Reproductive phenology of 233 species from four herbaceous–shrubby communities in the Gran Sabana Plateau of Venezuela

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Abstract

Background and aims
Herbaceous–shrubby communities in the Gran Sabana (Great Savanna) Plateau of Venezuela grow under non-zonal conditions. We speculated that this would produce specific patterns of reproductive phenology within these different soil–climate–vegetation associations. Specifically, we tested the hypothesis that the reproductive phenology patterns of four herbaceous–shrubby communities are determined by climate, plant life-forms and soil properties.

Methodology
The reproductive phenology of 233 plant species of the Gran Sabana Plateau of the Venezuelan Guayana Highlands was studied taking into account their life-forms (i.e. trees, shrubs, climbers, annual herbs, perennial herbs, epiphytes and parasites/hemiparasites) in four herbaceous–shrubby communities: (i) shrubland, (ii) secondary bush, (iii) savanna and (iv) broad-leaved meadow. Patterns of flowering, and occurrence of unripe fruit and ripe fruit were studied at two levels of intensity for 24 months within a 5-year span. Two phenological records for each month of the year and between two and four replicates for each community type were made. Randomly selected 2–3 ha plots were used. General phenological patterns were established using <25% of the plants of each species in each plot to give the total duration of each phenological phase. High-intensity phenological patterns were established using >25% of individuals in each plot to establish times of high abundance of flowers, and presence of unripe fruit and/or ripe fruit on individual plants. This generated phenological peaks for each species.

Principal results
Non-seasonality of general flowering and unripe fruiting in each of the four communities was related to non-seasonal flowering and unripe fruiting patterns in the plant life-forms studied and to low variation in precipitation throughout the year. Flowering activity in the shrubland and broad-leaved meadow peaked twice. The bush community had only one flowering peak while the savanna gave a non-seasonal flowering peak. The peak unripe fruiting pattern was not clearly related to unripe fruit phenological patterns of the most abundant life-forms. Unripe fruit patterns and precipitation were only correlated for shrubs, climbers and trees in the shrubland. Ripe fruiting patterns peaked during the short-dry season in the bush and shrubland, and were negatively correlated with precipitation in the shrubland. General and peak ripe fruiting patterns were non-seasonal in the savanna and broad-leaved meadow.

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and related to the dominance of herbaceous species with prolonged ripe fruiting times, low climate seasonality, high plant species richness and diversity, and dispersal syndromes.

Conclusions
The reproductive phenology of the herbaceous–shrubby communities is mainly influenced by the composition of the life-forms, the precipitation regime and soil type.

**Introduction**

The timing of reproductive phenology provides the basic framework for reproductive events in higher plants and is determined by both biotic and abiotic factors and the interactions between them. Diverse patterns of reproductive phenology have been associated with different plant life-forms (shrubs, climbers and trees) in tropical communities. Woody species tend to flower and fruit during the dry season (Daubenmire 1972; Frankie et al. 1974; Lieberman 1982; van Schaik et al. 1993; Morellato and Leitão-Filho 1996; Bhat and Murali 2001; Ramirez 2002; Batalha and Martins 2004; Stevenson et al. 2008), whereas herbaceous species tend to flower and fruit during the rainy season in tropical seasonal communities (Bhat and Murali 2001; Ramirez 2002; Batalha and Martins 2004; Joshi and Janarthanam 2004). In addition, each life-form may show a particular correlation with specific climatic factors (Bhat and Murali 2001; Batalha and Martins 2004; Joshi and Janarthanam 2004). However, climatic factors are not always directly correlated with reproductive phenology, especially when local climatic conditions do not change drastically during the year, such as in montane and submontane forests (Heideman 1989; Hamann 2004; Wanderley de Madeiros et al. 2007). Differences in the reproductive phenology of life-form categories are also influenced by both abiotic and biotic factors. Flowering patterns may be related to the abundance of pollinators and the optimal time for pollination (Daubenmire 1972; Rathcke 1988; Newstrom et al. 1994; Bhat and Murali 2001), and the ripening of fruits tends to peak during the best time for dispersal according to life-form categories. Thus, climatic conditions determine the timing of fruit ripening for climbers and trees: the fruit of wind-dispersed species ripens during the dry season and that of animal-dispersed species during the rainy season (Morellato and Leitão-Filho 1996; Ramirez 2002). In general, however, fruit ripening peaks tend to occur prior to favourable conditions for the germination of seeds and the development of seedlings (Frankie et al. 1974; van Schaik et al. 1993).

Few studies have described the reproductive phenology of tropical herbaceous–shrubby communities. According to a recent revision (Morellato 2003), most studies on herbaceous–shrubby tropical communities have been restricted to regions or zones with a seasonal climate, in which (i) flowering and fruiting phenologies tend to peak during the rainy season such as for littoral and psamophil herbaceous vegetation (Lemus-Jiménez and Ramirez 2002), thorny shrubland (Guevara de Lampe et al. 1992) and open savanna (Ramia 1977, 1978; Ramirez 2002) or (ii) flowering peaks during the rainy season and fruiting occurs during the dry season, as in Brazilian seasonal savanna (De Almeida 1995; Tannus et al. 2006; Silva et al. 2009). On the other hand, it has been reported that flowering and fruiting both peaked towards the end of the dry season and at the beginning of the wet season in a seasonal palm swamp in association with a reduction in flood levels and the abundance of herbaceous species (Ramirez and Brito 1987).

Descriptions of reproductive phenology patterns in tropical herbaceous–shrubby communities are almost non-existent in montane regions. A preliminary study by Ramirez et al. (1988) showed long overlapping flowering and fruiting periods in the Gran Sabana Plateau. However, the precise patterns of reproductive phenology for this shrubby community under mild climate conditions remain unknown. In this context, most studies of tropical reproductive phenology where climate seasonality is not pronounced are basically restricted to submontane and montane rainforest, where climatic factors are not directly responsible for the triggering and synchronization of phenological events (Heideman 1989; Sun et al. 1996; Hamann 2004).

