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Phenology of Tree Species Populations in Tropical Dry Forests of Southeastern Brazil

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1. Introduction

Tropical dry forests (TDFs) are forest formations that occur in regions with two marked seasons (dry and wet) and are characterized by some degree of foliar deciduousness (Murphy & Lugo, 1986). Recent estimates show that 1,048,700 km² of TDFs exist worldwide (Miles et al., 2006). The two largest continuous areas of this physiognomy are located in South America and include northeastern Brazil and the region incorporating southeastern Bolivia, Paraguay and northern Argentina (Miles et al., 2006).

In Brazil, these forests, usually called dry forests (Seasonally Deciduous Forests *sensu* Veloso et al., 1991), lose over 50% of their leaf area (Nascimento et al., 2004) as a physiological response to water shortages (Zalamea & González, 2008). Thus, the structural and ecophysiological properties of TDFs are significantly determined by the duration and timing of the dry season, which selects for adaptations associated with avoidance, resistance or tolerance to water stress (Singh & Kushwaha, 2005). Therefore, the floristic composition of TDFs is diverse, and they contain numerous liana, shrub and large tree species (Madeira et al., 2009). In particular, these forests show a great diversity of phenological patterns and large inter-annual variations, particularly at the level of individuals (Singh & Kushwaha, 2005).

In general, Brazilian TDFs are naturally fragmented and occur in different biomes: Cerrado and Caatinga in the Southeast, Central West and Northeast, and they are interspersed with evergreen formations, such as the Amazon and Atlantic Forest, in the North and South, respectively (Scariot & Sevilha, 2005). TDFs also occur in the transition zones of different biomes. However, according to the Brazilian classification of vegetation, Seasonally Deciduous Forests are included as part of the Atlantic Forest biome, specifically that found in Minas Gerais State (Veloso et al., 1991), and this biome is one of the most endangered in Brazil, with only 8% its original forest cover remaining. Therefore, human use is restricted in TDFs and is legally enforced by Brazilian environmental laws (Lima, 2001).

Although protected by law, TDFs are continuously converted to agricultural uses (Maass, 1995), as they generally occur on high fertility soils (Ribeiro & Walter, 1998). Moreover, different political, social and economic pressures have increased the human impact on these

forests, leading to severe disturbance and intense deforestation (Murphy & Lugo, 1986; Maass, 1995). In fact, tropical dry forests are the most threatened tropical ecosystems (Miles et al., 2006; Pezzini, 2008). Additionally, most studies in tropical forests were conducted in tropical humid or wet forests, and only 14% of the published articles on tropical forests focused on dry forests (Sánchez-Azofeifa et al., 2005). Therefore, given their relevance and degree of threat, studies on TDFs at the population and community level are essential to understanding their dynamics, maintaining their biodiversity and developing conservation policies to protect these ecosystems (Pezzini, 2008).

In this context, phenological studies of plant species in TDFs may help to understand the dynamics of plant communities (Spina et al., 2001) and act as an indicator of plant responses to climate and soil conditions in a region (Fournier, 1974). Information gathered from phenology studies can be used as a tool to support forest management when developing conservation strategies for the regional fauna and flora (Fournier, 1974).

The phenology of plants in TDFs has been largely associated with exogenous factors, such as precipitation, temperature and photoperiod (Bullock & Solís-Magallanes, 1990), which mainly influence vegetative phenophases (Lobo et al., 2003), and endogenous factors, such as competition for pollinators and dispersers and pressure from flower, fruit and seed predators (Lobo et al., 2003). Thus, because seasonal cues are more pronounced in TDFs, phenological patterns are particularly important to understanding how dry forests function (Justiniano & Fredericksen, 2000). The mix of evergreen and deciduous species gives the forest a phenological complexity that is not found in other tropical forest formations (Burnham, 1997). Nevertheless, information on the phenology of TDF species is scarce (however, see Borchert, 1994; Borchert et al., 2002; Borchert et al., 2004; Nunes et al., 2005; Nunes et al., 2008). This study addresses two basic questions aimed at increasing knowledge regarding the phenology of TDF tree species populations: (i) whether there any reproductive and vegetative phenological patterns in TDF tree species populations and (ii) whether the phenological responses of these populations are determined primarily by precipitation and temperature.

2. Methods

2.1 Study sites

This study was conducted in three sites located in northern Minas Gerais State (Fig. 1): Parque Estadual da Mata Seca (Mata Seca State Park, hereafter PEMS) (Site 1), CROS Reserve (Site 2) and Juramento Reservoir Reserve (Site 3). According to the Thornthwaite climate classification (Thornthwaite, 1948), the climate in northern Minas Gerais is dry sub-humid (C1), with two marked seasons (dry and wet) during the year (Antunes, 1994). The average annual precipitation ranges from 733-1,305 mm, with average annual temperatures between 16.8ºC and 26.2ºC. Rain usually falls from October to March, with November, December and January as the wettest months, while the driest period occurs from June to August (Nimer & Brandão, 1989). The study sites are located in the transition between the Cerrado and Caatinga biomes (Rizzini, 1997).

The PEMS was created in 2000 and currently has an area of 15,360 ha. The park is located in the city of Manga (14º97'02"S and 43º97'02"W) and represents the only conservation area on

the left margin of the São Francisco River with dry forests growing in flat soils (Madeira et al., 2009). Based on its forest structure, the PEMS is a mosaic of different successional stages (Madeira et al., 2009). The average annual temperature in the PEMS area is 24.4ºC, and the average annual precipitation is 871 mm (Antunes, 1994), with less than 60 mm of this rain falling in a seven month period (Espírito-Santo et al., 2008).

The CROS Reserve, owned by the Rocha & Souza Mining Construction Company, is located in the city of Montes Claros (16°38′53″S and 43°53′30″W) approximately 10 km from the urban area. The total area of the property is 49 ha, with 20% (9.8 ha) assigned as a permanent protection area (PPA). Dry forests and cerrado (savanna) are the main vegetation types in this area. Exposed rocks can be found on the soil surface and are typical of soils under limestone outcrops of basaltic origin (Silva & Scariot, 2004). The average annual precipitation is 1,000 mm, and the average temperature is 23ºC.

