and fruits were transformed into the numbers 0, 1 and 2, respectively. The categories "present" and "absent" for the new leaves were transformed into 0 and 1. These values (phenological scores) were used for statistical analyses to test for consistency in flowering and fruiting patterns and differences in leafing, flowering and fruiting activities between the different *Piper* species. To obtain a monthly phenological pattern of individuals, the bi-weekly scores of an individual were averaged. To assess the monthly phenological pattern of a species, the monthly scores of all individuals of a species were averaged. To obtain the overall monthly phenological pattern for all *Piper* species, the mean monthly scores of all species were averaged.

Statistical analysis

Consistency in flowering and fruiting patterns (measured as described above) between years was tested by the Spearman rank correlation test (Sokal and Rohlf 1995). We applied Wilcoxon's signed-ranked test to determine if there were significant differences in flowering/fruiting activity of the 12 monitored species between the first half (January to June; dry to early wet season) and the second half of the year (July to December; wet season). To assess significant differences in the amount of yearly flower, fruit, and leaf production between forest and gap *Piper* species, we used the two-tailed Mann-Whitney U-test. We chose $p < 0.05$ as level of significance for all tests.

To determine whether the level of flowering or fruiting overlap observed among *Piper* species differed significantly from expectations obtained by chance, we used a null model described in Pleasants (1980, 1990)

and Wright and Calderón (1995). Here, an overlap index (Pianka 1974) based on monthly values is calculated for each pairwise combination of *Piper* species (Pleasant 1980, 1990). The mean overlap of these combinations was compared with 99 values of a randomization test as described in Wright and Calderón (1995). The simulations randomized mean flowering and fruiting times while preserving the form of the observed distribution of flowering and fruiting around the year. Here, the year is not represented on a linear time scale, but on a circle with a rotation of 360° and an arbitrary origin. Mean flowering and fruiting times were determined as described in Wright and Calderón (1995). The length of the flowering and fruiting season in our analyses encompasses all 12 months of the year because flowering and fruiting could be observed year-round in *Piper*.

Flowering or fruiting times were regarded as “staggered” (temporally uniform) whenever the observed flowering or fruiting overlap value was smaller than that of at least 95 of the 99 simulations and as “aggregated” whenever the observed overlap value was greater than that of at least 95 simulations.

Results

Overall leaf production, flowering and fruiting activity of *Piper*

On our scale from 0 to 1, leaf production of all *Piper* species was intermediate (mean value of 0.63) and almost constant throughout the year with a slight drop in April and an increase at the onset of the wet season in May (Fig. 1). There were two smaller peaks in the wet season, the first one in June and the second in September. However, there was no significant difference in leafing activity between the first and second half of the year (Wilcoxon's signed ranks test: $n = 12$, $T_s = 22$, $p = 0.2094$).

Like leaf production, flowering was continuous throughout the year. On a scale from 0 to 2, overall activity was low with a mean value of 0.43 (Fig. 1). Annual flowering activity increased during the dry season and peaked in April, the last month of the dry season, when leaf production was lowest. However, differences in flowering activity between the first, mostly dry and the second, wet half of the year were not significant (Wilcoxon's signed-ranks test $n = 11$, $T_s = 17$, $p = 0.1823$).

The fruiting phenology of all *Piper* species together did not show a seasonal pattern on BCI (Fig. 1). On a scale from 0 to 2, ripe fruits were present at a very low level (mean value of 0.15) during the entire year with a slight increase at the end of the wet season in November and December. Wilcoxon's signed-ranks test did not show a significant difference in fruit production

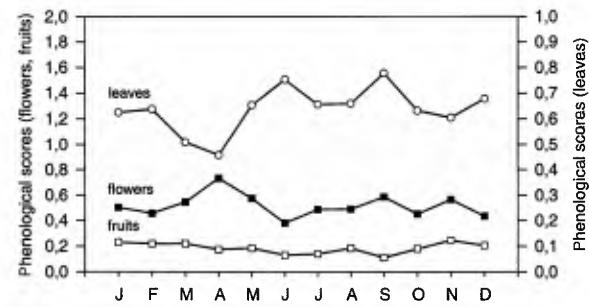


Fig. 1. Leafing, flowering, and fruiting activity of all *Piper* species studied on BCI ($n = 12$). Flowering and fruiting activities were categorized as “none”, “few”, or “many” flowers or fruits present. Categories were transformed into phenological scores with numbers between 0 and 2. Leafing activity was categorized as “presence” or “absence” of new leaves and transformed into the numbers 0 and 1. The phenological scores from the same months of the 28-month study period (1994–1996) were averaged taking all *Piper* species together. Averaged monthly phenological scores of flowering and fruiting are depicted on the left y-axis, and the averaged monthly phenological scores of leafing on the right y-axis.

between the two halves of the year ($n = 12$, $T_s = 37.5$, $p = 0.9375$).

Phenology of forest and gap *Piper* species

Based on the major habitat types where the 12 monitored species of *Piper* occurred, we discriminated between forest and gap *Piper* species. Forest *Piper* species are only found within the forest with low light conditions typical for the understory. Daws et al. (2002) measured in the understory on BCI 0.89% photosynthetically active radiation relative to full sunlight. On BCI, the group of forest *Piper* species includes *P. aequale*, *P. arboreum*, *P. carrilloanum*, *P. cordulatum*, *P. culebranum*, *P. dartenense*, *P. grande*, and *P. perlasense*. With the exception of *P. cordulatum*, all other forest *Piper* species prefer steep, moist areas and thus are found mainly in ravines. *Piper cordulatum* occurs under more closed canopy in drier and flatter habitats.

The group of gap *Piper* includes *P. dilatatum*, *P. hispidum*, *P. marginatum*, and *P. reticulatum*. With the exception of *P. reticulatum*, all gap *Piper* species are found in cleared, open areas (clearing sizes over 50 m^2) with light levels typical for gap conditions. Daws et al. (2002) measured between 5.7% and 34.0% photosynthetically active radiation relative to full sunlight for gap sizes between 67 m^2 and 320 m^2 . *Piper reticulatum*, which is a small tree 3 to 7 m in height, is intermediate in its habitat requirements. It grows within the forest, in forest gaps, and at forest edges. However, during the study period *P. reticulatum* produced inflorescences and fruits only in forest gaps and edges where the crowns of the trees were exposed to direct sunlight. We never observed flowering or fruiting trees within the forest.

Leaf production, flowering, and fruiting activity of forest *Piper* species

Leaf production in forest *Piper* species decreased during the dry season (Fig. 2a). It increased again to a high and even level during the wet season. Two smaller peaks of leaf production occurred in June and September. There was no significant difference in leafing activity between the two halves of the year (Wilcoxon's signed ranks test: $n = 8$, $T_s = 10.5$, $p = 0.3270$).

Flowering of forest *Piper* species peaked strongly in the dry season between February and April (Fig. 2a). With the beginning of the wet season, the activity dropped sharply to almost none in June and July but increased slightly at the end of the wet season. Flowering activity was significantly higher in the first half of the year than in the second half (Wilcoxon's signed-ranks test: $n = 8$, $T_s = 0$, $p = 0.0117$).

Flowering of individual species of forest *Piper* species peaked mostly in April and May (Fig. 2b). *Piper carri-*

loanum and *P. cordulatum* started flowering in the middle of the wet season and reached a peak at the beginning of the year, leading to the slight increase in overall flowering activity in forest *Piper* species at the end of the year (Fig. 2a). In the randomization test, the observed overlap value ($= 0.1331$) was greater than the simulated values of 84 runs, indicating a random distribution of flowering times within forest *Piper* species with only a slight tendency towards aggregation.

Generally, fruiting activity of forest *Piper* species was relatively constant at a low level throughout the year (Fig. 2a). Fruiting activity in the first half of the year was not significantly different from fruiting activity in the second half (Wilcoxon's signed-ranks test: $n = 8$, $T_s = 13.5$, $p = 0.4838$). There was a small increase in fruit production at the end of the dry and at the beginning of the wet season. Highest fruit production occurred in November and December, while it dropped slightly in February and March.

In contrast to leafing and flowering, fruiting activity of individual species showed a staggered pattern (Fig. 2c). Almost every month a different species peaked in fruit production, resulting in the observed continuous fruiting activity of this group throughout the year. *Piper aequale* and *P. grande*, two morphologically rather similar and very common species, had distinct and narrow peaks in November and December, when almost all individuals of a species fruited synchronously, leading to the increase in fruit production in the overall activity of this group at the end of the year.

In the randomization test, the observed overlap in fruiting times ($= 0.6563$) was smaller than all 99 simulations, indicating a temporally uniform (staggered) distribution of the fruiting times of the eight species of forest *Piper* species.

