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Fire and the reproductive phenology of endangered Madagascar sclerophyllous tapia woodlands



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ABSTRACT

Tapia woodland vegetation is a remnant of Madagascar sclerophyllous forest that has developed under the selective pressure of fire and is dominated by the endemic tree *Uapaca bojeri* (Phyllanthaceae), locally named tapia. We carried out a 2-year study in tapia woodland at Ibity mountain, a new protected area in central highlands of Madagascar. We aimed to describe the reproductive phenology of this vegetation type and to determine whether it is affected by fire. We addressed two main questions: 1) does fire frequency affect the proportion of reproducing individuals and the intensity of each flowering and fruiting event?; and 2) does fire frequency influence the reproductive synchrony of species across the landscape? Thirteen woody species (373 individuals) were sampled at six sites selected across the Ibity mountain, where three that were burned three times between 2000 and 2010 and three burned just once during the decade. We found that (1) fire reduced the percentage of individuals that participate in each phenophase, and flower and fruit production was lower at the more frequently burned sites; and (2) increased fire frequency reduced the reproductive synchronization of species throughout the landscape. Fire is recognized as one of the major disturbances affecting mortality and recruitment of trees in tapia woodland. Our study indicates that fire also impacts the timing of plant reproduction at community and landscape levels.

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1. Introduction

Reproductive phenology is a key issue in plant community ecology that has a fundamental role in the coexistence and maintenance of species (Frankie et al., 1974; Hagen et al., 2012; Seghieri et al., 1995). Precipitation, photoperiod and temperature are regarded as the primary drivers of plant phenology in tropical seasonal vegetation (Borchert, 1999; Morellato et al., 2013; Seghieri et al., 1995). Pollination, seed dispersal and germination can further shape phenological cycles (Rathcke and Lacey, 1985; Staggemeier et al., 2010; Waser, 1978). However, the

influence of local environmental drivers such as the biochemical composition of soil, as well as natural or human-induced disturbances such as fires and fragmentation, in controlling phenology are still poorly understood (Cardoso et al., 2012; Hagen et al., 2012).

Disturbance may have an effect on the phenology, density, abundance and distribution pattern of plant populations (Agrawal, 1990). Because phenology defines the temporal structure of a community, it is important to understand how disturbances can modify plant life cycles and their consequences, for instance, on interactions between plants and animals. Fire, whether of natural or anthropogenic origin, is generally regarded as a disturbance (Whelan, 1995), which can have positive effects – considered an integral process in some ecosystems or negative effects, regarded as a catastrophic disturbance. Fire alters the structure and composition of vegetation (Baeza et al., 2006; Drobyshchev et al., 2008; Kirkman et al., 2001) and leads to modifications in environmental conditions, such as increases in solar radiation, temperature and nutrient availability in the soil (Andersson et al., 2004; Certini, 2005; Kim et al., 2008). As a result, fire can stimulate flowering and fruiting (Pausas et al., 2004; Silva et al., 1996), increase fruit

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production (Paritsis et al., 2006), and/or accelerate the phenological cycle by shifting the starting date of flowering/fruitletting (Paritsis et al., 2006; White et al., 1991; Wroblewski and Kauffman, 2003). However, fire can destroy buds, flowers and fruits, affecting species that reproduce during the fire season (Hoffmann, 1998). While numerous studies have been carried out on the effects of fire on diversity (Agrawal, 1990; Drobyshchev et al., 2008; Kirkman et al., 2001), ecological succession (Engle et al., 2000), regeneration (Caturla et al., 2000) and germination (Crosti et al., 2006; Moreno and Oechel, 1991), its effects on phenology are still poorly understood (Fatubarin, 1985; Haddad and Valio, 1993; Hoffmann, 1998; Paritsis et al., 2006). The study of environmental drivers such as fire is important for understanding how fire disturbance affects phenology and, as a consequence, its potential to affect reproduction rates and success, a key consideration for vegetation management.

Tapia woodland vegetation is a vestige of Madagascar sclerophyllous forest dominated by *Uapaca bojeri* (Phyllanthaceae), locally named tapia (Koechlin et al., 1974), which has evolved under the selective pressure of fire. Most endemic woody species in tapia woodland are fire-tolerant, and while a natural fire regime is needed to maintain this type of vegetation (Kull, 2002; Virah-Sawmy, 2009), the current regime of annual or biannual fires may be causing its degradation (Alvarado et al., in press; Kull, 2002). Several woody species of tapia woodland likewise present the typical characteristics of pyrophytic trees, such as the capacity to regenerate by sprouting, thick bark and weakly flammable leaves (Campbell, 1996).

