

# Phenology and seasonal variation in stomatal conductance of rosewood tree, an important legume tree in the Sudanian savanna-woodland

---

ZIDA Didier<sup>1</sup>, SANOU Lassina<sup>1\*</sup>, SAVADOGO Patrice<sup>1</sup>

## Abstract

In the present study, we evaluated for the period 2010-2011, the leaf phenology and photosynthetic characteristics of planted rosewood tree (*Pterocarpus erinaceus* Poir.), an important browse legume tree in the Sudanian savanna-woodland. All observed individual trees reduced leaf physiological function between the wet and dry seasons. Photosynthetic capacity, leaf area, nitrogen concentration of leaves decreased significantly ( $P < 0.05$ ) with the leaves aging and the seasons. These physiological parameters of the species, however, are not significantly correlated with the climatic parameters (temperature, relative humidity, solar radiation, wind speed and direction) recorded during each measurement. Further work involving several populations of the species with longer time span is required to increase our understanding of its physiological responses to seasonal climate variation.

**Keywords:** *Pterocarpus erinaceus*, leaf longevity, photosynthetic acclimation, stomatal conductance, dry tropical forest.

## Phénologie et variation saisonnière de la conductance stomatique du vène, un important arbre légumineux dans la savane soudanienne boisée

### Résumé

Dans la présente étude, nous avons évalué pour la période 2010-2011, la phénologie des feuilles et des caractéristiques photosynthétiques du vène (*Pterocarpus erinaceus* Poir.), un arbre fourrager légumineux de la savane soudanienne boisée. Tous les individus observés ont réduit la fonction physiologique de leurs feuilles entre les saisons sèche et humide. La capacité photosynthétique, la surface foliaire, et la concentration en azote des feuilles ont diminué significativement ( $P < 0,05$ ) avec le vieillissement des feuilles et la saisonnalité. Ces paramètres physiologiques de l'espèce, toutefois, ne sont pas significativement corrélés avec les paramètres climatiques (température, humidité relative, rayonnement solaire, vitesse et direction du vent) enregistrés lors des mesures. D'autres travaux impliquant plusieurs populations de l'espèce avec un temps expérimental plus long est nécessaire pour accroître notre compréhension de ses réactions physiologiques aux variations climatiques saisonnières.

**Mots-clés :** *Pterocarpus erinaceus*, Longévité des feuilles, Acclimatation photosynthétique, Conductance stomatique, Forêt sèche tropicale.

---

<sup>1</sup> Centre National de la Recherche Scientifique et Technologique, INERA, Département Productions Forestières, 03 BP 7047, Ouagadougou 03, Burkina Faso.

\* Corresponding author: lassina.sanoulassina@gmail.com

## Introduction

*Pterocapus erinaceus* Poir. is widely distributed in West Africa and its foliage and timber are sought for various purposes. The high demand of its products leads to high pressure which is threatening its survival in some areas (IUCN, 2011). Despite the threat to this valuable native species, very few studies (SEGHIERI *et al.*, 2012) have been conducted to improve the knowledge on its phenology and ecophysiology. Such knowledge is essential for greater understanding of expected climate change on species' productivity and resilience and for its incorporation in conservation and rational management schemes in seasonally-dry savannas.

Understanding the determinants of phenological patterns of plant community is critical to predict their responses to global climate change (VAN VLIET et SCHWARTZ, 2002). Considering marked seasonality various phenological events (e.g. leafing, flowering, fruiting, seed germination), the new climatic pattern is supposed to greatly change tree pheno-phases (VICO *et al.*, 2014) and any deviation in the onset, degree and duration of wet and dry periods may lead to significant change in phenological events (KUSHWAHA *et al.*, 2011). The environmental change, in addition to affecting the tree phenological behavior, would affect photosynthesis and growth. Photosynthesis is the fundamental basis of plant's growth. This is the most important metabolic activity performed by green plants, which regulates primary productivity and carbon cycle (TAIZ et ZEIGER, 2006).

Plants productivity is a response to the availability of climatic and environmental factors essential to their functioning. Thus, plants are exposed to seasonal abiotic factors that show irregular and regular diurnal and seasonal variations (ZHANG *et al.*, 2012) and influence their metabolic responses (photosynthesis and growth rate). The role of seasonal changes in photosynthetic efficiency is demonstrated for many species with more efficiency gains related to changes in light intensity, temperature, nutrient concentration, or the state of development or phenology of the plant (LARCHER, 2003a). Seasonal variations in precipitation, soil moisture and evaporative demand have a significant impact on stomatal conductance leaf water potential and phenology (CHOAT *et al.*, 2006). The objective of this study was to investigate variation patterns in the phenological behavior and seasonal change in photosynthesis to gain better understanding.

