PHENOLOGY OF CANOPY TREES IN THE EVER-WET LOWLAND FOREST MOSAIC OF PICO DA NEBLINA NATIONAL PARK, AMAZONAS, BRAZIL

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Abstract. We report here on a phenological study of 436 canopy trees in three different forest habitats, i.e., terra firme, *caatinga* (forest on white soil), and *chavascal* (waterlogged forest) in the ever-wet forests of Pico da Neblina National Park, Brazil. At the community level, leafing peaked in October (1994), flowering in December, and fruiting in March. Flowering activity in *caatinga* preceded that of the other two forests types by approximately two months. Fruiting activity coincided in the three habitats. Contrary to theoretical predictions, *caatinga* species were on average more productive than terra firme and *chavascal* but the difference was not significant. Despite a lack in rainfall seasonality, at the community level the phenological patterns recorded here conform to the pattern exhibited by more seasonal Neotropical rainforest sites elsewhere. At the population level, however, several species showed phenological patterns not conforming to the overall pattern recorded. Hence we suggest that a larger sample of trees per species might have revealed a more complex pattern at the community level. In addition, we believe there to be an inter-annual variation in phenology in Pico da Neblina not detected in our 12-month study. *Accepted 31 January 2007.*

Keywords: Amazonia, Brazil, phenology, Pico da Neblina, tropical rain forest, tropical trees.

INTRODUCTION

The production of plant parts in many Neotropical rainforest sites that have been investigated to date seem to conform to rainfall seasonality (Borchet 1983, Reich and Borchert 1984). Most of the flower production is restricted to the dry or at least drier season (for the less seasonal tropical areas), immediately after a peak in new leaf production, and fruits to the early and mid-wet season. Sometimes there are two peaks, one major peak in the early wet season followed shortly thereafter (a month or two) by a smaller peak (Alencar *et al*. 1979, Terborgh 1983, Ayres 1986, Peres 1991, Setz 1995).

Around the ever-wet equatorial regions however, where seasonal variation in climatic parameters is negligible and in some cases variable from year to year, plant species are expected to be less constrained by abiotic factors (Putz 1979, Hilty 1980, Heideman 1989) and more in tune with biotic elements, such as herbivores, predators, competitors, pollinators, and dispersers (Janzen 1971, Aide 1988, van Schaik *et al*.

1993). Under such conditions, a complex phenological pattern may be the result at the community level due to the individual nature of each tree species' interaction with its set of biotic factors.

In this study, we investigate the phenological pattern of the ever-wet forests of Pico da Neblina National Park, Brazil. The study site is located 43 km north of the equator, where variation in climatic parameters (temperature and rainfall) and photoperiod are minimal. We examine the overall pattern at the community level and also the pattern at the population level of a few selected tree species that were abundant enough in our sample. Newstrom *et al*. (1994) suggest that tropical tree phenology should be conducted at the individual, population, guild and community level in order to recognize the patterns of plant reproductive part production in tropical ecosystems. This is important because individual and population-level patterns can be obscured when data are lumped together in community-level analysis. The forest at the study site is a mosaic of 'terra firme', 'caatinga' (forest on white sands) and 'chavascal' (waterlogged forests on loamy soils) forests. These forests are adjacent to one

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another and the boundaries between them are well marked. The distinct physiognomy is created mostly by variation in underlying soil conditions (water saturation and nutrients) (Boubli 1997). In this study, we wanted to observe if these different but adjacent forest types presented different phenological rhythms. Haugaasen & Peres (2005) have documented an asynchrony in the production of plant parts in abutting terra firme and flooded forest types in Amazonia and pointed to the importance of this phenological complementarity to animal consumers.

Finally, we wanted to observe the phenological pattern at the population and community levels in Pico da Neblina, in particular to investigate if the caatinga forest, a habitat known to be strongly nutrient-limited (Jordan, 1989, Coomes 1995), was less productive than the other two forests as theory would predict (Janzen 1971). This study is the first to document the phenological cycle of plant communities in this region of Amazonia, and in particular in caatinga forest type anywhere.

