Phenology of different vegetation types in Tsimanampetsotsa National Park, southwestern Madagascar

Rakotomalala Yedidya Ratovonamana[1,2], Charlotte Rajeriarison[1], Edmond Roger [1] & Jörg U. Ganzhorn[2]

[1]Département de Biologie et Ecologie Végétale, Faculté des Sciences, P.O Box 906, Université d'Antananarivo, Antananarivo 101, Madagascar
E-mail: ryrorch@yahoo.fr, charlotte.rajeriarison@moov.mg, rogeredmond1@yahoo.fr

[2]Department of Animal Ecology and Conservation, University of Hamburg, Biozentrum Grindel, Martin-Luther-King Platz 3, D-20146 Hamburg, Germany
E-mail: ganzhorn@zoologie.uni-hamburg.de

Abstract

From June 2007 to March 2009, phenological studies were carried out in Tsimanampetsotsa National Park, a spiny forest ecosystem in southwestern Madagascar. Six phenological plots of 5 x 200 m were installed and monitored biweekly in three vegetation types (dry forest on sandy soil, xerophytic bush on calcareous soil, and dry forest on ferruginous soil). The different phenophases could be linked to ambient conditions. The majority of plant species lost their leaves during the dry season (April to November). In all plots, flowering showed a bimodal distribution: one group of species flowered during the dry season and the other group had their maximum flowering peak during the wet season (December to March). Fruiting started at the end of the dry and beginning of the wet season (December, January), a period when strong winds prevail. This period also coincides with the start of the hot-wet season when possibly seed dispersing animals increase their activity or have come out of hibernation (*Microcebus griseorufus*). Both phenomena can be interpreted as facilitation for seed dispersal. The presence of leaves was linked to actual rainfall. However, day length rather than the actual rainfall triggered flowering and fruiting. This indicates that plants adapted their reproductive cycles to long-term climatic averages (reflected by day length), which seem to be more reliable in evolutionary terms than using erratic rains as a cue to initiate reproduction.

Key words: plant phenology, phenophase, Tsimanampetsotsa National Park, Madagascar

Résumé détaillé

Cette étude a été réalisée dans le Parc National de Tsimanampetsotsa, localisé dans la partie Sud-ouest de Madagascar, et un des écosystèmes les plus secs de l'île. Depuis juin 2007, six parcours phénologiques de 0,1 ha (soit 5 x 200 m) ont été installés dans trois différents types de végétation dont deux parcours phénologiques dans la forêt sèche décidue sur sol sableux ; deux dans le fourré xérophytique sur substrat calcaire et deux dans une forêt sèche sur sol ferrugineux. 1337 individus appartenant à 111 espèces ont été étiquetés et observés de juin 2007 à mars 2009 toutes les deux semaines. La présence des feuilles, des fleurs ou des fruits chez les individus sélectionnés a été notée. Pour l'analyse des données, des calendriers phénologiques ont été dressés pour chaque phénophase (feuillaison, défeuillaison, floraison et fructification). Les données par phénophase ont été corrélées avec plusieurs variables climatiques telles que la température, l'amplitude thermique journalière, la photopériode, l'insolation et la précipitation.

Les résultats de cette étude ont montré l'absence d'une grande différence entre le comportement phénologique des trois communautés végétales. La période de feuillaison des espèces dans les trois communautés végétales s'étale de janvier à mai ; la défeuillaison maximale de mai à décembre. Pour la forêt sèche, la durée de la saison de défeuillaison est plus longue que celle de feuillaison. Dans tous les parcours phénologiques, la perte des feuilles chez les espèces correspond à la diminution de la température pendant des mois où la longueur du jour est courte, puis augmente progressivement à cause des effets de stress hydrique. La reprise de la phase végétative active (maximum feuillaison) débute à la tombée de la première pluie, même si la quantité est relativement minime. La floraison, s'étale durant toute l'année, mais est marquée par une activité bimodale : un pic de floraison qui coïncide avec la période de défeuillaison de la saison sèche (octobre-novembre) avant la saison de pluie ; puis un pic de floraison maximale durant la période pluvieuse (janvier-février), lors du maximum de feuillaison. Dans tous les parcours phénologiques, la floraison des espèces est liée à la variation de la longueur du jour. La majorité des espèces fleurissent

Ratovonamana, R. Y., Rajeriarison, C., Roger, E. & Ganzhorn, J. U. 2011. Phenology of different vegetation types in Tsimanampetsotsa National Park, south-western Madagascar. *Malagasy Nature*, 5: 14-38.

durant les périodes chaudes, lors du jour long avec une forte insolation. Pour la fructification, elle se déroule entre la fin de la saison sèche et le début de la période pluvieuse. Chez certaines espèces, la période de fructification est plus longue, parfois elle s'étale entre deux périodes de floraison successive. Mais la période maximale de fructification a été enregistrée vers la fin de la saison sèche, la période où des espèces animales sont sorties du stade d'hibernation ou sont devenus plus actives.

La phénologie de la reprise de la feuillaison est en relation avec le facteur humidité. Alors que la floraison et la fructification sont liées à la variation de la longueur du jour. Ce qui fait que les cycles reproductifs des plantes sont corrélés avec la variation à long terme du climat (longueur du jour).

Mots clés : phénologie de plantes, phénophase, Parc National de Tsimanampetsotsa, Madagascar

Introduction

Knowledge of plant phenological patterns is important to understand effects of climate change (Elisabeth & Johnson, 1993), forest regeneration processes (Kruesi, 1981; Sorg & Rohner, 1996), and forest functions and services such as pollination, seed dispersal, and seed predation (Selwyn & Parthasarathy, 2007). Finally, plant phenological data provide the basis to measure food availability for animals and to link the temporal and spatial resource distribution to population characteristics of the consumer (van Schaik *et al.,* 1993; Chapman *et al*., 1999; Anderson *et al*., 2005). While plant-animal interactions are important to understand ecosystem functioning and ecosystem services from a biotic point of view, it is important to understand the abiotic factors that drive phenological phenomena.

Climate change has developed into one of the major issues discussed as a possible driver threatening Madagascar's ecosystems (Hewitson & Crane, 2006; Malcolm *et al*., 2006; Hannah *et al*., 2008). In general, weather conditions in Madagascar seem to be less predictable than in many other parts of the world (Dewar & Richard, 2007). With respect to bioclimatic classification, southwestern Madagascar constitutes the most unpredictable part of the island (Donque, 1975). The combination of an arid and variable climate might require rapid and specific responses of plants towards ambient conditions in order to complete their reproductive cycles. On the other hand, erratic rainfall might not reliably indicate the onset of the wet season. Therefore, initiation of the flowering and fruiting cycle based on unpredictable rain may not be advantageous and responding to proxies, such as day-length, might reflect long-term averages of rainfall patterns, which in turn would lead to more reliable reproductive success.

The goal of this study was to document the phenological characteristics of different vegetation types in Tsimanampetsotsa National Park. The analyses focus on the plant community level. Specific objectives were: 1) to record general leaf, flower, and fruit phenology of plant species of the different vegetation types; 2) to determine the effects of ambient conditions on the phenology of different vegetation types; 3) to test whether plant phenology follows actual rainfall patterns or whether it uses long-term conditions and associated day lengths as a more reliable environmental proxy in this unpredictable environment.

Materials and methods

Study site

The study was carried out from June 2007 to March 2009 in southwestern Madagascar, in the northern portion of the Tsimanampetsotsa National Park. Our study area is situated between 24°00' and 24°23'30" S and 43°44' and 43°46' E.

The study area is characterized by a semi-arid tropical climate with an average annual rainfall of less than 500 mm (Mamokatra, 1999), but annual variation is considerable. The dry season usually lasts eight to nine months, between March and October/November. Annual mean temperature is approximately 24°C.

The Tsimanampetsotsa forest is part of the southwestern spiny forest flora of Madagascar. The various formations that compose the Tsimanampetsotsa forest contain some of the most unique plant communities on the island and the spiny bush harbors the highest level of plant endemism with 48% of the genera and 95% of the species endemic (Elmqvist *et al.,* 2007). The forest is characterized by many xerophytic and drought tolerant woody species of the families Didiereaceae and Euphorbiaceae. Our study area in the Tsimanampetsotsa National Park is characterized by distinct topographical features and associated vegetation types (Table 1, Figure 1):

1) The coastal plane adjacent to the soda lake (Tsimanampetsotsa) with dry forest and hydro-hallomorphic soil with complex herbaceous formation in the littoral zone on sandy soil ("dry forest on sandy soil" or DFS),

Table 1. Characteristics of the different phenological plots; elevation ± standard deviation; n = 4 reading: 2 at the beginning and 2 at the end of each phenological plots).

Plot	Longitude E	Latitude S	Elevation [m]	Number of plant individuals per 0.1 ha	Substrate
DFS 1	43°44'16,441"	24°1'30,075"	7 ± 2	219	Sandy soil
DFS2	43°44'34,617"	24°2'7,096"	8 ± 3	207	Sandy soil
XBC3	43°44'49,783"	24°1'18,812"	42 ± 2	209	Calcareous soil
XBC 4	43°44'57,812"	24°2'1,409"	29 ± 3	223	Calcareous soil
DFF5	43°45'15,096"	24°1'10,895"	27 ± 1	245	Ferruginous soil
DFF 6	43°45'23,682"	24°1'53,715"	17 ± 1	234	Ferruginous soil

2) Calcareous soil with xerophytic bush on the grade rising to the Mahafaly Plateau ("xerophytic bush on calcareous soil" or XBC),
3) Ferruginous soil with low dry forest on the limestone of the Mahafaly Plateau ("dry forest on ferruginous soil" or DFF).

Phenological data collection

In each vegetation type, two replicate phenological plots, each measuring 0.1 ha (5 x 200 m) were established along access trails, resulting in six phenological plots (Figure 1, Table 1). The two plots per vegetation type were combined for the analyses presented here. We monitored only individuals of the different species considered large enough to flower and fruit. For shrubs and herbs, these were all individuals higher than 1 m and for trees, individuals with a diameter at breast height (DBH) ≥ 10 cm. Each plant was individually labeled with a serial number (indicating the plant number) and a letter code (indicating the phenological plot). Phenological data were recorded for all marked individuals within the six plots from June 2007 to April 2009. Every two weeks we recorded presence-absence of leaves, flowers or fruits (young or mature). For the sake of simplicity and since it is sometimes difficult to identify the onset of leaf flush, we noted the period when plants did not have leaves. Hence, this is the inverse measure for plants with leaves. The phenological characteristics (phenophase) used in this study were leafing, flowering, and fruiting. We chose this simple method to allow for long-term monitoring by different investigators and to facilitate comparisons between studies. In total, 1337 individuals from 111 plant species were observed.

Vegetation description

The structural description of the different vegetation types was based on two 100 m linear transect per type of vegetation (Godron, 1972; Gautier *et al*., 1994). This method has been used to analyze vegetation characteristics, and to determine the different strata for each phenological plot. In another set of 30 x 30 m² plots (six plots in DFS, six in XBC, five in DFF), we measured for each individual plant (tree, shrub, liana, and herb), the maximal height (in m), trunk diameter (DBH) at breast height (for trees, in cm), maximal (D_{max}) and minimal (D_{min}) diameter of the crown (in m); based on these two measurements, the average radius of the crown was calculated as: $r = (D_{max} + D_{min})/4$. Crown area of individual plants was calculated as the area covered by the crown projected vertically onto the ground and representing a circle (individual crown cover = $3.14 * r^2$). Total cover of woody vegetation was calculated as the sum of the cover of all individual trees and scrubs.

Climate

In order to assess possible effects of environmental factors on the phenological (leafing, flowering, and fruiting) of different plant species in the three communities, we monitored temperature and rainfall in the phenological plots. Average daily length and average daily insolation was taken from http://www.geocities.com/jjlammi/ and http://aom.giss.nasa.gov/srlocat.html by using the coordinates of the study area. Temperature data were collected from June 2007 to March 2009 with i-buttons. In each vegetation type, one i-button was installed in a shaded spot of a tree (on the south side) some 1.5 m above the ground. Each i-button was programmed to record temperature every two hours. The precipitation was measured with a rain gauge installed in our camp, which was localized in the study area, from 2006 to 2009.

