Phenological Variation Within and Among Populations of *Plathymenia reticulata* in Brazilian Cerrado, the Atlantic Forest and Transitional Sites

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● *Background and Aims Plathymenia reticulata* (Leguminosae) is a Brazilian tree that occurs in two biomes: Cerrado, a woody savanna vegetation, and the Atlantic Forest, a tropical forest. In this study, phenological patterns and their variability within and among populations located in these biomes and in transitional zones between them were assessed.
● *Methods* During a 15-month period, individuals from two populations in Cerrado, two in the Atlantic Forest, and six in transitional zones (three in a cerrado-like environment and three in forest fragments) were evaluated in Minas Gerais State, Brazil. The individuals were evaluated monthly according to the proportion of the canopy in each vegetative phenophase (leaf fall, leaf flush and mature leaves) and each reproductive phenophase (floral buds, flowers, immature fruits and mature fruit/seed dispersal). In order to assess the phenological variability within and among populations, habitats and biomes, the Shannon–Wiener diversity index, the Morisita–Horn similarity index and genetic population approach of partitioning diversity were used.
● *Key Results* Populations of *P. reticulata*, in general, showed similar phenology; the main differences were related to leaf fall, a process that starts months earlier in the Cerrado than in transitional sites, and even later in forest areas. Considerable synchrony was observed for reproductive phenology among populations and between biomes. Most phenological diversity was due to differences among individuals within populations.
● *Conclusion* In spite of environmental differences, *P. reticulata* from the Atlantic Forest and Cerrado showed similar phenological behavior with only about 10 % of the total diversity being attributed to differences between biomes.

Key words: Atlantic Forest, Cerrado, Morisita–Horn similarity index, leaf phenology, *Plathymenia foliolosa*, *Plathymenia reticulata*, reproductive phenology, Shannon–Wiener diversity index.

INTRODUCTION

Flowering and fruiting phenology may have an important influence on reproductive success, as it determines reproductive synchrony among potential mates (Marquis, 1988) and may influence the attraction of pollinators and seed dispersers (Augspurger, 1981). Additionally, the phenology of vegetative stages is important as cycles of leaf flush and leaf fall are intimately related to processes such as growth, plant water status and gas exchange (Reich, 1995).

Augspurger (1983) noted that the understanding of tropical phenology was best developed at the community level and this view has not changed in the intervening years. Many studies have evaluated a single species' phenology, but, in general, they have not examined differences among or within populations (but see Marquis, 1988; Seghieri and Simier, 2002). Few studies have made comparisons among populations located at sites characterized by marked environmental differences (e.g. Frankie *et al.*, 1974; Borchert, 1980). This approach is valuable as it may help to understand the extent of phenological variability as a survival strategy in different environments and how abiotic factors influence phenological patterns.

The genus *Plathymenia* (Leguminosae, Mimosoideae) is a good model to study in relation to this perspective as it is adapted to biomes with environmental differences, namely the Brazilian Cerrado, a woody savanna vegetation, and the Brazilian Atlantic Forest, a tropical forest. These habitat differences were considered in distinguishing two *Plathymenia* species, with *P. foliolosa* growing in forest areas and *P. reticulata* in Cerrado (Heringer, 1956). However, in a recent revision of this genus, Warwick and Lewis (2003) proposed it to be monospecific, containing only *P. reticulata*. This tree is known as 'vinhático' and occurs in at least 15 Brazilian states. It has been classified by the Brazilian Agricultural Research Corporation (EMBRAPA) as one of the most important and useful plant species from the Cerrado (Almeida *et al.*, 1998) due to its high quality wood and potential use for the recovery of degraded areas (Heringer and Ferreira, 1972).

As noted by Adler and Kielpinski (2000), the first step in studying phenology is to identify spatial and temporal patterns, as such information is important in laying the foundation for identifying factors that underline those patterns. The main objective of this work was to describe the phenology of *P. reticulata*, evaluating populations from Cerrado, Atlantic Forest and transitional sites. Some studies on the phenology of Cerrado flora (e.g. Oliveira, 1998; Batalha and Mantovani, 2000; Bulhão and Figueiredo, 2002) and

the Atlantic Forest flora (e.g. Morellato *et al.*, 2000; Fisher and Santos, 2001) are available in the literature but, to our knowledge, this is the first comparison of phenological patterns among populations of a species that occurs in both biomes.

In a study evaluating populations of *Plathymenia* from Cerrado and Atlantic Forest, Lacerda *et al.* (2002) showed that 60 % of molecular variation was due to differences among plants from the different biomes. Furthermore, evaluating Cerrado populations of this species, Lacerda *et al.* (2001) reported that most of the genetic variation in this biome was attributable to differences among plants within populations. Considering that abiotic factors affect phenological patterns (Reich, 1995) and also that genetic components can influence these patterns (Murfet, 1977), we predicted that most of the phenological differences in *Plathymenia* would be found between biomes, and that within a biome most of the differences would be between individuals within populations. To assess phenological variability and its distribution within and among populations, habitats and biomes, an approach based on the Morisita–Horn similarity index, the Shannon–Wiener diversity index and genetic population methodology of partitioning diversity was applied.

MATERIAL AND METHODS

Study biomes

The phenology of natural populations of *P. reticulata* occurring in areas of the Atlantic Forest and Cerrado was evaluated. These Brazilian biomes are both considered priority 'hot spots' for conservation due to the high levels of biodiversity and endemic species, and the fact that they are among the most endangered eco-regions on Earth (Myers *et al.*, 2000).

The Brazilian Atlantic Forest once covered more than 1 million km^2, but human activities have reduced it to about 5 % of the biome's original cover (Mittermeier *et al.*, 1999). Different vegetation types of the Atlantic Forest are recognized; in Minas Gerais State semi-deciduous inland forest is the most common type and characterizes the forest sites studied here. Brazilian Cerrado covered almost 2 million km^2, but today it is reduced to only 20 % of the original area (Fonseca *et al.*, 1999). Several Cerrado vegetation types are recognized, and populations of *P. reticulata* are found particularly in the strict woodland/savanna and grassland formations (Lacerda *et al.*, 2001) where the study took place.