METHODS

Study area. The study area was located on the right bank of the Cauaburi river (0°24'N, 66°18'W), in the lowlands of Pico da Neblina National Park, Amazonas, Brazil (100 m elevation), in the extreme northwestern part of Brazilian Amazonia, on the border with Venezuela (Fig. 1) (see Boubli 2002). Cauaburi is a white-water river and a left bank tributary of the Rio Negro. Pico da Neblina National Park is covered by dense, tall, evergreen lowland, submontane, and montane forests. On the highlands (2,000 m and above), there are a variety of shrublands and broad-leaved meadows (Hubber 1995, Steyermark 1986). In the lowlands (100 m), terra firme forest predominates, interspersed by areas of caatinga forest (forest on white sands) and chavascal (swamp forest). 'Igapó' (flooded forest) also occurs but is restricted to small areas along rivers (Boubli 2002).

At the study site, terra firme forest is the predominant habitat, where the large *Micrandra spruceana* tree is abundant, occurring in large groves. Also abundant is the palm *Jessenia bataua*. Caatinga forests are also well represented at the study site. *Eperua leucantha* (Caesalpinoideae) and *Hevea brasiliensis* (Euphorbiaceae) trees are dominant in the caatinga forest studied comprising more than 53% of all trees with diameter at breast height (DBH) greater than 10

cm in the area (Boubli 2002). Chavascal forest is restricted to areas where the soils are waterlogged for most of the year. *Chromolucuma rubiflora*, *Iryarthera* sp., and *Hevea brasiliensis* are the most common trees in this forest type. In the wettest parts of the chavascal, the palm *Mauritia flexuosa* becomes locally abundant. There is little overlap in tree species composition between caatinga and the other two forest types sampled. Chavascal and terra firme however, overlapped greatly although they differ markedly in tree importance values (Boubli 2002).

Climate. The rainfall for the region averages 3000 mm/year, corresponding to the rainiest region in Brazil (RADAM 1978). There is no dry season in the area. The period with least rain is from August to November, when on average 200 mm of rain per month is the norm. Inter-annual variation in rainfall is common in the region and it is more marked where total annual rainfall is highest. Average temperature is 25°C (ranging from 20°C to 30°C). According to the Köppen classification the climate is of the type Af, (A-wet tropical; f- humid) (RADAM 1978). Rainfall data for this study was gathered on a daily basis using a rain gauge (All-Weather Rain Gauge, 27.9 cm x 2 mm capacity) installed at camp. Whenever the camp-site was left vacant, the rain gauge recorded cumulative rain data. In February 1995 the rain gauge spilled over before it could be read again so no rainfall data were collected on that month. Rainfall was recorded from September 1994 through October 1995. As no data were collected in February, this month was treated as the average between January and March of 1995.

