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# Environmental influence on canopy phenology in the dry tropics

Frederic C. Do [a,*], Venceslas A. Goudiaby [b], Olivier Gimenez [c], Amadou L. Diagne [d], Mayecor Diouf [b], Alain Rocheteau [a], Leonard E. Akpo [b]

[a] IRD-UR060, Centre d'Ecologie Fonctionnelle et Evolutive, 1919 Rte de Mende, 34293 Montpellier, France

[b] Faculté des Sciences et Techniques (Biologie Végétale), Université Cheikh Anta Diop, BP 5005 Dakar, Senegal

[c] CNRS, Centre d'Ecologie Fonctionnelle et Evolutive, 1919 Rte de Mende, 34293 Montpellier, France

[d] Institut des Sciences de l'Environnement, Université Cheikh Anta Diop, BP 5005 Dakar, Senegal

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## Abstract

Canopy phenology of *Acacia tortilis* ssp. *raddiana*, a dominant semi-deciduous species of the northern Sahelian zone, was monitored for 39 mature individuals, each month and bi-weekly in the rainy season, over a 5.5-year period in North Senegal. To investigate the relationships between leaf phenology and environmental variables, soil water availability and several climatic variables were monitored.

Over six rainy seasons, annual rainfall ranged between 146 and 367 mm. The full canopy stage lasted between 5 and 8 months, broadly including the rainy season (July–September) and the ''cool'' dry season (November–January). A significant inter-annual variation, up to 2.0 months, affects both the timing of the peaks of leaf flush and leaf fall. The canopy was maintained during the dry season despite low upper soil water availability and tree roots had access to a deep water table (31 m). These results support the current view that in the dry tropics, groundwater availability is the major environmental variable controlling leaf phenology. However, inter-annual variation in the peaks of leaf flush and leaf fall could not be explained by ground water, genetics or day length. In such water-controlled biome, we focused on a comparison between two additional drivers, upper soil water availability and climatic variables which contribute to evaporative demand. Models predicting changes in canopy fullness from environmental variables were investigated by polynomial logistic regression. We considered each tree and pooled all the years, distinguishing periods of leaf flush (April–August) and leaf fall (January–April). Then, the ability of such models to predict inter-annual variation in the timing of peaks of leaf flush and leaf fall was tested.

Inter-annual variation in the timing of leaf flush peak was well predicted by models based on air relative humidity or vapour pressure deficit or global radiation (root mean square error = 0.5 month and $R^2$ = 0.8). Inter-annual variation of leaf fall peak was also significantly predicted by models based on atmospheric variables (temperatures or maximum value of vapour pressure deficit) however with weaker relationships (root mean square error = 0.7 month and $R^2$ = 0.7). By contrast, models based on upper soil water availability or rainfall did not predict either leaf flush or leaf fall inter-annual variation. It appears that inter-

* Corresponding author. Tel.: +33 467 613 263.
*E-mail address:* frederic.do@cefe.cnrs.fr (F.C. Do).


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annual variation of canopy phenology is mainly tuned to atmospheric conditions. Such behaviour maximizes the duration of high photosynthetic activity below a threshold of evaporative demand.


*Keywords:* Sahelian Africa; *Acacia tortilis*; Canopy fullness; Leaf flushing; Leaf fall; Evaporative demand; Soil water availability

## 1. Introduction

In dry tropical regions, such as Sahelian Africa, green leaves of dominant woody species in the dry season are a keystone resource for domestic herbivores, wildlife and ecosystems as a whole (Le Houérou, 1989). Prediction of the potential impact of climate change on the deciduousness extent and the timing of leaf flushing and leaf fall, i.e. leaf phenology, is a major challenge in ecology of dry tropics.

The Sahelian zone *sensu stricto* represents one of the driest savannas with 200–400 mm year$^{-1}$ of rainfall and with high inter-annual variability (coefficient of variation equal to 37%), potential evaporation is in excess of 2000 mm year$^{-1}$ and groundwater usually located deeper than 30 m (Le Houérou, 1989). *Acacia tortilis* (Forsk.) Hayne ssp. *raddiana* (Savi) Brenan, is a dominant tree of the area which is classified as semi-evergreen or semi-deciduous (Breman and Kessler, 1995; Le Floc'h and Grouzis, 2003), i.e. the loss of leaves which takes place in the late dry season is rarely complete and the deciduousness extent varies with years, sites and individuals. Moreover, trees of this species regularly exhibit inter-annual variation of leaf flush before the onset of rains.

