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Phenology of Woody Species Along the Climatic Gradient in West Tropical Africa

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1. Introduction

West tropical Africa (WTA) is known to be one of the most exposed regions in the world to climate change. The seasonality of rainfall and of atmospheric conditions, including a dry season lasting for several months in most of the area, strongly influences vegetation activity (Bourlière & Hadley, 1983; Breman & Kessler, 1995). Indeed, this region was already affected by severe and prolonged droughts in the 1970s-1980s. These events represent one of the major climate variations of the 20th century recorded at the global scale (Giorgi, 2002; Neelin et al., 2006; Redelsperger et al., 2006). The average annual rainfall deficit varied by ± 20% in higher rainfall zones and by 50% in lower rainfall zones. However, while these droughts were relatively uniform over most of WTA, the 1990–2007 period was characterised by a more complex pattern including large spatial variability (Lebel & Ali, 2009). Current projections of global change predict higher temperatures and lower rainfall, although opinions on temperatures are contradictory (Mearns et al., 2001; Haarsma et al., 2005; IPCC, 2007; Funk & Brown, 2009). More frequent extreme events are also expected in some parts of Africa (Hély et al., 2006; Frappart et al., 2009; Lebel & Ali, 2009).

In WTA, the current vulnerability of agro- and eco-systems to climate change is dramatically amplified by the rapidly growing population (Thornton et al., 2008; Heubes et al., 2011). In the next half century, the fastest growing populations will be mainly located in sub-Saharan Africa (Garrity et al., 2010). Current projections predict a doubling of the population (Funk & Brown, 2009). To feed these increasing numbers of people, between 1990 and 2006 the area of cultivated land already grew by more than 10% annually, to the detriment of the natural woody cover. However, woody cover is still a crucial component of the agro-sylvo-pastoral ecosystems in WTA.

The phenology of woody plants could be thus a significant indicator of the vulnerability and ability of existing agro-sylvo-pastoral ecosystems to respond to local and global changes, through their relationships with regional climate, soil distribution, and land use (Chuine & Beaubien, 2001; Scheiter & Higgins, 2009). On the other hand, changes in the woody cover

may also interact with the effect of global change on ecosystems through changes in leaf phenology (variations in the leaf area index). The relationships between environmental conditions and woody plant phenology are still poorly known, notably in seasonally dry tropics (Eamus & Prior, 2001). Studies on this topic and long-time series of phenological data are particularly rare in WTA. Deciduous and evergreen species are recognized as being the two extremes of a continuum of survival strategies which optimise annual carbon gain and water use under environmental constraints such as seasonal or prolonged droughts (Givnish, 2002; Scheiter & Higgins, 2009). Knowledge of their distribution along the WTA bioclimate gradient and of the factors that control their phenophases is thus of great value for large scale modelling of carbon and water cycles, and for forecasting land surface responses to climate change (Harrison et al., 2010). This chapter thus has three objectives: (1) to present a state of the art of the knowledge on woody species phenology along the WTA bioclimatic gradient, (2) to examine available information on the environmental causes of phenological variation, and on phenophase predictors and triggers, (3) to make recommendations for future phenological studies to help identify the possible consequences of global changes in WTA.

The first phenological studies in the humid part of the gradient were conducted in the 1960s and mainly concerned leaf shedding and increments of the stand basal area, especially in forests. Studies in the driest part of the gradient were mainly classical qualitative characterisation of leafing, flowering and fruiting at the population scale. However, the most recent studies conducted in Sahelian and Sudanian bioclimates included quantitative data analyses and modelling and made a thorough study of the most probable determining factors of phenology. Given their importance, these approaches are presented in this chapter.

Most studies were conducted along a transect from Guinean to Sahelian areas, and focused on the description of specific phenological strategies. The aim of most of these studies was to determine the distribution of the availability of woody forage over the year (Le Houerou, 1980; Hiernaux et al., 1994; Breman & Kessler, 1995; Ickowicz et al., 2007; Sanon et al., 2007). The aim of more theoretical studies was to understand the functioning of the savanna by characterising the general phenological patterns of their components at the community scale. Most authors concentrated on the adaptive strategies which enable species both to survive in a particular local environment and to coexist with other species (Fournier 1991; Seghieri et al. 1995; De Bie et al., 1998; Devineau 1999, Mahamane et al., 2007). They described species-specific annual phenology. We reviewed these studies to identify the distribution of phenological strategies along the WTA bioclimatic gradient.

2. Methods used

2.1 Definitions of bioclimates and phenological strategies

In WTA, the strong gradient of climate and surface conditions from the sub-humid area in the south to the arid area in the north, and its possible impacts at global scale have attracted international research programs on climate and global changes including the Hydrological and the Atmospheric Pilot Experiment (HAPEX-Sahel, Goutorbe et al., 1994), the SAvannas on the Long Term (SALT, core IGBP program, Koch et al., 1995), and more recently, the African Monsoon Multidisciplinary Analysis (AMMA, Redelsperger et al., 2006). WTA supports a wide range of natural vegetation along its south-north bioclimatic gradient:

moist forests, mosaics of forests and wooded savannas, dry deciduous forests, bush-grass savannas, and arid steppes (grass bush and thickets) just before the Sahara desert begins. The area is characterised by two rainy seasons which progressively decrease to become one summer rainy season which, in turn, becomes progressively shorter. In parallel, the average annual rainfall decreases, and the variability of rainfall distribution increases. The part of the transect used for the analysis of the phenological strategies along the bioclimate gradient stretches from the Guinean to the north-Sahelian bioclimates (table 1).

Vegetation zones	Annual rainfall (mm)	AETFAT, 1959	Aubreville, 1949	Knapp, 1973	Peyre de Fabrègues, 1980	White, 1983	Saadou, 1990	Adjanohoun et al., 1989	Le Houérou, 1989
Sahara	0-200	Subdesert steppe and desert	Saharian	Vegetation of the southern Sahara	Steppe vegetation: sparse and contracted	Sahara regional transition zone	Southern-Saharian contracted steppe		Contracted and diffuse steppes
Northern Sahel	200-400	Woody steppe with abundant *Acacia* and *Commiphora*	Sahelo-Saharian	Very dry, semi-desert, thorny-bush savanna	Open shrubby steppe	Semi-desert grassland and shrubland	Thorny and shrubby steppe		Sahel *sensu stricto*, Mimosaceae savanna with annual grass layer
Southern Sahel	400-600		Sahelo-Sundanian (woody savannas)	Moderate dry savanna	Shrubby and woody steppe	Sahelian *Acacia* woody grassland and deciduos bushland	*Combretum* thickets, steppes, savannas		Sudano-Sahelian Combretaceae savanna with annual grass layer
Northern Sudanian zone	600-900	Relatively dry type of woodlands, savannas, and steppes		Dry savanna	Shrubby and woody savanna	Undifferentiated Sundanian woodland	Low dry forest, open forest, savannas, riparian forests	Dry forests with dominant Combretaceae and enclosed thorny steppes	Sahelo-Sudanian Combretaceae savanna and woodland with perennial grasses
Southern Sudanian zone	900-1100					Sudanian woodland with abundant *Isoberlinia*		Savanna with enclosed miombo (Brachystegia genus tree)	Sudanian *sensu stricto* mixed savanna and woodland, perennial grass layer
Northern Guinea zone	1100-1200	Woodlands and savannas with abundant *Isoberlinia doka* and *I. dalzielii*	Sudano-Guinea (woody savannas)	Northern moist savanna				North Guineo-Sudanian zone Miombo	Sudano-Guinean zone
Southern Guinea zone	1100-1200	Relatively moist types of woodlands and savannas						South Guineo-Sudanian zone Dense dry forest	
Guinea-Congolia zone	1100-1400	Forest-savanna mosaic	Guinea forest (old dense litoral forests)	Southern moist savanna		Mosaic of lowland rain forest and secondary grassland		Semi-deciduous forest and impoverished deciduous forest	
Coastal zone	900-1400		Togo and Benin coasts	Coastal type of derived savanna					

Table 1. Definition of WTA bioclimates according to several authors , and areas concerned in the present work (boxes surrounded by dotted lines).

In the studies we reviewed, which mainly focused on savannas and steppes, we identified four groups:

1. Deciduous species with a short leafing period whose canopies are bare for more than two months in the year;
2. Deciduous species with a long leafing period. These include species for which no case of canopy evergreeness has yet been reported, despite the shortness of the leafless

period, which rarely lasts more than two months. The flush of new leaves rapidly follows leaf shedding.

3. Semi-evergreen species. Unfortunately the authors used different criteria when assigning this strategy to species, which makes them difficult to compare. The group includes species which shed their leaves over a short period, two months at the most according to Breman & Kessler (1995) (which corresponds to our group 2), but also species in which a smaller proportion of trees in the sample population shed their leaves than those which remained evergreen (Devineau, 1999; Seghieri et al., submitted), and finally species which lose more than 50% of their canopy (Eamus & Prior, 2001; Do et al., 2005). We found it more convenient to classify as "semi-evergreen" species referred to in the literature as evergreen (if not riparian) in at least one location, and otherwise as "long leafing". In this way, we show that these species can actually be both evergreen and deciduous, depending on environmental conditions.

4. Evergreen species. This group comprises species for which no leafless period of the canopy has been reported in the literature at any time during the year and irrespective of where their phenology was studied, except due to damage to the canopy by fire or locust attacks, for example. In these species, old leaves were still on the tree when the new leaf flush occurred.

Before presenting the results, we summarise the most widely used methods of field observation at the tree scale and at the twig scale, then the more common and the more recent data analysis. The discussion focuses on the explanation of the group distribution along the bioclimate gradient and on the role of leafing in the maintenance of the tree water balance.

2.2 Inventory of field observation methods

In WTA, most field observations at local scale were qualitative and concerned the individual tree. However, some authors quantified leaf development, and the number and density of leaves at the twig scale. These observations were generally combined with monitoring of environmental variables (rainfall, soil water availability, radiative energy, evapotranspiration, temperature, air humidity, day length, etc.).

2.2.1 At the tree scale

At the wettest end of the gradient, phenological studies mainly concerned leaf shedding patterns and variations in trunk size. Periodic observations identified variations in leaf shedding, and band dendrometers were used to measure variations in trunk girths. Annual variations in cambial activity (Liming, 1957) and periods of water stress undergone by trees (Borchert, 1999) can be deduced from the latter. An important study was carried out in the semi-deciduous forest at Lamto (Guinean bioclimate) by Devineau (1984, 1991). Band dendrometers were installed on all trees with a trunk diameter of more than 20 cm at breast height. Leaf shedding and trunk girths were monitored monthly over a period of ten years (1972-1981).