Phenology. From September 1994 to October 1995, at approximate monthly intervals, the crowns of 436 canopy trees ≥ 10 cm DBH, including 145 species (137 species and 8 morphospecies), were scanned with binoculars (10 x 40). The 436 trees in the study were taken from a pool of 818 trees with DBH ≥ 10 cm within a 1-ha continuous botanical plot (1000 x 10 m) which was part of a 2-ha botanical inventory conducted at the site (Boubli 2002). Given that individual trees of *Eperua leucantha* and *Hevea brasiliensis* were extremely abundant, the sample of these two species was arbitrarily reduced to 10% of *E. leucantha* and 20% of *H. brasiliensis* – every 10th *E. leucantha* and every 5th *H. brasiliensis* were included in the botanical plot. Trees that died during the study (7) or trees that could not be properly observed from
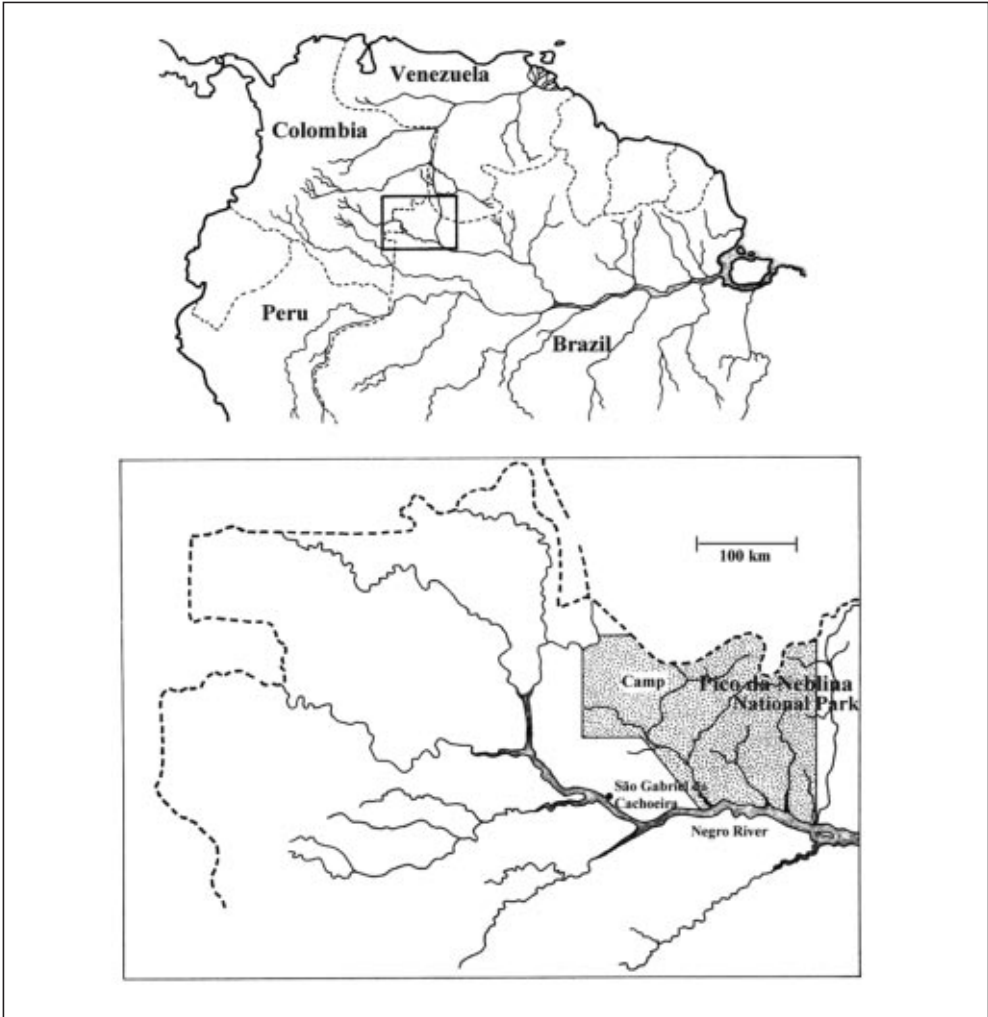
FIG. 1. Location of the study site in Pico da Neblina National Park, Brazil.

the ground (76) were also excluded. The latter trees however, represented a small proportion of the total (9%) and they did not consist of only tall trees as one might imagine; the average height of excluded trees did not differ from the average height for the total sample (Z = 0.3, *p* = 0.7). Finally, the mid-section of the botanical transect was crossed by a creek which made access to marked trees in this area impractical. Therefore the 28 trees found in this area were also excluded from this study resulting in the forest on that side of the study site not being sampled. The botanical plot used for the phenology study contained three habitat types: terra firme, caatinga, and chavascal. Data on leafing, flowering, and fruiting activity were recorded and each of these phenophases was ranked from zero to four according to its abundance relative to crown volume (Intensity index, Fournier 1974). We sampled approximately equal numbers of trees from terra firme (150 individuals), caatinga (152), and chavascal (135). Due to logistical difficulties the intervals between phenological samples were uneven and in several instances greater than a month. Data were gathered in 1994 (23 September, 26 October, 17 November) and 1995 (20 January, 11
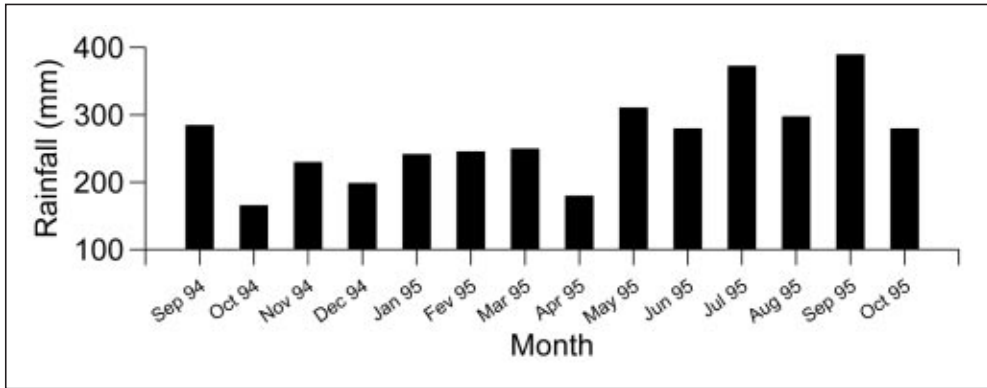
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FIG. 2. Monthly rainfall data recorded at the study site in Pico da Neblina National Park, Brazil (1994–1995). Rainfall for February 1995 is plotted as the average of January and March.

