



Characterization of the variability of the daily course of leaf water potential in the dominant shrub species within Sahelian fallows in south-west Niger

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Abstract

Around Niamey, in Niger, the shrub *Guiera senegalensis* dominates all of the fallows in almost totally monospecific stands. The species has a strong resprouting ability enabling it to survive cutting when clearing land for crops, whereas all other species succumb to cutting. However, in this dry environment (560 mm of annual rainfall from June through September), this remnant-increaser species has to cope with variations of available water in space and time. The daily course of its water status is an indicator of the variation of the intensity of water flux between the soil, vegetation and atmosphere, and it is often estimated with Soil Vegetation Atmosphere Transfer (SVAT) models.

We assessed the water status of *G. senegalensis* through its daily cycle leaf water potential (Ψ), using six populations representative of the local diversity by measuring three shrubs per population on two excised leaves per shrub for each measurement. We made our measurements over two vegetative cycles (from July 1994 to December 1995), fortnightly during the rainy season, and once a month during the dry season, until the sample shrubs lost their leaves in their deciduous cycle.

We used linear models to characterize the daily Ψ cycle of the shrubs, and of the populations during each season. For each population, three sources of variation were considered: the shrub number, the date and the hour in day. Date and hour in day effects are presented as trend surface models defined by the degrees of polynomials and the status of shrub effects. The status of shrub effects characterizes the variability in accounting for environmental conditions.

The group of plant populations that explain the least variability in every model as well as the least total variance among the shrubs and between seasons were in locations with the best water supply. Two other groups were defined according to the median and the highest explained variability of Ψ , respectively. For all stations, the most temporal variability is explained by models accounting for the interaction between shrubs and the temporal variation, with the least variability for models that do not account for the shrub effect at all. Models accounting only for the additive effect of shrubs explain intermediate values. The models used herein indicate the large range of variability in *G. senegalensis* water status, both for inter- and intra-populations. This high physiological plasticity must contribute to the strong species-dominance stability in its current distribution area.

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Keywords: Dry savanna; *Guiera senegalensis*; Linear model; Physiological heterogeneity; Water status

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1. Introduction

The savannas in Niger around Niamey are now mainly composed of a patchwork of fallows varying in age which are growing on sandy soils, classified as an arenosol using the FAO classification system (Gaze et al., 1998). Fallows are covered by an annual herbaceous stratum, and a species woody stratum comprised of Combretaceae, *Guiera senegalensis* J.L. Gmel. (Hutchinson and Dalziel, 1954–1972), which is an extremely dominant multi-stemmed and basal-resprouting shrub. In this area, *G. senegalensis* has benefited for several decades by the elimination of other native woody species due to the increasing intensity of repeated clearing for millet production (Delabre, 1998; Gaze et al., 1998). While the native previously-in-place suite of Combretaceae (dominated by *Combretum micranthum* G. Don, Hutchinson and Dalziel, 1954–1972) has disappeared, *G. senegalensis*, with its high survival rates following cutting combined with its high resprouting ability, has filled the gaps. In the study area, the spatial variability of soil water availability is due as much to soil aridification after over-exploitation of the pre-existing vegetation as to the topographic variation. *G. senegalensis* clearly has the capacity to deal with the spatial and temporal variations in levels of available water across its area distribution. It is of fundamental importance for the regional vegetation management to provide a better understanding of the species ecophysiology. We contribute to this priority by analyzing the hour and spatial variabilities of the water status in six local populations differing in fallow age, past intensity of exploitation, and topographic location. As a Sudano–Sahelian species, the study shrub is commonly dominant in sandy Sahelian fallow lands from Senegal east to Sudan (Aubreville, 1950, p. 90). It appears to be a typical case of a “human-mediated vegetation switch” *sensu* Barstow and McG King (1995), which is probably amplified by recent droughts (1973, 1981, and 1984). Consequently our study is likely to be relevant to a broader area than only that of the study site.

