

LEAF PHENOLOGICAL PATTERNS OF TREES, SHRUBS AND LIANAS
IN A DRY SEMI-DECIDUOUS FOREST OF NORTH-WESTERN MADAGASCAR:
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RÉSUMÉ.— *Phénologie de la foliaison des arbres, arbustes et lianes dans une forêt semi-décidue du nord-ouest de Madagascar : types fonctionnels et adaptations à l'environnement.*— Dans le cadre d'une étude sur la phénologie des arbres, arbustes et lianes d'une forêt semi-décidue (Badralla, au nord-ouest de Madagascar), nous avons trié et pesé les éléments de la litière ramassée deux fois par mois dans 20 paniers-collecteurs au cours d'une période couvrant les saisons sèches de deux années successives. Notre base de données quantifiées, constituée principalement par les poids des feuilles des espèces identifiées, a été complétée par les résultats des observations bimensuelles des repousses des feuilles, des floraisons et des fructifications d'une série d'arbres, d'arbustes et de lianes étiquetés. Les rythmes de chute de feuilles de 36 espèces (parmi les 90 espèces dont les feuilles ont été identifiées au cours des tris de litière) a permis une classification en 4 catégories phénologiques : décidue précoce, décidue progressive, décidue tardive et sempervirente. Bien que chacune de ces catégories soit caractérisée par des réponses aux facteurs climatiques significativement différentes, il existe un gradient des caractéristiques phénologiques de l'ensemble des espèces. La discussion porte sur les caractéristiques adaptatives de ces différentes catégories de réponses, sur leurs implications dans l'écosystème en fonction des rôles complémentaires joués par chacune d'elles et sur leurs possibilités d'adaptation à de futurs changements climatiques.

SUMMARY.— Plant phenology was studied in the dry semi-deciduous forest of Badralla (northwestern Madagascar). All categories of litterfall collected bi-weekly in 20 traps from the beginning of one year's to the end of the next year's dry season were separated, identified and weighed. The quantitative database on leaf litter production by different tree, shrub and liana species was supplemented by direct bi-weekly observations of their leaf flush, flowering and fruiting. Although distributed along a continuum, leaf-shedding rhythms of 36 species, out of about 90 species identified in leaf litterfall, could be classified into four categories (early deciduous, progressively deciduous, late deciduous, and evergreen) each having significantly different responses to variations of meteorological factors. The adaptation of the phenological responses, the complementary ecological role they played and the possible responses of the forest ecosystem to future climate changes are finally discussed.

Documenting and interpreting patterns of plant phenology provide insights into the ecological processes organizing a plant community (e.g. Negi & Singh, 1992; Kikuzawa & Lechowicz, 2011; Reich 1995) and might help us predicting how climate changes will affect that community (Díaz & Cabido, 1997; Richardson *et al.*, 2013). Leaf phenology is especially likely to reveal the selective pressures that are placed on plant characteristics. Leaves fuel a plant's growth and its competitive success, so leaf dynamics mainly reflects how plants invest in using vs storing resources (Reich *et al.*, 2004; Singh & Kushwaha, 2005).

Although plant phenological patterns result from various interactions between biotic and climatic factors, seasonal variation in precipitation, which influences soil moisture and tree water status, is often the primary influence on the timing of plant growth and reproduction in tropical plants (Reich & Borchert, 1984). As a result, the timing and severity of dry periods influence the

structure and ecophysiological characteristics of dry tropical forest ecosystems, by favouring adaptations for avoiding, resisting or tolerating water stress. Previous studies in such forests (Hladik, 1980; Reich & Borchert, 1984; see also the review of Singh & Kushwaha, 2005) showed that some species shed their leaves at (or just before) the onset of the dry season, whereas phenological pattern of other species is close to late deciduousness and even evergreen. Thus, even though deciduous and evergreen species in the same habitat experience similar availability of major resources, they differ in the way they acquire these resources, as well as in their morphological adaptations to reduce water loss. Furthermore, in sites with moderately severe dry seasons, leaf phenology of different species and, even, individuals of the same species, would reflect distinct leaf-shedding synchronization at species and plant community level (Reich & Borchert, 1984; Wright & Cornejo, 1990). Accordingly, most dry tropical forests are mosaics of plant species exhibiting various adaptations to dryness and duration of deciduousness (Borchert *et al.*, 2002; Singh & Kushwaha, 2005). Whether specific patterns in the timing of leaf-shedding might correspond to phenological categories remains debated mainly because current quantitative data on leaf fall phenology are scarce, involving a few tree species. In particular, neither lianas nor shrubs were taken into account in most of these studies, hampering a global analysis of leaf phenology in dry tropical forests.

In our study, carried out in a dry, semi-deciduous forest on sandy soil in north-western Madagascar, we characterized both the annual variation in litter production (leaf, reproductive parts, wood, etc) and leaf phenology of tree, shrub and liana species using quantitative data obtained by sorting out leaves of the species identified in litter traps and measuring their biomass. Although this approach is particularly time consuming, it appears to be the best way for gathering reliable data on leaf-shedding rhythms (especially for liana species) and to examine the effect of abiotic factors on these rhythms. It also allows to assess food availability for folivorous animals which exert considerable selective pressure on plants (Pichon, 2012, and unpubl. data). Thus, while the timing and intensity of deciduousness vary in a continuum among plant species, we assessed whether different categories of leaf phenological patterns can be identified in the study forest, and whether these patterns were correlated with climatic variables. We discuss implications of the variation within each type for how they adapt to their dry forest climate and how they might adapt to future climate changes.

MATERIALS AND METHODS

STUDY SITE

Data presented here were collected in one fragment of the dry semi-deciduous forest called Badrala. This study site located at 15°42'-15°50'S / 46°-46°15'E encompasses a 24-ha area surrounded by savannahs and a littoral dune (Gauthier *et al.*, 2001). It is a part of the Station Forestière à Usages Multiples of Antrema (SFUM of Antrema, presently Nouvelle Aire Protégée, interministerial order 5002/2010) covering 12 300 ha located along the Mozambique Channel, on the left riverside of the Betsiboka estuary, in north-western Madagascar.

Mean annual rainfall in the region is 1425 mm. Precipitation mostly occurs from November to March, and the heaviest rainfall is recorded in January-February (Service de météorologie de Mahajanga, 1990-2011). The thick layer of white sand covering the forest ground constitutes a very permeable substratum to rainwater (Leclerc-Cassan & Gauthier, 2000). Temperature also fluctuates seasonally, reaching its highest values in October and its lowest ones between June and August with an annual mean of 27°C. These climatic data indicate a severe dry season of 6 to 7 months from April to October, characteristic of the dry bioclimate (Schatz, 2001). Relative humidity in this littoral area, where there is morning dew, remains high all the year (Gauthier *et al.*, 2001), with mean monthly values fluctuating between 51.7 % (August) and 76.9 % (January). Inside a somewhat similar dry forest near Morondava, relative humidity recorded during the dry season remains above 90 % most of the time, except at midday when it drops to 50 % (Hladik, 1980). Although most of the cyclones coming from the Indian Ocean turn into heavy rainfall when arriving in the western part of Madagascar, some damage the forest reserve severely (Roger & Ravaomanalina, 2005).

Variation in day length (h) and solar irradiation (daily annual mean: 262 W.m⁻²), two meteorological variables related to photosynthetic activity and primary productivity were taken for the study period from internet databases

(<http://www.mindspring.com/~cavu/sunset.html> and <http://re.jrc.ec.europa.eu/pygis/apps4/pvest.php?map=africa&lang=en>, respectively) by using geographical coordinates of the study site.

Vernacular names of plant species were first given by local guides before herbarium specimens were collected for taxonomic identification. Voucher specimens and associated information registered at the Paris herbarium (MNHN) can be viewed through the Sonnerat database (<http://science.mnhn.fr/institution/mnhn/collection/p/search>).

