

# Phenology of different vegetation types in the dry forest of Andohahela National Park, southeastern Madagascar

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## Abstract

This paper presents results from 20 months of phenological observations in three vegetation formations of the dry part of Andohahela National Park, southeastern Madagascar. Data were recorded from September 2007 to April 2009. Patterns of leafing, flowering, and fruiting were documented for 668 individual trees of 77 species from 32 families growing in xerophytic bush, gallery and transitional forests. Data were recorded twice per month in 13 plots of 500 m<sup>2</sup> each. The tree phenologies in the different types of vegetation were analyzed for relationships to season, ambient temperature, relative humidity, day length, and insulation. Most of the species had leaves in the wet season. Leaf fall occurred throughout the year but was pronounced during the dry season. Flowering and fruiting were strongly seasonal. Flowering peaked at the end of the dry and the beginning of the rainy season. Most trees produced fruits at the beginning and during the rainy season. Some species produced fruits during the dry season.

**Key words:** Phenology, phenophase, dry forest, Andohahela, Madagascar

## Résumé détaillé

Cette étude décrit la phénologie des arbres (feuilles, fleurs et fruits) dans trois types de formations végétales de la partie sèche du Parc National d'Andohahela. Treize quadrats mesurant chacun 500 m<sup>2</sup> ont été installés dans les sites d'étude dont huit

dans le fourré xérophile, trois dans la forêt galerie et deux dans la forêt de transition. Six cent soixante et huit arbres appartenant à 77 espèces et 32 familles ont été observés deux fois par mois entre septembre 2007 et avril 2009. La présence de feuilles, de fleurs et de fruits sur chaque individu sélectionné a été notée.

Pour l'analyse des données obtenues, des phénogrammes et des graphes synthétisant chaque phénophase (feuillaison, floraison et fructification) ont été élaborés. Ils indiquent mensuellement chaque espèce qui est susceptible de porter des feuilles, des fleurs et des fruits pendant la période d'étude. Les relations entre chaque phénophase et les données stationnelles du milieu en termes de longueur du jour, d'humidité relative et de la température ambiante ont été analysées en utilisant un test de corrélation.

Les résultats obtenus ont montré l'absence de grandes différences entre l'apparition de chaque phénophase entre les trois types de végétation. En général, chaque phénophase est annuelle. Les feuilles sont présentes de novembre/décembre jusqu'au mois de mai, correspondant à la saison chaude et humide et où le jour est long. Pendant la saison sèche (juin à octobre/novembre), la chute des feuilles semble être continue pour la plupart des espèces. La floraison et la fructification sont saisonnières. Par ailleurs, même si la présence de feuilles ou de fruits varie le long de l'année, la plupart des espèces fleurissent à la fin de la saison sèche, juste avant les premières pluies. Les pics correspondent à la période de défeuillaison avant la saison de pluies : d'août à novembre. Pour certaines espèces la floraison s'effectue pendant la saison chaude et est liée à l'activité des bourgeons et de la longueur du jour. Le pic de fructification est visible entre le mois d'octobre et janvier. Cette période coïncide à la saison chaude et humide qui est une bonne période pour la dispersion des graines par les animaux et leur germination. L'apparition de chaque phénophase est donc basée directement aux variations écologiques annuelles du milieu et au besoin de chaque type de végétation.

**Mots clés :** Phénologie, phénophase, forêt sèche, Andohahela, Madagascar

## Introduction

In Madagascar, relief, altitude, and soil type have a significant impact upon the distribution and adaptation of the island's flora and fauna (Carbonnell, 1963). Climate change imposes new constraints on the biota and evokes various forms of responses (Adger *et al.*, 2005). Plant phenology, the science of natural recurring events, is a good indicator of climate change as it can be recorded with high-temporal resolution and thus, changes in leafing, flowering, and fruiting of plants can illustrate climate change impacts on the natural vegetation (Menzel *et al.*, 2006). The different phenophases of plants are determined by temperature and/or photoperiod; particularly in temperate zones (Menzel, 2002). Irradiance also varies seasonally in relation to cloud cover, day length, and solar angle (Wright & van Schaik, 1994). The three phenophases (leafing, flowering, and fruiting) are not independent in individual woody plants (van Schaik *et al.*, 1993). The various boundary conditions result in an enormous variety in temporal patterns of flowering and fruiting of trees in tropical forests in general (van Schaik *et al.*, 1993) as well as in Madagascar (Bollen & Donati, 2005).

The goal of this study was to collect and to compare data on tree phenology and to determine the period and the duration of each phenophase in different types of vegetation along an environmental gradient in the dry western part of the Andohahela National Park, southeastern Madagascar. This area contains a variety of vegetation formations ranging from xerophytic bush to evergreen humid rain forest (Goodman, 1999; Rakotomalaza & Messmer, 1999; Andriaharimalala *et al.*, 2011; Rakotondranary *et al.*, 2011).

Specific aims were: (I) to record the phenophases of different tree species in different types of vegetation; (II) to explore possible correlations between the percentage of plant species in different phenophases and monthly means of day length (h), relative humidity (%), and ambient temperature (°C); (III) to compare the phenology of individuals of the same species growing in different types of vegetation; and (IV) to compare our data with the results from other areas in Madagascar.

## Materials and methods

### Study site

The study was carried out in the Andohahela National Park located, between the “Anosy” and the “Androy” region in the southeast of Madagascar (between 46°32'E, 24°30'S and 46°55'E, 25°02'S). It currently covers 78 220 ha (MNP, 2003) and is divided in three non-contiguous “parcelles” (Goodman, 1999; Helme & Rakotomalaza, 1999; Rakotomalaza & Messmer, 1999; MNP, 2003; Rasoarimanana, 2005). This area has a unique concentration of different types of habitats and species of southeastern Madagascar. They fall into three main categories of ecosystems: evergreen rainforest, xerophytic bush, and transitional forest, crossed by gallery forest along permanent or ephemeral streams (MNP, 2003). Our study was performed in the western part of the park in “parcelle 2”. The phenological sampling plots were established in the dry forest around five villages: Ambatoabo, Ankoba, Ihazofotsy, Mangatsiaka, and Tsimelahy. The coordinates of the plots are given in Table 1.

**Table 1.** Characteristics and location of the different phenological plots in the Andohahela National Park. Site identifications A, B, C, D, and E refer to plots described by Andriaharimalala *et al.* (2011).

Village	Site identification	Vegetation	Latitude (S)	Longitude (E)	Altitude (m)
Ihazofotsy	A	Xerophytic bush	24°50.317'	46°31.629'	90
	E	Xerophytic bush	24°49.703'	46°32.319'	75
Ambatoabo	B	Xerophytic bush	24°49.245'	46°40.085'	160
	A	Gallery forest	24°49.103'	46°40.271'	150
Ankoba	A	Gallery forest	24°47.763'	46°41.100'	160
	B	Xerophytic bush	24°48.069'	46°41.365'	240
	C	Xerophytic bush	24°47.700'	46°41.344'	190
Mangatsiaka	A	Xerophytic bush	24°57.878'	46°33.381'	120
	B	Xerophytic bush	24°58.068'	46°33.818'	80
	C	Xerophytic bush	24°57.992'	46°33.176'	110
Tsimelahy	A	Gallery forest	24°57.334'	46°37.135'	100
	B	Transitional forest	24°57.053'	46°37.082'	170
	D	Transitional forest	24°57.278'	46°36.882'	170

## Phenological records

Phenological patterns were recorded in 13 plots of 500 m<sup>2</sup> each, the size suggested by Hemingway & Overdorff (1999). Due to constraints imposed by the shape of different habitats, plots measured 5 x 100 m<sup>2</sup> in xerophytic bush and in the transitional forest and 10 x 50 m<sup>2</sup> in gallery forest because it was impossible to fit a continuous plot of 100 m length in the gallery forests remaining at these sites. Eight plots were located in the xerophytic bush, three in the gallery forest, and two in the transitional forest (Table 1). Each woody plant (tree or shrub) with a stem diameter at breast height (dbh)  $\geq$  10 cm was colored and marked with a numbered flagging tag. Their phenology was recorded twice per month from September 2007 through April 2009. Observations were made with the help of one field assistant and one agent from Madagascar National Parks (MNP). We recorded only the presence or absence of leaves, flowers, and fruits on each individual tree. We chose this simple method to allow for long term monitoring by different investigators and to facilitate comparison between studies (Ratovonamana *et al.*, 2011). Analyses are based on species. Our methodology of recording follows Ratovonamana *et al.* (2011). According to their definition, a plant species was considered to have entered a specific phenophase when 25% of the individuals of the species in question had entered that state. If a species matched this criterion only for one half of the month, the plant part in question (leaves, flowers, fruits) was considered to be present in that month. The community-level phenology of the different vegetation types is described as the percentage of plant species that were in a given phenophase.