During HAPEX-Sahel (Hydrological and Atmosphere Pilot Experiment in the Sahel, 1990–1992), several models of the flux of water, energy, and matter in several fallows were supplied with inputs from very localized and hour limited data collections in a one-degree square (100 km × 100 km) around Niamey

(Goutorbe et al., 1997). These types of results are difficult to extrapolate up to the vegetation canopy as a whole, except through the use of more or less complex up-scaling models (Hanan and Prince, 1997). Another purpose of this analysis of large data sets at a local scale (six situations under the same climate conditions) is to provide regional investigators with better understanding of field heterogeneity. Our work assesses the actual magnitude of the water status variability that the modellers need to take into account when scaling up the vegetation physiological process. Leaf water potential following the soil water storage variation combined with the atmospheric demand (Ritchie and Hinkley, 1975) is an indicator of the water flux intensity between the vegetation and the atmosphere. However, in Soil Vegetation Atmosphere Transfer (SVAT), it is generally calculated through the presumed equality between the root extraction and the transpiration (Braud et al., 1995; Lo Seen et al., 1997). We propose to model the direct measurements of an estimator of the flux intensity frequently enough to outline its daily course over two growing seasons.

In the Sahel, a dataset on the fine dynamics of vegetation water status remains rare (Ullman, 1989; Berger et al., 1996; Seghieri and Galle, 1999), and should considerably contribute to understanding this type of cover functioning.

The study took place for fallows within the HAPEX one-degree square. We characterized the daily course of the water status in *G. senegalensis* by monitoring the leaf water potential (Ψ) in six populations at the HAPEX-Sahel Central super-site during two successive rainy seasons and the dry season between.

To quantify Ψ variability, we used linear models. They provided an overview of the inter- and intrastation variability of the Ψ daily course accounting for shrub, date, and hour effects. Furthermore, linear trend surface models also provide a visual “descriptive” analysis based on the shape of trend surfaces that gives a lot of original 3-D information.

2. Material and methods

2.1. The study species and the study sites

G. senegalensis can grow up to 3 m in height. Being semi-evergreen, leaf shedding occurs as a drought-

Table 1
Characteristics of the stations studied

Stations	Topographic situation	Fallow age (after Delabre, 1998)	Crop/fallow duration (%) (after Delabre, 1998)
1	Sandy field at middle-slope	3	42
2	Bottom-slope dune bulges	2	55
3	Hydrographic network	2	55
4	Very degraded at middle-slope	23	≈0
5	Degraded at middle-slope	19	12
6	Hydrographic network	1	≈100

avoiding strategy in the dry season in proportion to and during a period that varies with shrub location (Breman and Kessler, 1995, pp. 140–146; Seghier and Simier, 2002). We monitored the daily course of the leaf water potential (Ψ) in six fallow stands of *G. senegalensis* considered as representative of the fallow diversity in the square degree around Niamey (Delabre, 1998). The fallows were selected around the Banizoumbou village in Southwest Niger (13°32'N and 2°42'E), 75 km north-east of Niamey. In all of them, *G. senegalensis* was strongly dominant in the woody cover, with an annual understorey and a few other scattered woody shrubs (mainly *Combretum micranthum*). Mean annual rainfall over the period 1905–1989 was 560 mm (Le Barbé and Lebel, 1997). A single rainy season extends from June to September. Long-term average potential evaporation exceeds rainfall in all months except August when it is similar in magnitude (Peugeot et al., 1997). Mean annual ETP is about 2300 mm (Gaze et al., 1998). The soil is composed of aeolian sandy deposits from ergs, which are 15,000–50,000 years old (Delabre, 1998). It overlies a weathered lateritic layer, below which lies a sequence of Continental Terminal Miocene deposits of siltstones and mudstones (Gaze et al., 1998). Soils are about 88% sand, 3% silt and 9% clay.

The six fallows studied differ in their disturbance histories. We assessed each site in terms of time since last cutting (the fallow age) and the ratio of crop/fallow duration displayed in Delabre (1998). This ratio defined as “cumulated length of crop periods/cumulated length of fallow periods” indicates the intensity of exploitation pressure the shrubs suffered. Fallows also differ in their topographic situation. Their characteristics are displayed in Table 1. *G. senegalensis* stands in clumps of stems that could be several square meters in extent, according to their resprouting intensity after cutting.

