



ORIGINAL RESEARCH PAPER

Agriculture

ECO-PHYSIOLOGICAL BEHAVIOR OF TAMARIND (*TAMARINDUS INDICA* L.) IN DRY ENVIRONMENT OF WEST AFRICA (CASE STUDY OF SENEGAL).

KEY WORDS: Water deficit, Tamarind, Drought, West Africa

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ABSTRACT

Water deficit is considered by several authors to be the most limiting factor for agricultural production in the subtropics (Kizito et al., 2006; Porcel and Ruiz-Lozano, 2004; Bader et al., 2006; Logan et al., 2010; Rodriguez-Gamir et al., 2011; Conedera et al., 2011). On woody plants, only a few isolated studies (on *Acacia*, and *Combretaceae*) exist in the tropical zone south of the Sahara. Noteworthy are the works done on Sahelian forest species, *Acacia tortilis* (Diouf, 1996), *Combretum glutinosum*, *Guiera senegalensis*; *Piliostigma reticulatum*; *Balanites aegyptica*, *Boscia senegalensis*, *A. senegal* and *Ziziphus mauritiana* (Fournier, 1995; Kizito et al., 2006; Lufafa et al., 2008). Characterization of plant water functioning is a tool for selecting plants and/or varieties for their tolerance to water deficit (Lufafa et al., 2008; Zhu Qian et al., 2011; Logan et al., 2010). It is most often done at young age for ease of use (nursery and early field establishment of seedlings). However, even as adults, woody plants remain dependent on climatic factors such as rainfall (Kisito et al., 2007; Lufafa et al., 2008). It is therefore important to understand the *in situ* water functioning of adult plants to better explain the depressive effects of such complex water stress at a young age. However, the behavior of plants *in situ* is influenced by the climatic conditions and the uniformity (age) of the subjects (tamarind plants) to be followed. The present work was carried out on adult *T. indica* plants *in situ* in Senegal (Niokhoul in the Sahelian zone and Mbassis in the Sudano-Sahelian zone) and aimed mainly to: (1) understand and describe the physiological water management strategies of tamarind under arid conditions; and (2) understand the impact of this water management strategy on phenology and productivity. The study was conducted in Senegal, characterized by a dry and arid climate. It adopted a field approach (Seghier, 2010; Conedera et al., 2010) based on adult stands and climatic data collected at the study sites. Ultimately, the adaptation mechanism of tamarind to water deficit would be that of avoidance, described by various authors (Khalfaoui, 1985; Lacape, 1996; Nwalozie and Annerose, 1996; Rouhi et al., 2007; Roussel, 2008; Maes et al., 2009). Indeed, the plant first proceeds to a decrease in water potential (case of the Mbassis stand) and in case of continuous water deficit, it integrates the reduction of the leaf surface by the progressive fall of the leaves and flowers which can go up to the total defoliation (case of the stand of the Sahelian zone in Niokhoul).

INTRODUCTION

The water deficit is considered by many authors as the most limiting factor for agricultural production in sub-tropical zone (Kizito et al., 2006; Porcel and Ruiz-Lozano, 2004; Bader et al., 2006; Logan et al., 2010; Gamir-Rodriguez et al., 2011; Conedera et al., 2011). In the Sahel, the drought problem is mainly due to the decrease and the spatio-temporal variability of the precipitation (Moiwo et al., 2011). The observed effects on agricultural production are in several orders lower and / or fluctuations in annual crop yields. Moreover, the drought also affects the environment (degradation of landcover crops and gradual disappearance of wood) to the point that food requirements of animals are rarely satisfied (Van Horn, 2002; Stokes et al., 2011; Lambers et al., 2011a; Lambers et al., 2011b). If the effects of drought on annual crops seem to be known, few studies have made the observation on the degradation of wood in terms of their production and operation especially in the Sahel (Lufafa et al., 2008). Various authors (Gao et al., 2009; Moiwo et al., 2011, Stokes et al., 2011) have attributed the phenomenon of landcover crops degradation effects to drought.

Facing to the emergences of food crisis, it is necessary to promote agricultural diversification as an alternative to existing agricultural production systems (monoculture). The integration of multipurpose woody species in the current agricultural production system requires a better knowledge of plant material and its behavior vis-à-vis annual plants. This knowledge could be demonstrated by the characterization of its water relations. Characterization of water management

strategies of plants was discussed on several species such as *Vigna unguiculata*, *Zea mays*, *Arachis hypogaea*, etc.. (Davies et al., 1993; Falalou, 2006; Drame, 2005; Deblonde and Ledent, 2000; Moiwo et al., 2011). On woody plants, only a few isolated studies (on *Acacia*, and *Combretaceae*) exist in the tropical south of the Sahara. It may be noted the work carried out on forest species Sahelian *Acacia tortilis* (Diouf, 1996), *Combretum glutinosum*, *Guiera senegalensis*; *Piliostigma reticulatum*, *Balanites aegyptiaca*, *Boscia senegalensis*, *A. senegal* and *Ziziphus mauritiana* (Fournier, 1995; Kizito et al., 2006; Lufafa et al., 2008). The role of fruit species such as *Adansonia digitata* and *Tamarindus indica* in improving rural incomes has been shown by De Caluwé et al. (2010) and Buchmann et al. (2010). Indeed, the tamarind tree (*Fabaceae*) is a multipurpose plant. The leaves and bark are used in traditional medicine, fruits consumed as acidulate and seeds in animal feed, among others (Morton, 1987; Diallo, 2001; El-Siddig et al., 2006; Bowe, 2007).