## Meteorological measurements

Climatic conditions vary between the three “parcelles” of Andohahela National Park. “Parcelle 1” belongs to the eastern region that is hot and humid with an annual precipitation between 1 500 and 2 000 mm and without any dry month (Vincelette *et al.*, 2007; rainfall recorded in the city of Tolagnaro). Dry months were defined as months with less than 50 mm of rain. The driest conditions are observed in the “parcelle 2” where our study was located. There, the dry season lasts for 5 to 6 months with an annual precipitation between 600 and 700 mm. Detailed records of rainfall are not available for the study area. The closest contemporary records are from Berenty, about 30 km west of “parcelle 2” (Jolly *et al.*, 2002). There, annual

rainfall varied between 317 and 894 mm between 1983 and 2000. Monthly average rainfall was above 50 mm in the months of November to February. In Petriky, located some 30 km southeast of “parcelle 2”, the months with more than 50 mm of rain extend up to July (Vincelette *et al.*, 2007). The rainfall pattern of “parcelle 2” is somewhere between these two rainfall patterns. Based on the rainfall pattern during our study, we consider the dry season to extend between April and November and the wet season from December to March. The climate in “parcelle 3” is intermediate between the extremes of “parcelles” 1 and 2. There, annual precipitation is 700 to 800 mm (MNP, 2003; Rasoarimanana, 2005).

We measured air temperature (in °C) and relative humidity (in %) in the different habitat types with data loggers (Hygrochron IButton/DS1923, Dallas Semiconductor, USA) placed in shaded places at the different study sites. Loggers were programmed to record data every two hours (Rakotondranary *et al.*, 2011). Monthly means were calculated based on daily means of relative humidity (%) and mean temperature (°C). The daily minimum and maximum temperatures were also averaged per month. Data were analyzed with Excel. Variation in day length (h) and insolation (W/m<sup>2</sup>) with the sun at its highest position were taken from the Astronomical Application Department U.S Naval Observatory (<http://aom.giss.nasa.gov/srlocat.html>) by using central geographical coordinates of the study region (46°40'E, 24°49'S).

## Statistical analyses

Spearman's rank correlations ( $r_s$ ) were computed between the percentage of species in each phenophase (leafing, flowering, and fruiting) and between phenophases and the monthly means of day length (h), mean relative humidity (%), and mean temperature (°C) (Morellato *et al.*, 2000). The phenological characteristics for different species in the different types of vegetation were compared as well. Data from the different plots were pooled for the different vegetation types. All statistical tests were carried out with SPSS 17 for Windows.

## Results

### Abiotic conditions

In Figure 1 we show the monthly minimum, mean and maximum temperatures (°C), and the mean relative humidity (%) for each vegetation type between September 2007 and April 2009. During the study period, relative humidity varied substantially. The

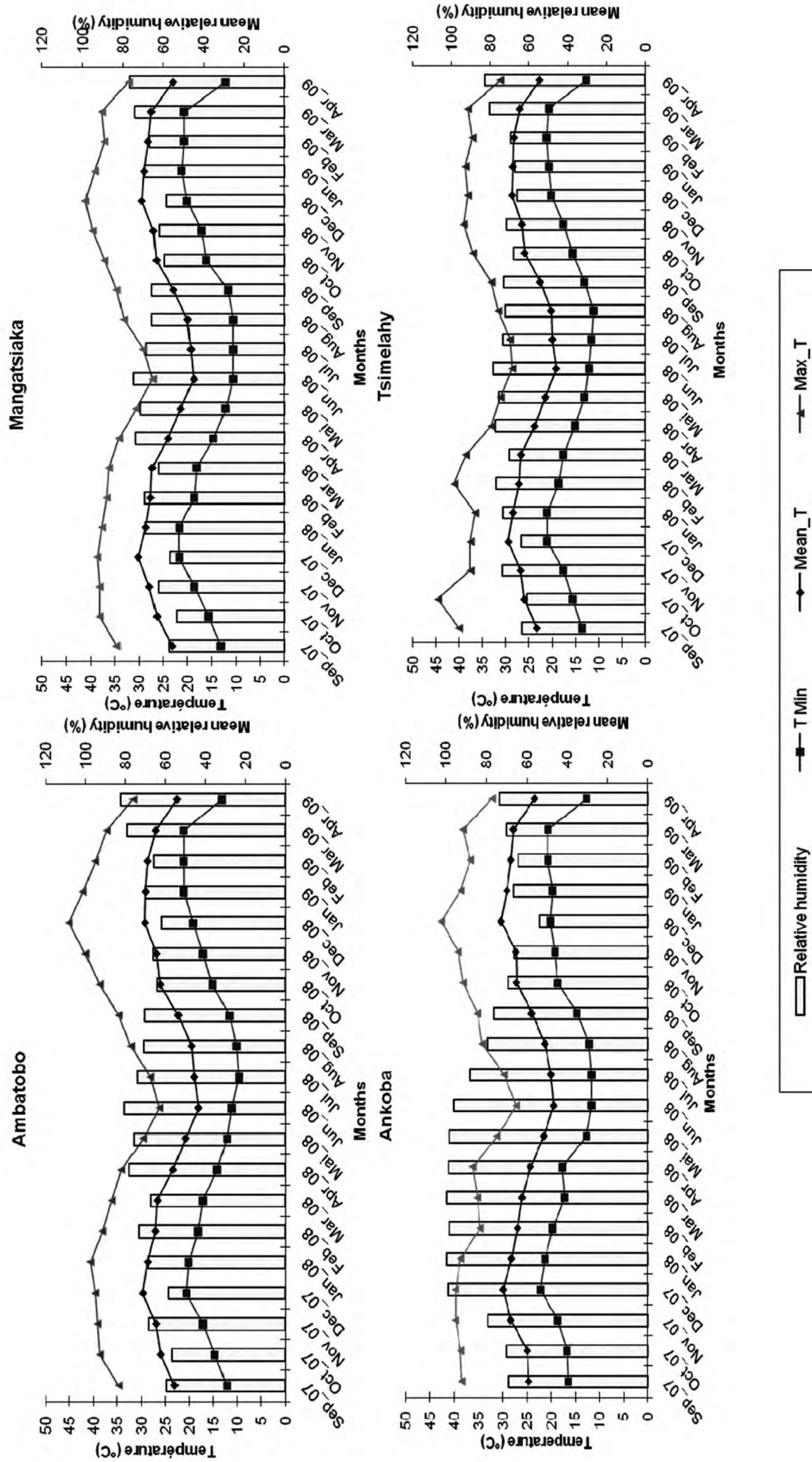
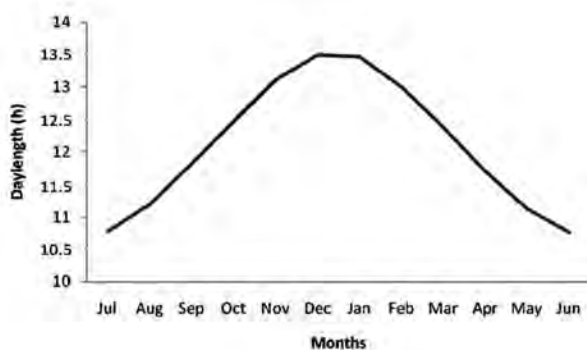
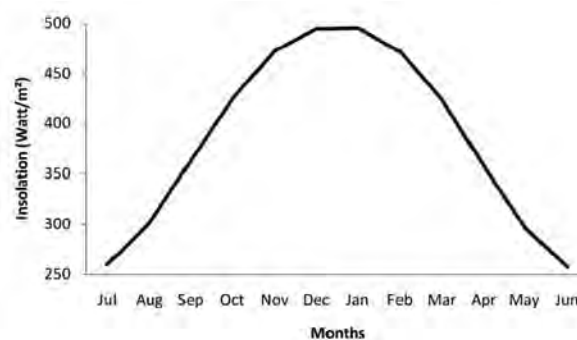