The Juramento Reservoir Reserve is located in the city of Juramento (16º46′20″S and 43º39′56″W) and has an area of 3,100 ha. The reserve, owned by the Minas Gerais State Water Company (COPASA), has a 7.63 km² reservoir. This reservoir was formed by the damming of the Juramento, Saracura and Canoas Rivers, which are part of the Verde Grande River sub-basin and the São Francisco River basin. The area surrounding the reservoir is 23.37 km² and has been under protection since the reservoir's construction in 1986 (Nunes et al., 2005). The average annual temperature is 23ºC, and precipitation is approximately 1,000 mm/year (Nunes et al., 2005).

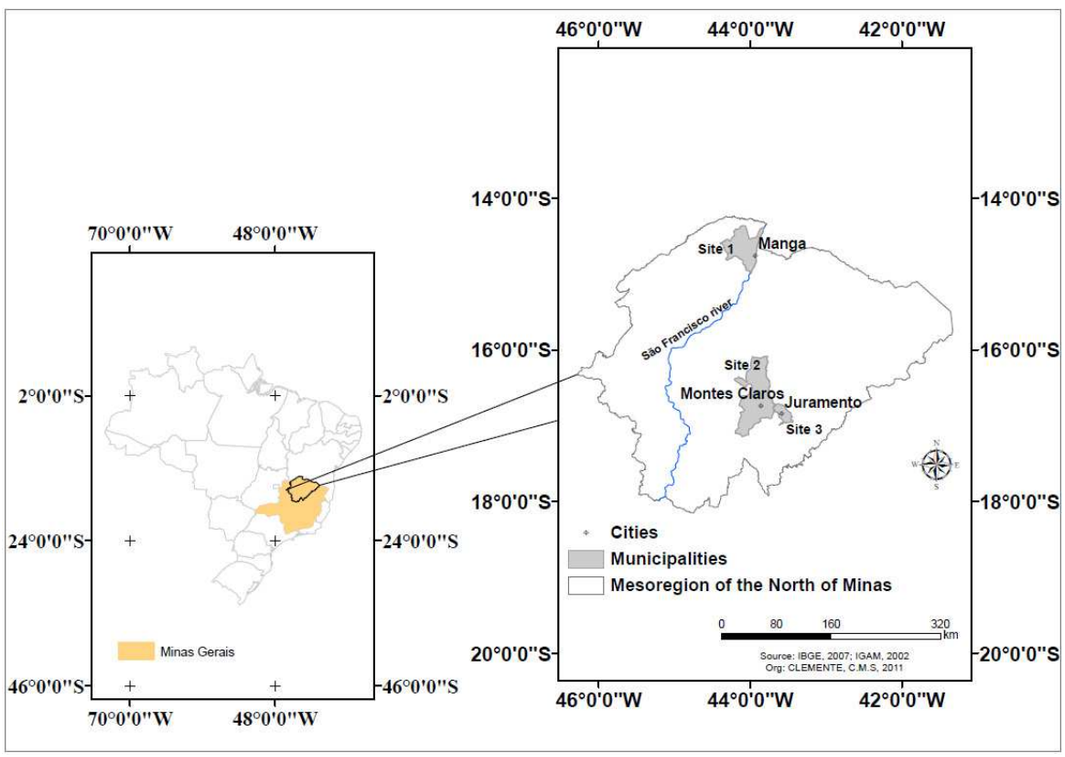


Fig. 1. Geographical location of the study sites in southeastern Brazil (Minas Gerais State). Site 1: Parque Estadual da Mata Seca, PEMS (Manga); Site 2: CROS Reserve (Montes Claros); Site 3: Juramento Reservoir Reserve (Juramento).

2.2 Sampling of phenological data

Populations from 20 TDF tree species were selected for monitoring of phenological patterns (Table 1). The circumference of marked trees at breast height (cbh, 1.3 m above ground) was greater than 15 cm. Each species had 20 individuals marked (Nunes et al., 2005; 2008), except for *Cedrela odorata* L. and *Sapium glandulosum* (L.) Morong, which had 14 and 15 individuals

Family	Species	Dispersion syndrome	Study Site	Source
Anacardiaceae	*Astronium fraxinifolium* Schott ex Spreng.	Ane	3	Maragon et al. 2010
	Myracrodruon urundeuva Allemão	Ane	1	Barbosa et al. 2005
	Spondias tuberosa Arruda	Zoo	1	Maia 2004
Burseraceae	*Commiphora leptophleos* (Mart.) J. B. Gillet	Zoo	1	Barbosa et al. 2005
Cactaceae	*Pereskia bahiensis* Gurke	Zoo	1	Britton & Rose 1963
	Pilosocereus pachycladus Ritter	Zoo	1	Obs. pes. [1]
Euphorbiaceae	*Jatropha mollissima* (Pohl) Baill.	Auto	1	Santos et al. 2005
	Sapium glandulosum (L.) Morong	Zoo	1	Maia 2004
Fabaceae	*Anadenanthera colubrina (Vell.) Brenan*	Auto	3	Barbosa 2005
	Chloroleucon tortum Mart. Pittier	Zoo	3	Obs. pes. [1]
	Copaifera langsdorffii Desf.	Zoo	3	Pereira et al. 2008
	Senna spectabilis DC. H. S. Irwin & Barneby	Auto	1	Barbosa et al. 2005
	Senegalia polyphylla DC.	Auto	2	Obs. pes. [1]
	Mimosa hostilis Benth.	Auto	1	Barbosa et al. 2005
	Pseudopiptadenia contorta (Benth.)	Auto	1	Obs. pes. [1]
Malvaceae	*Guazuma ulmifolia* Lam.	Zoo	3	Moreira et al. 2009
	Heteropterys byrsonimifolia Lam.	Ane	3	Stefanello et al. 2009
Meliaceae	*Cedrela odorata* L.	Ane	2	Silva e Rodal 2009
Polygonaceae	*Ruprechtia fagifolia* Meisn.	Ane	2	Obs. pes.[1]
Sapindaceae	*Dilodendron bipinnatum* Radlk.	Zoo	2	Obs. pes.[1]

Table 1. Species selected for phenological survey at three tropical dry forest sites in Minas Gerais, southeastern Brazil. (Ane = anemochorous, Auto = autochorous, Zoo = zoochorous). 1- Personal observation.

marked, respectively. In each field trip, phenophases were recorded through careful observation of the canopy with binoculars. The phenology of individual trees was recorded for 12 months, beginning in July and ending in June of the following year. The phenological survey at Site 1 was conducted in 2008 and 2009, at Site 2 in 2007 and 2008 and at Site 3 in 2002 and 2003.