The present-day vegetation cover of the Gran Sabana Plateau appears as a complex mosaic consisting of several vegetation types, resulting from different soil properties and human disturbance (Fölster et al. 2001). Fire represents the main factor driving landscape dynamics in the Gran Sabana Plateau, principally in the transformation of forest into savanna. The forest–savanna mosaic may also be partly explained by the marginal soil conditions (Deezeo and Fölster 1994). These may vary according to texture, water retention and chemical characteristics. From a general climatic point of view, the upland plateau of the Gran Sabana should be covered by evergreen montane and submontane forest (Huber 1995). Thus, herbaceous–shrubby communities in the Gran Sabana Plateau are under...
non-zonal conditions: vegetation types differing from the vegetation that would be present based on climate because several factors (e.g. fire, local soil properties) have given rise to plant communities that differ from the predicted regional vegetation. Therefore, the current vegetation may have produced specific reproductive phenological patterns in these soil–climate–vegetation associations that differ from those expected from the regional climate. Under the same climatic conditions, variations in soil properties and differences in the composition of the life-forms of these communities may lead to staggered sequences in reproductive phenology, reached by different routes within each community. In this context, we tested the hypothesis that the reproductive phenology patterns of the herbaceous–shrubby communities are determined by climate and the composition of life-forms. In addition, differences in the physical soil properties among herbaceous–shrubby communities in the Gran Sabana Plateau (Ramírez et al. 1988; Dezzeo and Fölster 1994; Ramírez et al. 2007) could represent another factor explaining variation between reproductive phenology patterns. Alternatively, under the same mild climate regime, reproductive phenology at the community level may exhibit non-seasonal patterns irrespective of life-form composition.

**Materials and methods**

**Study sites**

Fieldwork was conducted in the Gran Sabana on an elevated plateau (800–1500 m a.s.l.) located in the Canaima National Park, in southeastern Venezuela (04°45′–05°30′N and 60°30′–61°22′W). The Gran Sabana belongs to the Central Guayana Province of the Guayana Region (Huber 1994) and the expected vegetation type is evergreen montane forest according to the climate regime (Huber 1995). The climate of this region has been considered as humid seasonal, with a 3-month dry season (January–March) with <100 mm precipitation (Ramírez et al. 1988). However, this period cannot be considered as a pronounced dry season as some precipitation, a minimum of 60 mm, occurs from January to February with maximum precipitation occurring in August. In addition, annual precipitation rates vary between 1815 and 3400 mm year$^{-1}$, and mean monthly temperature does not vary drastically throughout the year: 19.9–21.4 °C (Ramírez et al. 1988). The soils are in an advanced state of weathering and are characterized by low pH, a deficiency of basic cations, the accumulation of acidic cations and a low Ca/Al ratio in the soil solution (Dezzeo and Fölster 1994; Fölster et al. 2001; Ramírez et al. 2007). Although the fire regime may be an important factor affecting plant reproductive phenology (McFarland 1990; Ish-Shalom-Gordon 1993), our study in the Gran Sabana Plateau did not include fire effects because the communities under study were not burned during the observation period, and there was no evidence of recent fire activity in these areas. However, the savanna is burnt regularly causing a gradual conversion of the forests into bush savanna or savanna (Fölster 1986), which have modulated the landscape of the Gran Sabana Plateau.

The fieldwork was carried out at ~1300 m a.s.l. in the northern part of the Gran Sabana Plateau in four different herbaceous–shrubby community types: shrubland, savanna, broad-leaved meadow and secondary vegetation (bush). These vegetation types were the most representative herbaceous–shrubby communities on the plateau. The shrublands have a physiognomy and floristic composition typical of white-sand associations in Guayana, dominated by herbs and shrubs and a few small trees (Ramírez et al. 1988) growing on sandy soils that are nutrient poor and have low water-retaining properties (Dezzeo and Fölster 1994). They are surrounded by Trachypogon savanna and, at their lowest elevation, frequently associated with broad-leaved meadows (Ramírez et al. 1988). The savanna was a typical grassland community, distributed on flat or sloping areas with sandy loam, acidic and nutrient-poor soils, dominated by perennial and annual herbs with Trachypogon plumosum being the most abundant species (Ramírez et al. 2007). Broad-leaved meadows occur on a peat substrate, which originated by soil compaction and low water permeability of hydromorphic horizons (Dezzeo and Fölster 1994). They are dominated by herbaceous species, with the main distinctive plant families being Xyridaceae, Rapateaceae and Eriocaulaceae. Stegolepis ptaritapuiense (Rapateaceae) is the most frequent species. Secondary vegetation (bush) was represented by the re-growth of a forest deeply disturbed by anthropogenic activity and dominated by perennial herbs, shrubs and annual herbs, followed by trees and climbers (Ramírez et al., in preparation) growing on clayey, acidic and nutrient-poor soils (Dezzeo and Fölster 1994).

**Plant life-forms**

Plant species were categorized as trees, shrubs, climbers, annual herbs (short-lived species were noted during phenological observations), perennial herbs, epiphytes and parasitic, mostly hemiparasitic, species. Short-lived species are defined as plants that complete their life cycle within 1 or 2 years. This life-form was important because it is assumed to have evolved in direct response to the climatic environment and therefore allows a more
Reproductive phenology

A total of 233 plant species belonging to 55 families were surveyed. Because the field sites were located in a remote area, phenological observations were made over 24 months during a 5-year period, with two phenological records for each month of the year and between two and four replicates for each community type. Permanent plots of ~2–3 ha each were randomly delimited for three shrublands, four savannas, two broad-leaved meadows and two areas of secondary forest (bush) sites. At each site, phenological data were recorded at a population level (multiple individuals of each species were surveyed). Each plant species population was phenologically surveyed in one or more of the communities, which could be either of the same or a different community type according to the distribution of each plant species. Some of the phenological information of the savanna areas recorded at the same time and places was taken from technical reports (Ramírez 2000; Varela 2001). The abundance of each developmental stage (flowers, unripe fruit and ripe fruit) for each population of plant species was scored on a scale from 0 to 2, where 0 = none, 1 = few and 2 = abundant. ‘None’ represents the absence of a particular reproductive activity, ‘few’ corresponds to less than one-fourth of individual plants undergoing a particular reproductive activity and ‘abundant’ corresponds to more than one-fourth of individuals undergoing a particular reproductive activity for each permanent plot. In addition, massive reproductive activity, a high number of flowers, unripe fruit and/or ripe fruit on individual plants, mainly trees and shrubs, was also considered in the ‘abundant’ category in order to correct for the low density of some species (from one to four individuals per area).

Flowering was considered to be the occurrence of open flowers. The occurrence of unripe fruit was considered to be between flower disappearance and ripe fruit, including fruit in immature stages, from small fruits to full size, and without any signal (e.g. full size, colour change, smell and dehiscence) for dispersal. Fruit was considered to be ripe when fully developed; green fruits displayed a change of colour and/or texture between successive observations. For fruit that ripened without apparent change, the full development of the seeds was examined. An individual plant or particular population could be in more than one phenological state at a given time, depending on the synchronization of reproductive events. Reproductive phenological patterns were analysed in two ways: firstly, general phenological patterns, which consider the total time of each phenological phase, irrespective of the intensity; secondly, a maximum value or high-intensity phenology, which considers only the phenological peaks for each plant species. In both cases, the phenological data recorded over a 24-month observation period were polled for flowering, unripe fruit and ripe fruit, respectively, and then the monthly presence of each phenological phase was established for each plant species in order to obtain an overall impression of the phenological patterns. For example, if one species was recorded as having flowered from January to April during the first observation period and from December to March during the second observation period, the general flowering period was taken to be December to April. In a similar way, the high-intensity values of each phenological phase were determined per month from the pool of the two observation periods. The observations of the flowering, unripe fruit and ripe fruit patterns for each community were then analysed at two levels: (i) general phenological patterns, representing the total time of each phenological phase, and (ii) high-intensity phenology, considering only the phenological peaks for each plant species.