Figure 1. Monthly means of temperature and relative humidity (%) in representative samples of different vegetation types in the Andohahela National Park listed in Table 2 between September 2007 and April 2009.

highest temperatures were observed in December. At all sites, temperature during the wet season was higher than during the dry season (Table 2). In Figure 2 we present the variation of day length (h), and Figure 3 the insolation with sun at its highest position ( $W/m^2$ ). In the region, the longest day has 13.5 h and the shortest day has 10.8 daylight hours.



**Figure 2.** Variation of day length in the study region ( $46^{\circ}40'E$ ,  $24^{\circ}49'S$ ) (from <http://aom.giss.nasa.gov/srlocat.html>).



**Figure 3.** Variation of the insolation at noon in Watt per  $m^2$  (b) in the study region ( $46^{\circ}40'E$ ,  $24^{\circ}49'S$ ) (from <http://aom.giss.nasa.gov/srlocat.html>).

## Phenology

At all study sites, 668 trees of 77 species and 32 families were included in the phenological plots. Analyses were based on species. Sixty one species were monitored in the xerophytic bush; 14 species in the gallery forest; and 15 in the transitional forest (Appendix 1).

**Table 2.** Temperature ( $^{\circ}C$ ) and relative humidity (%) in different vegetation types of the Andohahela National Park. Values are means  $\pm$  standard deviation. N = number of months.

Vegetation	Locality	Season	Mean humidity (%)	Maximum temperature ( $^{\circ}C$ )	Mean temperature ( $^{\circ}C$ )	Minimum temperature ( $^{\circ}C$ )
Xerophytic bush	Mangatsiaka	Dry (n = 12)	$65.7 \pm 6.0$	$34.7 \pm 4.9$	$23.2 \pm 2.7$	$14.0 \pm 2.2$
		Wet (n = 8)	$65.8 \pm 7.4$	$38.2 \pm 1.3$	$28.0 \pm 0.9$	$20.1 \pm 1.3$
Gallery forest	Ambatoabo	Dry (n = 12)	$67.9 \pm 6.4$	$34.9 \pm 4.1$	$23.8 \pm 2.9$	$15.2 \pm 3.0$
		Wet (n = 8)	$70.5 \pm 8.1$	$38.0 \pm 2.6$	$28.2 \pm 1.5$	$20.1 \pm 1.5$
Transitional forest	Tsimelahy	Dry (n = 12)	$70.9 \pm 5.6$	$34.0 \pm 3.8$	$23.3 \pm 3.1$	$13.6 \pm 2.8$
		Wet (n = 8)	$72.6 \pm 6.1$	$38.0 \pm 1.6$	$28.4 \pm 1.0$	$20.3 \pm 1.3$
Xerophytic bush	Ankoba	Dry (n = 12)	$80.6 \pm 11.9$	$34.0 \pm 4.4$	$22.8 \pm 2.7$	$14.3 \pm 2.7$
		Wet (n = 8)	$80.7 \pm 17.2$	$37.6 \pm 2.79$	$27.4 \pm 2.1$	$19.1 \pm 2.5$

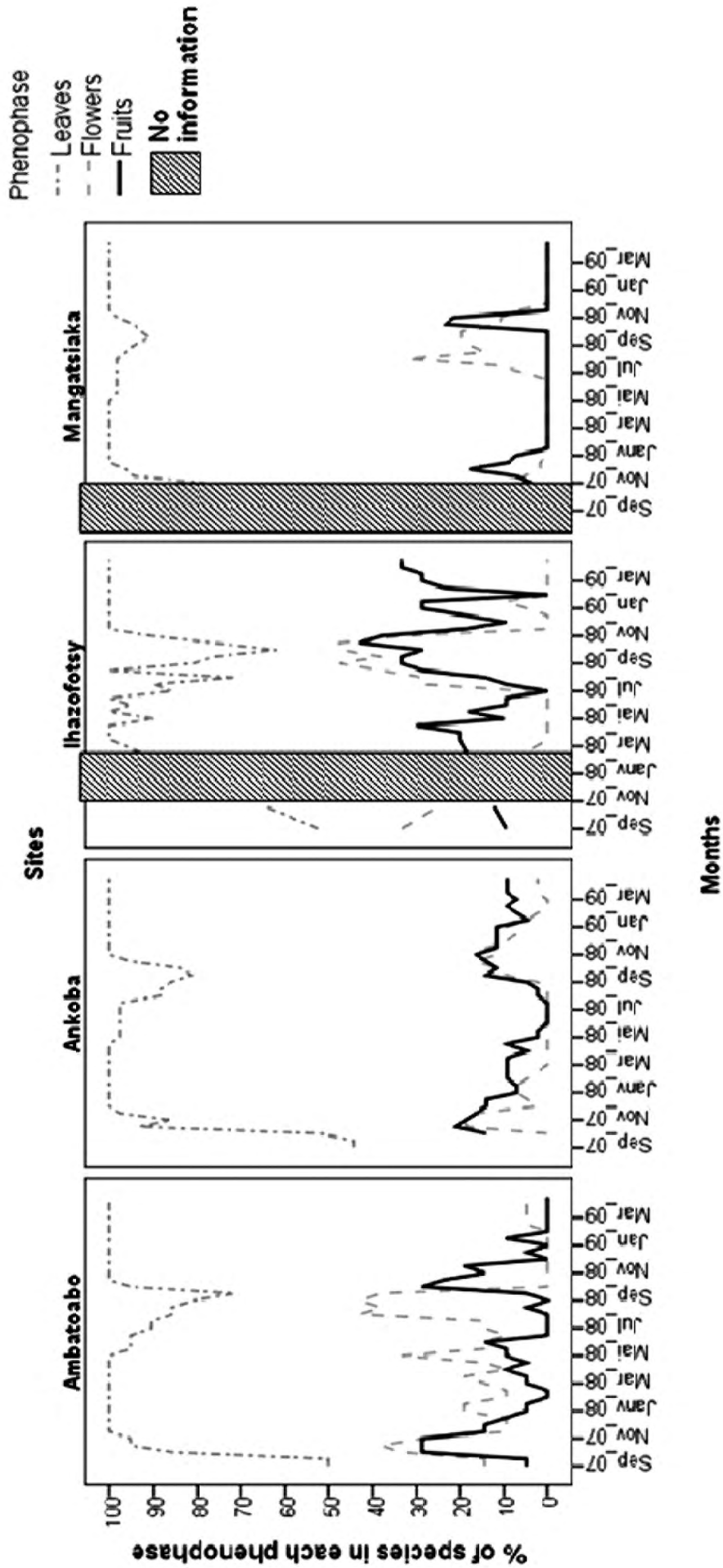
## Community level analysis

### Xerophytic bush

The phenologies of the species recorded in the xerophytic bush are summarized in Appendix 2. On a community level, the number of species with leaves varied seasonally. During the dry season, some species lost their leaves. During the wet season (October/November to April), more than 92% of the plant species had leaves. Over the course of the year, flowering was inconsistent between sites but at all sites, maximum flowering occurred in and towards the end of the dry season between July and October. The presence of fruits varied between years. Fruiting followed the flowering period with most trees fruiting at the end of the dry and during the wet season (Figure 4).