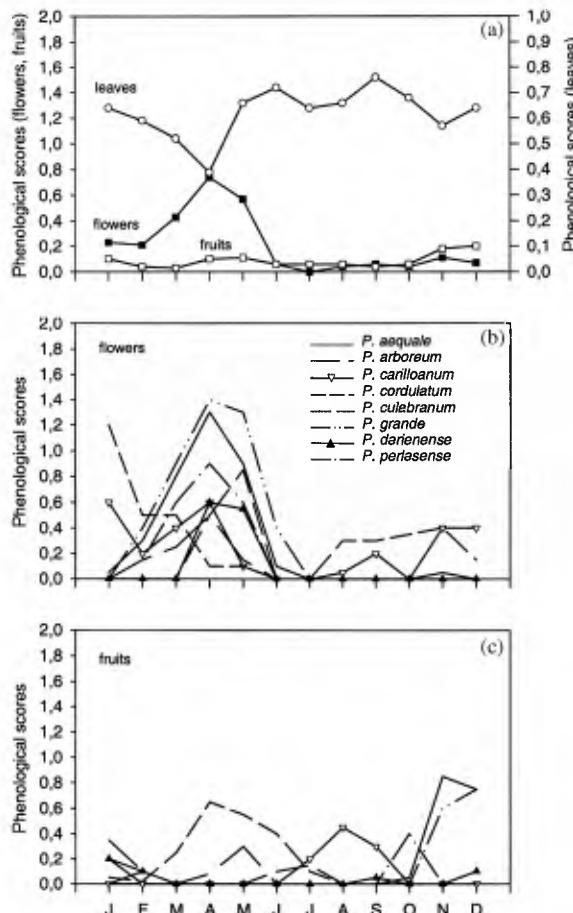


Fig. 2. (a) Leafing, flowering, and fruiting activity of eight forest *Piper* species on BCI averaged for the same months over the 28 month study period (1994–1996); (b) flowering activity and (c) fruiting activity of individual forest *Piper* species ($n = 8$) averaged for each forest *Piper* separately.

Ripening pattern, fruit availability, and removal rates of forest *Piper* species

Fruits of forest *Piper* species started to mature in the late afternoon after 3:30 pm. A fruit that would be ripe in a given night could not be distinguished from immature fruits the morning before maturation. Mature fruits were soft and produced a fruity smell (Thies et al. 1998). Ripe fruits remained light green as unripe fruits and persisted for only one night. If a ripe fruit was not removed during this night, it fell off the next morning or was eaten by ants. At night, mostly bats and very rarely katydids (Tettigoniidae) or crickets (Gryllidae) were observed feeding on ripe fruits. The mean nightly availability of fruits was 0.2 ± 0.1 ripe fruits per plant for *P. aequale* ($n = 1314$ plants), 0.4 ± 0.2 fruits per plant for *P. grande* ($n = 322$), and 0.4 ± 0.2 fruits per plant for *P. culebranum* ($n = 180$). To conclude, the number of ripe fruits per night and plant was very low,

but remained relatively constant from night to night throughout the fruiting period.

Removal rates of marked ripe fruits were observed on 50 plants of *P. aequale* once a week over seven weeks in 1996, and over 9 weeks in 1997 as well as on 26 plants of *P. grande* over 8 weeks in 1997. Bats removed entire ripe fruits in flight (Thies et al. 1998; pers. field obs.). The proportion of ripe *P. aequale* fruits taken at night was $88.6 \pm 9.0\%$ in 1996, and $89.0 \pm 18.2\%$ in 1997. Nightly removal rate was equally high for *P. grande* ($89.1 \pm 16.1\%$).

Leaf production, flowering, and fruiting activity of gap *Piper* species

Similarly to forest *Piper* species, leaf production in gap *Piper* species did not show a marked annual pattern (Fig. 3a). A slight drop in leaf production occurred in

the second half of the dry season but not as pronounced as in forest *Piper* species. During the wet season, leafing activity was continuously at a medium level with a small peak in June and September. There was no difference in relative leaf production between forest and gap *Piper* (Mann-Whitney U-test: $U = 59.5$, $p = 0.4689$). However, because both groups of *Piper* have only few leaves and flush them at very low rates, these results are also applicable to absolute leaf production of forest and gap *Piper*.

The flowering activity of gap *Piper* species was high during the year, suggesting high synchrony within species. However, in contrast to forest *Piper* species, flowering activity in gap *Piper* species was lowest during the dry season and highest during the wet season (Fig. 3a). Forest and gap *Piper* species differed significantly in flowering activity over the year (Mann-Whitney U-test; $U = 5$, $p = 0.0001$) with gap *Piper* species producing more inflorescences than forest *Piper* species.

With the exception of *P. reticulatum*, each species of gap *Piper* produced flowers throughout the year with several subsequent months of high flowering activity (Fig. 3b). Flowering peaks were distributed broadly throughout the wet season and with a broad overlap in flowering activity between species (Fig. 3b).

In the randomization test, the observed overlap in flowering times ($= 0.7094$) was smaller than the simulated overlap in 94 simulations indicating that the overlap in flowering times was not significantly different from a random distribution. However, a certain trend towards uniformity was visible. This result has to be viewed with caution because gap *Piper* consisted of only four species to run the randomization test and because, by averaging, multiple peaks converge into one.

Fruit production of gap *Piper* species was significantly higher than in forest *Piper* species (Mann-Whitney U-test: $U = 2$, $p = 0.0001$); it was fairly homogeneous during the year, reaching the lowest value in September (Fig. 3a). In contrast to forest *Piper* species, fruit production was highest at the beginning of the dry season and then decreased slowly.

Individual gap *Piper* species did not show the alternating fruiting activity between species with single, rather narrow peaks as seen in forest *Piper* species, but had multiple or broad fruiting peaks that overlapped widely between species (Fig. 3c). Within species, only one to five months per year were without fruit production in contrast to forest *Piper*, where individual species did not fruit for 7–11 months in a year. *Piper reticulatum*, the intermediate species between forest and gap *Piper* species, showed three fruiting peaks, two higher ones in June and October and a smaller one in March. *Piper hispidum* had fruiting peaks in March, May and September. *Piper dilatatum* and *P. marginatum* each had one broad peak per year. *Piper dilatatum* fruited most heavily between July and October with highest

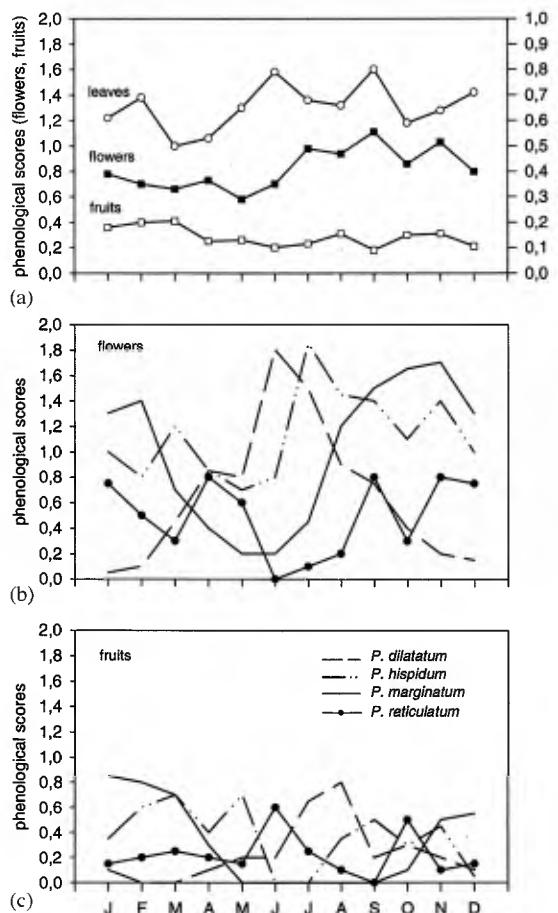


Fig. 3. (a) Leafing, flowering, and fruiting activity of four gap *Piper* species on BCI averaged for the same months over the 28 month study period (1994–1996); (b) flowering activity and (c) fruiting activity of individual gap *Piper* species ($n = 4$) averaged for each forest *Piper* separately.

fruiting activity in August. *Piper marginatum* had maximum fruiting activity between November and March.