Statistical analyses

To determine whether plant communities differ from each other according to life-form composition, the level of dependence and interaction among life-forms and communities was established using a log-linear analysis of frequency. Log-linear analysis provides a way of looking at cross-tabulation tables (Statsoft 2007). The concept of interaction in log-linear analysis is analogous to that used in analysis of variance. When the log-linear analysis of frequency was significant, the residual frequencies, i.e. the observed minus expected frequencies, were estimated for each cell of the two-factor comparison and then standardized and tested for significance. This analysis allowed us to establish which pairs of variables deviated significantly from the expected values (Legende and Legende 1993), and therefore made a larger contribution to the association. This analysis of dependence was performed excluding some categories where data distribution resulted in >20% of cells with low or zero counts of the expected frequency (Maruscuilo and Levin 1983). Because of these limitations, the data set was modified for statistical analysis by grouping epiphytic and parasitic species into one category.

On the basis of the floristic census performed in these communities (Ramirez et al., in preparation), plant species were selected in such a way that the largest possible number of plant families and species was included in the study (64% of the total number of plant species...
sampled in the four communities). To evaluate the effect of phylogeny on the associations between pairs of characters, and consequently on reproductive phenology, we used a slightly modified version of Bawa et al. (2003). The null hypothesis was that large plant families do not determine the associations between pairs of characters. To test for a possible effect of the largest families, the average number of plant species per family was first determined to establish the maximum number of plant species per plant family. The independence tests were then run with the total number of species and repeated using only four species from each family. These species were selected maintaining a similar life-form frequency per plant family to that of the life-form frequency when considering the total number of species in each family. We postulated that if the results of the independence tests in both data sets were similar, the effects of phylogeny were not important.

Significant changes in the number of plant species in flower and with unripe and ripe fruits during the year were grouped according to life-form and community type, respectively. To test whether the patterns of each phenological phase deviate from a non-seasonal distribution and therefore exhibited significant changes throughout the year, the annual distribution of the number of species in flower and with unripe and ripe fruit throughout the year was compared with a rectangular discrete distribution (no significant changes along the year) using the Kolmogorov–Smirnov one-sample test (StatSoft 2007). In addition, differences between the phenological pattern pairs of life-forms and communities, respectively, were compared using the Kolmogorov–Smirnov two-sample test (StatSoft 2007) to establish whether life-forms and communities exhibited specific phenological patterns.

We tested whether monthly precipitation was related to the patterns of reproductive phenology along the year. Spearman rank order correlations were calculated between average monthly precipitation rates, recorded over 26 years in the meteorological station at Kavanayén (Ramírez et al. 1988), and the frequency of species in flower and with unripe and ripe fruit in the different life-forms and community types, respectively. To test whether the precipitation regime had an immediate or delayed effect on each phenological event, correlation coefficients were calculated as follows: (i) correlations between precipitation and each phenological phase occurring in the same month, (ii) correlations between precipitation and each phenological phase occurring 1 month later, and (iii) correlations between precipitation and each phenological phase occurring 2 months later.

For the results of the Kolmogorov–Smirnov one-sample and two-sample tests and the correlation analyses, a sequential Bonferroni technique was used to increase the power for detecting more than one false null hypothesis (Rice 1989). The sequential Bonferroni test was used to adjust probability values for simultaneous tests. A significance level of $P < 0.05$ was applied for each separate test of the relationships between each phenological phase (flower, unripe fruit and ripe fruit) and level of intensity (general and peak phenology) according to life-forms and communities, respectively.

Cluster analysis based on the arcsine transformed monthly frequencies of yearly phenological patterns was performed using the general phenological patterns of flowering, unripe fruit and ripe fruit as grouping variables to classify the months of the year irrespective of plant life-forms and community type. Our hypothesis was that the months of the year show groups related to the climate of the area when they are classified according to reproductive phenology. In this analysis, however, some months tended to show similar information, since succeeding months sometimes had overlapping conditions. Consequently, the number of plant species in a given month may have depended on that of the previous month, thus violating the independence assumption for cluster analysis. This effect should be exploited, however, in order to demonstrate association (Anderberg 1973). Thus, the null hypothesis assumes that the number of plant species is similar for all months during the year. Linkage was measured using Ward’s method, which uses an analysis of variance approach to evaluate the Euclidean distances between clusters (StatSoft 2007). The hierarchical tree diagrams summarize the results of the joining analysis. To corroborate statistically the groups generated from cluster analysis, discriminant function analysis was performed, using the category to which each month of the year was assigned in the cluster analysis as the grouping variable and the frequency of the arcsine transformed plant species (flower, unripe fruit and ripe fruit) for each month of the year as independent variables. In addition, low levels of multicollinearity were corroborated, whereby tolerance values of up to 0.3 were established. The average values of the frequency of each phenological phase (flowering, unripe fruiting and ripe fruiting) were determined and compared using a one-way analysis of variance (ANOVA) (Sokal and Rohlf 1995). An a posteriori comparison of means, Tukey’s honestly significant difference for unequal sample sizes, was performed for each significant ANOVA.

**Results**

Plant life-forms, community types and the phenological records of 233 plant species belonging to 55 families are listed in Appendix 1 [see Additional Information].
plant families with the largest number of species in the four habitats studied were Melastomataceae ($N = 27$; 11.5%), Cyperaceae ($N = 17$; 7.3%), Asteraceae ($N = 16$; 6.8%), Orchidaceae ($N = 14$; 5.9%), Poaceae ($N = 14$; 5.9%), Xyridaceae ($N = 12$; 5.1%) and Rubiaceae ($N = 10$; 4.3%), with an average number of species per family of 4.2 (SD = 5.1).

The relationship between life-form and community type was statistically significant (df = 15, $\chi^2 = 54.06$, $P = 0.000003$). Perennial herb was the most abundant life-form in all communities. The broad-leaved meadow and savanna habitats had the highest proportion of perennial and annual herbs, and the lowest proportion of trees and shrubs (Table 1). The shrublands and bush were also dominated by perennial herbs, as well as having the highest proportion of shrubs and trees (Table 1). The largest plant families had no phylogenetic effect on the relationship between life-form and community type: the independence tests carried out using all plant species per family and four plant species per plant family (df = 15, $\chi^2 = 35.3$, $P = 0.002257$) gave similarly significant results.