QUANTIFICATION OF LITTERFALL

Litter traps were woven by traditional methods from *Bismarkia nobilis* leaves, so as to allow rainwater to leave the trap. Sixty litter traps were installed on wooden frames 1 m above ground level, 10 m apart from each other within transects inside Badrala forest. Due to irregular shaping, the surface of each litter trap was measured to allow further calculation of total litterfall (mean \pm SD: $0.17 \text{ m}^2 \pm 0.03$). The material from each individual trap was collected every two weeks (except during two longer periods; see Fig. 1), from May 2008 to August 2009, and stored in paper bags. The smallest items (e.g. flowers, leaflets, and feces of arthropods) were collected with the mouth-operated aspirator used by entomologists. Paper bags were first dried in an oven in the field and later in the lab at 60°C for at least 48 h.

From each separate paper bag identified by location and date of collect – allowing to know the exact surface area of the trap and the total number of days between two collections of litterfall –, all items were sorted into five main categories: leaves (including petioles), reproductive plant parts (flowers, fruits, and seeds), wood and twigs, faeces, and miscellaneous (arthropod fragments, feathers, galls, debris, and unidentified material). Leaves (and reproductive parts whenever possible) were identified to the species level following voucher specimens. About ninety species of different life form (i.e. trees, shrubs and lianas) were identified, most at the species level, but some at the genus level (see Annex). Each identified part was weighed ($\pm 0.01\text{g}$). Preliminary results had been obtained by botany students (Ranaivoson, 2010; Ranaivoson *et al.*, 2010) before all taxonomic identifications could be confirmed. Voucher specimens collected during the field work carried out between 2008 and 2011 allow a comprehensive analysis of the litterfall collected from the 20 litter traps installed along one of the transects. Focusing on this subset of 20 litter traps from the larger sample of traps installed reflects the intense effort at separating and identifying plant fragments collected over 16 months. Although transects varied somewhat in their plant species composition and densities, we will discuss later how representative the litterfall analysis is of the Badrala forest.

SUPPLEMENTARY QUALITATIVE OBSERVATIONS OF PHENOPHASES

In parallel to the quantitative study of leaf litterfall, we observed variations in leafing, flowering and fruiting status between May 2008 and August 2009, on a bimonthly basis during five periods of fieldwork (May 2008, July 2008, November 2008, May-June 2009, November 2009). These phenological data have been recorded on labelled trees (DBH ≥ 10 cm, $N = 280$) within two botanical transects (10 m x 210 m and 10 m x 150 m, respectively). Understorey species (shrubs and young trees >70 cm high and 2.5 cm $<$ DBH < 10 cm, $N = 156$) and lianas (woody and herbaceous species ≥ 1 m high, $N = 129$) were monitored in two quadrats (10 m x 10 m).

These qualitative phenological observations that will be presented in parallel to the quantitative patterns of leaf fall have been supplemented by information from voucher specimens collected in the Mahajanga area and consulted in the Paris Herbarium, as well as the observation of phenophases during a field study on lemurs' dietary behaviour (Pichon, 2012). The qualitative information will help to discussing and understanding the phenological patterns obtained through accurate quantification of species leaf shedding.

DATA ANALYSIS

We calculated litter production rates ($\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) in terms of dry weight of litterfall for each plant species, by averaging production rates from all litter traps (i.e. individual weights divided by the litter trap area and the number of days between collections). In order to allow comparisons with other forests, the annual production has been separately calculated using only data obtained between May 2008 and April 2009.

Thirty six species providing enough material reliably determined in the litter collected are presented here. Some abundant species in the forest are not presented, due to the difficulty of differentiating one species from another (e.g. *Chadsia flammea* vs *Mundulea* spp.) or because of their very light leaf-fall biomass (e.g. tiny leaflets of *Abrus aureus*).

On the basis of leaf-fall patterns (timing and intensity) and of all observations of phenophases in our database, we categorized plant species into four main groups along a gradient of deciduousness.

(1) *Early deciduous species* rapidly drop their leaves early in the dry season (i.e. May-June), and remain leafless for several dry months.

(2) *Progressively deciduous species* lose leaves continuously during the dry season, with leaf fall generally peaking in the mid-dry season (i.e. July-August).

(3) *Late deciduous species* keep their leaves longer, and finally drop them at the very end of the dry season (i.e. September-October).

(4) *Evergreen species* exhibit overlapping periods of leaf fall and leaf flush during the dry and/or the wet season.

We carried out correlation analysis to examine the relationship between litterfall (and leaf-falls) and the following meteorological variables: relative humidity (%), rainfall (mm), minimum temperature ($^\circ\text{C}$), horizontal irradiance ($\text{W}\cdot\text{m}^{-2}$),

and photoperiod change (min). Since available meteorological data were provided as monthly rainfall, etc., monthly lags were introduced so that phenology could be correlated with climate up to four months before the current month. Used data are monthly averages (without using data cumulated on longer periods) for the specific study period (i.e. January 2008-August 2009), except relative humidity that consists of monthly averages over 11 years (1990-2000). The five main variables at their respective five time lags (25 variables in total) were correlated with total litterfall and leaf-falls using Pearson correlation when binormality was fulfilled, and Spearman correlation otherwise. To test the importance of all meteorological variables altogether, multiple regression analysis was used. We included, in the full model, all five meteorological variables at the time lag that was shown to have the strongest correlation with total litterfall and leaf-falls, regardless of the correlation significance. Following the stepwise procedure, the final resulting model contained the combination of variables that best explained the relationship between the selected meteorological variables and phenology.

RESULTS

TOTAL LITTERFALL

The whole litterfall pattern obtained throughout the study period including two dry seasons, is presented in parallel to monthly variations of rainfall and temperature (Fig. 1) after calculating the total weight of the different items during each phase of collecting. The annual litterfall, calculated only between May 2008 and April 2009, is $6.4 \text{ t.ha}^{-1}.\text{y}^{-1}$ (Tab. I). Leaves account for more than 70 % ($4.6 \text{ t.ha}^{-1}.\text{y}^{-1}$ including $0.7 \text{ t.ha}^{-1}.\text{y}^{-1}$ for lianas), while reproductive plant parts and wood respectively represent 15 % and 10 % of total litterfall. The remaining items together constitute less than 5 % of total litterfall.

TABLE I

Litterfall per item category, calculated between May 2008 and April 2009, in the Badrala forest

Category	Annual litterfall ($\text{kg.ha}^{-1}.\text{y}^{-1}$)	Percentage of annual litterfall
Wood	637	9.9
Leaves (total)	4609	71.7
(trees and shrubs)	3682	
(lianas)	749	
(unidentified)	178	
Flowers, fruits and seeds	946	14.7
Fecal matter	139	2.2
Other miscellaneous productions (leaf buds, gall, fungus, animal parts, debris...)	101	1.6
<i>Total Litterfall</i>	<i>6432</i>	<i>100</i>

GENERAL PHENOLOGICAL PATTERN OF THE COMMUNITY

The variations in litterfall categories recorded during 16 months are shown in Fig. 1. Over this study period, leaves and reproductive parts followed the overall unimodal pattern of litterfall: leaf-shedding peaks between June and October, and flowers and fruits mainly fall between July and the first rainfalls (i.e. November).

LEAFING PATTERNS

Quantitative variations of leaf fall for the 36 selected species are presented in Figs 2 to 5. This sample of species constitutes 74 % of total leaf fall. Based on their leafing patterns, the 36 species can be classified as one of the four major phenological types (see methods). However, some species show intermediate characteristics, suggesting that the leafing pattern of all species actually reflects a continuum.

Early deciduous species (Fig. 2) are characterized by heavy leaf-fall at the onset of the study period (May and early June). Some of the tree species rapidly become bare (e.g. *Operculicarya*

gummifera) whereas other species including two lianas (*Combretum sphaeroides* and *Sphedammocarpus multiflorus*) keep shedding their leaves up to August. All species then remain leafless until the onset of the wet season.