## I. Material and Methods

### 1.1. Study site

The investigations were conducted from October 2010 to May 2011 on an experimental site located at Saria research station (12°16'N and 2°09'W) of the Institute of Environment and Agricultural Research (Burkina Faso). The site is an open flat terrain (300 m a. s. l.) with climate characterized by marked seasonality, with the majority of precipitation occurring during a rainy season lasting for 6 months from May to October. For the period 1999-2010, the average annual rainfall was  $835 \pm 88$ mm with large inter-annual variability. The number of rainy days per annum during this period was  $64 \pm 8$  days. The mean annual evapotranspiration is 2000mm in dry years and 1 720mm in wet years (OUATTARA *et al.*, 2006). For the year 2010, the cumulated monthly rainfall indicates that August is the wettest with 267.2mm of rain in 15 days. The mean daily temperature varied from 30°C during the rainy season to 45°C in April and May (MANDO *et al.*, 2005). The major soil type is Ferric Lixisols which have generally low fertility (OUATTARA *et al.*, 2006).

The vegetation of the locality is characterized by savanna grasses, trees and shrubs and an agricultural landscape. The experiment was first designed in 2004 to study the effect of seedling age and water stress on the subsequent growth performance of transplanted seedling of *P. erinaceus* and *Acacia macrostachya* Rchb. ex G.Don (ZIDA, 2007). After 2007 these investigations stopped and the experimental site was manually weeded twice per year at the beginning and the end of the rainy season, partly to reduce competition from grass during the growth season and partly to reduce risk of fire. The experimental site is permanently fenced to exclude large herbivores.

## 1.2. Plant species description

*P. erinaceus* Poir. (family of Leguminosae, subfamily of Papilionoideae) is a small to medium-sized tree 12–15 m tall with a diameter of 1.2–1.8 m. It is a deciduous legume tree indigenous to African savannas from the Sudanian and Guinean climate areas and dry forests, famous for producing one of the finest woods (African rosewood) in its native region (ARBONNIER, 2009). It also produces leafy fodder high in protein, which makes an excellent animal feed crucial for the survival of livestock during the dry season (OUÉDRAOGO-KONÉ *et al.*, 2008). The leaves are once-compound, imparipinnate, and 30 cm long, with 10–15 alternate or sub-opposite leaflets, 6–11 cm long and 3–6 cm wide (ARBONNIER, 2009). The tree produces showy and attractive golden-yellow flowers and has considerable potential as an ornamental. *P. erinaceus* is also a medicinal plant used to treat several diseases, as the whole plant including stem bark, leaves, roots and resin have medicinal properties (OUEDRAOGO *et al.*, 2011). *P. erinaceus* provides high-quality leaf fodder with an average nutritive value in dry matter of 5.3 MJ kg<sup>-1</sup> net energy, 16–19 % crude protein, and 0.15 % phosphorus (OUEDRAOGO *et al.*, 2011). *P. erinaceus* is a good species for fodder bank technology, which involves intensive coppicing through periodic cuttings (KY-DEMBELE *et al.*, 2016). Increasing demand for its high-value timber and fodder threat the existing natural stands. However, the tree fruits abundantly and is easy to propagate, making it a good candidate for reforestation programs.

## 1.3. Phenological analysis

The present study is conducted on individuals of *P. erinaceus* planted in 2004; they were all on average 7.26 cm diameter at 1.30 m and 4.5 m high. These individuals were transplanted on the site after spending three months in the nursery (ZIDA *et al.*, 2008). Bi-weekly observations were carried out from 4-October 2010 to 23 May 2011, on 15 marked individuals. Floc'h (1968) and Grouzis and Sicot (1980), reported the following main phenophases studies: (L) Leaf initiation, development and abscision; (F) anthesis and flower senescence; and (V) fruit maturation. The phenological phases were calculated as the ponderate average of the observed phenophases, every phenophase being indicated by a number of progressive stages (table I).

**Table I:** The different phenological phase of development observed.

<b>(L) Leaf initiation, development and abscission</b>	<b>(F) Anthesis and flower senescence</b>	<b>(V) fruit maturation</b>
L1: no new leaf development	F1: no flowers	P1: no fruits (pods)
L2: first appearance of new leaves	F2: Initial anthesis of inflorescence	P2: early development of pods
L3: approximately 50% of leaves fully expanded	F3: approximately 50% of inflorescence fully open	P3: green pods fully developed but still unripe
L4: Beginning of leaf senescence	F4: beginning of flower senescence	P4: pods brown and seeds fully ripe
L5: virtually all leaves fallen from tree	F5: flowering finished or nearly so	P5: end of fruit maturation ; some pods fallen from tree

Stages L2, F2 and P2 thus corresponded to the beginning of successive phenophases, stages “3” and “4” to intermediate development, and stage 5 to the culmination of a phenophase.

#### 1.4. Stomatal conductance

Stomatal conductance was determined with a porometer (model PRM-5) designed to be used with EGM-4 CO<sub>2</sub> analyzer (EGM-4, environmental gas monitors, PP systems, Hertfordshire, UK). The PMR-5 is a hand-held unit using an « open system » measurement of leaf transpiration. The porometer was calibrated as required following instructions given in the manual at commencement of each measurement session, and repeated if there was appreciable change in temperature and/or humidity. Care was taken during measurement to ensure that the light sensor on the porometer head receives the incidental radiation by holding the porometer head as parallel to the ground surface as possible. Stomatal apertures were measured at each date of phenological observations until the onset of leaf senescence to help understand how the photosynthetic assimilation changes with the seasonal period and the plant phenology. At each date, the measurements were done in the morning from 9:00 to 11:00 on six individual trees randomly chosen. At each of the measurement times, a group of six youngest fully expanded leaves on each tree were tagged. All tagged leaves were randomly selected throughout the sun illuminated side of canopy. After each measurement they were harvested, stored in paper envelopes and sent to the laboratory for further analysis.