The climate in both Cerrado and semi-deciduous Atlantic Forest is characterized by rainfall concentrated from November to March, making monthly variation in precipitation greater than the variation in temperature. The two biomes differ in the length and severity of the dry season. In the studied regions in Minas Gerais, semi-deciduous forest has a mean annual precipitation of about 1480 mm (Stallings *et al.*, 1991), while Cerrado sites have 1200 mm of rain (data from the 5th Brazilian Meteorological District, Belo Horizonte). Data for temperature and rainfall for the regions for 2003 are shown in Fig. 1.
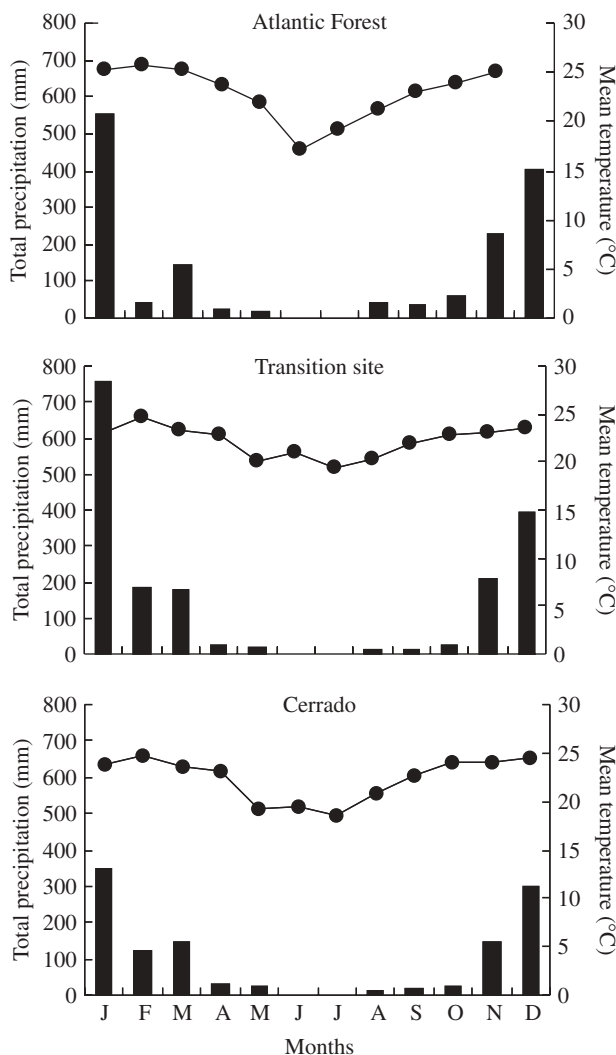

FIG. 1. Meteorological data for the studied regions in Minas Gerais State during 2003 (precipitation = bars, temperature = lines): Atlantic Forest (data from meteorological stations located in Dionísio and João Monlevade), transition site between biomes (Belo Horizonte) and Cerrado (Pompéu and Sete Lagoas).

Study sites

The study was performed following a three-level perspective: populations, habitats and biomes. Ten populations of *P. reticulata* were evaluated from Minas Gerais State, located in two different biomes (Atlantic Forest and Cerrado) and four different habitat types as follows. (1) Atlantic Forest core area: two populations located in the Rio Doce valley, Parque Estadual do Rio Doce (RD, 19°48′S 42°36′W) and Bom Jesus do Amparo (BJ, 19°45′S 43°31′W), where *Plathymenia* trees reach 20 m in height and until recently were classified as *P. foliolosa*. (2) Cerrado core area: two populations located in the central State area, Felixlândia (FE, 18°43′S 45°03′W) and Paraopeba (PA, 19°18′S 44°30′W), where *P. reticulata* trees are shorter and twisted. (3) Atlantic Forest in a transition site with Cerrado: three populations, Belo Horizonte (BH1, 19°56′S
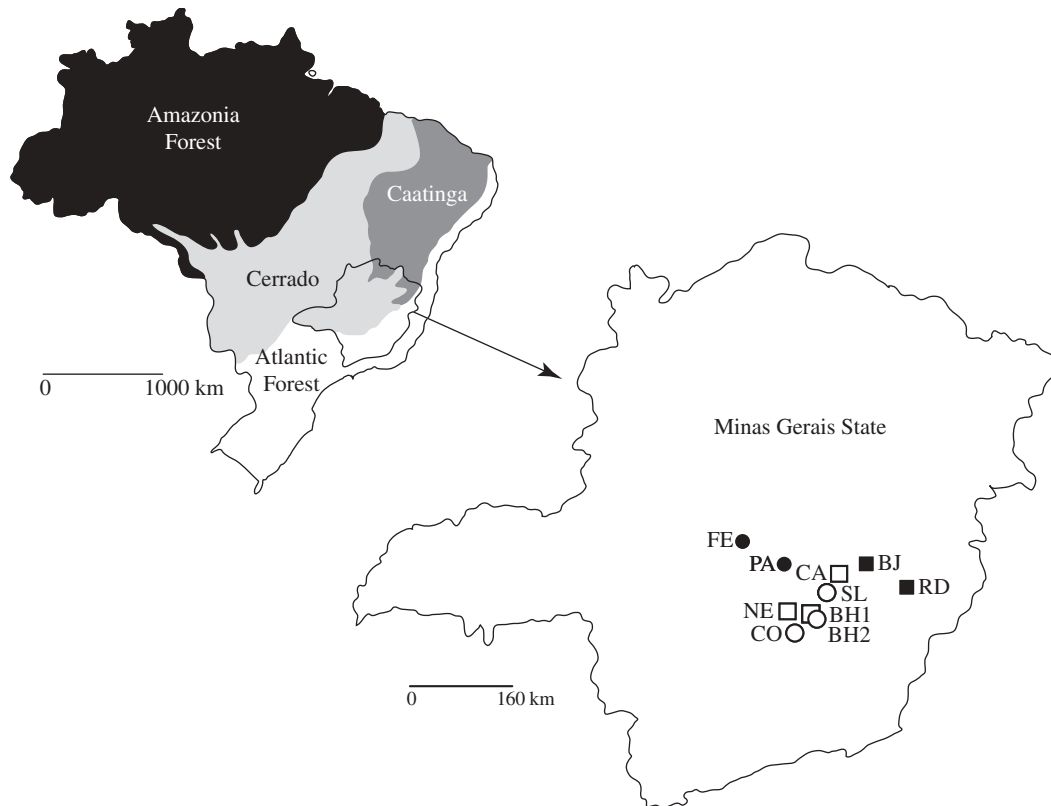
FIG. 2. Brazil's main biomes, with detail of Minas Gerais State and approximate locations of the *P. reticulata* populations studied: Atlantic Forest core area (black squares), Cerrado core area (black circles), in transition sites between biomes with forest characteristics (white squares), and transitional sites with Cerrado characteristics (white circles).