Characterization of water managements of plants is a tool for plant breeding and / or varieties for their tolerance to water deficit (Lufafa et al., 2008; Qian Zhu et al., 2011, Logan et al., 2010). It is most often performed at a young age for reasons of convenience (nursery and early installation of plants in the field). But even adults, trees are dependent on climatic factors such as rainfall (Kizito et al., 2007; Lufafa et al., 2008). It is therefore important to understand and to explain *in situ* the depressive and complex effects of water stress on mature plants. However, the behavior of plants *in situ* is influenced by climatic conditions and uniformity (age of plants). This work

was performed on adult trees of *T. indica*, *in situ* in Senegal (Niokhoul in the Sahel and Mbassis and Sudano-Sahelian zone) and focuses on: (1) understand and describe the physiological strategies of water management in arid conditions of the tamarind tree, and (2) understand the impact of this strategy of water management on the phenology and productivity.

METHODOLOGY

The study was conducted in Senegal, characterized by a dry and arid climate. It was on field methodology approach (Seghieri, 2010; Conedera et al., 2010) based on adult populations trees associated with climate data collected.

II.1- Climate data collection

Senegal is composed of three agro-ecological zones (Sahelian, Sudano-Sahelian and Sudanian) (Sarr et al., 2005). Two tamarind population sites were selected respectively in the Sahelian agro-ecological zone (Niokhoul, in the north characterized by tamarind density of one tree per Km²) and in the Sudano-Sahelian zone (Mbassis) located in the Senegalese peanut basin (tamarind density of seven trees per Km²). For each site, an automatic weather station (HOBO weather station, model H21-002) was installed for continuous measurement and daily climatic parameters: the air temperature, atmospheric pressure, humidity relative wind speed, rainfall and global radiation. The Weather stations had been previously calibrated at CERAAS Thies (Senegal).

II.2- Trees sampling

For both sites, 70 trees were randomly selected. For each tree, the circumference at 1.3 m (considered here as the diameter at breast height of 1.3 m, Dbh) was measured using a graduated meter. Stand structure (distribution of individuals in class of Dbh) was performed based on the rule of Yule (Grouzis and Akpo, 2006) which states that:

$$K = 2,5 \sqrt[4]{n}$$

Where n= size sample; K = class number

The interval between classes was obtained as follows:

$$A = \frac{X_{max} - X_{min}}{K}$$

With Xmax and Xmin, respectively the highest and the smallest value of X in the data series, and A = the range of classes.

Three trees were selected per site based on the diameter of the tree height (1.3 m), moreover that these trees must have the same port, similar in phenology and location on the same soil top-sequence. This choice is made based on the assumption that trees with Dbh (+/- 0.5 cm), and similar in phenology could have similar age (Fournier, 1995; Sillett et al., 2010, Qiuhan Zhu et al., 2011).

II.2- Observations and measures frequency

Phenological observations and eco-physiological measurements were made half (15 months) of each month throughout the growing season 2009/2010 (1 year). They concerned the physiological variables that best explain the water-plant mechanism (Lufafa et al., 2008; Seghieri, 2010; Rodriguez-Gamir et al., 2011). These parameters include: leaf water potential, gas exchange and phenology (leafing and fruiting).

a)- Leaf water potential

Measures of the water potential were performed using the pressure chamber (Scholander-type PMS Instruments, Corvallis, model 1001) at an average frequency of 30 days. Measures focused on three individuals phenotypically equivalent (phenology, age, size and port) which belongs to the class Dbh distribution from 1.93 to 2.38 m. At each measurement, the samples (leafy branches) were selected from those which are located at the same height of the crown and this on all four cardinal sides (north, south, east and west)

of each specimen followed by the method proposed by Grouzis and Akpo (2006) and Fournier (1995). These samples should be healthy looking, and phenological similar and with a minimum morphological variability among samples.

Once the leafy branch cut, it was immediately introduced into the sealed chamber of the pressure bomb leaving exceed its cut end for measurement (Figure 6.3). With the aid of a supply of compressed air pressure is applied into the chamber. By observing the cut end of the leafy branch through a magnifying glass, it is determined with the aid of a pressure gauge, the voltage at which the meniscus of the sap appears on the cut surface. This measure corresponds to leaf water potential *in situ* expressed in MPa. Kinetics day that is to say, the potential fluctuation on a leaf water potential, it was measured in January (for the cool dry season), May (for the hot dry season) and August (for the hot and wet season) at two sites (Niokhoul and Mbassis). The stated hypothesis was that the recovery physiological time of the plant will be function of climate season (Seghieri et al., 2010, Logan et al., 2010). Measures began with basal water potential (Ψ_{bs}) (Seghieri et al., 2010, Logan et al., 2010), measured around 4 am (before sunrise). This parameter is considered as an indicator of water stress in the plant (Logan et al., 2010).

This measure of water potential is followed by repeated measurements every 2 h up to 24 h (midnight) in universal time. During the day they will reach a maximum value, called minimum water potential (Ψ_{min}) (maximum in an absolute value), which is the maximum daily water stress resulting from the internal balance between transpiration and water absorption (Aussenac et al., 1984; Kasraoui et al., 2005; Seghieri et al., 2010). Water recovery potential (Ψ_{rec}) was observed at 22 h (Kasraoui et al., 2005, Logan et al., 2010). It represents the water potential of the plant where there is more water loss and when the plant recovers partially or entirely water lost during the day (Aussenac et al., 1984; Seghieri et al., 2010). This is also an indication of both the capacity and the speed recovery of the plant to restore its water balance with the soil and the atmosphere.