**Table 1** Relationship between life-form and community. The sample size exceeds the total number of plant species because plant species occurred in more than one community. $N$ = sample size. The figures in parentheses represent percentages of the total-row value.

| Community     | Life-form |       |       |       |       |       |       | Total |
|---------------|-----------|-------|-------|-------|-------|-------|-------|-------|
|               | Tree      | Shrub | Climber | Perennial herb | Annual herb | Epiphyte | Parasitic |       |
| Shrubland     | 14 (8.7) | 45 (28.1) | 5 (3.1) | 70 (43.7) | 17 (10.6) | 2 (1.3) | 7 (4.4) | 160   |
| Broad-leaved meadow | 2 (2.1) | 14 (14.9) | 2 (2.1) | 60 (63.8) | 16 (17.0) | 0 (0.0) | 0 (0.0) | 94    |
| Bush          | 12 (12.2) | 23 (23.5) | 10 (10.2) | 35 (35.7) | 13 (13.3) | 0 (0.0) | 5 (5.1) | 98    |
| Savanna       | 1 (1.3)  | 8 (10.5)  | 4 (5.3)  | 51 (67.1) | 12 (15.8) | 0 (0.0) | 0 (0.0) | 76    |

The general patterns of reproductive phenology

Cluster analysis of the monthly frequency of plant species in flower, and with unripe and ripe fruit for all plant species studied, allowed us to establish three groups of months according to reproductive phenology, irrespective of life-form and community type (Fig. 1). The first group, January–March, represents the short-dry period (SDP); the second group, from April to June, represents the first 3 months of the rainy period, beginning rainy period (BRP); and the third group, from July to December, represents the second half and end of the rainy period (RP). Discriminant function analysis statistically supported the presence of these three groups ($F(6,14) = 7.82$; $P < 0.0008$); group SDP differed from BRP ($P = 0.0052$) and RP ($P = 0.0150$), and group BRP differed from RP ($P = 0.0114$). In addition, all members within each group were correctly classified. On average, the frequencies of flowering and unripe fruiting phenology differed statistically between groups (Table 2). The number of species in flower was significantly lower during BRP than during SDP and RP, and the number of species with unripe fruit was significantly higher during SDP than during BRP and RP. Although the frequency of species with ripe fruit decreased from group SDP to group RP, no statistical differences were found (Table 2).

Reproductive phenology and precipitation

The correlation coefficients between the general patterns of each phenological phase according to life-forms and community type, and the average monthly precipitation rates, are given in Table 3. The frequency of climbers in flower correlated negatively with precipitation...
values for the same month, and monthly precipitation was negatively correlated with the frequency of tree species in flower both 1 and 2 months later. In contrast, high-intensity flowering phenology was not significantly correlated with precipitation. The frequency of plant species with unripe fruit correlated negatively with precipitation values for trees, shrubs and climbers in the same month, and, in the case of trees and shrubs, precipitation was also negatively correlated with the frequency of species with unripe fruit 1 month later (Table 3). Similarly, peak phenology patterns of unripe fruit correlated negatively with precipitation values for trees and shrubs. In contrast, the frequency of perennial herbs with unripe fruit correlated positively with precipitation values 2 months later. The frequency of plant species with unripe fruit correlated negatively with precipitation values for the same month and 1 month later in the shrubland (Table 3).

Life-forms and flowering phenology

General and peak patterns of flowering phenology did not differ statistically from a rectangular discrete distribution for any of the life-forms studied (Table 4). However, flowering patterns during the year showed some variation among life forms: for example, climbers and trees tended to have more flowers during the short-dry season and at the end of the rainy season compared with during the rainy season (Fig. 2A). Specifically, general flowering patterns between life-forms were found to be statistically different between trees and annual herbs, and trees and parasitic plants (Table 5). All life-forms tended to show a peak flowering period during the mid-rainy season, when maximum precipitation occurs. The annual herbs exhibited the most drastic variations between maximum and minimum flowering values. In addition, shrubs, perennial herbs and climbers exhibited another peak during the late short-dry season (Fig. 3A). High-intensity flowering patterns during the year differed statistically between some pairs of life-forms: annual herbs—all life-forms and trees—climbers (Table 5).

Life-forms and unripe fruit phenology

General and peak patterns of unripe fruit phenology did not differ statistically from a rectangular discrete distribution for any of the life-forms studied (Table 4). However, the frequency of unripe fruit in trees and climbers tended to decrease from the dry to the rainy season (Fig. 2B). Statistical comparisons between life-form pairs demonstrated that differences in general unripe fruit patterns were not significant (Table 5). The frequency of unripe fruit in trees, shrubs and climbers tended to decrease from the short-dry to the rainy season and that of annual herbs to increase from the first months of the year to the rainy season (Fig. 3B). The peak phenology of unripe fruit patterns differed statistically between annual herbs and all other life-forms, and climbers and all other life-forms throughout the year (Table 5).

Life-forms and ripe fruit phenology

General and peak patterns of ripe fruit phenology did not differ statistically from a rectangular discrete distribution for any of the life-forms studied (Table 4). However, the frequency of ripe fruit in trees and climbers tended to decrease from the dry to the rainy season (Fig. 2C). Statistical comparisons between life-form pairs demonstrated that ripe fruit patterns were not significant (Table 5). The frequency of ripe fruit in trees, shrubs and climbers tended to decrease from the short-dry to the rainy season and that of annual herbs to increase from the first months of the year to the rainy season (Fig. 3C). The peak phenology of ripe fruit patterns differed statistically between annual herbs and all other life-forms, and climbers and all other life-forms throughout the year (Table 5).

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Table 2 Mean values and statistical results of ANOVA between phenological groups of each phenological phase.

| Phenological phase | Phenological group | Short-dry period | Beginning rainy period | Rainy period | Statistical |
|--------------------|--------------------|------------------|------------------------|-------------|-------------|
|                    |                    | X (SD)           | X (SD)                 | X (SD)      | $F_{(2,9)}$ (P=) |
| Flowering (%)      | 77.8 (2.4)$^a$    | 63.7 (3.5)$^b$  | 74.3 (3.0)$^a$        | 17.8 (0.000735) |
| Unripe fruit (%)   | 79.4 (1.6)$^a$    | 66.2 (3.4)$^b$  | 69.6 (3.1)$^b$        | 18.3 (0.000673) |
| Ripe fruit (%)     | 67.0 (7.7)        | 62.9 (9.6)       | 54.4 (9.2)            | 4.1 (n.s.)  |

Different superscripts indicate significant difference between values of each row at $P < 0.000920$. 