46°56′W), Ribeirão das Neves (NE, 19°48′S 44°06′W) and Caeté (CA, 19°46′S 43°39′W), all showing forest characteristics with denser vegetation, higher trees and *P. reticulata* individuals being morphologically similar to forest individuals. (4) Cerrado in a transition site with Atlantic Forest: three populations, Belo Horizonte (BH2, 19°56′S 46°56′W), Santa Luzia (SL, 19°49′S 43°48′W) and Contagem (CO, 19°54′S 44°03′W), with *P. reticulata* trees showing Cerrado characteristics. Henceforth the habitats are identified by the letters F (forest), FT (forest in transition), C (Cerrado) and CT (Cerrado in transition) following the population name. Locations and other population characteristics are shown in Fig. 2.

Phenological data sampling

Eleven to 20 individuals of *P. reticulata* in each population were sampled, totaling 182. Trees were chosen randomly, but in forest sites only trees with visible crowns were included. The distance among individuals within a population varied from 10 m to 1 km.

Trees were marked and observations were made monthly from October (BJ-F, CA-FT, NE-FT, BH1-FT, BH2-CT, SL-CT and CO-CT) or November 2002 (RD-F, PA-C and FE-C) through to December 2003. A single person made all observations of individual tree crowns using binoculars to evaluate the vegetative phenological phases (leaf fall, leaf flush and mature leaf) and reproductive phases

(floral buds, open flowers, immature and mature fruit/seed dispersal; as the difference between closed mature pods and mature pods releasing seeds is very hard to determine under field conditions, both forms were considered as the same phase). Characteristics were graded relatively as follows: 0 = absence of the characteristic; 1 = presence of the characteristic in 1–25 % of the crown; 2 = 26–50 %; 3 = 51–75 %; and 4 = 76–100 %. For each group of phenological phases, individuals were characterized by the combination of assessed grades. For example: a tree evaluated as 1-2-1 for vegetative phenology would show grade 1 for leaf fall, grade 2 for leaf flush and grade 1 for mature leaf (the grades totalling 4, or 100 % of the crown). Note that these grades always follow the order specified in this example. For the reproductive phases, the combination 1-2-1-0 would mean that this individual was grade 1 for floral buds, grade 2 for open flowers, grade 1 for immature fruits and grade 0 for mature fruit/seed dispersal (again totaling 4, or 100 % of the crown). The grades henceforth always follow the order specified here. For both reproductive and vegetative phenology, each grade combination represented a specific phenological state.

Analysis of data

In order to describe monthly variability in phenology, for each individual a grade combination was attributed and three different analyses were performed separately for the

vegetative and reproductive phases. For reproductive data, only individuals that flowered at least once during the observation period were considered. A diversity index was used to estimate synchrony among and within populations, habitats and biomes. Higher values for this index indicate higher phenological diversity, meaning lower phenological synchrony. This index was also used to estimate the partitioning of diversity; for example, which percentage of the total phenological diversity that was due to differences in behaviour among individuals within populations and among different populations. Finally, a similarity index was used to estimate synchrony among populations, with higher values indicating higher phenological synchrony. Details about each of the analyses are given below.

Diversity of phenological behaviour was estimated using the Shannon–Wiener diversity index. This index is widely used among community ecologists and is commonly adapted to other scientific areas (e.g. population genetics; Lacerda *et al.*, 2001). According to Magurran (1988), the index is:

$$H' = -\sum p_i \ln(p_i)$$

Frequencies of different phenological states (given by the grade combination) were used instead of frequencies of different species in a community. Accordingly, p_i was considered as the proportion of individuals found in the *i*th combined grade, with $p_i = n_i/N$; n_i being the number of individuals showing the phenological status i, and N the total number of individuals in the population. Populations with greater numbers of phenological states show higher values of this index, and less phenological synchrony.

Four different calculations were performed for each month. (1) Diversity index for each one of the ten populations, in which a mean value was attributed to the level of phenological diversity within populations (H_{pop}). (2) Mean values for each one of the four habitats (H_{hab}) without considering the population effect. (3) Mean values for the two biomes (H_{bio}), without considering population or habitat effect. (4) Total diversity using data from all evaluated individuals (H_{total}). Using these indexes, partitioning of total diversity was determined. In a way similar to Lacerda *et al.* (2001), (H_{pop}/H_{total}) × 100 was considered to be the percentage of diversity attributable to differences in phenology among individuals within populations, and $[(H_{total} - H_{pop})/H_{total}] \times 100$ the diversity attributable to differences among populations. (H_{hab}/H_{total}) × 100 was considered the percentage of diversity attributable to differences among individuals within habitats, and $[(H_{total} - H_{hab})/H_{total}] \times 100$ the diversity attributable to differences among habitats. Finally, (H_{bio}/H_{total}) × 100 was considered the percentage of diversity attributable to differences within biomes, and $[(H_{total} - H_{biol})/H_{total}] \times 100$ the diversity attributable to differences between biomes.

Besides diversity, similarity among populations also was evaluated monthly by the Morisita–Horn similarity index (Magurran, 1988):

$$MH = \frac{2\sum(n_{Ai}n_{Bi})}{(da + db)N_A N_B}$$

where $da = (\sum n_{Ai}^2)/N_A^2$, $db = (\sum n_{Bi}^2)/N_B^2$, N_A is the total number of individuals in population A, N_B the total number of individuals in population B, n_{Ai} is the number of individuals in the *i*th combined grade in A, and n_{Bi} is the number of individuals in the *i*th combined grade in B. Mean similarity indexes were used in cluster analysis (UPGMA; Ludwig and Reynolds, 1988) to group populations, both for vegetative and reproductive data.