Ibity mountain, a new protected area located in Madagascar's highlands (Alvarado et al., 2012), is a mosaic of grassland vegetation and isolated remnants of tapia woodland. This mosaic is a result of human activities, with fire being one of the most important practices, providing a well suited context to examine phenology. The date since the last fire or the response during the 12 months following fire is the most frequently studied issues considered when evaluating the influence of fire on reproductive phenology (Paritsis et al., 2006). In order to evaluate the resilience of tapia woodland to fire, we studied the influence of fire frequency on plant phenology. Resilience is defined here as the time an ecosystem needs to return to its reference trajectory after an exogenous disturbance (Hirst et al., 2003). Specifically, we studied the phenological cycles of the 13 most abundant woody plant species of tapia woodland on Ibity to describe general phenological patterns that were previously unknown for this vegetation and to answer two main questions: 1) does fire frequency affect the proportion of reproducing individuals and the intensity of each flower and fruit event? and 2) does fire frequency influence the reproductive synchrony of species across the landscape? We expect that frequent fires affect phenological cycles by reducing the production of flowers and fruits and the synchronization of flowering and fruiting within and among sites. The current knowledge on ecological processes (including plant phenology) is scarce for Madagascar's highly endangered tapia woodlands, where fire is a frequent disturbance. Thus, the phenological data gathered in this study are relevant for the basic characterization of the biodiversity of tapia woodlands, and also provide key information for developing conservation strategies. The management plan for the new protected area on Ibity includes a restoration program to improve the regeneration of the main endangered species of this endemic vegetation type. A good understanding of the biology and ecology of these species will provide a baseline for this program, and our phenology study thus represents an important step for making the connection between studies in fundamental and applied ecology.

2. Methods

2.1. Study site

Ibity mountain is located 200 km south of Madagascar's capital city, Antananarivo, and 25 km south of the town of Antsirabe (47°01'E 20°07'S). Ibity, situated between 1400 and 2254 m altitude, was

declared a New Protected Area in 2008 (Alvarado et al., 2012) and is now classified in IUCN category V: "Landscape/seascape conservation and recreation" (Dudley, 2008).

2.2. Climate

The climate of Ibity mountain is characteristic of highland areas in the tropics, and classified as CWB (C: warm temperate, W: dry winter, B: hot in summer) according to the Köppen classification (Peel et al., 2007). Average rainfall reaches 1583 mm and average temperature is 17.5 °C (1961–1990), with a mean maximum temperature of 20.0 °C in December and a mean minimum temperature of 13.3 °C in July (Fig. 2). During the rainy season (summer months with >100 mm of rain), between November and May, the total monthly rainfall ranges from 100.2 mm to 343.1 mm while during the dry season (winter months with <100 mm of rain), between June and October, monthly precipitation is below 70 mm, ranging from 5.7 to 68.7 mm.

2.3. Vegetation

Tapia woodlands are characterized by two strata: a woody stratum dominated by *U. bojeri*, the tapia, in association with other woody species of the family Sarcolaenaceae (Madagascar's largest endemic family), and an herbaceous stratum represented primarily by species of Asteraceae, Cyperaceae, Lamiaceae, Poaceae, and Rubiaceae (Alvarado et al., in press). This vegetation type has been transformed and degraded by human activities, including bush fires, which are a major cause of fragmentation (Birkinshaw et al., 2006; Kull, 2002, 2003).

Preliminary fieldwork in all the remnants of tapia woodland on the Ibity mountain was conducted in order to identify suitable places to carry out the present study and to make field observations to detect the effects of on vegetation (e.g., fire scars on vegetation, re-sprouts). This field work showed that fire results in plant defoliation and that regeneration by sprouts is very common and occurs rapidly after fire for most of the studied species (Pers. Obs.). All the tapia remnants have been burned at least once between 2000 and 2010; no sites were observed that did not show traces of burning (Alvarado, 2012; Ramahefamanana, 2012). Tapia woodlands are reduced to ten isolated remnants on the Ibity mountain. Six of these remnants, hereafter referred to as sites, were selected for the study. We excluded fragments that were dangerous to access or were disturbed by a short but intense presence of gold diggers. During the decade preceding the study, three of the six sites were burned once (Fire1) whereas the three others each burned three times (Fire3) (see Table 1 for site details and Fig. 1 the location map). The number of times each site burned was determined using a map of fire frequency over a period of 10 years (2000–2010) compiled by Ramahefamanana (2012). To evaluate the resilience of tapia woodland exposed to frequent fires, we assumed that fire frequency was a more relevant factor to our study goals than time since the last fire because: 1) fire frequency is increasing and three fire events in ten years are regarded as a rather high frequency and 2) for four of the six sites, the last fire occurred at least three years before the beginning of the phenology monitoring; the two other sites, for which the last fire occurred less than two years before the beginning of the phenology monitoring, were distributed equally, with one haven burned once and three times (Table 1).

2.4. Reproductive phenology of woody species

The thirteen most common endemic woody species (Alvarado et al., in press), belonging to seven families, were selected for this study (Table 2). For each species, 3 to 15 reproductive individuals (>1 m) were marked and numbered at each site within a randomly placed 40 × 40 m plot, with a total of 373 individuals recorded and monitored. Observations of flowering and fruiting were performed every two months over a period of two years (February 2010 to December 2011). Flowering