In the randomization test, the observed overlap in fruiting times ($= 0.4840$) was lower than 99 simulations, indicating a uniform distribution for the four gap *Piper* species throughout the year. Although a uniform distribution of fruiting times was also found in forest *Pipers*, the fruiting pattern that leads to the uniform distribution in both groups of *Piper* is strikingly different. In forest *Piper*, individual species had only one rather narrow main fruiting peak per year with little overlap between species whereas in gap *Piper*, individual species had multiple or broad fruiting peaks with large overlap between species. Both patterns result in continuous fruit production throughout the year (Fig. 2a and 3a).

Ripening pattern, fruit availability, and removal rates of gap *Piper* species

With the exception of *P. reticulatum*, 95% of gap *Piper* fruits started to ripen in the morning at about 06:00 am while 5% of the fruits began to ripen after 2:00 pm. Fruits of *P. reticulatum* ripened between 14:00 and 4:00 pm as in forest *Piper* species. Ripe fruits smelled spicy and persisted for up to two days on the branch before they fell off. After the first night, however, they became mushy with a rotten smell. Fruits that were not eaten during the first day or night of maturation were not taken on the second day.

Availability of gap *Piper* fruits was about 4 to 10 times higher than that of forest *Piper* species, with 0.9 ± 0.5 ripe fruits per plant and day/night for *P. dilatatum* ($n = 133$ plants), 0.4 ± 1.4 fruits for *P. marginatum* ($n = 346$), and 8.5 ± 11.4 fruits for *P. reticulatum* ($n = 64$).

Fruits were eaten by ants, birds and bats. During the day, we frequently observed ants stripping off fruit tissue and seeds from the axis of the infructescence (rachis) that then remained empty on the branch. Occasionally, flycatchers (Tyrannidae) and tanagers (Thraupinae) took entire fruits during the day. The majority of the fruits, however, was removed by bats at night.

Removal rates of marked fruits were determined quantitatively in 1997 on 44 plants of *P. dilatatum* once a week over 5 weeks. During the day, ants took $26.3 \pm 16.9\%$ of the available ripe fruits and birds $3.8 \pm 7.4\%$. At night, bats took $48.5 \pm 20.3\%$. The fruits that remained untouched until the next morning ($21.4 \pm 6.1\%$) fell off during the day. In contrast to forest *Piper* species, the available number of ripe fruits declined steadily during each species' fruiting season. Parallel to this decline, the removal rate by bats also declined.

Differences in phenological patterns between years

Each species of *Piper* that we monitored on BCI had at least one flowering and one fruiting period per year. The overall flowering activity of all *Piper* species showed a peak in the late dry season. Compared to 1995 and 1996, the flowering peak of 1994 occurred one month earlier, in March. Because of this early peak in 1994, the flowering patterns of 1994/95 and 1994/96 were less consistent (Spearman rank correlation: flowering in 1994/95, $r_s = 0.39$, $p > 0.05$, $n = 7$, n.s.; flowering in 1994/96, $r_s = 0.6$, $p > 0.05$, $n = 5$, n.s.) than the flowering periods of 1995/96 (Spearman rank correlation: $r_s = 0.83$; $n = 8$; $p = 0.02$). Individual species of *Piper* varied in their flowering peaks from year to year, usually by a month, thus the consistency in flowering activity between years was low for many species (Table 1).

Overall fruiting activity of *Piper* species did not show a significant consistency between years because of the lack of pronounced peaks (Spearman rank correlation: fruiting in 1994/95, $r_s = 0.10$, $p > 0.05$, $n = 7$, n.s.; fruiting in 1994/96, $r_s = 0.58$, $p > 0.05$, $n = 5$, n.s.; fruiting in 1995/96, $r_s = 0.64$, $p > 0.05$, $n = 8$, n.s.). However, individual species had fruiting peaks. For most species these peaks were highly predictable and significantly consistent between years, even when the flowering peaks differed by a month from year to year (Table 1). Consistency between years was stronger for forest *Piper* species than for gap *Piper* species. *Piper reticulatum* showed the least consistency, since some individuals fruited more often per year than others.

Duration of flowering and fruiting periods

To categorize the duration of flowering and fruiting periods, we defined four categories. "Short" flowering or fruiting extends from 2 weeks to 4 months, "multiple, short" flowering or fruiting shows several periods per year that last 2 to 4 weeks each, "extended" flowering or fruiting ranges from 5 to 10 months, and "continuous" refers to flowering or fruiting encompassing 11 months to a whole year.

Based on flowering periods, we found two groups in forest *Piper* species: one group with short flowering periods (*P. aequale*, *P. arboreum*, *P. culebranum*, *P. grande*, *P. darienense* and *P. perlasense*) and a second group with extended flowering periods (*P. carilloanum* and *P. cordulatum*, Table 2). Gap *Piper* species showed more types of flowering duration with a trend to longer flowering periods than forest *Piper* species. *Piper hispidum* and *P. marginatum* had continuous flowering periods, while the flowering period of *P. dilatatum* fell into the category "extended" with 10 months of flowering. *Piper reticulatum* differed from all other *Piper* species in having multiple, short flowering periods that lasted only 2 to 4 weeks (Table 2).

Table 2. Duration of flowering and fruiting within species in forest and gap *Piper* species on BCI. Numbers in parentheses indicate the number of flowering/fruiting months.

Species	Flowering	Fruiting
Forest <i>Piper</i> species		
<i>P. aequale</i>	short (3–4)	short (4)
<i>P. arboreum</i>	short (2–4)	short (2)
<i>P. carilloanum</i>	extended (6–8)	short (3)
<i>P. cordulatum</i>	extended (9)	short (4–5)
<i>P. culebranum</i>	short (1–2)	short (1–2)
<i>P. darienense</i>	short (1–2)	short (3–4)
<i>P. grande</i>	short (4–5)	short (4)
<i>P. perlasense</i>	short (2–4)	short (1)
Gap <i>Piper</i> species		
<i>P. dilatatum</i>	continuous (11–12)	continuous (11)
<i>P. hispidum</i>	continuous (12)	continuous (11)
<i>P. marginatum</i>	continuous (12)	extended (8)
<i>P. reticulatum</i>	multiple, short (0.5–1)	multiple, short (0.5)

All forest *Piper* species had short fruiting periods that lasted either 1 to 4 months or were very short (i.e., 2 to 4 weeks, Table 2). In gap *Piper* species, fruiting periods generally extended from 8 to 11 months (Table 2). As in its flowering period, *P. reticulatum* differed from all other *Piper* species by having multiple, short fruiting periods of 2 to 4 weeks.

Duration of fruit maturation

The period of fruit maturation encloses the time between the end of flowering and the onset of the production of ripe fruits. We distinguish two fruit maturation periods: a “short” period of 1–4 months, and an “extended” period lasting 5 months and more. Half of the forest *Piper* species had extended maturation times preceded by relatively short flowering periods (*P. aequale*, *P. perlasense*, *P. grande* and *P. darienense*, Table

3). Typically, the fruits of these species reached their final size and shape including seed set within two months after flowering. The fruits remained in this stage until ripening occurred very quickly at the end of the maturation time. The other half of the forest *Piper* species were divided into species with short maturation times preceded by an extended flowering period (*P. carilloanum* and *P. cordulatum*) and species with short maturation times following directly after a short flowering period (*P. arboreum* and *P. culebranum*). To summarize, all forest *Piper* species, except *P. darienense*, flowered together at the beginning of the rainy season and bore ripe fruits in the same year but at different times. *Piper darienense* was the only species that produced ripe fruits at the beginning of the following year.

In general, gap *Piper* species had short maturation times. In *P. dilatatum*, *P. hispidum* and *P. marginatum*, flowers and ripe fruits occurred simultaneously on the same branches (Table 3). These species also produced a few immature fruits shortly after the fruiting period. These fruits stayed immature for 2–4 months and ripened in the following fruiting period. *Piper reticulatum* also had short maturation periods that lasted between 2 weeks and 2 months and occurred shortly after or simultaneously with a very short flowering period (Table 3).

Diet of *C. perspicillata* and *C. castanea*

Ripe fruits of *Piper* were the core diet of both *Carollia* species. Diet analyses based on fecal samples revealed that large numbers of *Piper* seeds were present in both *Carollias’* year-round, including seeds of all *Piper* species that are common on BCI. In *C. perspicillata*, more than half (58.3%) of the total seed samples ($n = 84$) contained *Piper*. In *C. castanea*, *Piper* seeds occurred in 92% of the total seed samples ($n = 187$). However, although *Piper* formed the principal diet of the two

Table 3. Maturation times (time between end of flowering and occurrence of first ripe fruits) of forest and gap *Piper* species fruits on BCI. For definitions see text.