Drought recuperation index (Gt) is defined from the recuperation level (Maes et al., 2009) by the formula:

$$Gt = \frac{\Psi_{rec} - \Psi_{min}}{\Psi_{bs} - \Psi_{min}}$$

With: Ψ_{rec} = Recovery water potential; Ψ_{bs} = Basal water potential; Ψ_{min} = Minimum water potential.

The transpiration intensity of the plant, called delta (δ) is an index which include transpiration rate and hydraulic conductivity (Maes et al., 2009) of the soil-plant system (Fournier, 1995). It may be determined by the following formula.

$$\Delta (\delta) = \Psi_{bs} - \Psi_{min} Res;$$

It is used to determine indirectly the intensity of the plant's transpiratory flow.

b)- Gas exchange

Gas exchanges provide information on the water status of the plant. They bring together a cohort of variables calculated or measured after a direct reading of a number of parameters (net photosynthesis, transpiration, stomatal conductance and / or photosynthetically active radiation (PAR)). These variables are for the most part fundamental parameters of the eco-physiological functioning of plants (Annerose, 1990; Falalou, 2006; Rouhi et al., 2007; Maes et al., 2009). The measuring device used here was the LCi CO₂ analyzer (ADC BioScientific Ltd, model EN1 10DB). It operates on the basis of an open circuit system, the measuring chamber is permanently supplied with air taken 4 m from the ground using a rod of the IRGA model LCi type. Five (5) healthy and fully developed leaves were sampled from each cardinal side (north, east, west and south) of the tree. The daily kinetics

(every 2 hours) were followed each month and the results were represented by seasonal averages (SSF: cold dry season, SSC: hot dry season and SHC: wet and hot season). The instantaneous water use efficiency (EUEi) expressed in $\mu\text{molm}^{-2}\text{s}^{-1}$ was calculated by the Jones (1993) formula cited by Roussel (2008), which states that:

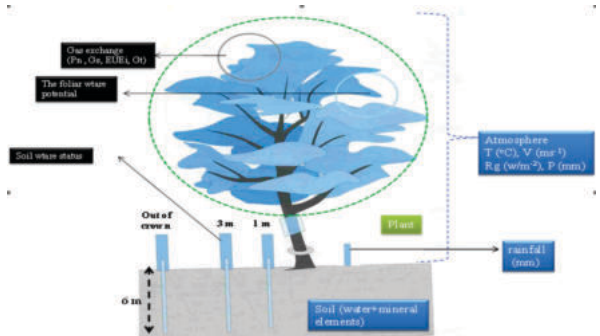
$$EUEi = A/E$$

Where A = net photosynthesis, E = transpiration or evaporation, Y = yield and B = biomass.

Indeed, EUEi ($\mu\text{molm}^{-2}\text{s}^{-1}$) represents the ratio of the CO₂ flux entering the leaf to the water vapor flux leaving the leaf during photosynthesis (Rouhi et al., 2007; Roussel, 2008).

c)- Water status of the soil

The evaluation of soil water potential allows an assessment of the soil water status. The neutron method was chosen for determining soil moisture because of its speed of implementation, reliability, and the possibility of in situ and continuous moisture monitoring over time (Roussel, 2008; Logan et al., 2010). Twelve PVC probe access tubes were installed around each tree (3 trees/site) selected for soil volume moisture measurements. Measurement was made on the four cardinal sides (north, south, east, and west) with three replicates for the same side at 1 m and 3 m from the trunk and one outside the crown canopy (Moiwo et al., 2011), at a depth of 6 m.



Eco-physiological monitoring device.

Pn (net photosynthesis); Gs (stomatal conductance); EUEi (instantaneous water use efficiency); Gt (tension gain); T (temperature); Rg (global radiation); P (rainfall); V (Wind speed).

Measurements were taken on the 0-100 cm horizon every 10 cm and then every 20 cm for the rest of the profile i.e. up to 6 m (Moiwo et al., 2011). Measurements were made monthly during the 2009/2010 crop year. The use of the neutron probe type Solo 25, model T7 must be preceded by a calibration. This calibration is necessary because there are other hydrogen atoms in the soil (organic matter, clays) than those of water molecules (Granier and Colin, 1990). In addition, the soil may contain chemical elements capable of absorbing neutrons (chlorine, boron).

We used the gravimetric method (Moiwo et al., 2011), which consists of taking gravimetric soil samples with an Edelman auger, model 022308, and in situ neutron counts during the installation of the probe access tubes. These gravimetric and neutron measurements were carried out on all the tubes during their installation, every 10 cm from the surface to 100 cm and then every 20 cm, from 100 cm to 600 cm. These pairs of gravimetric samples/probe pulses were also obtained for other measurement dates (April 23, 2009 and August 27, 2009) corresponding to very different degrees of soil moistness (dry and wet spots). After each set of samples, the determination of the weight moisture (Hp) (defined as the mass value of water contained in a soil sample) (Moiwo et al., 2011) of the soil samples obtained from the in situ collections is performed. The fresh weight of the samples was obtained by weighing using an electronic precision balance ($\pm 0.01\text{g}$)

brand Mettler, model AIP419W. Then, they were dried in an oven (Jouan type, model EU170) at 105°C until a constant weight was obtained. The weight humidity (Hp) was obtained by the formula:

$$Hp = \frac{PF - PS}{PS - Ta} \times 100$$

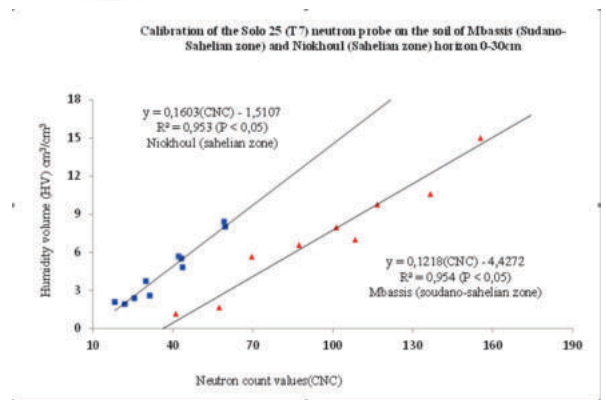
where FP = fresh weight of the soil sample, DW = dry weight of the soil sample, and Ta = empty weight of the sample container.

Soil bulk density was measured in situ by a density meter (gamma type model 3430-M). Moisture content (Hv) is calculated from the weight moisture (Hp) and bulk density (Da), using the formula (Granier and Colin, 1990; Moiwo et al., 2011):

$$Hv = Hp \times Da$$

The moisture content is expressed in cm³ of water per cm³ of dry soil (cm³.cm⁻³). Because of the electronic drift that can cause variations in the neutron count values, these count values must be corrected. This correction was made by establishing a ratio of the in situ count (NC) to the reference count (NCe) performed in a water drum (called water point), and which was brought back to the count of a probe that gives 1000 pulses per second in water. The corrected neutron count (CNC) is expressed as:

$$CNC = \frac{CN}{CNe} \times 1000$$



Calibration of the Solo 25 neutron probe (T7) on the soils of Mbassis (Sudano-Sahelian zone) and Niokhoul (Sahelian zone) in Senegal, horizon 0-30 cm Calibration of the Solo 25 neutron probe (T7) on the soils of Mbassis (Sudano-Sahelian zone) and Niokhoul (Sahelian zone) in Senegal, horizon 30-600 cm The corrected probe measurements (CNC) were thus converted to volume moisture following the linear relationship equation of the form (Moiwo et al., 2011): where a is the slope of the equation, and b is the constant value characteristic of the soil type.

The measurements were made with a Troxler neutron probe, type Solo 25, model T7, in average time option with a counting time of 30 seconds. The water monitoring was done at a monthly measurement time step and the monthly averages of the seasonal monitoring (SSF, SSC and SHC) were calculated. The time series of data obtained was used to determine the water profiles (Moiwo et al., 2011).

d)- Soil water balance

The water balance of a site expresses the evolution, between any two dates, of the water mass present in the soil-plant-atmosphere system. This water is divided between the water stored in the soil and the plant on the one hand and the flows in and out of these reserves on the other hand (Kizito et al., 2006; Moiwo et al., 2011). The water balance appears to be a determining factor in understanding the water behavior of plants in the natural environment. For a given period, this balance can be written as follows:

$$\Delta S = P + I - E - T - D - R + \Omega$$

Where we have:

ΔS : the variation of the water stock in the soil layer under consideration of the other parameters of the equation; P: rainfall received between these two dates; I: irrigation; E: soil evaporation; T: plants transpiration; D: Drainage below the mined soil area to the water table; R: water loss through surface runoff; and Ω : capillary rise.

In this relationship, only E, D, and R are difficult to measure. For the case of woody plant water functioning, E, D and R are negligible (Lufafa et al., 2008; Seghieri, 2010; Moiwo et al., 2011; Carter and Nippert, 2012). We freed ourselves from D by prospecting a 0-200 cm soil slice beyond which there is little or no variation in moisture. Such a situation makes us assume zero drainage. At the same time, this profile is part of the water absorption zone of the tamarind tree, the limit of which would be at 400 cm (El-Siddig et al., 2006). In the absence of an observed water table near the sites, we considered capillary rise to be negligible (Aussenac et al., 1984; Kisito et al., 2006). We did not apply water by irrigation. Thus, the "I" component of the water balance equation should not be considered. Note that the actual evapotranspiration (water loss through evapotranspiration) is obtained by the following formula:

$$ETR = Tr + Ip$$

where Tr represents transpiration and Ip represents Net Interception.

The fairly strong relationship (64.3%) obtained between rainfall recorded outside the canopy (by the weather station) and under the canopy (by rain gauges installed under the trees), leads us to neglect the amount of water intercepted. For a given soil water status and a given evaporative demand from the atmosphere, the relative shares of evaporation and transpiration in REE depend on the proportion of radiative energy intercepted by the foliage compared to that reaching the ground, and thus on the leaf area index (LAI) (Le Maire et al., 2011). Thus, following the method of Dancette (1983) adopted by several authors (Kisito et al., 2007; Moiwo et al., 2011) and taking into account the above, calculating the periodic water balance is reduced to estimating the difference between the rainfall and the variation of the water stock during the given period:

- The water stock variation ($\Delta S(0-600\text{cm})$) is obtained by the difference of the volume moisture at 600 cm and the horizon (0-10cm);
- The periodic stock change (ΔSPe) is defined as the difference between the stock change at date 1 ($\Delta S(0-600\text{cm})_{\text{date1}}$) and the stock change at date 2 ($\Delta S(0-600\text{cm})_{\text{date2}}$);
- The daily water balance (daily consumption) is obtained by the ratio between the periodic water balance and the number of days between the measurement dates (T).

$$\Delta s = \Delta s_{\text{per}} / T$$

where represents the water balance, Per. represents the periodic water balance and T the number of days.

e)- Data processing and analysis

The phenological data obtained at a frequency of monthly observations are presented in percentage and in graphical form. The percentage of trees with leaves (foliage) and trees with mature fruits is calculated from the following formula:

$$f = \frac{n}{N} \times 100$$

where f = percentage of trees; n = number of trees with leaves or ripe fruit; and N = total number of trees observed.

