Reproductive phenology of sympatric taxa of *Chamaecrista* (Leguminosae) in Serra do Cipó, Brazil

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(Accepted 9th February 1999)

ABSTRACT. Reproductive phenology of 13 sympatric taxa of *Chamaecrista* in three sections was surveyed at Serra do Cipó, south-east Brazil. Mean abundance of flowers and fruits per plant and mean number of aborted, predated, and surviving seeds per fruit were estimated. Monthly average number of developed seeds per fruit multiplied by the monthly mean number of fruits per plant gave the monthly average number of seeds produced by a plant of each taxon. Five types of phenological behaviour were differentiated by cluster analyses according to the season during which each species produced most of its mature seeds. This behaviour was related to the taxonomic section to which the taxa belong, to plant architecture, to geographical range, to seed predation and to local climatic seasonality. Herbs were more affected by variation in rainfall than shrubs and trees. Two species did not show any clear seasonal behaviour. Widespread taxa produced most of their mature seeds in the rainy season or immediately after it, and all but one of the narrowly distributed species produced most of their mature seeds in the dry season or in the transition from dry to rainy season. Seed predation is probably not an important selective force affecting reproductive phenology of larger taxa, while the smaller taxa seemed too constrained by abiotic factors for biotic factors to influence their phenology significantly.

KEY WORDS: flowering, fruiting, rupestrian field, seasonality, seed abortion, seed predation, sympatric congenerics, tropical savanna

INTRODUCTION

The distribution over time of life-history events, such as growth, leaf flux and fall, flowering, fruiting, and seed dispersal, can greatly affect individual fitness and population or species survival (Augspurger 1981, English-Loeb & Karban...
1992, Eriksson 1995, Grimm 1995, Haddock & Chaplin 1982, Lee & Bazzaz 1982, Mosquin 1971, Opler et al. 1976, Rathcke & Lacey 1985, Schemske et al. 1978, Wheelwright 1985, Zimmerman 1980a, b). Phenological studies generally seek cyclic patterns related to environmental seasonality. In temperate regions, these cycles are linked to large annual variations in temperature and photoperiod, and are readily detectable. However, tropical ecosystems also have seasonal variation, and although usually more subtle than in temperate regions, the variation is large enough to induce cyclic patterns in plants (Frankie et al. 1974, Lieberman 1982, Machado et al. 1997, Medway 1972, Monasterio & Sarmiento 1976, Rathcke & Lacey 1985, Seghieri et al. 1995). The primary difference between temperate and tropical plant phenology is that the main cue for phenological patterns in the tropics is usually precipitation (Opler et al. 1976), although temperature and photoperiodism and biotic factors may also have a role.


Most phenological studies in the tropics have been carried out at the level of community, including large numbers of mostly arboreal species at a time, and have been qualitative (Frankie et al. 1974, Kinnaird 1992, Medway 1972, Morellato et al. 1989, 1990; Morellato & Leitão-Filho 1990, Murali & Sukumar 1994, Shukla & Ramakrishnan 1982, Wheelwright 1985). Few detailed quantitative phenological studies have been carried out in tropical systems (Augspurger 1981, Grimm 1995) and phenology of other growth forms, i.e. shrubs and herbs, is relatively unknown (but see Croat 1975, Koptur et al. 1988, Lieberman 1982, Machado et al. 1997, Monasterio & Sarmiento 1976, Opler et al. 1976, 1980, Seghieri et al. 1995), despite their importance for community diversity and structure.

A small number of phenological studies compared phylogenetically related species, at the family level (Gentry 1974, Proença & Gibbs 1994). However, a detailed study of sympatric congeneric species may provide important insights into the ecology and evolution of phenological traits. Sympatric species are subjected to similar abiotic pressures, and congenerics presumably diverged relatively recently from a common ancestor. Therefore, one can control for
Reproductive phenology of sympatric *Chamaecrista* factors resulting from phylogenetic relatedness and environmental similarities. Probably because of the usually small number of congeneric species co-occurring on a relatively small area, this kind of study has dealt with very few species (Haddock & Chaplin 1982, Pickering 1995, Siemens *et al.* 1992).