In the tropics, authors agree on a primary genetic control and an influence of day length on leaf phenology (Halevy and Orshan, 1973; Reich and Borchert, 1984; Borchert, 1994a,b; Reich, 1995; Williams et al., 1997; Morellato et al., 2000). The controversy is over which environmental controls explain inter-annual and inter-site variations in the timings of leaf flush and leaf fall. In the dry tropics, the general view is that groundwater availability is the major environmental variable controlling canopy dynamics (Borchert, 1994a,b,c; Eamus and Prior, 2001).

Such hypothesis is relevant to explain inter-site variation of *A. tortilis* phenology in the northern Sahelian zone of Senegal (Ferlo). In this area, it is particularly notable that the deciduousness extent of *A. tortilis* changes with variation of the water table level, e.g. near the Senegal river where the water table is close to the top soil, trees behave like evergreen species. Moreover, this tree is known for its phreatophytic habit and its roots reach deep water tables (Lhote, 1961; Deans et al., in press) in common with numerous woody species of low-rainfall areas.

However, the influence of groundwater availability is not always relevant to explain inter-annual variation of leaf fall and leaf flush in the same site. In the northern Ferlo, the water table, located between 30 and 40 m depth, is very slowly recharged from the top soil (several decades) and no large fluctuation of its level is expected (Gaye and Edmunds, 1996).

To explain inter-annual variation of leaf fall, the depletion of upper soil water availability after the rainy season is the main hypothesis (Grouzis and Sicot, 1980; Diouf and Zaafouri, 2003). High seasonal fluctuations of predawn leaf water potential attest influence of soil water availability near the soil surface on *A. tortilis* water status (Berger et al., 1996). However, in the tropics, several irrigation experiments in the field have shown little impact of soil water availability on leaf phenology (Wright and Cornejo, 1990; Myers et al., 1998). Several authors have suggested that evaporative demand may also be an important environmental variable controlling leaf phenology (Wright and Cornejo, 1990; Duff et al., 1997; Myers et al., 1998).

Such response to climatic conditions (relative humidity and vapour pressure deficit) have been often mentioned to explain leaf flush in the transition period between dry season and rainy season (Le Houérou, 1989). However, we are not aware of quantitative data supporting this hypothesis.

In conducting a multi-annual study (5.5 years) on 39 individuals of *A. tortilis* in the Sahelian zone with concurrent measurements of climatic conditions and upper soil water availability, we wanted to address the two following questions: (1) Can changes in evaporative demand explain inter-annual variation of the timing of leaf flush peak? (2) Can changes in upper soil water availability explain inter-annual variation of the timing of leaf fall peak.

The full canopy stage of a tree was assessed when the proportion of the branches supporting green expanded leaves represented more than 50% of those in the canopy. The timings when the full canopy stage rose above or fell beneath the 50% value in the tree population defined the timings of leaf flushing and leaf fall peaks, respectively.

The study had three steps. The first step was to assess the seasonal course of canopy fullness and the inter-annual variation in the timings of leaf flushing and leaf fall peaks. The second step was to build and compare, by regression analysis pooling individuals and years, predictive models of canopy fullness based on upper soil water availability, rainfall and different variables contributing to the evaporative demand: temperature, global radiation, relative humidity and vapour pressure deficit. The third step was to test the ability of such models to predict inter-annual variation of the timing of leaf flush and leaf fall peaks.

## 2. Methods

### 2.1. Location, climate and vegetation

The study was carried out in northern Senegal, near Souilene Village (16°20′N, 15°25′W) located 20 km south of Dagana in the grazing land ecosystem of the sandy Ferlo. Annual rainfall averages 280 mm, mean annual temperature is 28.7 °C and average maximum and minimum temperatures are, respectively, 41 and 22 °C for the hottest month (May) and 31 and 14 °C for the coldest month (January). The sparse woody community is dominated by three species: *A. tortilis* and *Balanites aegyptiaca* (L.) Del, for the tree layer (90 individuals $ha^{-1}$) and *Boscia senegalensis* (Pers.) Lam for the shrub layer (50 individuals $ha^{-1}$). The soil is very deep and sandy (90% sand).