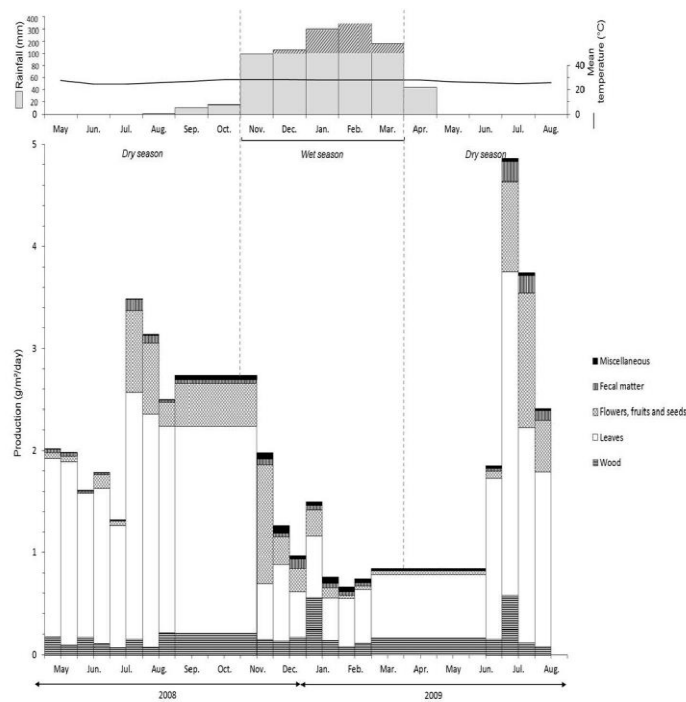


Figure 1.— Litterfall pattern in the Badrara forest according to monthly variations in rainfall and temperature. In the upper graph, a dry month is determined when rainfall is below the temperature curve (respective scales with 1°C corresponding to 2 mm of rainfall according to the ombrothermic graph of Bagnouls and Gaussen, 1953). Note that above 100 mm of rainfall (hatched area), a different scale highlight the part of the water that is generally considered as runoff due to water-saturated soil. In the bottom graph, litter productions have been recorded over periods of 2 weeks. However, when it was only possible to collect the litter after a longer period than two weeks, litterfalls are shown as a block for which the mean production per day allows comparison with other periods.

In *progressively deciduous species* (Fig. 3), leaves fall throughout the dry season although leaf-shedding mainly occurs between July and September. Leaflessness lasts less than one month.

Species described as *late deciduous* (Fig. 4) retained their leaves until the end of the dry season. Then, they rapidly become bare, and new leaves flush simultaneously to –or just after–shedding.

Evergreen species (Fig. 5) are characterized by various profiles of leaf shedding: leaf-fall remains weak all year round in some species (e.g. *Memecylon boinense*, *Trilepisium madagascariense*), whereas other ones (e.g. *Noronhia boinensis*, *Xylopia sericolampra*, *Anisocycla cf. grandidieri*) undergo a peak of leaf-shedding after new shoots regrowth.

METEOROLOGICAL VARIABLES AND LITTERFALL

Among the meteorological variables tested (Tab. II), solar radiation recorded with a time lag

of two months prior to total litterfall records has a significant negative effect on litterfall. Humidity and rainfall also have a significant negative effect, but without time lag. A meteorological influence reaching statistical (photoperiod variation) or marginal significance is also found when considering leaf-shedding only. Meteorological variables together explain 93 % of the observed variation in leaf-shedding. Particularly interesting is the negative effect of photoperiod variation on the temporal pattern of leaf-fall: the larger the change of day length within each month, the weaker the leaf-fall four months later.

TABLE II
Regression models of the relationships between litterfall and meteorological variables at Badrala for various life forms and phenological types

Dependent variable	Independent variables included in the final model ^a					R^2
	Humidity	Rainfall	Minimum temperature	Horizontal irradiance	Photoperiod variation	
Total litterfall	0 / -	0 / -	(1 / -)	2 / -		0.87
Total leaf-fall	(0 / -)	(0 / -)	(0 / -)	(2 / -)	4 / -	0.93
Trees	(1 / -)	(2 / -)	(1 / -)	2 / -	0 / +	0.96
Understory	1 / -	2 / -				0.84
Lianas	3 / +					0.64
Early deciduous	3 / +					0.79
Progressively deciduous	(1 / -)	(2 / -)	(1 / -)	(2 / -)	0 / +	0.95
Late deciduous	(1 / -)	2 / -	(3 / -)	4 / -	0 / +	0.93
Evergreen	(3 / -)	(2 / -)	(3 / -)	(1 / +)	(1 / +)	0.06

^aLag in months and sign of the regression coefficient are given for each independent variable included in the final model. Significant relationships ($P < 0.05$) are in bold, and marginally important ones ($0.08 > P > 0.05$) are shown in parenthesis.

Each life form (i.e. trees, understory and lianas) responds differently to meteorological variables. Those variables explain much of the defoliation patterns observed for trees (96 %), which are significantly sensitive to photoperiod changes (immediate) and solar radiation (time lag of two months). In contrast, they have a smaller impact on understory (small trees, shrubs) and lianas (84 % and 64 %, respectively), which are mostly sensitive to water availability (i.e. humidity and rainfall).

Meteorological factors appear to be linked to leaf-shedding pattern of the different phenological types, evergreen species apart (Tab. II, evergreen species: $R^2 = 0.06$; deciduous species: $R^2 \geq 0.79$). Unusual high values of R^2 might be due to small sample, however, it is particularly noteworthy that relative humidity is sufficient to explain 79 % of leaf-fall in early deciduous species, whereas two phenological types (progressively and late deciduous species) – that are less sensitive to water stress *a priori* – also depend on other meteorological variables. Photoperiod changes have significant, positive effect on leaf-fall of progressively and late deciduous species, and the latter are also negatively dependent of rainfall (with a time lag of 2 months) and solar irradiance (with a time lag of four months).

DISCUSSION

PHENOLOGICAL PATTERNS AND METEOROLOGICAL VARIABLES

The presence of trees, shrubs and lianas within four different phenological categories suggest that species in the sandy soil dry forest at Badrala use different means to cope with water stress. Meteorological constraints probably trade-off against other constraints, whether environmental (e.g. pollinators, predators) or internal (e.g. physiological, phylogenetic).