Species	Flowering peak	Fruiting peak	Maturation time
Forest <i>Piper</i> species			
<i>P. aequale</i>	April	November	extended
<i>P. arboreum</i>	April	May	short, after a short flowering period
<i>P. carilloanum</i>	January, April	August	short, after an extended flowering period
<i>P. cordulatum</i>	January	April	short, after an extended flowering period
<i>P. culebranum</i>	May	July	short, after a short flowering period
<i>P. darienense</i>	May	January next year	extended
<i>P. grande</i>	April	December	extended
<i>P. perlasense</i>	April	October	extended
Gap <i>Piper</i> species			
<i>P. dilatatum</i>			short, simultaneously with flowering
<i>P. hispidum</i>			short, simultaneously with flowering
<i>P. marginatum</i>			short, simultaneously with flowering
<i>P. reticulatum</i>			short, after a short flowering period or simultaneously

Carollia species, they differed in the consumption of forest versus gap *Piper* species. *Carollia perspicillata* consumed more gap *Piper* species (71.4%; total number of fecal samples containing *Piper* = 49), while *C. castanea* ate equal parts of forest (43.6%) and gap *Piper* species (56.4%; total number of fecal samples containing *Piper* = 172).

Discussion

General patterns of *Piper* phenology on BCI in comparison to other neotropical forests

Our 28-month study of the phenology of 12 *Piper* species on BCI showed strong seasonality in flowering with a peak at the transition time between dry and wet season in April and May. Leafing and fruiting was less seasonal. Leaf production was almost constant with two small peaks in June and September. Fruiting occurred at a low but constant level throughout the year with a slight increase at the end of the year. This pattern coincides largely with the phenological patterns of other understory plants on BCI (Croat 1975, 1978, Foster 1990, Leigh and Windsor 1990, Leigh 1999).

Flowering

Compared with the flowering patterns of understory plants of a wet forest in La Selva and a dry forest in Guanacaste, both in Costa Rica (Opler et al. 1980), the flowering activity of *Piper* on BCI resembles more that of the highly seasonal Guanacaste dry forest that is influenced by the Pacific Ocean climate. While the flowering activity of understory plants in forests with relatively constant rainfall throughout the year such as the wet forest in La Selva shows a tendency towards aseasonality (see also Hilty 1980, Newstrom and Frankie 1994), flowering activity in forests with marked seasonality such as the dry forest in Guanacaste mostly peaks at the end of the dry season. It has been suggested that the onset of flowering is triggered by the first rainfalls at the end of the dry season (Janzen 1967, Opler et al. 1976, 1980, Borchert 1983). However, higher light levels during the dry season are also likely to affect time of flowering (van Schaik et al. 1993, Wright and van Schaik 1994, Wright 1996).

Fruiting

In contrast to flowering, fruiting of understory plants does not show marked seasonal patterns, whether in wet or in dry forests (Opler et al. 1980, Foster 1990). As differences in rainfall and light conditions in the forest do not appear to strongly affect fruiting patterns, we conclude that the observed continuity of fruiting events throughout a year in *Piper* and other understory plants can be seen as a response of the plants to competition for the same seed dispersers

(Snow 1965, Janzen 1967, Hilty 1980, Rathcke and Lacey 1985, Foster 1990).

Fruiting activity in *Piper* is constant throughout the year and increases slightly in November and December. This increase is characteristic for understory plants on BCI and coincides with the period of fruit scarcity of canopy trees (Croat 1978, Foster 1990). Because of this continuity, *Piper* represents a reliable food source for frugivores year-round. This is well-documented in its continuous presences in the fecal samples of its main dispersers, the short-tailed fruit bats *C. perspicillata* and *C. castanea*. However, *Carollia*, in particular *C. perspicillata*, supplement their *Piper* diet with fruits from other understory plants as well as fruits from canopy trees (Bonaccorso 1979, unpubl.). Since fruit production of the latter decreases at the end of the year on BCI (Foster 1990), *Piper* becomes even more important for *Carollia* during this period.

Productivity and the onset of fruiting periods in *Piper* are very consistent from year to year in contrast to the overall fruit-production on BCI that shows large seasonal fluctuations, in particular in association with the El Niño Southern Oscillations (Wright et al. 1999). They do not seem to be strongly influenced by climatic changes such as prolonged rainy seasons or displaced dry seasons. This results in a stable resource base not only throughout one year but also over several years and could be one of the underlying reasons for the observed stability in the long-term population trends of both *Carollia* on BCI (Kalko et al. 1996a).

Leafing

Leaf production of pioneer plants in light gaps on BCI is strongly seasonal with most leaves flushing in the wet season (Coley 1990). Leafing in *Piper* resembles that of canopy trees on BCI with a major peak in May or June and a minor one in September (Leigh and Windsor 1990). The pronounced peak in leaf production of canopy trees on BCI in May/June is interpreted as a response to high herbivory pressure (Lieberman and Lieberman 1984, Aide 1988, 1993, Reich 1995, Coley and Barone 1996, Coley and Kursar 1996) where synchronized leafing may satiate herbivores.

In contrast to canopy trees, leaf production of *Piper* is more even throughout the year and the peak in June is less pronounced. Species with less seasonal leaf flush appear to suffer less damage by herbivores which is corroborated by observations on young and old leaves of *Piper* (Aide 1993). This is presumably due to chemical defenses (Aide 1993) as extracts of plant material of some *Piper* species revealed antifertility effects on insect herbivores and insecticidal properties (Schultes and Raffauf 1990). The simultaneous decline in leaf production at the peak of flowering may facilitate resource and energy allocation necessary for the strong and short burst of flowers.

Phenology of forest and gap *Piper* species

As our study shows, forest and gap *Piper* species differ also in phenological patterns of flowering and fruiting. We ask what roles abiotic factors such as rainfall or light environment and biotic factors such as the community of pollinators and dispersers might play for the timing of these reproductive activities.

Flowering

There was a strong tendency towards synchronous peaks of flowering at the end of the dry season in forest *Piper* species, while gap *Piper* species had broader or multiple peaks and flowered mostly in the wet season. In forests with a distinct dry and wet season, the highly synchronized and pronounced flowering peaks of many plants in the drier months of the year may reflect the higher abundance of insect pollinators (Wolda 1978, Foster 1990, Foster and Brokaw 1990, Smythe 1990, but see Borchert 1983). Synchronized flowering then may also enhance pollination success. As *Piper* is pollinated by small insects such as *Trigona* bees, small beetles, and syrphid flies (Semple 1974, Fleming 1985, pers. obs.), the distinct flowering peak of *Piper* species on BCI can be interpreted as a response to pollinator availability. However, whereas pollinator availability during the dry season can explain the narrow dry season peak of flowering in forest *Piper* species, it is not sufficient to explain the flowering activity of gap *Piper* species that flowered mostly in the wet season.

It has been predicted for plants of dry forests (Reich and Borchert 1984) and for plants of seasonal forest with limited access to dry season water (i.e. gap plants) (van Schaik et al. 1993, Wright and van Schaik 1994, Wright 1996), that water stress during the dry season should promote flower production during the wet season. Plants, however, that have access to sufficient water during dry season should flower during peak irradiance when it is energetically more efficient to transfer assimilates produced during the peak of irradiance (drier months of the year) directly to growing organs. Therefore, many plants produce flowers in the dry season instead of storing assimilates for later translocation. However, this is only true for plants that do not suffer severe water stress in the dry season. Opler et al. (1978) showed that plants in dry forests that grow close to rivers flower during the dry season and use the peak of irradiance for higher photosynthesis rates whereas plants that grow farther away from water courses flower only at the onset of the rains. They avoid water stress but miss the peak of irradiance.

These ideas are in accordance with our results for forest and gap *Piper* species. While forest *Piper* species on BCI occur mainly along streams and ravines and therefore have continuous access to water, they flower at highest light levels during the dry season. In contrast, gap *Piper* species in open habitats are presumably more

water-limited (Greig 1991) and thus flower mostly during the wet season.

We conclude that the observed difference in timing of flowering between forest and gap *Piper* species is related primarily to abiotic constraints (water and light). The observed difference in the shape of the flowering peaks of forest and gap *Piper* species, however, could also be attributed to biotic factors. Whereas the highly synchronized and narrow flowering peaks of forest *Piper* species may reflect the higher availability of insect pollinators in the dry season, the broad and/or multiple flowering peaks of gap *Piper* species may be associated with a low but continuous abundance of insect pollinators throughout the wet season.