To assess possible climate change over time, we analyzed inferred rainfall data of the study area during the period from 1950 to 2000 with the help of the DIVAGIS program (http://www.diva-gis.org) and measured rainfall from 2006 to 2009. Rainfall data

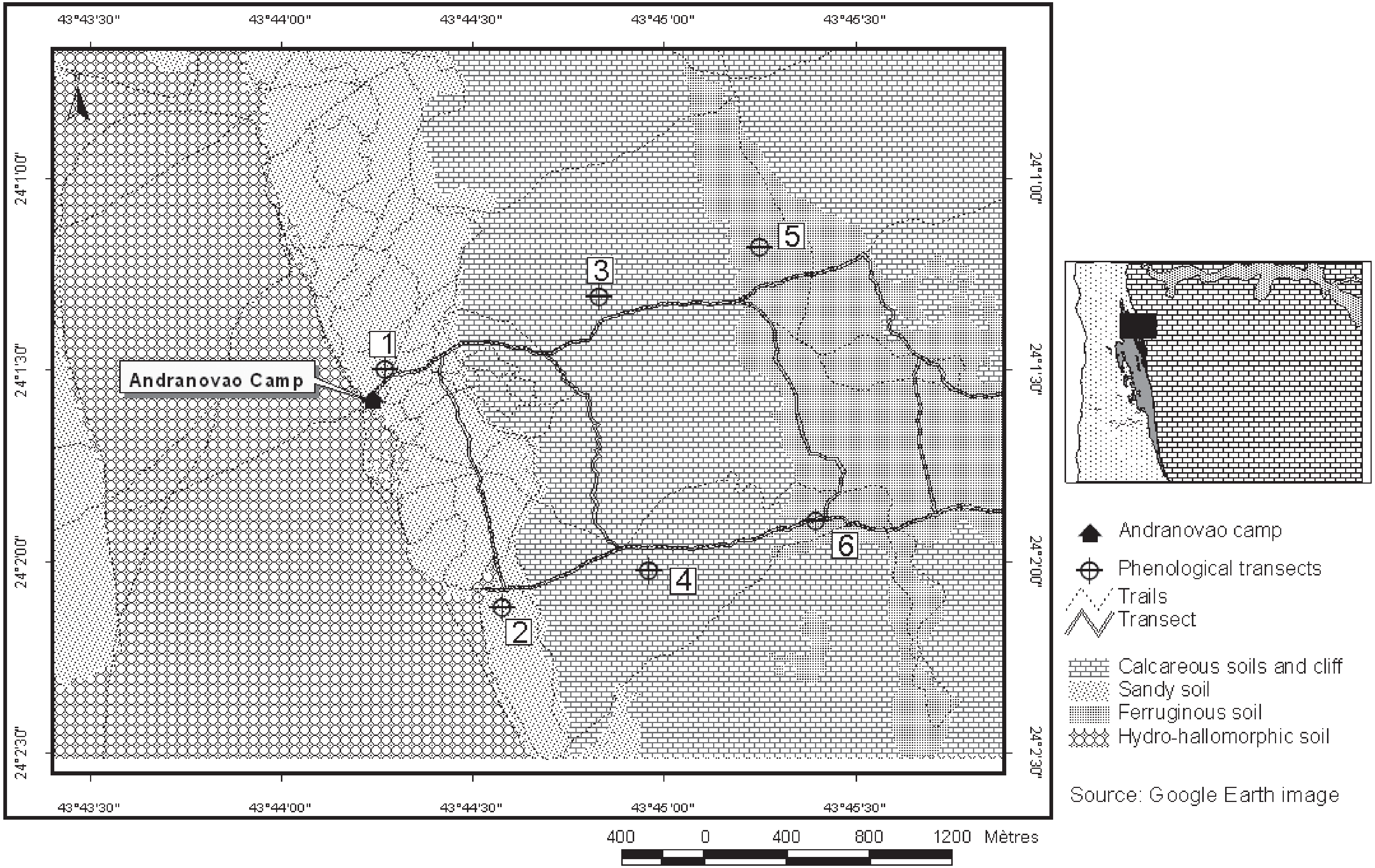

Figure 1. Localization of the different phenological plots in the study area in the dry forest on sandy soil (DFS) in the littoral zone (1,2), in the xerophytic bush on calcareous soil (XBC) (3,4), and in the dry forest on ferruginous soil (DFF) on limestone (5,6).

were related to the monthly average temperature and were used to define the different seasons. The wet season was defined as the months in which the monthly rainfall (R) was higher than twice the mean temperature: R > 2T (Moral, 1964).

Plant specimens collected in the field were identified in the herbaria of the Département de biologie et Ecologie végétales, FOFIFA, and the Parc Botanique et Zoologique de Tsimbazaza. Since scientific binomials are often revised, we used the names listed by Tropicos.org (http://tropicos.org/name/22900091). The voucher specimens are currently held in the Arboretum d'Antsokay in Toliara.

Data analyses

A plant species was recorded as having entered a specific phenophase when at least 25% of the individuals of that species had entered that state. We quantified community-level phenology of the different vegetation types by the percentage of plant species that were in a given phenophase. We calculated the duration of each phenophase for each species and combined the data for each community. This allowed us to compare the phenological characteristics for different species and to compare phenological pattern of different vegetation types.

To detect effects of ambient temperature, rainfall, insulation or day length on phenological parameters at the community level, we correlated the percentage of plant species in different phenophases with these variables. For this, the numbers of plant species in each phenophase per month were correlated with the monthly means of daily minimum temperature, maximum temperature, difference between average night and average day temperature, minimum temperature and maximum temperature, and monthly rainfall. Statistical tests were performed with SPSS 13.

Results

Vegetation description

The structural differences between the three vegetation types are illustrated in Figure 2. The forest on sand at the base of the cliff was the highest, followed by forest on ferruginous soil and the xerophytic bush on calcareous soil (Table 2). Mean canopy height (F = 85.7, $P < 0.001$), vegetation cover (F = 8.96, $P = 0.01$), and the crown diameter (F = 8.82, $P = 0.001$) varied significantly between the three vegetation types.

In each phenological plot, the number of plant species observed was lower than in the 30 x 30 m² plots used to record the horizontal structure per vegetation type.

Climate variables

According to the historical weather records, the study area is characterized by two different seasons: eight dry months (April - November) and four wet months (December - March; Figure 3). However, peak rainfall has shifted since the year 2000. Based on our data recorded between 2007 and 2009, mean maximum and minimum temperatures were 32.6°C and 17.8°C during the dry season. During the wet season, mean

Table 2. Characteristics of the three vegetation formation, with n = 6 (30 x 30 m²) plots: dry forest on sandy soil, n = 6 (30 x 30 m²) plots: xerophytic bush on calcareous soil and n = 5 (30 x 30 m²) plots: dry forest on ferruginous soil and each phenological plot.

	Dry forest on sand soil	Xerophytic bush on calcareous soil	Dry forest on ferruginous soil
Plots of 30 x 30 m² Number of plant species in plots	93	81	75
Number plant families in plots	39	35	36
Mean canopy height (m)	6.1 ± 0.2	3.0 ± 0.7	4.6 ± 0.7
Mean crown diameter (m)	1.6 ± 1	1.6 ± 0.9	1.9 ± 1.2
Cover (%)	76 ± 5	58 ± 11	75 ± 12
Mean plant density (ind/ha)	10 994 ± 3376	26 407 ± 17 292	18 222 ± 16 923
Plots of 5 x 200 m² Number plant species in the two phenological plots	63	58	63
Number plant families in the two phenological plots	27	27	29

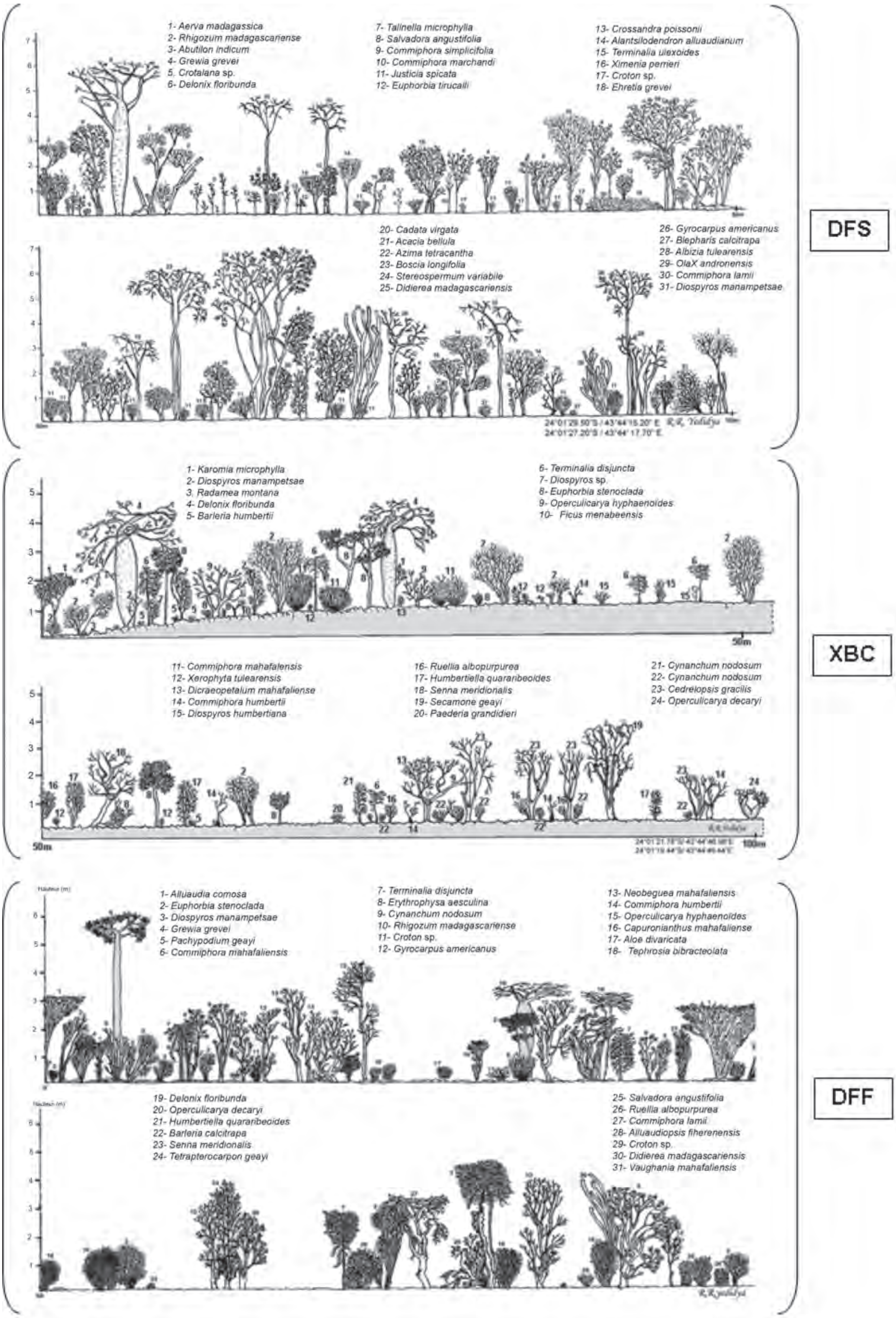

Figure 2. Structural aspect of the different vegetation types. Dry forest on sandy soil (DFS), xerophytic bush on calcareous soil (XBC), and dry forest on ferruginous soil (DFF).

Table 3. Comparison of ambient temperatures in the different phenological plots during the dry and the wet seasons from 2007 - 2009, with mean maximum temperature (max. temp.), mean minimum temperature (min. temp.), mean temperature (mean temp.), and diurnal temperature range (DTR = difference between mean maximum and minimum temperature). n = 8 months for the wet season and n = 14 months for the dry season.

Plots	Seasons	Max. temp. (°C)	Min. temp. (°C)	Mean temp. (°C)	DTR (°C)
DFS	Dry (n =14)	30.9 ± 3.1	17.3 ± 3.5	24.1 ± 3.0	13.6 ± 2.7
	Wet (n = 8)	34.2 ± 2.9	23.6 ± 2.0	28.9 ± 2.1	10.6 ± 2.8
XBC	Dry (n =14)	31.8 ± 3.5	17.4 ± 3.3	24.6 ± 3.1	14.4 ± 2.7
	Wet (n = 8)	35.7 ± 2.9	23.5 ± 1.7	29.6 ± 1.9	12.3 ± 2.8
DFF	Dry (n =14)	35.2 ± 3.1	18.8 ± 3.3	27.0 ± 2.6	16.4 ± 3.8
	Wet (n = 8)	35.8 ± 3.1	25.1 ± 1.8	30.5 ± 2.1	10.7 ± 3.0
Study area	Dry (n =14)	32.6 ± 3.7	17.8 ± 3.4	25.2 ± 3.2	14.8 ± 3.3
	Wet (n = 8)	35.3 ± 3.1	24.0 ± 2.0	29.6 ± 2.1	11.2 ± 2.9

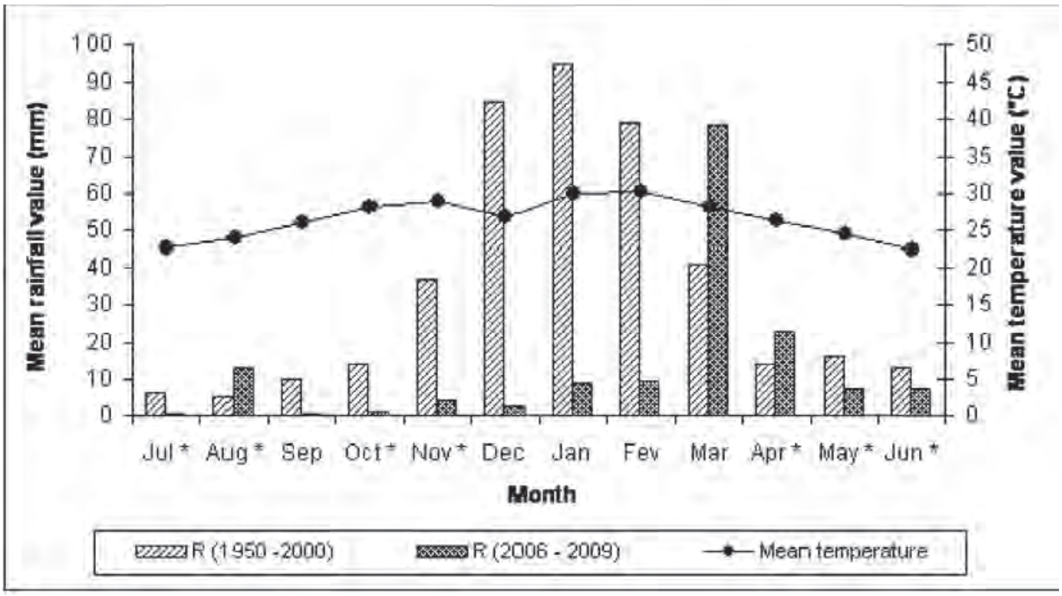

Figure 3. Climate diagram of the study area: (*) indicates dry months where rainfall value was less than twice the mean temperature value (R < 2T). Data from 1950 to 2000 from DIVAGIS (http://www.diva-gis.org) and data recorded in the study area from 2006 to 2009.

maximum and minimum temperatures were 35.5°C and 24.0°C. Based on the difference between mean maximum temperature and mean minimum temperature, the diurnal temperature range (DTR) during the dry season was much higher than during the wet season (Table 3, Figure 4). Monthly sunlight and fluctuations in day length are illustrated in Figure 5.

Leaf phenology

The relative abundance of plant species at leaf phenophase in the different plots are summarized in Table 4. The number of plant species with leaves decreases from June to the end of December (Table 4, Figure 6). In general, the plant species in each phenological plot reached their maximum vegetative activity (90-98% of plant species with leaves) between January and May/June, with a peak between February and April. The period of leaf fall began in May/June and lasted to December, with a maximum in October/November (Figure 6, Table 5).