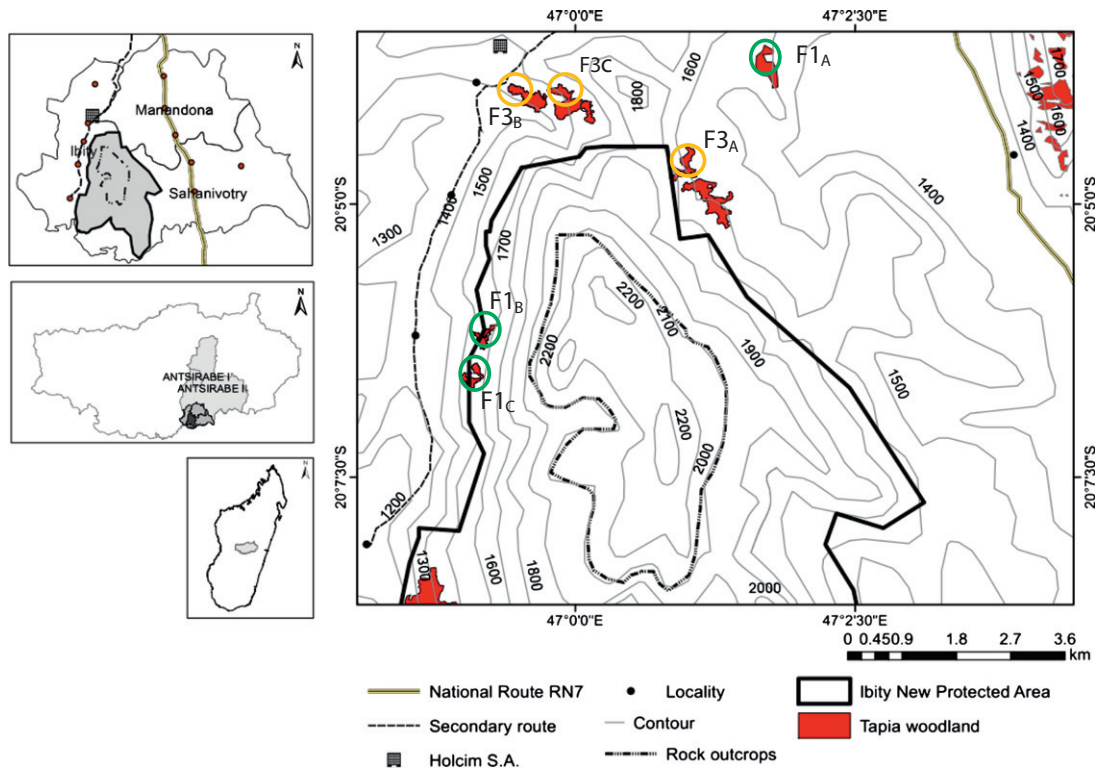


Fig. 1. Location of study sites at Ibity mountain, Madagascar, with different fire frequencies. Green circles: sites burned once (F1A, F1B and F1C); yellow circles: sites burned three times (F3A, F3B and F3C).

was defined by the presence of flower buds and/or open flowers and fruiting by the presence of unripe and/or ripe fruits. The method of Fournier (1974) was used to assess the intensity of these four individual phenophases by assigning one of the five categories of Fournier (0, 1 = 1–25%; 2 = 26–50%; 3 = 51–75% and 4 = 76–100%). This was done by estimating the percentage of an individual flowering (buds and flowers) and fruiting (green and ripe). Each Fournier category indicates the percent of branches in each phenophase among the total number of branches on each individual.

2.5. Data analysis

To assess phenology, data were described at two different scales: landscape (Ibity mountain, all sites combined) and community (site

by site, all species). Three types of information were gathered – at the landscape level: 1) the number of species in each phenophase, 2) the total number of individuals of each species in each phenophase; and at the community level: 3) the number of individuals of all species per site in each phenophase. At both scales (landscape and community), the data were grouped for analysis according to fire frequency: burned once or three times.

Fournier's percentage of intensity, calculated for each species at each site and for the two fire frequencies, was used to determine the reproductive peaks and to describe the phenology of a given species (Benke and Morellato, 2002; San Martin-Gajardo and Morellato, 2003). The percent of intensity of each phenophase was calculated according to Fournier's equation (1974) (for details see Supplementary Material S1).

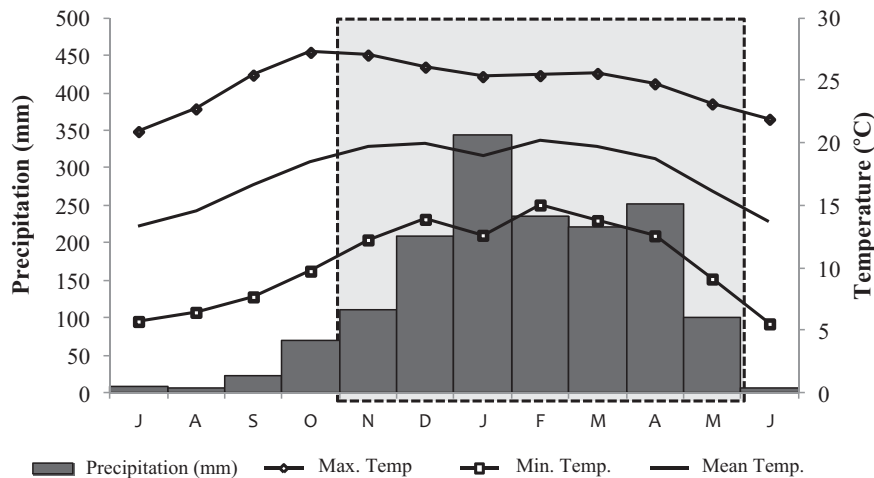


Fig. 2. Distribution of precipitation, mean, mean maximum and mean minimum temperatures for Ibity mountain, Astirabe district, Madagascar (data from 1961 to 1990); source: Meteorology Service of Ampandrianomby. Dotted box includes the rainy season from November to May when rainfall is >100 mm per month.