Fruiting

A different picture emerges from the fruiting patterns of forest and gap *Piper* species. Although all forest *Piper* species flowered in a narrow time window of two months, fruits matured asynchronously among species. Further, fruiting peaks were relatively short with a relatively uniform distribution throughout the year. This leads to a continuous and reliable fruit supply. On the other hand, fruiting periods of gap *Piper* species were extended and overlapped strongly. Snow (1965) proposed that displaced (staggered) fruiting seasons of plant species that share the same dispersers have evolved as a response to competition for these dispersers. In spite of the presumed link between fruiting seasons and dispersers, little is known about the actual distribution of fruiting seasons, particularly for phylogenetically related species of plants that share the same seed dispersers (Smythe 1970, McKey 1975, Hilty 1980, Cruz 1981, Wheelwright 1985, Smith-Ramírez et al. 1998, Poulin et al. 1999), including bat-dispersed plants (Heithaus et al. 1975, Fleming 1985, Marinho-Filho 1991). Poulin et al. (1999) studied the fruiting phenology of two common understory plants, *Miconia* and *Psychotria*, and found that these bird-dispersed shrubs benefit more from an aggregated fruiting pattern (*Psychotria*) when they have small crops produced mainly for nomadic frugivores, while segregated fruiting (*Miconia*) will be beneficial to plants with large crops taken mainly by sedentary frugivores. The few studies on bat-dispersed plants suggest that there is relatively low overlap between fruiting periods. Up to now, however, the hypothesis that fruiting seasons are staggered because of competition for the same dispersers has not been verified as studies have either focused on only few and closely related plant species with shared dispersers or on many, mostly unrelated species of plants with multiple dispersers (Gleeson 1981).

Our study tried to overcome these problems. Eight common to abundant forest *Piper* species on BCI are mainly dispersed by two closely related short-tailed fruit bats, *C. castanea* and *C. perspicillata* that are abundant on the island (Handley et al. 1991, Kalko et

al. 1996a). Further, *Piper* fruits are the most important dietary item for both *Carollia*. By displacing their fruiting peaks to different periods of the year, all forest *Piper* species can make use of the small spectrum of dispersers, thus avoiding overlap in fruit ripening with other congeners which could increase the risk of losing opportunities for dispersal because of disperser limitation. Thus, potential competition between *Piper* species for those dispersers can be reduced (Fleming 1981). It could be argued that the staggered fruiting periods are the result of species-specific differences in the time the fruits need to grow until they reach maturity. However, our results show that the fruits of half of the forest *Piper* with extended maturation times already reach their final size and shape shortly after flowering and remain in this stage for several more months until ripening occurs quickly within a few days. To our opinion, this further supports the hypothesis that staggered fruiting in forest *Piper* could be a response to disperser limitation.

Another explanation could be that staggered fruiting in forest *Piper* species reduces competition for limited germination sites. This would imply temporally staggered germination in the different forest *Piper* species and scattered dispersal patterns by the bats. The latter holds true for both *Carollia* as shown with radio-tracking on BCI (unpubl.). Unfortunately, little is known about the germination patterns of *Piper* species. Garwood (1990) describes one main germination peak per year on BCI at the beginning of the rainy season. Here, moisture and gap formation due to increased numbers of tree falls are high (Brokaw 1990), thus providing good germination conditions. Therefore, if all forest *Piper* species germinate only during this peak, we would expect dormancy capabilities of seeds in those *Piper* species that fruit late in the wet season.

Gap *Piper* species, on the other hand, have extended, overlapping fruiting seasons and are visited by bats, birds and ants (O'Donnell 1989, this study). Whereas bats and birds are known seed dispersers of *Piper*, ants are regarded mainly as seed predators (Perry and Fleming 1980) but might also act to a limited degree as seed dispersers of *Piper* (Dalling, pers. com.). It has been suggested (Howe 1977, Howe and Estabrook 1977, Howe and Smallwood 1982) that plants with specific requirements for seedling establishment, i.e. gaps whose formation is not predictable in space and time (Brokaw 1986, Martinez-Ramos and Alvarez-Buylla 1986, Murray 1986), should have longer fruiting seasons and use a broader spectrum of dispersers than plants whose habitat requirements are more predictable (e.g. forest understory).

There are several advantages associated with a broad range of dispersers. Ants carry seeds only small distances ranging from 1–12 meters (Heithaus 1986, Ohkawara and Higashi 1994, Ohkawara et al. 1996, Passos and Ferreira 1996, Leal and Oliveira 1998).

Thus, most seeds remain close to their parent plants. Frugivorous birds often also transport seeds only short distances since they tend to stay for a prolonged time in fruiting trees and frequently deposit seeds from a tree at the same site during fruit processing or defecation (Pratt and Stiles 1983, Stiles and White 1986, Murray 1988, Thomas et al. 1988, Wheelwright 1991). However, it is unclear whether this behavior also applies for birds eating fruits from bushes (Murray 1988). In contrast to many frugivorous birds, frugivorous bats (Phyllostomidae) always carry fruits away from fruiting trees or bushes to a feeding roost (Fleming 1988, unpubl.). This behavior promotes dispersal of seeds away from the vicinity of the parent plant. The tiny seeds of *Piper* are either dropped during feeding at a temporary roost or they are swallowed and afterwards excreted undamaged with the feces (Fleming 1988, unpubl.). This way seeds can sometimes be transported over long distances. Foraging distances (and hence potential dispersal distances) of frugivorous neotropical bats vary between 50 m to several kilometers (Morrison 1980, Fleming 1988, Kalko et al. 1996b, unpubl.).

Based on these observations, it appears that the dispersal of seeds of gap *Piper* species by birds and ants results mostly in short-range dispersal with a high probability that the seeds are deposited close to the parent plants. Although mortality of seeds and seedlings might be high closer to parent plants (Janzen 1970, Augspurger 1984, Dalling et al. 1998, Harms et al. 2000, Wenny 2000), short-distance dispersal by ants and to some smaller extent also by birds could be advantageous for plants depending on gaps. The unpredictability of favorable germination sites for gap plants in space and time could favor seed dispersal systems where seeds that have a low probability of survival under closed canopy, are mostly dispersed locally within the patch (i.e. the gap) of the parent plant (Horvitz and Schemske 1986).

Dispersal of gap *Piper* seeds by bats, on the other hand, may often lead to long-range dispersal and colonization of new sites. However, because nothing is known yet about the population dynamics of gap *Piper* species and the effects of seed predation on distributional patterns of *Piper* seeds (Perry and Fleming 1980), our propositions about the effects of dispersal by different dispersers must remain tentative.

Is the dispersal system *Piper/Carollia* specialized?

As fecal analyses from several studies have revealed and our study confirms, both *C. perspicillata* and *C. castanea* are the main dispersers of *Piper* in most parts of the neotropics (Goodwin and Greenhall 1961, Fleming et al. 1972, Howell and Burch 1974, Bonaccorso 1979, de Foresta et al. 1984, Charles-Dominique 1986, 1991, Fleming 1988, 1991, Palmeirim et al. 1989, Marinho-

Filho 1991, Ascorra and Wilson 1992, Muller and dos Reis 1992, Gorchov et al. 1995). Fleming (1981) proposed that the dispersal system of *Piper* is specialized sensu model 1 proposed by Howe and Estabrook (1977). Specialized dispersal systems are characterized by plants that produce small numbers of nutrient rich fruits per day or night over a prolonged period and that are associated with a small number of reliable, specialized dispersers (see also Howe 1993). Because our results on BCI have shown clear differences in the phenologies and number of dispersal agents between gap and forest *Piper* species, this raises the question whether this proposition is valid for all *Piper* species.

On BCI, forest *Piper* species meet all the conditions for a specialized system. Only about every third to fifth plant produces a ripe fruit per night. The time of ripening occurs in late afternoon which suggests that forest *Piper* species are highly specialized for bat dispersal. Furthermore, our fecal samples demonstrate that only one species of bat, *C. castanea*, is the major seed disperser. Although the number of ripe fruits per night and plant is very low, the production of forest *Piper* fruits is predictable because the number of ripe fruits per night in a given area is almost constant throughout the fruiting period of a species. The fruits are probably a nutritionally rich food source with high protein content (Dinerstein 1986, Fleming 1986, Herbst 1986, but see Bizerril and Raw 1997). Furthermore, each forest *Piper* species produces fruits at a predictable time of the year and fruit production is consistent from year to year. We conclude that these characteristics promote a specialization between forest *Piper* species and their dispersers, mainly *C. castanea*.