#### 1.5. Weather variables

During the measurements of gas exchange in the field, solar radiation, rainfall, temperatures, wind speed, wind direction, relative humidity and air temperature were recorded with a WS-GP1 Ultra Portable Weather Station equipped with a GP1 Data Logger and a 2 m tripod mast. The data logger was set to automatically save every 15 minutes the minimum, maximum and average values of the different climatic parameters cited above.

## 1.6. Evaluation of leaf area, weight and chemical analysis

The area per unit leaf weight (specific leaf area) was determined after measuring leaf area using an Area Measurement System, CI-202 Portable Laser Area Meter, CID Inc., USA. For the sake of clarity, leaf area measurements were performed *ex situ* in the laboratory on collected leaflets. After measurement of leaf area, the fresh weight of leaflets was immediately determined using an electronic scale of  $210 \text{ g} \pm 0.01 \text{ g}$  (Brand PL Mettler Toledo Model 203-S). The dry weight was then obtained after drying in an oven at  $60^\circ\text{C}$  for 48 h. After drying the leaves samples were kept in ambient room conditions and later subject to chemical investigation. The leaflets on each day of measurement for each individual tree were put together and sent to Burkina Faso's Bureau National des Sols (BUNASOL) for the determination of nitrogen (N) and potassium (K) total using the Houba method. The nitrogen content of the leaflets was determined after mineralization of samples. The sample is heat treated with a mixture of concentrated sulfuric acid ( $\text{H}_2\text{SO}_4$ ) and salicylic acid ( $\text{C}_6\text{H}_7\text{O}_3$ ). The sulfuric acid through its oxidizing action destroys the organic matter and releases the N as ammonium ( $\text{NH}_4^+$ ), which was immediately fixed in the form of  $(\text{NH}_4)_2\text{SO}_4$  and  $(\text{NH}_4)\text{HSO}_4$ . The Nitrate ( $\text{NO}_3^-$ ) and traces of nitrite ( $\text{NO}_2^-$ ) present in the sample are first fixed by the salicylic acid and subsequently reduced to ammonia by the sodium thiosulfate. The mineralization is accelerated by using a catalyst (selenium) and an increase in temperature by adding hydrogen peroxide ( $\text{H}_2\text{O}_2$ ). After mineralization, N is determined by spectrometry at 420 nm by the method of Nessler's reagent. The K was dosed with flame photometer. The N and K content are derived from the following formula:

$$\% (\text{N or K}) = (\text{L}-\text{B}) \times \text{K} \times \text{VT} \times \text{D} / \text{P} \times 10000$$

With L the absorbance of the sample, B the blank absorbance, the constant K series range, the total volume VT (75 ml), D the dilution factor and P the weight of the sample (0.05 g).

## 1.7. Data analysis

At the end of the measurements, the data is transferred into the computer. Climate data are aggregated by date of measurement, respectively, for averages, maxima and minima. Phenogram was established for *P. erinaceus*. It was possible to construct a phenological calendar in which the phenological events of the species are related to time. To understand the temporal variability on the measured parameters, a time series analytical procedures was used. The data for stomatal aperture, leaf area, dry weight, nitrogen and potassium content for each of the six individual samples are subjected to repeated measured analysis of variance (DAVIS, 2002). Analysis of variance was performed separately for each parameter following a general linear model (GLM) for repeated measures:

$$Y_{ik} = \mu + \lambda_i + \varepsilon_{i(k)}$$

Where Y is the response variable,  $\mu$  is the grand mean,  $\lambda$  is time (measurement date).  $\varepsilon_i$  parameter (k) is the random error with the number of repetitions  $k = 6$ . Before the statistical analysis, the normality of the data was checked. When the homogeneity of variance assumption was violated, according to Mauchly's test of Sphericity, the degrees of freedom for testing the significance of the within-subject factors were adjusted using Huynh-Feldt correction factor, which is less biased than other correction factors (DAVIS, 2002). Given that only one or two individuals had leaves at the last measurement date, data for this measurement time were excluded from the