Table 1
Local names, altitude and fire information concerning the six study sites at Ibity mountain, Madagascar.

Site code	Local name of the site	Altitude	Area (km ²)	Frequency and year of fire	Longitude	Latitude
Fire1 _A	Manandona	1461 m	0.18	Burned once before 2008	47°2'10.49"E	20°3'37.15"S
Fire1 _B	Maneva-Ihasy II	1501 m	0.05	Burned once in 2006	46°59'10.74"E	20°6'13.07"S
Fire1 _C	Maneva-Ihasy III	1560 m	0.06	Burned once in 2006	46°59'4.57"E	20°6'34.53"S
Fire3 _A	Faliandro	1620 m	0.08	Burned three times: 2006/2007/2010	47°0'58.33" E	20°4'38.24"S
Fire3 _B	Kiboy 1	1547 m	0.12	Burned three times: 2003/2005/2007	46°59'31.25"E	20°3'59.15"S
Fire3 _C	Kiboy 2	1605 m	0.19	Burned three times: 2003/2005/2007	46°59'49.57"E	20°3'58.66"S

Synchrony of species and individuals was also calculated to determine if synchronization varies depending on the scale (landscape and community) and on fire frequency (burned once or three times). At the landscape level we analyzed four phenophases: flower buds, open flowers, unripe and ripe fruits. At the community level, just the presence of open flowers and ripe fruits were considered because these two phenophases have the greatest ecological importance for pollination and seed dispersal (Smith-Ramírez and Armesto, 1994).

We applied the Augspurger's (1983) index of synchrony to estimate the degree of synchronization of an individual i (X_i), measured as the amount of flowering/fruitlet overlap (months) compared to each of the other individuals in the sampled population (for details see Supplementary Material S1). Synchrony of a population ($Z_{\text{population}}$) is a measure of the overlap of flowering/fruitlet between individuals of the same species in a given population, and is equal to the average values of the individual synchronies (X_i), calculated according to the population synchrony index proposed by Augspurger (1983, Supplementary Material S1). Flower/fruitlet synchrony of one individual or of all individuals in a population is perfect when the value of Z_i and $X_i = 1$, and absent when Z_i and $X_i = 0$.

To verify whether synchrony increases, decreases or remains unchanged according to geographic scale and fire frequency, the indices mentioned above were adapted to calculate: 1) the synchrony of all species at Ibity mountain ($Z_{\text{Landscape}}$), and 2) the synchrony of all species for sites burned once ($Z_{\text{Landscape/Fire1}}$ and $Z_{\text{Community/Fire1}}$) or three times ($Z_{\text{Landscape/Fire3}}$ and $Z_{\text{Community/Fire3}}$) (at the landscape and community levels). For these calculations, in the index X_i species were considered as the individuals in the original formula (see formula and explanations above) and the Z index, comparing the values for each species, which yields a value of synchrony at the community or landscape level. In all cases, species or individuals that were not observed in any reproductive phenophase or did not produce any flowers and/or fruits were included in the calculations of the index and their X_i synchrony value was considered to be 0.

Kruskal–Wallis tests were performed to identify possible differences in synchrony (X_i) for both main phenophases for which the synchrony

index was calculated (open flowers and ripe fruits) between sites burned once and three times. At the landscape level, the test was calculated by taking the value X_i of each species and comparing the two fire frequencies in all locations pooled together. At the community level, the test was performed to determine the differences in synchrony among the 6 sites and between the two fire frequencies, taking the value X_i of each species at each site. Results for each species are presented in Supplementary Material S2 and S3. Statistical analyses were performed using the R software package (The R Foundation for Statistical Computing, version 2.15.1).

3. Results

3.1. Reproductive phenology at Ibity mountain

The onset of flowering among the 13 species studied was marked by an increase in the number of species with flower buds at the end of the dry season in July and August (Fig. 3). Peak flowering occurred at the beginning of the rainy season in October–November (Fig. 3). Fruits were produced throughout the year (Fig. 3), with unripe fruits peaking in the beginning to the middle of the rainy season. The peak of ripe fruits was observed at the end of the rainy season in February, and another peak occurred in the beginning of wet season in October (Fig. 3).

The percentage of individuals with flowers and fruits was below 50% in all months, but was highest from August (end of dry season) to December (peak of the rainy season) (Fig. 4). The percentage of individuals with fruit was irregular during the two years of monitoring (Fig. 4), and an evident decrease was observed in the dry season (May to September).

3.2. Fire frequency and phenology

Sites burned once during the decade prior to observation showed a higher percentage of individual flowering than those burned three times (Fig. 5). A similar trend was observed for fruit production: sites

Table 2
List of the studied species (Note: photos are available for some species via the on-line *Catalog of the Vascular Plants of Madagascar*; see Additional information).