By comparison with forest *Piper* species, gap *Piper* species on BCI do not fully meet the conditions for a specialized dispersal system. Gap *Piper* species produce two to ten times as many fruits per plant as forest *Piper* species. Fruit ripening starts in early morning and the seeds are dispersed by a wider range of dispersers: birds, bats, and probably also ants. The number of fruits available per plant from night to night is not as constant throughout the fruiting period as in forest *Piper* species, but shows a pronounced peak in the middle of the fruiting period with a subsequent decline thereafter. As indicated by removal rates, bats remove most of the fruits opportunistically at the peaks of fruit production. They remove proportionately more fruits when fruit numbers are high and less when fruit numbers decline. Therefore, they are not very reliable visitors to gap *Piper* species. *Carollia castanea* probably eats gap *Piper* species only as an addition to other, more predictable forest *Piper* species. The diet of *C. perspicillata* includes, in addition to gap *Pipers*, large portions of other available fruits from shrubs and trees, most of them with large crops (unpubl.). Therefore, we propose that dispersal of gap *Piper* species resembles more a generalized system, corresponding to model 2

proposed by Howe and Estabrook (1977). In generalized systems, large crops of relatively nutritional poor fruits are produced over short periods, as in *Miconia* (Snow 1965) or *Muntingia calabura* (Fleming 1985) for a wide range of "opportunistic" frugivores (McKey 1975, Howe and Estabrook 1977). However, more data are needed to substantiate the proposition for the two dispersal systems within *Piper*. For example, it is still unclear whether forest and gap *Piper* species differ in nutritional value, a prerequisite necessary for either a specialized or unspecialized system.

Overall, it is necessary to test the general usefulness of this concept, i.e. the proposition of two dispersal systems (specialized versus generalized) for explaining the evolutionary and ecological relationships between plants and their dispersers. No studies are available so far that give strong support to the suggested patterns on a community level or offer convincing alternatives.

Conclusions

Our study on the phenology of *Piper* on BCI showed distinct differences in flowering and fruiting patterns between forest and gap *Piper* species. While the differences in flowering appear to be influenced primarily by abiotic factors such as site-specific differences in water and light availability, the factors that influence fruiting patterns of *Piper* on BCI are more complex. We propose that competition for a limited disperser spectrum favors the staggered fruiting pattern observed in forest *Pipers*. In contrast, the larger spectrum of possible seed dispersers as well as long and overlapping fruiting periods in gap *Pipers* appear to be associated with the low probability of seed dispersal into favorable germination sites. Continuous availability of *Piper* fruits throughout the year permits dietary specialization of two bat species of the genus *Carollia*. We suggest that the relationship between fruit availability of *Piper* and the degree of dietary specialization of *Carollia* found in our study on BCI reflects a particularly tight association between plants and a small group of dispersers. Because of this tight association, we propose that the distribution and fruiting phenologies of sympatric *Piper* species influence the composition and abundance of coexisting *Carollia*. To substantiate these assumptions, studies comparing differences of *Piper* phenologies and dispersal modes at sites with different climatic conditions as well as different *Piper* and disperser assemblages are crucial. Overall, it cannot be ruled out that phylogeny, in addition to ecological characteristics, might also influence the observed phonological differences among *Piper* species as it has been demonstrated on the family level for the understory shrubs *Piper* and *Miconia* with regard to chemical plant defenses (i.e. phenolics, Kochmer and Handel 1986, Baldwin and

Schultz 1988). To test whether and how phylogenetic relationships may constrain the evolution of phenological patterns among *Piper* requires a sound phylogeny on the species level. As the systematics of the genus *Piper* are still in flux, the possible effects of phylogeny on phenology patterns cannot be fully addressed so far.

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References

- Aide, T. M. 1988. Herbivory as a selective agent on the timing of leaf production in a tropical understory community. – *Nature* 336: 574–575.
- Aide, T. M. 1993. Patterns of leaf development and herbivory in a tropical understory community. – *Ecology* 74: 455–466.
- Ascorra, C. F. and Wilson, D. E. 1992. Bat frugivory and seed dispersal in the Amazon, Loreto, Peru. – *Publ. Mus. Hist. Nat. UNMSM (A)* 43: 1–6.
- Augsburger, C. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. – *Ecology* 65: 1705–1712.
- Baldwin, I. T. and Schultz, J. C. 1988. Phylogeny and the patterns of leaf phenolics in gap- and forest-adapted *Piper* and *Miconia* understory shrubs. – *Oecologia* 75: 105–109.
- Bizerril, M. X. and Raw, A. 1997. Feeding specialization of two species of bats and fruit quality of *Piper arboreum* in a Central Brazilian gallery forest. – *Rev. Biol. Trop.* 45: 913–918.
- Bonaccorso, F. J. 1979. Foraging and reproductive ecology in a Panamanian bat community. – *Bull. Florida State Mus.* 24: 359–408.
- Borchert, R. 1983. Phenology and control of flowering in tropical trees. – *Biotropica* 15: 81–89.
- Brokaw, N. V. L. 1986. Seed dispersal, gap colonization, and the case of *Cecropia insignis*. – In: Estrada, A. and Fleming, T. H. (eds), *Frugivores and seed dispersal*. Dr. W. Junk, Dordrecht, pp. 323–331.
- Brokaw, N. V. L. 1990. Caída de árboles: frecuencia, cronología y consecuencias. – In: Leigh, E. G., Jr., Rand, A. S. and Windsor, D. M. (eds), *Ecología de un Bosque Tropical. Ciclos estacionales y cambios a largo plazo*. Smithsonian Press, pp. 163–172.
- Charles-Dominique, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guiana. – In: Estrada, A. and Fleming, T. H. (eds), *Frugivores and seed dispersal*. Dr. W. Junk, Dordrecht, pp. 119–135.
- Charles-Dominique, P. 1991. Feeding strategy and activity budget of the frugivorous bat *Carollia perspicillata* (Chiroptera: Phyllostomidae) in French Guiana. – *J. Trop. Ecol.* 7: 243–256.
- Charles-Dominique, P. 1993. Speciation and coevolution: an interpretation of frugivory phenomena. – In: Fleming, T. H. and Estrada, A. (eds), *Frugivory and seed dispersal*. – *Vegetatio* 107/108. Kluwer, pp. 75–84.
- Coley, P. D. 1990. Tasas de herbivorismo en diferentes árboles tropicales. – In: Leigh, E. G., Jr., Rand, A. S. and Windsor, D. M. (eds), *Ecología de un Bosque Tropical. Ciclos estacionales y cambios a largo plazo*. Smithsonian Press, pp. 191–200.
- Coley, P. D. and Barone, J. A. 1996. Herbivory and plant defenses in tropical forests. – *Ann. Rev. Ecol. Syst.* 27: 305–335.
- Coley, P. D. and Kursar, T. A. 1996. Anti-herbivore defenses of young tropical leaves: physiological constraints and ecological trade-offs. – In: Smith, A. P., Mulkey, S. S. and Chazdon, R. L. (eds), *Tropical forest plant ecophysiology*. Chapman & Hall, pp. 305–336.
- Croat, T. B. 1969. Seasonal flowering behavior in central Panama. – *Ann. Missouri Bot. Gard.* 56: 295–307.
- Croat, T. B. 1975. Phenological behavior of habitat and habitat classes on Barro Colorado Island (Panama Canal Zone). – *Biotropica* 7: 270–277.
- Croat, T. B. 1978. Flora of Barro Colorado Island. – Stanford Univ. Press.
- Cruz, A. 1981. Bird activity and seed dispersal of a montane forest tree (*Dunalia arborea*) in Jamaica. – *Biotropica* 13 (Suppl.): 34–44.
- Dalling, J. W., Swaine, M. D. and Garwood, N. C. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. – *Ecology* 79: 564–578.
- Daws, M. I., Burslem, D. F. R. P., Crabtree, L. M. et al. 2002. Differences in seed germination responses may promote coexistence of four sympatric *Piper* species. – *Funct. Ecol.* 16: 258–267.
- Denslow, J. S., Schultz, J. C., Vitousek, P. M. et al. 1990. Growth responses of tropical shrubs to treefall gap environments. – *Ecology* 71: 165–179.
- de Foresta, H., Charles-Dominique, P., Erard, C. et al. 1984. Zoothorie et premiers stades de la régénération naturelle après coupe en forêt guyanaise. – *Revue Ecologie (Terre et Vie)* 39: 369–400.
- Dinerstein, E. 1986. Reproductive ecology of fruit bats and the seasonality of fruit production in a Costa Rican cloud forest. – *Biotropica* 18: 307–318.
- Fleming, T. H. 1981. Fecundity, fruiting pattern, and seed dispersal in *Piper amalago* (Piperaceae), a bat-dispersed tropical shrub. – *Oecologia* 51: 42–46.
- Fleming, T. H. 1985. Coexistence of five sympatric *Piper* (Piperaceae) species in a tropical dry forest. – *Ecology* 66: 688–700.
- Fleming, T. H. 1986. Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. – In: Estrada, A. and Fleming, T. H. (eds), *Frugivores and seed dispersal*. Dr. W. Junk, Dordrecht, pp. 105–118.
- Fleming, T. H. 1988. The short-tailed fruit bat. A study of plant-animal interactions. – Univ. of Chicago Press.
- Fleming, T. H. 1991. The relationship between body size, diet and habitat use in frugivorous bats, genus *Carollia* (Phyllostomidae). – *J. Mammal.* 72: 493–501.
- Fleming, T. H., Hooper, E. T. and Wilson, D. E. 1972. Three Central American bat communities, structure, reproductive cycles and movement patterns. – *Ecology* 53: 555–569.
- Fleming, T. H. and Maguire, J. 1988. Patterns of diversity, density, and distribution in a wet tropical forest *Piper* flora. – *Bull. Ecol. Soc. Am.* 69: 133.
- Foster, R. B. 1990. Ciclo estacional de caída de frutos en la isla de Barro Colorado. – In: Leigh, E. G., Jr., Rand, A. S. and Windsor, D. M. (eds), *Ecología de un Bosque Tropical. Ciclos estacionales y cambios a largo plazo*. Smithsonian Press, pp. 219–242.
- Foster, R. B. and Brokaw, N. V. L. 1990. Estructura e historia de la vegetación de la isla de Barro Colorado. – In: Leigh, E. G., Jr., Rand, A. S. and Windsor, D. M. (eds), *Ecología de un Bosque Tropical. Ciclos estacionales y cambios a largo plazo*. Smithsonian Press, pp. 113–128.