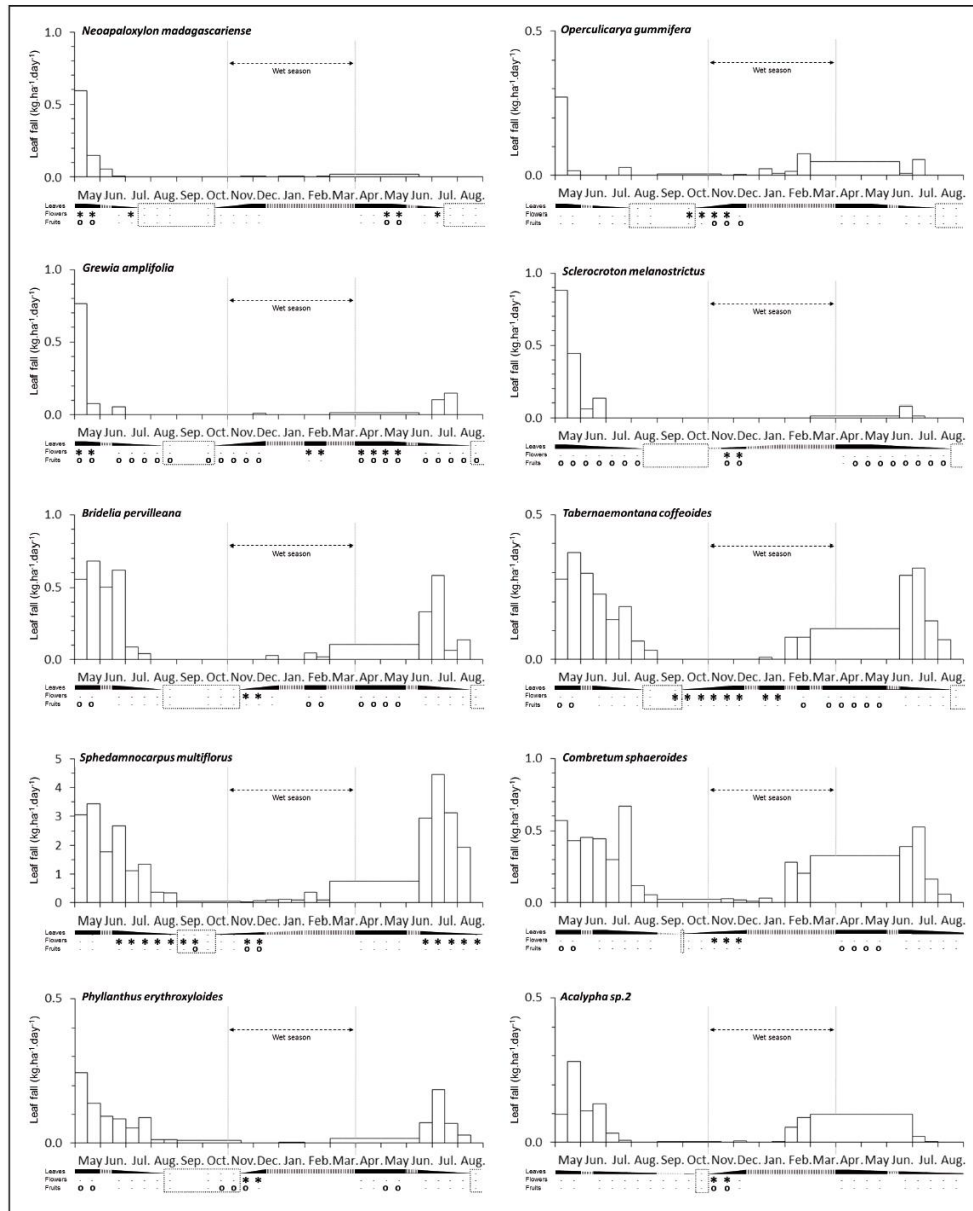


Figure 2.— Early deciduous species of the Badrara forest, according to the leaf litterfall recorded during 16 months including two dry seasons (scales are adapted for comparing phenological profiles). Individual graphs are ordered according to the general pattern (*i.e.* timing and amplitude) of leaf-shedding. Below each graph is a timeline displaying qualitative observations on leaf-shedding, total bareness and leaf-regrowth, as well as the presence of flowers and fruits. Total leafless periods are highlighted by empty rectangles followed by flushing of new leaves (shown by the increase of the corresponding thick line). Negative observations of phenophases are indicated by dashes.

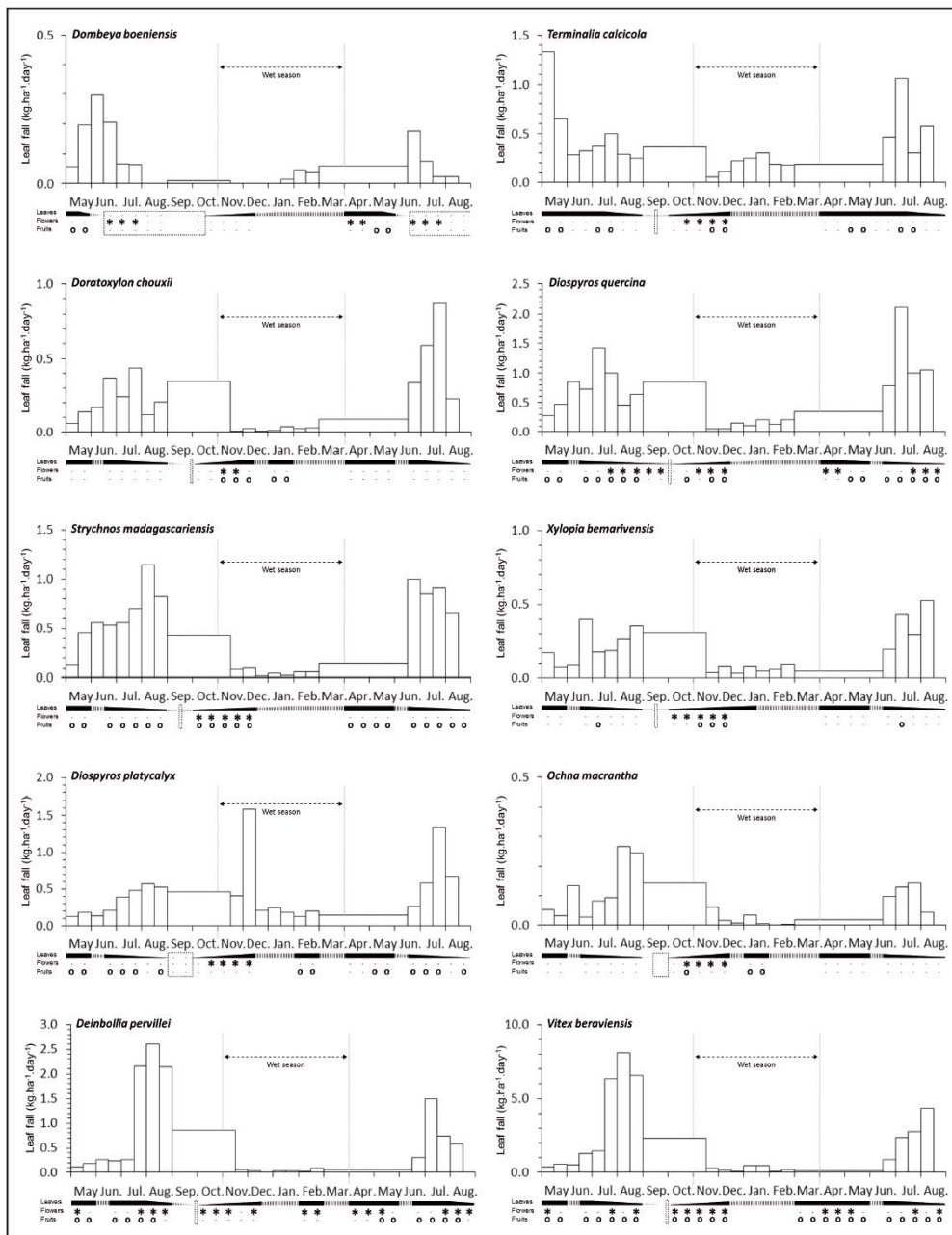


Figure 3.— Progressively deciduous species of the Badrala forest, according to the leaf litterfall recorded during 16 months including two dry seasons (scales are adapted for comparing phenological profiles). Individual graphs are ordered according to the general pattern (i.e. timing and amplitude) of leaf-shedding. Below each graph is a timeline displaying qualitative observations on leaf-shedding, total bareness and leaf-regrowth, as well as the presence of flowers and fruits. Total leafless periods are highlighted by empty rectangles followed by flushing of new leaves (shown by the increase of the corresponding thick line). Negative observations of phenophases are indicated by dashes.