Statistical analysis of the data was performed using Statistix (8.1) software. All data were tested for normality and homogeneity of variances using Levene's test before analysis of variance. Comparison of means was done using the 5% Newman-Keul test. Spierman correlation coefficients were calculated between all variables.

III. RESULTS

III. 1. Climate factors

The cumulative rainfall obtained at the two sites during the 2009/2010 season (April 2009-March 2010) was 335.3 mm and 602.2 mm, respectively for Niokhoul and Mbassis (Tables 6.1a and 6.1b). The climatic data obtained are summarized in Table 6.1 below (a & b) for climatic parameters such as rainfall (P in mm), maximum temperature (Tmax in °C), minimum temperature (Tmin in °C), wind speed (V in ms-1) and global radiation (Rg in Wm-2).

Table 1: Seasonal average values of microclimatic parameters (rainfall, temperature, wind speed and global radiation) of Niokhoul (a) and Mbassis sites (2009/2010 crop year)

Niokhoul

Climatic season	P (mm)	Tmax (°C)	Tmin (°C)	V (ms-1)	Rg (Wm ⁻²)
CFS	0	36,3(±0,6)	19,64(±0,8)	1,4	2126,8
HDS	55,1	32,6(±0,7)	18,30(±0,7)	2,6	2828,0
WCH	280,2	37,8(±0,9)	21,08(±1,0)	1,0	2380,2
Sum	335,3				

Mbassis

Climatic season	P (mm)	Tmax (°C)	Tmin (°C)	V (ms-1)	Rg (Wm ⁻²)
CFS	0	38,5(±0,8)	15,6(±0,6)	0,9	1662,8
HDS	23,5	40,5(±0,6)	20,7(±0,7)	1,8	2699,1
WCH	581,7	33,9(±0,9)	22,0(±0,8)	0,9	2216,5
Sum	602,2				

It can be deduced from the values presented in Table 1 that temperatures were close to the averages obtained from the literature as presented in Table 6.1 (a and b) (Sarr et al., 2005; Grouzis and Akpo, 2006). However, a large deviation is observed during the cold dry season with amplitudes between maxima and minima of 22.87°C at Mbassis and 16.71°C at Niokhoul. Two types of wind generally occur in this region: the harmattan, coming from the north and northeast during the dry season (CFS and HDS: November to March) and the monsoon blowing from the southwest during the rainy season (WCH: June to September) (Fournier, 1995). The highest monthly mean velocities grouped by climatic season were observed during the HDS and were of the order of 6.7 ms-1 and 1.88 ms-1 at Niokhoul and Mbassis, respectively.

III.2- Leaf water potential

The maintenance of a good water status (a state of equilibrium between plant consumption and atmospheric water demand, called leaf water potential) by the plant most often reflects a form of tolerance of the water deficit, whereas the decrease in water potential is all the more accentuated the more severe the intensity of the water constraint experienced (Maes et al., 2009; Seghieri, 2010). The results of the measurements of the variation of the kinetics of the leaf water potential according to the climatic seasons are presented in Figure 6.8. The latter figure shows that during the three climatic seasons (cold dry season, hot dry season and hot wet season), the increase in water stress intensity (in the day) is accompanied by a decrease in leaf water potential (increase in absolute value). It can also be observed that the base potential (between 4 and 6 h) drops by half whatever the season of the year, depending on whether one goes from the Mbassis site (-0.75 MPa) located in the Sudano-Sahelian zone to the Niokhoul site (-1.45 MPa) located in the Sahelian zone. On the other hand, there is little variation in the recovery period, which begins at 10 p.m. (in universal time), regardless of the site. Within the same site, the cold dry season shows the lowest leaf water potentials (-3.15 to -3.8 MPa).

Indeed, at the end of the rains, the response of the tamarind tree was a loss of turgor at the leaf level (Boyer, 1982; Sorrells et al., 2000). This decrease could be attributed to the high

temperature range (16.71°C to 22.87°C) observed during this climatic season. Maintaining a low water potential is related to the ability to extract available water from the soil and the ability to limit water loss through transpiration (Turner et al., 2001; Sorrells et al., 2000; Rouhi et al., 2007). It characterizes a dehydration avoidance strategy (Turner et al., 2001). During the hot dry season and during the rainy season, a similar level of leaf water potential is noted. This could be explained by the adaptive character developed by tamarind (ability to fully defoliate during the hot dry season).