On average, in the DFS habitat, leaves remain on the plants for 151 days (22 weeks) from January to May. This corresponds to a period without leaves of 214 days (31 weeks) from June to December. In October, about 50% (± 10) of the 63 plant species in the phenological plots had leaves. In the XBC habitat, the average duration of leaves remaining on the trees (maximum vegetative activity) and time without leaves was 182 days (26 weeks), with a maximum number of plants without leaves in November (49%; ± 1 of the plant species; n = 58 plant species). In the DFF, the maximum vegetative activity was observed between January and June for 161 days (23 weeks),

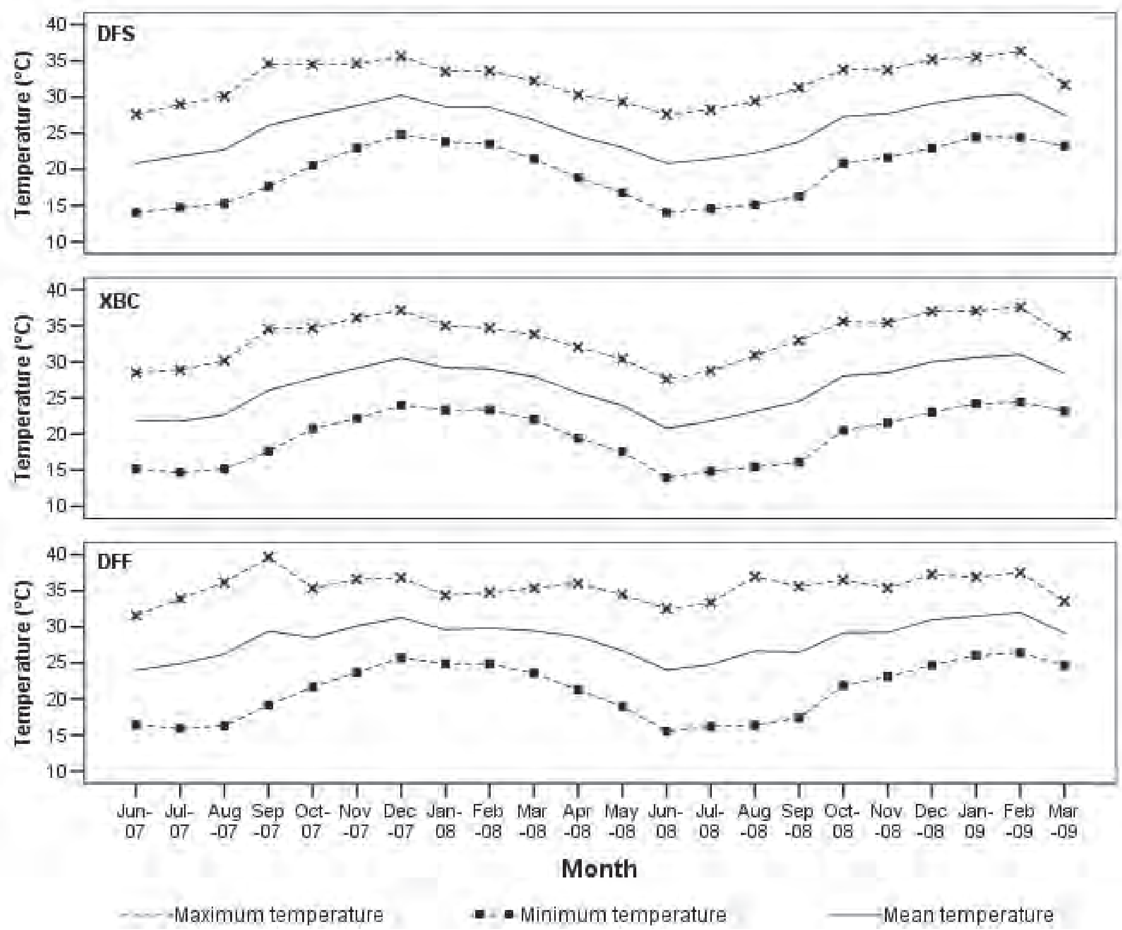

Figure 4. Minimum, maximum, and mean temperature in the different phenological plots.

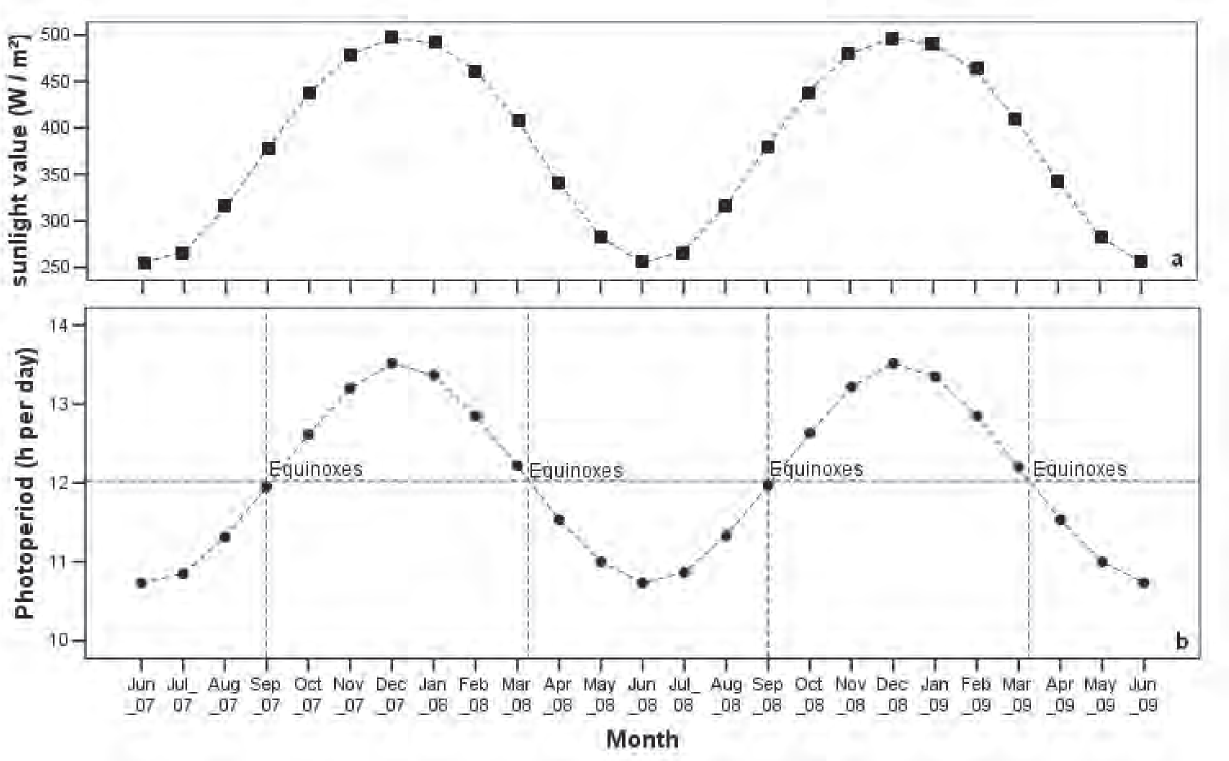

Figure 5. Variation of monthly sunlight (insulation) in watt per m² (a) and average day length (photoperiod) in hours per day (b) from http://www.geocities.com/jjlammi/; and http://aom.giss.nasa.gov/srlocat.html.

Table 4. Percentage of plant species with or without leaves in the different phenological plots from June 2007 to March 2009. Means and standard deviations are based on monthly averages. Phen: phenophase, Veg. type: vegetation types, n = number of plant species.

Phen.	Veg.-type	N	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
With leaves	DFS	63	66 ± 24	97 ± 1	96 ± 1	97 ± 1	94 ± 1	90 ± 1	83 ± 5	78 ± 7	66 ± 7	50 ± 10	51 ± 11	56 ± 10
	XBC	58	64 ± 25	97 ± 1	98 ± 1	97 ± 1	97 ± 1	94 ± 1	89 ± 2	81 ± 9	66 ± 11	50 ± 6	51 ± 1	56 ± 5
	DFF	63	75 ± 20	91 ± 1	91 ± 1	90 ± 1	89 ± 2	86 ± 1	82 ± 4	72 ± 8	62 ± 10	49 ± 6	52 ± 6	60 ± 1
Without leaves	DFS	63	34 ± 24	3 ± 1	4 ± 1	3 ± 1	6 ± 1	10 ± 1	17 ± 5	22 ± 7	34 ± 7	50 ± 10	49 ± 11	44 ± 10
	XBC	58	35 ± 25	3 ± 1	1 ± 1	2 ± 1	3 ± 1	5 ± 1	11 ± 2	19 ± 9	32 ± 11	48 ± 6	49 ± 1	46 ± 5
	DFF	63	25 ± 20	8 ± 1	8 ± 1	9 ± 1	11 ± 2	13 ± 1	17 ± 4	27 ± 8	38 ± 10	50 ± 5	48 ± 6	40 ± 1

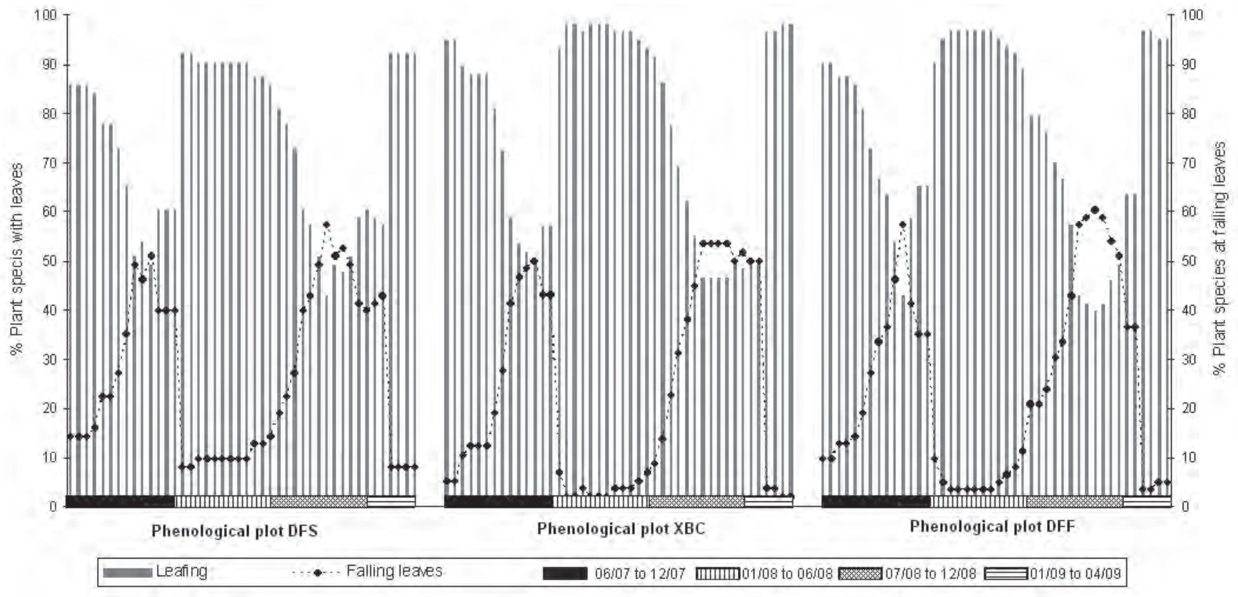

Figure 6. Leaf phenology of the different phenological plots in Tsimanampetsotsa National Park.

Table 5. Presence of leaves for all plant species in the study area from June 2007 to March 2009; X = months with leaves; **....** variation between different vegetation types (C). L.F.: life form, T: tree, S: shrub, L: liana, H: herbs.

			2007							2008													2009		
Scientific name	**Family**	**L.F.**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**
Blepharis calcitrapa	Acanthaceae	H	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Crossandra poissonii	Acanthaceae	S	X	X	X					X	X	X	X	X	X	X							X	X
Justicia spicata	Acanthaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Ruellia albopurpurea	Acanthaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Aloe divaricata	Aloeaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Aerva madagassica	Amaranthaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Aerva sp.	Amaranthaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Poupartia minor	Anacardiaceae	T	X	X						X	X	X	X	X	X								X	X
Operculicarya decaryi	Anacardiaceae	T	X	X	X				X	X	X	X	X	X	X	X					X	X	X	X
Operculicarya hyphaenoïdes	Anacardiaceae	S	X	X	X	X			X	X	X	X	X	X	X	X							X	X
Cynanchum nodosum	Apocynaceae	L																						
Secamone geayi	Apocynaceae	L	X	X	X					X	X	X	X	X	X	X							X	X
Roupellina boivinii	Apocynaceae	S	X	X	X				X	X	X	X	X	X	X	X	X						X	X
Secamone sp.	Apocynaceae	L	X	X	X	X				X	X	X	X	X	X	X	X						X	X
Secamone tenuifolia	Apocynaceae	L	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Pluchea grevei	Asteraceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Distephanus subluteus	Asteraceae	H	X	X	X	X	X			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Polycline proteiformis	Asteraceae	L	X	X	X	X	X			X	X	X	X	X	X	X							X	X
Stereospermum nematocarpon	Bignoniaceae	T	X	X	X	X				X	X	X	X	X	X	X	X	X	X	X		X	X	X
Rhigozum madagascariense	Bignoniaceae	S	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X			X	X
Ehretia sp.	Boraginaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Table 5. (cont.)