March, 14 April, 24 June, 20 July, 16 August, 8 September, 6 October). Due to the long intervals between sampling periods, on many occasions flowering and fruiting episodes were missed in some individual trees, and so in several cases we recorded fruits in an individual tree for which no flowers had been observed and vice-versa.

We present population-level data for the 10 most abundant species in the sample, namely *Hevea brasiliensis, Eperua leucantha, Caraipa densiflora, Mucoa duckei, Gustavia pulchra, Senefeldera macrophyla, Pachira insignis, Licania octandra, Clathrotropis macrocarpa, Caraipa* sp.

RESULTS

Rainfall. Rainfall for the 12-month period spanning September 1994 to August 1995 was 3048 mm. No marked distiction between wet and dry seasons could be made given that even during the driest month, October 1994, 165 mm of rain was recorded. Also, as is the case for this region (see above), rainfall varied from year to year, with considerably more rain in September and October of 1995 than for the same months in 1994 (Fig. 2).

Phenology at the community level. In total, 39% of the individual trees sampled, corresponding to 54% of
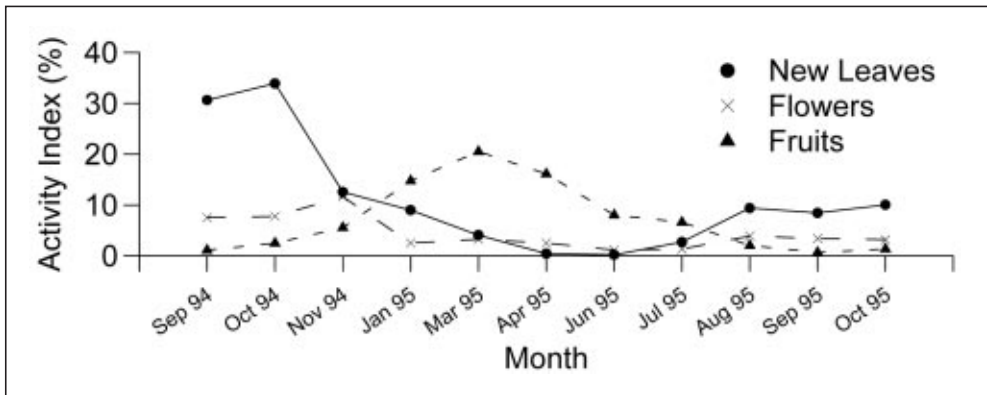