However, most reports on dry forests, savannas, and steppes in WTA were based on periodic observations of successive phenophases of the canopy: leafing, flowering and fruiting. A few individuals to a few dozen trees were usually sampled per species. Phenophases were recorded at different stages, which varied in number depending on author. They

corresponded to the percentage of the canopy covered by buds, mature, or senescent organs. By far the most commonly used method in WTA was developed by Grouzis & Sicot (1980). The stages of each phenophase were recorded using the following classification:

1. Organs are absent.
2. Beginning of the phase, buds are swelling, expanded leaves and open flowers are rare, fruits are in the early setting stage.
3. Early development, both buds and open organs are present, 10-50% of the canopy is covered with mature or ripe organs, fruits are at all stages up to maturity.
4. Peak development, most leaves and flowers are open, more than 50% of the canopy is covered with mature or ripe organs, fruits are mature.
5. Decline, leaves and flowers are open and dry, 10-50% of the canopy is covered with senescent organs, fruits are ripe and dissemination is beginning (fruits starting to fall).
6. End, over 50% of the canopy is covered with senescent, dry, and falling organs, shedding flower elements, fruits falling or in open pods.

More often, to establish phenograms, the stages were combined as follows:

0, 1 and 5 combined as "non occurring",
2, 3 and 4 combined as "occurring".

Considering a tree as leafing, flowering or fruiting from stage 2 to 4 enabled exclusion of miscarrying primary states and long periods during which woody plants still displayed sparse organs at the end of a phenophase (especially fruiting, Grouzis & Sicot, 1980; Seghieri et al., 1995; Seghieri & Simier, 2002). But to express the magnitude of canopy fullness, Do et al. (2005) preferred to use the midrange percentage values of the stages to estimate the percentage of branches bearing mature green leaves: stage 0 = 0%; stages 1 and 5 = 5%; stages 2 and 4 = 30%, stage 3 = 75 %.

2.2.2 At the twig scale

Although small-scale approaches at the twig scale are time and labour consuming, they provide significant details about phenological processes such as the number of leaves, leaf area, biomass, and life span, and facilitate quantitative analysis. First, Hiernaux et al. (1994) randomly selected one calibrated twig, whose basal diameter was 1 cm, from 6-20 shrubs per species. The twig was representative of the mean phenological stage and leaf density of the canopy. Total leaf biomass and leaf area were estimated for each twig. Samples were harvested every two weeks, once a month during the rainy season, and less frequently during the dry season. Later, Goudiaby (2003) combined classical phenological observations on leafing at the canopy scale on 40 individual trees with detailed observations on 12 tagged twigs on three trees. Following tree architectural concepts (Hallé et al., 1978), the terminal branches or twigs were divided into growth units of successive age according to their length and basal diameter. The appearance and development of buds, leaves, stem ramification and growth, average leaf area and average leaf life span were quantified.

2.3 Summary of data analyses

2.3.1 Characterisation of phenology and its variations

Analyses of time series from dendrometer data revealed trends and periodic components of trunk growth for each indivual tree. Multifactorial analysis made it possible to ordinate trees

according to the seasonal distribution of their trunk growth (Devineau 1984, 1991). Cumulative trunk growth provided the stand basal area increments.

Over time, analytical approaches based on observations of the canopy stages (0-5) of each phenophase (leafing, flowering and fruiting) evolved from qualitative to more quantitative analyses. In the first studies, individual phenograms (figure 1) showed inter-individual variability, and enabled the calculation of the mean duration of each phenophase or each stage. Phenological spectra (figure 1) were the basic tools used to describe phenological patterns of woody species. They revealed the same characteristics as phenograms but at the population scale. In this way, variations in the magnitude of stages or phenophases were quantified and linked to the seasonal course of environmental variables (Grouzis & Sicot, 1980). Until recently, the influence of environmental factors was mainly assessed using this type of analysis (Poupon, 1979; Menaut, 1983; Seghieri et al., 1995; De Bie et al., 1998).

An original analysis based on the same observations consisted of comparing species plasticity using a synchrony index (Devineau, 1999). For each species sampled, the index was the ratio of the mean individual duration of a given phenophase to its overall duration at the scale of the sample population. The higher the ratio, the greater the coincidence between individuals.

To describe between-species variability, Seghieri & Simier (2002) used centred principal components analysis (PCA). This graphical representation was enhanced by plotting the centres of gravity for each site and the link between shrubs and sites, representing respectively between- and within-site variability. In addition, to obtain an unbiased typology of fallows, these authors performed hierarchical cluster analysis using the average-linkage method originally developed by Sokal & Michener (1958).
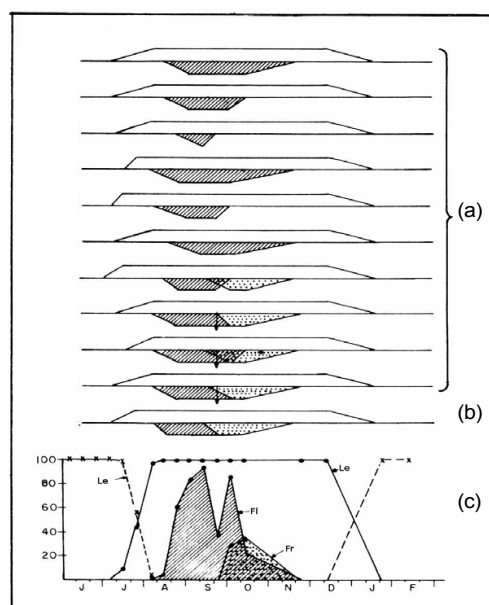

Fig. 1. Examples of phenograms of ten woody individuals among a sample population (a), average phenogram of the same sample population (N=35 individuals) (b), phenological spectrum of the same sample population over one phenological cycle, i.e., percentage of the trees leafing (Le, solid line) and without leaf (Le, dotted line), flowering (Fl, hatch patterns), and fruiting (Fr, stippling pattern) (c), after Grouzis & Sicot (1980).

2.3.2 Quantification of the relationships between phenophases and environmental factors

Recently, attempts have been made to quantify the relationships between ordinal phenological observations and quantitative environmental predictors in WTA (Do et al., 2005; Seghieri et al., 2009, Seghieri et al., submitted). These studies tackled difficulties inherent in analysing time series dealing with temporal auto- and inter-correlations among variables. These authors quantified the level of statistical significance of the correlation between the occurrence of phenophases and variations in environmental variables using logistic regression models. Do et al. (2005) focused on the predictions of interannual variations in leaf flush and leaf shedding peaks respectively, while Seghieri et al. (2009) and Seghieri et al. (submitted) analysed the global occurrence of the phenophases in the sample population. The models linked the cumulative log of the odds of an occurrence of a given phenophase to quantitative (environmental) predictors in linear form (Agresti, 1996).

Generally, different time lags of environmental variables were included as predictors to account for the inertia of the vegetation response. The coefficients of the models were computed using maximum likelihood estimation. The global quality of each model was assessed by the Akaike information criterion (AIC), which compares the fit of a given model including predictors (constrained model) with the fit of a model excluding predictors (unconstrained model). McFadden's Pseudo R^2 indicated the proportion of the phenophase variance explained by the model (Seghieri et al., 2009). The level of significance of the model coefficients (validity of the regression for each variable) was assessed by the Wald test. The c-statistic provides a measure of the discriminative power of the logistic equation, i.e., a comparison of the predictive power of environmental variables (Do et al., 2005). It measures the degree to which probabilities agree with actual outcomes, and is a quick and simple indicator of the accuracy of a predictive model.

However, to obtain relevant results from logistic regression models certain conditions have to be fulfilled. Indeed, the multicolinearities between environmental variables (especially climate variables) are rarely taken into account, which may lead to bias in the results. To avoid skewed results, Seghieri et al. (submitted) ran logistic regression models with uncorrelated pseudo-predictors generated from the principal axis of a PCA applied to original environmental predictors. However, the direct meaning of the coefficients obtained in the models is then lost. To identify the most significant predictors, these authors mapped the PCA pseudo-variables back to the original environmental predictors, i.e. they fitted a multivariate linear regression model that links pseudo-observations in the PCA space to observations in the environmental space.

The main results synthetized from the literature are displayed in the following part. They focus on the characteristics of each phenological group and their distribution along the bioclimate gradient, and then on environmental and human factors that have been reported as determining.

3. Review of main results

3.1 Phenological strategies: characteristics and distribution

In the literature we reviewed, the phenophases (leafing, flowering, fruiting) of 125 species were described along a transect from the Guinean to the Sahelian bioclimate (table 1).

Riparian species were excluded from our analysis since in the three studies which mention this particular category of tree, they were all classified as evergreen (Breman & Kessler, 1995; De Bie et al., 1998; Mahamane et al., 2007).

Fifty-seven percent of the species were deciduous, including short-leafing and long-leafing types. Twenty-six percent were evergreen, and 17% were semi-evergreen species (according to our definition).

Short-leafing deciduous species: 89% started leafing at the end of the dry season or at the beginning of the rainy season (figure 2). Forty-nine percent shed their leaves at the beginning of the following dry season, and 33% later. Eighteen percent had a short leafing period limited to the rainy season *sensu stricto*, including *Acacia seyal*, *Adenium obesum*, *Commiphora africana*, *Euphorbia balsamifera*. Most often, they flowered at the same time as leafing during the rainy season, and 55% started flowering at the end of the dry season or at the beginning of the rainy season (figure 3). However, 25% completed reproduction entirely during the dry season, including *Pterocarpus erinaceus* and *Ziziphus mucronata*. Consequently, only 20% reproduced during the most favourable season after a minimum of photosynthetic activity (*Acacia adansonii*, *Feretia apodanthera*, *Acacia gerardii*, *Detarium microcarpum*). Several species were also reported to have either variable or several flowering periods, including *Adansonia digitata*, *Grewia bicolor*, *Grewia lasiodiscus*, *Grewia venusta*. Atypical phenologies were also found in this group, especially in the Sahel. This is the case of *Leptadenia pyrotechnica* which bears atrophied ephemeral leaves and is able to flower continuously, the peak of abundance being at the end of the rainy season (Seghieri et al. submitted).
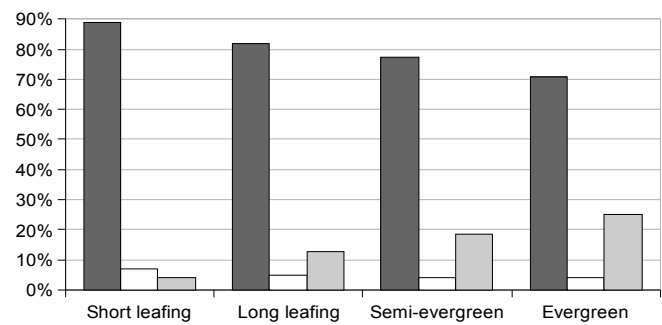

Fig. 2. Distribution of the start of leafing periods for each phenological strategy (see definition in section 2.1.) of the woody species in west tropical Africa cited in the literature. Leafing started at the end of the dry season or at the beginning of the rainy season (dark grey), leafing started in the middle of the rainy season (white), leafing started in the middle of the dry season (light grey).