2.2. The data collection

A rectangular enclosure of around 10,000 m² was set up during 1993 in each site. Data were collected within these enclosures (called “stations” below) from July 1994 to December 1995, which included two successive rainy seasons and the intervening complete dry season. There were three rainfall recorders: one close to the isolated station 1, another close to stations 2 and 3, and the third close to stations 4, 5 and 6. Rain recorders were provided and monitored by the EPSAT¹ Program (which validates in the field rainfall assessment by remote sensing through a dense network of rain recorders).

In each station, the basal circumference of each clump was measured. Three shrubs per station were sampled at random among the dominant classes of circumference size, and among individuals in an apparent good state (taking account of parasite attack and plant diseases, etc.). A hydraulic press (HP, Objectif K model, France) was used to measure the leaf water potential, because it was much stronger, more convenient and less dangerous than classic devices (using highly compressed air such as a pressure chamber) to implement in the field (stations were as far as 5 km apart). Calibration was not required for comparative analysis. In addition, rather good correlations were found between the HP and pressure chamber (Jones and Carabaly, 1980; Hicks et al., 1986; Sojka et al., 1990). Data were collected fortnightly during the rainy seasons and once a month during the dry season. Ψ was measured at each time interval for one small piece of each leaf, on two different leaves per sampled clump. Measurements were made every hour from predawn until the daily maximum of Ψ was reached

¹ Etablissement des Pluies par SATellite—Niger (ORSTOM project).

for the three sampled shrubs in a station. Cuts were taken from mature leaves in well-lighted conditions at eye level (about 6 ft off the ground).

2.3. The data processing

During the study period, leaf water potential (Ψ) was measured on a set of 12,540 leaves (6270 two leaf samples) taken from the 18 sampled shrubs in the six fallows. For data analysis, we used the natural logarithm of Ψ .

2.3.1. Reference model

We sought to clearly show the magnitude of the possible variability of the daily course of Ψ in the study species in Sahelian conditions at both the population scale (intra-station differences) and between populations (inter-stations comparison). We first considered those 6270 samples in an ANOVA with “sample effect.” This reference model takes into account the two-leaf effect. When this reference model is applied to each of the six stations, the residual mean squares are considered as indicators of the variance of the distribution of the Ψ logarithm among the “leaf population” of a given shrub at a given hour for a given day.

2.3.2. Linear trend surface models

For each station, we considered nine general linear models, accounting for shrub, date, and hour effects. Those models correspond to surface response “descriptive” analysis (Draper and Smith, 1981) which is sometimes used for spatial analysis with polynomials of two spatial coordinates. Here, the coordinates are days and hours in each day (hereafter noted j and k). If we consider one given shrub, the expectation of the variable of interest is

$$Y_{jkl} = a + \sum_{d=1}^D b_d j^d + \sum_{h=1}^H c_h k^h + \sum_{d,h=1,1}^{D',H'} \gamma_{dh} j^d k^h + e_{jkl}, \tag{1}$$

where Y_{jkl} is $\log(\Psi)$ of leaf l of the shrub at day j and hour k . The j and k values are obtained by standardization of values of the day number (day “1” is January 1, 1994) and of the hours between 0 and 24, e_{jkl} are random variables (residuals) which are assumed to be independent, and identically distributed with nil

expectation, a is a constant. D is the maximal degree of the polynomial for the day effect, H is the maximal degree of the polynomial for the hour effect, D' and H' are the maximal degrees of polynomials for the day and hour in crossed terms accounting for interactions between day and hour effects.

For a given shrub, such a model is entirely identified with degrees D, H, D' and H' .

Effect of the three shrubs for a station may be accounted for by considering three hypotheses.