Family	Species	Life form	Geographic distribution	Additional information
Anacardiaceae	<i>Abrahamia ibityensis</i> (H. Perrier) Randrian. & Lowry ined.	Shrub	Endemic to Madagascar (Ibity and Itremo areas only)	www.tropicos.org/Name/50297889?projectid=17
Anacardiaceae	<i>Rhus taratana</i> (Baker) H. Perrier	Tree	Endemic to Madagascar (widespread)	www.tropicos.org/Name/1300041?projectid=17
Araliaceae	<i>Schefflera bojeri</i> (Seem.) R. Vig.	Shrub	Endemic to Madagascar (widespread)	www.tropicos.org/Name/2200727?projectid=17
Asteraceae	<i>Vernonia ibityensis</i> Humbert	Shrub	Endemic to Madagascar (Ibity and Itremo areas only)	www.tropicos.org/Name/2703641?projectid=17
Asteraceae	<i>Distephanus polygalifolius</i> (Less.) H. Rob. & B. Kahn	Shrub	Endemic to Madagascar (widespread in central region)	www.tropicos.org/Name/2736862?projectid=17
Ericaceae	<i>Erica andringitrensis</i> (H. Perrier) Dorr & E.G.H. Oliv.	Shrub	Endemic to Madagascar (known from <5 localities in central region)	www.tropicos.org/Name/50150825?projectid=17
Ericaceae	<i>E. cryptoclada</i> (Baker) Dorr & E.G.H. Oliv.	Shrub	Endemic to Madagascar (widespread)	www.tropicos.org/Name/50142789?projectid=17
Ericaceae	<i>Vaccinium secundiflorum</i> Hook.	Shrub	Endemic to Madagascar (widespread)	www.tropicos.org/Name/12303017?projectid=17
Orobanchaceae	<i>Radamaea montana</i> Benth.	Liana, shrub	Endemic to Madagascar (widespread)	www.tropicos.org/Name/29205927?projectid=17
Phyllanthaceae	<i>Uapaca bojeri</i> Baill.	Tree	Endemic to Madagascar (widespread in central region)	www.tropicos.org/Name/12800490?projectid=17
Sarcolaenaceae	<i>Pentachlaena latifolia</i> H. Perrier	Shrub, tree	Endemic to Madagascar (Ibity only)	www.tropicos.org/Name/28800063?projectid=17
Sarcolaenaceae	<i>Sarcolaena oblongifolia</i> F. Gérard	Shrub, tree	Endemic to Madagascar (widespread in central region)	www.tropicos.org/Name/50264106?projectid=17
Sarcolaenaceae	<i>Xerochlamys bojeriana</i> (Baill.) F. Gérard	Shrub	Endemic to Madagascar (widespread in central region)	www.tropicos.org/Name/28800034?projectid=17

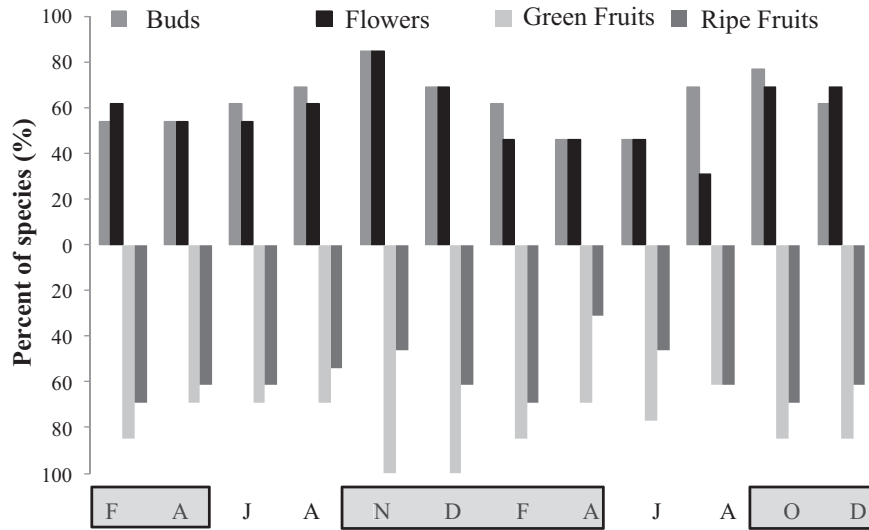


Fig. 3. Percentage of woody species with flower buds and flowers (above the x-axis), unripe fruits and ripe fruits (below the x-axis) during the two years of study at Ibity mountain, Madagascar. The shaded months correspond to the rainy season.

burned once had a higher percentage of individual fruiting than those burned three times during the two years of monitoring (Fig. 5).