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Table 3  Spearman rank order correlation coefficients between monthly mean values of precipitation and the frequency of species in flower, and with unripe and ripe fruit occurring simultaneously (0), 1 month later (1) and 2 months later (2) in the different life-form and community types, respectively (N = 12).

|                          | General phenology |                  | Peak phenology |                  |
|--------------------------|-------------------|------------------|----------------|------------------|
|                          | 0                 | 1                | 2              | 0               | 1               | 2               |
| **Flowering**            |                   |                  |                |                 |                 |                 |
| **Life-form**            |                   |                  |                |                 |                 |                 |
| Tree                     | 0.65              | -0.87            | -0.81          | -0.01           | -0.07           | -0.20           |
| Shrub                    | 0.54              | -0.65            | -0.72          | -0.19           | 0.03            | 0.12            |
| Climber                  | -0.91             | -0.77            | -0.46          | -0.07           | 0.19            | 0.30            |
| Perennial herb           | -0.68             | -0.68            | -0.54          | 0.36            | 0.67            | 0.66            |
| Annual herb              | -0.19             | -0.42            | -0.63          | 0.07            | -0.19           | -0.51           |
| Parasitic                | -0.31             | -0.22            | -0.01          | -0.05           | -0.05           | 0.11            |
| **Community**            |                   |                  |                |                 |                 |                 |
| Bush                     | -0.74             | -0.53            | -0.16          | -0.43           | 0.04            | 0.49            |
| Shrubland                | -0.35             | -0.62            | -0.77          | -0.48           | -0.46           | -0.16           |
| Broad-level meadow       | -0.15             | -0.42            | -0.65          | -0.29           | -0.30           | -0.14           |
| Savanna                  | 0.19              | -0.08            | -0.40          | 0.35            | 0.38            | 0.37            |
| **Unripe fruit**         |                   |                  |                |                 |                 |                 |
| **Life-form**            |                   |                  |                |                 |                 |                 |
| Tree                     | -0.94             | -0.87            | -0.48          | -0.83           | -0.58           | -0.21           |
| Shrub                    | -0.89             | -0.88            | -0.68          | -0.81           | -0.52           | -0.21           |
| Climber                  | -0.80             | -0.53            | -0.03          | -0.47           | -0.03           | 0.45            |
| Perennial herb           | -0.33             | -0.29            | 0.03           | -0.02           | 0.48            | 0.81            |
| Annual herb              | -0.02             | -0.05            | -0.28          | -0.08           | -0.42           | -0.64           |
| Parasitic                | -0.64             | -0.34            | 0.03           | -0.46           | -0.17           | -0.17           |
| **Community**            |                   |                  |                |                 |                 |                 |
| Bush                     | -0.49             | -0.06            | 0.42           | 0.02            | 0.47            | 0.74            |
| Shrubland                | -0.83             | -0.82            | -0.62          | -0.70           | -0.54           | -0.20           |
| Broad-leaved meadow      | -0.52             | -0.59            | -0.56          | -0.29           | -0.20           | 0.04            |
| Savanna                  | 0.54              | 0.24             | -0.14          | 0.66            | 0.65            | 0.46            |
| **Ripe fruit**           |                   |                  |                |                 |                 |                 |
| **Life-form**            |                   |                  |                |                 |                 |                 |
| Tree                     | -0.49             | -0.02            | 0.39           | -0.33           | 0.19            | 0.60            |
| Shrub                    | -0.58             | -0.12            | 0.29           | -0.46           | 0.02            | 0.45            |
| Climber                  | -0.02             | 0.48             | **0.78**       | 0.53            | **0.78**        | **0.90**        |
| Perennial herb           | -0.06             | 0.39             | 0.58           | 0.35            | 0.68            | 0.71            |
| Annual herb              | -0.23             | -0.24            | -0.17          | -0.20           | -0.55           | -0.69           |
| Parasitic                | -0.36             | -0.01            | 0.15           | -0.66           | -0.36           | 0.01            |
| **Community**            |                   |                  |                |                 |                 |                 |
| Bush                     | 0.18              | 0.65             | **0.90**       | 0.34            | 0.75            | **0.81**        |

Continued
season and that of annual herbs tended to increase from the beginning of the rainy season to the end of the year. Parasitic plants exhibited two peaks, the first during the short-dry season and the second during the rainy season (Fig. 3C). High-intensity patterns differed statistically between annual herbs and all other life-forms, climbers and trees–shrubs–perennial herbs, and trees and perennial herbs (Table 5) throughout the year.

Communities and flowering phenology

General patterns of flowering phenology did not differ statistically from a rectangular discrete distribution for any of the communities studied (Table 4). The frequency of plants in flower decreased during the beginning of the rainy season in the shrubland and broad-leaved meadows, and during September–October in the bush community (Fig. 4A). Neither were general flowering patterns statistically different between communities (Table 6). However, peak flowering patterns for bush and shrubland departed statistically from a rectangular distribution throughout the year (Table 4). Flowering frequency in the shrubland, broad-leaved meadow and savanna tended to exhibit a bimodal pattern (a minor first peak during the short-dry season and a second peak during the rainy season), whereas in the bush, flowering only peaked during the short-dry season (Fig. 5A). Thus, the bush communities differed in their peak flowering patterns from the

### Table 3 Continued

| Life-form       | General phenology | Peak phenology |
|-----------------|------------------|----------------|
|                 | 0    | 1    | 2    | 0    | 1    | 2    |
| Shrubland       | -0.64| -0.16| 0.21 | -0.41| 0.09 | 0.39 |
| Broad-leaved meadow | -0.54| -0.19| 0.07 | -0.20| -0.02| 0.14 |
| Savanna         | 0.26 | 0.46 | 0.49 | 0.19 | 0.21 | -0.05 |

Coefficients in bold are significant at $P < 0.05$ according to the sequential Bonferroni test.

### Table 4 $D_{max}$ values (Kolmogorov–Smirnov test) of the comparisons of general and peak phenology throughout the year with rectangular discrete distribution grouped according to life-form and community.

| Life-form       | General phenology | Peak phenology |
|-----------------|------------------|----------------|
|                 | Flower | Unripe fruit | Ripe fruit | Flower | Unripe fruit | Ripe fruit |
|                 | $D_{max}$ | $D_{max}$ | $D_{max}$ | $D_{max}$ | $D_{max}$ | $D_{max}$ |
| Tree            | 0.0563 | 0.0694 | 0.1505 | 0.0958 | 0.1167 | 0.3150 |
| Shrub           | 0.0176 | 0.0415 | 0.0878 | 0.1288 | 0.1186 | 0.2586 |
| Climber         | 0.0566 | 0.0841 | 0.1900 | 0.1929 | 0.2593 | 0.1905 |
| Perennial herb  | 0.0186 | 0.0181 | 0.0242 | 0.1085 | 0.0954 | 0.0862 |
| Annual herb     | 0.0415 | 0.0278 | 0.0398 | 0.2281 | 0.2180 | 0.1886 |
| Parasitic       | 0.0385 | 0.0523 | 0.0500 | 0.0894 | 0.0291 | 0.0962 |
| Community       |        |        |        |        |        |        |
| Bush            | 0.0305 | 0.0435 | 0.0622 | 0.1216 | 0.1162 | 0.1119 |
| Shrubland       | 0.0273 | 0.0256 | 0.0608 | 0.0731 | 0.1116 | 0.1607 |
| Broad-leaved meadow | 0.0253| 0.0145 | 0.0396 | 0.0588 | 0.0667 | 0.0979 |
| Savanna         | 0.0135 | 0.0149 | 0.0096 | 0.0464 | 0.0554 | 0.0351 |