RESULTS

General phenological pattern

Individuals of *P. reticulata* showed marked drought-deciduousness (Fig. 3). In Atlantic Forest, leaf fall was minor in the months before June and became pronounced after that. In Cerrado, some level of leaf fall occurred in all months of the year, but was most pronounced in the dry season. In all ten populations, leaf fall peaked in August, when the majority of observed individuals were completely deciduous. In September leaf flush began and two months later the individuals showed mature leaves throughout the tree crown.

Of the 182 evaluated individuals, 146 showed a reproductive event. In all populations most trees reproduced at least once (70–100 % of the individuals observed), except in RD-F where only six out of 20 did so. Flowering occurred in the beginning of the wet season (Fig. 3). Light-green floral buds started to develop in September in some individuals in Cerrado, and in October in most populations. After inflorescence development, flowering peaked in November in all populations and soon small, dark-green fruits were observed. Fruit development took several months and the appearance of big, brown fruits started to be observed in June. Mature pods split in two parts and released winged seeds. Seed dispersal peaked in August, but its duration was not easily determined as many empty pods remained on trees. In November, wherever possible, some remaining pods were collected and evaluated. They either had no seed or seeds that were damaged by fungi and insects. Therefore, October was considered the possible end of the seed dispersal period.

Variability in phenological pattern

Populations exhibited different levels of diversity in vegetative phenology (Table 1), with means for monthly diversity ranging from 0·61 to 0·98. BJ-F showed the lowest value of diversity, meaning it was the most synchronous population, while BH1-FT was the least synchronous. Mean values for habitats demonstrated that Cerrado and the two transitional habitats showed similar and higher diversity levels when compared to the Atlantic Forest core sites. Similar levels of total diversity were found in the two biomes.

Relative to vegetative phenology, lower levels of diversity for reproductive phases were found, indicating greater synchrony (Table 1). Monthly mean population diversity ranged from 0·41 to 0·56. BJ-F, the population with the lowest level of diversity for vegetative phenology,

had the highest diversity for reproductive phenology. Again, similar levels were found when comparing biomes.

For both vegetative and reproductive phenology, mean values of diversity increased succesively from populations, to habitats and to biomes, indicating a structured diversity (Table 1).

The partitioning of phenological diversity, both for vegetative and reproductive phases, showed that more variation
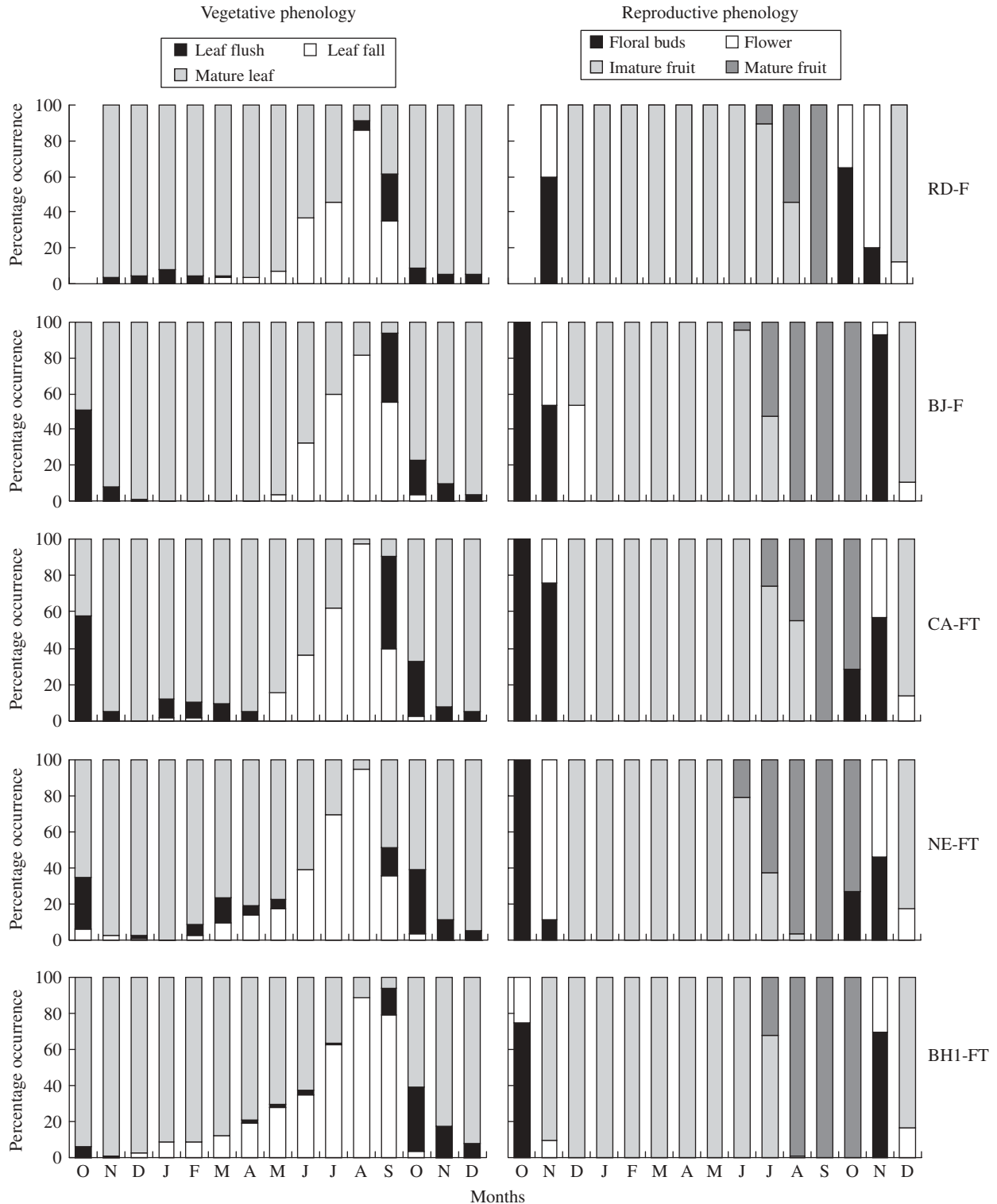