3.3. Fire and reproductive synchrony

For the 13 species analyzed, flowering synchrony at the landscape level showed an average synchrony of $Z_{Landscape} = 0.64$ for flower buds and $Z_{Landscape} = 0.62$ for flowers (Table 3). The values of flower synchrony decreased but were not significantly different for sites burned once and three times (Table 3). Likewise, the difference in population synchrony at the landscape scale between the two fire frequencies was not significant (Table 3). At the community level, the flowering synchrony index of each site was also low but significantly different between sites burned one and three times: $Z_{Community/Fire1}$ ranged from 0.16 to 0.54 for sites burned once vs. values of $Z_{Community/Fire3}$ from 0.18 to 0.48 for sites burned three times (Table 3). The lower values of $Z_{Community/Fire3}$ for sites burned three times were not significantly different from the values $Z_{Community/Fire1}$ for sites burned once (Table 3).

At the landscape level, the synchrony of unripe fruit production was high ($Z_{Landscape} = 0.80$) while ripe fruit synchrony was lower ($Z_{Landscape} = 0.55$) for the 13 species analyzed (Table 3). When comparing for the two fire frequencies, the synchrony of ripe fruits was lower for sites burned once than for those burned three times

($Z_{Landscape/Fire1} = 0.43$ and $Z_{Landscape/Fire3} = 0.55$, respectively) and this difference was significant (Table 3). At the community level, the synchrony indices for each site were also low and significantly different: $Z_{Community/Fire1}$ ranged between 0.16 and 0.63 for sites burned once, whereas $Z_{Community/Fire3}$ was between 0.20 and 0.43 for sites burned three times (Table 3). The synchrony of sites burned three times ($Z_{Community/Fire3}$) was lower but not significantly different from that of sites burned once ($Z_{Community/Fire1}$) (Table 3).

4. Discussion

4.1. Reproductive phenology at Ibity Mountain

At Ibity, flowering began at the end of the dry season (August) and peaked at the beginning of the rainy season (November) suggesting a relation to the increase in day length and the onset of seasonal rains, as observed elsewhere in the southern hemisphere (Morellato et al., 2000, 2013; Van Schaik et al., 1993). Similar flowering patterns have been reported in Neotropical moist, seasonal and dry forests (Justiniano and Fredericksen, 2000; Rubim et al., 2010; Wright and Calderón, 2006) and also for Cerrado woodlands (Silberbauer-Gottsberger, 2001; Wallace and Painter, 2002) and Restinga vegetation found on sandy and salty soils in northeastern Brazil (Medeiros et al., 2007). In African

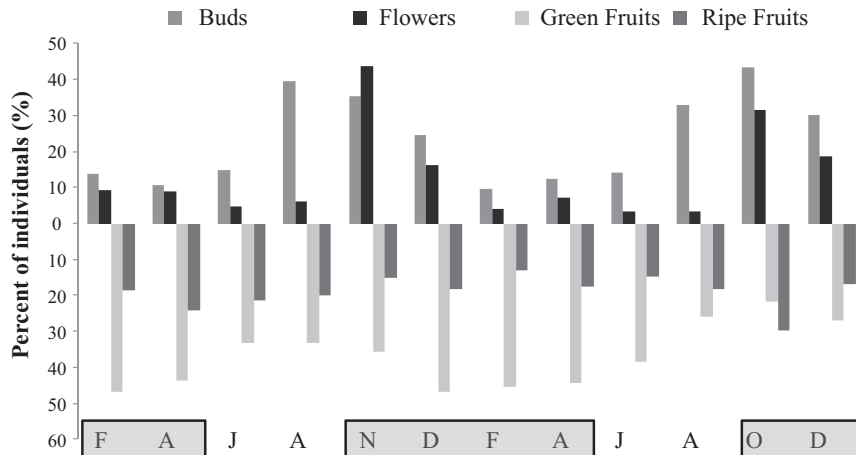


Fig. 4. Percentage of individuals with flower buds and flowers (above the x-axis), unripe fruits and ripe fruits (below the x-axis) during the two years of study on Ibity mountain, Madagascar. The shaded months correspond to the rainy season.

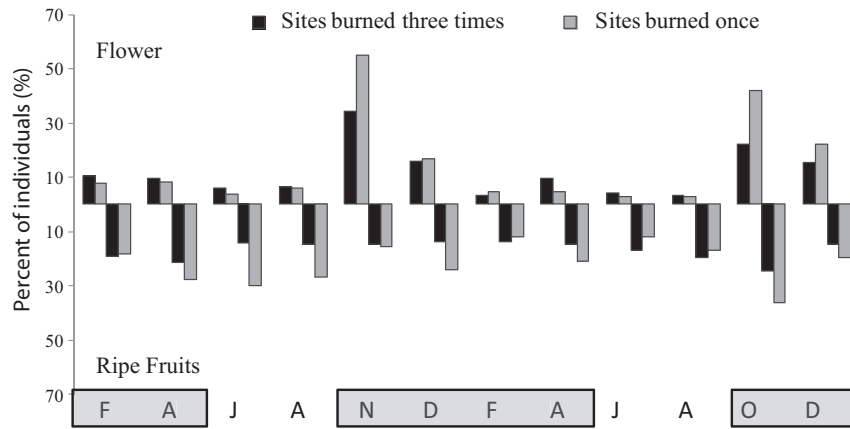


Fig. 5. Percentage of individuals with flowers (above the x-axis) and ripe fruits (below the x-axis) at sites burned once and three times during the two years of study at Ibity mountain, Madagascar. The shaded months correspond to the rainy season.

savannas and woodlands, which are under similar climatic conditions and situated at latitudes similar to Ibity mountain, phenology is determined by precipitation and temperature (Chidumayo and Frost, 1996). Flowering of most woody species occurs before the rainy season (September to October), although some species flower in the middle or at the end of the rainy season and only a small number produce flowers in the dry season (Chidumayo and Frost, 1996). On Ibity mountain, the strategy used by woody species in which fruiting occurs mainly in the wet season is likely linked to increase water availability, which promotes seed germination and seedling establishment, as observed in wood savannas in Africa and Australia (Ngulube et al., 1998; Williams et al., 1999).