- Garwood, N.C. 1990. Ciclo estacional de germinación de semillas en un bosque semicaducifolio tropical. – In: Leigh, E. G., Jr., Rand, A. S. and Windsor, D. M. (eds), Ecología de un Bosque Tropical. Ciclos estacionales y cambios a largo plazo. Smithsonian Press, pp. 243–255.
- Gilbert, L. E. 1980. Food web organization and the conservation of neotropical diversity. – In: Soule, M. E. and Wilcox, B. A. (eds), Conservation biology, an evolutionary-ecological perspective. Sinauer, pp. 11–33.
- Gleeson, S. K. 1981. Character displacement in flowering phenologies. – *Oecologia* 51: 294–295.
- Goodwin, G. G. and Greenhall, A. M. 1961. A review of the bats of Trinidad and Tobago. – *Bull. Am. Mus. Nat. Hist.* 122: 191–301.
- Gorchov, D. L., Cornejo, F., Ascorra, C. F. et al. 1995. Dietary overlap between frugivorous birds and bats in the Peruvian Amazon. – *Oikos* 74: 235–250.
- Greig, N. 1991. Ecology of co-occurring species of neotropical *Piper* (Piperaceae): distribution, reproductive ecology, and seed predation. PhD thesis, Univ. of Texas, Austin.
- Handley, C. O., Wilson, D. E. and Gardner, A. L. 1991. Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panamá. – *Smithsonian Contr. Zool.* 511: 1–173.
- Harms, K. E., Wright, S. J., Calderón, O. et al. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. – *Nature* 404: 493–495.
- Heithaus, E. R. 1986. Seed dispersal mutualism and the population density of *Asarum canadense*, an ant-dispersed plant. – In: Estrada, A. and Fleming, T. H. (eds), Frugivores and seed dispersal. Dr. W. Junk, Dordrecht, pp. 199–210.
- Heithaus, E. R., Fleming, T. H. and Opler, P. A. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. – *Ecology* 56: 841–854.
- Herbst, L. H. 1986. The role of nitrogen from fruit pulp in the nutrition of the frugivorous bat *Carollia perspicillata*. – *Biotropica* 18: 39–44.
- Hilty, S. L. 1980. Flowering and fruiting periodicity in a premontane rain forest in pacific Colombia. – *Biotropica* 12: 292–306.
- Horvitz, C. C. and Schemske, D. W. 1986. Seed dispersal and environmental heterogeneity in a neotropical herb: a model of population and patch dynamics. – In: Estrada, A. and Fleming, T. H. (eds), Frugivores and seed dispersal. Dr. W. Junk, Dordrecht, pp. 169–186.
- Howe, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. – *Ecology* 58: 539–550.
- Howe, H. F. 1993. Specialized and generalized dispersal systems. Where does “the paradigm” stand? – In: Fleming, T. H. and Estrada, A. (eds), Frugivory and seed dispersal. *Vegetatio* 107/108. Kluwer, pp. 3–13.
- Howe, H. F. and Estabrook, G. F. 1977. On intraspecific competition for avian dispersers in tropical trees. – *Am. Nat.* 111: 817–832.
- Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. – *Annu. Rev. Ecol. Syst.* 13: 201–228.
- Howell, D. J. and Burch, D. 1974. Food habits of some Costa Rican bats. – *Rev. Biol. Trop.* 21: 281–294.
- Janzen, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. – *Evolution* 21: 620–637.
- Janzen, D. J. 1970. Herbivores and the number of tree species in tropical forests. – *Am. Nat.* 104: 501–528.
- Janzen, D. H. 1979. How to be a fig. – *Annu. Rev. Ecol. Syst.* 10: 13–51.
- Kalko, E. K. V., Handley, C. O. and Handley, D. 1996a. Organization, diversity, and longterm dynamics of a neotropical bat community. – In: Cody, M. and Smallwood, J. (eds), Longterm studies in vertebrate communities. Academic Press, pp. 503–553.
- Kalko, E. K. V., Herre, E. A. and Handley, C. O., Jr. 1996b. Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. – *J. Biogeogr.* 23: 565–576.
- Karr, J. R. 1976. Seasonality, resource availability and community diversity in tropical bird communities. – *Am. Nat.* 110: 973–994.
- Kochmer, J. P. and Handel, S. N. 1986. Constraints and competition in the evolution of flowering phenology. – *Ecol. Monogr.* 56: 303–325.
- Korine, C., Kalko, E. K. V. and Herre, E. A. 2000. Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. – *Oecologia* 123: 560–568.
- Laska, M. S. 1997. Structure of understory shrub assemblages in adjacent secondary and old growth tropical wet forests, Costa Rica. – *Biotropica* 29: 29–37.
- Leal, I. R. and Oliveira, P. S. 1998. Interactions between fungus-growing ants (Attini), fruits and seeds in cerrado vegetation in southeast Brazil. – *Biotropica* 30: 170–178.
- Leigh, E. G. 1999. Tropical forest ecology. A view from Barro Colorado Island. – Oxford Univ. Press, pp. 1–245.
- Leigh, E. G. and Windsor, D. M. 1990. Producción del bosque y regulación de consumidores primarios de la isla de Barro Colorado. – In: Leigh, E. G., Jr., Rand, A. S. and Windsor, D. M. (eds), Ecología de un Bosque Tropical. Ciclos estacionales y cambios a largo plazo. Smithsonian Press, pp. 179–190.
- Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. – *Ecology* 69: 1076–1089.
- Lieberman, D. and Lieberman, M. 1984. The causes and consequences of synchronous flushing in a dry tropical forest. – *Biotropica* 16: 193–201.
- Marinho-Filho, J. S. 1991. The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. – *J. Trop. Ecol.* 7: 59–67.
- Marquis, R. J. 1988. Phenological variation in the neotropical understory shrub *Piper arieianum*: causes and consequences. – *Ecology* 69: 1552–1565.
- Martinez-Ramos, M. and Alvarez-Buylla, E. 1986. Seed dispersal, gap dynamics and tree recruitment: the case of *Cecropia obtusifolia* at Los Tuxtlas, Mexico. – In: Estrada, A. and Fleming, T. H. (eds), Frugivores and seed dispersal. Dr. W. Junk, Dordrecht, pp. 333–346.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems. – In: Gilbert, L. E. and Raven, P. H. (eds), Coevolution of animals and plants. Univ. of Texas Press, pp. 159–191.
- Milton, K., Windsor, D. M., Morrison, D. W. et al. 1982. Fruiting phenologies of two neotropical *Ficus* species. – *Ecology* 63: 752–762.
- Morrison, D. W. 1980. Foraging and day-roost dynamics of canopy fruit bats in Panama. – *J. Mammal.* 61: 20–29.
- Murray, K. G. 1986. Consequences of seed dispersal for gap-dependent plants: relationships between seed shadows, germination requirements, and forest dynamic processes. – In: Estrada, A. and Fleming, T. H. (eds), Frugivores and seed dispersal. Dr. W. Junk, Dordrecht, pp. 187–198.
- Murray, K. G. 1988. Avian seed dispersal of three neotropical gap-dependent plants. – *Ecol. Monogr.* 58: 271–298.
- Muller, M. F. and dos Reis, N. R. 1992. Partição de recursos alimentares entre quatro espécies de morcegos frugívoros (Chiroptera, Phyllostomidae). – *Rev. Bras. Zool.* 9: 345–355.
- Newstrom, L. E. and Frankie, G. W. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. – *Biotropica* 26: 141–159.
- O'Donnell, S. 1989. A comparison of fruit removal by bats and birds from *Piper hispidum* SW. (Piperaceae), a tropical second growth shrub. – *Brenesia* 31: 25–32.
- Ohkawara, K. and Higashi, S. 1994. Relative importance of ballistic and ant dispersal in two diplochorous *Viola* species (Violaceae). – *Oecologia* 100: 135–140.