Here we present data on the phenology of 13 sympatric taxa of the genus *Chamaecrista* [Breyne] Moench (Leguminosae), all occurring within an area in south-east Brazil. The reproductive phases (flower, fruit and seed production) of all species were studied during 1996. The 13 taxa belong to three sections (Irwin & Barneby 1982), and among them there are eight herbs, two subshrubs, two shrubs and one tree. For the analysis of the phenological patterns identified, we considered the phylogenetic relation between the taxa (sections), the geographical range of each taxon, the plant habit, and the biotic and abiotic pressures.

**STUDY AREA AND TAXA**

The study was conducted in a rupestrian field area of c. 28 km², located in Serra do Cipó, Minas Gerais State, a region of high diversity and endemism of higher plants (Giulietti *et al.* 1987). Serra do Cipó is in the southern portion of Serra do Espinhaço, a quartzitic mountain chain 1100 km long, running north–south, with two distinct parts – Chapada Diamantina in the north and Serra do Espinhaço in the south. The study area varies in altitude, between 900 m to 1250 m above sea level, and is predominantly covered by low-growing vegetation, with few shrubs and small trees, except near watercourses where small riverine forests are found (Giulietti *et al.* 1987). Both parts of Serra do Espinhaço are included in the savanna-like vegetation (‘cerrado’) domain of Central Brazil (Ab’Saber 1977). Hereafter the southern portion will be referred to as ‘Serra do Espinhaço’ and the northern portion as ‘Chapada Diamantina’.

Relevant plant traits of the study taxa are summarised in Table 1. Varieties of *C. desvauxii* have conspicuous differences in the phenology, seed package, seed size, fruit pubescence, microhabitat and/or plant architecture (J.A. Madeira, unpubl. data), hence, we have treated them here as separate entities.

**METHODS**

*Climatic data*

To determine whether our study was conducted in a typical year, we obtained monthly total precipitation and mean maximum and minimum temperatures for the period 1987–1996, from the nearest meteorological station, at Conceição do Mato Dentro, c. 30 km from the study site. With these data we calculated the 10-y averages for each month and each year, and compared them with the 1996 data.

A cluster analysis with this precipitation data indicated four groups of
Table 1. Studied species and relevant information concerning them.

<table>
<thead>
<tr>
<th>Species</th>
<th>Section</th>
<th>Habit</th>
<th>Geogr. range</th>
<th>Situation in the area studied</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chamaecrista cathartica (Mart.) var. paucijuga Irwin &amp; Barneby</td>
<td>A</td>
<td>3</td>
<td>V</td>
<td>Rare. Only one small patch.</td>
</tr>
<tr>
<td>Chamaecrista cipoana (Irwin &amp; Barneby) Irwin &amp; Barneby</td>
<td>A</td>
<td>4</td>
<td>I</td>
<td>Only one big and dense patch.</td>
</tr>
<tr>
<td>Chamaecrista dentata (Vog.) Irwin &amp; Barneby</td>
<td>A</td>
<td>5</td>
<td>III</td>
<td>Found in three patches, relatively close to each other.</td>
</tr>
<tr>
<td>Chamaecrista echinacea (Vog.) var. purpurascens (Benth.) Irwin &amp; Barneby</td>
<td>A</td>
<td>1</td>
<td>II</td>
<td>Patchily distributed along all the studied area.</td>
</tr>
<tr>
<td>Chamaecrista semaphora (Irwin &amp; Barneby) Irwin &amp; Barneby</td>
<td>A</td>
<td>4</td>
<td>II</td>
<td>Found in three patches, distant from each other.</td>
</tr>
<tr>
<td>Chamaecrista choriophylla (Vogel) Irwin &amp; Barneby var. latifolia (Benth.) Irwin &amp; Barneby</td>
<td>C</td>
<td>2</td>
<td>IV</td>
<td>The most abundant along all the studied area.</td>
</tr>
<tr>
<td>Chamaecrista mucronata (Spreng.) Irwin &amp; Barneby</td>
<td>C</td>
<td>1</td>
<td>VII</td>
<td>Found in patches, preferentially in more shaded habitats, near watercourses.</td>
</tr>
<tr>
<td>Chamaecrista venulosa (Benth.) Irwin &amp; Barneby</td>
<td>C</td>
<td>1</td>
<td>IV</td>
<td>Found in patches, preferentially in more shaded habitats, near watercourses.</td>
</tr>
<tr>
<td>Chamaecrista desvauxii (Collad.) Killip var. latifolia Irwin &amp; Barneby</td>
<td>X</td>
<td>1</td>
<td>VI</td>
<td>Relatively isolated individuals found in all the area studied.</td>
</tr>
<tr>
<td>Chamaecrista desvauxii (Collad.) Killip var. malacophylla Irwin &amp; Barneby</td>
<td>X</td>
<td>2</td>
<td>III</td>
<td>Found in patches, some of them very dense and carpet-like, others sparse.</td>
</tr>
<tr>
<td>Chamaecrista desvauxii (Collad.) Killip var. mollissima (Benth.) Irwin &amp; Barneby</td>
<td>X</td>
<td>1</td>
<td>VI</td>
<td>Relatively rare, found in two patches.</td>
</tr>
<tr>
<td>Chamaecrista ramosa (Vog.) var. parvifolia (Irwin) Irwin &amp; Barneby</td>
<td>X</td>
<td>3</td>
<td>V</td>
<td>Easily found at lower altitudes in the area studied, in dense patches.</td>
</tr>
</tbody>
</table>