### 2.2. Population and measurements

The studied population included 39 mature individuals of *A. tortilis* located in a 1 ha area that has been protected since 1989. Trunk diameter, which was measured 30 cm above the soil, varied from 5 to 45 cm, with 70% of the population having diameters between 15 and 30 cm. Tree height ranged from 5 to 10 m. Local microclimate was automatically monitored by a datalogger (21×, Campbell Scientific Ltd., Leics, UK), which recorded hourly values of air temperature, relative humidity, global radiation and rainfall. Soil moisture was measured to a depth of 4 m by neutron probe (Solo 25, Nardeux S.A., Les Ulis, France) using six access tubes. The soil wetting front rarely exceeded 1 m depth. Soil water availability (SWA) is expressed for the layer of 0–100 cm depth, calculated between moisture contents at field capacity and the driest moisture contents which were less than those prevailing at a water potential of −1.5 MPa. The soil profile down to the water table was augered by the Geological Department of Dakar University (Dr. Abdoulaye Faye). Samples were taken every 0.5 m. Actual moisture content and moisture equivalent to −1.5 MPa were determined in the laboratory. Over the period June 1995–August 2000, phenological observations and soil measurements were carried out every month in the dry season and twice a month in the rainy season, except in August 1995 and 1997.

Climatic data were not available between 13 and 18 April 1996, and between 29 September and 10 October 1996.

### 2.3. Assessment of phenological stages

For each tree, a phenological stage for the foliage was allocated according to the six following categories taking into account the proportion of branches bearing green expanded leaves in the canopy (Grouzis and Sicot, 1980): 0, leafless, 0%; 1, leaf buds opening, <10%; 2, start of leaf expansion, 10–50% of the branches; 3, full canopy, >50%; 4, start of leaf senescence, changing colour, <50%; 5, full leaf senescence or fall, <10%.

### 2.4. Data analysis

To express canopy fullness, the phenological stages were converted to their midrange percentage value of branches bearing green expanded leaves in the canopy: 0, 0%; 1, 5%; 2, 30%; 3, 75%; 4, 30%; 5, 5%. Thus, the maximum value of canopy fullness is 75 by definition. The timings of leaf flush or leaf fall peaks were calculated for each tree by linear interpolation, such as the time when the canopy fullness rose above or fell below the 50% value in the long term (>1 month). Time is expressed in numerical values of months (mo.), e.g. 6.5 for the middle of June. Because phenological cycles are displayed across 2 years, we use for simplicity's sake, the year of the rainy season to name the phenological cycle, e.g. 1998 for 1998/1999. Timings of leaf fall peak located at the beginning of the second year are expressed as greater than month 12, e.g. 13.5 for the middle of January. The duration of full canopy was calculated for each tree by difference between the timings of leaf fall and leaf flush peaks.

Year effects on the duration of full canopy and the timings of leaf flush and leaf fall peaks were tested using a repeated-measures analysis of variance (SAS Proc. Mixed, SAS Institute Inc., 1999). Predictive model of canopy fullness changes based on environmental variables were investigated by regression analysis considering each tree and pooling all years, distinguishing periods of leaf flush and leaf fall. Since at the tree level, canopy fullness values were qualitative and ordinal response variables, classified as 0, 5, 30 and 75, we specifically performed ordered polynomial logistic regressions with a cumulative logit link (SAS Proc. Genmod, SAS Institute Inc., 1999). This model relates the cumulative log of odds of the response variable to the explanatory variable in a linear form (Agresti, 1984). The validity of regressions was assessed by computing the significance of each variable using Wald tests (Agresti, 1984).

Because we wanted to compare the predictive power of environmental variables, the *c*-statistic was computed (Hosmer and Lemeshow, 2000). It measures the degree to which predicted probabilities agree with actual outcomes. It is computed as the proportion of times where the relative ranking of individual prediction is in the correct order. The *c*-statistic ranges from 0.5 to 1. A 0.5 value means that the model is no better than assigning observations randomly into outcome categories. Variables with *c*-statistic value greater than 80% were therefore selected as having high predictive power. The analysis gives the values of the explanatory variable (environmental variable) corresponding to the selected probability of each response (0, 5, 30 and 75). For atmospheric variables (temperature, relative humidity, vapour pressure deficit and global radiation), the average value for the 15 days preceding phenological observations was considered. For soil water availability, the actual SWA and the amount of rainfall were used. A period of 30 days before phenological observation was also tested.

For environmental variables having high predictive power, models were test to predict for each year, the times of leaf flush and leaf fall peaks, such as the day when the probability of full canopy (response 75) rose above or fell below the 50% value in the long term (>1 month). Inputs were climatic data for the 15 days preceding each day. Quality of prediction was evaluated by the root mean square error: $\mathrm{RMSE} = \sqrt{\sum_1^n (s_i - m_i)^2/n}$, where $s_i$ is the model prediction, $m_i$ the corresponding observation, $i$ the year and $n$ is the total number of years.