The first hypothesis assumes that shrub behaviors may be different, and thus we consider three different trend surfaces. This corresponds to a hypothesis of an interaction between the shrub and the trend surface. This model is given by Eq. (1) with the addition of indice i for Y and each parameter (a_i, b_{di}, c_{hi} and γ_{dhi}). This indicates that those values depend on the shrub.

$$Y_{ijkl} = a_i + \sum_{d=1}^D b_{di} j^d + \sum_{h=1}^H c_{hi} k^h + \sum_{d,h=1,1}^{D',H'} \gamma_{dhi} j^d k^h + e_{ijkl}. \tag{2}$$

Using symbol (*) for an interaction, such a model may be simply written as Shrub* $P(D, H, D', H')$.

The second hypothesis considers the additive effects of shrubs only, so differences between the response surfaces of two shrubs are constant. From equation 1, those differences are accounted for by different values of parameters a_i in Eq. (2):

$$Y_{ijkl} = a_i + \sum_{d=1}^D b_d j^d + \sum_{h=1}^H c_h k^h + \sum_{d,h=1,1}^{D',H'} \gamma_{dh} j^d k^h + e_{ijkl}. \tag{3}$$

Using the symbol (+) for an additive effect, such models are written in the following way: Shrub + $P(D, H, D', H')$.

The third hypothesis supposes no shrub effect. The three surfaces are equal. This means equal values of a_1, a_2 and a_3 from the “additive” models (3):

$$Y_{ijkl} = a + \sum_{d=1}^D b_d j^d + \sum_{h=1}^H c_h k^h + \sum_{d,h=1,1}^{D',H'} \gamma_{dh} j^d k^h + e_{ijkl}. \tag{4}$$

They can be simply written as $P(D, H, D', H')$.

Each model is fitted using the usual least squares method which provides the values of the parameters

(a_i , b_{di} , c_{hi} and γ_{dhi}) for which the sum of squared differences between observed and fitted values (i.e. the residual sum of squares) is a minimum. The quality of each fit and comparisons between them can be discussed through standard statistical linear modeling theory. It can also be discussed through examination of the distribution of the residuals.

The nine models are classified into three groups, according to the status of shrub effect. Models 2–4 [Shrub* $P(16, 5, 9, 4)$, Shrub* $P(9, 4, 9, 4)$, Shrub* $P(16, 5, 0, 0)$] account for the interaction between shrubs and the temporal variation. Models 5–7 [Shrub + $P(16, 5, 9, 4)$, Shrub + $P(9, 4, 9, 4)$, Shrub + $P(16, 5, 0, 0)$] consider only an additive effect of the shrub, which means that the temporal patterns are the same for each shrub with a constant difference between them. The last three models 8–10, [$P(16, 5, 9, 4)$, $P(9, 4, 9, 4)$, $P(16, 5, 0, 0)$] assume no shrub effect at all. For each group of models, the first one (2, 5, 8) considers the additive effects of day and hour with degrees 16 and 5, and interactions limited to degrees 9 and 4. The second models (3, 6, 9) consider the additive effect and the interactions for which both of the polynomials are limited to degrees 9 and 4. The third models (4, 7, 10) consider only the additive effects of the day and hour (degrees 16 and 5).

We considered polynomials with rather high degrees (up to 16 for model 2). Such high degrees are needed to represent the observed variability. For example, for each of the six stations, the usual F tests for the comparison of models 2 and 3, the later having “lower” degrees (up to 9, Table 3), led to the rejection of model 3 with an “ α ” risk level lower than 0.001.

2.3.3. Shape of the trend surfaces

The estimated values of the parameters are of no great interest, since we are looking for the shape of response surfaces which may be presented in a figure. As for non-parametric models, where the usual linear function of covariates is replaced with an unspecified function (Hastie and Tibshirani, 1990), may be presented in a graphic. With the given values of the parameters, we may compute the expected values of the variable of interest for each shrub and for given values of days and hours in a grid. This operation was illustrated from the fit of model 2 for stations 1, 2 and 6 considering day–shrub combinations for which at least six observations were available. For each of

these day–shrub combinations, we estimated the expectation of Y in half-hour time steps between 08:00 and 17:00 LST.