Fig. 3. Monthly mean percentages of vegetative and reproductive phenologies found in individuals of *P. reticulata* from ten populations. Note that for reproductive data, in each month, only individuals that showed reproductive characteristics were considered.
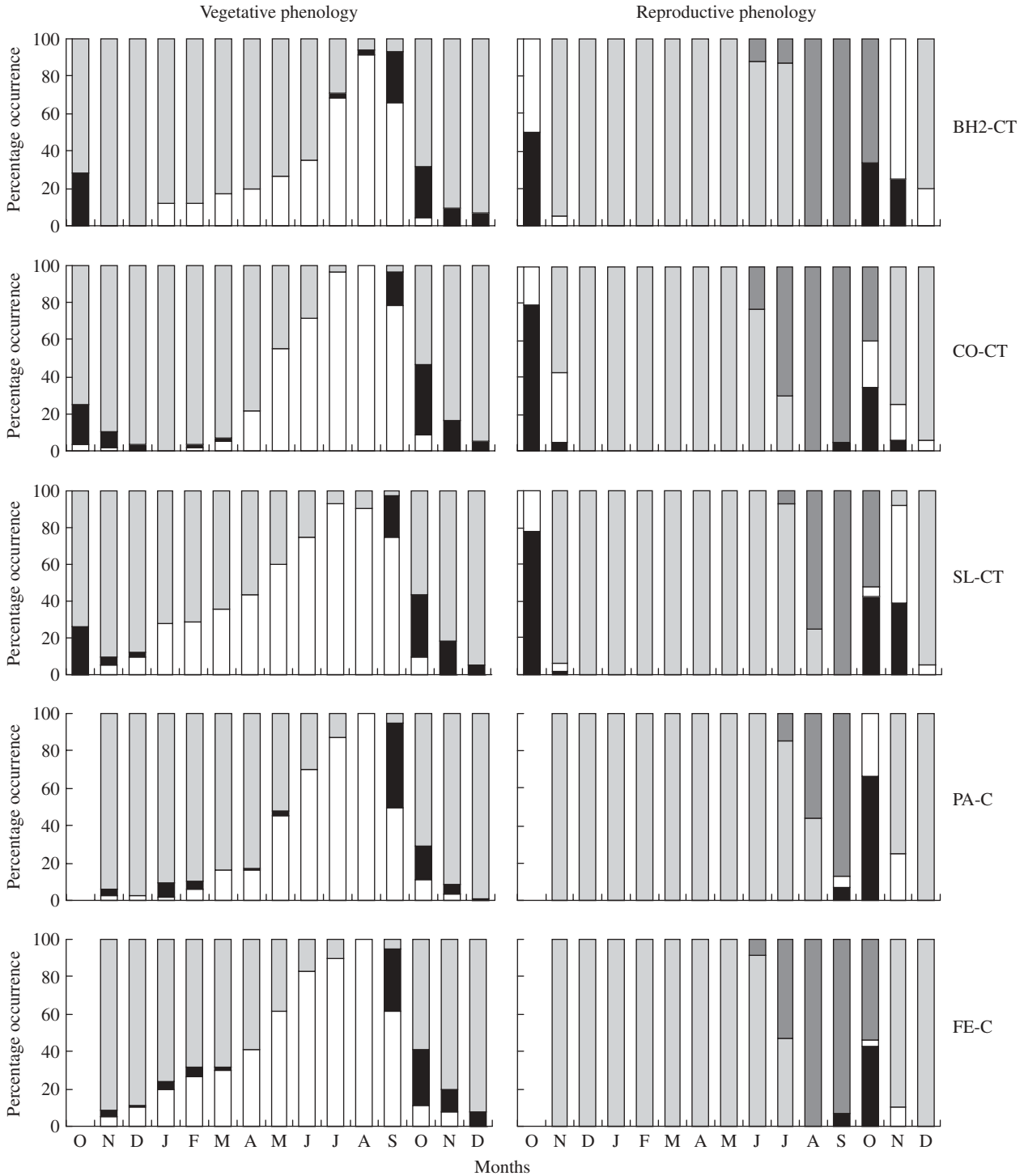
FIG. 3. Continued.

was due to differences in phenological behaviour among individuals in the same population than among populations (Table 2). A similar pattern was found when individuals within habitats (without considering population effects) and individuals within biomes (without considering population and habitat effects) were considered. Considerable variation in percentages of diversity within and bewteen populations,

habitats and biomes was observed during the study. Diversity within populations, for example, ranged from 55·5 to 94·4 % for vegetative phenology and from 47·1 to 69·7 % for reproductive phenology (Table 2). Approximately 90 % of the total variation in phenology found in *P. reticulata*, for both vegetative and reproductive data, was due to differences in behaviour of individuals located in the same biome,

TABLE 1. *Shannon–Wiener diversity index means (±s.d.) for vegetative and reproductive phenology of P. reticulata individuals within populations, habitats and biomes, for data collected from October 2002 to December 2003*

	Vegetative	Reproductive
Population		
RD-F	0·80 ± 0·44	0·50 ± 0·57
BJ-F	0·61 ± 0·53	0·56 ± 0·58
CA-FT	0·81 ± 0·45	0·50 ± 0·57
NE-FT	0·82 ± 0·44	0·48 ± 0·44
BH1-FT	0·98 ± 0·47	0·49 ± 0·51
BH2-CT	0·75 ± 0·43	0·41 ± 0·47
CO-CT	0·79 ± 0·47	0·50 ± 0·61
SL-CT	0·91 ± 0·25	0·52 ± 0·57
PA-C	0·78 ± 0·45	0·47 ± 0·56
FE-C	0·90 ± 0·37	0·47 ± 0·55
H_{pop}	0·82 ± 0·10	0·49 ± 0·04
Habitat		
Forest core	0·80 ± 0·50	0·70 ± 0·60
Forest trans.	1·06 ± 0·48	0·69 ± 0·62
Cerrado core	1·03 ± 0·31	0·69 ± 0·68
Cerrado trans.	1·02 ± 0·44	0·60 ± 0·65
H_{hab}	0·98 ± 0·12	0·67 ± 0·05
Biome		
Atlantic Forest	1·03 ± 0·48	0·76 ± 0·64
Cerrado	1·11 ± 0·37	0·74 ± 0·71
H_{bio}	1·08 ± 0·05	0·75 ± 0·01