Values in bold are significant at $P < 0.05$ according to the sequential Bonferroni test separately for each phenological phase (flower, unripe fruit and ripe fruit) and level of intensity (general and peak phenology) according to life-form and community, respectively.
Communities and unripe fruit phenology

Patterns of unripe fruit phenology at the community level did not differ statistically from a rectangular discrete distribution (Table 4). However, the frequency of unripe fruit decreased from the dry season to the beginning of the rainy season for shrubland and bush communities and from the dry season to the end of the rainy season for the savanna community (Fig. 4B). Unripe fruit phenology in the savanna exhibited few changes over the year but did increase towards the mid-rainy season. Pairwise comparisons between communities did not differ according to general phenology (Table 6). Furthermore, high-intensity unripe fruiting patterns for the shrubland and bush communities departed statistically from a rectangular distribution over the year (Table 4). Peak unripe fruit phenology in the savanna, broad-leaved meadow and bush communities tended to exhibit a bimodal pattern with a peak during the short-dry season. This was followed by a less pronounced second peak during the mid-rainy season. In contrast, only one peak during the short-dry season was found for the shrubland community (Fig. 5B). In addition, the high-intensity phenology of unripe fruit throughout the year differed statistically between the bush and the other three communities, and between savanna, and shrubland and broad-leaved meadow (Table 6).

Communities and ripe fruit phenology

General and peak patterns of ripe fruit phenology departed statistically from a rectangular discrete distribution for bush and shrubland (Table 4) with a peak during the short-dry season that decreased until the end of the rainy season (Fig. 4C). However, there were no significant differences in general patterns between pairs of communities (Table 6). Ripe fruiting patterns peaked during the last month of the short-dry season and then decreased until the end of the rainy season for all communities (Fig. 5C). Despite the similarities in the peak ripe fruiting patterns among communities throughout the year, all ripe fruiting patterns were found to be statistically different, except between the bush and the broad-leaved meadow (Table 6).

Discussion

General phenology

Reproductive patterns of groups of plant species established according to their reproductive phenology were related to the climate conditions in the Gran Sabana Plateau, suggesting that climate conditions are an important factor in determining within-year patterns of reproductive phenology and may bias the seasonality of reproductive events for plant species, life-forms and communities. Variation in precipitation between the short-dry season and rainy seasons seems to have some effect on reproductive phenology depending on community and life-form types. Moreover, seasonal and non-seasonal reproductive phenology at the community level may be explained by the reproductive phenology patterns of the life-forms, the frequency or abundance of each life-form in the community and/or...
Table 5 Comparison between each phenological phase according to life-form. Chi-square values below the diagonal correspond to the general phenology, and values above the diagonal correspond to peak phenology throughout the year (df = 2).

| Life-form | Tree | Shrub | Climber | Perennial herb | Annual herb | Parasitic |
|-----------|------|-------|---------|---------------|-------------|-----------|
|           | $\chi^2$ | $\chi^2$ | $\chi^2$ | $\chi^2$ | $\chi^2$ | $\chi^2$ |
| Tree      |       |       |         |               |             |           |
| F         | -     | 4.79  | 10.53   | 4.54          | 10.59       | 7.59      |
| U         | -     | 0.55  | 12.67   | 3.17          | 21.83       | 2.56      |
| M         | -     | 1.51  | 11.63   | 25.91         | 59.89       | 6.86      |
| Shrub     |       |       |         |               |             |           |
| F         | 0.66  | -     | 3.84    | 3.79          | 30.18       | 2.82      |
| U         | 0.57  | -     | 13.28   | 6.11          | 47.04       | 2.59      |
| M         | 1.42  | -     | 13.22   | 52.80         | 89.92       | 7.34      |
| Climber   |       |       |         |               |             |           |
| F         | 0.39  | 1.14  | -       | 7.15          | 24.33       | 1.79      |
| U         | 0.46  | 1.60  | -       | 9.96          | 62.67       | 9.55      |
| M         | 1.42  | 4.17  | -       | 3.45          | 28.01       | 4.71      |
| Perennial herb |       |       |         |               |             |           |
| F         | 1.02  | 0.53  | 0.72    | -             | 28.45       | 2.89      |
| U         | 1.28  | 0.95  | 1.61    | -             | 66.66       | 1.93      |
| M         | 5.98  | 4.79  | 7.06    | -             | 39.78       | 1.94      |
| Annual herb |     |       |         |               |             |           |
| F         | 266.09 | 0.43  | 1.64    | 1.29          | -           | 17.11     |
| U         | 2.08  | 1.48  | 2.44    | 0.78          | -           | 11.85     |
| M         | 6.12  | 5.04  | 9.58    | 2.49          | -           | 13.47     |
| Parasitic |       |       |         |               |             |           |
| F         | 135.82 | 0.80  | 0.32    | 0.40          | 1.25        | -         |
| U         | 0.52  | 0.76  | 0.30    | 0.54          | 1.32        | -         |
| M         | 1.49  | 0.32  | 3.17    | 0.33          | 0.82        | -         |

Values in bold are significant at $P < 0.05$ according to the sequential Bonferroni test separately for each phenological phase (flower (F), unripe fruit (U) and ripe fruit (M)) and level of intensity (general and peak phenology), respectively.

the response of each life-form to the precipitation regime. However, these parameters do not always influence reproductive phenology in a similar way or act synergistically and, in some cases, may even have a null or opposite effect on reproductive events.

**Flowering patterns**

Non-seasonal general phenological patterns suggest a lack of climatic constraints during the year on flowering activity at a community-wide level (Opler et al. 1980; Heideman 1989; Seres and Ramirez 1993; Sun et al. 1996; Wanderley de Madeiros et al. 2007). According to this, an unpronounced dry season is largely influencing the non-seasonal flowering patterns found in the herbaceous–shrubby communities in the Gran Sabana Plateau. The non-seasonality of flowering patterns in the four community types studied is consequently related to the non-seasonal flowering patterns of the life-forms. Many plant species exhibited low intensity and extended periods of flowering activity, related to water availability throughout the year. In contrast, the general pattern of the flowering phenology of tree species was found to be different to that of annual herbs and parasitic species. Differences in flowering patterns between life-forms during the year are probably part of an evolutionary strategy to develop a non-seasonal flowering pattern and thus reduce overlapping at the community level.
General and peak flowering phenologies were not correlated with precipitation in the four herbaceous–shrubby communities studied and for most of the life-forms. Thus, flowering phenology is not influenced by the precipitation regime. High levels of precipitation throughout the year seemed to bias the non-flowering–precipitation correlations at the community level. General patterns of flowering phenology were only negatively correlated with precipitation for climbers and with a lag time of 1–2 months for tree species, which could be due to the association between high precipitation and a decrease in insect activity (Roubik 1989). Most of the plant species in the shrubland are pollinated by insects (Ramírez 1989), and flowers may also be affected by strong rains. Thus, high precipitation during the rainy period could be negatively affecting pollination performance and consequently selecting for flowering activity during the optimum period for pollination.