4.2. Fire frequency and phenology

We observed a reduction of the number of individuals producing flowers and fruits, and of the intensity of each phenophase at the landscape scale in the frequently burned tapia woodland (subjected to fire 3 times) compared to those burned just once. Some studies have shown that fire frequency has an effect on phenological patterns of woody species in various ecosystems via an increase in fruit production and/or an acceleration of the phenological cycle by shifting the starting date of flowering/fruiting forward by several days (Paritsis et al., 2006; Pausas et al., 2004; Setterfield, 1997). On Ibity we found that flowering began at the end of the dry season (August) when the risk of fire is still high

(Govender et al., 2006), which may explain the reduction of flower and fruit production in vegetation that is burned at that time of year because fire results in defoliation of plants (Pers. Obs.). Contrary to what we have observed at Ibity, flowering of several woody species in some African savannas that are burned frequently (e.g. in Cameroun, Seghier et al., 1995) occurs in the middle or at the end of rainy season, after the risk of fire has subsided. On Ibity, Rasoafaranaivo (2005) found no indication of flowering or fruiting of *Abrahamia ibityensis* or *Pentachlaena latifolia* one year after fire, while *Distephanus polygalifolius* and *Xerochlamys bojeriana* flowered the year after burning.

The analysis of fire frequency on Ibity over a 10-year period (2000–2010) showed that most burning occur between the end of the dry season and the beginning of the wet season, with a peak in the number of fires in September and October (Alvarado, 2012; Ramahefamanana, 2012). Early fires, during the transition from wet to dry season (April and May), are less severe because there is less accumulated biomass and the available fuel is not completely dry (Govender et al., 2006; Knapp et al., 2004). Frequent low-intensity fires in the dry season in Australian savannas resulted in a significant reduction in flower and seed production for some woody species (Setterfield, 1997). Late fires during the transition from dry to wet season are much more severe because of the greater amount of accumulated dry biomass, leading to a reduction in flower, fruit and seed abundance of woody species in Australian savannas (Setterfield, 1997; Williams et al., 1999).

Table 3

Synchrony indices of flowering and fruiting in tapia woodlands on Ibity mountain, Madagascar, calculated at the landscape and community scales (by fire frequency and site), and comparison between sites burned once (Fire1_A, Fire1_B, Fire1_C) and three times (Fire3_A, Fire3_B, Fire3_C). Total: all six sites pooled together sites included. Fire 1 and Fire 3: pooled data for fire frequency (three sites per fire frequency); Details regarding Z (synchrony index) are given in the Methods section.

Phenophase	Site	No. of species	% species	No. of Individuals	Z _{Landscape}	Z _{Community}	Kruskal–Wallis χ^2
Buds	Total	13	100	373	0.64		
Flowers	Total	13	100	373	0.62		
	Fire 1	11		171	0.51		Kruskal–Wallis $\chi^2 = 0.81$, p-value = 0.37
	Fire 3	13		202	0.44		
	Fire1 _A	6	100.0	57		0.54	Xi by Fire
	Fire1 _B	9	78	54		0.16	Kruskal–Wallis $\chi^2 = 2.49$, p-value = 0.11
	Fire1 _C	8	100.0	60		0.52	Xi by Site
	Fire3 _A	9	67	56		0.18	Kruskal–Wallis $\chi^2 = 34.95$, p-value < 0.001
	Fire3 _B	9	100	59		0.48	
	Fire3 _C	11	91	87		0.25	
	Unripe fruits	Total	13	100	332	0.80	
Ripe fruits	Total	13	100	332	0.55		
	Fire 1	11		149	0.43		Kruskal–Wallis $\chi^2 = 10.70$, p-value = 0.001
	Fire 3	13		183	0.55		
	Fire1 _A	6	100	48		0.63	Xi by Fire
	Fire1 _B	9	88.9	47		0.16	Kruskal–Wallis $\chi^2 = 1.53$, p-value = 0.22
	Fire1 _C	8	75	54		0.20	Xi by Site
	Fire3 _A	9	88.9	51		0.20	Kruskal–Wallis $\chi^2 = 28.54$, p-value < 0.001
	Fire3 _B	9	89	52		0.35	
	Fire3 _C	11	91	80		0.43	

4.3. Fire and reproductive synchrony

We observed an asynchronous phenology among woody species on Ibity mountain at the two scales considered: landscape and community. Sites burned three times were less synchronous than those burned just once, and our results suggest that frequent fire can affect the reproductive success of species by reducing synchrony. Fire increases synchronicity at local scales when all plants are stimulated to flower after a fire event (Sarmiento, 1992). However, in our study, fire decreased synchronicity at landscape scales because plants are responding differently to different fire histories (fire intensity and frequency, date of fire event, etc.). Synchrony in reproduction may enhance plant ability to attract pollinators and seed dispersers (Augspurger, 1983) and the chances for outcrossing (Aguilar et al., 2006), thus increasing reproductive success (Rathcke and Lacey, 1985).