FIG. 3. Phenological patterns of flushing, flowering and fruiting at the community level in Pico da Neblina National Park, Brazil, showing percentage of individuals in each phenophase (Activity Index).
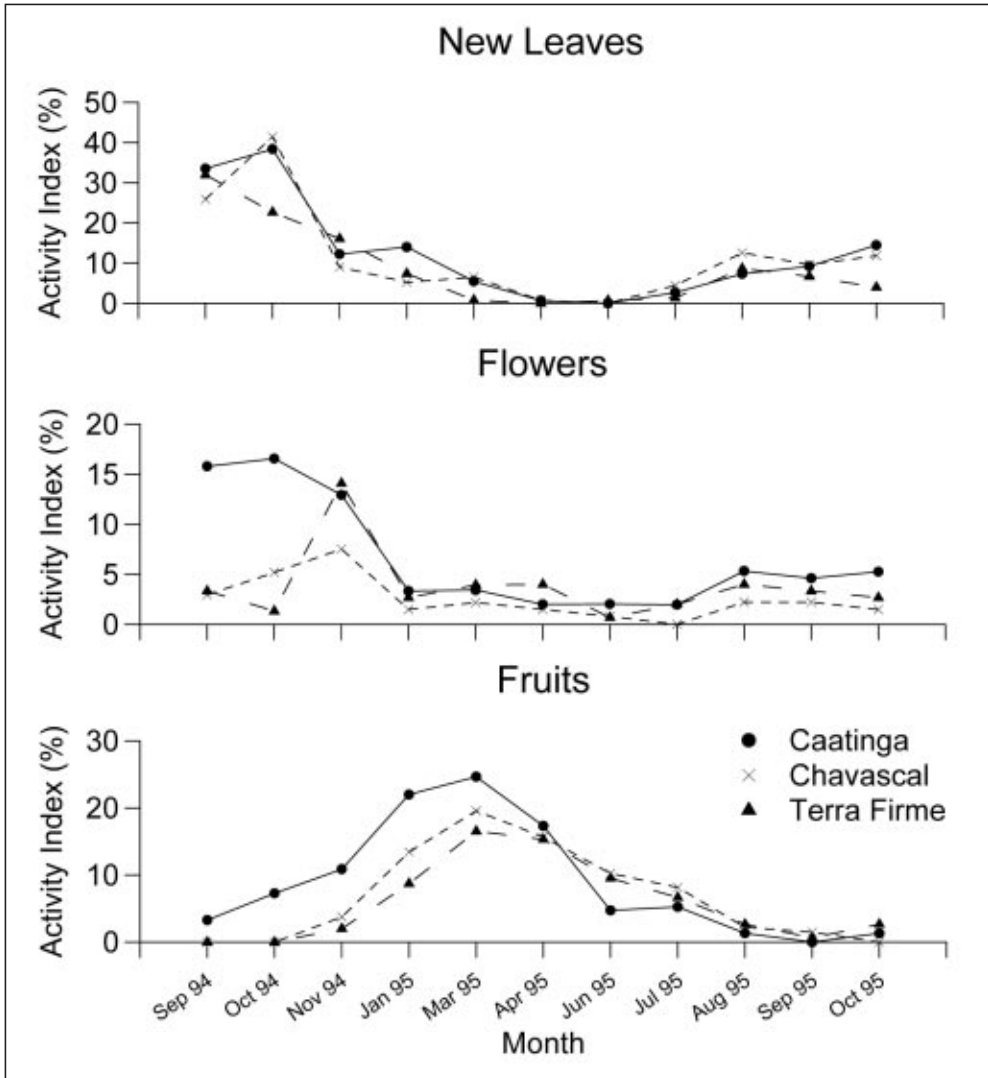
FIG. 4. New leaf, flower and fruit phenology per habitat type in Pico da Neblina National Park, Brazil.

the species, were fertile (presence of flowers, and/or fruits) during the study period. New leaves were observed in 305 individuals (70%) during the study period at the community level, including all forest types, and maximum young leaf production occurred in October 1994 preceeding the flowering peak in December. Most fruits were produced from January to July. March corresponded to the peak of fruiting activity in the forest (Fig. 3). Peaks in phenophase shown by the intensity index, or by percentage of

individuals (Activity Index), coincided. Leaf flushing peaked with the driest months recorded in this study. Finally, the leafing and flowering pattern for 1995 appeared to differ from that observed in 1994. In 1994, September and October were peak months in new leaf production in all habitats. By Ocotober 1995 new leaf production had not yet peaked. Similarly, flowering in caatinga and chavascal peaked around September–November in 1994 but in 1995, by October there were no signs of increased flowering ac-

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tivity. Multi-year difference in the timing of fruiting could not be detected in this study as the fruiting season was sampled only once in 1995 (there were no data for 1994 or 1996). Overall, at the peak of fruiting (March) 20% of the trees produced fruits, whereas from August to October (the trough for fruits) only 0.6% of the trees had fruits.