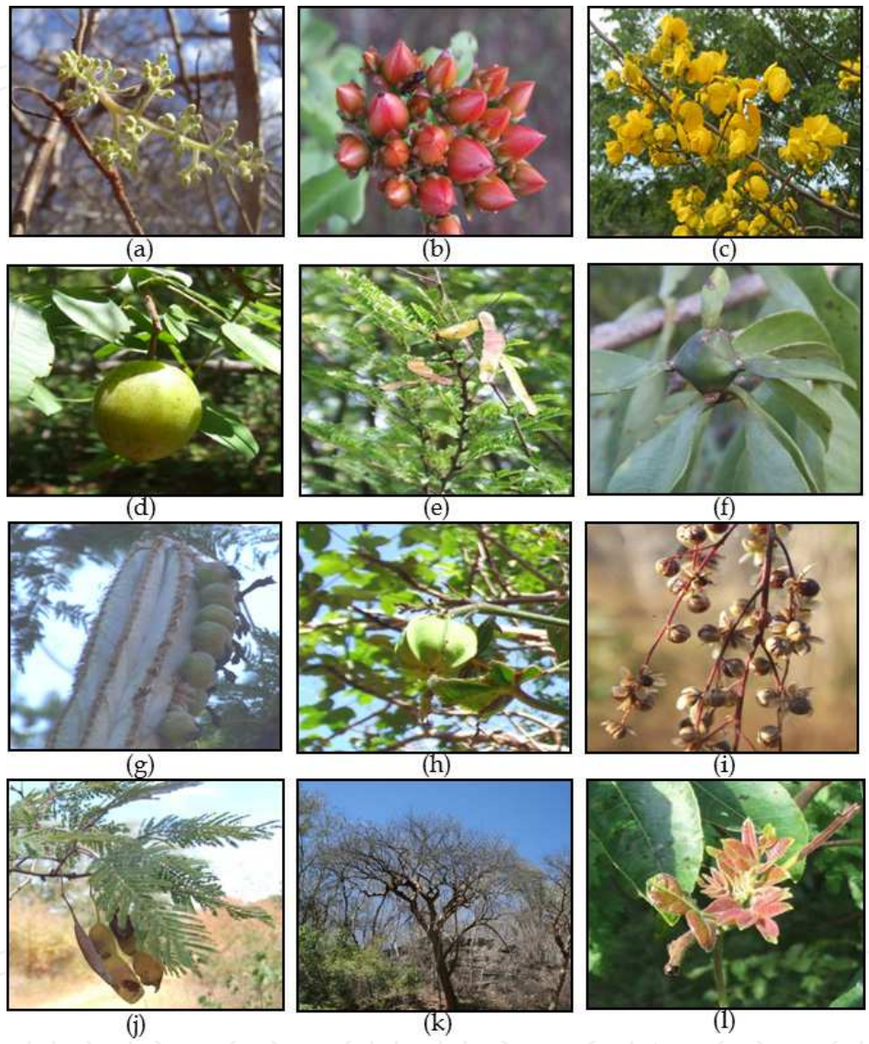


Fig. 2. Phenophases observed in the species studied: flower buds of *Spondias tuberosa* Arruda (a) and *Pereskia bahiensis* Gurke (b); flower opening in *Senna spectabilis* DC. H. S. Irwin & Barneby (c); ripe fruits of *S. tuberosa* (d); fruiting in *Mimosa hostilis* Benth. (e), *P. bahiensis* (f), *Pilosocereus pachycladus* Ritter (g), *Jatropha molissima* (Pohl) Baill. (h), *Myracrodruon urundeuva* Allemão (i) and *Pseudopiptadenia contorta* (Benth.) (j); total deciduousness (k) and young leaves (l) in *M. urundeuva.*

The following reproductive phenophases were recorded: (1) flower buds, from the formation of the floral structure to the opening of flower buds; (2) flower opening (anthesis), from the opening of flower buds to flower fall; (3) fruiting, from fruit formation until ripening, represented by the presence of green fruits; and (4) ripe fruits, represented by the

presence of dark-brown, yellow or yellowish-green fruits, depending on species. The following vegetative phenophases were also recorded: (5) leafing, represented by emergence of small leaves of different coloration (bright green or red); (6) leaf fall, characterized by leaves falling under a soft breeze and fallen leaves under the tree canopy; and (7) full deciduousness, characterized by total absence of leaves (Nunes et al., 2005; 2008) (Fig. 2).

2.3 Data analyses

The activity index observation method was used to quantify phenological events of the species (Bencke & Morellato, 2002). The activity index refers to the percentage of individuals displaying an event at each sampling date, with the presence or absence of the particular phenophase being recorded. In addition to indicating the occurrence of an event, this method also estimates the synchrony among individuals in a population (Pedroni et al., 2002).

To test whether species populations are differently affected by climate variables, the phenological data of each phenophase were correlated with total precipitation and average temperature, in the same period (month), using Spearman correlation tests (Zar, 1996) and were qualitatively compared with the climatological norms for each site (Fig. 3). The average temperature and total precipitation data for each month were collected at three weather stations located near the study sites in the cities of Itacarambi (Site 1), Montes Claros (Site 2) and Juramento (Site 3). Climatological norms for each city from 1991-2007 (Site 1), 2001-2006 (Site 2) and 1987-2002 (Site 3) were also used to discriminate between dry and wet seasons. So, for the climatological norms we used total precipitation and mean temperature of each year and extract the mean of these variables for all the period, 17 years to Site 1, five years to Site 2 and 16 years to Site 3. These differences in data period are associated to the time of station installation and the availability of the data.