			2007							2008												2009		
Scientific name	**Family**	**L.F.**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**
Ehretia decaryi	Boraginaceae	T	X	X	X	X	X			X	X	X	X	X	X	X	X	X	X				X	X
Boscia longifolia	Brassicaceae	T	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Cadaba virgata	Brassicaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Maerua filiformis	Brassicaceae	T	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Androya decaryi	Buddlejaceae	T	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Commiphora marchandii	Burseraceae	T							X	X	X	X	X								X	X	X	X
Commiphora orbicularis	Burseraceae	S							X	X	X	X	X	X	X						X	X	X	X
Commiphora humbertii	Burseraceae	S						X	X	X	X	X	X	X	X								X	X
Commiphora simplicifolia	Burseraceae	S	X	X					X	X	X	X	X	X	X						X	X	X	X
Commiphora lamii	Burseraceae	T	X	X	X					X	X	X	X	X	X	X							X	X
Commiphora monstruosa	Burseraceae	S	X	X	X	X			X	X	X	X	X	X	X	X							X	X
Commiphora mahafaliensis	Burseraceae	S	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X				X	X	X
Cassinodea sp.	Celastraceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Gymnosporia linearis	Celastraceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Salvadoropsis arenicola	Celastraceae	T	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Loeseneriella urceolus	Celastraceae	S	X	X	X	X	X			X	X	X	X	X	X	X	X	X	X		X	X	X	X
Combretum grandidieri (C)	Combretaceae	L	X	X	X			.	.	.	X	X	X	X	X	X	.				.	.	X	X
Terminalia ulexoïdes	Combretaceae	S	X	X	X	X				X	X	X	X	X	X	X	X						X	X
Terminalia disjuncta	Combretaceae	T	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X
Kalanchoe millotii	Crassulaceae	S	X	X	X			X	X	X	X	X	X	X	X	X				X	X	X	X	X
Alluaudiopsis fiherenensis (C)	Didieraceae	S	X	X	X	X	.		X	X	X	X	X	X	X	X	X					X	X	X
Didierea madagascariensis (C)	Didieraceae	T	X	X	X	X	.		.	X	X	X	X	X	X	X	X	.			.	.	X	X
Alluaudia comosa	Didieraceae	T	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Diospyros humbertiana	Ebenaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X
Diospyros manampetsae	Ebenaceae	S	X	X	X	X	X	.	.	X	X	X	X	X	X	X	X	X	X	X	.	.	X	X
Erythroxylum retusum (C)	Erythroxylaceae	S	X	X	X	X	X	.	.	X	X	X	X	X	X	X	X	.					X	X
Euphorbia stenoclada	Euphorbiaceae	S																						
Euphorbia tirucalli	Euphorbiaceae	S																						
Acalypha decaryana	Euphorbiaceae	S	X	X					X	X	X	X	X	X	X	X						X	X	X
Securinega seyrigyi	Euphorbiaceae	T	X	X	X	X			X	X	X	X	X	X	X	X	X	X	X				X	X
Croton sp. 1 (C)	Euphorbiaceae	S	X	X	X	X	.	.	.	X	X	X	X	X	X	X	X	.	.	.	.	.	X	X
Croton salviformis (C)	Euphorbiaceae	S	X	X	X	X	X	.	.	X	X	X	X	X	X	X	X	.	.	.	.	.	X	X
Croton sp. 2 (C)	Euphorbiaceae	S	X	X	X	X	X	X	.	X	X	X	X	X	X	X	X	X	X	.	.	.	X	X
Croton sp. 3	Euphorbiaceae	S	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X
Croton cotoneaster	Euphorbiaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X
Croton geayi	Euphorbiaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Croton sp. 6	Euphorbiaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Delonix floribunda (C)	Fabaceae	T	X	.				.	X	X	X	X	X	X	X	X				.	X	X	X	X
Albizia mahalao (C)	Fabaceae	T	X	X	X	.			X	X	X	X	X	X	X	X	.	.			X	X	X	X
Albizia tulearensis	Fabaceae	T	X	X	X				X	X	X	X	X	X	X	X	X			X	X	X	X	X
Dichrostachys tennifolia	Fabaceae	S	X	X	X					X	X	X	X	X	X	X							X	X
Bauhinia grandidieri	Fabaceae	S	X	X	X					X	X	X	X	X	X								X	X
Crotalaria androyensis	Fabaceae	S	X	X	X					X	X	X	X	X	X	X							X	X
Lemuropisum edule (C)	Fabaceae	S	X	X	X	.	.	.		X	X	X	X	X	X	X	.	.			.	.	.	X
Senna meridionalis (C)	Fabaceae	T	X	X	X	X	.	.	X	X	X	X	X	X	X	X	X	.		X	X	X	X	X
Dicraeopetalum mahafaliense	Fabaceae	T	X	X	X	X			X	X	X	X	X	X	X	X	X						X	X
Mimosa delicatula (C)	Fabaceae	S	X	X	X	X	.	.	.	.	X	X	X	X	X	X	X	.	.	.	.	.	X	X
Tetrapterocarpon geayi (C)	Fabaceae	T	X	X	X	X	.		.	X	X	X	X	X	X	X	X	X	.		.	X	X	X
Chadsia grevei	Fabaceae	S	X	X	X	X	X			X	X	X	X	X	X	X	X	X					X	X
Indigofera mouroundavensis	Fabaceae	S	X	X	X	X	X			X	X	X	X	X	X								X	X
Indigofera sp.	Fabaceae	S	X	X	X	X	X			X	X	X	X	X	X	X							X	X
Tephrosia alba	Fabaceae	S	X	X	X	X	X	.	.	X	X	X	X	X	X	X	X	X	X			.	X	X
Vaughania mahafaliensis	Fabaceae	S	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Alantsilodendron alluaudianum	Fabaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Acacia bellula	Fabaceae	T	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Albizia atakataka	Fabaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Gyrocarpus americanus (C)	Hernandiaceae	T						.	X	X	X	X	.							.	X	X	X	X

Table 5. (cont.)

			2007							2008												2009		
Scientific name	**Family**	**L.F.**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**
Clerodendrun sp.	Verbenaceae	S	X	X	X	X				X	X	X	X	X	X	X	X	.					X	X
Karomia microphylla (C)	Lamiaceae	S	X	X	X	X	.			X	X	X	X	X	X	X	X	X	.				X	X
Capuronianthus mahafaliense	Lythraceae	S	X	X	X	X				X	X	X	X	X	X	X	X	X	.				X	X
Lawsonia inermis	Lythraceae	S	X	X	X	X	X			X	X	X	X	X	X	X	X	X					X	X
Adansonia rubrostipa	Malvaceae	T	X	X	X				X	X	X	X	X	X								X	X	X
Grewia sp. (C)	Malvaceae	S	X	X	X	.				X	X	X	X	X	X	X	.	.					X	X
Grewia grevei (C)	Malvaceae	S	X	X	X	.	.		.	X	X	X	X	X	X	X	.	.				.	X	X
Grewia tulearensis	Malvaceae	S	X	X	X					X	X	X	X	X	X	X							X	X
Grewia mahafalensis	Malvaceae	S	X	X	X						X	X	X	X	X	X							X	X
Grewia humblotii (C)	Malvaceae	S	X	X	X	.				.	X	X	X	X	X	X	.	.					X	X
Grewia sp. 2	Malvaceae	S	X	X	X	X				X	X	X	X	X	X	X	X	X					X	X
Humbertiella quararibeoides	Malvaceae	S	X	X	X	X					X	X	X	X	X	X	X	X					X	X
Indetermined_Kotaky	Malvaceae	S	X	X	X	X	X			X	X	X	X	X	X	X	X	X					X	X
Humbertiella quararibeoides	Malvaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Neobeguea mahafaliensis (C)	Meliaceae	T	.			.	.	.	X	X	X	X	X	X				.	.	X	X	X	X	X
Olax andronensis (C)	Olacaceae	T	X	X	X	X	.	.	X	X	X	X	X	X	X	X	X	X	X	.	.	X	X	X
Ximenia perrieri	Olacaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Adenia olaboensis (C)	Passifloraceae	L	.					.	X	X	X	X	X	X	.					X	X	X	X	X
Uncarina stellulifera (C)	Pedaliaceae	S	X	X			.	X	X	X	X	X	X	X	X	.				.	X	X	X	X
Plumbago aphylla	Plumbaginaceae	H																						
Polygala greveana (C)	Polygalaceae	S	X	X	X	X	.	.	.	.	X	X	X	X	X	X	X	X	.	.	.	.	X	X
Polygala sp. 2	Polygalaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X
Talinella microphylla (C)	Portulacaceae	S	X	X	.			.	.	.	X	X	X	X	X	.				.	.	.	X	X
Cedrelopsis gracilis	Ptaeroxylaceae	T	X	X	X	X				X	X	X	X	X	X	X	X	X					X	X
Cedrelopsis grevei (C)	Ptaeroxylaceae	T	X	X	X	X	X	.		X	X	X	X	X	X	X	X	.					X	X
Paederia grandidieri	Rubiaceae	L	X	X	X					X	X	X	X	X	X	X							X	X
Golonium adenophorum	Rubiaceae	S	X	X	X	X				X	X	X	X	X	X								X	X
Catunaregam spinosa subsp. *spinosa*	Rubiaceae	S	X	X	X	X	X			X	X	X	X	X	X	X	X	X	X				X	X
Azima tetracantha	Salvadoraceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Salvadora angustifolia	Salvadoraceae	T	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Erythrophysa aesculina	Sapindaceae	T	X	X	X		X	X	X	X	X	X	X	X	X					X	X	X	X	X
Leucosalpa poissonii	Scrophulariaceae	L	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X	X
Lycium acutifolium	Solanaceae	S	X	X	X	X	X			X	X	X	X	X	X	X	X						X	X
Solanum hippophaenoïdes	Solanaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Xerophyta tulearensis	Velloziaceae	H	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Cissus boseri	Vitaceae	L	X	X	X				X	X	X	X	X	X	X	X				X	X	X	X	X
Zygophyllum depauperatum	Zygophyllaceae	S	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

with the maximum between February and March. Leaf fall occurred from June to December/January and lasted for 196 day (28 weeks). The maximum number of plant species in the phenological plots without leaves was reached in October with 50% (± 5; n = 63 plant species). The period when trees did not have leaves differed by 32 days between DFS and XBC, by 18 days between DFF and XBC, and by 14 days between DFS and DFF. These differences were not significant, neither for the duration when trees did not have leaves (F = 2.4, $P > 0.05$), nor for the time with leaves (F = 2.17; $P > 0.05$; ANOVAs were based on the duration of the leafing phenophase per species in each vegetation type). Species specific variation will be addressed in a forthcoming manuscript.

Flowering

The relative abundance of plant species flowering per month from June 2007 to March 2009 is summarized in Tables 6 and 7 and Figure 7. The number of flowering species decreased from March until June/July and then increased in August. The season of flowering varied between years and between the three types of vegetation, but in all phenological plots flowering occurred in two different periods. One group of species had flowers at the end of the dry season. A second group peaked during the wet and the beginning of following dry season (Figure 7). The majority of plant species flowered when plants did not have leaves. In the DFS vegetation, the annual maximum of flowering occurred in November, with 36 ± 6% of the plant species flowering during that time. Another peak occurred between February (30 ± 10%) and March (32 ± 5%) when most trees had leaves. In the XBC vegetation, the maximum peak of flowering occurred in October with a mean of 31 ± 2% of the plant species. The second peak of flowering was between January (28 ± 12%) and February (32 ± 5%). In the DFF vegetation, the peak during the time without leaves occurred in November with 29 ± 2% and the second peak in January with 34 ± 6% of the plant species.

Fruiting

The annual fruiting phenology in the different phenological plots from June 2007 until March 2009 is summarized in Tables 7 and 8 and Figure 8. In all phenological plots, the different plant species started to bear fruit at the end of the dry season and extended fruiting into the wet season. Several fruiting peaks were found in each phenological plot with fruiting peaks corresponding to earlier flowering peaks. In general, the first maximum peak of fruiting occurred in December before the maximum rainy period and the second peak occurred between February and April, during the height of the wet season.

Table 6. Percentage of flowering plant species with flower in the different phenological plots from June 2007 to March 2009. Mean and standard deviation are based on monthly averages. Veg. type: vegetation types. N: number of plant species.

Veg.-type	N	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
DFS	63	29 ± 4	30 ± 10	32 ± 5	22 ± 2	16 ± 2	17 ± 4	21 ± 3	22 ± 2	29 ± 2	33 ± 5	36 ± 6	35 ± 2
XBC	58	28 ± 12	32 ± 5	22 ± 2	19 ± 2	17 ± 0	19 ± 1	20 ± 7	22 ± 2	26 ± 2	31 ± 2	29 ± 2	28 ± 12
DFF	63	34 ± 6	22 ± 6	25 ± 5	15 ± 1	6 ± 0	8 ± 6	8 ± 5	13 ± 2	16 ± 5	22 ± 3	29 ± 2	27 ± 4

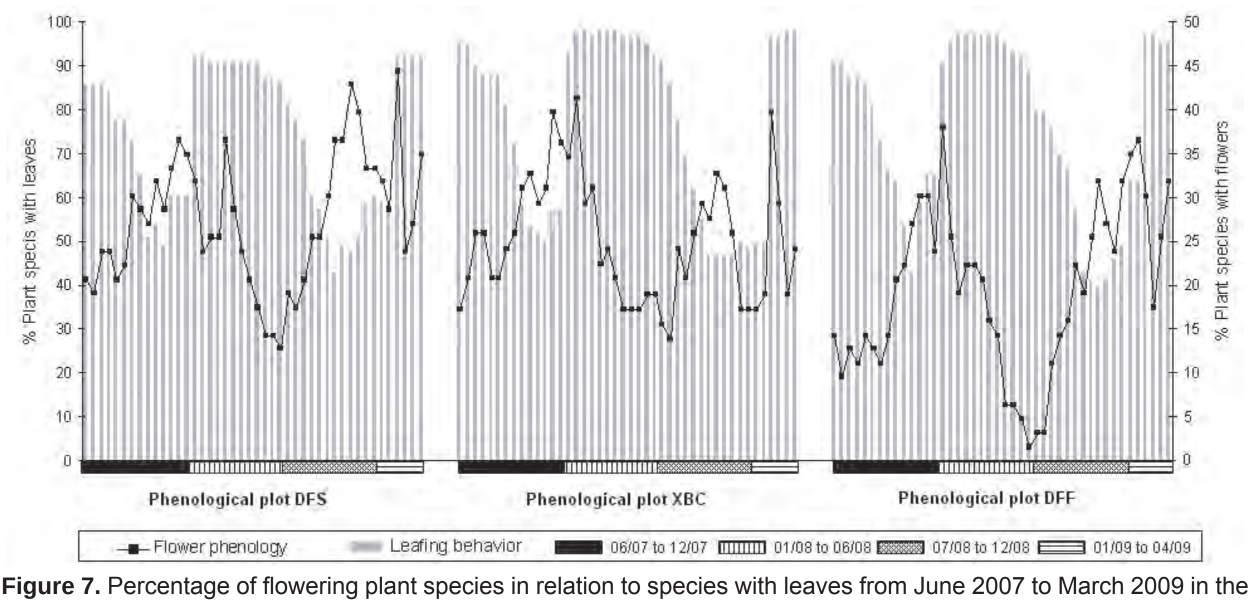

Figure 7. Percentage of flowering plant species in relation to species with leaves from June 2007 to March 2009 in the three vegetation types of Tsimanampetsotsa National Park.