Contrast between the forest types. New leaves were produced by 113 (74%) trees in caatinga, 97 (72%) in chavascal, and 96 (64%) in terra firme. New leaf production in terra firme peaked in Ocotber 1994, one month in advance of both caatinga and chavascal. Flushing was very noticeable in the caatinga forest because the most abundant tree, *Eperua leucantha*, was leafing at that time of the year. Flowers were observed in 63 (41%) caatinga trees, in 28 (20%) chavascal trees, and 41 (27%) terra firme trees, whereas fruits were seen in 59 caatinga trees (39%), 43 chavascal trees (32%), and 46 terra firme trees (31%). Flowering activity in caatinga preceeded that of terra firme and chavascal by approximately two months whereas the peak in fruit production coincided in the three habitats. However, fruit production declined faster in caatinga than in the other two habitats (Fig. 4). In terms of plant part productivity, caatinga tree species were on average more productive than trees from the other two forest types but the difference was not significant (ANOVA, F = 1.96, *p* = 0.14). On average, 51% of the individuals of each caatinga tree species were fertile in this study vs 40% for terra firme and 35% for chavascal.

Phenology at the population level. Although at the community level the overall pattern was of production of new leaves followed by one peak in flower and a subsequent peak in fruit production, at the population level a closer examination of the phenology of the ten most abundant species revealed a more heterogeneous pattern (Fig. 5). Of the 10 species analyzed, four were restricted to caatinga forests (*Eperua leucantha* n = 17, *Caraipa densiflora* n = 18, *Mucoa duckei* n = 16, *Pachira insignis* n = 18), one (*Hevea brasiliensis* n = 32), was common in all habitats but attained codominance with *E. leucantha* in caatinga , and the remaining five were restricted to terra firme and chavascal forests. The four caatinga trees examined here appeared to stick to the overall pattern of new leaf production in September–October of 1994 followed by flowering in December and fruiting around March-April. Some minor flowering activity was recorded for *E. leucantha* in April as well but that was in one in-

dividual tree that flowered twice. Outside the study plot other *E. leucantha* trees were seen flowering but this appeared to consist of a very small fraction of the population of this species. Also, one individual in our sample fruited twice, in the main peak and again in July. As was the case in most species studied here, most new leaf activity was observed in September–October 1994 but this pattern did not repeat itself in 1995. Another caatinga species, Mucoa duckei, also flowered and produced new leaves in October but fruiting in this species was extended, from December to July. *Mucoa duckei* produced small fruit crops in a piecemeal fashion. The last caatinga species, *Pachira insignis*, had only four individuals fertile in this study, one producing flowers in March and the other three in June. Fruiting was only observed in one individual for which flowering was not observed during the sample periods.

Hevea brasiliensis, the second most abundant tree in the forest, had two flowering episodes in this study; one in September–October and the other in January–March. That resulted in a prolonged fruiting season lasting from around January through to July. But of the nine fertile individuals in this study, three produced fruits before June, one produced fruits twice, once in March and once in June, and the remaining five produced fruits after April into June–July. So individual trees were active at different times to produce such a seemingly prolonged fruiting season. Outside the sampling plots, mature fruits and seeds of *H. brasiliensis* appeared to be most abundant in July. Leafing in this species had one peak in September 1994 and leafing remained high until March. However, no signs of leafing again were observed until Ocotber of 1995.