To verify whether populations of the different species exhibit similar reproductive and vegetative phenophases at the different sites, a cluster analysis of the activity index of each species was performed, with Euclidean distance as the coefficient of association (Ludwig & Reynolds, 1988). Moreover, the species studied were also classified according to seed dispersal syndrome (Table 1), following van der Pilj (1982) classification, in zoochorous, when the dispersal is done by animals; anemochorous, when the dispersion is carried by the wind; and autochorous, when the dispersion occurs by explosive dehiscence or gravity. The species classification was made according to information on the biology of the species found in literature (Briton & Rose 1963; Maia 2004; Barbosa 2005; Barbosa et al. 2005; Santos et al. 2005; Pereira et al. 2008; Moreira et al. 2009; Silva & Rodal 2009; Stefanello et al. 2009; Maragon et al. 2010), expert consultation and increased knowledge of the authors. This classification was intended to detect patterns related to reproductive strategies of species.

3. Results and discussion

3.1 Reproductive phenology

Synchronous flowering within populations and among species is more frequent in dry areas (Bullock, 1995). In general, flower bud (late dry season) and anthesis (late wet season)

phenophases were concentrated in the wet season. Flower buds occurred in September and October for 50% of the species at Site 1, from August to November for 50% of the species at Site 2 and in October for 67% of the species at Site 3 (Fig. 4a). For most species, anthesis was recorded from September to November; 60% of the species displayed this event in September at Site 1, 50% from September to November at Site 2 and 50% in September and October at Site 3 (Fig. 4b). This pattern seems to be common in seasonal tropical forests with well-defined dry and wet seasons, as several authors (Morellato et al., 1989; Morellato & Leitão-Filho, 1990; 1992; 1996) have also observed flowering in the wet season or during the

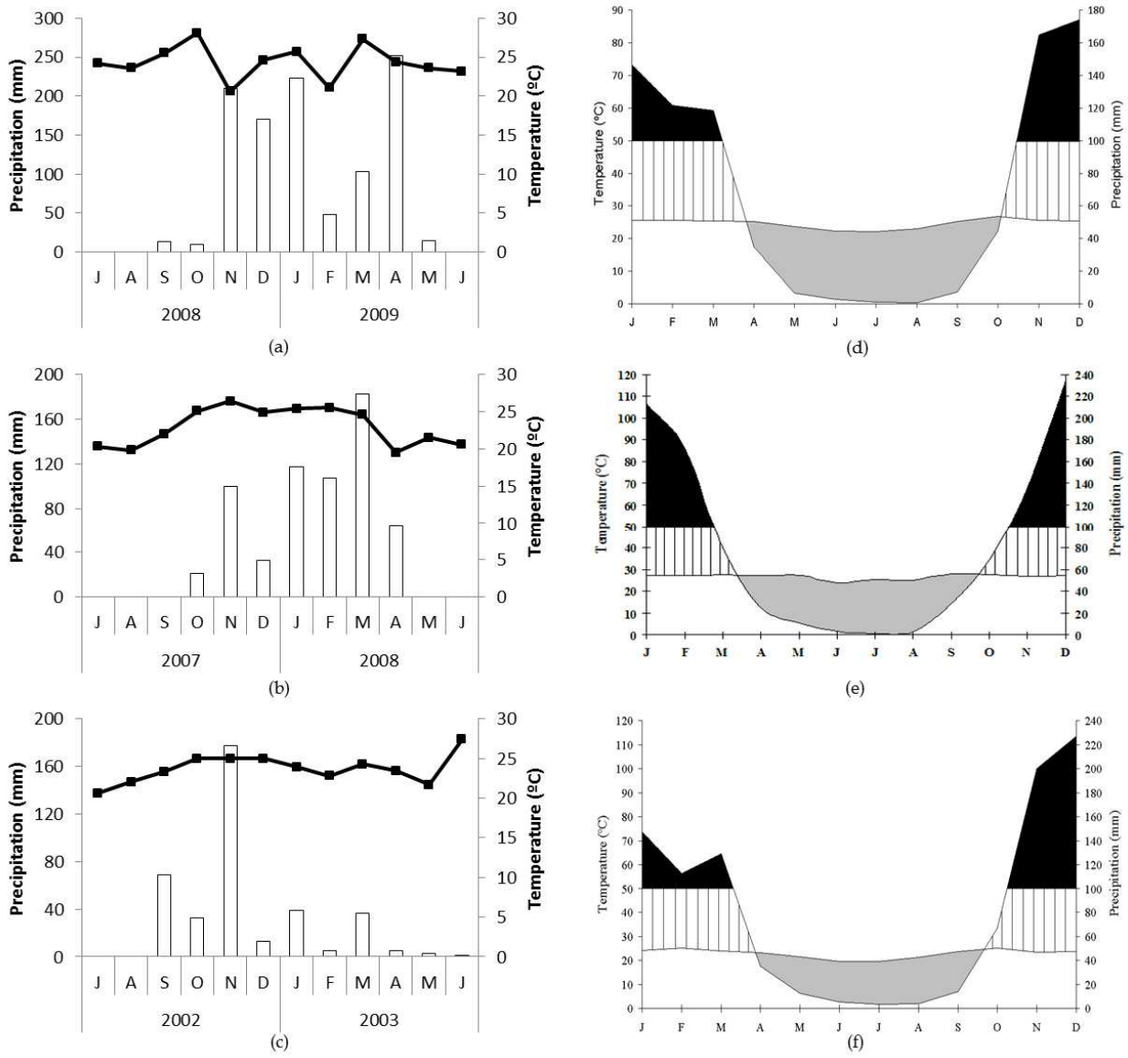


Fig. 3. Climate description of the study sites in southeastern Brazil: total precipitation (bars) and average monthly temperatures (line) for (a) Site 1 (Parque Estadual da Mata Seca, Manga: 2008-2009), (b) Site 2 (CROS Reserve, Montes Claros: 2007-2008) and (c) Site 3 (Juramento Reservoir Reserve, Juramento: 2002-2003); climatological norms for (d) Site 1 (Itacarambi, 1991-2007), (e) Site 2 (Montes Claros, 2001-2006) and (f) Site 3 (Juramento, 1987-2002). For d, e and f the black color refer to the monthly rainfall greater than 100 mm (hydric surplus), the gray color to the drought period and the ratched the humid period.