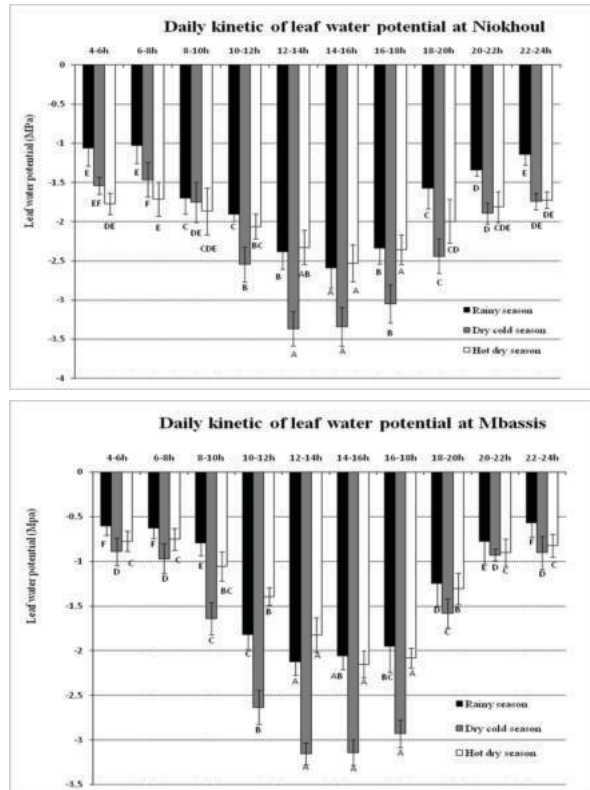


Figure 1: Evolution of daily kinetics of leaf water potential of tamarind in two contrasting agro-ecological zones of Senegal. Vertical bars represent standard deviations.

III.2- Seasonal evolution of gas exchange (net photosynthesis and instantaneous water use efficiency)

Net photosynthesis and instantaneous water use efficiency were monitored in Mbassiss and Niokhoul during the cropping season.

Net photosynthesis

The averages of seasonal net photosynthesis observed at Niokhoul (in the Sahelian zone), show significant differences ($P < 0.05$), contrary to the averages obtained at Mbassiss which are similar from one season to another. This situation is explained by the fact that the strategy of reducing plant transpiration by closing the stomata from the onset of water stress has led to a reduction in the photosynthetic activity of stands in the Sahelian zone during so-called dry periods

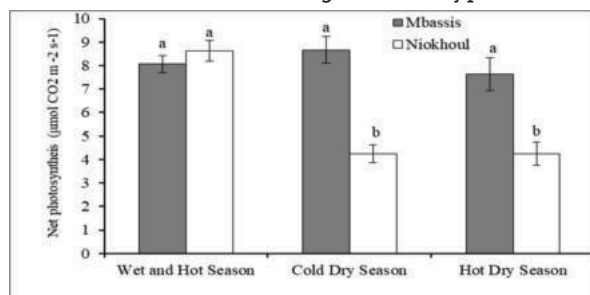


Figure 2: Comparative seasonal evolution of the

photosynthetic activity of two tamarind stands in two contrasting agro-ecological zones in Senegal. The vertical bars represent standard deviations.

Water use efficiency

Figure 3 shows a seasonal evolution of the instantaneous water use efficiency (WUE) for the stands of the two agro-ecological zones studied, according to the different climatic periods of the year. During the period of unrestricted water availability (rainy season), tamarind stands in the Sahel zone have a higher WUEi ($P < 0.05$) than trees in the Sudano-Sahelian zone.

The tendency to limit plant transpiration (more pronounced in Sahelian zone plants) during the dry period could be explained by the low level of water use in the dry period. On the other hand, the fact that during the rainy period (wet and hot season), the difference observed between the trees of Mbassiss and Niokhoul in terms of their WUEi (Figure 3) would be the effect of the water stress avoidance character of the stands in this agro-ecological zone of the Sahel.

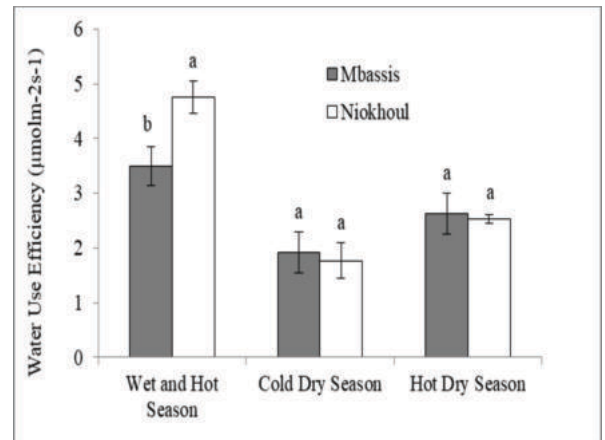


Figure 3: Comparative seasonal evolution of water use efficiency of two tamarind stands in two contrasting agro-ecological zones of Senegal. The vertical bars represent the standard deviations

Soil water potential

The water profiles (Figures 4a and 4b) show that at the beginning of the rainy season (CHS) only the surface horizons (50 cm) are moistened.

This would be the effect of the low and irregular rainfall during the experimental period. The water profiles obtained under the tamarind trees (solid line in figures 6.12 and 6.13) and the control (dashed line in the same figures) are similar in terms of surface water availability (horizon 0-50 cm). Furthermore, regardless of the site, on the 50-200 cm horizon there was a difference (not significant) between the water profiles obtained under the tamarind trees and the controls. This could suggest that the water supply horizon of the tamarind trees is located between 50 cm and 200 cm in depth.

This water consumption of the plants (characterised by the difference between the profile curve under the tamarind and the control) nevertheless remains variable from one site to another and from one climatic season to another.