A, Section *Absus*; C, Section *Chamaecrista*; X, Section *Xerocalyx*; 1, small herb (small isolated rosettes); 2, bushlike herbs; 3, sub-shrub; 4, shrub; 5, tree. I, endemic to Serra do Cipó; II, endemic to Serra do Cipó and vicinity; III, endemic to southern portion of Serra do Espinhaço; IV, endemic to all Serra do Espinhaço; V, widespread in Brazil; VI, widespread in Central and South America; VII, cosmopolitan.
months showing similar mean monthly precipitation. These groups of months were treated as seasons.

Flowering and fruiting phenology

In December 1995 and January 1996, 20 individuals from each taxon were chosen at random and labelled for phenological surveys. Around the 20th day of each month, all the fruits, flowers and flowerbuds on each labelled individual were counted. No destructive sampling was performed on these plants. Only the senescent or opened fruits (with dispersed seeds) were taken, to avoid counting them again in the subsequent survey.

*C. cathartica*, *C. cipoana* and *C. semaphora* were added later to the study, the first in February, and the latter two in May 1996, because they were discovered while the survey was in progress. *C. cathartica* was found later probably because of its local rarity. *C. cipoana* and *C. semaphora* were found only during flowering, and we are confident that these species did not flower between January and May, given the conspicuous nature of their flowers. Hence, the year for the survey of these species was delayed in relation to the others. The same situation occurred with *C. dentata* owing to methodological problems with flower and fruit counts which caused us to prolong the observations on this species until January 1997. To facilitate comparisons with the other taxa studied, we placed all these data in a sequence from January to December, irrespective of the year in which the data were recorded (1996 or 1997).

Some plants were lost through burning, trail-clearing and other accidents, or through natural mortality. These plants were replaced every time the number of plants of a given taxon was less than 15. The rarity of *C. choriophylla* and *C. cathartica* did not allow such replacement, and for these species alone, a sample of about 10 individuals was used.

Seed production

To evaluate seed production, abortion, and predation, fruits were gathered from non-labelled individuals, two or three times per month. All ripe fruits were collected whenever a fruiting plant was found. For each sampling, we sought as many plants as possible and sampled up to 25 plants per taxon. The collection of all fruits per individual was not possible for *C. dentata*, as many fruits were inaccessible because of plant height. Sample size per taxon and per month was variable, since they depended on the proportion of available fruiting individuals.

Multiplying the monthly mean number of fruits per plant by the monthly mean number of completely developed seeds per fruit, we obtained an estimate of the monthly mean number of mature seeds produced per individual plant, representative of the period in which plants of each taxon are dispersing their seeds. To make the results of each taxon easily comparable, the monthly mean number of seeds was divided by the total mean number of seeds produced in
the whole year, to give the percentage of all mature seeds produced during each month by a ‘mean plant’ from each taxon.