transition from the dry to wet season. According to Morellato et al. (1989), most species produce flowers during this period because the first rains and the increasing photoperiod stimulate the onset of flowering. This notion has also been advanced by Pereira et al. (2008) who suggested that, prior to anthesis, flower primordia are in a dormant state imposed by drought, which can be interrupted when moisture levels in the environment increase. Moreover, higher precipitation levels and temperatures in the wet season lead to increased litter decomposition and nutrient availability to plants (Morellato, 1992), which in turn are able to invest in reproductive phenophases. During this period, population density and pollinator activity are also higher (Wikander, 1984).

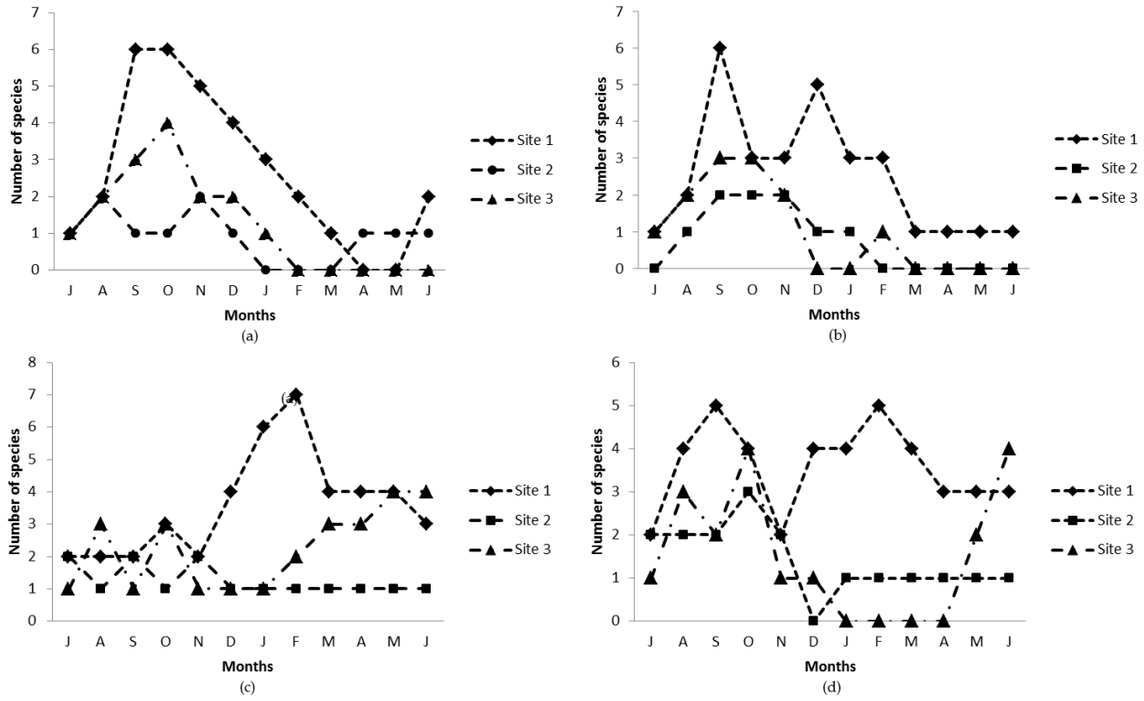


Fig. 4. Reproductive phenology of 20 tropical dry forest tree species in southeastern Brazil from July to June (12 months). Number of species displaying phenophase (a) flower buds, (b) anthesis, (c) green fruits and (d) ripe fruits at the three study sites in Minas Gerais (Site 1 = Parque Estadual da Mata Seca - Manga; Site 2 = CROS Reserve - Montes Claros; and Site 3 = Juramento Reservoir Reserve - Juramento).

Fruiting varied among sites, with 50% of the species fruiting in February at Site 1, 50% between July and November at Site 2 and 67% in May and June at Site 3 (Fig. 4c). The emergence of ripe fruits occurred from September to February at Site 1 for 50% of the species, in October at Site 2 for 75% of the species and at from October to June Site 3 for 67% of the tree species analyzed (Fig. 4d). Thus, unlike flowering, green fruits and ripe fruits appear at different times during the year, both in the dry and wet seasons. The timing and duration of reproduction may differ greatly among plant groups with different pollination or dispersal vectors (Bullock, 1995). The fruiting patterns observed in this study are likely associated with the seed dispersal mode of each species. In TDFs, fleshy fruits are abundant in the wet season and rare in the dry season, while anemochorous and autochorous fruits

are almost inconspicuous in the wet season but abundant in the dry season (Frankie et al., 1974). In fact, five species fruiting in the dry season and five in the wet season. The majority of species that fruiting in the dry season (60%) was wind-dispersed (anemochorous), while the fruiting for most species in the wet season (80%) was dispersed by animals (zoochorous). Another interesting pattern, several species (45%) had fruits in both season, most of these (44.4%) belonging to autochorous syndrome. However, one species (*Dilodendron bipinnatum* Radlk.) not fruiting during the study period.

In tropical forests, the most frequent seed dispersal syndrome is zoochory, followed by anemochory and autochory (Howe & Smallwood, 1982). Nevertheless, wind dispersal is relatively common in deciduous forests (Van Schaik et al., 1993) and is largely present in TDFs (Bullock, 1995). In these forests, plants lose leaves seasonally, allowing for greater wind movement not only in the canopy but also in lower vegetation strata (Griz & Machado, 2001). Thus, reduction in physical obstacles resulting from greater deciduousness of tree species promotes the longer distance transport of anemochorous seeds (Janzen, 1967). Conversely, as activity of dispersers is higher in wet seasons (Smythe, 1970), the fruiting of most zoochorous species was concentrated in this season. It should also be noted that autochorous species (e.g., *Mimosa hostilis* Benth. and *Senna spectabilis* DC. H. S. Irwin & Barneby) with fruiting distributed throughout the year do not rely on any single dispersal agent and maximize seed dispersal over time (Piña-Rodrigues & Aguiar, 1993). Although dispersal is not primarily zoochorous, fruiting spread throughout the year provides an important food source to fauna. As food availability is limited during dry seasons, the dispersal of several species relies on secondary zoochorous dispersal.