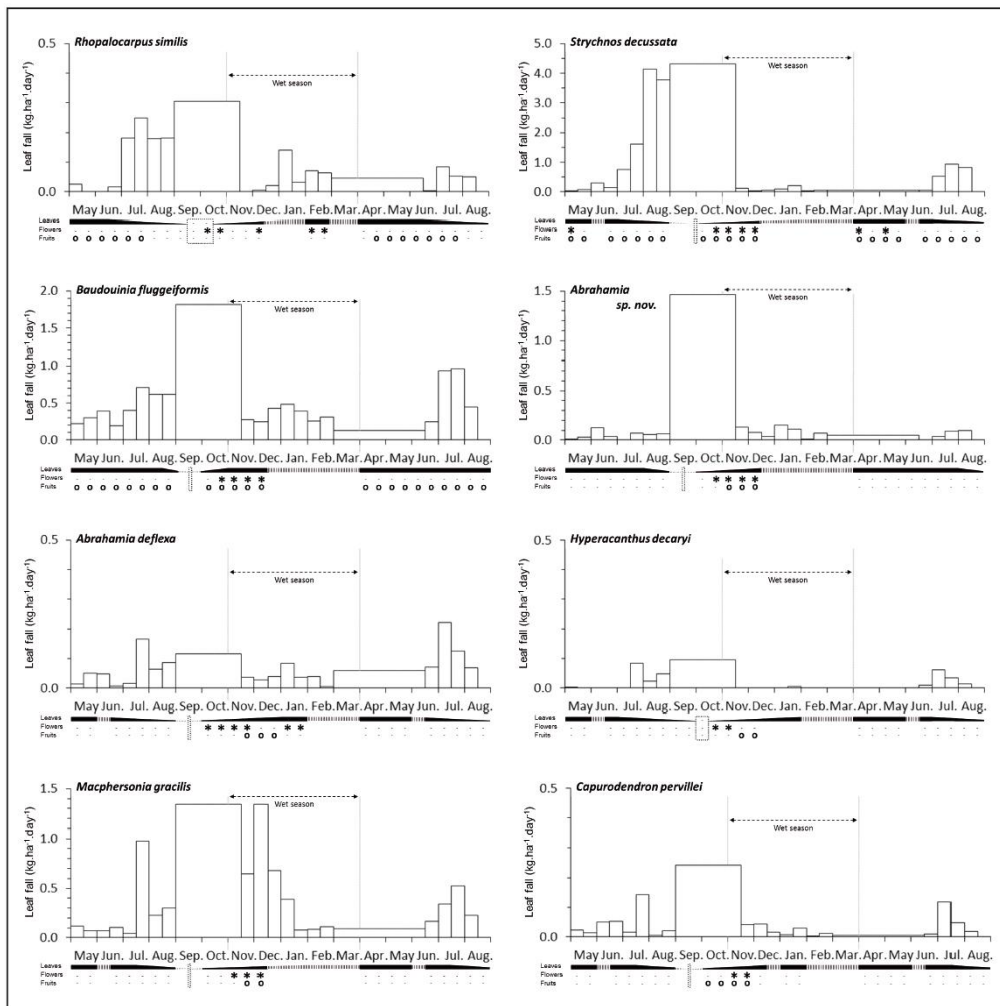


Figure 4.— Late deciduous species of the Badrara forest, according to the leaf litterfall recorded during 16 months including two dry seasons (scales are adapted for comparing phenological profiles). Individual graphs are ordered according to the general pattern (i.e. timing and amplitude) of leaf-shedding. Below each graph is a timeline displaying qualitative observations on leaf-shedding, total bareness and leaf-regrowth, as well as the presence of flowers and fruits. Total leafless periods are highlighted by empty rectangles, followed by flushing of new leaves (shown by the increase of the corresponding thick line). Negative observations of phenophases are indicated by dashes.

Early deciduous species respond particularly to relative humidity (Tab. II). In these species, high sensitivity to water stress probably triggers early leaf shedding and mobilizes most remaining endogenous resources to prepare flower buds to open just when rainy season begins, or even before. A phase of total leaf bareness is a remarkable characteristic of these species (Fig. 2), especially when flowers are visible on a bare plant (e.g. the liana *Sphedammocarpus multiflorus*, and the trees *Tabernaemontana coffeoides* and *Operculicarya gummifera*). Such an ability to flower during the dry season, after leaf shedding, undoubtedly reflects a particular trade-off between growth and reproduction. Some early deciduous species, such as *Neopaloxylon madagascariense* and *Operculicarya gummifera*, are also remarkable by their pachycaulous trunk, a morphological adaptation that secure water uptake even in open habitats.

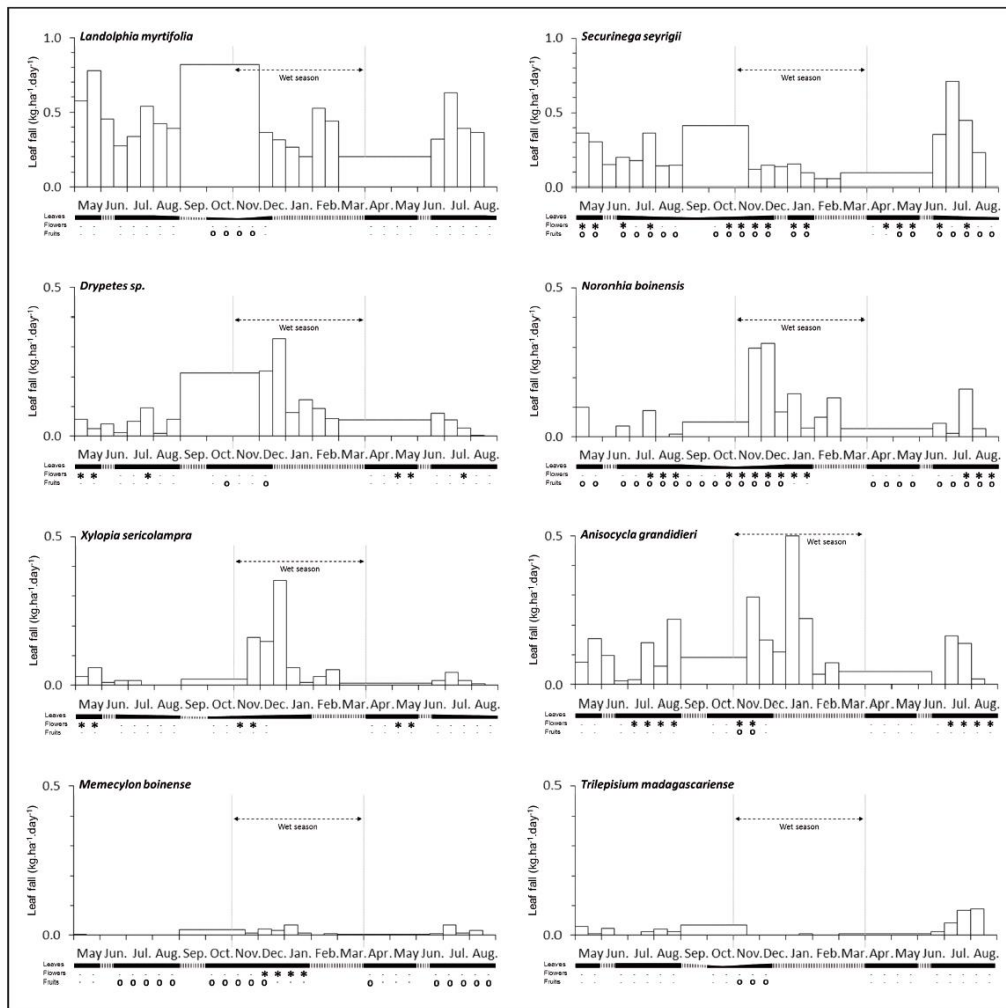


Figure 5.— Evergreen species of the Badrala forest, according to the leaf litterfall recorded during 16 months including two dry seasons (scales are adapted for comparing phenological profiles). Individual graphs are ordered according to the general pattern (i.e. timing and amplitude) of leaf-shedding. Below each graph is a timeline displaying qualitative observations on phenophases (negative observations are indicated by dashes) of leaves, flowers and fruits. Some flushing of new leaves are indicated by the increase of the corresponding thick line.

Species of other phenological categories do not respond so quickly to dryness. Progressively and late deciduous species indeed immediately respond to more predictable environmental cues, such as day length variation (Tab. II). Litterfall phenology of progressively deciduous species appears to be tightly linked to light cycles. Late deciduous species however shed their leaves in response to day length variations as well as to a variety of factors including irradiance and rainfall. This suggests, for the latter phenological group, a more flexible physiology related to photosynthetic capacity. In progressively deciduous species, leaf flushing and leaf regrowth generally occur at the same time as flowering (e.g. *Ochna macrantha*, *Diospyros platycalex*; Fig. 3). Furthermore, among the *Diospyros* species present at Badrala (e.g. *D. quercina* and *D. platycalex*), the occurrence of large quiescent buds is another trait adapted to periodical drought.

Finally, litterfall phenology of evergreen species is weakly related to meteorological factors (Tab. II). Morphological adaptations such as coriaceous or hairy leaves allow these species to avoid shedding leaves throughout the longest dry seasons.

These adaptations are also found in late deciduous species. Flowering and fruiting occurs during the wet season and allows fruit maturation throughout the following months (e.g. *Macphersonia gracilis*, *Abrahamia* sp. nov.; Fig. 4). It is noteworthy that some evergreen species that repeatedly exchange their leaves also flower several times each year, and they produce fruits throughout the year (e.g. *Anisocycla grandidieri* and *Securinea seyrigii*; Fig. 5).