### Gallery forest

The phenology of the species recorded in the gallery forests are summarized in Appendix 3. During the 20 months of phenological observation, most of trees had leaves except for a short period at the end of the dry season when about half of the species lost their leaves. The minimum number of tree species with leaves was observed at Ankoba in October 2007 with 47.3% having leaves. The main period of flowering was similar in Ambatoabo and Ankoba, where trees flowered at the end of the dry and the beginning of the wet season. In Tsimelahy, very few tree species of the phenological plot were actually recorded with flowers except between the second half of November and the end of December 2007 (49.6%). The fruiting period is similar at all three sites. It started at the beginning



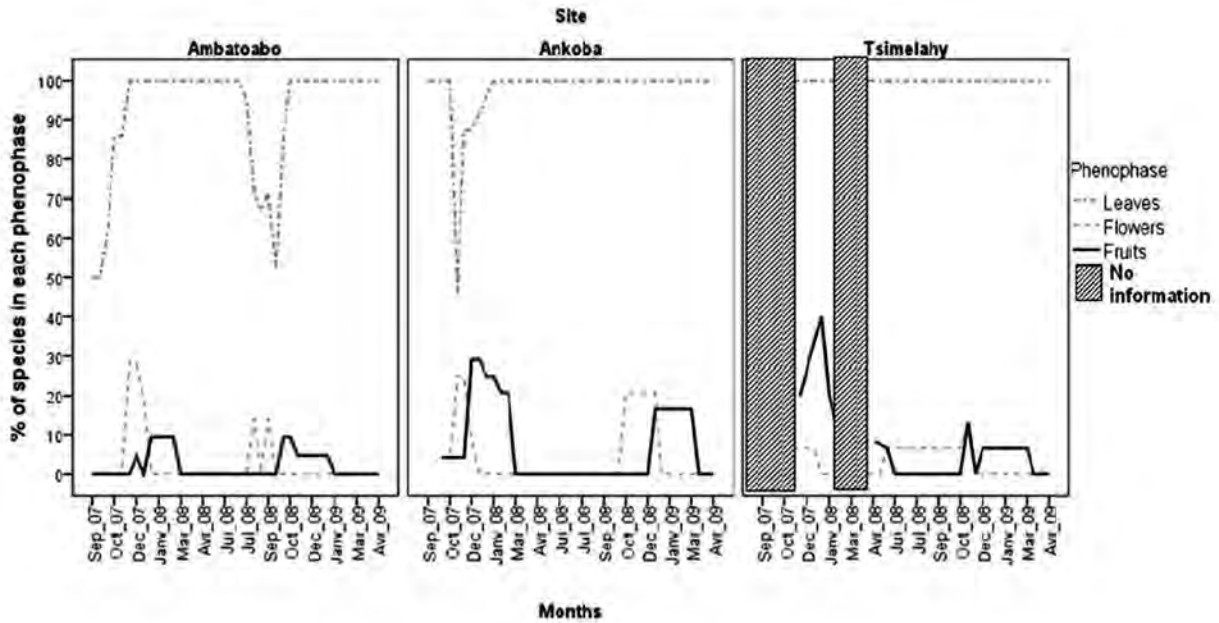
**Figure 4.** Monthly variation of each phenophase in the four sites of xerophytic bush in the Andohahela National Park; dotted line: leaves; stippled line: flowers; solid line: fruits; gray bars: no data available.

of the rainy season and lasted from November until March/April. However, a peak of fruiting was observed by the end of July 2008 (Figure 5).

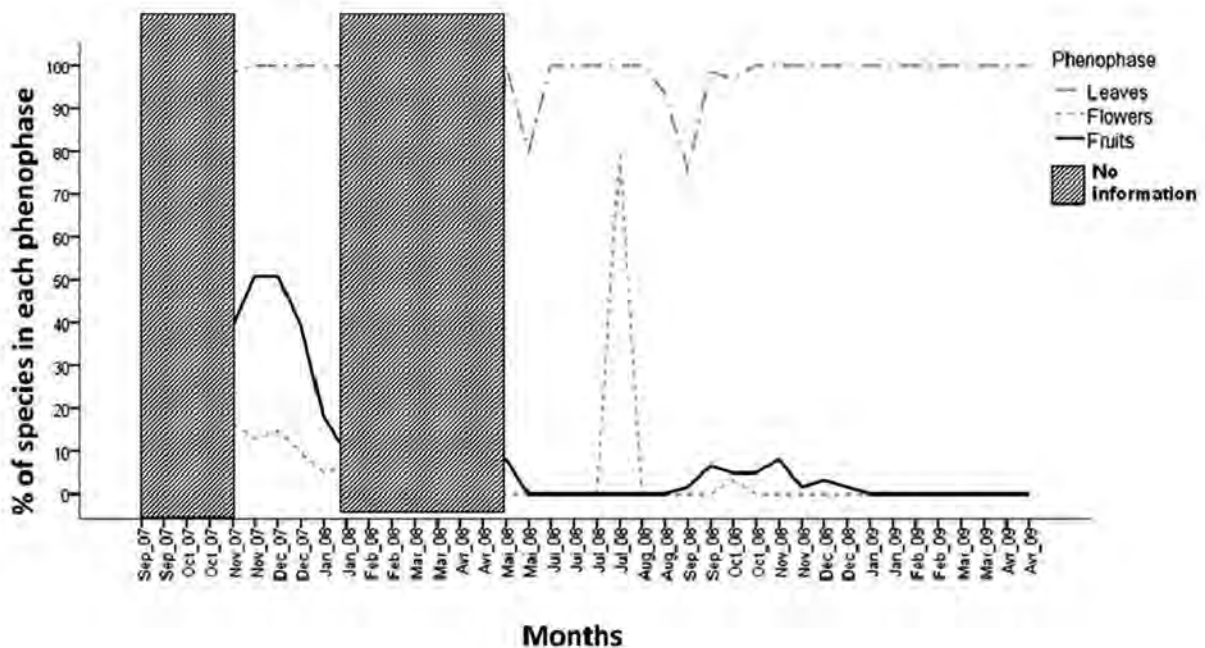
*Transitional forest*

The phenology of the species recorded in the transitional forest of Tsimelahy is summarized in Appendix 4. This type of vegetation, leaves were present throughout the year except for two short periods in May and September, when 15-20% of the

trees lost their leaves. Flowering seemed to have been inconsistent between years. In 2007 flowering extend from the middle of the dry season into the wet season while in 2008 there was a sharp flowering peak in July but no flowering afterwards. Similarly, fruits were present at least from November 2007 to January 2008, but in the wet season from November 2008 to March 2009 next to no trees were recorded to have had fruits (Figure 6).



**Figure 5.** Monthly variation of each phenophase in three gallery forests in the Andohahela National Park; dotted line: leaves; stippled line: flowers; solid line: fruits; gray bars: no data available.



**Figure 6.** Monthly variation of each phenophase in the transitional forest at Tsimelahy in the Andohahela National Park; dotted line: leaves; stippled line: flowers; solid line: fruits; gray bars: no data available.