3.2 Vegetative phenology

All of the species studied produced new leaves in the wet season. Leafing pick was recorded from October to February at Site 1, in October and November at Site 2 and from October to December at Site 3 (Fig. 5a). Conversely, leaf fall occurred from March to May for 90% of the species at Site 1, from July to October and in May and June for 100% of the species at Site 2 and from July to September and in May and June for 100% of the species at Site 3 (Fig. 5b). Full deciduousness was recorded for 90% of the species in August and September at Site 1, for all of the species from July to October at Site 2 and for 66% of the species in October at Site 3 (Fig. 5c). Thus, the onset of leafing at all sites occurred during the dry/wet season transition, whereas leaf fall was strongly associated with dry seasons, with the full absence of leaves observed for some species during these periods.

A widespread feature of tropical dry forests is the seasonal production of new leaves (Longman & Jenik, 1987), which is stimulated by increased water and light availability (Lieberman & Lieberman, 1984; Borchert, 1994). Besides, the existence of synchrony in leafing, in tropical dry forests, has been suggested as a strategy to avoid the emergence of young leaves at unfavorable times (van Schaik et al., 1993). This synchrony, observed in the present study, affects herbivore communities leading to fluctuations in population size, as most food resources are present for only a few months (Peters et al., 2001). Therefore, leaves produced during flushing peaks sustain less damage than those produced out of synchrony because herbivores are more easily satiated when food availability increases (Janzen, 1975).

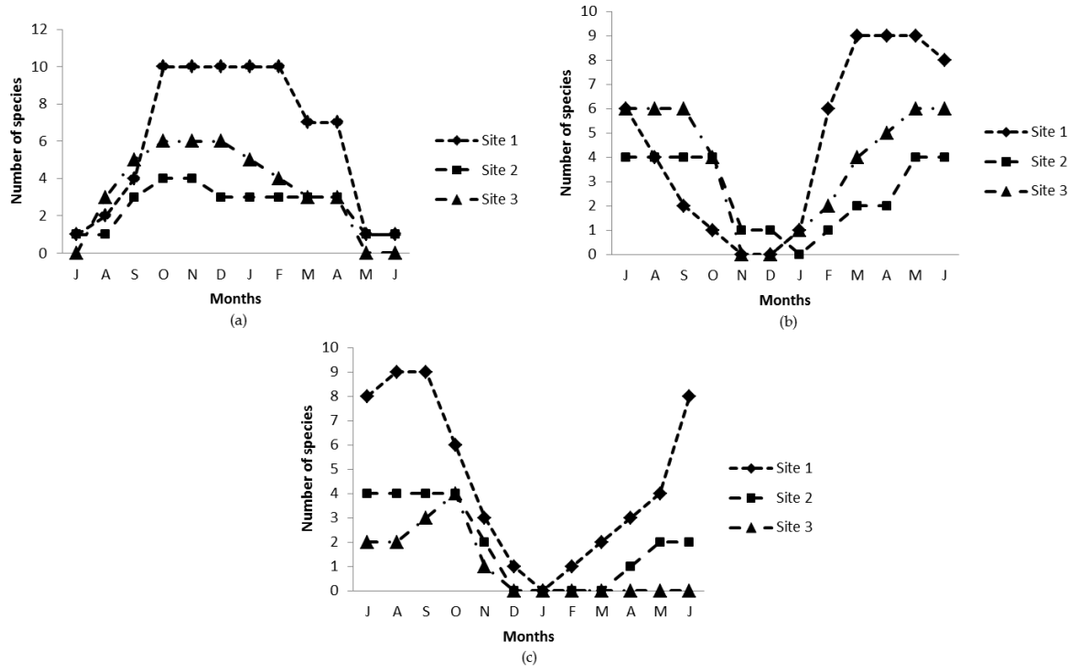


Fig. 5. Vegetative phenology of 20 tropical dry forest tree species in southeastern Brazil. Number of species displaying phenophase (a) leafing, (b) leaf fall and (c) full deciduousness at the three study sites in Minas Gerais (Site 1 = Parque Estadual da Mata Seca - Manga; Site 2 = CROS Reserve - Montes Claros; and Site 3 = Juramento Reservoir Reserve – Juramento).

Leaf fall, on the contrary, is likely a consequence of increased water stress and leaf ageing (Elliott et al., 2006). Leaf fall is intense during the early dry season because evapotranspiration increases, leading to greater nutrient removal from soil by roots (Morellato, 1992). At the end of the dry season, the air is drier and water availability decreases, nutrient uptake is inhibited and most species shed their leaves, reducing evapotranspiration (Morellato, 1992). Synchronous leaf fall, showed in this study, may be the result of various processes (Janzen, 1980), for example, for many deciduous species in tropical forests, the retention of leaves may be costly when water availability is reduced; besisde, as trees shed leaves with the arrival of the dry season, the need for any individual tree to retain its leaves for canopy space is reduced; and also, when green foliage disappears from the community, plant species without major anti-herbivore defenses will likely sustain greater damage to the rest of their leaves.