Other plant species of the Badrala forest that were not collected in the litter traps (or were present in too small quantity) show drought adaptations. These include geophytes such as plants with storage tubers, whose aerial parts disappear during the wet season that are mostly small lianas (e.g. *Dioscorea* sp.), and plants with no (or with very small) leaves (aphylly and succulent photosynthetic stems, e.g. Euphorbs and *Vanilla madagascariensis*).

Water stress might also be solved by other morphological characters such as life-span of leaves, or density and capacity for stem water storage (such as a pachycaulous trunk), and also depth and density of roots systems (Borchert, 1994). Furthermore, Devineau (1999) mentioned other factors to be considered, such as phylogenetic constraints which might be related to phenological plasticity as for leguminous tree species in African savannah versus Combretaceae tree species.

Although life forms (trees, shrubs and lianas) respond differently to rainfall and to the resulting saturation/dryness of the soil, rainfall is not a consistent factor associated to (and eventually triggering) leaf-fall and other phenophases in most phenological groups (Tab. II). As a matter of fact, in their attempt at experimentally changing the phenological cycles of trees and liana species of the Barro Colorado forest (Panama) by watering large plots during the dry season, Wright & Cornejo (1990) indirectly demonstrated that rainfall was not a key factor triggering litterfall and/or flowering in deciduous trees and lianas.

In contrast, daylength variation is suspected to be a major factor linked to the timing of phenological phases, allowing synchrony with other meteorological variables. Although most research on photoperiod have been focused on the adaptive responses of species of temperate areas, where flowering and leaf flushing should not occur in the coldest conditions, Borchert (2002) shows that most tropical species also benefit from this signal, constant each year and allowing a precise seasonal response, even near the equator where the variation of the daylength is small. This was partly observed in the present study with an important effect of the daylength variation played in some phenological category but with various time lags and combination with other meteorological factors (Tab. II).

PHENOLOGICAL PATTERNS AND ECOSYSTEM

The resilience of ecosystems in the West coast of Madagascar results of an association between various phenological types and co-evolved animals acting as seed dispersers and pollinating agents. In spite of a long dry season following rainstorms and flooding, plant species can benefit from the diversification of adaptive responses to seasonal variation in the physical environment. After seed dispersal by animals, seedlings can grow in the shade of trees, where humidity is maintained by plant species that do not shed leaves simultaneously.

As a global result, litterfall in the Badrala forest ($6.4 \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$) is close to the maximum litterfall reported for other dry, semideciduous (e.g. Sri Lanka: $4.6 \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$, Hladik, 1978) or deciduous forests (see also review in Proctor, 1984, e.g. India: $5.8 \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$, Singh, 1992). The same figure is found when comparing the annual leaf-fall at Badrala ($4.6 \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$) with that in other dry forest sites. For instance, A. Hladik (1978, 1980) reported leaf-fall to be as low as 2.4

t.ha⁻¹.y⁻¹ in Sri Lanka and close to 3 t.ha⁻¹.y⁻¹ in southwestern Madagascar, whereas Indian deciduous forests may produce 4.0 t.ha⁻¹.y⁻¹ of leaves (Singh, 1992). This may explain why the major folivorous primate species, the lemur *Propithecus coronatus*, can reach the impressive density of 9.7 kg.ha⁻¹ (Pichon *et al.*, 2010; Pichon, 2012), despite the fact that the biomass of folivorous primates is commonly limited by their territorial behavior (Hladik, 1975).

There are a few comparable phenological studies carried out in dry forests: in continental Africa, at a slightly higher latitude (16° S) than Badrala, but in a cooler climate due to altitude, Malaisse *et al.* (1970) found a similar global leaf litterfall in small patches of forest (Muhulu forest, inside the Miombo dry forest) with a small peak of leaf-fall at the beginning of the dry season followed by high leaf-fall before the rains start. In a similar type of dry forest in Costa Rica (Guanacaste), Borchert *et al.* (2002) observed that most of the tree species shed their leaves during the dry season when the photoperiod was decreasing, which matches the phenological pattern found in Badrala (taking into account that Guanacaste is located in the northern hemisphere). In all instances, the forest includes species with different phenological patterns, with a major peak of defoliation preceding the rainy season. Andriaharimalala *et al.* (2012) also described similar phenological patterns based on direct observations of trees, in a dry forest of south-eastern Madagascar.

Concerning liana phenology, a study using litter traps allowed description of phenological patterns (Hladik, 1980) before Zalamea & González (2008) described some unimodal and bimodal patterns. In the present study we observed liana species of early deciduous phenological type (e.g. *Sphedamnocarpus multiflorus* and *Combretum sphaeroides*) producing an important leaf biomass (Annex 3), and at least two evergreen species (*Anisocycla grandidieri* and *Landolphia myrtifolia*) which appear as the most common phenological type in dry tropical forests (Opler *et al.*, 1991). The total leaf-fall of lianas accounts for almost 12 % of total litterfall of the Badrala forest as reported in other tropical forests (Leigh, 1999), although being much smaller than in a Gabon rainforest where a similar analysis was carried out (33 %, Hladik, 1974).

In the long term, diversification of phenological responses resulted from the climatic variations after the Gondwana was separated from the continental plate. At this time, the climate of Madagascar was extremely dry (as at present in the south) and species later differentiated in the various bioclimates presently observed (Wells, 2003). Badrala currently hosts dry-adapted plant species (e.g. *Rhopalocarpus similis* Sphaerosepalaceae) deriving from families that already existed during this ancient dry period. Presently, temperature at Badrala never falls as low as those recorded in southern parts of Madagascar and allows a greater diversity of species. In a close future, this current diversity of species with various phenological patterns could be an important factor for maintaining the dry forest ecosystem. However, the most important species in terms of plant biomass at Badrala (i.e. *Strychnos decussata* and *Vitex beraviensis*; Annex 1) are progressively deciduous species, and according to the meteorological factors tested in our study, leaf phenology in these species potentially depends on the predictable variations in photoperiod. Hence, they could be particularly sensitive to future climate changes (for instance if humidity, nebulosity and irradiance patterns would become disconnected from seasonal variations of daylight). Furthermore, since the large seeds of these species are dispersed by fruit-eating vertebrates, their fate might also depend on the protection of the fauna in these dry deciduous types of forest, as well as on how seed dispersers will respond to new assemblages of fruits made available at a given season according to climate change.

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ANNEX

1.— Tree species (DBH>10cm, N=280) of the Badrala forest listed by decreasing order of basal area within 3 transects (5300 m²)