In the DFS vegetation, annual maximum fruiting occurred generally in December with 48 ± 1% of the plant species bearing fruits. This corresponded to the end of the dry season and the beginning of the wet season, before the flush of new leaves. The peaks during the raining period were generally in April with about 45 ± 1% of the total number of plant species. In the XBC vegetation, the fruiting peaks occurred during the time of leaf fall in September with a mean of 20 ± 8% of the plant species and during the renewal of leaves in December with 27 ± 2% of the plant species. The second peak of fruiting was in February with 34 ± 3% of the plant species, corresponding to the maximum peak of flowering during the wet season. In the DFF vegetation, the first fruiting peak occurred in December during the beginning of leaf renewal with 36 ± 1% of the plant species. The second peak was

Table 7. Flowering and fruiting of all plant species in the study area, from June 2007 to March 2009. …………flowering; ▬▬ fruiting, SD: short day; LD: long day; DRY: dry season and WET: wet season, L.F.: life forms, T: tree, H: shrub, L: liana, H: herb.

Scientific name	Family	L.F.
Abutilon indicum	Malvaceae	H
Croton sp. 3	Euphorbiaceae	S
Croton sp. 6	Euphorbiaceae	S
Croton salviformis	Euphorbiaceae	S
Zygophyllum depauperatum	Zygophyllaceae	S
Cadaba virgata	Brassicaceae	S
Croton sp. 1	Euphorbiaceae	S
Croton sp. 2	Euphorbiaceae	S
Senna meridionalis	Fabaceae	T
Loeseneriella urceolus	Celastraceae	S
Crossandra poissonii	Acanthaceae	S
Diospyros manampetsae	Ebenaceae	S
Plumbago aphylla	Plumbaginaceae	H
Justicia spicata	Acanthaceae	S
Delonix floribunda	Fabaceae	T
Ximenia perrieri	Olacaceae	S
Aerva madagassica	Amaranthaceae	S
Indigofera sp.	Fabaceae	S
Grewia grevei	Malvaceae	S
Crotalaria androyensis	Fabaceae	S
Salvadoropsis arenicola	Celastraceae	T
Stereospermum nematocarpon	Bignoniaceae	T
Commiphora simplicifolia	Burseraceae	S
Karomia microphylla	Lamiaceae	S
Tetrapterocarpon geayi	Fabaceae	T
Mimosa delicatula	Fabaceae	S
Acacia bellula	Fabaceae	T
Paederia grandidieri	Rubiaceae	L
Androya decaryi	Buddlejaceae	T
Aerva sp.	Amaranthaceae	S
Polycline proteiformis	Asteraceae	L
Pluchea grevei	Asteraceae	S
Polygala greveana	Polygalaceae	S
Aloe divaricata	Aloeaceae	S
Distephanus subluteus	Asteraceae	H
Blepharis calcitrapa	Acanthaceae	H
Leucosalpa poissonii	Scrophulariaceae	L
Gymnosporia linearis	Celastraceae	S
Maerua filiformis	Brassicaceae	T
Croton cotoneaster	Euphorbiaceae	S
Neobeguea mahafaliensis	Meliaceae	T
Cynanchum nodosum	Apocynaceae	L
Dicraeopetalum mahafaliense	Fabaceae	T
Tephrosia alba	Fabaceae	S
Acacia rovumae	Fabaceae	T
Albizia mahalao	Fabaceae	T
Indigofera mouroundavensis	Fabaceae	S
Vaughania mahafaliensis	Fabaceae	S
Commiphora monstruosa	Burseraceae	S
Erythroxylum retusum	Erythroxylaceae	S
Secamone geayi	Apocynaceae	L
Terminalia ulexoïdes	Combretaceae	S
Solanum hippophaenoïdes	Solanaceae	S
Secamone sp.	Apocynaceae	L
Securinega seyrigyi	Euphorbiaceae	T
Ruellia albopurpurea	Acanthaceae	S
Salvadora angustifolia	Salvadoraceae	T
Boscia longifolia	Brassicaceae	T
Commiphora lamii	Burseraceae	T
Operculicarya hyphaenoïdes	Anacardiaceae	S
Commiphora orbicularis	Burseraceae	S
Commiphora humbertii	Burseraceae	S
Commiphora mahafaliensis	Burseraceae	S

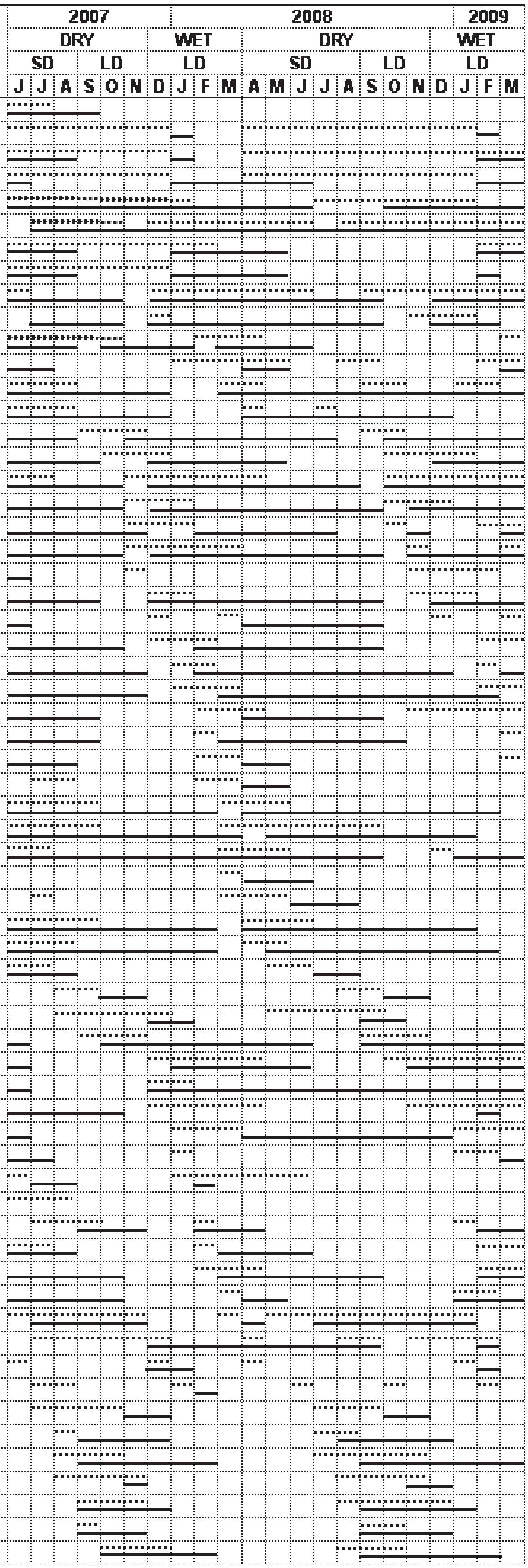

Table 7. (cont)

Scientific name	Family	L.F.
Poupartia minor	Anacardiaceae	T
Uncarina stellulifera	Pedaliaceae	S
Azima tetracantha	Salvadoraceae	S
Euphorbia tirucalli	Euphorbiaceae	S
Erythrophysa aesculina	Sapindaceae	T
Euphorbia stenoclada	Euphorbiaceae	S
Gyrocarpus americanus	Hernandiaceae	T
Terminalia disjuncta	Combretaceae	T
Olax andronensis	Olacaceae	T
Operculicarya decaryi	Anacardiaceae	T
Combretum grandidieri	Combretaceae	L
Adenia olaboensis	Passifloraceae	L
Secamone tenuifolia	Apocynaceae	L
Alluaudiopsis fiherenensis	Didieraceae	S
Cedrelopsis gracilis	Ptaeroxylaceae	T
Cedrelopsis grevei	Ptaeroxylaceae	T
Albizia tulearensis	Fabaceae	T
Croton geayi	Euphorbiaceae	S
Rhigozum madagascariense	Bignoniaceae	S
Lemuropisum edule	Fabaceae	S
Didierea madagascariensis	Didieraceae	T
Talinella microphylla	Portulacaceae	S
Ehretia sp.	Boraginaceae	S
Commiphora marchandii	Burseraceae	T
Acalypha decaryana	Euphorbiaceae	S
Lycium acutifolium	Solanaceae	S
Alluaudia comosa	Didieraceae	T
Cissus boseri	Vitaceae	L
Alantsilodendron alluaudianum	Fabaceae	S
Xerophyta tulearensis	Velloziaceae	H
Diospyros humbertiana	Ebenaceae	S
Gonolium adenophorum	Rubiaceae	S
Capuronianthus mahafaliense	Lythraceae	S
Chadsia grevei	Fabaceae	S
Ehretia decaryi	Boraginaceae	T
Undetermined	Malvaceae	S
Grewia mahafalensis	Malvaceae	S
Grewia tulearensis	Malvaceae	S
Grewia sp.	Malvaceae	S
Lawsonia inermis	Lythraceae	S
Adansonia rubrostipa	Malvaceae	T
Humbertiella quararibeoides	Malvaceae	S
Dichrostachys tennifolia	Fabaceae	S
Catunaregam spinosa subsp.spinosa	Rubiaceae	S
Grewia humblotii	Malvaceae	S

Table 8. Percentage of fruiting plant species with fruit in the different phenological plot from June 2007 to March 2009. Mean and standard deviation are based on monthly average. Veg. type: vegetation types. N: number of plant species.

Veg. type	N	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
DFS	63	38 ± 1	40 ± 4	40 ± 1	45 ± 1	37 ± 2	24 ± 9	25 ± 5	25 ± 3	24 ± 5	29 ± 3	37 ± 4	48 ± 1
XBC	58	28 ± 8	34 ± 3	29 ± 4	32 ± 1	29 ± 2	16 ± 12	14 ± 6	16 ± 6	20 ± 8	18 ± 3	22 ± 2	27 ± 2
DFF	63	37 ± 2	37 ± 7	31 ± 2	35 ± 2	27 ± 2	16 ± 6	12 ± 2	14 ± 2	17 ± 1	21 ± 1	27 ± 5	36 ± 1

during the wet season in February (37 ± 7%) after the maximum peak of flowering.

In all phenological plots, the first maximum fruiting period was synchronized with the end of the dry season and before the time of maximum rainfall. However, during the wet season, maximum fruiting was asynchronous between the different phenological plots. The fruiting peak in the phenological plot of dry forest on sandy soil (DFS) is one month later than in the phenological plot in the xerophytic bush on calcareous soil (XBC), and the phenological plot of dry forest on ferruginous soil (DFF). DFS contained

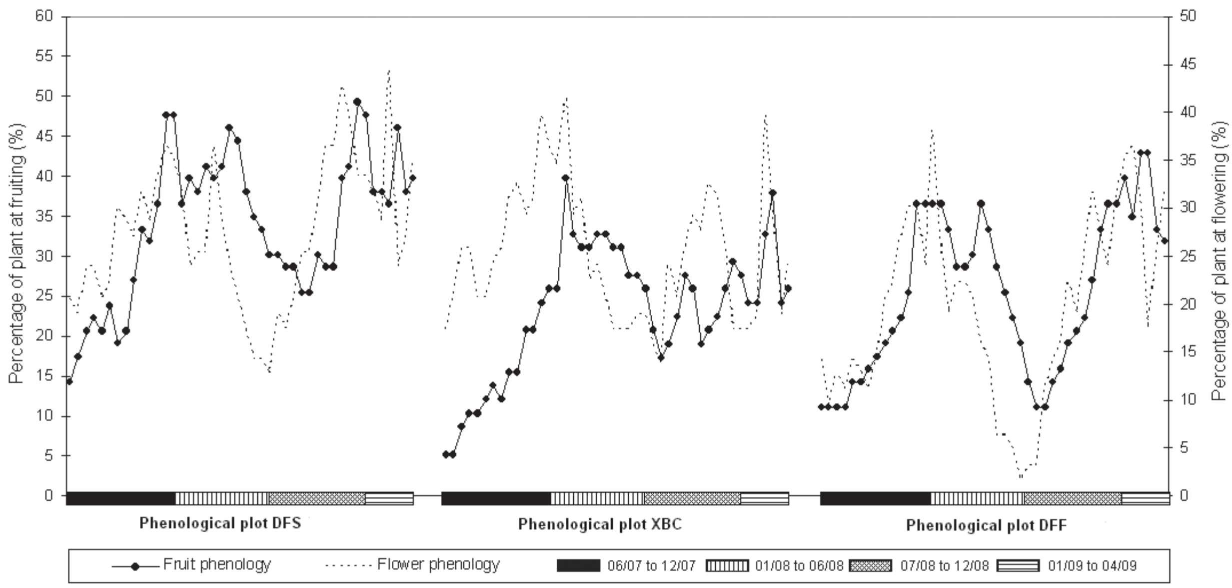

Figure 8. Fruit phenology of the different phenological plots in relation to flowering from June 2007 to March 2009 in Tsimanampetsotsa National Park.

more fruiting plant species than the phenological plot on dry forest on ferruginous soil and the phenological plot in the xerophytic bush on calcareous soil.