- Ohkawara, K., Higashi, S. and Ohara, M. 1996. Effects of ants, ground beetles and the seed-fall patterns of myrmecochory of *Erythronium japonicum* Decne. (Liliaceae). – *Oecologia* 106: 500–506.
- Opfer, P. A., Frankie, G. W. and Baker, H. G. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. – *J. Biogeogr.* 3: 231–236.
- Opfer, P. A., Frankie, G. W. and Baker, H. G. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. – *J. Ecol.* 68: 167–188.
- Palmeirim, J., Gorchov, D. L. and Stoleson, S. 1989. Trophic structure of a neotropical frugivore community: is there competition between birds and bats? – *Oecologia* 79: 403–411.
- Passos, L. and Ferreira, S. O. 1996. Ant dispersal of *Croton priscus* (Euphorbiaceae) seeds in a tropical semideciduous forest in southeastern Brazil. – *Biotropica* 28: 697–700.
- Paton, S. 1996. Meteorological and hydrological summary for Barro Colorado Island. – Smithsonian Tropical Res. Inst.
- Perry, A. E. and Fleming, T. H. 1980. Ant and rodent predation on small, animal-dispersed seeds in a dry tropical forest. – *Brenesia* 17: 11–22.
- Pianka, E. R. 1974. Niche overlap and diffuse competition. – *Proc. Natl Acad. Sci.* 71: 2141–2145.
- Pleasants, J. M. 1980. Competition for bumblebee pollinators in rocky mountain plant communities. – *Ecology* 61: 1446–1459.
- Pleasants, J. M. 1990. Null-model tests for competitive displacement: the fallacy of not focusing on the whole community. – *Ecology* 71: 1078–1084.
- Poulin, B., Wright, S. J., Lefebvre, G. et al. 1999. Interspecific synchrony and asynchrony in the fruiting phonologies of congeneric bird-dispersed plants in Panama. – *J. Trop. Ecol.* 15: 213–227.
- Pratt, T. K. and Stiles, E. W. 1983. How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. – *Am. Nat.* 122: 797–805.
- Pyke, G. H. 1983. Seasonal pattern of abundance of honeyeaters and their resources in heathland areas near Sydney. – *Aust. J. Ecol.* 8: 217–233.
- Rathcke, B. and Lacey, E. P. 1985. Phenological patterns of terrestrial plants. – *Annu. Rev. Ecol. Syst.* 16: 179–214.
- Reich, P. B. 1995. Phenology of tropical forests: patterns, causes, and consequences. – *Can. J. Bot.* 73: 164–174.
- Reich, P. B. and Borchert, R. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. – *J. Ecol.* 72: 61–74.
- Schlüter, R. E. and Raffauf, R. F. 1990. The healing forest. Medicinal and toxic plants of the northwest Amazonia. – Dioscorides Press, Portland, Oregon.
- Seppé, K. S. 1974. Pollination in Piperaceae. – *Ann. Missouri Bot. Gard.* 61: 868–871.
- Smith-Ramírez, C., Armesto, J. J. and Figueroa, J. 1998. Flowering, fruiting and seed germination in Chilean rain forest Myrtaceae: ecological and phylogenetic constraints. – *Plant Ecol.* 136: 119–131.
- Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. – *Am. Nat.* 104: 25–35.
- Smythe, N. 1990. Abundancia estacional de insectos nocturnos en un bosque neotropical. – In: Leigh, E. G., Jr., Rand, A. S. and Windsor, D. M. (eds), *Ecología de un Bosque Tropical. Ciclos estacionales y cambios a largo plazo*. Smithsonian Press, Washington, D.C., pp. 393–402.
- Snow, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. – *Oikos* 15: 274–281.
- Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. – *Ibis* 113: 194–202.
- Sokal, R. R. and Rohlf, F. J. 1995. Biometry. The principals and practice of statistics in biological research, 3rd ed. – WH Freeman and Company.
- Sosa, M. and Soriano, P. J. 1996. Resource availability, diet and reproduction in *Glossophaga longirostris* (Mammalia: Chiroptera) in an arid zone of the Venezuelan Andes. – *J. Trop. Ecol.* 12: 805–818.
- Stiles, F. G. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. – *Am. Nat.* 116: 668–670.
- Stiles, E. W. and White, D. W. 1986. Seed deposition patterns: influences of season, nutrients, and vegetation structure. – In: Estrada, A. and Fleming, T. H. (eds), *Frugivores and seed dispersals*. Dr. W. Junk, Dordrecht, pp. 45–54.
- Tebbs, M. C. 1990. Revision of *Piper* (Piperaceae) in the New World. 2. The taxonomy of *Piper* section Churumayu. – *Bull. Br. Mus. Nat. Hist.* 20: 193–236.
- Terborgh, J. 1983. Ecological relationships in the Manu primate community. – In: Terborgh, J. (ed.), *Five New World primates. A study in comparative ecology*. Princeton Univ. Press, pp. 190–210.
- Terborgh, J. 1986. Keystone plant resources in the tropical forest. – In: Soule, M. E. (ed.), *Conservation biology*. Academic Press, pp. 330–344.
- Thies, W., Kalko, E. K. V. and Schnitzler, H.-U. 1998. The roles of echolocation and olfaction in two neotropical fruit-eating bats, *Carollia perspicillata* and *C. castanea*, feeding on *Piper*. – *Behav. Ecol. Sociobiol.* 42: 397–409.
- Thomas, D. W., Cloutier, D., Provencher, M. et al. 1988. The shape of bird- and bat-generated seed shadows around a tropical fruiting tree. – *Biotropica* 20: 347–348.
- Thompson, J. N. and Willson, M. F. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. – *Evolution* 33: 973–982.
- van Schaik, C. P., Terborgh, J. and Wright, S. J. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. – *Annu. Rev. Ecol. Syst.* 24: 353–377.
- Wenny, D. 2000. Seed dispersal of a high quality fruit by specialized frugivores: high quality seed dispersal? – *Biotropica* 32: 327–337.
- Wheelwright, N. T. 1983. Fruits and the ecology of resplendent Quetzals. – *Auk* 100: 286–301.
- Wheelwright, N. T. 1985. Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. – *Oikos* 44: 465–477.
- Wheelwright, N. T. 1991. How long do fruit-eating birds stay in the plants where they feed? – *Biotropica* 23: 29–40.
- Windsor, D. M., Rand, A. S. and Rand, W. M. 1990. Características de la precipitación de la isla de Barro Colorado. – In: Leigh, E. G., Jr., Rand, A. S. and Windsor, D. M. (eds), *Ecología de un Bosque Tropical. Ciclos estacionales y cambios a largo plazo*. Smithsonian Press, Washington, D.C., pp. 53–71.
- Wolda, H. 1978. Fluctuations in abundance of tropical insects. – *Am. Nat.* 112: 1017–1045.
- Worthington, A. H. 1990. Comportamiento de forrajeo de dos especies de saltarines en respuesta a la escasez estacional de frutos. – In: Leigh, E. G., Jr., Rand, A. S. and Windsor, D. M. (eds), *Ecología de un Bosque Tropical. Ciclos estacionales y cambios a largo plazo*. Smithsonian Press, Washington, D.C., pp. 285–304.
- Wright, S. J. 1996. Phenological responses to seasonality in tropical forest plants. – In: Smith, A. P., Mulkey, S. S. and Chazdon, R. L. (eds), *Tropical forest plant ecophysiology*. Chapman & Hall, pp. 440–460.
- Wright, S. J. and van Schaik, C. P. 1994. Light and the phenology of tropical trees. – *Am. Nat.* 143: 192–199.
- Wright, S. J. and Calderón, O. 1995. Phylogenetic patterns among tropical flowering phenologies. – *J. Ecol.* 83: 937–948.
- Wright, S. J., Carrasco, C., Calderón, O. et al. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. – *Ecology* 80: 1632–1647.