Bimodal flowering phenologies have been recorded in a Bolivian dry forest (Justiniano and Fredericksen 2000) and in a tropical lowland forest (Stevenson et al. 2008). According to peak flowering phenology, the shrubland, broad-leaved meadow and most life-forms showed two flowering peaks, the first during the short-dry season and the second during the rainy season. At this point, the following question arises: why do the same life-forms have similar bimodal flowering patterns in structurally contrasting communities? Probably each flowering peak is represented by different plant species belonging

![Fig. 3 Phenological patterns of life-forms. These are based on maximum values of flower (A), unripe fruit (B) and ripe fruit (C) production.](image1)

![Fig. 4 General phenological patterns of plant species at the community level. (A) flowering, (B) fruiting and (C) ripe fruiting.](image2)
to the same life-form. Alternatively, each plant species may exhibit two flowering peaks. In addition, the specific combinations of life-forms, together with soil type and water availability in each community, seem to strongly influence the timing of the major peak during the SDP at the community level. In herbaceous plant communities, such as broad-leaved meadows that are under conditions of permanent soil water availability, flowering activity increases towards the end of the dry season. A reduction in soil water during the dry season has been associated with increased flowering activity in a palm swamp, a permanently flooded herbaceous community (Ramírez and Brito 1987). In addition, it is recognized that soil moisture content is the main determinant of phenological patterns in different life-forms in tropical evergreen forests (Joshi and Janarthanam 2004). Hence, flowering peaks in the SDP in the broad-leaved meadow could be related to the reduction of water in the soil. In the bush community, a high number of trees, shrubs and climbers with flowering peaks during the SDP could be biasing the peak high-intensity phenology results of only one flowering peak during the short-dry season. Similar patterns have been found in wet, mostly non-seasonal forests (Heide- man 1989; Bhat and Murali 2001). Moreover, flowering in the bush seems to be related to the moisture content of the soil, as reported for a tropical evergreen forest (Joshi and Janarthanam 2004). A flowering appears to be triggered more by the dry conditions created by low river levels than by local rainfall in riverine forests (Kinnard 1992). In our case, the bush community was located along the banks of the Aponguao River, where low river levels during the dry period could be enhancing flowering activity.

Conversely, non-seasonal flowering patterns in the savanna could be related to six main factors. (i) Low climate seasonality in the area may enhance the non-seasonality of flowering patterns. (ii) The particular floristic composition and structure of the grassland savannas, where Poaceae and Cyperaceae are the most abundant plant families (Ramírez et al. 2007), may be associated with non-seasonal flowering patterns. Flowering season encompassing the whole year may result from relatively mild environmental conditions and high ecophysiological heterogeneity of plant species (Herrera 1986). (iii) Herbaceous life-forms tend to have prolonged flowering times (Ramírez and Brito 1987; Seres and Ramírez 1993) and, consequently, flowering phenology at the community level may be extended throughout the year. (iv) Soil properties may determine the non-seasonal flowering patterns in the savanna. Soils in the savanna differ from those in the other

| Table 6 | Comparison between each phenological phase according to community. Chi-square values below the diagonal correspond to the general phenology, and values above the diagonal correspond to peak phenology (df = 2). |
| Community phenology | Bush | Shrubland | Broad-leaved meadow | Savanna |
|----------------------|------|-----------|---------------------|--------|
| Bush                 |      |           |                     |        |
| F                    | –    | 30.05     | 34.66               | 32.69  |
| U                    | –    | 11.49     | 12.36               | 19.28  |
| M                    | –    | 20.48     | 9.19                | 26.92  |
| Shrubland            |      |           |                     |        |
| F                    | 5.39 | –         | 1.31                | 5.86   |
| U                    | 6.12 | –         | 4.94                | 28.41  |
| M                    | 2.72 | –         | 14.79               | 40.54  |
| Broad-leaved meadow  |      |           |                     |        |
| F                    | 3.96 | 0.11      | –                   | 2.94   |
| U                    | 4.96 | 0.42      | –                   | 9.38   |
| M                    | 3.15 | 1.31      | –                   | 9.50   |
| Savanna              |      |           |                     |        |
| F                    | 2.22 | 0.94      | 0.22                | –      |
| U                    | 6.04 | 2.42      | 5.81                | –      |
| M                    | 4.04 | 5.21      | 1.45                | –      |

Values in bold are significant at $P < 0.05$ according to the sequential Bonferroni test for flowering, unripe fruit and ripe fruit phenology, respectively.
communities studied, which together with the dominance of herbaceous life-forms may produce a particular combination resulting in non-seasonal flowering phenology. (v) Environmental heterogeneity of the savanna due to disturbance and topography enhances plant species richness and diversity shown by the different life-forms (Ramírez et al. 2007). Consequently, a high diversity of phenological strategies may occur throughout the year. (vi) The savanna grassland is characterized by a high proportion of wind-pollinated species, which produce fruit and seed at different times throughout the year (Ramírez 2000; Varela 2001), avoiding heavy overlap among species. Therefore, non-seasonal flowering patterns in the savanna may also be modulated by the segregation of flowering times, ensuring a better distribution of pollination classes.

**Unripe fruit patterns**

The general patterns of unripe fruit phenology were non-seasonal in the four communities studied, which can be related to the non-seasonal unripe fruiting patterns of all life-forms. In contrast, the availability of unripe fruit is related to periods of high rainfall in seasonal riverine forests (Kinnard 1992). Non-seasonal unripe fruit phenology in the herbaceous–shrubby community in the Gran Sabana Plateau seems to be largely influenced by an unpronounced seasonal climate. A fruiting season encompassing the whole year in a Mediterranean shrubland is a result of relatively mild environmental conditions (Herrera 1986), and a weak and extended fruiting peak may be a common feature of forests in weakly seasonal environments (Heideman 1989). In addition, non-seasonal unripe fruiting patterns seem to be influenced by non-seasonal flowering phenology.