Seed production during each season was used to group the taxa by a cluster analysis. As the four seasons were different in terms of the number of months, data were averaged according to the number of months in each season. For this averaging, the number of seeds produced by a given taxon during a given season was divided by the number of months in the season. The sum of the average production of this taxon gave the annual production, this was used to calculate the percentage production during each season.

RESULTS

Climatic data

The climate in 1996 was quite similar to the average climatic data over the last 10 y. Data from August 1996 were lacking, because of technical problems at the meteorological station. Monthly maximum and minimum temperatures showed very small variation between years, indicating the predictability of these variables. Temperature had narrow annual and monthly variation. Precipitation showed much stronger seasonality and a wider range of variation (Figure 1a), with a rainy period around summer and a dry period around winter. Mean annual precipitation for the 10-y period was 1374 mm, and total annual precipitation for 1996 was very similar – 1354 mm, with the data from August lacking, but for which the 10-y mean was 9.7 mm.

The cluster analysis with precipitation data indicated four distinguishable seasons (Figure 1b): a rainy season, from November to January; a ‘post-rain’ transition season, from February to April; a dry season, from May to September; and a ‘post-dry’ transition season, during October only.

Phenological syndromes

Summaries of the phenological data observed for the studied taxa, grouped by taxonomic section are shown in Figures 2 to 4. Among all the three sections there was some variation in phenological behaviour, although section Xerocalyx showed more homogeneity. We encountered a sampling problem with the C. rotundifolia plants chosen to follow the phenological behaviour, because they did not flower in November and December (Figure 3), in spite of many other plants, out of our sample, observed flowering in these months.

Figure 5a shows the distribution of averaged seed production through the four seasons for each taxon. The cluster analysis grouped the taxa into four phenological syndromes according to the period during which most of their mature seeds were produced. There was a fifth group that did not present a clear seed production peak, and was considered ‘aseasonal’ (Figure 5b). As the results are percentages, the absolute numbers of seeds produced by each taxon were not considered, but they were roughly proportional to each taxon’s characteristic plant size, as shown by the maximum mean number of fruits and flowers produced by each taxon during one month (Table 2).
Reproductive phenology of sympatric Chamaecrista

Figure 1. (a) Monthly total rainfall and mean maximum and minimum temperatures – data for the year of the study (1996) and mean values for the 10 y (January 1987 – December 1996), with the range of the monthly total precipitation in the 10y period. □, total monthly rainfall in 1996; ○, average total monthly rainfall in 10 y; —, monthly minimum temperature in 1996; --, average monthly minimum temperature in 10 y; —, monthly maximum temperature in 1996; --, average monthly maximum temperature in 10 y. (b) Dendrogram showing the result of the cluster analysis grouping the months according to their mean rainfall in the 10 y (1987–1996).
Figure 2. Phenological data of the *Chamaecrista* taxa that belong to the section *Absus*. Percentage of plants with flowers (---) and with fruits (-----) in each monthly survey. Bars represent the estimated monthly mean number of developed seeds per plant (percentage, from the mean number of developed seeds per plant in the year, produced in each month).
The first group (C. desvauxii latistipula, C. d. mollissima and C. ramosa) consisted of three taxa that produce most of their mature seeds during the rainy season (November to January). All the taxa in this group belong to section Xerocalyx and were widely distributed. Two taxa were herbaceous and one was a sub-shrub. A second group of three taxa (C. cathartica, C. ochnacea and C. rotundifolia)
produced most of their seeds during the ‘post-rain’ transition season, although *C. cathartica* and *C. ochnacea* also produced some flowers and fruits at other times. *C. ochnacea* was the only one in this group with narrow geographical distribution, and the other two are widely distributed. Two of these three taxa

Figure 4. Phenological data of the *Chamaecrista* taxa that belong to the section *Xerocalyx*. Symbols and explanation as Figure 2.
Reproductive phenology of sympatric Chamaecrista