4.4. The case of *U. bojeri*

Members of the genus *Uapaca* also occur in tropical Africa, and some are common in “miombo” woodland, an African vegetation type homologous to tapia woodland, while others are found in closed canopy forests of lowland Africa (Campbell, 1996; Chidumayo and Frost, 1996; Ngulube et al., 1998). The ecology and reproductive biology of *U. bojeri* are still largely unknown, but can be compared with such African species as *Uapaca kirkiana*, *Uapaca pilosa* and *Uapaca nitida*. The response of woody species after fire in “miombo” and tapia woodland is similar, and in both vegetation types fire plays a major role in their degradation (Alvarado et al., in press; Campbell, 1996; Chidumayo, 1989).

U. bojeri, which represents 82% of the trees in Ibity tapia woodlands (Alvarado et al., in press), is thus a good model to illustrate phenology patterns in this vegetation and the response to fire frequency at local and landscape levels. We found that *U. bojeri* flowering peaks in October and November, and fruiting peaks in October, although fruits were also present until December for sites burned once and three times (Fig. 6). Seed dispersal has been recorded in the rainy season and is likely related to the requirements for germination since the seeds of this species are recalcitrant, losing their viability a few days after being dispersed (Kull et al., 2005; Randrianavosa et al., 2011). Concerning fire, we observed a similar response to that of other members of the community. *U. bojeri* has a higher production of flowers and fruits in sites burned once than those burned three times. Our results also confirm the vulnerability of this species to fire. Adult individuals of *U. bojeri*, as well as some other woody species in tapia woodland, can tolerate fire because adult they typically have thick, spongy bark, weakly flammable leaves, and underground reserves, and can re-sprout after fire (Campbell, 1996; Kull, 2002). However, fire changes its structure and composition of tapia woodland (Alvarado et al., in press) and reduces natural regeneration by killing seedlings (Gade, 1996). Thus, a reduction in the intensity of

reproductive events can have strong implications for the potential of this species to achieve reproduction by cross-pollination and regeneration by seeds.

5. Conclusions

Flower and fruit production of woody species on Ibity mountain occurred at the end of the dry season and continued throughout the wet season. With regard to our initial questions, we have demonstrated that fire affected phenology by reducing the percentage of individuals that participated in each event, and that the effect of fire on flower and fruit production was greater in more frequently burned sites. It should be noted that a bi-monthly monitoring regime limited the interpretation of some of our results (Morellato et al., 2010). An increase in the frequency of observations would be desirable to refine our understanding of possible variation in the starting date and the duration of the phenophases impacted by fire.

Fire is recognized as one of the major disturbances affecting mortality and recruitment of trees in savannas, and our study confirms that fire also impacts the timing of plant reproduction at the landscape and community levels. We suggest that future management actions for the new protected area on Ibity must take the fire regime into account in order to maintain a balance among the vegetation types and to sustain other system functions that are affected by fire, such as vegetative regeneration and seed germination. The response of woody species to pressure from human-caused fires, whose current regime differs from the naturally occurring regime in which the studied species have evolved, may alter the interactions with pollinators and predators, and thus affect the demographic cycle of species and reduce natural regeneration.

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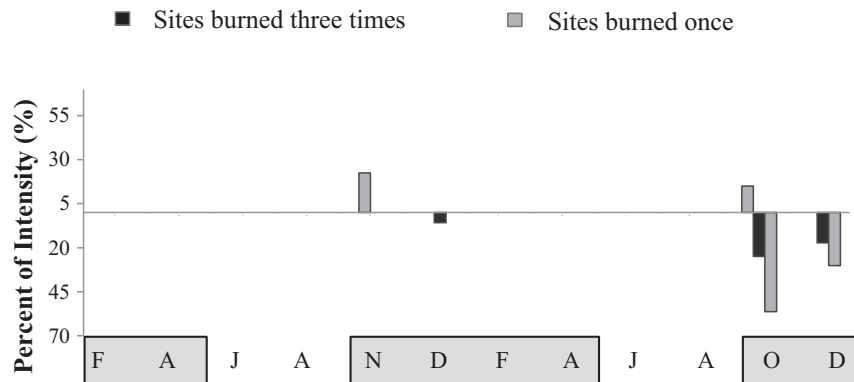


Fig. 6. Percentage of individuals with flowers (above the x-axis) and ripe fruits (below the x-axis) at sites burned once and three times for the dominant species of tapia woodland, *Uapaca bojeri*, during the two years of study at Ibity mountain, Madagascar. The shaded months correspond to the rainy season. $N_{F1} = 46$ individuals, $N_{F3} = 45$ individuals.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.sajb.2014.06.001>.

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