Similarities between general unripe fruiting patterns for shrubland, savanna and broad-leaved meadow suggest the existence of variables other than life-form frequency which could influence their unripe fruit phenologies. The general pattern of unripe fruit phenology was negatively correlated with precipitation for the shrubland community, following negative correlations between the unripe fruit phenologies and precipitation of the most abundant life-forms. A decrease in unripe fruiting activity during the rainy season could be related to an increase in cloudiness, which reduces radiation during this period. Several lines of evidence point to the enhancement of photosynthetic and reproductive productivity during sunny periods (Rathcke and Lacey 1985). Consequently, daily energy input is lower during the rainy season than the dry season, which could negatively affect plant physiology. Hence, unripe fruit phenology is not completely favoured during the rainy season. Moreover, the moisture content of the soil is the main determinant of phenological patterns for different life-forms in tropical evergreen forests (Joshi and Janarthanam 2004). In this context, differences between the peak unripe fruiting patterns of bush vegetation compared with the other communities could also be associated with differences in soil type: sandy soil in the shrubland (Ramírez et al. 1988), sandy loam in the savanna (Ramírez et al. 2007), peat substrate in the broad-leaved meadow, and clayey soils in the bush (Dezzeo and Fölster 1994). Soils under the same climatic conditions have different water-holding capacities; the sandy shrubland and savanna soils dry out far more rapidly than the clayey bush vegetation soils, enhancing unripe fruiting activity. In addition, the bush is located

![Fig. 5 Phenological patterns of communities. These are based on maximum values of flower (A), unripe fruit (B) and ripe fruit (C) production.](https://academic.oup.com/aobpla/article-abstract/doi/10.1093/aobpla/plr014/148427)
along the banks of the Aponguao River, and soil water may remain at saturation levels for a longer period of time both during and after the rainy season, thus shaping unripe fruit production patterns.

Ripe fruit patterns
The seasonality of the ripe fruiting patterns, which peaked during the short-dry season in the bush and shrubland, was primarily related to the abundance of trees, shrubs and climbers possessing seasonal-equivalent ripe fruit phenologies in these communities. Similar ripe fruiting patterns among different life-forms were also found in a tropical dry evergreen forest (Selwyn and Parthasarathy 2007), which seems to indicate a general adaptation of these life-forms to produce ripe fruit during the dry season. Fruit ripening has been shown to be primarily determined by internal factors that control the rate of fruit development rather than by environmental cues (Rathcke and Lacey 1985). Probably, woody life-forms and plant physiology are combined in such a way as to allow the ripening of fruit during the dry period in both seasonal and non-seasonal plant communities. Dispersal syndromes have been recognized as important attributes associated with the timing of ripe fruit production. Most trees and lianas produce wind-dispersed fruit during the dry season (Lieberman 1982; Guevara de Lampe et al. 1992; Morellato and Leitão-Filho 1996; Bhat and Murali 2001; Ramirez 2002), whereas fruiting peaks for shrubs during the rainy season are related to the production of animal-dispersed fleshy fruits in seasonal and humid forests (Shukla and Ramakrishnan 1982; Funch et al. 2002; Ramirez 2002). However, wind dispersal was only slightly higher than animal dispersal during both the short-dry and rainy seasons in the shrublands (López and Ramirez 1998). Thus, ripe fruiting patterns during the year are not clearly associated with specific dispersal modes, mainly because woody species, which peak during the dry season, are strongly tied to animal dispersal. Although relationships between fruiting and climatic factors remain unclear (Rathcke and Lacey 1985; van Schaik et al. 1993), peaks of ripe fruit production during the short-dry season are in some way influenced by the precipitation regime. In the bush, general and peak ripe fruiting patterns were positively correlated with precipitation 2 months later, thus showing a delayed response in ripe fruit phenology, this being influenced by the positive correlation between ripe fruit phenology and precipitation 2 months later for climbers. Moreover, the ripe fruit production peak in seasonally dry tropical forests has evolved to precede favourable conditions for the survival of seeds, germination and the development of seedlings (Frankie et al. 1974; van Schaik et al. 1993; Bhat and Murali 2001), which could also be applicable to tropical montane communities such as the bush vegetation in the Venezuelan Guayana Highlands.

The general and peak patterns of ripe fruit phenology during the year were seasonal for the bush and for shrubland, which is associated with ripe fruit production peaks for trees during the same period. There are almost certainly other variables apart from climate and life-form, such as soil properties and plant physiology, which may play an important role in determining the ripe fruit production peak of trees in the dry season. The fruiting peak was higher towards the end of the dry season and at the beginning of the wet season in a palm swamp community, associated with the reduction of soil water availability and the abundance of herbaceous species (Ramirez and Brito 1987). Apparently, the reproductive phenologies of most herbaceous species that grow in habitats such as broad-leaved meadows are influenced by the flooded substrates of these communities. Low water availability in the soil during the short-dry season may stimulate ripe fruit production in the herbaceous species of the broad-leaved meadow, a phenomenon that may be associated with the forthcoming rainy season and subsequent water dispersal of mostly hydrochorous species in the broad-leaved meadow (Ramirez, unpubl. data). In contrast, ripe fruit phenology was non-seasonal for the savanna, which differs from that reported for other tropical savannas (Ramia 1977, 1978; Tannus et al. 2006; Silva et al. 2009) and from the other three communities in the Gran Sabana Plateau (this study). As was mentioned above for the non-seasonal flowering patterns found for the savanna, the non-seasonality of both the general and peak ripe fruit patterns in this community may be related to the dominance of herbaceous species with prolonged ripe fruiting times, sandy loam soils, low local climatic seasonality, and high plant species richness and diversity, as shown by the high number of different life-forms. In addition, seed dispersal syndromes for plant species in the savanna grassland are represented by similar proportions of wind dispersal (40 %) and granivorous animals (40 %) (Ramirez 2000), which may also influence the segregation of the timing of ripe fruit production in the savanna grassland, ensuring a more efficient distribution of dispersal syndromes throughout the year.

Conclusions and forward look
The reproductive phenology of herbaceous–shrubby communities in the Gran Sabana Plateau is characterized by (i) three discrete periods during the year, (ii) independence (in general) of the precipitation regime, (iii) non-seasonal flowering and fruiting phenologies for...
all life-forms and seasonal phenology in the bush and shrubland communities, and (iv) one or two peaks during the year due to the high-intensity reproductive phenologies of the life-forms and at the community level. Further studies in the herbaceous–shrubby communities in the Gran Sabana have to evaluate overlapping in reproductive phenology and the consequences of extended phenological periods in pollination and seed dispersal.

Additional information
The following additional information is available in the online version of this article –

Appendix 1. Life-form, community and phenological patterns (general and peaks of flowering, unripe fruit and ripe fruit monthly production) for 233 plant species from four herbaceous–shrubby communities in the Venezuelan Gran Sabana Plateau.

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Contributions by the authors
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Conflicts of interest statement
None declared.

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