Long-leafing deciduous species: 82% started leafing at the end of the dry season or at the beginning of the rainy season vs. 13% which started leafing in the middle of the dry season. Only five percent of species in this group started leafing in the middle of the rainy season (figure 2). Forty-four percent bore leaves during the dry season and shed them in the middle or at the end of the dry season. But 52% shed their leaves at the beginning of the dry season like in the previous group. This is not surprising since 37% of the species in this group were observed in the Sudanian bioclimate vs. 31% in the Sudano-Sahelian area (figure 4), despite the fact that most species recorded in the literature were monitored in the Sudano-Sahelian area (50% *vs.* 25% in the Sudanian area). Forty-five percent of species belonging to this group started flowering while leafing at the end of the dry season or at the beginning of the

rainy season, while 30% completed reproduction entirely during the dry season (figure 3). The contribution of this group to flora were higher in Sudanian and Guinean bioclimates - including in the mosaic landscape of savannas and forests in the Lamto region (Menaut, 1971; Menaut & César, 1979) - than in drier bioclimates (figure 5). One species with reverse phenology was observed in this group: *Faidherbia (Acacia) albida.* This species bore leaves during the dry season and was leafless during the rainy season (Hiernaux et al., 1994; Depommier, 1998; Roupsard et al., 1999).
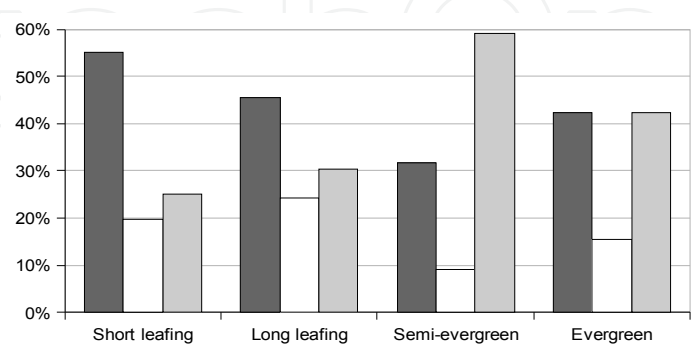

Fig. 3. Distribution of reproductive periods according to each phenological strategy (see definition in section 2.1.) of the woody species in WTA reported in the literature: flowering started at the end of the dry season or at the beginning of the rainy season (dark grey), in the middle of the rainy season (white), reproduction completed during the dry season (light grey).

Semi-evergreen species: like in the previous group, most (78%) of the species replaced their leaves at the end of the dry season or at the beginning of the rainy season (figure 2). Only 18% replaced their leaves in the middle of the dry season. However, 42% shed their leaves in the middle or at the end of the dry season. Twenty-nine percent shed their leaves during the rainy season and 29% at the beginning of the dry season. Unlike in the two previous groups, in this group, 59% reproduced entirely during the dry season, and started flowering at the end of the rainy season, at the beginning or in the middle of the dry season (figure 3). Only *Guiera senegalensis* was observed by Devineau (1999) to flower at any time in the Sudanian bioclimate.
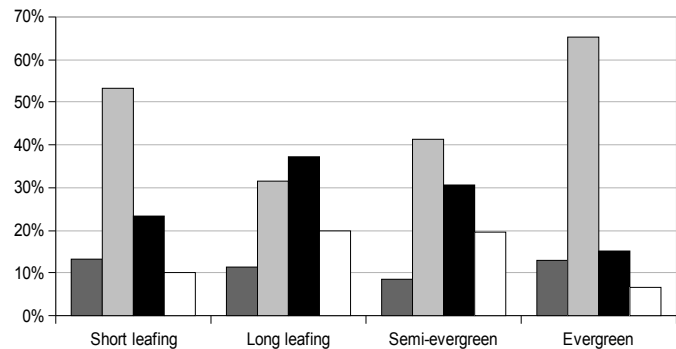
Fig. 4. Proportions of the bioclimates investigated along the WTA latitudinal gradient in the literature as a function of each phenological strategy (definition in section 2.1.), from the driest to the wettest bioclimate: Sahelian (dark grey), Sahelo-Sudanian (light grey), Sudanian (black), Guinean (white).

Evergreen species: these species were mainly observed in Sahelo-Sudanian bioclimate (figure 4), in which they contribute to a greater part of the flora (figure 5). Their contribution

was also high in the Sahel. They replaced their old leaves at any time (*Balanites aegyptiaca*, *Cadaba farinosa*, *Maytenus senegalensis*) or at a specific period, mostly (72%) at the end of the dry season or at the beginning of the rainy season (figure 2), and 25% in the middle of the dry season (*Balanites aegyptiaca*, *Maytenus senegalensis*, *Nauclea latifolia*, *Piliostigma reticulatum*). Their reproductive period mostly occurred at a fixed time of the year: 42% started flowering at the end of the dry season or at the beginning of the rainy season, and 42% completed reproduction during the dry season (figure 3). Several flowering periods were observed in *Balanites aegyptiaca*, but generally only one was followed by fruiting (Seghieri et al., 1995; Seghieri et al., submitted), with peak flowering during the dry season.

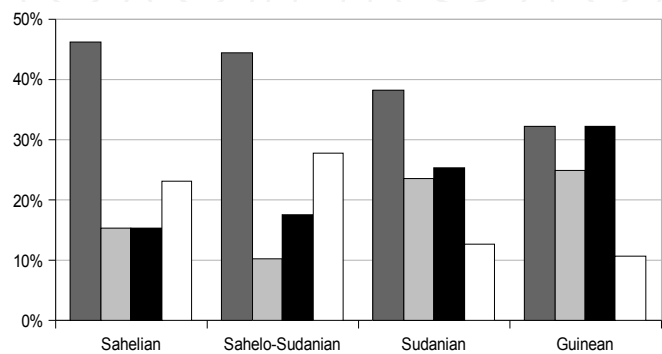Fig. 5. Contribution of each phenological strategy cited in the literature (see definition in section 2.1.) to the woody flora investigated in the successive bioclimates along the WTA latitudinal gradient: short leafing deciduous species (dark grey), long leafing deciduous species (light grey), semi-evergreen species (black), evergreen species (white).

There was a clear decrease in the proportion of short-leafing deciduous woody plants from the driest to the wettest bioclimate, along with an increase in the proportion of semi-evergreens (figure 5).

3.2 Factors controlling phenology and its variations

3.2.1 Environmental factors

The total rainfall amount and the length of the rainy season were most often suggested to explain global variations in woody phenology along the south-north gradient of increasing climatic aridity (Fournier, 1991). This explanation is well illustrated along the whole WTA bioclimatic gradient from rain forests to Sahelian steppes (table 1).

At the wettest extremity of the gradient, studies were performed in a natural tropical rain forest in southern Ivory Coast (Bernhard, 1970; Bernhard-Reversat et al., 1972), which has a typical equatorial climate. At the community level, a distinct unimodal seasonal rhythm of leaf shedding was observed during the main dry season, although leaf shedding continued throughout the year (litter-fall, figure 6a). In a tropical dry semi-deciduous forest in the Guinean bioclimate (Hall & Swaine, 1981), both basal area increment and leaf shedding were found to be more seasonal (figure 6b; Devineau, 1976).

Further north in the dry forests and savannas, basal area increment and leaf shedding were found to be more closely linked to climate seasonality. The period with no (or reduced) cambial activity, which lasted one month in the semi-deciduous forest (figure

6b), lasted almost three months in the *Anogeissus leiocarpa* dry forest (figure 7a) and for five to eight months in the North Sudanian savanna (figure 7b). However, in both the dry forest and the savanna, where woody plants are not active throughout the year, the proportion of leafing trees varied between communities but was never nil (Devineau 1982, 1999).

(a)