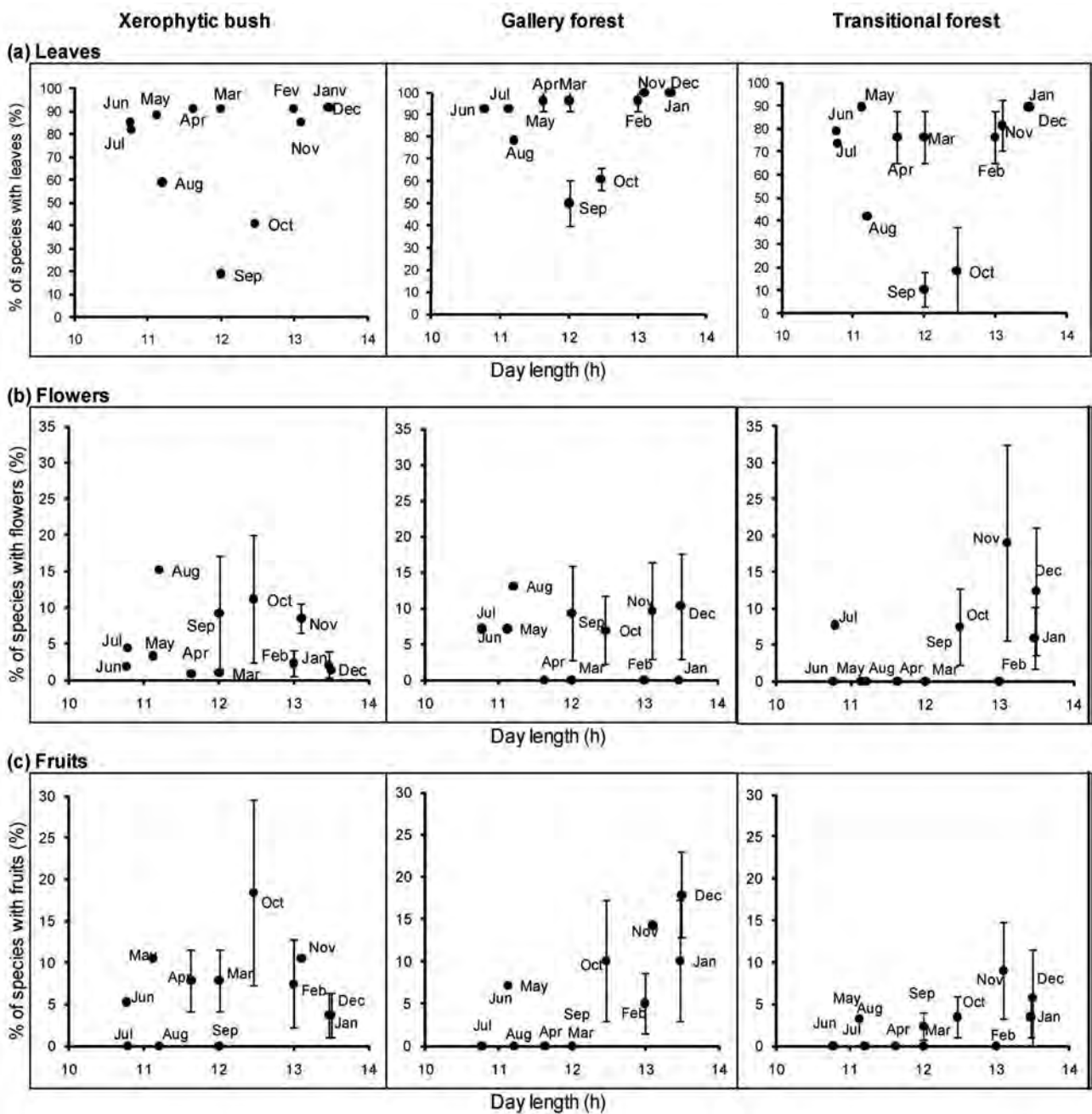
**Correlation between phenophases and climatic conditions**

To investigate correlations between the three phenophases and day length, relative humidity and temperature, we summarized the monthly means for all years into single values per month (Figures 7, 8 & 9).

*Day length and phenophases*

Leafing period showed a clear relation with increasing day length. The percentage of species with leaves increased in November/December (Figure 7a). The

presence of flowers varied in relation to day length. The minimum was observed during the short day length (day length < 12 hours) between January and June and the maximum between September and November, when the days become longer (Figure 7b). The number of species with fruits was correlated with day length in the gallery forest ( $r_s = 0.72$ ;  $n = 12$  months for all correlations;  $P < 0.05$ ), but not in the xerophytic bush and transitional forest ( $r_s = 0.57$  and  $0.52$ ; respectively  $P > 0.05$ ). The percentage of trees with fruits is high when the days are longer than 12 hours (November and January).



**Figure 7.** Day length in relation to the monthly averages of species with a) leaves, b) flowers, and c) fruits in each vegetation type in the Andohahela National Park.



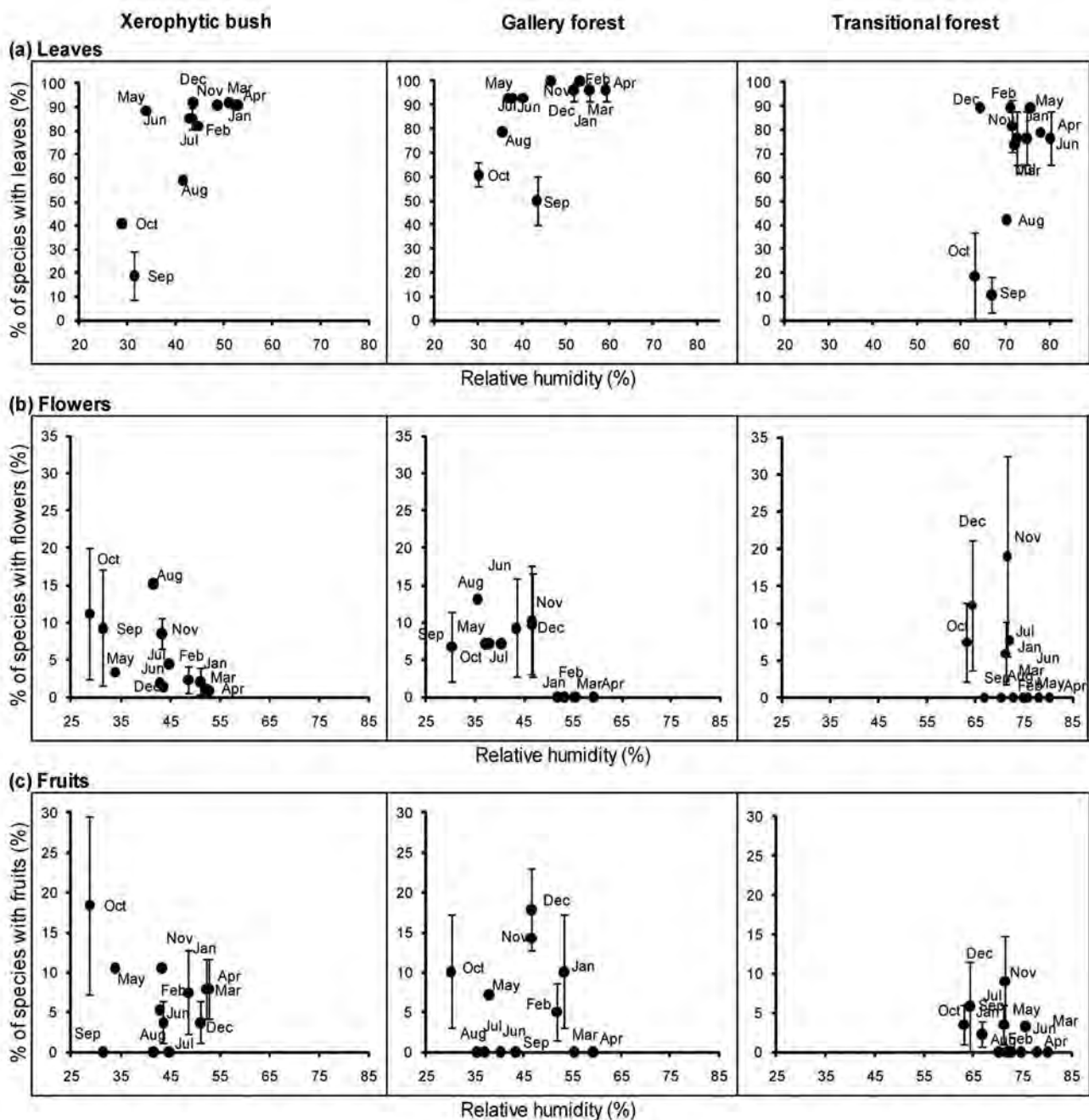
*Mean relative humidity and phenophases*