Table 1
Mean values of timing of leaf flush peak, timing of leaf fall peak, and duration of full canopy stage expressed in months for 39 individuals of *Acacia tortilis* growing at Souilène in North Senegal

| Annual cycle | Rainfall amount (mm) | Leaf flush peak | | Leaf fall peak | | Full canopy duration | |
|---|---|---|---|---|---|---|---|
| | | Mean (month) | S.D. | Mean (month) | S.D. | Mean (month) | S.D. |
| 1995–1996 | 251 | 7.8 | 0.5 | 15.2 | 0.5 | 7.4 | 0.8 |
| 1996–1997 | 153 | 7.8 | 0.4 | 13.1 | 1.4 | 5.3 | 1.5 |
| 1997–1998 | 146 | 8.4 | 0.3 | 14.5 | 0.8 | 6.1 | 1.1 |
| 1998–1999 | 272 | 7.3 | 0.7 | 14.8 | 0.9 | 7.6 | 1.3 |
| 1999–2000 | 367 | 6.3 | 1.1 | 13.7 | 0.6 | 7.4 | 1.3 |
| 2000–2001 | 190 | 6.0 | 0.3 | – | | – | |
| Total mean | 230 | 7.3 | 1.0 | 14.3 | 1.2 | 6.8 | 1.5 |

Repeated-measures ANOVA revealed highly significant effects of year ($P < 0.001$) on the three variables. The study ended in August 2000 before observation of the timing of leaf fall for the phenological cycle 2000–2001.

## 3. Results

During the study period (1995–2000), annual precipitation averaged 230 mm with minima of 146 and 153 mm in 1997 and 1996, and a maximum of 367 mm in 1999 (Table 1; Fig. 1a). It is noteworthy that inter-annual variability over the 6-year period (CV = 37%) was similar to the long-term variability for the area. Rains occurred mainly between July and September. The dates for onset of the rains were variable, i.e. about the start of June in 1996 and 1997, but the end of July in 1998. August and September were the wettest months. On average, 70% of the total annual precipitation fell during these 2 months. SWA in the upper layer (0–100 cm) was closely correlated with annual rainfall (Fig. 1b). In the wet season, SWA increased proportionally with rainfall and reached 80% for the wettest year 1999. However, by January, SWA decreased to similar values between years (from 7 to 9%). Subsequently, SWA declined to small values of 3–5%, before the start of the rains. The top of the water table was found at 31 m depth, consistent with the water level found in village wells in the study area. Between the upper layer of soil and the water table, SWA for plants was very limited because the actual moisture contents were equivalent to a water potential of $-1.5$ MPa. Living root fragments of *A. tortilis*, which can be identified from their very special smell, were collected at 25 m depth. These observations confirmed that the trees have access to the water table.

Atmospheric conditions in the rainy season were characterized by highest relative humidities (RH), above 50%, with mean temperatures around 30 °C (Fig. 1a). This was the time of the lowest evaporative demand: daily means of vapour pressure deficit (VPD) were less than 2 kPa (Fig. 1b). RH increased between May and June, from 1 to 2 months before the start of the rains. This is a common phenomenon induced by the northerly movement of the Inter-Tropical Convergence Zone but there were notable differences between years (Fig. 1a). RH decreased sharply after the rainy season, then it fluctuated, from 10 to 50%, with notable differences between years. In the dry season, two climatic seasons are usually distinguished according to air temperature: the "cool" dry season lasting from December until February and the hot dry season lasting from March until June (Fig. 1b, months 15–17). The hot dry season with low RH and increasing temperatures is characterized by the highest evaporative demand: mean VPD generally exceeds 2 kPa and maximum VPD regularly exceeds 5 kPa.