Terra firme/chavascal trees had a more heterogeneous pattern. *Gustavia hexapetala* (seven fertile individuals) showed two peaks in flowering, one in December and one in April. Five individuals flowered twice, once in December and once in April but only one produced fruits twice (January–March and June). Only one fruiting peak was recorded in this study from January to April. *Senefeldera macrophyla* had seven individuals fertile in this study, although flowering was observed in only two individuals (having been missed in the others) in the month of March. Two fruiting episodes were observed, one in January and the other in June–July. Leafing was high in September–October 1994 but no significant leafing activity was recorded in 1995. In *Licania octandra* six individuals were fertile but flowering was witnessed in only two in December. All six individuals fruited from January to April. Leafing was high in September–Oc-
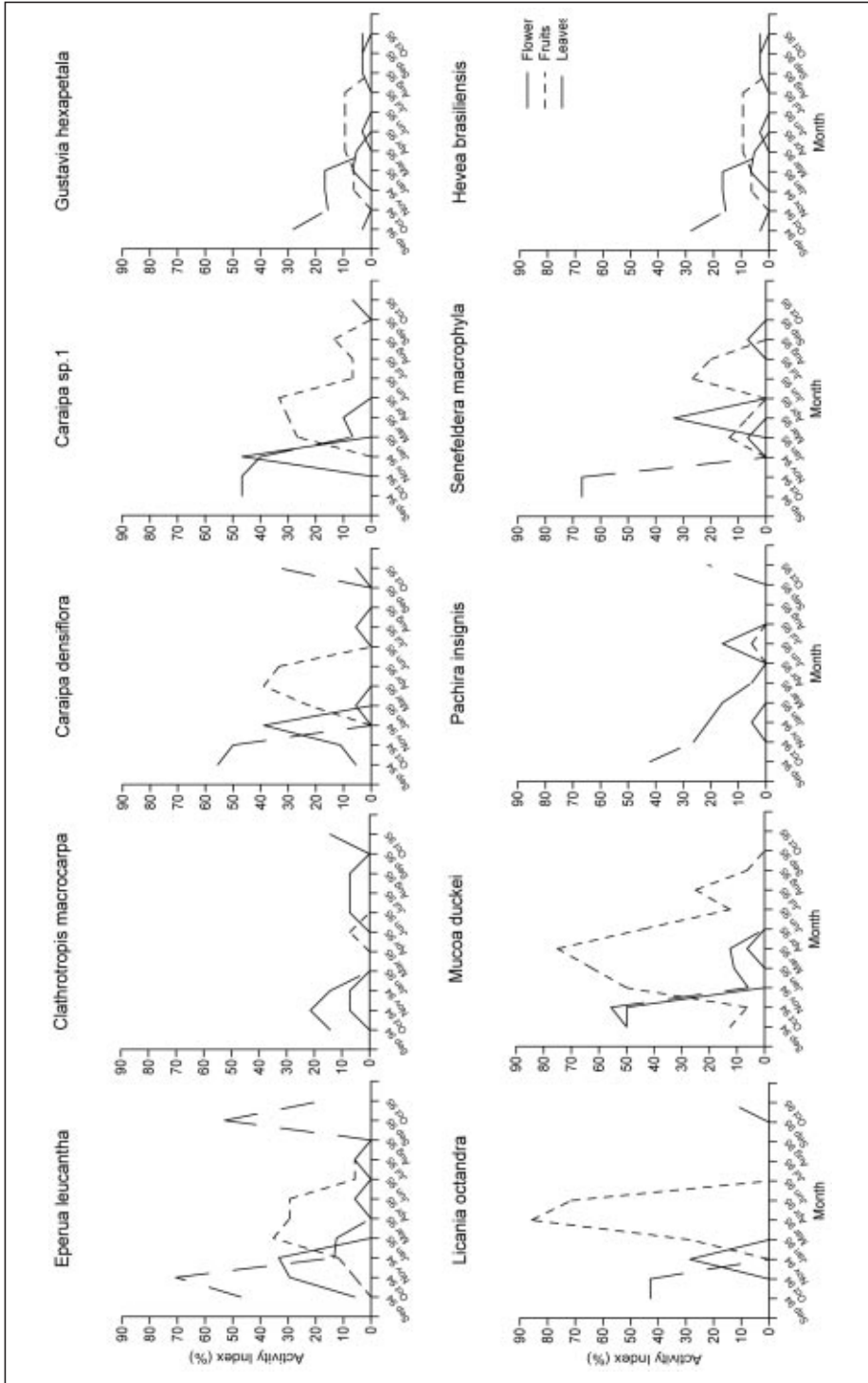
FIG. 5. Phenological patterns of flushing, flowering and fruiting at the population level, showing percentage of individuals by species in each fenofase (Activity Index)

tober of 1994 but not in 1995. In *Clathrotropis macrocarpa*, five individuals were fertile, where flowers but no fruits were observed in four and fruits but no flowers in one in May. Two individuals flowerd in October 1995, one in October 1994, and one in December 1994, corresponding to one annual flowering peak around October–December. Leafing appeared to show two peaks, one in September–October 1994 and the other in June–August. Finally, *Caraipa* sp. had nine fertile individuals, flowering and fruiting was observed in six, only flowers in one, and only fruits in two. All flowering was restricted to December whereas fruiting extended from January to August with a peak in April. Leafing was concentrated in October 1994.