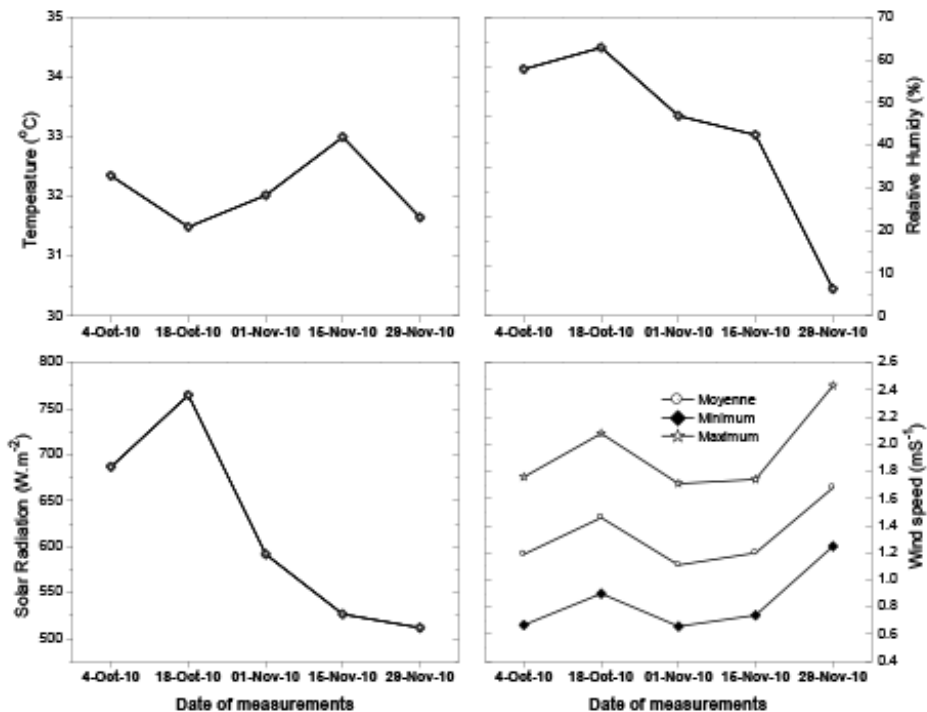
analysis. In addition to determining whether the temporal variability in the parameters studied was linked to climatic variables recorded during measurement, correlation analysis was made between these two groups of parameters. All statistical analyses were performed using the statistical analysis software SPSS 19.0 for Windows (SPSS Inc. Copyright ©.1989-2010. All rights reserved). Graphic plotting was conducted with Origin 7.5 software (Origin Lab Copyright © 1998-2008 Corporation).

## II. Results

### 2.1. Weather conditions during the study

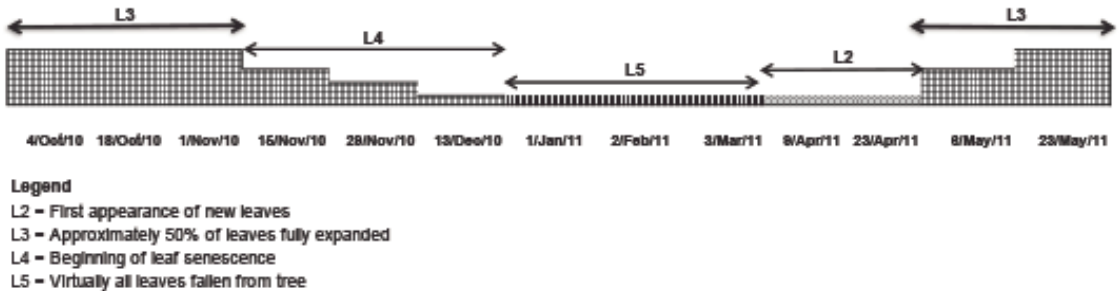
Automatic weather data recording lasted about 2 hours on each date of measurement. During this period there was no difference between the values recorded for the average, minimum and maximum for temperature, solar radiation and relative air humidity (the three separate curves are overlapping on figure 1). From mid-October to late-November, solar radiation decreases steeply of about 33% (from 764.8  $W m^{-2}$  to 511.75  $W m^{-2}$ ), at the same time relative air humidity decreased with a magnitude of 75.8% (from 63.89 to 15.46%). The temperature during the measurement varied from 31.50°C to 33°C. The average wind speed was the highest at late November 1.68  $ms^{-1}$  compared with all other recorded values. The direction in which the wind was blowing during the first two measurements in October was 175 degrees then it dropped of about 2 degrees in late November. There was no rain, trace included during the period of investigation.

### 2.2. Phenology



**Figure 1:** Variation in the climatic data recorded during the measurement of leaf stomatal conductance.

The phenological observations indicated that generally the growth cessation (i.e. leaf fall) at the end of growing season and subsequent growth resumption (i.e. leaf flushing) were separated by a period where most of the individuals were leafless. According to the phenogram (figure 2) from October to early November, all observed individuals had mature leaves. From mid-November the leaf senescence and the leaf fall begun; it increased with the progressive dryness and in late December all individuals were leafless and remain so till March. From April two major events were observed: the beginning of bud break or when more than 1/3 of the individuals' buds had burst followed by leaf flush and completion of leaf expansion which was achieved in mid-May when more than 2/3 of leaves were fully extended. No reproductive growth (flowering and ripeness of fruits) was observed.