Figure 5. (a) Mean percentage of completely developed seeds produced by plants of each taxon during each season, averaged by the number of months each season lasted. Rainy season from November to January; post-rain transition came from February to April; dry season from May to September and post-dry transition for October only (see Figure 1). ■ rainy season; ■ post-rain transition; ■ dry season; ■ post-dry transition. (b) Dendrogram showing the result of the cluster analysis grouping Chamaecrista taxa according to the percentage of their completely developed seeds produced during each season (numbers of produced seeds were averaged according to the number of months in each season; see text for details). Cd, Chamaecrista desvauxii latistipula; Cr, C. ramosa; Cdm, C. d. mollissima; Co, C. ochacea; Crm, C. rotundifolia; C, C. cathartica; Cs, C. semaphora; Cc, C. venulosa; Cd, C. devistata; Cm, C. mucronata; Cdm, C. d. malacophylla; Cch, C. choriophylla; Gc, C. cipoana; Cs, C. semaphora.

were herbs and one (C. cathartica) was a sub-shrub. Seeds of C. ochacea were the most heavily predated by insects (Table 2).

The shrub species, C. cipoana and C. semaphora (section Absus), and the herb C. choriophylla (section Chamaecrista) had their flowering peak at the beginning of the dry season, and the fruiting peak was at the end of the dry season, when
Table 2. Mean number of ovules per fruit of each *Chamaecrista* taxon and their fate, maximal mean number of flowers and fruits observed per individual plant of each taxon, with the month when these maximal means were observed between brackets, and the total number of individuals where mature fruits were collected throughout the year.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Total number of ovules</th>
<th>Unfertilised ovules or aborted seeds</th>
<th>Developed seeds</th>
<th>Predated seeds</th>
<th>Surviving seeds</th>
<th>Maximal mean number of flowers per individual plant (month)</th>
<th>Maximal mean number of fruits per individual plant (month)</th>
<th>Number of individuals from which fruits were collected</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Section Abus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. cathartica</em></td>
<td>4.765</td>
<td>1.062</td>
<td>3.680</td>
<td>0.0</td>
<td>2.062</td>
<td>20.89 (Feb)</td>
<td>18.50 (Oct)</td>
<td>23</td>
</tr>
<tr>
<td><em>C. cipoana</em></td>
<td>3.996</td>
<td>1.787</td>
<td>2.210</td>
<td>0.267</td>
<td>1.943</td>
<td>165.60 (Apr)</td>
<td>36.05 (Aug)</td>
<td>110</td>
</tr>
<tr>
<td><em>C. dentata</em></td>
<td>4.6</td>
<td>1.171</td>
<td>3.478</td>
<td>0.648</td>
<td>2.721</td>
<td>146.35 (Apr)</td>
<td>32.10 (Jul)</td>
<td>193</td>
</tr>
<tr>
<td><em>C. ochnacea</em></td>
<td>5.866</td>
<td>3.502</td>
<td>2.364</td>
<td>1.009</td>
<td>1.355</td>
<td>30.55 (Jan)</td>
<td>17.00 (Feb)</td>
<td>213</td>
</tr>
<tr>
<td><em>C. semaphora</em></td>
<td>4.530</td>
<td>2.787</td>
<td>1.744</td>
<td>0.074</td>
<td>1.668</td>
<td>332.80 (May)</td>
<td>138.15 (Jul)</td>
<td>92</td>
</tr>
<tr>
<td><strong>Section Chamaecrista</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. choriophylla</em></td>
<td>12.528</td>
<td>7.465</td>
<td>5.063</td>
<td>0.0</td>
<td>5.063</td>
<td>17.95 (Jun)</td>
<td>2.77 (Aug)</td>
<td>6</td>
</tr>
<tr>
<td><em>C. mucronata</em></td>
<td>6.318</td>
<td>4.974</td>
<td>1.344</td>
<td>0.078</td>
<td>1.266</td>
<td>35.00 (Jul)</td>
<td>41.30 (Sep)</td>
<td>127</td>
</tr>
<tr>
<td><em>C. rotundifolia</em></td>
<td>12.099</td>
<td>2.241</td>
<td>9.858</td>
<td>0.213</td>
<td>9.643</td>
<td>10.05 (Feb)</td>
<td>16.15 (Feb)</td>
<td>112</td>
</tr>
<tr>
<td><em>C. senuhua</em></td>
<td>8.541</td>
<td>3.084</td>
<td>5.489</td>
<td>0.943</td>
<td>4.547</td>
<td>12.18 (Jun)</td>
<td>9.15 (Jul)</td>
<td>140</td>
</tr>
<tr>
<td><strong>Section Xerocalyx</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C.d. latistipula</em></td>
<td>19.479</td>
<td>13.729</td>
<td>5.773</td>
<td>0.168</td>
<td>5.493</td>
<td>11.55 (Nov)</td>
<td>4.22 (Jan)</td>
<td>77</td>
</tr>
<tr>
<td><em>C.d. malacophylla</em></td>
<td>13.027</td>
<td>8.306</td>
<td>4.721</td>
<td>0.0</td>
<td>4.721</td>
<td>91.88 (Jul)</td>
<td>69.33 (Oct)</td>
<td>133</td>
</tr>
<tr>
<td><em>C.d. mollissima</em></td>
<td>18.077</td>
<td>9.214</td>
<td>8.864</td>
<td>0.772</td>
<td>8.091</td>
<td>31.95 (Dec)</td>
<td>23.65 (Jan)</td>
<td>38</td>
</tr>
<tr>
<td><em>C. ramosa</em></td>
<td>15.692</td>
<td>7.741</td>
<td>7.951</td>
<td>1.111</td>
<td>6.839</td>
<td>28.06 (Jan)</td>
<td>32.88 (Jan)</td>
<td>108</td>
</tr>
</tbody>
</table>
most of their mature seeds were produced. The sample size for *C. choriophylla* were considerably reduced by burning in July, eliminating most of the individuals of the larger population used in the study. As this population contained the larger individuals, the results were probably affected. The absence of seed predation in this species may be a result of this rarity or because of a small sample size (Table 2).