DISCUSSION

Despite the lack of marked seasonality in rainfall and temperature, the phenological pattern in the three forest types investigated in this study conformed with that of more seasonal Neotropical rain forest sites, with flower production during the months with less rainfall, immediately after a peak in new leaf production, and fruit production at the beginning of the wetter period. Given the relative constancy of abiotic conditions in Neblina, we believe that the observed synchrony in the production of each plant part might correlate more directly with biotic interactors (pollinators and seed dispersers or herbivores and seed predators) as has been suggested by a number of authors (e.g., Janzen 1967, Aide 1992, van Schaik *et al.* 1993).

A slight difference in the timing of flowering and flushing activities was observed between caatinga, terra firme and chavascal forests, but the peak time of fruit production coincided in these three forest types. Thus a case for habitat complementarity as suggested by Haugaasen & Peres (2005) cannot be made for the forest mosaic of Neblina.

In terms of overall plant part production, typically in Amazonia, over an annual cycle, approximately 30 to 40 % of the individual trees produce flowers and fruits and only about 10 to 15 % at the peaks (e.g., Ayres 1986, Peres 1991, Setz, 1995). With 39 % of the individuals trees producing flowers and fruits and 20 % at the peak, Neblina forest was relatively productive. This result also holds when the three habitats are considered independently. This finding is somewhat puzzling given that caatinga forests are considered to be an oligotrophic system, where plants are 'starved' of most nutrients and consequently less productive (Coomes 1995). It is possible however, that there is an inter-annual difference in plant productivity in Neblina. As noted in this study, the phenological pattern for leaf and flower production differed between 1994 and 1995. Moreover, as noted by Boubli (1999), some abundant tree species found at the study site, such as *Micrandra sprucei*, but that were not sampled in this study, failed to produce a fruit crop in our study site in 1995, while bearing fruits in other parts of Pico da Neblina. So, it is possible that we sampled a productive year for this forest patch in this study.

At the population level, we found a variation in flowering, fruiting, and leafing phenology as proposed by Sakai (2001). Some species had individuals with two distinct episodes of flowering and fruiting in the same year (e.g., *Gustavia pulchra* and *Eperua leucantha*) and some species had individuals that were asynchronous. However in both of these cases, in our sample very few individuals of each species behaved in that unpredictable fashion. But our sample size was of necessity too small to uncover the more intricate patterns shown by Newstrom *et al.* (1993) in La Selva, where despite the existence of a regular annual pattern at the community level, at the population level only 29 % of the species had an annual rhythm and 55 % were actually sub-annuals. A larger sample size in Neblina would no doubt reveal a more complex pattern similar to this. The fact that a more heterogeneous pattern was documented for terra firme/chavascal trees than caatinga species may be a consequence of biotic factors. Most trees in terra firme produced endozoochorous fruits (Boubli 2002) and their more asynchronous pattern might be a result of the trees competing for dispersers. In caatinga forest, on the other hand, most fruits produced were dry, hard-shelled barochorous fruits (Boubli 2002). These plants usually invest heavily in their seeds, which are generally large except for wind-dispersed ones. Consequently, they are a target for seed-predators and are expected to be produced in synchrony, at the community-level, as a defense mechanism (predator satiation – Smythe 1970, Janzen 1971, Frankie *et al.* 1974, Augspurger 1981, van Schaik *et al.* 1993, Curran and Leighton 2000).

In conclusion, in this study we observed a marked seasonal rhythm in plant part production in Pico da Neblina, despite a lack of seasonality in rainfall, temperature, and photoperiod. The most likely factor producing this observed annual cycle is the small but existing difference in rainfall between the wetter (July–September) and drier (October–June) months. Bor-

chert (1980) believes that the excess of evapotranspiration over precipitation can synchronize leaf fall and subsequent leaf flush or flowering on trees, even in the ever-wet conditions of equatorial regions. The three habitat types examined in this study showed similar patterns of plant part production although, unexpectedly, caatinga forest trees were slightly (but not significantly) more productive than trees in the other two habitats. This study, however, lasted only one year, and it is likely to have produced an incomplete picture of the long-term overall pattern of plant part production for this area. Given the documented inter-annual variation in rainfall for this ever-wet region, an important inter-annual variation in phenology is to be expected. Studies of longer duration are thus required to fully understand the patterns of plant part production in the different forest types of Pico da Neblina.

ACKNOWLEDGMENTS

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