TABLE 2. *Partitioning of phenological diversity (Shannon–Wiener index) in populations of P. reticulata. Data are percentages attributable to differences within and among populations, within and among habitats and within and between biomes. Values refer to 15-month means (October 2002 to December 2003)*

	Vegetative	Reproductive
Within populations	69·7 ± 10·3	58·9 ± 7·8
Among populations	30·3 ± 10·3	41·1 ± 7·8
Within habitats	83·0 ± 6·6	82·3 ± 7·3
Among habitats	17·0 ± 6·6	17·7 ± 7·3
Within biomes	91·0 ± 5·8	90·1 ± 7·4
Between biomes	9·0 ± 5·2	9·9 ± 7·4

while the remaining 10 % variation was attributable to the differences among plants from Cerrado and Atlantic Forest (Table 2).

Indices for both similarity among populations and diversity within populations showed great monthly variation (Fig. 4). Vegetative phenology for April to July, the dry season, was marked by high diversity within populations and low similarity between them, indicating a low synchrony among trees both within and among populations. This result is due to the fact that some individuals start leaf fall earlier than others (Fig. 3). However, in August, the peak dry season, most trees had lost all leaves (Fig. 3), and therefore low diversity within populations and high similarity among them were observed. In the transition to the rainy season (September and October), the highest levels of diversity within populations were observed, as all vegetative phases occurred at the same time at the population level.

Higher similarity among populations and lower diversity within populations occurred in November and December.

For reproductive phenology, populations had relatively high diversity during the flowering period (October and November) and intermediate levels of similarity among them. In months when only immature fruit were present, individuals showed no diversity within populations, and hence similarity reached its maximum. This pattern changed when seed dispersal began (June and July) and was characterized by higher diversity and lower similarity. Similar to vegetative phenology, low diversity and high similarity were observed in August when seed dispersal characterized most individuals (Fig. 4).

Similarities among populations differed within habitats both for vegetative phenology (Atlantic Forest = 0·89, forest in transitional sites = 0·82, Cerrado = 0·66, Cerrado in transitional sites = 0·66) and reproductive phenology (0·72, 0·79, 0·81 and 0·82, respectively). The vegetative phenologies of populations in Atlantic Forest were more similar to each other (0·84) than for populations in Cerrado (0·77), while the opposite was observed for reproductive phenology (0·77 and 0·83, respectively). The clusters generated by the similarity indices demonstrated that the observed patterns for vegetative and reproductive phenology were equivalent. Populations in core areas of Atlantic Forest and Cerrado were less similar, while populations in transitional sites showed a more intermediate position (Fig. 5).

DISCUSSION

General phenological pattern

Some phenological aspects of *P. reticulata* reported here have also been described by other authors who have evaluated this species at different locations. Funch *et al.* (2002) classified *Plathymenia* individuals as showing episodic production and loss of leaves in a gallery forest in Cerrado in Bahia State. Flowering and fruiting patterns were annual, regular and of an intermediate duration. Similarly, Bulhão and Figueiredo (2002) emphasized the deciduousness found in *P. reticulata* in a marginal area of Cerrado in Maranhão State. The similar phenological patterns reported for *P. reticulata* populations at widely separated locations are in accordance with the results of Frankie *et al.* (1974), who showed that other tropical species occurring in both dry and wet sites exhibited a similar phenology in all populations. The tree species *Erythrina poeppigiana*, however, shows a transition from an evergreen to a deciduous habit with an increase in water stress (Borchert, 1980). Borchert (1980) suggested that this transition might be widespread in tropical trees, thus making *P. reticulata* an exception.

Reich *et al.* (1992) stated that deciduous species are probably favoured wherever annual variation in temperature or water availability results in marked favourable versus unfavourable periods of carbon gain. For *P. reticulata*, water availability could have been an environmental pressure promoting deciduousness, as this neotropical species occurs in an area characterized more by dry and wet seasons than by seasons of high and low temperature. However,
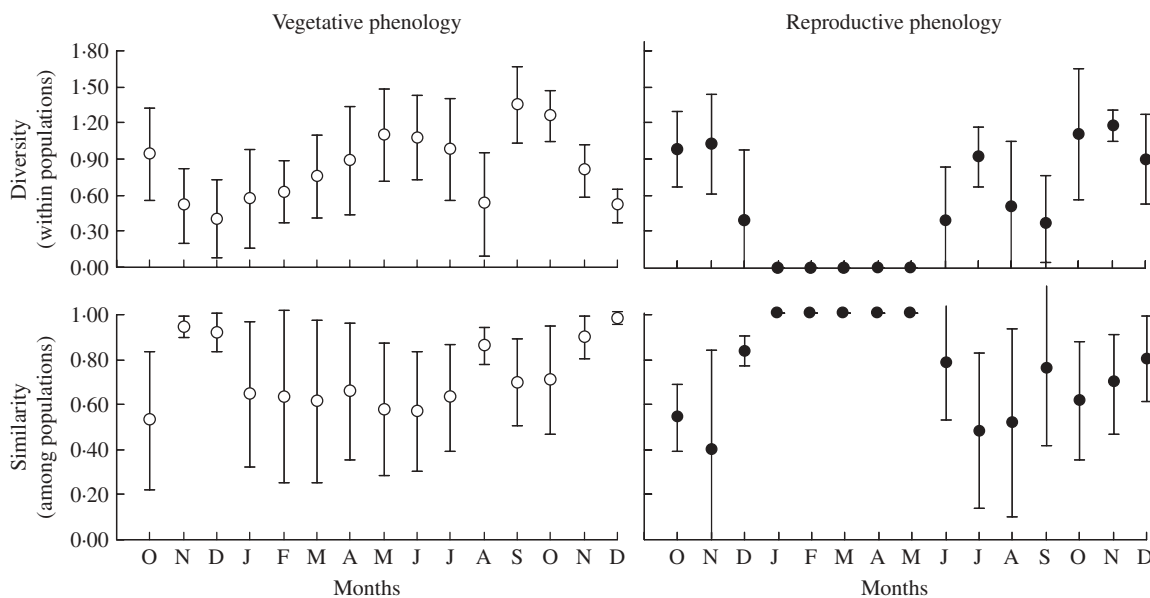
FIG. 4. Monthly variation in the mean of phenological indexes of diversity within populations (Shannon–Wiener index), and similarity among populations (Morisita–Horn index) of *P. reticulata*. Bars indicate ± s.d.