In some species, the duration of the fruiting phase (young and mature fruit) is long, including almost both flowering seasons. These species are: *Aerva madagassica*, (Amaranthaceae), *Polycline proteiformis, Pluchea grevei* (Asteraceae), *Blepharis calcitrapa, Justicia spicata* (Acanthaceae), *Cadaba virgata* (Brassicaceae), *Acacia bellula, Crotalaria androyensis, Delonix floribunda, Dicraeopetalum mahafaliense, Indigofera* sp., *Mimosa delicatula, Senna meridionalis, Tetrapterocarpon geayi* (Fabaceae), *Loeseneriella urceolus* (Celastraceae), *Leucosalpa poissonii* (Scrophulariaceae), *Neobeguea mahafaliensis* (Meliaceae), *Polygala greveana* (Polygalaceae), *Plumbago aphylla* (Plumbaginaceae), *Secamone* sp. (Apocynaceae), *Solanum hippophaenoïdes* (Solanaceae), *Stereospermum nematocarpon* (Bignoniaceae), and *Zygophyllum depauperatum* (Zygophyllaceae).

Abiotic triggers for phenological changes

Insulation, monthly mean, maximum and minimum temperatures, and daily temperature ranges were highly correlated with day length in all three types of vegetation. Therefore, we only used day length and monthly rainfall to illustrate possible effects of abiotic factors on phenophases. Day length was significantly correlated with the average monthly rainfall from 1950 – 2000 (r_s = 0.79, n = 12, P = 0.002), but not with the monthly averages of rain between 2007 and 2009 (r_s = 0, n = 12, P > 0.05). If environmental changes (such as rainfall) could be reliably associated with day length over evolutionary time scales, evolution would have favored plants that use day length as the trigger to initiate a specific phenophase. This would give plants a head start once the actual environmental change begins. Alternatively, if the link between day length and seasonal changes is unreliable, evolution would have favored individuals that wait with the initiation of a given phenophase until the environmental change has actually become effective. Thus, the onset of phenophases represent either the response to photoperiod (day length) as a proximate factor associated with long-term averages in abiotic conditions (historical rainfall), or to contemporary rainfall (years 2007 – 2009) as an ultimate factor for

Table 9. Spearman correlations between day-length, historical rainfall data from 1950 – 2000, contemporary rainfall from 2007 – 2009, and phenological data recorded from 2007 – 2009 in different vegetation formations. Correlations are based on monthly means (n = 12). Values are correlation coefficients; asterisks indicate significance levels: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

	Abiotic factor	Leaf fall	Flowers	Fruits
DFS	Day length	0.37	**0.87*** **	**0.65***
	Rain 1950 – 2000	-0.11	0.55	**0.75** **
	Rain 2007 - 2009	**-0.76***	-0.08	0.44
XBC	Day length	0.47	**0.80** **	0.46
	Rain 1950 – 2000	-0.01	0.48	**0.72** **
	Rain 2007 - 2009	**-0.71***	-0.08	**0.70***
DFF	Day length	0.41	**0.94*** **	**0.76** **
	Rain 1950 – 2000	-0.04	**0.74** **	**0.92*** **
	Rain 2007 - 2009	**-0.72** **	0.12	0.47

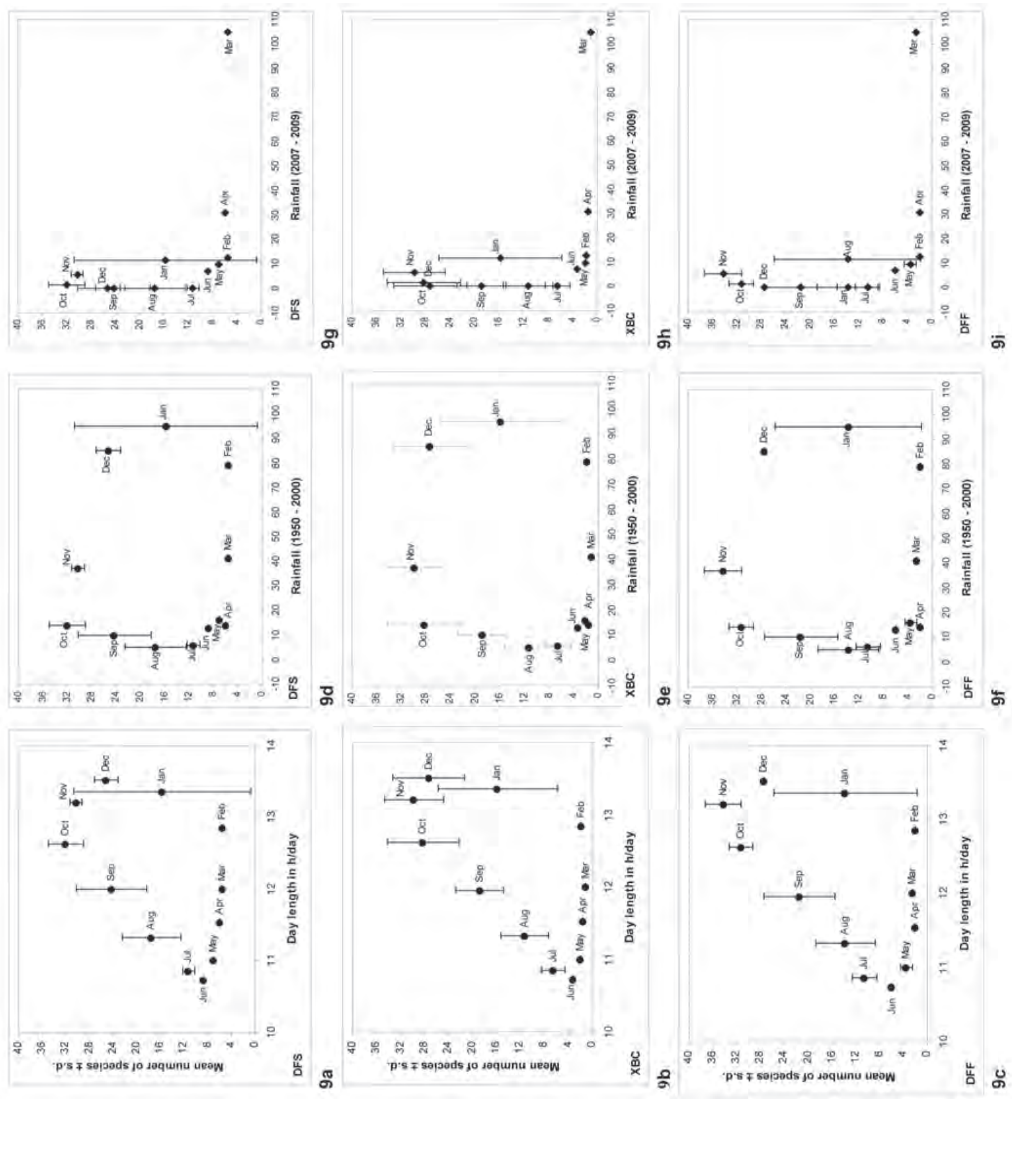

Figure 9. Day length, historical (1950 – 2000), and recent (2007 – 2009) rainfall effects on the number of plant species without leaves in the different phenological plots; phenological data from June 2007 to March 2009.

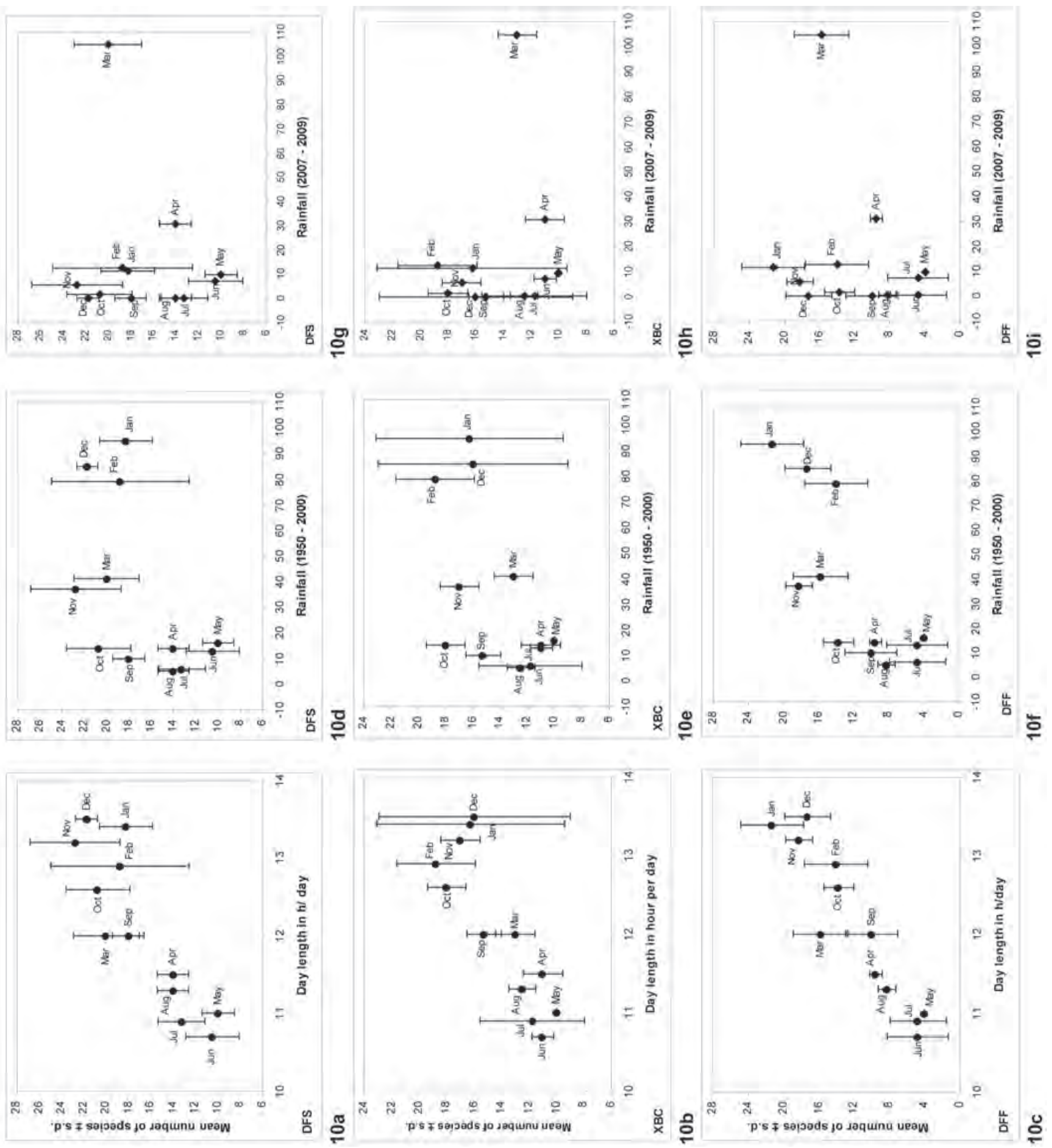

Figure 10. Day length, historical (1950 – 2000), and recent (2007 – 2009) rainfall effects on the number of plant species with flowers in the different phenological plots; phenological data from June 2007 to March 2009.

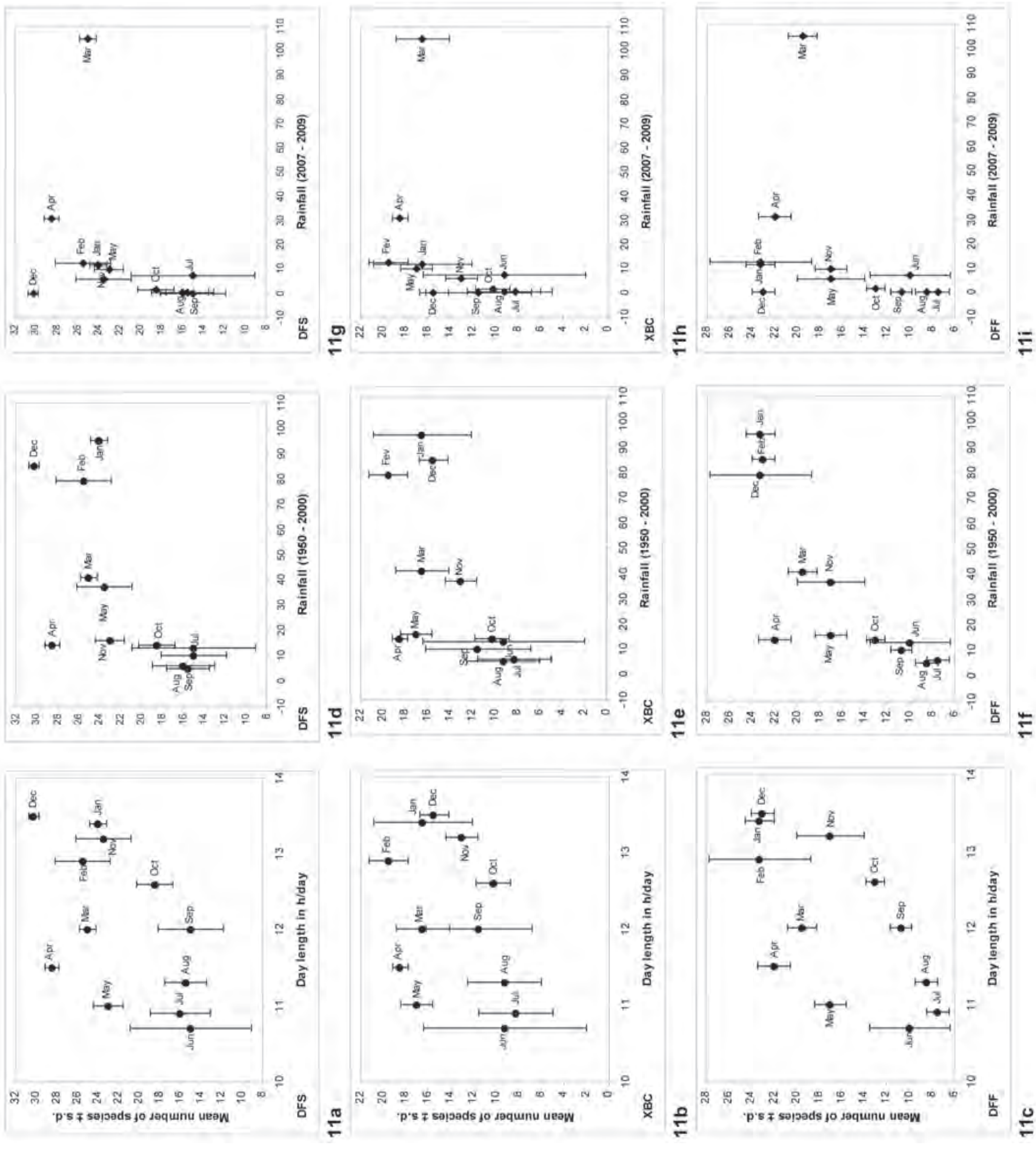

Figure 11. Day length, historical (1950 – 2000), and recent (2007 – 2009) rainfall effects on the number of plant species with fruits in the different phenological plots; phenological data from June 2007 to March 2009.

metabolic activity. The shift in rainfall patterns between the last century and the past few years (Figure 3) allows a separation of the proximate trigger from the ultimate factor.