Figure 8a shows the relations between the mean relative humidity and the number of species with leaves in the xerophytic bush and the gallery forest ( $r_s = 0.74$  and  $0.70$ , respectively;  $P < 0.05$ ). The correlation was not significant in the transitional forest ( $r_s = 0.37$ ,  $P > 0.05$ ). Flowering is negatively correlated with the humidity in the gallery forest ( $r_s = -0.76$ ;  $P < 0.05$ ). However, there was no significant correlation in the xerophytic bush ( $r_s = -0.50$ ) and in the transitional forest ( $r_s = -0.48$ ;  $P > 0.05$ ; Figure 8b). No significant correlation were found between the

number of species with fruits and the humidity in any of the vegetation types (xerophytic bush:  $r_s = 0.15$ ; gallery forest:  $r_s = -0.16$ ; transitional forest:  $r_s = -0.51$ ;  $P > 0.05$  for all these correlations; Figure 8c).

*Mean temperature and phenophases*

Temperature was significantly correlated with the leaf patterns in the xerophytic bush ( $r_s = 0.62$ ;  $P = 0.05$ ); the gallery forest ( $r_s = 0.71$ ;  $P < 0.05$ ), but not in the transitional forest ( $r_s = 0.50$ ; Figure 9a). Mean temperature did not show any significant correlation with flowering (xerophytic bush:  $r_s = -0.37$ ; gallery



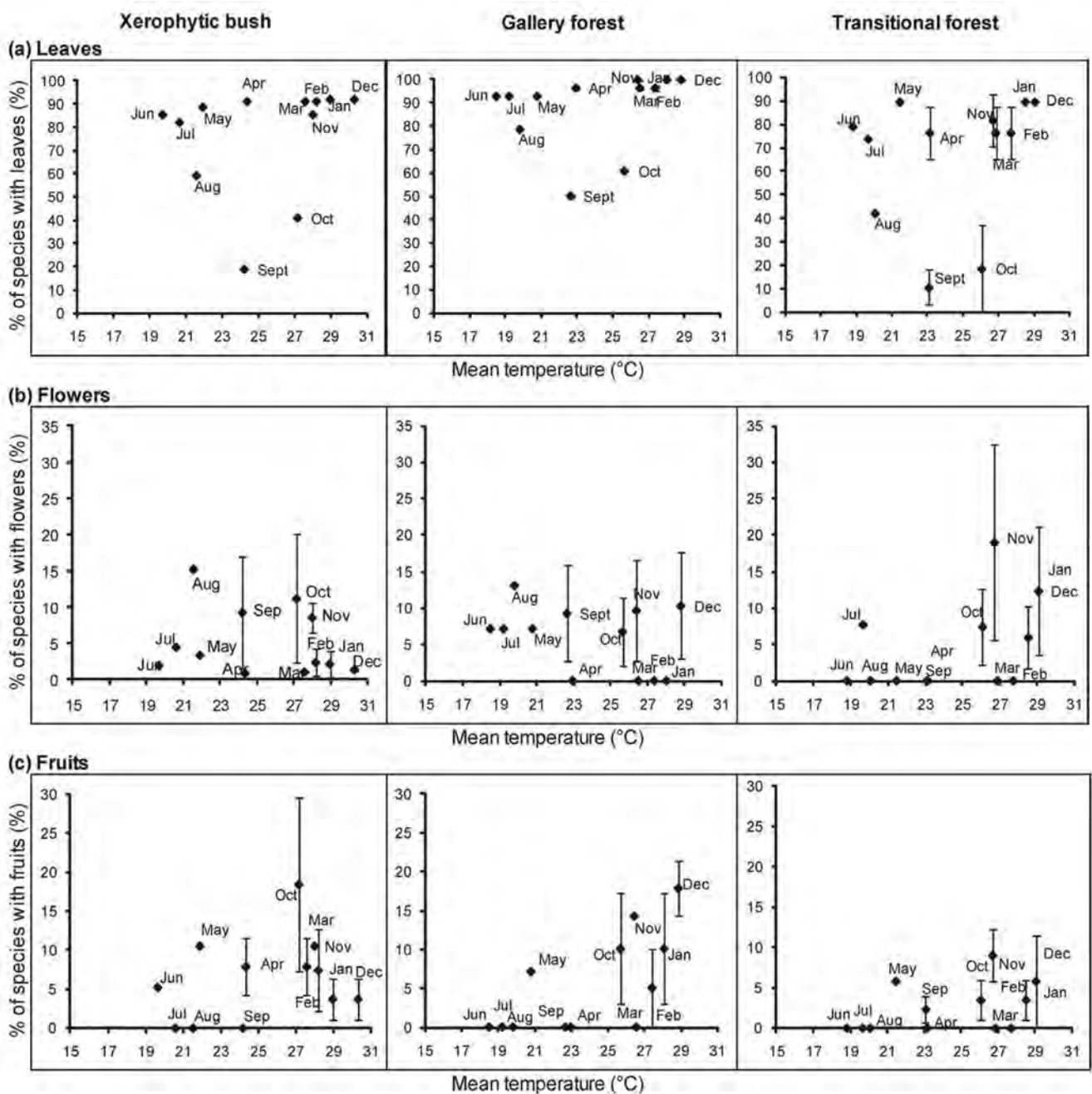
**Figure 8.** Mean monthly relative humidity in relation to the monthly averages of species with a) leaves, b) flowers and c) fruits in each vegetation type of the Andohahela National Park.

forest:  $r_s = 0.28$ ; transitional forest:  $r_s = 0.31$ ;  $P > 0.05$ ; Figure 9b). The proportion of species in fruit was correlated significantly with the mean temperature in the gallery forest ( $r_s = 0.88$ ) and the transitional forest ( $r_s = 0.80$ ) but not in the xerophytic bush ( $r_s = 0.42$ ) (Figure 9c).

### Species level

Comparisons between phenophases of species growing under different conditions but under the same day length and similar temperature provide the means to assess the role of relative humidity for leaving, flowering, and fruiting. The analyses on the

species level were restricted to species that occurred in more than one vegetation type. Three species were shared between the xerophytic bush and the gallery forest. These were *Cerbera venenifera* (Apocynaceae), *Terminalia seyrigii* (Combretaceae), and *Helmiopsis hily* (Malvaceae). Fourteen species were shared between the xerophytic bush and the transitional forest: *Albizia viridis* (Fabaceae), *Alluaudia ascendens* (Didiereaceae), *Androya decaryi* (Buddlejaceae), *Canthium* sp. 1 (Rubiaceae), *Capuronianthus mahafalensis* (Meliaceae), *Cedrelopsis grevei* (Ptaeroxylaceae), *Commiphora brevicalyx* (Burseraceae), *Dicoma*



**Figure 9.** Mean temperature in relation to the monthly average of species with leaves, flowers and fruits in each vegetation type of the Andohahela National Park.

*grandidieri* (Asteraceae), *Diospyros mirtyfolia* (Ebenaceae), *Euphorbia leucodendron*, *E. stenoclada* (Euphorbiaceae), *Opercularia decaryi* (Anacardiaceae), *Rhigozum madagascariense* (Bignoniaceae), and *Vaughania interrupta* (Fabaceae). No species were shared between the gallery forest and the transitional forest. The leafing season of species started at the same time in all three types of vegetation. The onset of flowering and fruiting of the species occurring in more than one type of vegetation varied inconsistently between the xerophytic bush and the gallery and the transitional forest.