**Figure 2:** Phenogram

### 2.3. Seasonal variation of the measured parameters

The repeated measures analysis of variance revealed a significant ( $P < 0.05$ ) temporal variation of most measured parameters excepted potassium where the value of  $P$  was 0.543 (table II, figure 3) which remained relatively unchanged through the measurement periods with values ranging from  $10.37 \pm 2.58$  to  $9.66 \pm 1.12$ g/kg from the first to last measurement. Leaf potassium content slightly increases of 2.5% before the litter fall in early December. Leaf area had a tendency ( $P = 0.059$ ) to decrease through the dry season. From the first date to the last measurement, leaf area decreased from  $28.29 \pm 2.01$  to  $25.53 \pm 1.89$  cm<sup>2</sup>. The total nitrogen in the harvested leaflets decreased of about 16% from early October to mid-November. Stomatal conductance (gs) rose of three fold from the first measurement to the second (from  $84.08 \pm 24.96$  to  $255.15 \pm 20.60$ mmol. m<sup>2</sup>.s<sup>-1</sup>). However with the onset of the dry season, gs declined and fell gradually to a value close to the first measurement ( $93.16 \pm 22.80$ mmol. m<sup>2</sup>.s<sup>-1</sup>) early in the dry season.

**Table II:** Summary of the repeated measures analyses of variance of leaf area, stomatal conductance, fresh and dry weight matter and Ntot and K content

Parameter	F-value	p-value
Leaf area	F[3,15]= 3.101	P= 0.059
Stomatal conductance	F[3,15]= 10.337	P= 0.001
Fresh weight	F[3,12]= 22.640*	P< 0.001
Dry weight	F[3,15]= 6.939	P= 0.004
Ntot	F[3,15]= 8.364	P= 0.003
K	F[3,5]= 0.750*	P= 0.543

\* Huynh-Feldt correction applied

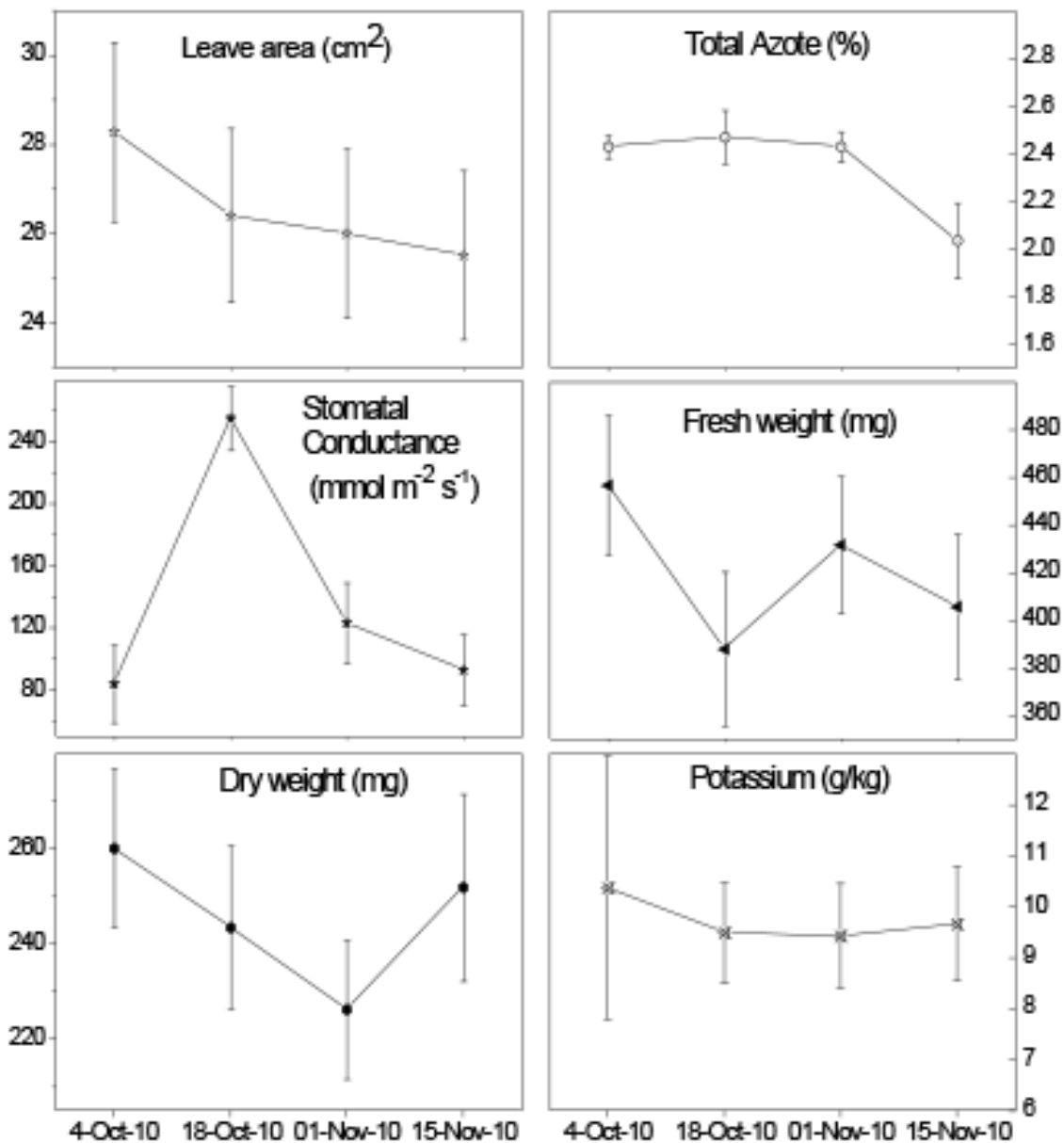
#### 2.4. Relationship between stomatal conductance and climate data