A progressive decrease in the 'wetting belly' (Aussenac et al., 1984; Moiwu et al., 2011) is observed from the CHS to the SSC (Figures 4a and 4b). The wetting belly is defined as the deviation of the water profile curve that indicates the level of wetting of the different soil horizons. In fact, from the first rains onwards, the wetted profiles increase and this successive displacement of the wetted horizons in relation to the starting line constitutes the wetting belly (Moiwu et al., 2011; Mendham et al., 2011)

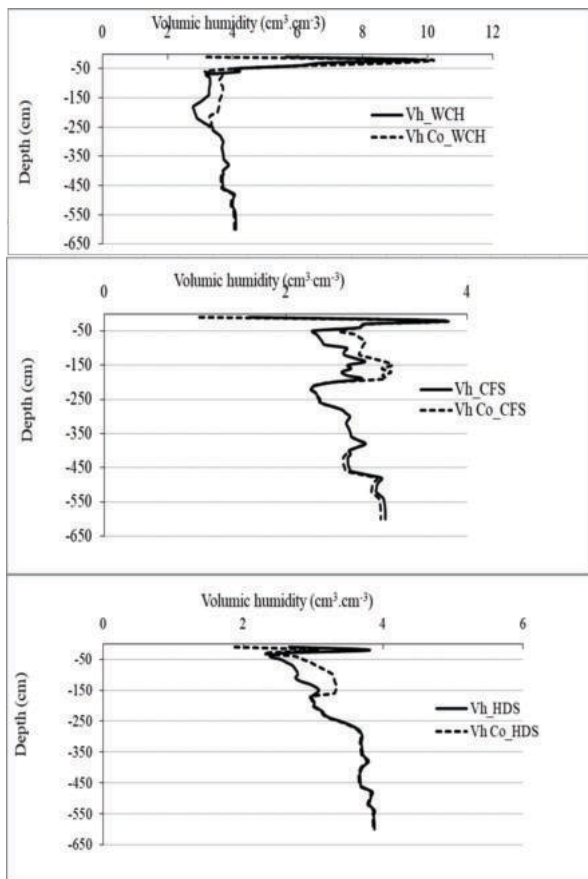


Figure 4a: Soil moisture profiles under tamarind trees studied during the WCH, CFS and HDS seasons of the agricultural season at the Niokhoul site in the Sahel zone of Senegal

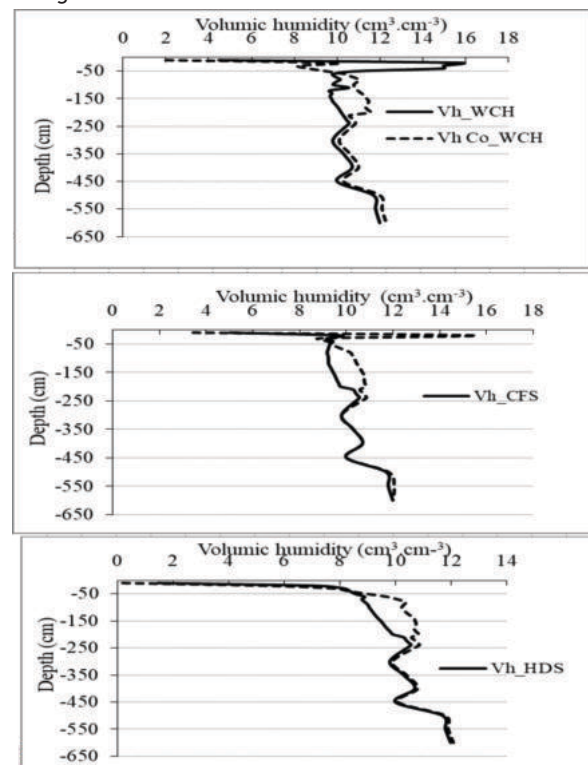


Figure 4b: Soil moisture profiles under tamarind trees studied during the WCH, CFS and HDS seasons of the agricultural season at the Mbassiss site in the Sudano-Sahelian zone of Senegal

However, the water content (volumetric humidity) of the Mbassiss soils is higher in WCH (10cm³.cm⁻³) than in Niokhoul (4 cm³.cm⁻³). In addition to the higher rainfall at Mbassiss (602.2 mm), this difference in water retention at the Mbassiss site would be the effect of the soil characteristics. Indeed, in Niokhoul we have a sandy soil (90.5%) and a clay rate of 3.4%, contrary to Mbassiss where we have a sand rate of 82.3% and 7.8% of clay (Bourou et al., 2010).

Water Balance

The results of the water balance calculation are summarised in Table 6.2 below. It can be seen that the daily water consumption of the tamarind tree is almost zero in the dry period. This result is observed at both sites. On the other hand, this consumption is proportional to the variation of the soil water stock and tends to increase when the water factor becomes non-limiting. It can also be seen that water consumption is closely related to the amount of available water at all sites.

Table 6.2: Water balance and daily consumption of tamarind in two agro-ecological zones of Senegal

(a) Niokhoul

Date	12 June	25 July	19 Aug	23 Oct.	13 Feb.	23 Mar
Rain (mm)	0	82,8	91,9	160,6	0	0
Times (Days)		43	25	65	113	38
Water stock variation over 0-600 cm (mm)	195,4	197,7	210,8	175,4	173,5	186,2
Total water stock variation (mm)		2,2	13,1	-35,4	-1,8	10,8
Periodic water balance (mm)		80,57	78,79	196,00	1,83	-10,81
Daily water consumption (mm)		1,9a	3,2b	3,0b	0,02b	0,3b

(b) Mbassiss

Date	1st may	24 July.	17 Aug	21 Oct.	10 Feb.	13 Mar
Rain (mm)	0	82,8	202,4	321	0	0
Times (Days)		84	24	65	112	31
Water stock variation over 0-600 cm (mm)	583,9	596,9	633,5	625,3	536,3	516,3
Total water stock variation (mm)		13,0	36,6	-8,2	-89,0	-20,0
Periodic water balance (mm)		69,7	165,8	329,2	88,9	20,0
Daily water consumption (mm)		0,8a	6,9a	5,1a	0,8a	0,6a

DISCUSSION

Under drought conditions, the decrease in plant water potential induces a significant loss of turgidity in the leaves (Sorrells et al., 2000; Maes et al., 2004). The maintenance of a low water potential in plants is linked to their ability to continue to extract water from the soil and to the capacity to limit water losses by transpiration (Turner et al., 2001). This is the case observed in this study of tamarind stands. This situation characterises a dehydration avoidance strategy (Logan et al., 2011). The most sensitive species or varieties then show more negative water potential values than drought resistant plants (case of Niokhoul stand) (Maes et al., 2004).