## Discussion

The forests of southern Madagascar display different phenological patterns, along a gradient from east to west (Bollen & Donati, 2005; Ratovonamana *et al.*, 2011). Phenological phenomena vary in time and space, in relation to seasons and the status of each individual tree (Newstrom *et al.*, 1994). Among abiotic factors, water availability is most important as all plants need water for their survival. However, the conditions that plants perceive as a drought can vary in relation to temperature, humidity, and the availability of water in the soil (van Schaik *et al.*, 1993). The objectives of the present study were to explore the relationships between phenological characteristics of tree species and tree communities and various abiotic environmental conditions.

In Andohahela National Park, trees had leaves during the hot and humid season. Leaf drop was observed during the dry season between August and September and, hence, before the rainy season. Leafing patterns varied between the different vegetation types, but leaf flushes were concentrated at the beginning of the rainy season. Leaf fall was asynchronous between plants but is concentrated during the driest part of the year from August to October. This seems to be a general pattern as leaf production, which often coincides with peak irradiance when water is available (Lieberman, 1982; Wright & van Schaik, 1994; Sorg & Rohner, 1996). Though in relatively small quantities, it appears that rain is needed to induce leafing in other Malagasy dry forests (Sorg & Rohner, 2002).

Flowering and the subsequent production of fruit can be triggered by changes in photoperiod with some species flowering with declining day length, others with increasing day length, and some without relationship to day length. Within this framework, temperature thresholds initiate the actual onset

of flowering (Sitte *et al.*, 2002). Changing climatic conditions might thus affect the onset of flowering and fruit production with far reaching consequences for animal consumers (Begon *et al.*, 1990). In Andohahela, flowering occurred during the time of leaf fall (July/August – September) and before the rainy season. In more mesic dry deciduous forests, many species also flower during the dry season before the first rains (Sorg & Rohner, 1996) with subsequent fruiting peaks (van Schaik *et al.*, 1993). Here, the flowering cycles showed substantial variation over the year. Some species had no flowers while others flowered at different times of the year in different types of vegetation. The presence of flowers was irregular; the flowering cycle could stop and be resumed in the same year but after a long interruption (Rohner & Sorg, 1987). This may be a consequence of the growing conditions, other external factors or the physiology of each species that are unlikely to reproduce regularly. In general, flowering (and subsequent fruiting) was related more to day length than to the current abiotic conditions.

Most species were observed having fruits at the end of the dry season (September/October) and the first part of the rainy season (December). Most dry forest species are seasonal in their production of mature fruits (Frankie *et al.*, 1974). The majority of wind-dispersed species ripen and release fruits near the end of the dry season (Howe & Smallwood, 1982). However, several species with a late flowering period also produced fruits between April and May (at the end of the rainy season).

The data from Andohahela National Park differed from Tsimanampetsotsa National Park, a site located further west with identical day lengths but distinctly less annual rainfall. There, the maximum vegetation activity occurred between December and June (Ratovonamana *et al.*, 2011). In Andohahela National Park, the onset and the end of flowering and fruiting were one month earlier than in Tsimanampetsotsa National Park. At both sites, leafing was correlated with the wettest period of the year and the peak was during the rainy season (December-March). Flowering was divided in two seasons. Most of the species had flowers during the dry season. Some species flowered before the rainy season. Fruiting patterns occurred in two peaks that coincided with the end of the dry season and the beginning of the rainy season. This corresponds to high temperatures and days longer than 12 hours. In many cases, higher temperatures speed up plant development (Saxe *et al.*, 2001). During the fruiting period, several animal

species are notably active. Thus, food availability is higher during the wet than during the dry season (Wright, 1999; Bollen & Donati, 2005).

Apart from abiotic conditions, plants occupying the same above-ground stratum and the same soil horizons are likely to compete over water, thus adding biotic interactions to the abiotic boundary conditions that affect plant phenology (Seghieri *et al.*, 1995). These biotic effects ought to be most pronounced in an environment where water is limiting. This component was not considered here but might be of interest in subsequent studies.

## Conclusion

In extreme southeastern Madagascar, phenological patterns vary in relation to local conditions that are most likely to be related to water availability. Leaf production seems to be linked to day length, though day length is highly correlated to various abiotic conditions, such as temperature and rainfall. These correlations make analyses of causal relationships impossible without experimental approaches. Nevertheless, while small-scale comparisons between vegetation formations within the Andohahela National Park did not reveal clear differences between vegetation types, an inter-site comparison between Andohahela and the even drier Tsimanampetsotsa National Park revealed clear differences in the timing of leaf production and flowering. These patterns are likely due to differences in abiotic conditions (most likely rainfall) as both sites are subject to the same photoperiodic regime.

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## References

- Adger, W. N., Arnell, N. W. & Tompkins, E. L. 2005.** Successful adaptation to climate change across scales. *Global Environmental Change*, 15: 77-86.
- Andriaharimalala, T., Roger, E., Rajeriarison, C. & Ganzhorn, J. U. 2011.** Analyse structurale des différents types de formation végétale du Parc National d'Andohahela (Madagascar) comme habitat des animaux. *Malagasy Nature*, 5: 39-58.
- Begon, M., Harper, J. L. & Townsend, C. R. 1990.** *Ecology*. Blackwell Scientific Publications, Boston.
- Bollen, A. & Donati, G. 2005.** Phenology of the littoral forest of Sainte Luce, southeastern Madagascar. *Biotropica*, 37: 32-43.
- Carbognell, M. 1963.** Les formations végétales du Sud Est de Madagascar. *Etudes Rurales*, 8: 84-91.
- Frankie, G. W., Baker, H. G. & Opler, P. A. 1974.** Comparative phenological studies of trees in tropical wet dry forest in the lowland of Costa Rica. *Journal of Ecology*, 62: 881-919.
- Goodman, S. M. 1999.** Description of the Réserve Naturelle Intégrale d'Andohahela, and the 1995 biological inventory of the reserve. In A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With reference to elevational variation, ed. S. M. Goodman. *Fieldiana: Zoology*, new series, 94: 1-9.
- Helme, N. A. & Rakotomalaza, P. J. 1999.** An overview of the botanical communities of the Réserve Naturelle Intégrale d'Andohahela, Madagascar. In A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With reference to elevational variation, ed. S. M. Goodman. *Fieldiana: Zoology*, new series, 94: 11-23.
- Hemingway, C. A. & Overdorff, D. J. 1999.** Sampling effects on food availability estimates: Phenological method, sample size, and species composition. *Biotropica*, 31: 354-364.
- Howe, H. F. & Smallwood, J. 1982.** Ecology of seed dispersal. *Annual Review of Ecology and Systematic*, 13: 201-228.
- Jolly, A., Dobson, A., Rasamimanana, H. M., Walker, J., O'Connor, S., Solberg, M. & Perel, V. 2002.** Demography of *Lemur catta* at Berenty Reserve, Madagascar: Effects of troop size, habitat and rainfall. *International Journal of Primatology*, 23: 327-353.
- Lieberman, D. 1982.** Seasonality and phenology in a dry tropical forest in Ghana. *Journal of Ecology*, 70: 791-806.
- Menzel, A. 2002.** Phenology: Its importance to the global change community: An editorial comment. *Climate Change*, 54: 379-385.
- Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F. M., Crepinsek, Z.,**

- Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Mage, F., Mestre, A., Nordli, O., Penuelas, J., Pirinen, P., Remisova, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A. J. H., Wielgolaski, F.-E., Zach, S. & Zust, A. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12: 1969-1976.
- MNP. 2003. Plan de gestion de la conservation du Parc National Andohahela. Madagascar National Parks (MNP), Toliara.
- Morellato, L. P., Talora, D. C., Takahasi, A., Benke, C. C., Romera, E. C. & Zipparro, V. B. 2000. Phenology of Atlantic rain forest trees: A comparative study. *Biotropica*, 32: 811-823.
- Newstrom, L. E., Frankie, G. W. & Baker, H. G. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica*, 26: 141-159.
- Rakotomalaza, P. J. & Messmer, N. 1999. Structure and floristic composition of the vegetation in the Réserve Naturelle Intégrale d'Andohahela Madagascar. In A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With reference to elevational variation, ed. S. M. Goodman. *Fieldiana: Zoology*, new series, 94: 51-96.
- Rakotondranary, J. S., Hapke, A. & Ganzhorn, J. U. 2011. Diversity of *Microcebus* spp. along an environmental gradient. *International Journal of Primatology*, 32: 1037-1057. DOI 10.1007/s10764-011-9521-z
- Rasoarimanana, J. 2005. Suivi des lémuriens diurnes dans le Parc National d'Andohahela. *Lemur News*, 10: 27-29.
- Ratvonamana, 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.
- Rohner, U. & Sorg, J.-P. 1987. *Observation phénologique en forêt dense sèche*. Fiche technique N° 13. Tome 2. Centre de formation professionnelle forestière, Morondava.
- Saxe, H., Cannell, M. G. R., Johnsen, O., Ryan, M. G. & Vourlitis, G. 2001. Tree and forest functioning in response to global warming. *New Phytologist*, 149: 369-399.
- Seghieri, J., Floret, C. & Pontanier, R. 1995. Plant phenology in relation to water availability: Herbaceous and woody species in the savannas of Northern Cameroon. *Journal of Tropical Ecology*, 11: 237-254.
- 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: 57-80.
- Sorg, J.-P. & Rohner, U. 2002. *Cycles phénologiques des arbres de la forêt dense sèche dans la région de Marofandilia/Morondava*. Eidgenössische Technische Hochschule, Zürich.
- Sitte, P., Weiler, E., Kadereit, J. W., Bresinsky, A. & Körner, C. 2002. *Strasburger: Lehrbuch der Botanik für Hochschulen*. 35. Auflage. Spektrum Akademischer Verlag, Heidelberg.
- 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 Systematics*, 24: 353-377.
- Vincelette, M., Dumouchel, J., Giroux, J. & Heriarivo, R. 2007. The Tolagnaro (Fort Dauphin) region: A brief overview of the geology, hydrology, and climatology. In Biodiversity, ecology and conservation of littoral forest ecosystems in southeastern Madagascar, Tolagnaro (Fort Dauphin), eds. J. U. Ganzhorn, S. M. Goodman & M. Vincelette, pp. 9-17. Smithsonian Institution Press, Washington, D.C.
- Wright, J. S. & van Schaik, C. P. 1994. Light and phenology of tropical trees. *The American Naturalist*, 143: 192-199.
- Wright, P. C. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook of Physical Anthropology*, 42: 31-72.

**Appendix 1.** Number of individual trees observed in each vegetation type within the Andohahela National Park. Scientific names and taxonomy are based on <http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php?langue=an>.

Family	Species	Number of individual trees observed in each vegetation type		
		Gallery forest	Transitional forest	Xerophytic bush
Anacardiaceae	<i>Abrahamia grandidieri</i>	27		
	<i>Mangifera indica</i>	3		
	<i>Operculicarya decaryi</i>		2	17
	<i>Poupartia silvatica</i>			1
	<i>Rhus taratana</i>			1
Apocynaceae	<i>Cerbera venenifera</i>	3		2
	<i>Pachypodium lamerei</i> var. <i>lamerei</i>			18
	<i>Rauvolfia media</i>			1
Asteraceae	<i>Dicoma grandidieri</i>		1	1
Bignoniaceae	<i>Rhigozum madagascariense</i>		5	1
Brassicaceae	<i>Maerua filiformis</i>		1	
Buddlejaceae	<i>Androya decaryi</i>		1	1
	<i>Nuxia oppositifolia</i>	2		
Burseraceae	<i>Commiphora brevicalyx</i>		6	109
	<i>Commiphora humbertii</i>			5
	<i>Commiphora marchandii</i>			32
	<i>Commiphora simplicifolia</i>			19
	<i>Commiphora stellulata</i>			12
Celastraceae	<i>Cassine micrantha</i>		1	
	<i>Salvadoropsis arenicola</i>			2
Combretaceae	<i>Terminalia fatraea</i>			3
	<i>Terminalia gracilipes</i>			5
	<i>Terminalia seyrigii</i>	3		1
Crassulaceae	<i>Kalanchoe beharensis</i>			1
Didiereaceae	<i>Alluaudia ascendens</i>		2	42
	<i>Alluaudia dumosa</i>			5
	<i>Alluaudia humbertii</i>			1
	<i>Alluaudia procera</i>			62
Ebenaceae	<i>Diospyros danguyana</i>			31
	<i>Diospyros humbertiana</i>	1		
	<i>Diospyros myrtifolia</i>		1	9
Euphorbiaceae	<i>Croton menabeensis</i>			2
	<i>Euphorbia intisy</i>			2
	<i>Euphorbia leucodendron</i>		1	9
	<i>Euphorbia plagiantha</i>			26
Euphorbiaceae	<i>Euphorbia pyrifolia</i>			2
	<i>Euphorbia stenoclada</i>		1	2
Fabaceae	<i>Albizia commiphoroides</i>			3
	<i>Albizia gummifera</i>	1		
	<i>Albizia tulearensis</i>	1		
	<i>Albizia viridis</i>		3	1
	<i>Cordyla madagascariensis</i>			11
	<i>Dalbergia pervillei</i>			1
	<i>Mimosa delicatula</i>			3
	<i>Mimosa grandidieri</i>			5
	<i>Senna viguierella</i>			1
	<i>Sesbania rostrata</i>	1		
	<i>Vaughania interrupta</i>		3	4
Hernandiaceae	<i>Gyrocarpus americanus</i>			26
Loganiaceae	<i>Strychnos decussata</i>			2
	<i>Strychnos madagascariensis</i>			3

## Appendix 1. (cont)

Family	Species	Number of individual trees observed in each vegetation type		
		Gallery forest	Transitional forest	Xerophytic bush
Malvaceae	<i>Adansonia za</i>			2
	<i>Dombeya valafotsy</i>			1
	<i>Helmiopsis hily</i>	1		7
	<i>Humbertiella henricii</i>			3
	<i>Capuronianthus mahafalensis</i>		1	2
	<i>Melia azedarach</i>	1		
	<i>Neobeguea mahafaliensis</i>			4
	<i>Quivisianthe papinae</i>		1	
Montiniaceae	<i>Grevea madagascariensis</i>			1
Myrtaceae	<i>Eugenia jambolana</i>	6		
Oleaceae	<i>Noronhia ovalifolia</i>			1
Pandanaceae	<i>Pandanus dauphinensis</i>	1		
Pedaliaceae	<i>Uncarina grandidieri</i>		5	
Ptaeroxylaceae	<i>Cedrelopsis microfoliolata</i>		2	
Rhamnaceae	<i>Berchemia discolor</i>			1
Rubiaceae	<i>Breonadia salicina</i>	9		
	<i>Canthium</i> sp. 1		7	3
	<i>Hymenodictyon decaryi</i>			1
	<i>Rothmannia</i> sp.			1
Rutaceae	<i>Cedrelopsis grevei</i>		17	15
Salicaceae	<i>Homalium tetramerum</i>			6
Salvadoraceae	<i>Salvadora angustifolia</i>			1
Sapotaceae	<i>Sideroxylon beguei</i>			8
Sphaerosepalaceae	<i>Rhopalocarpus lucidus</i>			1
Tiliaceae	<i>Grewia androyensis</i>			1
Urticaceae	<i>Obetia madagascariensis</i>			3