Evolution of canopy fullness showed an annual cycle with both similarities and differences between years (Fig. 1b; Table 1). The defoliation phase was centred around the hot dry season. Defoliation was never complete at population scale as shown by canopy fullness which never reached a zero value (Fig. 1b). The point closest to zero occurred in April 2000 (Fig. 1a: point at 16 mo. in "1999" or 4 mo. in "2000"), which corresponded to 63% of fully defoliated trees. The full canopy stage lasted an average 7 months (Table 1), from mid-July to the start of February, broadly including the rainy and cool dry seasons (Fig. 1). The inter-annual variation of full canopy stage duration was large, e.g. more than 2 months between the extreme years: 5.2 mo. in 1996 and 7.5 mo. in 1998 or 1999 (Table 1). The repeated-measures analysis of variance revealed a highly significant ($P < 0.001$) effect of year on canopy duration. The observation interval which was at the best bi-weekly and more often monthly precludes discussion of differences or equalities at less than 0.5 months. The magnitude of differences clearly distinguishes two groups, the group of the years 1996 and 1997 where duration was shortened by 25% in comparison with the group of the years 1995, 1998 and 1999. The duration differences resulted from variation in a 2 month range both in the timings of peaks for leaf flush and leaf fall (Table 1). The timing of leaf flush peak varied from the start of June (years 2000 and 1999), more than 1 month before the first rains (Fig. 1), to the end of July or the start of August in the rainy season (years 1995–1997). The situation in 1998 was intermediate: the start of leaf flushing was early, in May as in 1999 and 2000, but was followed by a defoliation before leaf flush peaked in July (Fig. 1). Initial leaf flush was generally observed between April and May overall years. The timing of leaf fall peak varied from the start of January (year 1996) to the start of March (year 1995). The years 1996 and 1997 had intermediate defoliation in December. The inter-individual variation was large and variable depending upon year (standard deviation in Table 1). For example, for the same average timing of leaf flush peak, the inter-individual variation was four-fold