The basic and minimum potential vary between minimum values in the hot humid season (-0.6 to 1 MPa) and higher values in the cold dry season (0.8 to 1.5 MPa). The increase in water potential starts gradually with the arrival of the first rains. The observed trends confirm those obtained on other tropical woody species such as *Acacia raddiana* (Sop et al., 2011), *Boscia senegalensis*, *Balanites aegyptiaca*, *Ziziphus*

mauritanica, *A. senegal*, *A. tortilis* and *Combretum glutinosum* (Jacques et al., 2010; Sop et al., 2011; Craven et al., 2011). This is because of the marked contrasts between the levels of environmental and seasonal water stress on the one hand and the variation in water potential and recovery on the other (Sop et al., 2011; Craven et al., 2011).

The ability to regain water balance (recovery) in plants that have been subjected to water stress has been highlighted by various authors (Eyog-Matig and Dreyer, 1991; Fournier, 1995; Maes et al., 2004; Logan et al., 2011; Craven et al., 2011; Carter and Nippert, 2012). It would be linked to a good protoplasmic tolerance (interest in maintaining cellular enzymatic activity for drought resistance), which would make it possible to minimise the effects of drought through the osmotic adjustment phenomenon. In this study, we observed an increase (over time) in the water potential of the plant linked to the increase in thermal amplitude and relative humidity. This reflects the levels of water availability in the rhizosphere and corroborates the results of Craven et al. (2011) on six tropical woody species (*Terminalia amazonia*, *Inga punctata*, *Colubrina glandulosa*, *Pseudosamanea guachapele* and *mangium*, *Acacia raddiana*, *Acacia mangium*). The evolution of water potential (baseline and minimum) shows a parallel progression to that of soil water availability. This has been highlighted by the results of several other authors (Kisito et al., 2007; Jacques et al., 2010; Sop et al., 2011). These results also confirm those of some authors (Fournier, 1995; Seguiéri, 2010) who indicate that the seasonal evolution of the water potential could be used as a criterion to assess the evolution of the soil water stock.

The δ (delta) of the factor decreases as the dry season progresses. According to the literature, this decrease translates into a reduction in leaf transpiration through stomatal closure or defoliation of plants under stress, accompanied by a loss of hydraulic conductance (Kisito et al., 2007; Roussel, 2008). In the case of tamarind, we observed a good recovery capacity of the plant in the hot wet season in Mbassis (> 80%) and Niokhoul (70%). However, this recovery decreases with the onset of drought (cold dry season), especially in the Sahelian zone (remaining at 55%) and remains stable in the Sudano-Sahelian zone (82%). These values in the Sudano-Sahelian zone remain similar to those observed on *Acacia mangium* in the Sahelian zone (Craven et al., 2011) and on *Guiera senegalensis* and *Piliostigma reticulatum* in the Sudano-Sahelian zone of Senegal (Kisito et al., 2007). This suggests that *A. mangium* may have a better tolerance capacity to water deficit than tamarind.

Concerning the gas exchange parameters measured here, in particular net photosynthesis, it was observed that the availability of water in the rainy season (SHC) allows a similar photosynthetic activity in the two sites. The significant difference ($P < 0.05$) observed during the dry season (cold or hot) would be due to the fact that in the Niokhoul site (in the Sahelian zone), the adaptive response of the tamarind stand to the effects of the water deficit was leaf drop, thus reducing the photosynthetically active surface. In Mbassis (Sudano-Sahelian zone), on the other hand, the plant first lowers its water potential, which would be sufficient to stabilise the water balance and thus to keep the leaves. This adaptation strategy, which consists of lowering its water potential, would be the main form of reaction of the tamarind to a water deficit. These results corroborate those obtained on cowpea (*Vigna unguiculata*) varieties by Falalou (2006) and on groundnut (*Arachis hypogaea*) by Annerose (1990) and Craven (2011) on tropical woody species.

Stomatal closure to control transpiration is first involved in the response to water stress (on a daily scale). Then, hydraulic architecture is affected (monthly scale), followed by leaf area index (annual scale) (Rambal, 1993; Rouhi et al., 2007). Our results confirm those obtained by Magnani et al. (2002) who

show that the different responses of plants to extreme drought are in the direction of conservation of the water use balance. Ultimately, the adaptation mechanism of the tamarind to water deficit would be that of avoidance, described by various authors (Khalifaoui, 1985; Lacape, 1996; Nwalozie and Annerose, 1996; Rouhi et al., 2007; Roussel, 2008; Maes et al., 2009). Indeed, the plant first decreases its water potential (case of the Mbassis stand) and in case of continuous water deficit, it integrates the reduction of the leaf surface by the progressive fall of leaves and flowers which can go as far as total defoliation (case of the stand in the Sahelian zone at Niokhoul).

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