In all phenological plots, flowering showed a clear correlation with day length (Table 9). In the edaphically dry xerophytic bush, flowering ceased after the longest day in November (Figure 7). The percentages of flowering plant species were remarkably similar in months with similar day lengths despite being in the opposite phase of increasing or decreasing day lengths. Rainfall did not show a consistent relationship with the percentage of plants flowering. The various plant species seem to have different strategies associated with flowering either at the end of the dry season or at the height of the wet season. Day-length and historical rainfall patterns also seem to be the overriding components determining fruiting as compared to the contemporary monthly rainfall. The sequence of the percentage of plant species with fruits is reversed compared to the situation of plants without leaves. The absence of leaves follows day length in a clockwise fashion, while fruiting patterns are counter-clockwise.

Discussion

In tropical forests, plant phenology shows complex links to environmental conditions such as air temperature (maximum and minimum temperature), precipitation, day length, and insolation (Mitchell, 1992; van Schaik *et al*., 1993; Bullock *et al*., 1995; Gwada *et al*., 2000). While seasonal variation in day length will remain unaffected, rainfall characteristics are expected to shift as the climate changes. These modifications in precipitation will have important consequences for plant growth and reproduction with far reaching consequences for natural and anthropogenic ecosystems. In the context of these climatic changes, the goal of this study was to document the phenological characteristics of different vegetation types in the spiny forest of southwestern Madagascar. Specific objectives were to record general leaf, flower, and fruit phenology of different plant species and their combined community wide pattern in different vegetation types in Tsimanampetsotsa National Park. In particular, we wanted to investigate whether plants use the actual rainfall or long-term conditions and day length as a proxy for long-term and evolutionary active forces that initiates specific phenophases in this seemingly unpredictable environment.

In all phenological plots, the maximum vegetation activity (maximum leaf phase) occurred between December and June. Prior to the recent shift in rainfall, this time represents the traditional time of the wet season (December to March) and the beginning of the dry season (April to June). The time during which plants had leaves lasted from 22 weeks in the dry forest on sandy soil, 23 weeks in the dry forest on ferruginous soil to 26 weeks in xerophytic bush on calcareous soil. The vegetative phase in the xerophytic bush was three to four weeks longer than in the dry forests on sandy or ferruginous soils.

Within a given vegetation formation, the deciduous plant species did not react in the same way to environmental factors. The loss of leaves was asynchronous among the different species in the same family. Of all plant taxa in the different vegetation types, 12 species were identified that shed their leaves coinciding with slight changes of external environmental conditions, such as a drop in temperature or shorter day length at the beginning of the dry season. These plant species belong to the families Burseraceae (*Commiphora marchandii*, *C. orbicularis*, *C. humbertii*, and *C. simplicifolia*), Anacardiaceae (*Poupartia minor*), Euphorbiaceae (*Acalypha decaryana*), Fabaceae (*Delonix floribunda*), Hernandiaceae (*Gyrocarpus americanus*), Meliaceae (*Neobeguea mahafaliensis*), Passifloraceae (*Adenia olaboensis*), Pedaliaceae (*Uncarina stellulifera*), and Portulacaceae (*Talinella microphylla*). Other plant species lost their leaves completely during the dry season with ongoing water stress and increased temperature. These are largely members of the Apocynaceae, Bignoniaceae, Celastraceae, Combretaceae, Didieraceae, Ebenaceae, Erythroxylaceae, Euphorbiaceae, Fabaceae (except *Delonix floribunda*), Lamiaceae, Lythraceae, Malvaceae, Polygalaceae, Ptaeroxylaceae, Rubiaceae, Solanaceae, and Scrophulariaceae.

Flowering in the different vegetation types was bimodal: one group of species flowered during the dry season (June to November), corresponding to the time of maximum leaf fall. The second group of species peaked during the wet season, thus coinciding with maximum leaf flush until the end of the wet season (December - April). This matches the situation found in other dry forests of Madagascar (reviewed by Bollen & Donati, 2005).

Of the 111 plant species followed in the phenological plot, only 17 species flowered during the cold months under short day conditions (less than 12h): *Abutilon indicum* (Malvaceae), *Blepharis calcitrapa*, *Justicia spicata* (Acanthaceae), *Boscia longifolia*, *Maerua filiformis* (Brassicaceae), *Commiphora lamii*, *C. orbicaulis* (Burseraceae), *Croton cotoneaster*, *C. salviformis*, *Croton* sp. 2, *Croton* sp. 3 (Euphorbiaceae), *Gymnosporia linearis* (Celastraceae), *Salvadora angustifolia* (Salvadoraceae), *Secamone* sp. (Apocynaceae), *Vaughania mahafaliensis* (Fabaceae), *Zygophyllum depauperatum* (Zygophyllaceae), and *Leucosalpa poissonii* (Scrophulariaceae). All other plant species flowered during the dry or wet season, but under long day conditions.

Fruiting also peaked twice per year. One peak occurred at the end of the dry season, which coincides with the period of high winds from the south (monsoon). The second peak was observed during the hot wet season and coincided with the period when animal-dispersers have come out of hibernation, such as *Microcebus griseorufus* or different bird species commence to breed. Several animal-dispersed plant species have fleshy fruits at the end of the dry season, and these include: *Adenia olaboensis* (Passifloraceae), *Azima tetracantha*, *Salvadora angustifolia* (Salvadoraceae), *Boscia longifolia, Maerua filiformis* (Brassicaceae), *Catunaregam spinosa* subsp. *spinosa* (Rubiaceae), *Commiphora humbertii, C. lamii, C. mahafaliensis, C. marchandii, C. monstruosa, C. orbicularis* (Burseraceae), *Cissus boseri* (Vitaceae), *Diospyros humbertiana* (Ebenaceae), *Ehretia* sp. (Boraginaceae), *Erythrophysa aesculina* (Sapindaceae), *Golonium adenophorum* (Rubiaceae), *Grewia mahafaliensis*, *G. tulearensis* (Malvaceae), *Olax andronensis* (Olacaceae), *Operculicarya decaryi*, *O. hyphaenoïdes*, *Poupartia minor* (Anacardiaceae), *Salvadora angustifolia* (Salvadoraceae), *Talinella microphylla* (Portulacaceae), *Terminalia disjuncta* (Combretaceae), and *Uncarina stellulifera* (Pedaliaceae). Species with wind-dispersed seeds include: *Alluaudia comosa*, *Alluaudiopsis fiherenensis*, *Didierea madagascariensis* (Didieraceae), *Cedrelopsis gracilis* (Ptaeroxylaceae), *Gyrocarpus americanus* (Hernandiaceae), *Humbertiella quararibeoides* (Malvaceae), *Polygala* sp. (Polygalaceae), and *Rhigozum madagascariensis* (Bignoniaceae). Thus, the presence of several fruiting peaks can be interpreted as adaptations to different forms of pollination, dispersal agents, and germination physiology (Phillipson, 1996). In seasonal tropical forest, most wind-dispersed species ripen and release fruits at the end of dry season. This coincides with the time of strong winds and the lack of leaves that could inhibit dispersal (Rathcke & Lacey, 1985; Jordano, 1992; Stevenson, 2004).

Water, available in the soil is presumably the ultimate factor for reproduction and survival. In a region characterized by aridity and highly variable weather conditions, organisms should respond quickly to favorable conditions and initiate flowering with the first rains. This is well known from the explosive growth and flowering of herbaceous plants of southern Africa and other savanna-type vegetation formations in the dry regions of the world.

However, there is a negative aspect of responding too quickly to falling rain. In the Kirindy/CFPF (now Centre National de Formation, d'Etudes et de Recherches en Environnement et Foresterie [CNFEREF]) forest, with some 800 mm of rain per year, water reserves for young plants last only for 4-7 days, if rain does not fall during the growing season (Sorg & Rohner, 1996). Thus, if plants initiate flowering and fruiting too early, they risk that their seeds are dispersed under unfavorable conditions for germination and sustained growth.

In many tropical forests it is difficult to identify the selective forces acting upon the evolution of fruit characteristics (Bollen *et al*., 2005) and phenological changes as day length, rainfall, and temperature are correlated (van Schaik *et al*., 1993).The recent shift of the wet season from December/January to March/April in southern Madagascar (Figure 3) allows separation of these effects to some extent. Correlations indicate that leaf flush is triggered by actual rainfall, while initiation of flowering and fruiting is linked to rainfall patterns prevailing in the recent past. Today, these historical rainfall patterns may best be represented by day length that serves as a proximate factor to trigger flowering and fruiting. If so, we have to assume that rainfall patterns were largely stable for long enough to allow the evolution of day length to be used as a proxy and reliable signal for the plants to optimize reproduction. This then implies that past climatic parameters were less variable than today (Ganzhorn, 1995; Dewar & Richard, 2007).

In the context of climate change, plants that respond to day length as a proxy for past rainfall patterns might face problems in reproduction if the shift of the peak precipitation becomes permanent. Certainly, this aspect will have far-reaching consequences for the functioning of natural ecosystems, as well as for agriculture and livestock practices in southwestern Madagascar.

However, we should not underestimate the speed of evolutionary change. Recent studies on bird migration and mammalian hibernation indicate that day length as a trigger for initiating these behavioral changes can be modified in just a few generations (Coppack *et al*., 2008). For example, the nocturnal lemur *Microcebus griseorufus* in the spiny bush of Madagascar can react in a very flexible manner to environmental change, which is not limited in its response by circadian phenomena (Kobbe *et al*., 2010). Hence, it is important to establish long-term monitoring in the southwestern Madagascar to create a model of the effects of climate change on the phenology of the endemic plant communities.

Acknowledgements

We would like to thank the Madagascar National Parks in Toliara (Tsimanampetsotsa) and the Commission CAFF/CORE, Direction of Environmental, and Tourism for research permits. The study was carried out under the Accord de Collaboration between ANGAP (now Madagascar National Parks [MNP], the Departments of Plant Biology and Ecology (University of Antananarivo), and the Department of Animal Ecology and Conservation (University of Hamburg). We also thank Jocelyn Rakotomalala and Domoina Rakotomalala (MNP Toliara, WWF Madagascar) for their logistical support. Special thanks go to Tolona Andrianasolo, Solofomalala Jacques Rakotondranary, Peggy Giertz, Jana Jeglinski, Susanne Kobbe, and to the para-ecologists Fisy Louis, Edson, Mahita, Odilizara, and Raoly. Marie Jeanne Raherilalao, Steven M. Goodman, Joelisoa Ratsirarson, and an anonymous reviewer provided excellent suggestions on the manuscript. The study was financed by WWF Sweden/WWF Madagascar (Project MG0911.03) with additional support from DFG/BMZ (Ga 342/15), Volkswagen Foundation, WWF Germany, and DAAD.

References

Anderson, D. P., Nordheim, E. V., Moermond, T. C., Gone, Z. B. & Boesch, C. 2005. Factors influencing tree phenology in Taï National Park, Côte d'Ivoire. *Biotropica*, 37: 631-641.

Bollen, A. & Donati, G. 2005. Phenology of the littoral forest of Sainte Luce, southeastern Madagascar. *Biotropica*, 37: 32-43.

Bollen, A., Donati, G., Fietz, J., Schwab, D., Ramanamanjato, J. -B., Randrihasipara, L., van Elsacker, L. & Ganzhorn, J. U. 2005. An intersite comparison on fruit characteristics in Madagascar: Evidence for selection pressure through abiotic constraints rather than through co-evolution. In *Tropical fruits and frugivores: The search for strong interactors*, eds J. L. Dew & J. P. Boubli, pp. 93-119. Springer, Dordrecht.

Bullock, S. H., Mooney, H. A. & Medina, E. 1995. *Seasonally dry tropical forests*. Cambridge University Press, Cambridge.

Chapman, C. A., Wrangham, R. W., Chapman, I. J., Kennard, D. K. & Zanne, A. E. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Biotropica,* 37: 189-211.

Coppack, T., Tindemans, I., Czisch, M., Van der Linden, A., Berthold, P. & Pulido, F. 2008. Can long-distance migratory birds adjust to the advancement of spring by shortening migration distance? The response of the pied flycatcher to latitudinal photoperiodic variation. *Global Change Biology*, 14: 2516-2522.

Dewar, R. E. & Richard, A. F. 2007. Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences, USA,* 104: 13723-13727.

Donque, G. 1975. *Contribution Géographique à l'étude de Climat de Madagascar.* Nouvelles Imprimerie des Arts Graphiques, Tananarive.

Elisabeth G. B. & Johnson D. L. 1993. Flowering plant phenology and weather in Alberta, Canada. *International Journal of Biometeorology*, 38: 23-27.

Elmqvist, T., Pyykönen, M., Tengö, M., Rakotondrasoa, F., Rabakonandrianina, E. & Radimilahy, C. 2007. Patterns of loss and regeneration of tropical dry forest in Madagascar: The social institutional contex. *PLoS ONE*, 2:e402.

Gautier, L., Chatelain, C. & Spichiger, R. 1994. Presentation of a relevé method for vegetation studies based on high resolution satellite imagery. *Proceedings of the 13th Plenary Meeting AETFAT,* Malawi, 2: 1339-1350.