most of the tree species co-occuring with *Plathymenia* in Cerrado or Atlantic Forest are not deciduous. In Cerrado, during the dry season the soil surface tends to dry but the zone located at 2 m depth remains moist (Oliveira, 1998). For this reason woody species are usually not severely affected by the dry season and deciduousness is more characteristic of herbs (Oliveira, 1998). In the part of the Atlantic Forest along the Brazilian coast, there is virtually no dry season and trees are evergreen (Morellato *et al.*, 2000). The inland Atlantic Forest displays a rather seasonal climate but severe soil water limitation probably does not occur (Lemos Filho and Mendonça Filho, 2000). Co-occurring tree species showing different phenological behaviour have been shown in other tropical environments (e.g. Myers *et al.*, 1997). The variation may be caused by differences in depth of the root system (Medina and Francisco, 1994; Myers *et al.*, 1997) or may be due to different physiological strategies related to water use and accumulation (Myers *et al.*, 1997).

The beginning of leaf fall represented the main differences found among populations from Cerrado and Atlantic Forest. In Cerrado, trees started to lose leaves earlier than in Atlantic Forest, while transitional regions exhibited an intermediate pattern. According to Reich (1995), the timing of leaf fall is usually a function of tree water status, and this is determined not only by the structural and functional state of the tree but also by the environmental water status, including soil water availability and air vapour pressure deficit (Lemos Filho and Mendonça Filho, 2000). Therefore, differences in timing of leaf fall observed in *P. reticulata* populations were probably related to differences in water status between sites, starting earlier in drier areas (Cerrado) and later where the drought period is less severe (Atlantic Forest).

Leaf flush began in September, when the wet period starts but rain is still minimal. Rain-induced flushing is possible but not very likely. On the other hand, the fact that flushing occurred around the spring equinox suggests flushing may be induced by increase in day length. This has been documented for several tropical species, including some from Cerrado (Rivera *et al.*, 2002).

The *P. reticulata* flowering season started in September or October, soon after flushing. This indicates that flowers are formed in new shoots and are not directly induced by environmental signals (Borchert *et al.*, 2004). The wet season flowering pattern observed in *P. reticulata* is in accordance with the findings of Morellato *et al.* (2000), who suggested that in Atlantic Forest flowering, in general, is highly seasonal and concentrated at the beginning of the wetter season. Phenological studies in Cerrado show that flowering is less seasonal, although it also tends to occur at the beginning of the wet season (Batalha and Mantovani, 2000) or in the late dry period (Oliveira, 1998).

In contrast to flowering, fruiting phenology is aseasonal in Atlantic Forest (Morellato *et al.*, 2000) but more periodic in Cerrado (Oliveira, 1998). In Cerrado, the time of seed dispersal is related to dispersal syndromes: zoochoric species usually release seeds in the wet season, while anemochoric species disperse seeds in the late dry season (Oliveira, 1998). *Plathymenia* exhibits anemochory (Batalha and Mantovani, 2000; Funch *et al.*, 2002) and its peak of dispersal in August is in accordance with the general pattern proposed by Oliveira (1998). In anemochorous fruit, the pericarp dehydrates before releasing seeds, making dry months a suitable period for this event (Batalha and Mantovani, 2000). Moreover, wind dispersal is more efficient in this season (Augspurger and Franson, 1987). After dispersal, *P. reticulata* seeds remain in the soil for a few months without germination, as the species shows dormancy imposed by a hard and impermeable seed coat (Lacerda *et al.*, 2004). Seedlings start to appear in November or December (M. F. Goulart, pers. obs.).
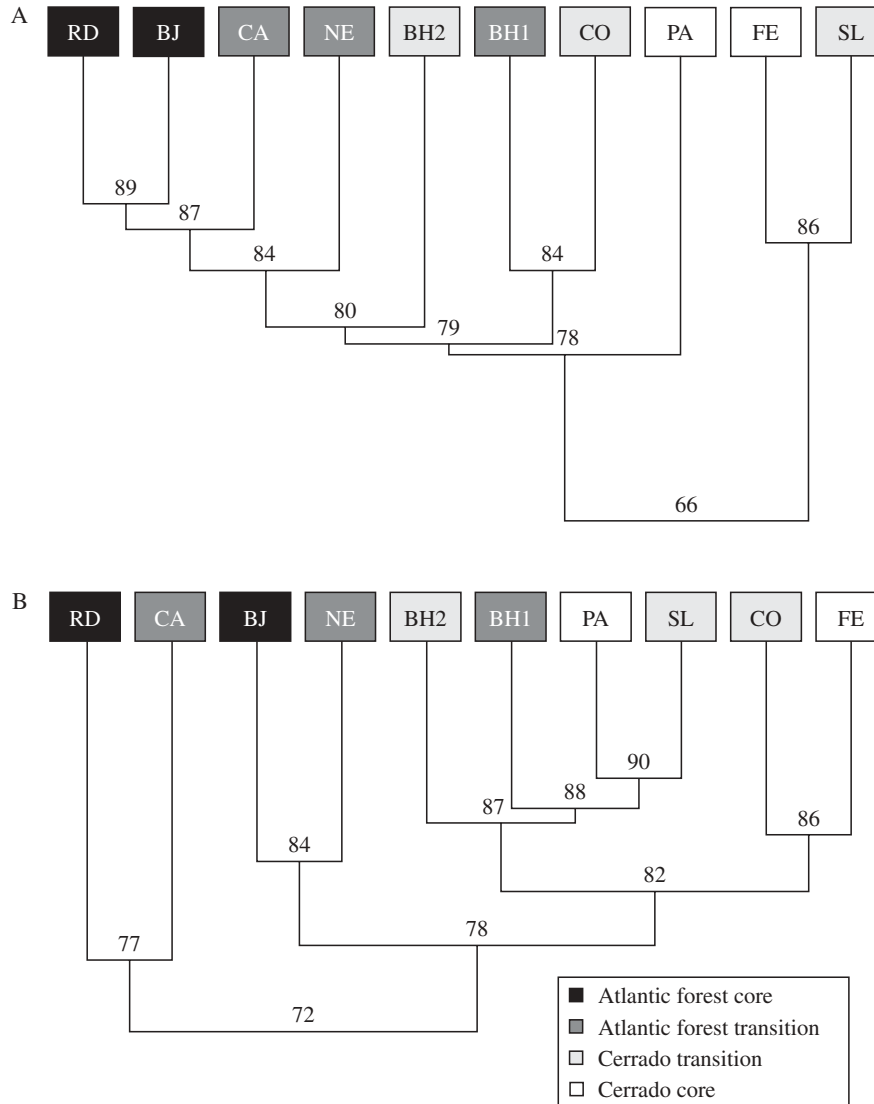
FIG. 5. Cluster analysis considering phenological similarity among populations (Morisita–Horn index) for (A) vegetative phases and (B) reproductive phases.