(b)
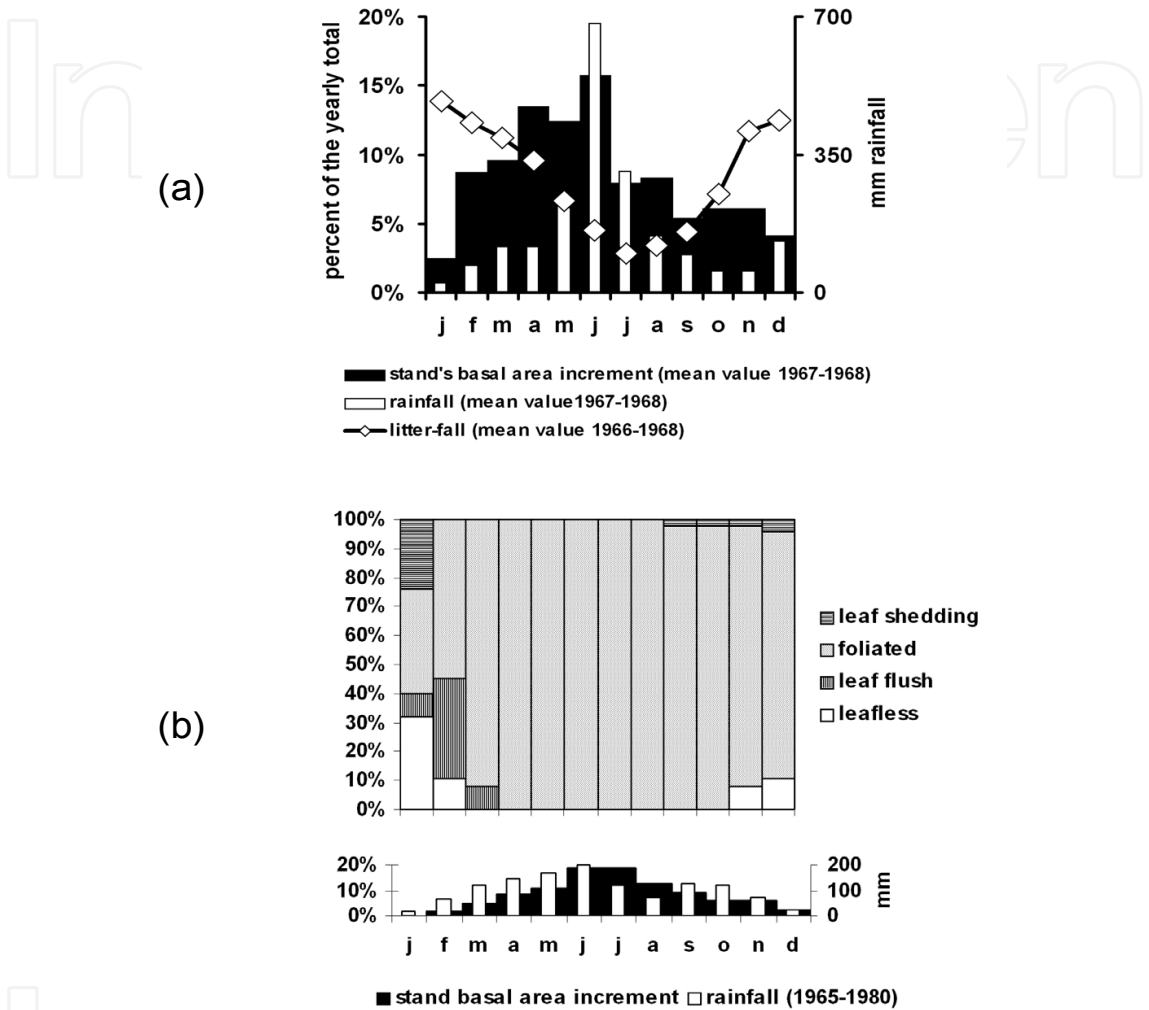
Fig. 6. Leaf phenology and stand basal area increments as a function of rainfall distribution in a typical equatorial bioclimate, the Banco National Park (5.39N -4.05W) with four seasons and 2 100 mm of mean annual rainfall (a) compiled from Bernhard-Reversat et al. (1972), and in a tropical dry semi-deciduous forest, at the Lamto research station (6.22° N, -5.02°W) with four seasons and 1 280 mm of mean annual rainfall (b) compiled from Devineau (1984, 1991).

In the most arid open environments along the bioclimate gradient, phenological variations gave way to a number of different strategies in response to water stress and its variations. Poupon (1979) found significant between-year variability in the beginning and in the length of the leafing period in a Sahelian woody community. Significant variations in the duration of the leafing period were also observed between years (up to two months over 5.5 years) and between individuals (25% of 39 individuals on average) in the semi-evergreen species *A. tortilis* ssp. *raddiana* in the northern part of the Sahel (Do et al., 2005).

Nevertheless, locally, a number of other factors were also reported to determine woody phenology. In the natural tropical rain forest in southern Ivory Coast (2 100 mm of annual rainfall), at the community level, leaf shedding was significant throughout the year and appeared to be correlated with the number of hours of sunshine, while the role of day length was questioned. In spite of this clear pattern, Bernhard (1970) and Bernhard-Reversat et al. (1972) reported wide diversity and asynchrony in leaf phenology and in cambial activity between species and between individuals. In these moist forests, a large part of the within and between species variability of growth patterns was mainly related to biotic interactions, resulting in competitive or niche partitioning strategies. For instance, Devineau (1984, 1991) showed that the phenology of cambial growth in a moist semi-evergreen forest (1 280 mm of annual rainfall) varied according to the position of the tree in the vertical strata, its biological type, and its stage of maturity. In dominant trees, cambial growth peaked during
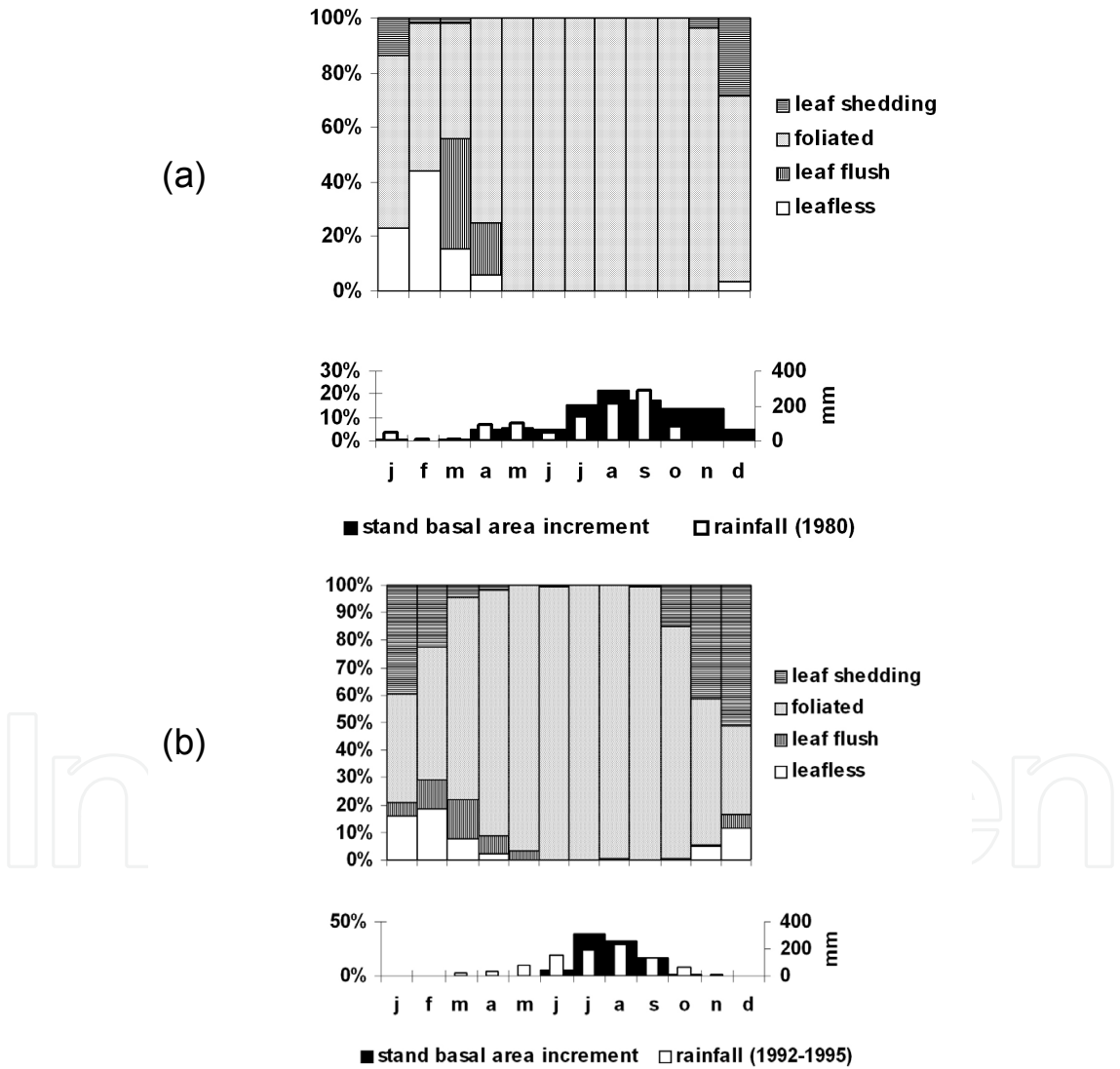

Fig. 7. Leaf phenology and stand basal area increments as a function of rainfall distribution in an *Anogeissus leiocarpa* dry forest, Ouango Fitini. (9.58N , 4.02W) with 1080 mm of mean annual rainfall (a) compiled from Devineau (1984, 1982), and in a north Sudanian savanna (Bondoukuy 11.85°N, -3.73 W) with 900 mm of mean annual rainfall (b) compiled from Devineau (1997, 1999).

the rainy season (June, July), whereas in the understory strata, significant cambial activity occurred during the dry season (December-May). Understory strata took advantage of leaf shedding by taller trees to access more light, and were consequently more active during this period. In this semi-evergreen forest, cambial activity peaked at the beginning of the main rainy season, but did not appear to be linked to rainfall distribution. However, the same author also reported that stand basal area growth rates varied according to rainfall distribution and to the evaporation rate, especially their extreme values, as well as to the water deficit in the preceding months (Devineau, 1989). Even if leaf shedding was most abundant during the main dry season, it also occurred during the rainy season. A large part of the dominant trees were deciduous whereas understory woody species were evergreen.

Menaut (1983) reviewed the most frequently cited determining factors of phenophase in studies conducted in African savannas. This author pointed to an increase in atmospheric vapour pressure or in relative humidity. Indeed, both occur just before the beginning of the rainy season, when most species start leafing. He also indicated the seasonal change in day length and an increase in temperature, in terms of values as well as diurnal ranges. In the north Sudanian savanna, in most species he studied at Bondoukuy, Devineau (1997) found that trunk shrinkage peaked just before the beginning of the rainy season, when the leaf flush occurred (*Entada africana, Terminalia avicennioides, T. laxiflora, Vittelaria paradoxa, Pteleopsis suberosa*). Then, at the beginning of the rainy season, trunk girth increased rapidly with the first regular heavy rainfalls and soil water supply. Growth generally did not begin before at least half the canopy was covered by new foliage (Ashton et al., 1983). As soon as the soil dried out at the end of the rainy season, trunks started to shrink again and continued throughout the dry season. In drier areas, phenological variability was also related to variations in both climatic and soil water conditions, depending on the individual and on the species. Seghieri et al. (1995), Seghieri & Galle (1999), and Seghieri & Simier (2002) confirmed the possibility of high phenological within-species variability according to soil water regimes in southern Sahel and northern Sudanian bioclimates (table 1). These authors showed that this determining factor depends not only on topography and soil texture (Seghieri et al., 1995; Seghieri & Simier, 2002), but also on the nature and distribution of soil surface crusts (Seghieri & Galle, 1999).