*Chamaecrista mucronata* (section *Chamaecrista*) and *C. desvauxii malacophylla* (section *Xerocalyx*), both herbs, showed flowering peaks from the middle to the end of the dry season, and produced most of their mature seeds at the transition from the dry to the rainy season. Nevertheless, they also produced a few flowers at other times, apparently responding to occasional rains. These flowers, however, did not develop into fruits, or resulted in fruits with 100% seed abortion. The seed abortion rates of *C. mucronata* were the highest among all the studied taxa (Table 2).

The two remaining species, *C. dentata* (tree, section *Absus*), and *C. venulosa* (herb, section *Chamaecrista*), did not present clear peaks of flowering, fruiting, and seed production, and are therefore grouped more by the lack of patterns than the similarity in their phenological behaviour. *C. dentata* produced flowers, fruits and seeds throughout the whole year. *C. venulosa* was the only herbaceous species without distinct seasonal behaviour. As the sampling effort was roughly the same for all the taxa, the number of individuals with fruits collected (Table 2) gives an idea of the relative abundance of each taxon in the area.

**DISCUSSION**

The climatological pattern found in Serra do Cipo was typical of the ‘cerrado’ region, which usually has rainy summers and dry winters (Freitas & Silveira 1977). This seasonal variation acts as a strong selective force shaping the phenological behaviour of species or populations submitted to these climatic conditions (Monasterio & Sarmiento 1976, Opler et al. 1976).

Within this group of 13 closely related *Chamaecrista* taxa, we found a wide variety of phenological behaviours in a relatively small, climatically uniform region. One of the main factors constraining the phenological behaviour of a plant species is its habit. Seghieri et al. (1995) found that herbs in a savanna in Cameroon are usually more affected by seasonal climatic variation, because they are less able to accumulate water and nutrient reserves. Within the eight herbaceous *Chamaecrista* taxa, four produced most of their mature seeds during the rainy season, or immediately after it, two produced seeds in the transition from the dry to rainy season, one produced seeds at the end of the dry season and one was aseasonal. The three herbaceous taxa that flowered during the dry season were small bushlike plants, probably with larger biomass than the other herbs, which should provide them with higher water storage capacity. *C. venulosa* was probably less affected by drought because of its habitat preferences, mainly near watercourses and more shaded places, but it was unable to produce mature seeds during the most unfavourable months (Figure 3).
The two sub-shrub species, in spite of their apparently slightly larger biomass, appeared to be very constrained by climatic seasonality, and both produced all their mature seeds during the rainy season or immediately after it. *C. cathartica* produced flowers and fruits throughout the year, but this reproductive effort did not result in mature seed production during drier periods. The species that seemed to be unaffected by drought were the shrubs, which flowered and fruited in precisely the dry season, and the arboreal species, which flowered and fruited throughout the year. However, the arboreal species did show a reduction in flower and fruit production during the drier months, but without a reduction in mature seed production, except in June (Figure 2). *C. choriophylla* was the only herbaceous exception, fruiting in the dry season, but a clear conclusion cannot be drawn, owing to small sample size. In general, plant biomass does not seem to correlate with the capacity to produce seeds out of the wetter months, but is a constraint for the smallest plants (in terms of biomass) to do so.