Species	Family	Vernacular name	Voucher specimen	Basal area (m ² .ha ⁻¹)	Density (ind.ha ⁻¹)	Leaf-shedding group
<i>Vitex beraviensis</i> Vatke	Lamiaceae	Mojiro	M1747	2.9	69.4	Progress. decid.
<i>Strychnos decussata</i> (Pappe) Gilg	Loganiaceae	Hazombo	AH7174	1.6	66.7	Progress. decid.
<i>Abrahamia</i> sp. nov.	Anacardiaceae	Manavodrevo	AH7169	1.0	12.1	Late deciduous
<i>Majidea zanguebarica</i> J. Kirk ex Oliv.	Sapindaceae	Tsipopoka	RNT109	0.6	16.0	-
<i>Mimusops occidentalis</i> Aubrév.	Sapotaceae	Natofotsy	M2045	0.5	27.6	-
<i>Baudouinia fluggeiformis</i> Baill.	Fabaceae	Manjakabentany	CP46	0.5	23.0	Progress. decid.
<i>Abrahamia deflexa</i> (H. Perrier) Randrian. & Lowry	Anacardiaceae	Motsolahy	AH7200	0.5	16.3	Late deciduous
<i>Securinega seyrigii</i> Leandri	Euphorbiaceae	Natolahy	CP228	0.5	12.9	Evergreen
<i>Strychnos madagascariensis</i> Poir.	Loganiaceae	Vakakoa	M1660	0.4	12.1	Progress. decid.
<i>Operculicarya gummifera</i> (Sprague) Capuron	Anacardiaceae	Atokonjo	CP30	0.4	16.7	Early deciduous
<i>Boscia plantefolii</i> Hadj-Moust.	Capparaceae	Maroaka	CP215	0.4	14.8	-
<i>Nesogordonia stylosa</i> H. Perrier	Malvaceae	Hazomena	CP180	0.4	11.1	-
<i>Macphersonia gracilis</i> O. Hoffm.	Sapindaceae	Antsingeny maroampototra	AH7143	0.3	25.5	Late deciduous
<i>Deinbollia pervillei</i> (Blume) Radlk.	Sapindaceae	Ampoly be	M1662	0.3	17.2	Progress. decid.
<i>Trilepisium madagascariense</i> DC.	Moraceae	Kililo	RNT94	0.3	14.9	Evergreen
<i>Xylopia bemarkensis</i> Diels	Annonaceae	Kipindropindro	M1671	0.3	13.7	Progress. decid.
<i>Rhopalocarpus similis</i> Hemsl.	Sphaerosepalaceae	Hazondringitra	M1727	0.3	7.7	Progress. decid.
<i>Diospyros quercina</i> (Baill.) G.E. Schatz & Lowry	Ebenaceae	Belomboka	M1688	0.2	20.3	Progress. decid.
<i>Lepisanthes perrieri</i> (Choux) Buerki, Callm. & Lowry	Sapindaceae	Tamborisa	M2043	0.2	12.8	-
<i>Hyperacanthus decaryi</i> Homolle	Rubiaceae	Sofin'akomba	AH7191	0.2	13.0	Late deciduous
<i>Campoplepis</i> sp.	Sapindaceae	Hazontsavaka	AH7147	0.2	10.4	-
<i>Terminalia calcicola</i> H. Perrier	Combretaceae	Taliala	CP75	0.2	11.2	Progress. decid.
<i>Allophylus</i> sp.	Sapindaceae	Ampoly kely	M1741	0.2	9.7	-
<i>Diospyros</i> sp.1	Ebenaceae	Hazomafana	M1683	0.2	3.2	-
<i>Lepidotrichilia convallarioidora</i> (Baill.) J.-F. Leroy	Meliaceae	Azofoty	AH7239	0.2	7.2	-
<i>Drypetes</i> sp.	Euphorbiaceae	Tainpapango	CP217	0.2	13.0	Evergreen
<i>Pachypodium rutenbergianum</i> Vatke	Apocynaceae	Vontaka	-	0.2	3.2	-
<i>Rinorea</i> sp.	Violaceae	Tsiambanirengy be	AH7230b	0.1	13.9	-
<i>Warneckea</i> sp.	Melastomataceae	Voatrotrokala	AH7234	0.1	6.1	-
<i>Grewia amplifolia</i> Baill.	Malvaceae	Sely be	CP195	0.1	11.0	Early deciduous
<i>Dialium occidentale</i> (Capuron) Du Puy & R. Rabev.	Fabaceae	Pingo fotsy	M2066	0.1	5.6	-
<i>Astrotrichilia asterotricha</i> (Radlk.) Cheek	Meliaceae	Andranoky	M2048	0.1	8.7	-

<i>Xylopia sericolampra</i> Diels	Annonaceae	Mbavy / Fanazavalahy?	M1709	0.1	1.6	Evergreen
<i>Diospyros</i> sp.2	Ebenaceae	Pingo be	RNT152	0.1	4.4	-
<i>Bridelia pervilleana</i> Baill.	Euphorbiaceae	Kitata	M1718	<0.1	4.9	Early deciduous
<i>Noronhia tubulosa</i> H. Perrier	Oleaceae	Tsilaitra lava	M2069b	<0.1	8.7	-
<i>Vitex perrieri</i> Danguy	Lamiaceae	Malazovoavy	M1684	<0.1	4.8	-
<i>Grewia</i> spp.	Malvaceae	-	AH7205, AH7206, CP196	<0.1	7.6	-
<i>Cedrelopsis grevei</i> Baill.	Rutaceae	Katrafay be	M1721	<0.1	3.3	-
<i>Crateva excelsa</i> Bojer	Capparaceae	Bevoa	AH7173	<0.1	4.8	-
<i>Noronhia boinensis</i> H. Perrier	Oleaceae	Tsilaitra be	M1676	<0.1	7.5	Evergreen
<i>Rauvolfia media</i> Pichon	Apocynaceae	Tsilanimboana	AH7133	<0.1	4.8	-
<i>Phyllanthus erythroxyloides</i> Müll. Arg.	Euphorbiaceae	Koropoko lahy	CP176	<0.1	3.3	Early deciduous
<i>Ochna ciliata</i> Lam.	Ochnaceae	Boramena be	M2042	<0.1	4.8	-
<i>Bathiorhamnus reticulatus</i> (Capuron) Callm., Phillipson & Buerki	Rhamnaceae	Tanibe	CP96	<0.1	5.6	-
<i>Commiphora pervilleana</i> Engl.	Burseraceae	Arofy mena	CP134	<0.1	3.3	-
<i>Mundulea</i> spp.	Fabaceae	Fanamohazo	AH7170, AH7187	<0.1	1.7	-
<i>Anacolsa pervilleana</i> Baill.	Olaceae	Maivalafika	CP149	<0.1	3.3	-
<i>Euclina suavissima</i> (Homolle ex Cavaco) J.-F. Leroy	Rubiaceae	Voalitsaka	AH7210	<0.1	1.7	-
<i>Commiphora grandifolia</i> Engl.	Burseraceae	Arofy fotsy	AH7159	<0.1	1.7	-
<i>Commiphora marchandii</i> Engl.	Burseraceae	Tsivokini lahy	M1693	<0.1	1.7	-
<i>Ochna macrantha</i> Baker	Ochnaceae	Boramena kely	AH7139	<0.1	3.3	Progress. decid.
<i>Memecylon boinense</i> H. Perrier	Melastomataceae	Tsilaitra kely	M1756	<0.1	3.2	Evergreen
<i>Capurodendron pervillei</i> (Engl.) Aubrév.	Sapotaceae	Natoboay	M2041	<0.1	1.7	Late deciduous
<i>Erythroxylum</i> sp.2	Erythroxylaceae	Koropoko ala	CP231	<0.1	1.7	-
<i>Albizia numidarum</i> Capuron	Fabaceae	Morango	AH7247	<0.1	1.7	-
<i>Diospyros platycalyx</i> Hiern	Ebenaceae	Pingo "fotsiny"	RNT202	<0.1	1.7	Progress. decid.
<i>Dombeya boentensis</i> Arènes	Malvaceae	-	M1735	<0.1	1.7	Early deciduous
[unknown]	Euphorbiaceae	Mazavaravina	RNT168	<0.1	1.7	-
[unknown]	Apocynaceae	Mandronono	RNT126b	<0.1	1.6	-
<i>Tabernaemontana coffeoides</i> Bojer ex A. DC.	Apocynaceae	Mamalipolahy	CP139	<0.1	1.6	Early deciduous
<i>Terminalia boivinii</i> Tul.	Combretaceae	Amanin'omby	AH7209	<0.1	1.6	-
<i>Neoapaloxylon madagascariense</i> (Drake) Rauschert	Fabaceae	Kolohoto	LT934	<0.1	1.6	Early deciduous
<i>Chadsia flammea</i> Bojer	Fabaceae	Fanamo	AH7141, CP214	-	-	-
<i>Sclerocroton melanostrictus</i> (Baill.) Kruijt & Roebers	Euphorbiaceae	Boroa	CP54	-	-	Early deciduous
<i>Diospyros subfalciformis</i> H. Perrier	Ebenaceae	Ledoleo	AH7192	-	-	-
<i>Schizenterospermum rundifolium</i> Homolle ex Arènes	Rubiaceae	Ndraniana	AH7138	-	-	-
<i>Blotia</i> sp.	Euphorbiaceae	Morasiro	RNT260	-	-	-
<i>Helmiopsis boivinii</i> (Baill.) Arènes	Malvaceae	Manaranja	M1714, CP233	-	-	-
<i>Polyalthia henricii</i> Diels	Annonaceae	Ambay lava	CP234	-	-	-
<i>Bauhinia</i> sp.	Fabaceae	Hotrombengy	RNT104	-	-	-
<i>Polysphaeria</i> sp.	Rubiaceae	Lavaravina	AH7181, CP148, RNT229	-	-	-
<i>Cinnamosma fragrans</i> Baill.	Cannellaceae	Motrobeantsinana	M1633	-	-	-
<i>Polycardia lateralis</i> O. Hoffm.	Celastraceae	Fanazava	M1639	-	-	-
<i>Phylloctenium</i> sp.	Bignoniaceae	Saritaila	AH7148	-	-	-