The correlations between environmental variables and leaf stomatal conductance were not significant. Nevertheless, most of the correlations were all above  $r^2=0.50$  except wind direction which had  $r^2=0.458$  of relationship with stomatal conductance. Among all, stomatal conductance had a negative response to temperature ( $r= -0.830$ ). Stomatal conductance rates were positively correlated with levels of incoming solar radiation, wind speed, wind direction relative air humidity (table III).

**Table III:** Relationship between stomatal conductance and climatic data.

	Pearson Correlation	Sig. (2-tailed)
Relative air humidity	0.647	0.353
Solar radiation	0.717	0.283
Air temperature	-0.830	0.170
Wind speed	0.889	0.111
Wind direction	0.458	0.542





**Figure 3:** Seasonal variation of stomatal conductance, leaves area, fresh and dry weight and Ntot (Total azote) and K content.

### III. Discussion

The phenological behavior of *P. erinaceus* observed in the present study is characteristic of many trees and shrubs of arid zones (VICO *et al.*, 2014) with the timing of leaf production and abscission appearing to be influenced by progressive dryness. Indeed, in deciduous species the growth cessation (i.e. leaf fall) at the end of the growing season and subsequent growth resumption (i.e. leaf flushing) are separated by deciduousness (leaflessness) of variable duration (KUSHWAHA *et al.*, 2010; DI LUCCHIO *et al.*, 2018). In deciduous ecosystems water stress is most frequently cited as a primary factor responsible for the timing of phenological events (CHOAT *et al.*, 2006 ; KEENAN *et al.*, 2009) and seasonal extent of drought is critical factor for growth regulation (VICO *et al.*, 2014). It has been suggested that leaf drop in drought-deciduous species is related to the internal water balance of the plant rather than to direct environmental cues such as photoperiod (CHOAT *et al.*, 2006 ; VINYA *et al.*, 2019). Given that leaf senescence is an evolutionarily acquired process (LIM *et al.*, 2007), variation in timing and pattern of leaf fall among phenological functional types may be the result of their adaptations to varying soil moisture levels. At the end of the dry season, there was development of buds and peak in leaves development despite rainfall event; this is an indication of the role of various factors in triggering the leaf flushing breaks in deciduous species in this region (DE BIE *et al.*, 1998).

The results show that seasonality plays an important role in the modulation of the photosynthetic activity of leaves. These findings are similar to those reported by BOWMAN and PRIOR (2005) for savanna species in Australia. Stomatal conductance was greatest during the measurement of mid-October which happens on a day following a rainfall event. This finding is in agreement with the results of other gas exchange studies in seasonally dry tropical forest trees (CHOAT *et al.*, 2006). These authors reported that tropical deciduous trees are predicted to have higher photosynthetic rates during the wet season in order to compensate for the lost opportunity for carbon gain while leafless in the dry season (EAMUS, 1999 ; CHOAT *et al.*, 2006). After the mid October, we observed a decline in the stomatal conductance most likely due to decrease of accessible soil water and increase in evaporative demand. This observation was expected as the water deficit is one of the most important environmental factors constraining plant photosynthesis and productivity in arid and semi-arid areas (BOWMAN et PRIOR, 2005 ; VINYA *et al.*, 2019). Indeed, seasonal water stress in many tropical regions, characterized by a decrease in soil water content and an increase in vapor pressure deficit, is shown to reduce the turgor of guard cells and induce stomatal closure, which decreases the absorption of CO<sub>2</sub> (EAMUS, 1999). This leads to the observed decrease in leaf area and a decrease in incoming shortwave absorption.

Our results indicated that photosynthetic capacity as well as nitrogen content of leaves decreased with increasing leaves age as leaves color changes from bright green to a yellowish color. This is consistent with other studies (LARCHER, 2003b ; WUJESKA-KLAUSE *et al.*, 2019) indicate that photosynthetic capacity is strongly influenced by leaf age. When dryness period extends, leaves senesce and the ability of photosynthesis and stomatal conductance decline in senescent leaves, in order to increase the efficient use of scarce water (ARES et FOWNES, 1999). The leaves are the primary photosynthetic organ for producing carbohydrate in most cases and its phenology is closely related to tree's growth rhythm (WANG *et al.*, 2018). The decline in photosynthetic capacity is often correlated with a decrease in stomatal conductance, nitrogen

concentration of the leaf, and photosynthetic activity of several enzymes (LARCHER, 2003a). This explains that the concentration of nitrogen in the dried material of leaves decreases progressively in our samples. The reduction of nitrogen in the aging tissue is well known (TAIZ et ZEIGER, 2006). With leaves aging, the leaf nitrogen is translocated in the stem or roots. This decrease in foliar nitrogen is accompanied by an increase in yellowish color of the foliage that we observed in the field before the leaf fall.