Based on observations at the twig scale, Goudiaby (2003) demonstrated that the annual phenological pattern observed over a year in *A. tortilis* ssp. *raddiana* in North Senegal (northern Sahel) corresponded to the overlap of successive leaf cohorts of different magnitudes, three of which appeared to be particularly high. The first leafing period started between April and May, two months before the onset of rains. The second started in July, in the middle of the rainy season, and had the longest leaf life span (6-7 months). The last occurred in December. This author deduced that in this species, the annual duration of leafing mainly depended on the life span and density of the first and the last cohorts because they are the most exposed to the risk of atmospheric and soil drought. In addition, Diouf (2003) found that the individuals with the longest annual leafing duration had a better leaf water status (less negative predawn leaf water potential) and were mainly located on the downslope of micro-topography with more water available in the upper soil layers.

Finally, whatever the bioclimate, the magnitude and duration of leafing and growth rates were found to be more closely linked to the regularity of rainfall distribution than to heavy rainfall events which do not infiltrate, or annual rainfall amount. Unfortunately, very few authors quantitatively tested the environmental factors actually most strongly related to woody phenology in WTA and evidence is consequently still very scarce.

3.2.2 Predictive power of some factors

Do et al. (2005) focused on the comparison of water environmental triggers which could explain inter-annual variation in the peaks of leaf flush and leaf shedding in *A. tortilis* ssp. *raddiana* in northern Senegal. Logistic models including upper soil water availability and rainfall as predictors did not predict variation in either of these two phenophases, but models including the daily maximum vapour pressure deficit, i.e., the driver of leaf transpiration, did.

Seghieri et al. (2009) tested a global predictive approach at the stand scale by mixing species and studying the occurrence of phases (binary response) over the course of the year. The test included data from a two-year monitoring period at a Sahelian site (370 mm mean annual rainfall) and from a three-year monitoring period at a Sudanian site (1 200 mm mean annual rainfall). Only a small proportion of phenophase variability was explained by environmental factors. Nevertheless, significant relationships were identified and provided global insights. Leafing probability was linked to an increase in cumulative rainfall at the Sahelian site but not at the Sudanian site. Conversely, 66% of leafing occurrence was highly significantly explained by an increase in day length and a decrease in air temperature at the Sudanian site but not at the Sahelian site. These results suggest that the water regime is not limiting at Sudanian sites but is at Sahelian sites at the scale of the community.

At the species scale, Seghieri et al. (submitted) found that at the same Sahelian site, temperature variations during the preceding months with different time lags were often the strongest environmental predictor of flowering in *Acacia raddiana* and *Acacia seyal*, and of leafing and flowering in *Balanites ægyptiaca* and *Acacia ehrenbergiana*. Day length, air relative humidity and/or cumulative rainfall with different time lags were the best predictors of flowering in *Combretum glutinosum*, *Leptadenia pyrotechnica* and *Acacia senegal*.

3.2.3 Human factors

It is now widely recognized that fires are fully integrated in savanna ecosystems and favour the resilience and pseudo-stability of the system (Wright, 1974). For this reason, savannas have been called "fire sub-climax" (Clements, 1936), despite the fact that in WTA, fires are currently mainly caused by human activities. As a result, a reduction in the number of -or an end to- fires can be observed in many Sudanian areas, where they were previously the most common. These modifications may lead to significant biological changes, particularly in phenology (Devineau et al., 2010). The main effect of fire is leaf burning. This synchronizes the natural diversity of leaf shedding patterns in a given site, but simultaneously desynchronizes leaf shedding between burned and unburned sites. Furthermore, in savannas, fires are mainly superficial. Their occurrence and intensity are mainly determined by existing biomass and the state of dehydration of the grass layer, which is the most abundant combustible. That is why Caillaut (2011) simulated current regional spatial patterns of fire in western Burkina Faso based on the simple assumption that fires occur as soon as the grass layer is flammable, i.e. has dried out. Consequently, the disturbance of leaf shedding-and-flush patterns of the woody cover depends on the phenological stage of the herbaceous layer when the fire occurs. However, no major phenological differences were observed by Menaut (1971) when he compared tree phenology between a burned savanna and a neighbouring unburned savanna. The phenological switch caused by fire disappeared after only a few weeks. Seghieri et al. (1995) reported limitation of the leafing period by fire

in northern Sudanian savannas, but only in semi-evergreen or evergreen species (*Piliostogma reticulatum, Acacia hockii, Combretum glutinosum, Balanites aegyptiaca, Ziziphus mauritiana, Acacia seyal, Combretum fragrans*), irrespective of when the fire occurred (early or late in the dry season). However, when fires occur early, they may also affect long leafing species. Finally, fire appears to exacerbate the impact of dryness, but does not seriously change phenophase periods, perhaps because of the long-term selection of adapted species to this human factor.

Devineau (1999) compared the phenological plasticity of species in the north Sudanian savanna (Bondoukuy), taking into account within-species synchrony/asynchrony in leafing and flowering duration, fruit ripening and seed dispersal periods. His results pointed to land use as the discriminating factor. Along the axis of increasing plasticity, species were distributed from trees to shrubs and from species which dominate uncropped savannas to species which dominate younger fallows. In addition, Leguminosae were separated from Combretaceae, the latter generally being considered as an indicator of fallow agrosystems (White, 1983). According to Kochmer & Handel (1986) and Pau et al. (2011), the segregation of species phenology according to families suggests the possible influence of phylogenetic constraints.

More particularly, it was reported that in south Sahelian agrosystems in Niger, there was a significant reduction in biodiversity due to pressure from crop and wood harvesting to the benefit of the semi-evergreen cut-resistant Combretaceae, *Guiera senegalensis* (Delabre, 1998; Seghieri & Simier, 2002; Seghieri et al., 2005). Thanks both to this species phenological and physiological plasticity (Seghieri & Simier, 2002, Seghieri & Laloë, 2004) combined with its relative drought resistance (Seghieri & Galle, 1999), it is increasingly dominating the woody cover on sandy soils (70-90% at present), a trend that is facilitated by its significant abundance in the original flora.

Another reason for dominant woody phenological patterns in WTA to change locally is that when farmers clear land for cultivation, they do not eliminate woody species that are of economic interest to them. These species are now sparsely distributed in north-Guinean, Sudanian, and south-Sahelian agricultural parklands. Following cultivation, they become dominant in fallows. This is mainly true of long-leafing and semi-evergreen species *Vittelaria paradoxa* (shea tree), *Parkia biglobosa* (African locust bean), *Faidherbia albida* (Gao), and the short leafing *Adansonia digitata* (Baobab). Further south, evergreen Anacardiaceae plantations are becoming progressively more common along with mango (*Mangifera indica*), and cashew trees (*Anacardium occidentale*). These changes in vegetation composition may show up in remote sensing images and may alter the balance of the energy transfers between the surface and the atmosphere through modifications of the leaf area index and the vegetation functioning.

4. Overall analysis

4.1 Balance between deciduous and evergreen species

Species which start leafing at the end of the dry season or at the beginning of the rainy season were found to be dominant in WTA, whatever the phenological group. In this way, these species minimise the risk of drought during the period of most intensive photosynthetic activity in young leaves, which do not yet have the necessary adaptative

traits to limit transpiration. However, this implies that the dry period just before the rainy season is critical for most species, particularly if the first regular and abundant rains are delayed, as observed by Devineau (1997) in the Bondouky savanna or by Seghieri & Galle (1999) after they have prevented the runoff from arriving on a banded thicket in southern Niger.

In dry tropical environments, deciduous species are acknowledged to "avoid drought", while evergreens are assumed to be "drought resistant", two contrasted strategies to optimize water use. But as we will see, the distinction between arido-passive and arido-active species is not really clear.

Short-leafing deciduous species were called also "drought deciduous" by Breman & Kessler (1995) because they almost always had no leaves during the dry season. These species limit water stress by reducing transpiration (leafing) during the unfavourable season, although most can survive short periods without rain. These species start leafing before regular abundant rains and are bare after the last rains of the season, often thanks to residual moisture available in the soil (Seghieri et al., 1995). However, in some Sahelian species in this group, other adaptative characters may compensate for the shortness of the leafing period. Hiernaux et al. (1994) reported thin chlorophyllous bark in *Commiphora africana* and *Euphorbia balsamifera*. An extreme case is *Leptadenia pyrotechnica*, which has flexible stems engorged with water which are permanently photosynthetically active. The stems compensate for atrophied and ephemeral leaves to such an extent that the species was classified among "evergreens" by Breman & Kessler (1995). Thanks to roots that were observed at a depth of 11.5 m, this shrub is able to tap sufficient water resources to grow and reproduce. Such stems and roots are an efficient adaptation to climatic droughts, even in desert conditions (Migahid et al., 1972; Batanouny & Abdel Wahab, 1973).

The majority of long-leafing deciduous species take advantage of the longer favourable period of the Sudanian bioclimate. The fact that the majority of species in this group shed their leaves at the beginning of the dry season and flower when leafing during the rainy season justifies the closeness of this group to the previous one. Their longer leafing period appears to be mainly linked to the longer rainy season in the Sudanian bioclimate. The reverse leafing cycle in the Sudanian-Sahelian species *Faidherbia albida* is possible thanks to its deep roots. Roupsard et al. (1999) observed roots at a depth of 7 m, where they vanished in the vicinity of a permanent water table. The fraction of annual rainfall used by these trees was estimated to be less than 5%.

Semi-evergreen species are generally assumed to have access to water resources during the dry season, e.g. internal plant reserves (root, trunk), deep soil layers, or the water table. Indeed, roots which accessed a 30 m deep water table were observed by Do et al. (2008) in *A. tortilis* ssp. *raddiana* at a north Sahelian site. These authors cited root depth as the main determining factor of the length of leafing (6.7 months) as well as the intensity of transpiration throughout most of the dry season (Do et al., 1998; Do et al., 2005; Do et al., 2008). Furthermore, some species (e.g. Combretaceae) have xeric traits or hairs on their leaves to limit transpiration, but not all (e.g. Fabaceae). Chlorophyllous bark was also observed in *Acacia seyal* by Hiernaux et al. (1994). These adaptations enable the majority of species in this group to reproduce during the dry season.

Like other arido-active plants, evergreen species are also assumed either to have access to water located deep below the surface or to mobilize reserves from the roots or the trunk. Most species in arid or semi-arid bioclimates have scleromorphic features (*Boscia* ssp., *Combretum* ssp.) to reduce water losses, but again not all.