2.— Shrub species of the Badrala forest (2.5 cm < DBH < 10 cm; height > 70 cm) within 3 plots of 100 m²

Species	Family	Vernacular name	Voucher specimen	Nb indiv.	Leaf-shedding group
<i>Canthium</i> sp.1	Rubiaceae	Rendry	RNT267	34	-
<i>Acalypha</i> sp.2	Euphorbiaceae	Tsiambanirengy kely	CP113	28	Early deciduous
<i>Doratoxylon chouxii</i> Capuron	Sapindaceae	Antsingeny lahy	AH7125	8	Progress. Decid.
<i>Vaughania</i> sp.	Fabaceae	Kifaity vavy	RNT212	7	-
[unknown]	Rubiaceae	Maintsoravina	-	2	-
[unknown]	Euphorbiaceae	Saravin-janahary	AH7236	2	-
<i>Omphalea occidentalis</i> Leandri	Euphorbiaceae	Somoro be	M1644	2	-
<i>Ivodea</i> sp.	Rutaceae	Ndramanamora lahy	CP238	2	-
<i>Evonymopsis</i> sp.	Celastraceae	Raiampy	CP212	1	-
<i>Phyllarthron</i> sp.	Bignoniaceae	Tohiravina	-	1	-
<i>Psorospermum</i> sp.	Hypericaceae	Tapapoasy	M2054	1	-
<i>Vitex pervillei</i> Bak.	Lamiaceae	Fanahaka	RNT268	1	-
<i>Croton boinensis</i> Leandri	Euphorbiaceae	Somoron'aliaka	M1648	1	-
<i>Tarenna</i> sp.	Rubiaceae	Kelimaity	M1700	1	-
<i>Psychotria</i> sp.	Rubiaceae	Maimbovitsika	CP136	1	-

3.— Climbers (liana, epiphyte, and parasite species, height > 70 cm) of the Badrala forest, within three plots of 100 m²

Species	Family	Vernacular name	Voucher specimen	Life form	Nb indiv.	Leaf-shedding group
<i>Acacia pervillei</i> Benth.	Fabaceae	Roity	M1657	Liana	23	-
<i>Salacia madagascariensis</i> (Lam.) DC.	Celastraceae	Hobohobo ala	AH7126	Liana	21	-
<i>Rhinacanthus</i> spp.	Acanthaceae	Felimafonty	CP56, CP126	Liana	15	-
<i>Combretum sphaeroides</i> (Tul.) Jongkind	Combretaceae	Fanstikakoholahy 1	CP53	Liana	11	Early deciduous
<i>Anisocycla grandidieri</i> Baill.	Menispermaceae	Vahilava	M1782	Liana	10	Evergreen
[unknown]	Apocynaceae	Vahimandronono	RNT200	Liana	9	-
<i>Abrus aureus</i> R. Vig.	Fabaceae	Mason'ombilahy	CP142	Liana	8	-
<i>Adenia</i> spp.	Passifloraceae	Kelibevoody / Holoboay	AH7137, AH7243	Liana	7	-
<i>Artabotrys madagascariensis</i> Miq.	Annonaceae	Vahimamy	M1807	Liana	6	-
<i>Dichapetalum bojeri</i> (Tul.) Engl.	Dichapetalaceae	Latakosy	CP81	Liana	5	-
<i>Combretum</i> sp.2	Combretaceae	Fanstikakoholahy 2	RNT103	Liana	5	-
<i>Reissantia angustipetala</i> (Tul.) Engl.	Celastraceae	Tsivoanino lava	CP84	Liana	5	-
<i>Sphedamnocarpus multiflorus</i> (Bojer ex A. Juss.) Nied	Malpighiaceae	Vahimaboraka	AH7211	Liana	4	Early deciduous
<i>Ptelidium</i> sp.	Celastraceae	Tsivoanino bory	CP236	Liana	4	-
<i>Leptadenia madagascariensis</i> Decne.	Apocynaceae	Sintak'ombilahy	CP163	Liana	4	-
<i>Deeringia densiflora</i> Cavaco	Amaranthaceae	Kifafa 1	CP114	Liana	4	-
<i>Jasminum pteropodum</i> H. Perrier	Oleaceae	Kifafa 2	RNT253	Liana	3	-
<i>Paederia</i> sp.	Rubiaceae	Laingo-maimbo	CP169	Liana	3	-
<i>Pentarrhopalopilina</i> sp.	Opiliaceae	Vahimaiky	CP165	Liana	3	-
<i>Bonania spectabilis</i> (Choisy) Hallier f.	Convolvulaceae	Vahimifota	CP198	Liana	1	-
<i>Maerua humbertii</i> Hadj-Moust.	Capparaceae	Vahimaimbolany	CP159	Liana	1	-
<i>Microstetra</i> sp.	Malpighiaceae	Vahimakofoka	AH7184	Liana	1	-
[unknown]	Solanaceae	Vahimalandy	CP143	Liana	1	-
<i>Landolphia myrtifolia</i> (Poir.) Markgr.	Apocynaceae	Vahipira 1	AH7140	Liana	1	Evergreen
<i>Monanthes boivinii</i> (Baill.) Verdc.	Annonaceae	Fotsiavadika lava (3)	M1699	Liana	1	-
<i>Ipomoea</i> sp.	Convolvulaceae	Vahimerajo	AH7188	Liana	1	-
<i>Plectaneaia thoursii</i> Roem. & Schult.	Apocynaceae	Vahipira 2	AH7207	Liana	-	-
<i>Aristolochia albidula</i> Duch.	Aristolochiaceae	Totonga	M1640	Liana	-	-
<i>Dalechampia</i> sp.	Euphorbiaceae	Vahimiamdambo 2	CP146	Liana	-	-
<i>Vanilla madagascariensis</i> Rolfe	Orchidaceae	Tohitohy	-	Epiphyte	9	-
<i>Bakerella ambongoensis</i> Balle	Loranthaceae	Hazosampona be	CP126	Parasite	-	-

4.— Meteorological variables given as monthly averages of the specific study period, except relative humidity that consists of monthly averages over 11 years (1990-2000)

Month	Day length variation (min)	Rainfall (mm)	Relative humidity (%)	Horizontal irradiance (Wh.m ⁻² .day ⁻¹)	Minimal temperature (°C)
Jan. 08	-0.25	373.8	82.1	5990	24.9
Feb. 08	-0.38	540.5	83.2	6170	23.8
Mar. 08	-0.43	70.7	78.8	6530	28.9
Apr. 08	-0.4	49.3	74.1	6310	23.4
May 08	-0.28	0	69.9	5670	21
June 08	-0.05	0	64.8	5230	18.9
Jul. 08	0.2	0	60.7	5390	18.6
Aug. 08	0.37	2	60.2	7430	19.7
Spt. 08	0.42	11	62.8	7090	21.4
Oct. 08	0.42	16	65	7670	22.8
Nov. 08	0.3	99	69.2	7430	24.9
Dec. 08	0.05	129	75.3	6980	24.6
Jan. 09	-0.25	297.8	82.1	5990	24.4
Feb. 09	-0.37	341.5	83.2	6170	24.1
Mar. 09	-0.43	180.7	78.8	6530	24.4
Apr. 09	-0.4	43.5	74.1	6310	23.5
May 09	-0.27	0	69.9	5670	21
June 09	-0.05	0	64.8	5230	20
Jul. 09	0.22	0	60.7	5390	19.3