3.3 Phenophases versus climate variables

Despite the variations in phenological behavior among species, the climate variables influenced more the vegetative phenology than the reproductive phenology. There was a correlation between the production of flower buds and precipitation in 20% of the species and with temperature only in *C. odorata* and *D. bipinnatum*. Precipitation and temperature also affected the opening of flowers in three (15%) species. These data show that both climate variables affect the flowering of tropical dry forest species. According to Mantovani & Martins (1988), these environmental variables affect pollinator availability, which are directly related to the flowering patterns of plant species. These individuals likely share the

same pollinator agents (mostly insects), which have high population densities at that time of year (Souza-Silva et al., 2001). Conversely, fruiting was only correlated with precipitation, and 20% of the species were influenced by this variable. Ripe fruits were negatively correlated with precipitation in *C. odorata* and *M. hostilis* and positively with temperature in *Ruprechtia fagifolia* Meisn. Water availability is an important factor in the production of fleshy, succulent fruits that are attractive to dispersers (Piña Rodrigues & Piratelli, 1993). Among the dispersal guilds of tree species, zoochory is positively correlated with precipitation (Bullock, 1995). Therefore, there is a connection between the production of energy-rich fruits and the attraction of effective dispersers. However, in the present study there is no association among dispersion guilds, climate variables and fruit production, because the association of precipitation and fruiting and ripe fruits phenophases occurred in different dispersion guilds.

Precipitation and temperature are important environmental variables that determine tree stem water stress in the dry tropics (Singh & Kushwaha, 2005). Precipitation positively influenced leafing in 55% of the species, while temperature positively influenced occurrence of this phenophase only in *Anadenanthera colubrina* (Vell.) Brenan. Leaf fall was also negatively correlated with precipitation in eight species (40%) and with temperature in *R. fagifolia*. There was a negative correlation between full deciduousness and precipitation in 50% of the species. Negative correlations between leaf fall and environmental variables indicate that this phenophase is associated with a reduction in temperature and precipitation (Nunes et al., 2005). Leaf fall during drier periods represents an economization of water by plants (Borchert et al., 2002), as it results in large nutrient losses. Full deciduousness is particularly evident in nutrient-rich soils, in which plants can retrieve nutrients that are lost in this process from the soil (Jaramillo & Sanford, 1995). Therefore, the soil conditions of TDFs enable plants to shed leaves because they grow in high fertility soils (Oliveira-Filho et al., 1998). A marked seasonality in vegetative phenological patterns has been observed in several studies focusing on dry forests (Lieberman, 1982; Bullock & Solís-Magallanes, 1990; Machado et al., 1997). Tree species in this study behaved consistently with this phenological pattern, which evolved through leaf fall to avoid water stress during dry periods, thus reducing transpiration and pronounced dehydration (Bullock & Solís-Magallanes, 1990).

Site	Species	Climate variable	Phenophase	Activity	
				r	p
1	*Commiphora leptophleos*	P	Full deciduousness	-0.63	0.03
1	*Jatropha mollissima*	P	Fruiting	0.58	0.05
		P	Leafing	0.67	0.02
		P	Full deciduousness	-0.72	0.01
1	*Mimosa hostilis*	P	Ripe fruits	-0.77	0.00
		P	Leafing	0.74	0.01
1	*Myracrodruon urundeuva*	P	Flower buds	-0.88	0.00
		P	Anthesis	-0.72	0.01
		P	Full deciduousness	-0.72	0.01
1	*Pereskia bahiensis*	P	Fruiting	0.61	0.04
		P	Full deciduousness	-0.75	0.01

1	*Pseudopiptadenia contorta*	P	Leafing	0.64	0.02
		P	Full deciduousness	-0.67	0.02
1	*Pilosocereus pachyladus*	P	Flower buds	-0.65	0.02
		P	Leafing	-0.63	0.03
1	*Sapium glandulosum*	P	Full deciduousness	-0.75	0.00
1	*Senna spectabilis*	P	Full deciduousness	-0.80	0.00
1	*Spondias tuberosa*	P	Full deciduousness	-0.74	0.01
2	*Cedrela odorata*	T	Flower buds	0.60	0.04
		P	Ripe fruits	-0.71	0.01
		P	Leafing	0.87	0.00
		P	Leaf fall	-0.86	0.00
		P	Full deciduousness	-0.86	0.00
2	*Dilodendron bipinnatum*	P	Flower buds	-0.67	0.02
		T	Flower buds	-0.82	0.00
		P	Leafing	0.79	0.00
		P	Leaf fall	-0.79	0.00
		P	Full deciduousness	-0.76	0.00
2	*Senegalia polyphylla*	P	Leafing	0.93	0.00
		P	Leaf fall	-0.82	0.00
2	*Rupretchia fagifolia*	T	Ripe fruits	0.67	0.02
		T	Leaf fall	-0.78	0.00
		P	Leaf fall	-0.74	0.01
3	*Anadenanthera colubrina*	T	Leafing	0.58	0.05
		P	Fruiting	-0.60	0.04
		P	Leaf fall	-0.65	0.02
3	*Astronium fraxinifolium*	T	Anthesis	-0.60	0.04
		P	Leafing	0.74	0.02
		P	Leaf fall	-0.68	0.02
3	*Chloroleucon tortum*	P	Fruiting	-0.59	0.04
		P	Leafing	0.59	0.05
		P	Leaf fall	-0.63	0.03
3	*Copaifera langsdorffii*	P	Leaf fall	-0.63	0.03
3	*Guazuma ulmifolia*	P	Flower buds	0.81	0.00
		P	Anthesis	0.63	0.03
		P	Leafing	0.70	0.01
		P	Leaf fall	-0.62	0.03
3	*Heteropterys byrsonimifolia*	P	Leafing	0.67	0.02

Table 2. Correlation between the climate variables precipitation (P) and temperature (T) and the reproductive and vegetative phenophase activity of 20 tropical dry forest tree species in southeastern Brazil (Site 1 = Parque Estadual da Mata Seca - Manga; Site 2 = CROS Reserve - Montes Claros; and Site 3 = Juramento Reservoir Reserve – Juramento).