However, information is still lacking on adaptative arido-active traits in most of the species mentioned here irrespective of the group. Insufficient detailed information is available on their phenology and physiology, as well as on the strategies they use to access water during the unfavourable season.

The dominance of deciduous species in WTA is assumed to be due to their higher competitive ability (Menaut, 1983). After Eamus & Prior (2001), analyses of the cost benefit of their maintenance and construction revealed significant differences in comparison with evergreens, not only in terms of water use. Species with short-lived leaves (e.g., < 6 months) displayed a suite of related characteristics including high N investment, high surface leaf area, a high rate of light-saturated assimilation, high relative growth rate, high maintenance cost, but low construction cost, high xylem hydraulic conductivity, but also marked sensitivity to embolism. These traits ensure high short term efficiency of carbon assimilation, and are an opportunistic strategy in terms of carbon gain. By contrast, long-lived leaves ensure long term efficiency and represent a conservative strategy in terms of carbon gain (Eamus & Prior, 2001). Evergreen species do not invest large amounts of nitrogen in their leaves. Their assimilation and relative growth rates are consequently lower. Despite the fact they do not dominate, the contribution of evergreens *sensu stricto* was found to be higher in the driest bioclimates where their carbon gain strategy must consequently be more efficient than in the others.

However, the schematic separation of deciduous and evergreen physiological traits concerns species at the extreme end of the two categories. A deciduous tree with a leaf life span of nine months probably has more in common with an evergreen tree with leaf life span of 12 months than with a deciduous tree with leaf life span of three months. This hypothesis is also supported by the following trend extracted from our review of the literature on WTA savannas and steppes (figure 2): the longer the leafing period, the lower the contribution of species which leaf at the end of the dry season or the beginning of the rainy season. The corollary, which we also stress in this chapter, is that the contribution of species that start leafing in the middle of the dry season increases with an increase in the length of the leafing period, at least in seasonally dry areas.

At the ecosystem scale, Eamus & Prior (2001) reported considerable variation in the relative proportions of different phenological strategies. These authors indicated that Indian savannas are dominated by deciduous species, whereas evergreen species dominate Llanos savannas in South America. In addition, seasonally dry forests in Costa Rica are dominated by semi-evergreen or deciduous species, whereas tropical dry forests in Venezuela are dominated by deciduous species. Australian savannas differ from other savannas in having approximately the same number of species in each of the equivalent of our four groups, but evergreens dominate in terms of canopy cover (90%). Eamus & Prior (2001) presumed that this was a consequence of the extreme dominance of the predominantly evergreen *Acacias* and *Eucalypts* families. But this pattern would also be consistent with these authors' emphasis on the relative photosynthetic return on the cost of investment. Indeed, the lower cost of replacing nutrients

and sclerophyllous leaves to better survive drought would be advantageous for evergreens in these savannas, which are drier and hotter than elsewhere (Bowman & Prior, 2005). In WTA, a detailed comparison of trends in terms of cover has not yet been made. Breman & Kessler (1995) claimed that semi-evergreens are important both in Sahelian and Sudanian bioclimates, especially with regard to their canopy cover, but this literature review relativized their assertion in terms of the number of species concerned (figure 5).

4.2 Leaf phenology: a physiological adjustment to the environment

The increase in the proportion of semi-evergreen woody plants with a decrease in the severity of drought along the gradient, along with a decrease in the proportion of deciduous species, has been reported in all continents except Australia (Williams et al., 1996; Eamus & Prior, 2001). This review confirmed that leafing duration and basal area increments largely depend on water conditions. The distribution of phenological strategies in WTA reported in this chapter supports the hypothesis that the alternation of leaf and leafless conditions, which gives the characteristic seasonal physiognomy of the woody component of WTA savannas and dry forests, is directly linked to the high periodicity of the dry season. Under this hypothesis, deciduous species would dominate in climates with a clear boundary between favourable and unfavourable seasons for plant growth, and with moderately long unfavourable periods. The greater contribution of evergreens in the driest bioclimates could thus also result from reduced predictability of rainfall accompanied by a decrease in annual rainfall amount. Breman & Kessler (1995) concluded that, in terms of contribution to species diversity and canopy cover, the proportion of evergreen but also, contrary to our results, of semi-evergreen species decreases from the north to the south of the Sahelo-Sudanian gradient. Paradoxically, these authors recognize that water availability is a determining factor of leaf flush and shedding, and of flowering and fruiting. This apparent contradiction emphasises the crucial need in WTA for 1) generic definitions of phenological observations, analyses and partitioning of strategies, 2) regional monitoring networks of land surface phenology with sufficient permanent field observation sites. This would enable precise and robust characterisation of the phenology of the woody cover and of its variability along the gradient, which is indispensable for validating data acquired by remote sensing.

Furthermore, it is now widely recognized that the general phenological patterns observed at the community scale conceal a wide range of behaviours both among species and among individuals (Seghieri & Galle, 1999; Seghieri & Simier, 2002; Pau et al., 2011). Seghieri & Simier (2002) showed that even if variability between topographical locations is highly significant, within-individual variability at the same topographical location could be even higher. Generally, species with highly variable phenological behaviour provide evidence for growth plasticity (Devineau, 1999). Studies in the literature report the existence of several competing climate drivers of phenology that are not directly linked to water conditions. This makes their initial interpretation difficult. However, all the drivers cited influence tree water status and support the hypothesis of control by endogenous plant water (Borchert et al., 2002). Leaf flush may be under genetic control, which makes it to depend on day length, hours of sunshine or temperature, while its success may depend on water conditions. Indeed, leaf phenology and shoot growth are increasingly considered to be a way for a plant to fine-tune its water status to atmospheric conditions (Devineau, 1989; Fournier, 1995; Do et al., 2005). The concomitance found by Devineau (1997) between periods of the greatest trunk

shrinkage and of leaf flush is in accordance with observations made in other tropical vegetation under contrasting climates (Jeffers & Boaler, 1966; Daubenmire, 1972; Lieberman, 1982; Asthon et al., 1983).). This suggests that defoliation could prevent tissue dehydration.

Indeed, it is increasingly acknowledged that differences in leaf phenology between species are linked to differences in their water regime and in their vulnerability to xylem cavitation, leading to differences in their responses to soil and atmospheric drought (Delzon et al., 2010). These new insights underline the role of leafing rhythms in the internal water balance of woody plants, especially in semi-arid and arid environments. Leaf shedding limits water loss under prevailing evaporative demand and water availability (rainfall, soil water regime and access to the water table). When environmental changes exceed the plasticity of a given species, the species is eliminated. It may or not have been replaced by one or more other species with different phenology and plasticity, and resulted in the distribution of phenological strategies observed along the climate gradient (Fournier, 1991; Fournier et al., 2001). Locally, whatever the location along the climate gradient, similar processes influenced by factors other than climate are thought to be at work. Topography and soil surface crusts, depth, texture, and fertility are probably the main factors that determine spontaneous species distribution through water and nutrient availability, as shown by Fournier & Planchon (1998) in herbaceous communities. The phenological plasticity of woody species and the wide range of strategies at the community scale contribute to the capacity of the woody plants to survive in the heterogeneous and unstable environments of WTA. Species plasticity, like their physiological independence from the rainy season, would be expected to increase with an increase in the length of the leafing period in the driest parts of the gradient.

4.3 Implications in terms of land use and climate change effects: lack of support studies

Phenological diversity between species allows vegetation in WTA to survive heterogeneous and changing conditions. Similarly, within-species phenological variability is a measure of species plasticity, which largely contributes to the survival and expansion of a species in such environments. Consequently, it is logical to claim that the most plastic species are predisposed to be the best candidates to survive global changes.

The increasing dominance of the semi-evergreen species *Guiera senegalensis* in southern Niger (Seghieri & Simier, 2002; Seghieri & Laloë, 2004; Seghieri et al., 2005) can thus be explained as follows. The species was able to fill the niche gaps previously occupied by several deciduous species disappeared under the pressure of crop and wood harvest. With their larger environmental tolerance, semi-evergreens obtained a decisive competitive advantage from the disappearance of less resistant species. The fact they are more flexible than obligate deciduous plants contributes to their survival and expansion in the most exploited agro-systems (Poupon, 1979; Devineau, 1999; Williams et al., 1997; Seghieri & Simier, 2002; Seghieri & Laloë, 2004; Seghieri et al., 2005). However, this makes natural regeneration of the other original native species difficult, as water balance generally deteriorates with vegetation degradation (Casenave & Valentin, 1992; Seghieri et al., 1994, 1995). That is why the WTA vegetation may follow the putative law of the "expansion drive of desert plants" reported in the Middle East and in Mediterranean areas (Blondel & Aronson, 1999): "when following human transformation of ecosystems, plants from more

xeric habitats, since they are pre-adapted to a large range of conditions, tend to invade more mesic ones rather than the reverse" (Zohary, 1973). In addition, the plasticity of leafing and flowering appears to be an adaptive trait to resist crop pressure as well as savanna fires (Devineau, 1999). Among species whose leaves persist up to the disturbance, those that should be preferentially selected are those whose leaves rapidly reappear afterwards and are still able to flower.

In WTA, the main climate changes expected are an increase in temperature and in rainfall variability, with an increasing proportion of extreme events (Hély et al., 2006; Frappart et al., 2009; Lebel & Ali, 2009). Lack of water disturbs carbon assimilation most when temperatures are too high. This could explain why in the Sahel, where temperatures can be very high and lack of water is a major limitation, most of the phenological processes were found by Seghieri et al. (submitted) to depend on variations in temperature. But the multiple environmental factors that appear to influence phenology may also contribute to species survival thanks to compensatory effects. For example, the effect of an increase in temperature may be compensated by the beneficial effects of an increase in CO_2 concentrations on carbon gain, especially in C3 plants. High plasticity and the many strategies which enable them to remain photosynthetically active independently of the presence of leaves, also probably buffer the negative effects of severe but temporary droughts on Sahelian species. Indeed, changes in the patterns of density, size and species composition of woody populations were documented in 24 rangeland sites along the north–south bioclimatic gradient in the Sahel monitored from 1984 to 2006 by Hiernaux et al. (2009). In the short term, woody populations were seriously affected by the droughts that occurred in 1983–1984. Drought-induced mortality was not more severe under drier climates but occurred sooner after drought in shallow soils. Active recruitment started immediately, i.e. in 1985, *Acacias* species being among the first pioneers. Thanks to the drought, which reduced competition from the other components of the vegetation cover, recruitment was successful. The resulting species composition was first interpreted as a shift towards more arid tolerant flora (*Balanites aegyptiaca*, *Maerua crassifolia* and *Commiphora africana*), but diversification started in the mid 1990s (*Combretum aculeatum*, *Combretum glutinosum* and *Guiera senegalensis*) supporting the hypothesis of the resilience of Sahelian vegetation. Unfortunately, no phenological observations were reported in this interesting study, which concerned only the Sahel.