Phylogenetic trends may also constrain phenological behaviour. Species from section *Absus* seem to be the less affected by drought, but this capacity probably reflects the larger biomass of three out of five species of this section, which may be itself the result of a phylogenetic trend. At the opposite extreme, the taxa from section *Xerocalyx* tended to be the most affected by drought. All three taxa of the group that produced mature seeds during the wettest months were from section *Xerocalyx*. But these taxa were also among those with smallest biomass. Section *Chamaecrista* was the most variable in phenological syndromes, with only one species in each of the other four groups. The presence of different phenological behaviours within each section suggests that these syndromes probably evolved independently within each section. Hence, phenology may be a relatively plastic or rapidly evolving feature, or selection may be very strong, or both.

Geographical range seemed to be the factor which correlated most with the phenological patterns found. Among the six taxa that produced most of their seeds during the rainy season or immediately after it, only one (*C. ochnacea*) is not a widespread species (Table 1). All the five taxa that produced most of their seeds during the transition from the dry to the rainy season or during the dry season are at least restricted to Serra do Espinhaço and Chapada Diamantina (*C. mucronata*) or more restricted (the other four) (Table 1). Among the aseasonal species, the tree *C. dentata* is restricted to Serra do Espinhaço, and was a particular case since it is the only arboreal species. The herb *C. venulosa* is also a special case, because it is associated with watercourses. In any case, none of them is widespread. Thus, more narrowly distributed taxa are characterised by earlier seed production, during the dry season or immediately after it. These taxa may represent a closer synchronisation with the climatic characteristics of their habitat, as they probably maximise survival of their seeds by dispersing them before or just at the beginning of the rainy season, with the
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prospect of three very wet and three moderately wet months for germination and establishment. The taxa that begin to flower in the rainy season, on the other hand, had their seed production peak around January, with fewer favourable months ahead. Again, phylogenetic factors may be in force, as the majority of the species from section Absus are narrowly distributed, and the majority of the taxa of section Xerocalyx are widespread.

The role of insect pollinators of these plants (mainly bees) would be interesting and could explain part of the picture described. Seed predation did not seem to influence decisively the phenological behaviour of the studied taxa, although some species are significantly attacked by bruchids (J.A. Madeira & G.W. Fernandes, unpubl. data). Taxa with larger biomass could have their phenology significantly affected by biotic factors, as those of smaller biomass are too constrained by abiotic factors for biotic factors to influence their phenological behaviour significantly.

The variety of phenological behaviour within a single genus contradicts the hypothesis of Ollerton & Lack (1992), that the flowering phenological behaviour would be selectively neutral due to phylogenetic constraints. Greater knowledge of the phylogenetic relations between the taxa studied here would be helpful for the interpretation of our results, and studies in this direction are now being undertaken.

ACKNOWLEDGEMENTS

Our special thanks to K.T. Ribeiro, D.A. Yanega, F.A. Silveira, P.S. Oliveira, G. Houle, R. Corlett and A. Ippolito for their critical revision of earlier manuscripts and their valuable suggestions, and to R. Barneby for all the plant identifications and a large amount of important information on the biology and geographical distribution of Chamaecrista. We also thank the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis – IBAMA, for permission to work and collect at the Parque Nacional da Serra do Cipó, and for staying overnight at the park house during some of the field excursions. This study was supported by the U.S. Fish & Wildlife Service, CNPq (521772/95–8, 133366/95–2), and FAPEMIG (1950/95). This study was in partial fulfilment of requirements for J. A. Madeira’s MSc. Thesis in Ecology, Conservation and Wildlife Management at the Universidade Federal de Minas Gerais.

LITERATURE CITED