Climatic parameters did not significantly correlate with photosynthetic capacity in the present study probably due to the small sample size (we had only 4 measurements). Nevertheless, the high correlations found are consistent with other studies (RIBEIRO *et al.*, 2009) which indicate that stomatal conductance and photosynthesis varied seasonally and with climatic parameters. Stomatal conductance rates negatively correlated with temperature, this corroborates previous evidence of decreasing gas in response to increasing temperature. The response of  $g_s$  to temperature is thought to be mainly the result of the effect of temperature on the energy metabolism of the cells (YAMAZAKI *et al.*, 2006). The results showed overall positive correlations between conductance rates and relative humidity during the measurement. Most likely explanation for these results is that leaves may minimize conductance to water vapor (TAIZ et ZEIGER, 2006). There was a positive correlation between leaf conductance and solar radiation. Light intensity affects photosynthesis rate through light receptors which drive CO<sub>2</sub> fixation and lower intercellular CO<sub>2</sub> concentration, and the guard cells are conditioned jointly by the water balance of the bulk leaf tissue and the CO<sub>2</sub> concentration in the substomatal cavity (TAIZ et ZEIGER, 2006). Further, stomatal conductance responded positively to wind. The mechanism of the stomatal response to wind observed could be explained on the basis of water balance within the stomatal complex and on the antagonistic relationship between turgors in guard and epidermal cells. Wind is one of the important environmental factors for plant growth and can be estimated to affect leaf gas exchange through change in leaf boundary layer conductance (ZHANG *et al.*, 2012).

## Conclusion

In conclusion, the results of this study suggested that phenological development and stomatal conductance of *P. erinaceus* were related to season. The seasonal change in the nitrogen concentration is intrinsically linked to the leaves aging. The seasonal change is related to decreasing soil moisture availability which induced adaptation strategies in deciduous trees through leaf fall. The results also show that several environmental variables such as temperature, wind speed, solar radiation, and relative humidity come into play for determining the stomatal conductance rates. Given the probable impact of climate variability on tree phenology and primary productivity, further work involving several populations of *Pterocarpus* with longer time span is required to increase our understanding of the species responses to global climate change.

## Acknowledgements

Financial support for this work was provided by the International Foundation for Science (IFS), Grant Agreement No C/4781-1. Special thanks to Santi Saidou and Meda Modeste for their continuous assistance during the fieldwork. Thanks are also due to Dr Bognounou Fidèle for lending us some equipment.