At present, woody cover is still an integral part of the whole agro-sylvo-pastoral system in WTA. Parkland systems are increasing in Sahelo-Sudanian areas. Some species of great economic interest are thus protected by farmers even if none are planted. In this way, some local agro-pastoral landscapes in the Sahel have considerably more tree cover than they did 30 years ago (Reij et al., 2009). Vast expanses of Sahelian farmlands which were devoid of uncontrolled vegetation in the early 1980s are now studded with trees, shrubs, and crops (WRI, 2008). Elsewhere, deep disturbances of agro-ecosystems have occurred due to crop pressure, which have 1) reduced the woody cover with major hydrological effects in Sahelo-Sudanian areas (Leblanc et al., 2008), 2) modified fire regimes in Guinean areas (Devineau, 1999), and 3) expanded tree plantations in the wettest areas. Impacts on remote sensing (Brown et al., 2010), and consequences in terms of the carbon and water balances (Boulain et al., 2009) remain to be analysed.

In the past decade, the study of phenology has acquired a new legitimacy in climate change research. A conference entitled "The times they are a-changin'; Climate change, phenological

responses and their consequences for biodiversity, agriculture, forestry, and human health" was held in Wageningen in December 2001 (Van Vliet & Schwartz, 2002). It revealed that a change in natural event timing is underway in a wide range of locations and is affecting a wide range of species. The recommendations made on this occasion are still applicable to future studies in WTA where the woody stratum is a key component of the surface-vegetation-atmosphere interface.

5. Challenges for the future

In the context of climate change, the increased interest in phenology sends a clear signal that long term monitoring networks on woody phenology are required in WTA to provide better regional understanding, and hence to improve global forecasting. The main defy at global scale is to foresee the possible consequences of environmental and socioeconomic changes on phenological responses. In WTA, the main challenges are 1) to measure the impacts of land use (wood harvest, pasture, fire, and agriculture) on the phenology of both woody species and canopy cover, 2) to increase our knowledge of the processes involved in their relationships with environmental factors. To take up the challenges, it is extremely important for phenologists to exchange information and ideas with scientists from other disciplines. There are many opportunities for collaborative studies, including methods of data analysis, scenario development, and ecological complexity modelling, as well as monitoring phenology at different scales. Remote sensing approaches, for instance, can provide appropriate tools for upscaling the results of functional (canopy phenology, leaf life span, plant physiological and morphological traits) and demographic (population dynamics) approaches combined. Finally, riparian species have rarely been studied up to now, despite the fact they play a major role in surface-vegetation-atmosphere transfers, given their high density along streams and their probable permanent access to free water.

In this chapter, we have described and explained the distribution of phenological strategies along the WTA gradient in terms of the number of species, and of the dominance of deciduous species. However, replications of environmental situations in which a given species can be found would improve the identification of specific survival strategies in changing environments. We have shed light on the role of leaf phenology in the plant water balance and its adaptation to periodically dry environments. This aspect now needs to be investigated at greater depth. In the future studies on phenology of the woody cover in WTA, we recommend to systematically include knowledge of the relative importance of a given species or of a given strategy in the stand cover. Studies that attempt to quantify relationships between environmental factors and woody phenology are rare and should be encouraged. Implementing these recommendations would provide the essential link with remote sensing data and surface-atmosphere transfer models.

6. Appendix

Phenology of woody species reported in the literature in West Tropical Africa, mostly in savannas and steppes, after Apko, 1992; De Bie et al., 1998; Depommier, 1998; Devineau, 1997; Devineau, 1999; Diouf, 1996; Diouf, 2003; Do et al., 2009; Fournier A., 1991; Grouzis & Sicot, 1980; Hiernaux et al., 1994; Ickowicz et al., 2005; Mahamane et al., 2007; Poupon, 1979; Roupsard et al., 1999; Sanon et al., 2007; Seghieri et al., 1995; Seghieri & Galle, 1999; Seghieri & Simier 2002 (full references in the reference list below).

Deciduous species				Phenology
Acacia adansonii		←		Leafing
		←		Flowering
			←	Fruiting
Acacia ataxacantha		←		Leafing
				Flowering
				Fruiting
Acacia dudgeoni		← ← ← — — — →		Leafing
		← ← ← — — — →		Flowering
			← — — — →	Fruiting
Acacia erythrocalyx		← ← ← — — — — — →		Leafing
			← — →	Flowering
	— — →		← — — —	Fruiting
Acacia gourmaensis		← — — — — — — →		Leafing
		← — — — — →		Flowering
			← — →	Fruiting
Acacia macrostachya		← — — — — — — →		Leafing
		← — — — →		Flowering
			← — — — →	Fruiting
Acacia nilotica		←		Leafing
				Flowering
				Fruiting
Acacia polyacantha		←		Leafing
				Flowering
				Fruiting
Acacia senegal		← ← ← — → — → — →		Leafing
		← — →		Flowering
		← — — — — — →		Fruiting
Acacia sieberiana	←			Leafing
				Flowering
				Fruiting
Adansonia digitata		← ← — → → →		Leafing
	↔		← — →	↔ Flowering
	↔	↔	← — — →	Fruiting
Adenium obesum		← — — — →		Leafing
			← — — →	Flowering
	← — — →			Fruiting
Albizia chevalieri		←		Leafing
				Flowering
				Fruiting
Bombax costatum		← — — — — — — →		Leafing
	→			← Flowering
	— — →			← Fruiting
Boswellia dalziellii		←		Leafing
				Flowering
				Fruiting
Bridelia ferruginea		← — — — — →		Leafing
		←	←	Flowering
			← ← — — →	Fruiting
Burkea africana		←		Leafing
				Flowering
				Fruiting
Cassia sieberana		← — ← — — — — — — →		Leafing
	↔ ↔ ↔ ← — ← — — → ↔ ↔ ↔ ↔			Flowering
	↔ ↔ ↔ ↔ ← — → ↔ ↔ ↔ ↔ ↔			Fruiting
Cassia singueana	←			Leafing
				Flowering
				Fruiting

Deciduous species		Phenology
Cochlospermum planchoni	← — — — →	Leafing
	← — →	Flowering
	← — →	Fruiting
Combretum lecardii		Leafing
	no detail available	Flowering
		Fruiting
Commiphora africana	← — — — →	Leafing
	→ · · · · · · · · · · · · · ← —	Flowering
	← — — →	Fruiting
Commiphora pedunculatum	← —	Leafing
		Flowering
		Fruiting
Cordyla pinnata	← —	Leafing
		Flowering
		Fruiting
Crateva adansonii	← —	Leafing
		Flowering
		Fruiting
Dalbergia melanoxylon	← —	Leafing
		Flowering
		Fruiting
Detarium microcarpum	← — — — — →	Leafing
	← →	Flowering
	→ → → · · · · · · ← — — →	Fruiting
Dichrostachys cinerea	← — — ← — → — →	Leafing
	← — — → →	Flowering
	← — →	Fruiting
Dichrostachys glomerata	← — — — →	Leafing
	← →	Flowering
	← →	Fruiting
Dombeya quiqueseta	← — — — →	Leafing
	— → · · · · · · · · · · ←	Flowering
	← — →	Fruiting
Entada abyssinica	← —	Leafing
		Flowering
		Fruiting
Entada africana	← ← — — → →	Leafing
	← — ← — →	Flowering
	← — →	Fruiting
Erythrina senegalensis	← —	Leafing
		Flowering
		Fruiting
Euphorbia balsamifera	← — ← — → →	Leafing
	← →	Flowering
	← →	Fruiting
Feretia apodanthera	← — — — ← — → — →	Leafing
	← — ← — →	Flowering
	— — → · · · · · ← — — → —	Fruiting
Gardenia ternifolia	← — ← — — — — — →	Leafing
	← → ← →	Flowering
	← ← — ← — — —	Fruiting
Grewia bicolor	← — ← — — → — →	Leafing
	↔ ← → ↔	Flowering
	← →	Fruiting
Grewia flavescens	←	Leafing
		Flowering
		Fruiting

Deciduous species			Phenology
Grewia lasidiscus		← — — — — → — →	Leafing
		↔ ↔	Flowering
		↔ ↔	Fruiting
Grewia tenax		← — — — — →	Leafing
		← →	Flowering
		↔	Fruiting
Grewia venusta		← — ← — — — → — →	Leafing
		↔ ← — ↔	Flowering
		← → ↔	Fruiting
Hexalobus monopetalus		← —	Leafing
			Flowering
			Fruiting
Lannea humilis		← — — — →	Leafing
		← →	Flowering
		← →	Fruiting
Pericopsis laxiflora		← — — — — — →	Leafing
		← — →	Flowering
		← →	Fruiting
Pseudocedrela kotschyi		←	Leafing
			Flowering
			Fruiting
Pteleopsis suberosa		← ← — →	Leafing
	— — — — — →	← — —	Flowering
		← →	Fruiting
Pterocarpus erinaceus		← — — — — — → — →	Leafing
	← →		Flowering
	← →		Fruiting
Pterocarpus lucens		← ← — — — → — →	Leafing
		← ↔ → →	Flowering
		← — — → →	Fruiting
Sclerocarya birrea		← ← — — — → — →	Leafing
	← — →	← →	Flowering
	← ← — — → →		Fruiting
Securidaca longipedunculata →		← ← — — — — → — —	Leafing
	— — — ← ← →	← —	Flowering
		↔ ↔ ↔	Fruiting
Securigena virosa		← ← — — — — → — →	Leafing
		← ← — — → →	Flowering
		← ← — — → — →	Fruiting
Sterculia setigera		← ← — — — — → — →	Leafing
	← — → ← ← →		Flowering
		← → ← — →	Fruiting
Stereospermum kunthianum		← —	Leafing
			Flowering
			Fruiting
Strychnos spinosa		← ← — — → — → — →	Leafing
		← — ← →	Flowering
		← — ← — — →	Fruiting
Terminalia laxiflora	← — ← — — — — →		Leafing
		← — →	Flowering
		← — →	Fruiting
Terminalia macroptera	← —		Leafing
			Flowering
			Fruiting
Xeroderris stühlmannii		← ← — — — → →	Leafing
		← — →	Flowering
			Fruiting
Ziziphus mucronata	← →		Leafing
			Flowering
			Fruiting