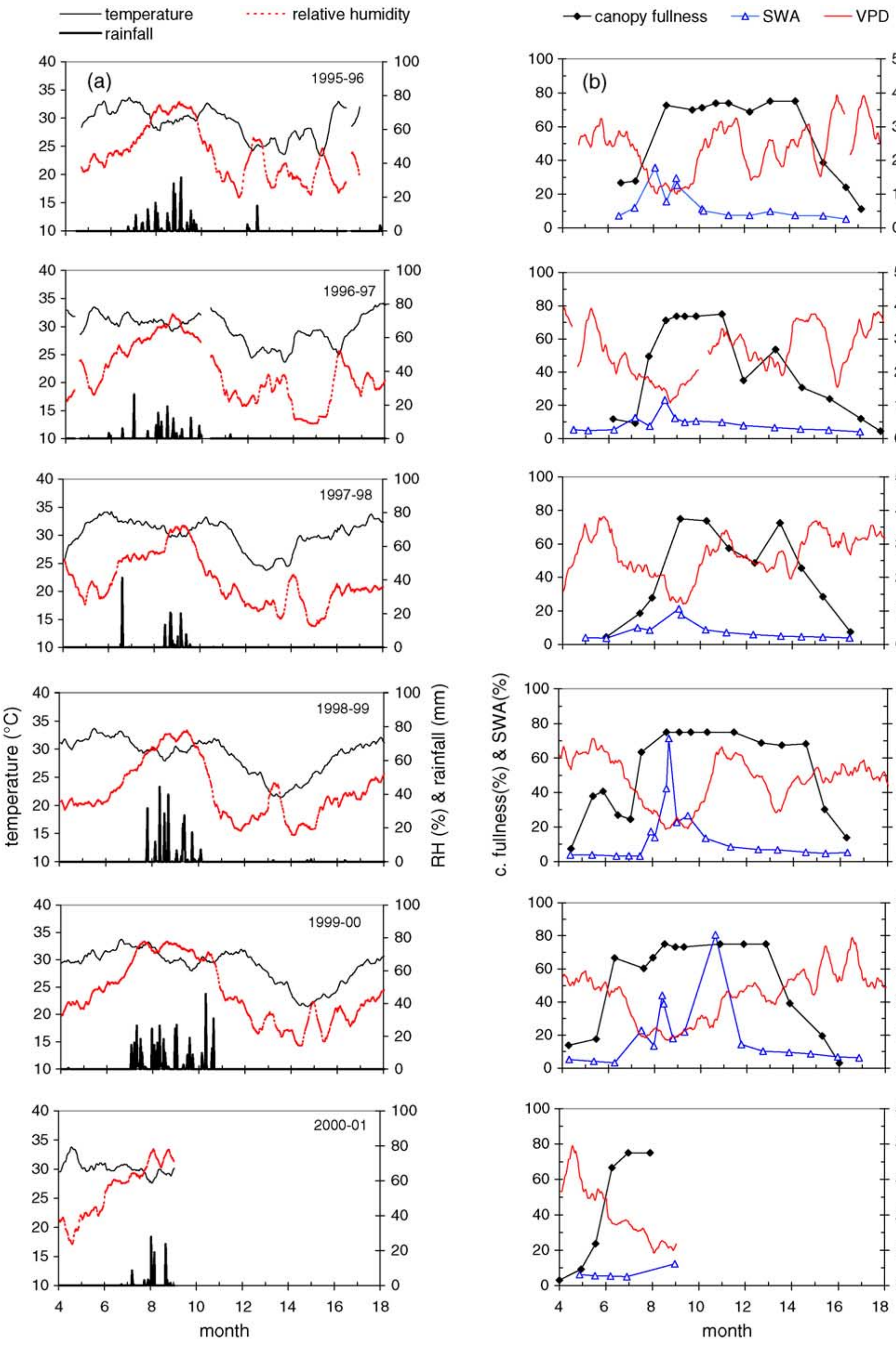


Fig. 1. Inter-annual variation of environmental conditions and leaf phenology for *Acacia tortilis* growing at Souilène in North Senegal. (a) Daily rainfall, 15 days moving average of mean air temperature and relative humidity (RH) and (b) average canopy fullness of 39 individuals, soil water availability (SWA) in the upper layer (0–1 m), 15 days moving average of mean air vapour pressure deficit (VPD). Time is expressed in numerical values of months, e.g. 6.5 for the middle of June. The study ended in August 2000.

Table 2
Parameters of regression–prediction analysis testing which environmental variable can best explain (1) changes in canopy fullness (CF) and (2) the annual timings of leaf fall and leaf flush peaks (T50)

| Variable | Leaf flush time (April–August) | | | | Leaf fall time (January–April) | | | |
|---|---|---|---|---|---|---|---|---|
| | CF models ($n$ = 1209) | | T50 prediction ($n$ = 6) | | CF models ($n$ = 819) | | T50 prediction ($n$ = 5) | |
| | 50% CF | $C$ | RMSE | $R^2$ | 50% CF | $C$ | RMSE | $R^2$ |
| $T_{mean}$ (°C) | 30.8 | 0.76 | – | | 25.6 | 0.82* | 0.7 | 0.63 |
| $T_{min}$ | 22.9 | 0.50 | – | | 17.5 | 0.79 | – | |
| $T_{max}$ | – | 0.78 | – | | 33.4 | 0.81* | 0.7 | 0.64 |
| $RH_{mean}$ (%) | 54.5 | 0.82* | 0.5 | 0.77 | – | 0.49 | – | |
| $RH_{max}$ | 78.5 | 0.82* | 0.4 | 0.76 | – | 0.55 | – | |
| $RH_{min}$ | 30.5 | 0.82* | 0.5 | 0.82 | 20.2 | 0.64 | – | |
| $VPD_{mean}$ (kPa) | 2.1 | 0.82* | 0.4 | 0.80 | 2.2 | 0.77 | – | |
| $VPD_{min}$ | 0.7 | 0.82* | 0.4 | 0.78 | 0.5 | 0.62 | – | |
| $VPD_{max}$ | 4.9 | 0.81* | 0.5 | 0.83 | 4.5 | 0.81* | 0.6 | 0.76 |
| RG (W m$^{-2}$) | 6689 | 0.80* | 0.5 | 0.88 | 5596 | 0.81* | 0.9 | 0.04 |
| SWA (%) | 11 | 0.68 | – | | 8.4 | 0.64 | – | |
| Rainfall (mm) | 14 | 0.72 | – | | – | | – | |

Variables were daily mean, minimum and maximum air temperatures ($T$), relative humidity (RH), vapour pressure deficit (VPD), global radiation (RG), upper soil water availability (SWA) and rainfall. Polynomial logistic regressions were performed between values of canopy fullness and each environmental variable, considering each tree and pooling all years, distinguishing times of leaf flush and leaf fall. "50% CF" indicates the value of variables corresponding to 50% of canopy fullness (peak of leaf flush or leaf fall). $C$ is the predictive power, which is high when (*) is added. RMSE is root mean square error of predicted timings of leaf flush peak ($n$ = 6 years) and leaf fall peak ($n$ = 5 years) against observed timings. $R^2$ is the determination coefficient of the linear relationship between predicted timings and observed timings.

larger in 1999 than in 2000. Similar results occurred between 1995 and 1996 for the timing of leaf fall peak. At the individual level, the time between the onset of flushing and full foliation was approximately 1–1.5 mo. (data not shown). Fig. 1b shows the average of canopy fullness in the population, so durations were increased by an averaging effect in the case of large inter-individual variation.