Ganzhorn, J. U. 1995. Cyclones over Madagascar: Fate or fortune? *Ambio,* 24: 124-125.

Godron, M. 1972. Echantillonnage linéaire et cartographie. *Investigacion Pesquera,* 36: 171-174.

Gwada, P., Makoto, T. & Uezu, Y. 2000. Leaf phenological traits in the mangrove *Kandelia candel* L. Druce. *Aquatic Botany*, 68: 1-14.

Hannah, L., Dave, R., Lowry, P.P., Andelman, S., Andrianarisata, M., Andriamaro, L., Cameron, A., Hijmans, R., Kremen, C., MacKinnon, J., Randrianasolo, H.H., Andriambololonera, S., Razafimpahanana, A., Randriamahazo, H., Randrianarisoa, J., Razafinjatovo, P., Raxworthy, C., Schatz, G.E., Tadross, M. & Wilmé, L. 2008. Climate change adaptation for conservation in Madagascar. *Biology Letters*, 4: 590-594.

Hewitson, B. C. & Crane, R. G. 2006. Consensus between GCM climate change projections with empirical downscaling: Precipitation downscaling over South Africa. *International Journal of Climatology*, 26: 1315-1337.

Jordano, P. 1992. Fruits and frugivory. In *Seeds: The ecology of regeneration in plant communities*, ed. M. Fenner, pp. 105-156. Commonwealth Agricultural Bureau International, Wallingford, Great Britain.

Kobbe, S., Dausmann, K. & Ganzhorn, J. U. 2011. Extreme individual flexibility of heterothermy in free-ranging Malagasy mouse lemurs (*Microcebus griseorufus*). *Journal of Comparative Physiology B*, 181: 165–173.

Kruesi, B. 1981. Phenological methods in permanent plot research the indicator value of phenological phenomena a study in limestone grassland in northern Switzerland. *Veröffentlichungen des Geobotanischen Institutes der Eidgenoessische Technische Hochschule Stiftung Ruebel in Zürich*, 75: 1-116.

Malcolm, J. R., Liu, C., Neilson, R. P., Hansen, L. A. & Hannah, L. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology*, 20: 538-548.

Mamokatra. 1999. Etude pour l'élaboration d'un plan d'aménagement et de gestion au niveau de la Reserve naturelle intégrale de Tsimanampetsotsa, Diagnostic physico-bio-écologique. Deutscher Forstservice GmbH, Feldkirchen et Entreprise d'Etudes de Développement Rural "Mamokatra", Antananarivo, Madagascar.

Mitchell, A. T. 1992. Dry season leaf production: An escape from herbivory. *Biotropica,* 244: 532-537.

Moral, P. 1964. Essai sur les régions pluviothermiques de l'Afrique de l'Ouest. *Annales de Géographie*, 73: 660-686.

Phillipson, P. B. 1996. Endemism and non-endemism in the flora of south-west Madagascar. In *Biogeography of Madagascar*, ed. W. R. Lourenço, pp. 125-136. ORSTOM, Paris.

Rathcke, B. & Lacey, E. P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematic,* 16: 179-214.

Selwyn, M. A. & Parthasarathy, N. 2007. Fruiting phenology in a tropical dry evergreen forest on the Coromandel coast of India in relation to plant life-forms, physiognomic groups, dispersal modes, and climatic constraints. *Flora,* 202: 371-382.

Sorg, J.-P. & Rohner, U. 1996. Climate and phenology of the dry deciduous forest at Kirindy. In Ecology and economy of a tropical dry forest in Madagascar, eds J. U. Ganzhorn & J.-P. Sorg. *Primate Report*, 46-1: 57-80.

Stevenson, P. R. 2004. Phenological patterns of woody vegetation at Tinigua Park, Colombia: Methodological comparisons with emphasis on fruit production. *Caldasia,* 26: 125-150.

van Schaik, C. P., Terborgh, J. W. & Wright, S. J. 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematic,* 24: 353-377.

APPENDIX. Different plant species found in the different phenological plots. DFS = dry forest on sandy soil; XBC = xerophytic bush on calcareous soil; and DFF = dry forest on ferruginous soil. The local name in Malagasy is given for undetermined plant species. The different life forms (LF) include: T = tree, S = shrub, L = liana, and H = herb.

				Presence in two phenological plots (5 x 200 m) per vegetation type		
Plant species	**Author**	**Family**	**LF**	**DFS**	**XBC**	**DFF**
Abutilon indicum	(L.) Sweet	Malvaceae	H	+	-	-
Acacia bellula	Drake	Fabaceae	T	+	-	-
Acacia rovumae	Oliv.	Fabaceae	T	+	-	-
Acalypha decaryana	Leandri	Euphorbiaceae	S	-	-	+
Adansonia rubrostipa	Jum. & H. Perrier	Malvaceae	T	-	-	+
Adenia olaboensis	Claverie	Passifloraceae	L	-	+	+
Aerva madagassica	Suess.	Amaranthaceae	S	+	-	-
Aerva sp.		Amaranthaceae	S	-	-	+
Alantsilodendron alluaudianum	(R. Vig.) Villiers	Fabaceae	S	+	-	-
Albizia atakataka	Capuron	Fabaceae	S	-	+	-
Albizia mahalao	Capuron	Fabaceae	T	+	-	+
Albizia tulearensis	R. Vig.	Fabaceae	T	+	-	-
Alluaudia comosa	(Drake) Drake	Didieraceae	T	-	+	+
Alluaudiopsis fiherenensis	Humbert & Choux	Didieraceae	S	-	+	+
Aloe divaricata	A. Berger	Aloeaceae	S	-	+	-
Androya decaryi	H. Perrier	Buddlejaceae	T	+	-	-
Polycline proteiformis	Humbert	Asteraceae	L	+	-	-
Azima tetracantha	Lam.	Salvadoraceae	S	+	-	-
Bauhinia grandidieri	Baill.	Fabaceae	S	-	-	+
Blepharis calcitrapa	Benoist	Acanthaceae	H	+	-	-
Boscia longifolia	Hadj-Moust	Brassicaceae	T	+	-	+
Cadaba virgata	Bojer	Brassicaceae	S	+	-	-
Capuronianthus mahafaliense	J.-F. Leroy	Lythraceae	S	-	+	+
Cassinodea sp.		Celastraceae	S	-	+	-
Catunaregam spinosa subsp. *spinosa*	(Thunb.) Tirveng	Rubiaceae	S	-	+	-
Cedrelopsis gracilis	J.-F. Leroy	Ptaeroxylaceae	T	-	+	-
Cedrelopsis grevei	Baill.	Ptaeroxylaceae	T	+	-	+
Chadsia grevei	Drake	Fabaceae	S	-	-	+
Clerodendrun sp.		Verbenaceae	S	-	+	+
Combretum grandidieri	Drake	Combretaceae	L	-	+	+
Commiphora humbertii	H. Perrier	Burseraceae	S	+	+	-
Commiphora lamii	H. Perrier	Burseraceae	T	+	-	+
Commiphora mahafaliensis	Capuron	Burseraceae	S	-	+	+
Commiphora marchandii	Engl.	Burseraceae	T	+	-	+
Commiphora monstruosa	(H. Perrier) Capuron	Burseraceae	S	-	+	+
Commiphora orbicularis	Engl.	Burseraceae	S	+	+	+
Commiphora simplicifolia	H. Perrier	Burseraceae	S	+	-	+
Crossandra poissonii	Benoist	Acanthaceae	S	+	-	-
Crotalaria androyensis	R. Vig.	Fabaceae	S	+	-	-
Croton cotoneaster	Müll. Arg	Euphorbiaceae	S	-	+	-
Croton geayi	Leandri	Euphorbiaceae	S	-	+	-
Croton salviformis	Leandri	Euphorbiaceae	S	+	+	+
Croton sp. 1		Euphorbiaceae	S	+	+	+
Croton sp. 2		Euphorbiaceae	S	+	+	-
Croton sp. 3		Euphorbiaceae	S	-	+	-
Croton sp. 6		Euphorbiaceae	S	-	+	+
Cynanchum nodosum	Desc.	Apocynaceae	L	+	+	+
Cissus bosseri	Desc.	Vitaceae	L	-	-	+
Delonix floribunda	(Baill.) Capuron	Fabaceae	T	+	+	+
Dichrostachys tennifolia	Benth.	Fabaceae	S	-	-	+
Dicraeopetalum mahafaliense	(M. Pelt.) Yakovlev	Fabaceae	T	-	+	-

APPENDIX. (cont.)

			Presence in two phenological plots (5 x 200 m) per vegetation type			
Plant species	**Author**	**Family**	**LF**	**DFS**	**XBC**	**DFF**
Didierea madagascariensis	Baill	Didieraceae	T	+	-	+
Diospyros humbertiana	H. Perrier	Ebenaceae	S	+	-	-
Diospyros manampetsae	H. Perrier	Ebenaceae	S	+	+	+
Ehretia decaryi	J. S. Mill.	Boraginaceae	T	+	+	-
Ehretia sp.	Benth.	Boraginaceae	S	+	-	-
Erythrophysa aesculina	Bail.	Sapindaceae	T	-	-	+
Erythroxylum retusum	Baill. ex O.E. Schulz	Erythroxylaceae	S	-	+	+
Euphorbia stenoclada	Baill.	Euphorbiaceae	S	+	+	+
Euphorbia tirucalli	L.	Euphorbiaceae	S	+	-	-
Golonium adenophorum		Rubiaceae	S	+	-	-
Grewia mahafalensis	Capuron & Mabb.	Malvaceae	S	-	+	-
Grewia grevei	Baill	Malvaceae	S	+	-	+
Grewia humblotii	Baill.	Malvaceae	S	+	-	+
Grewia sp.		Malvaceae	S	+	-	+
Grewia sp. 2		Malvaceae	S	+	-	-
Grewia tulearensis	Capuron	Malvaceae	S	-	+	-
Gymnosporia linearis	L.F.	Celastraceae	S	-	+	-
Gyrocarpus americanus	Hallier. F.	Hernandiaceae	T	+	+	+
Humbertiella quararibeoides	Hochr	Malvaceae	S	-	+	+
Indigofera mouroundavensis	Baill	Fabaceae	S	-	+	-
Indigofera sp.		Fabaceae	S	+	-	-
Kalanchoe millotii	H. Perrier	Crassulaceae	S	-	+	-
Karomia microphylla	(Moldenke) R.B. Fern.	Lamiaceae	S	-	+	+
Undetermined_Kotaky		Malvaceae	S	-	+	-
Lemuropisum edule	H. Perrier	Fabaceae	S	-	+	+
Leucosalpa poissonii	Bonati ex Humbert	Scrophulariaceae	L	-	-	+
Loeseneriella urceolus	(Tul.) N. Halle	Celastraceae	S	-	-	+
Lawsonia inermis	L.	Lythraceae	S	-	+	-
Lycium acutifolium	E. Mey ex. Dunal	Solanaceae	S	+	-	-
Maerua filiformis	Drake	Brassicaceae	T	+	-	+
Mimosa delicatula	Baill.	Fabaceae	S	+	+	+
Neobeguea mahafaliensis	Hallier f.	Meliaceae	T	+	+	+
Olax andronensis	Baker	Olacaceae	T	+	+	-
Operculicarya decaryi	H. Perrier	Anacardiaceae	T	+	+	+
Operculicarya hyphaenoïdes	H. Perrier	Anacardiaceae	S	-	+	+
Justicia spicata	(Nees) Baron	Acanthaceae	S	+	-	-
Paederia grandidieri	Drake	Rubiaceae	L	-	+	-
Plumbago aphylla	Boiss.	Plumbaginaceae	H	+	-	-
Polygala greveana	H.Bn	Polygalaceae	S	-	+	+
Polygala sp. 2		Polygalaceae	S	-	-	+
Poupartia minor	(Bojer) L. Marchand	Anacardiaceae	T	+	+	-
Pluchea grevei	(Baill.) Humbert	Asteraceae	S	+	-	-
Rhigozum madagascariense	Drake	Bignoniaceae	S	+	-	+
Roupellina boivinii	(Baill.) Pichon	Apocynaceae	S	-	-	+
Ruellia albopurpurea	(Benoist) Benoist	Acanthaceae	S	-	+	-
Salvadora angustifolia	Turill	Salvadoraceae	T	+	-	-
Salvadoropsis arenicola	H. Perrier	Celastraceae	T	-	-	+
Secamone geayi	Costantin & Gallaud	Apocynaceae	L	-	+	-
Secamone sp.		Apocynaceae	L	+	-	+
Secamone tenuifolia	Decne.	Apocynaceae	L	+	-	-
Securinega seyrigyi	Leandri	Euphorbiaceae	T	-	-	+
Senna meridionalis	(R. Vig.) Du Puy	Fabaceae	T	-	+	+

APPENDIX. (cont.)

			Presence in two phenological plots (5 x 200 m) per vegetation type			
Plant species	**Author**	**Family**	**LF**	**DFS**	**XBC**	**DFF**
Solanum hippophaenoïdes		Solanaceae	S	+	-	-
Stereospermum nematocarpon	A. DC.	Bignoniaceae	T	+	-	+
Talinella microphylla	Eggli	Portulacaceae	S	+	+	+
Tephrosia alba	Du Puy & Labat	Fabaceae	S	-	+	+
Terminalia disjuncta	H. Perrier	Combretaceae	T	+	+	+
Terminalia ulexoïdes	H. Perrier	Combretaceae	S	+	+	+
Tetrapterocarpon geayi	Humbert	Fabaceae	T	-	+	+
Uncarina stellulifera	Humbert	Pedaliaceae	S	+	-	+
Vaughania mahafaliensis	Du Puy & Labat	Fabaceae	S	-	-	+
Distephanus subluteus	(Scott-Elliot) Homolle	Asteraceae	H	-	+	-
Xerophyta tulearensis	H. Perrier	Velloziaceae	H	-	+	+
Ximenia perrieri	Cavaco & Keraudren	Olacaceae	S	+	-	-
Zygophyllum depauperatum	Drake	Zygophyllaceae	S	+	-	-