Long leafing species				Phenology
Acacia albida	— — — — — — →	← ← — —	Leafing
	→ — →	← — —	Flowering
	← — — →		Fruiting
Acacia gerardii	→ ← — — — — — — — — —		Leafing
	← — →		Flowering
	← — — →	Fruiting
Annona senegalensis	← — — — ← — — — — →		Leafing
	← — — — — — — ↔ →	← —	Flowering
	— — — — — — — ← →	← ←	Fruiting
Anogeissus leiocarpus	→ ← ← — — — — → — —		Leafing
	— — → ← — — — ← — → —		Flowering
	↔ — →	← ← —	Fruiting
Combretum aculeatum	← ← — — — — — →		Leafing
	← ← — ← →		Flowering
	— →	← ← — → —	Fruiting
Combretum micranthum	→ ← — ← ← — — — — — — —		Leafing
	← — ← ← → ← — →		Flowering
	→ — →	← ← — — —	Fruiting
Combretum molle	— — — → ← — — — — — —		Leafing
	← — — →		Flowering
		← —	Fruiting
Crossopteryx febrifuga	↔ — — ↔ ← — — — — → — —		Leafing
	— — — ← ← — →	← —	Flowering
	← — — — — →		Fruiting
Gardenia erubescens	← — — → ← — — — — → —		Leafing
	← — — — — — →	← —	Flowering
	↔ ↔ ↔ ↔ ↔ ↔ ← → ↔ ↔ ↔ ↔		Fruiting
Lannea acida	← — — — — — — — →		Leafing
	↔ ↔ ← — →		Flowering
	↔ ↔		Fruiting
Lannea microcarpa	← — — — — — — — →		Leafing
	← ← →		Flowering
	← → →		Fruiting
Lannea vetulina	← — — — — — — — →		Leafing
	← →		Flowering
	← →		Fruiting
Lonchocarpus laxiflorus	← — — — — — — — →		Leafing
	← →		Flowering
	← →		Fruiting

Semi-evergreen species		Phenology
Acacia hockii	→ ← — — — — → — →	Leafing
	← — →	Flowering
	← — →	Fruiting
Acacia raddiana	→ — → ← ← — — — — → —	Leafing
	← — — — → ← ← — →	Flowering
	— → ← — — ← — →	Fruiting
Acacia seyal	→ ← ← — — — — → — —	Leafing
	— — → ← ← — — — — — —	Flowering
	← — →	Fruiting
Combretum collinum	← — — ← — — — — → → →	Leafing
	— — — ← ← — → ← — —	Flowering
	— — → ← — — ← — — —	Fruiting
Combretum nigricans	→ ← ← — → — — — —	Leafing
	← — ← → — →	Flowering
	→ — → ← — — → — —	Fruiting
Cordya mixa		Leafing
		Flowering
		Fruiting
Daniellia oliveri	← — → ← — — — — — → →	Leafing
	← ← — →	Flowering
	← — — — — →	Fruiting
Diospyros mespiliformis	← — — — — — — — — →	Leafing
	← → ← →	Flowering
	→ ← — — → ←	Fruiting
Ficus thonningii		Leafing
		Flowering
		Fruiting
Gardenia sokotensis		Leafing
		Flowering
		Fruiting
Guiera senegalensis	→ — ↔ — ← — — ← — — — →	Leafing
	→ — → ← — ← — →	Flowering
	→ — — → → ← — —	Fruiting
Isoberlinia doka	← — — — ← — — — — — ↔	Leafing
	← — ↔ — — — →	Flowering
	← ← — — →	Fruiting
Ozoroa insignis	→ ← — — — — — — — —	Leafing
	← — — →	Flowering
	← — — →	Fruiting
Parkia biglobosa	← — — — — — — → →	Leafing
	← — → ← —	Flowering
	← — — →	Fruiting
Piliostigma thonningii	→ ← — — — — — — → → —	Leafing
	↔ ← — → ↔ →	Flowering
	↔ — ← — — — → ← ← — ↔ →	Fruiting
Prosopis africana	↔ — ↔ — — — — — — — —	Leafing
	← ← — →	Flowering
	→ ← — — — → —	Fruiting
Pterocarpus santalinoides		Leafing
		Flowering
		Fruiting
Tamarindus indica	→ ← — — — — — —	Leafing
	← — ← — ← → → ← — —	Flowering
	← → ← — — →	Fruiting
Terminalia avicennioides	← — — ← ← — — — — → →	Leafing
	← ← — →	Flowering
	← — ← → →	Fruiting
Vittelaria paradoxa	← — — → ← — — — — →	Leafing
	← — → ← — → ← — —	Flowering
	← ← — →	Fruiting
Ximenia americana	↔ — — — — — — — — — —	Leafing
	← — — → — — →	Flowering
	← — — ↔ →	Fruiting
Ziziphus mauritiana	→ ← ← — ← → — → — —	Leafing
	→ ← ↔ ↔ → ← — —	Flowering
	← → ← → ← →	Fruiting

Evergreen species		Phenology
Alfezia africana	— — ↔ — — — — — — — — —	Leafing
	← →	Flowering
	← — →	Fruiting
Balanites aegyptiaca (1)	↔ — — ↔ ↔ — ↔ — — — — —	Leafing
	← — →　　　　← — →　　← — →	Flowering
	← — — — ← — → — — →	Fruiting
Berlinia grandiflora		Leafing
	no detail available	Flowering
		Fruiting
Borassus aethiopium		Leafing
	no detail available	Flowering
		Fruiting
Boscia angustifolia		Leafing
	no detail available	Flowering
		Fruiting
Boscia salicifolia		Leafing
	no detail available	Flowering
		Fruiting
Boscia senegalensis	— — ↔ — — — — — — — ↔ —	Leafing
	→ 　　　　← — — — ← ← —	Flowering
	← — — — — — — — — — →	Fruiting
Cadaba farinosa (1)	— — ↔ — — — — — — — — —	Leafing
	← — — — — →	Flowering
	← — →	Fruiting
Calotropis procera		Leafing
	no detail available	Flowering
		Fruiting
Capparis fascicularis		Leafing
	no detail available	Flowering
		Fruiting
Capparis sepiaria (2)	— — — — — — — — — — — —	Leafing
	← — — →	Flowering
	← — — →	Fruiting
Celtis integrifolia		Leafing
	no detail available	Flowering
		Fruiting
Cola cordifolia		Leafing
	no detail available	Flowering
		Fruiting
Combretum fragrans	— — — — — ↔ — — — — — —	Leafing
		Flowering
		Fruiting
Combretum glutinosum	— — ↔ — — ↔ — — — — — —	Leafing
	← → ↔ — — → ← →　　　← —	Flowering
	— ← ↔ — — →　　　← — ← —	Fruiting
Ficus glumosa		Leafing
	no detail available	Flowering
		Fruiting
Ficus ingens		Leafing
	no detail available	Flowering
		Fruiting
Ficus platyphylla		Leafing
	no detail available	Flowering
		Fruiting
Ficus sycomor		Leafing
	no detail available	Flowering
		Fruiting
Flemingia faginea		Leafing
	no detail available	Flowering
		Fruiting
Hippocrates africana		Leafing
	no detail available	Flowering
		Fruiting
Holarrhena floribunda		Leafing
	no detail available	Flowering
		Fruiting

Evergreen species					Phenology
Leptadenia hastata					Leafing
		no detail available			Flowering
					Fruiting
Maytenus senegalensis (1)	↔ — — ↔ — — — — — — —				Leafing
	↔ — — ↔ — →				Flowering
	← — →				Fruiting
Nauclea latifolia	↔ ↔ ↔ — — — — — — — —				Leafing
	← — →				Flowering
	← — — — — →				Fruiting
Opilia celtidifolia					Leafing
		no detail available			Flowering
					Fruiting
Parinari curatellifolia	— — — — — ↔ — — — — — —				Leafing
	← — — — →				Flowering
	← — — — — — — — — — →				Fruiting
Piliostigma reticulatum	↔ — ↔ — — — — — — — —				Leafing
	← — — →				Flowering
	→ — →		← — —		Fruiting
Rotula aquatica riparian					Leafing
		no detail available			Flowering
					Fruiting
Saba senegalensis					Leafing
		no detail available			Flowering
					Fruiting
Salix subserrata riparian					Leafing
		no detail available			Flowering
					Fruiting
Sarcocephalus latifolius					Leafing
		no detail available			Flowering
					Fruiting
Syzygium guineense					Leafing
		no detail available			Flowering
					Fruiting
Vitex simplicifolia					Leafing
		no detail available			Flowering
					Fruiting

(1) several periods of leaf turn over and at any times

(2) period of leaf turn-over non mentionned

←	Beginning of the phenophase
—	Current phenophase
→	End of phenophase
↔	Overlape between the beginning and the end either on the same or between two sites
	Dry season
	Transition between seasons
	Sahelian sudanian and guinean rainy season

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8. References

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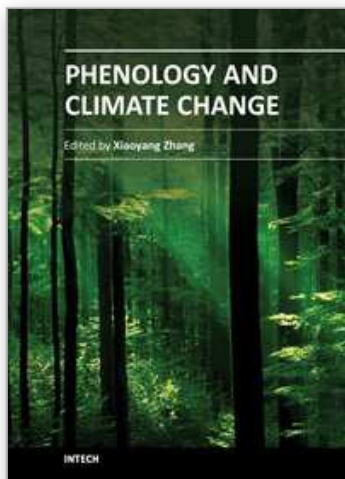
Phenology and Climate Change

Edited by Dr. Xiaoyang Zhang

Phenology, a study of animal and plant life cycle, is one of the most obvious and direct phenomena on our planet. The timing of phenological events provides vital information for climate change investigation, natural resource management, carbon sequence analysis, and crop and forest growth monitoring. This book summarizes recent progresses in the understanding of seasonal variation in animals and plants and its correlations to climate variables. With the contributions of phenological scientists worldwide, this book is subdivided into sixteen chapters and sorted in four parts: animal life cycle, plant seasonality, phenology in fruit plants, and remote sensing phenology. The chapters of this book offer a broad overview of phenology observations and climate impacts. Hopefully this book will stimulate further developments in relation to phenology monitoring, modeling and predicting.

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