Results of regression–prediction analysis between canopy fullness and environmental variables, distinguishing times of leaf flush (January–April) and leaf fall (April–August), are summarized in Table 2. For upper SWA, two variables were considered: the actual SWA and the amount of rainfall in the 15 days preceding phenological observations. In the completely dry season (timing of leaf fall), changes of SWA were slow and actual SWA, measured at monthly intervals, was a good integrator of soil conditions for the 15-day period of time. By contrast, during the transition between dry and rainy seasons (timing of leaf flush), due to the effect of rainfall, measured SWA was a poor predictor and rainfall amount (hourly recording) was used as a surrogate (see Fig. 1). Whatever the environmental variables there was a significant relationship ($P < 0.05$). This was due to the fact that during the considered periods, soil water and weather variables were all moving broadly at the same seasonal time as canopy fullness (see Fig. 1). The key point is the comparison between predictive powers of variables ($c$-values in Table 2). The values of environmental variables corresponding to a prediction of 50% of canopy fullness (leaf flush or leaf fall peaks) are also indicated in Table 2. The analysis considering a period of 30 days instead of 15 days before phenological observations gave similar results (data not shown).

For the timing of leaf flush, models based on air relative humidity (RH), vapour pressure deficit (VPD) and global radiation (RG) had high predictive powers ($c \geq 0.80$). Moreover, they could predict the inter-annual variation in the timing of leaf flush peak with a root mean square error (RMSE) of 0.4–0.5 month (Table 2). So, the 2 months difference noticed between the years with early leaf flushing peak (1999 and 2000) and the years with late leaf flushing peak (1995, 1996 and 1997) was explained by difference in weather conditions. It was foreseeable that upper soil water availability did not explain inter-annual variation of leaf flush because early leaf flush peaks (1999 and 2000) occurred more than 1 month before the first rains.

For the timing of leaf fall, models based on air temperature, $VPD_{max}$ and RG had high predictive powers. Between timings of leaf flush and leaf fall, there was a remarkable switch between the predictive powers of relative humidity (RH) and temperature ($T$), variables which are combined in VPD calculation (Table 2). Model based on soil water availability had a weak predictive power and did not predict inter-annual variation of leaf fall peak. By contrast, model based on temperature and $VPD_{max}$ predicted inter-annual variation of leaf fall peak with a RMSE equal to 0.6–0.7 months. The prediction ability of models based on atmospheric variables was better for leaf flush timing than for leaf fall timing. Moreover, determination of days when probability of full canopy fell below the 50% value (leaf fall peak) was less clear than for leaf flush due to larger fluctuation of climatic conditions and consideration of a ‘‘long-term’’ (>1 month) decrease was necessary.

Fig. 2 illustrates that a model based on a weather variable, such as $VPD_{max}$, significantly predicted inter-annual variation in both the timing of leaf flush peak and the timing of leaf fall peak, and consequently, duration and time location of the full canopy stage. However, we should mention that such model based on $VPD_{max}$, when applied to the whole year, predicted some defoliation during October and November which was not systematically observed (Fig. 1).

## 4. Discussion

In spite of very deep water table (31 m), the phreatophytic habit of *A. tortilis* was confirmed by several results: the similarity of the annual pattern of canopy phenology over 5 years, the full canopy maintenance during dry season while upper soil water availability is very low and constant, and the finding of roots at the top of the water table. The full canopy stage of *A. tortilis* sp. *raddiana* lasted between 6 and 8 months, broadly including the rainy season and the ‘‘cool’’ dry season. As for the majority of deciduous species in the seasonally dry tropics, the defoliation phase was centered around the hot dry season. The seasonal period and duration of full canopy stage is in agreement with the general description of its leaf phenology in Sahelian Africa (Grouzis and Sicot, 1980; Diouf and Zaafouri, 2003). These data support the general view that groundwater availability is the major environmental variable controlling canopy dynamics in the dry tropics (Borchert, 1994a,b,c; Eamus and Prior, 2001).

The second result was the assessment of a significant inter-annual variation in both the timing of leaf flush peak and the timing of leaf fall peak on the same site, up to 2 months in each case. One consequence was a 25% reduction in the duration of the full canopy stage for 2 years (1996 and 1997). Such variations show that ground water, genetics and day length are not the only factors controlling canopy phenology and that others have complementary influence on the timings of leaf flush and leaf fall peaks.