## References

- ARBONNIER M., 2009.** Arbres, arbustes et lianes des zones sèches d'Afrique de l'Ouest, 3e Ed.,QUAE/MNHN. 504 p.
- ARES A., et FOWNES J. H., 1999.** Water supply regulates structure, productivity, and water use efficiency of Acacia koa forest in Hawaii. *Oecologia*. 458-466.
- BOWMAN D. et PRIOR L., 2005.** Why do evergreen trees dominate the Australian seasonal tropics? Australian Journal of Botany, 53: 379–399.
- CHOAT B., BALL M. C., LULY J. G., DONNELLY C. F. et HOLTUM J. A. M., 2006.** Seasonal patterns of leaf gas exchange and water relations in dry rain forest trees of contrasting leaf phenology. *Tree Physiology*. 657-664.
- DAVIS, C. S. 2002.** Statistical methods for the analysis of repeated measurements. Springer, London.
- DE BIE S., KETNER P., PAASE M. et GEERLING C., 1998.** Woody plant phenology in the West African savanna. *Journal of Biogeography*. 883-900.
- DI LUCCHIO L. M., FENSHOLT R., MARKUSSEN B. et RAEBILD A., 2018.** Leaf phenology of thirteen African origins of baobab (*Adansonia digitata* (L.)) as influenced by daylength and water availability. *Ecology and Evolution*, 8: 11261-11272.
- EAMUS D., 1999.** Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends Ecology & Evolution*. 11-16.
- IUCN., 2011.** IUCN Red List of Threatened Species. Version 2011.2. www.iucnredlist.org. Downloaded on 02 December 2011.
- KEENAN T., GARCIA R., FRIEND A. D., ZAEHLE S., GRACIA C. et SABATE S., 2009.** Improved understanding of drought controls on seasonal variation in Mediterranean forest canopy CO<sub>2</sub> and water fluxes through combined in situ measurements and ecosystem modelling. *Biogeosciences*, 6:1423-1444.
- KUSHWAHA C. P., TRIPATHI S. K., SINGH G. S. et SINGH K. P., 2010.** Diversity of deciduousness and phenological traits of key Indian dry tropical forest trees. *Annals of Forest Science*.
- KUSHWAHA C. P., TRIPATHI S. K., TRIPATHI B. D. et SINGH K. P., 2011.** Patterns of tree phenological diversity in dry tropics. *Acta Ecologica Sinica*. 179-185.
- KY-DEMBELE C., BAYALA J., KALINGANIRE A., TRAORÉ F. T., KONÉ B. et OLIVIER A., 2016.** Vegetative propagation of twelve fodder tree species indigenous to the Sahel, West Africa. *Southern Forests: a Journal of Forest Science*, 78(3).
- LARCHER W., 2003.** Physiological plant ecology: Ecophysiology and stress physiology of functional groups (4th Ed.). Springer-Verlag, Berlin Heidelberg, Germany.
- LIM P. O., KIM H. J. et NAM H. G., 2007.** Leaf senescence. *Annual Review of Plant Biology*. 115-136.
- MANDO A., OUATTARA B., SEDOGO M., STROOSNIJDER L., OUATTARA K., BRUSSAARD L. et VAN-LAUWE B., 2005.** Long-term effect of tillage and manure application on soil organic fraction and crop performance under Sudano-Sahelian conditions. *Soil Tillage Research*. 95-101.
- OUATTARA K., OUATTARA B., AYEMOU A. et SEDOGO P. M. 2006.** Long-term effect of ploughing, and organic matter input on soil moisture characteristics of a Ferric Lixisol in Burkina Faso. *Soil Tillage and Research*. 217-224.
- OUÉDRAOGO-KONÉ S., KABORÉ-ZOUNGRANA C. Y. et LEDIN I. 2008.** Important characteristics of some browse species in an agrosilvopastoral system in West Africa. *Agroforestry Systems*. 213-221.
- OUÉDRAOGO N., TIBIRI, A., SAWADOGO R. W., LOMPO M., HAY A. E., KOUDOU J., DIJOUX M. E. et GUISSOU I. P., 2011.** Antioxidant anti-inflammatory and analgesic activities of aqueous extract from stem bark of *Pterocarpus erinaceus* Poir. (Fabaceae). *Journal of Medicinal Plants Research*. 2047-2053.
- RIBEIRO R. V., MACHADO E. C., SANTOS M. G. et OLIVIERA R. F., 2009.** Seasonal and diurnal changes in photosynthetic limitation of young sweet orange trees. *Environmental and Experimental Botany*, 66(2): 203-211.

- SEGHERI J., DO F. C., DEVINEAU J. L. et FOURNIER A., 2012.** Phenology of Woody Species Along the Climatic Gradient in West Tropical Africa. *Phenology and Climate Change*, 143p.
- VAN VLIET A. J. H. et SCHWARTZ M. D., 2002.** Phenology and climate: the timing of life cycle events as indicators of climate variability and change. *International Journal of Climatology*. 713-1714.
- VICO G., THOMPSON S. E., MANZONI S., MOLINI A., ALBERTON J. D., ALMEIDA-CORTEZ J. S., FAY P. A., FENG X., GUSWA A. J., LIU H., WILSON T. G. et PORPORATO A., 2014.** Climatic, ecophysiological, and phenological controls on plant ecohydrological strategies in seasonally dry ecosystems. *Ecohydrology*. DOI:10.1002/eco.1533.
- VINYA R., MALHI Y., BROWN N. D., FISHER J. B., BRODRIBB T. et ARAGAO L. E. O. C., 2019.** Seasonal changes in plant-water relations influence patterns of leaf display in Miombo woodlands: evidence of water conservative strategies. *Tree Physiology* 39: 1561-1571.
- WANG Y., GUANDE L., DIN N., CLOTHIER B., DUAN J., LI D., JIA L., XI B. et MA F., 2018.** Leaf Phenology Variation within the Canopy and Its Relationship with the Transpiration of *Populus tomentosa* under Plantation Conditions. *Forests*, 9, 603:1-17.
- WUJESKA-KLAUSE A., CROUS K. Y., GHANNOUM O. et ELLSWORTH D. S., 2019.** Leaf age and eCO<sub>2</sub> both influence photosynthesis by increasing light harvesting in mature *Eucalyptus tereticornis* at EucFACE. *Environmental and Experimental Botany* 167: 3857-3857.
- YAMAZAKI T., KATO K., KUWADA T., NAKAI T., PARK H. et OHTA T., 2006.** Land surface model simulation on CREST forest sites using measured leaf-scale physiological parameters. In: International workshop on H<sub>2</sub>O and CO<sub>2</sub> exchanges in Siberia. Amsterdam, 81–84.
- ZHANG Y. X., EQUIZA M. A., ZHENG Q.S. et TYREE M. T., 2012.** Factors controlling plasticity of leaf morphology in *Robinia pseudoacacia* L. II: The impact of water stress on leaf morphology of seedling grown in a controlled environment chamber. *Annales Forest in Sciences*, 69, 39–47. .
- ZIDA D., TIGABU M., SAWADOGO L. et ODEN P. C., 2008.** Initial seedling morphological characteristics and field performance of two Sudanian savanna species in relation to nursery production period and watering regimes. *Forest Ecology and Management*. 2151-2162.