3.4 Phenophases versus sites

Few phenological studies have compared populations located in sites under different environmental conditions (Frankie et al., 1974; Borchet, 1980). This experimental approach, however, is valid for understanding the extent of phenological variability as a survival strategy and to determine how environmental factors influence these patterns (Goulart et al., 2005). Although this study did not address variation between populations of the same species in different regions, phenological patterns generated by different populations may indicate local environmental variation, both in climate and soil conditions. In general, there

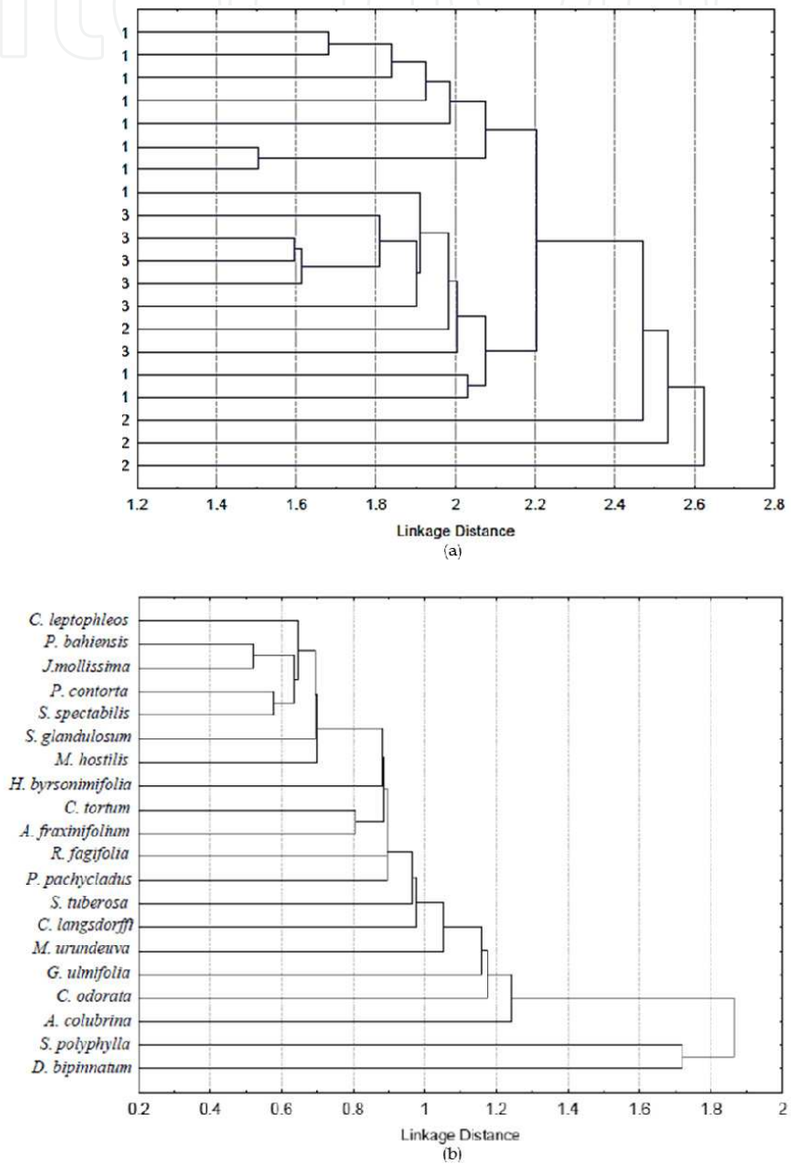


Fig. 6. Similarity dendrogram of the reproductive and vegetative phenophase activity of 20 tropical dry forest tree species in southeastern Brazil. (a) Species and (b) species location in the different study sites (Site 1 = Parque Estadual da Mata Seca - Manga; Site 2 = CROS Reserve - Montes Claros; and Site 3 = Juramento Reservoir Reserve – Juramento).

was a tendency of species to group by site (Fig. 6). This result suggests that there is a difference between phenological patterns of species in different sites and that these patterns are grouped by site. In fact, two large groups composed primarily of species from Sites 1 (PEMS, Manga) and 3 (Juramento Reservoir Reserve, Juramento) were formed in the cluster analysis, while species from Site 2 (CROS Reserve, Montes Claros) were not included in any of these groups.

The extent and intensity of seasonal drought may differ due to the geographical location of the study sites (Singh & Kushwaha, 2005). For instance, Site 1 is at a northern location, and this location determines its climatic differences to the other sites. According to the climatological norms of the study sites (Fig. 2), there are differences in the average temperature (Site 1 = 24.2ºC, Site 2 = 23ºC and Site 3 = 23ºC) and precipitation (Site 1 = 871 mm, Site 2 = 1,000 mm and Site 3 = 1,000 mm) among sites, especially between Site 1 and the others. In addition to climate variables, soil conditions may also determine the phenological behavior of plants (Morellato, 1992). The differences between Sites 2 and 3 are likely caused by such factors. In fact, the TDF at Site 3 is growing in limestone outcrops (slope seasonal dry forest or dry calcareous forest), while at Site 2, the TDF is growing in flat soils. Therefore, although the proximity of the sites results in similar climates, differences in soil and topography may determine the occurrence of similar phenological patterns in different species. The water availability in the soil is considered to be the determining factor of leaf dynamics in the dry tropics (Borchert, 1994). The amount and timing of water that is available to plants on rocky outcrops is likely different from that of plants growing in deep soils.

4. Conclusion

This study showed different reproductive and vegetative phenological patterns among TDF tree species. Flowering and fruiting occurred in the wet season, whereas leaf fall was concentrated in the dry season. Nevertheless, fruiting seemed to be associated with the dispersal guilds of the different species. Temperature and precipitation were correlated with all phenophases analyzed, and the correlations were more robust with vegetative phenology. Species occurring in the same site showed phenological patterns that were more similar than species from different sites.

Climate and soil conditions may influence the occurrence of adaptations that result in similar phenological patterns among different species. Despite strong biotic interactions with processes such as pollination, propagule dispersal, predation and herbivory, the environmental factors that act directly upon the phenological behavior of species also affect these biotic agents and determine the occurrence of both vegetative and reproductive phenological patterns in TDF species.

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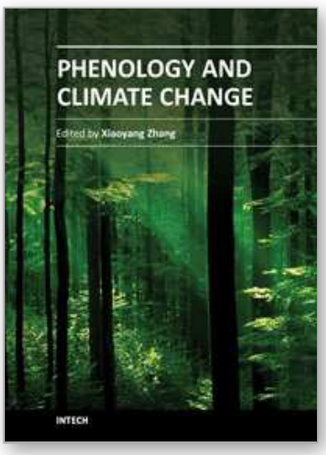
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