In most populations, the majority of individuals reproduced at least once during the study period, but RD-F is clearly an exception as only six of 20 trees reproduced. Supra-annual reproduction is not an uncommon event in tropical forests (Frankie *et al.*, 1974). Janzen (1969, 1970) proposed that the irregular reproduction in tropical species could be some kind of escape strategy against seed predators. In *P. reticulata* a considerable amount of seeds (35 %) were damaged by coleopterans (M. F. Goulart, pers. obs.), although this was not restricted just to forest sites, and reported data are insufficient to test Janzen's hypothesis.

Variability in phenological pattern

Variability among individuals within populations and among populations in vegetative phenology was more evident than variability in reproductive phenology. In vegetative phenology, in general, asynchrony among individuals and among populations was greater in the dry season. This pattern has also been documented in *E. poeppigiana*, in which trees were synchronous in the wet season but asynchronous in the dry season (Borchert, 1980). An explanation for this finding could be that genetic differences among individuals are more likely to be evident in a stressful situation, as shown by physiological data (Lemos Filho *et al.*, 2004). This same explanation may also apply to the fact that, for *P. reticulata*, greater asynchrony was observed within populations from Cerrado or transitional regions than within populations from Atlantic Forest sites. Cerrado could be considered to be a more stressful environment than the Atlantic Forest as it is characterized by a stronger and more prolonged drought season. This data agrees with that of Seghieri and Simier (2002), who also observed greater individual variability in phenology under less favourable conditions. These authors hypothesized that asynchrony among individuals may reflect population

flexibility, as the adaptation of individuals to a variety of conditions should contribute to population maintenance and expansion, certainly a hard task especially in a stressful environment.

Reproductive synchrony was not perfect among individuals and among populations of *P. reticulata*, as indicated by the diversity patterns found here. Similar patterns have been reported for other species (Murfet, 1977; Marquis, 1988). Rathcke and Lacey (1985) suggested that there should be some advantages in partial synchrony of flowering among individuals and populations, as it promotes cross-pollination among distant individuals, thus enhancing genetic diversity, and it also helps to avoid competition for pollinators. Variation in the initial date of flowering and the duration of this phase could be caused not only by genetic differentiation among individuals (e.g. Murfet, 1977) but also by microspacial variation in climatic conditions (e.g. Marquis, 1988; Borchert, 1994), plant size (e.g. Borchert, 1980) and herbivory (e.g. Marquis, 1988).

Partitioning of phenological diversity showed that the majority of the total diversity was due to differences among individuals within populations, and not among populations. This pattern is common in natural plant populations and has been reported both for phenological (e.g. Seghieri and Simier, 2002) and morphological data (e.g. Kocacic and Simic, 2001), and especially for genetic diversity in a great number of species (Hamrick and Godt, 1989; Nybom and Bartish, 2000), including *P. reticulata* (Lacerda *et al*., 2001). Populations of *P. reticulata* located in Atlantic Forest and in Cerrado have quite similar phenological behaviour, with only about 10 % of the total diversity being attributable to differences between the biomes. This level of differentiation between biomes is low when compared with genetic differentiation based on molecular data: Lacerda *et al*. (2002) reported that 60·5 % of genetic diversity in *Plathymenia* could be attributed to differences between biomes. However, it should be noted that in Lacerda's study only one population at a transitional site between biomes was evaluated. If more populations of this type had been included in the analysis, the proportion of the genetic diversity between biomes may have been lower. Nevertheless, comparisons between phenological diversity and genetic diversity suggest that the former is a more conserved characteristic, which is in agreement with Nicotra *et al*. (1997), who argued that physiological traits are under strong stabilizing pressures.

The diversity reported here in phenology is in accordance with other studies on the variability among populations of *Plathymenia* located in Cerrado, Atlantic forest and transitional sites. Lacerda *et al*. (2002) evaluated populations using RAPD markers and M. F. Goulart (unpubl. data) evaluated fruit and seed morphology. In both studies, differences among Atlantic Forest and Cerrado populations were found and individuals from transitional areas showed an intermediate pattern. All these results have some taxonomic value and the phenological data add to this pattern. Davies and Ashton (1999) reported that, when closely related species occur in sympatry, they usually flower at different times or show different flower morphologies and pollinators. In addition, Frankie *et al*. (1974) reported that congeneric species usually do not show strong synchrony in flowering phenology. Although there are exceptions to the reported patterns (e.g. Almeida and Alves, 2000), the fact that the flowering period is similar between Atlantic Forest and Cerrado populations of *Plathymenia* suggests, as pointed out by Stuessy (1990), that they may interbreed. Moreover, *Plathymenia* flower morphology is similar in both biomes and the same group of floral visitors was observed in different areas (mostly generalist bees and wasps; M. F. Goulart, pers. Obs.), reinforcing the possibility of gene flow. Gene flow along the cline could explain the intermediate pattern described for populations in transition zones between the biomes.

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