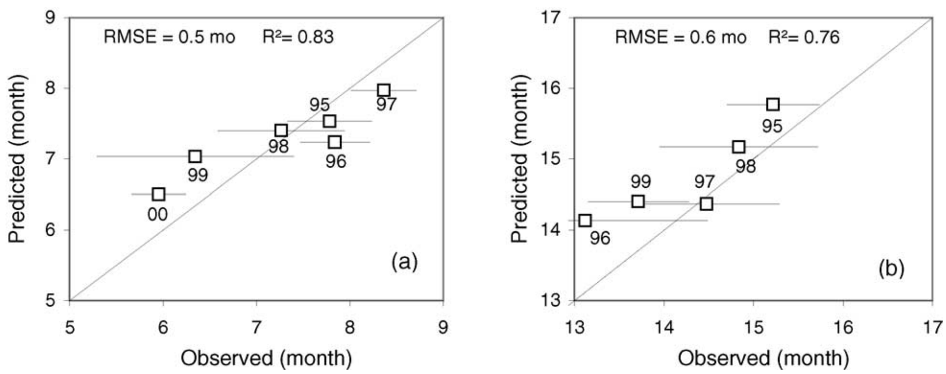


Fig. 2. Timings of leaf flush peak (a) and leaf fall peak (b) predicted by models based on the dynamics of maximum vapour pressure deficit ($VPD_{max}$) vs. observed timings. Input was the average value of $VPD_{max}$ for the preceding 15 days. Point labels specify annual phenological cycles. Horizontal bars indicate standard deviation of observed data (means of 39 individuals). RMSE is the root mean square error (see Section 2).

The third result was that evaporative demand explained inter-annual change of the timing of leaf flush peak in the dry–wet transition period. Variables particularly involved were relative humidity, vapour pressure deficit and global radiation. This result supports the current idea that in the Sahelian zone leaf flushing responds to the relative humidity increase, or the evaporative demand decrease, which is induced by the northerly movement of the Inter-Tropical Convergence Zone (Le Houérou, 1989).

The fourth result was that the depletion of upper soil water availability did not explain inter-annual variation in the timing of leaf fall peak in the dry season. This result does not support the current hypothesis that in the Sahelian zone, higher annual rainfall would induce a larger residual upper soil water availability in the dry season which could delay the timing of defoliation. Despite a large inter-annual variation in rainfall (from 146 mm in 1997 to 367 mm in 1999), upper SWA reached similar and very small values in all years 3 months after rainy season. How was this possible? The phenological stage or canopy fullness percentage does not describe leaf area or leaf number which were two times higher for 1998 than for 1997 (Goudiaby, 2003). Biomass of grass was also greater at the end of the wettest rainy seasons. These two factors involve greater water uptake, which can explain how SWA reached similar small values.

The fourth result was the most surprising: it showed that evaporative demand significantly explained inter-annual changes of the timing of leaf fall peak. Variables particularly involved were temperature and vapour pressure deficit. The relationships were weaker than for the timing of leaf flush. However, results showed that an atmospheric variable, such as the daily maximal value of VPD significantly predicted inter-annual variations both in the timing of leaf flush peak and in the timing of leaf fall peak.

Finally, these results give a new insight on the additional role of evaporative demand in canopy phenology of dry tropics species. One schematic idea is that the average phenological pattern fits the prevailing local available water, annual rainfall amount and groundwater availability, while inter-annual fluctuations are a fine tuning to atmospheric conditions. The conditions of water constraint (rainfall amount, evaporative demand and depth to the water table) in the ecosystem studied here were more extreme than in savannah situations detailed elsewhere in the literature (Eamus and Prior, 2001). It is fairly possible that these extreme conditions enhance the role of evaporative demand. Comparable data on these points are scarce in the literature. One reason may be that phenological studies on the same individuals lasting more than 1 or 2 years are not often found in the tropics (Poupon, 1979; Corlett and Lafrankie, 1998). Another reason is that up to now, evaporative demand was not always considered as a climatic variable influencing savanna tree phenology (De Bie et al., 1998; Chidumayo, 2001).

The mechanism of the influence of evaporative demand on canopy phenology is not known. However, we hypothesize that atmospheric conditions control development, demography and life span of initial and final leaf flushes. On the same trees, the study of Goudiaby (2003) made on terminal branches shows that the annual phenological pattern corresponds to continuous flushes of leaves except during a short period in the middle of the hot dry season. The initial flush of leaves systematically began between April and May, 2 months before the onset of rains. If the atmospheric conditions are favourable, such as in 1999 and 2000, the initial leaf flush succeeds and the leaf flush peaks occur around June. If the atmospheric conditions are not favourable, such as in 1996 or 1997, the initial leaf flush fails and the leaf flush peaks occur later around July. A similar phenomenon is assumed to explain variation of leaf fall peaks.

Finally, the tuning of canopy phenology to atmospheric conditions induced a maximum variation of 25% in the duration of the full canopy stage. Such behaviour maximizes the duration of high photosynthetic activity below a threshold of evaporative demand.

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