2.3.4. Checking models

The quality of the models must be checked and discussed through an examination of the distribution of the residual differences between the observed and the fitted values (Draper and Smith, 1981; Mac Cullagh and Nelder, 1989). In Fig. 2, residuals are plotted versus fitted values (points) together with the results (lines) of a spline regression (Hastie and Tibshirani, 1990) for each shrub of those residuals on fitted values. Two main aspects are evident (i) if the model is unbiased, those regressions are nil functions and (ii) if the variance of the residuals does not depend on the expectation of the variable of interest, the range of residuals doesn’t depend on the fitted values. We also present histograms of the residuals (Fig. 2).

In theory, the closer the residual variance of a model to the variance of the reference model, the more it accounts for shrub, date and hour effects. Such models only exhibit regular events. For example, at each date, the maximum value of Ψ occurs around the “solar midday,” i.e. when the sun is at its zenith. This type of model doesn’t exhibit outcomes from casual local changes occurring in environmental conditions, as does the reference model. For instance, clouds crossing the sun temporarily decrease the luminosity and reduce the stomatal opening, which then cause Ψ to decrease during a short time period. These sorts of casual events are not what we want to describe, so even a model with a higher residual variance than that of the reference model would not necessarily be rejected.

3. Results

Total seasonal rainfall was higher and the duration of the rainy period was longer in 1994 than in 1995 for each of the three rain gauge locations. Differences in rainfall between the locations were smaller during the dryer year (1995, Table 2).

Results of the fit of the nine general linear models for each of the six stations are summarized in Table 3. For each station and each model, the total variance, the percentage of total variance accounted for, and the residual mean square are given in this table. Fig. 1

Table 2
Total of annual rainfall (mm) recorded at each of the rain gauge

Stations	Years	
	1994	1995
1	648	536
2 and 3	594	537
4, 5 and 6	706	507

illustrates the surface responses for each shrub from model 2 [Shrub* $P(16, 5, 9, 4)$] for stations 1, 2 and 6. Considering model 2 [Shrub* $P(16, 5, 9, 4)$] and each shrub of a given station, we present in the left part of Fig. 2 graphs of residuals (points) and spline regression of residuals on fitted values (lines) versus fitted values. Histograms of those residuals are presented in the right part of the figure.

Analysis of these results is developed in the following section.

4. Discussion

4.1. The reference model

The residual mean square of the reference model is of the same order whatever the station (between 0.0041 and 0.0067, Table 3). Consequently, the relative part of the temporal variability (intra- and inter-day variability deduced from the total variability effect) accounted for by the model is logically reduced for stations of relatively lower total variability (stations 3 and 6, Table 3). For every station, the reference model explains 95–99% of the total variance. These very high values indicate a high similarity between the status of the two sampled leaves taken off the same shrub at the same hour. The other models explain less of the total variance (75–97%, Table 3). Whatever the station, F tests lead to the conclusion that all those models are significantly “less good” than the reference model. Despite this, they represent very well the $\log(\Psi)$ variations for the stations. This result, which indicates a relatively small sampled leaf effect, supports the hypothesis of either significant local space-time variations and/or of non-randomly selected pairs of leaf samples (cut at about the same height and light exposure).

4.2. Comparison between stations

For the reference model, the comparison of the percentage of the total variability explained (Table 1) between the stations leads to a linkage of their relative values to some station characteristics:

1. Among all the stations, and whatever the model, the least explained variability is for station 3, followed very closely by station 6. Thus, a group can be made with *stations 3 and 6* which is defined as having the least part of the variability explained by every model, but also having the least total variance for the station (0.13–0.14, Table 3). The minimum ranges are observed for stations of this first group (0.023–0.032 for station 3 and 0.021–0.030 for station 6). Being located in a catchment (Table 1), these two stations suffered less from intensive drought during the dry season than the other stations. The water status of the shrubs was maintained at relatively lower levels of Ψ values than for the other stations over the entire year. Stations 3 and 6 also recorded the longest period of 100% leafing rate during the same study period (Seghieri and Simier, 2002). This confirms that these stations provided the best water supply to shrubs, and it also explains the low Ψ variations (Fig. 1, station 6). The stations located within the area at the base of the hillslope incorporated vegetation which was supplied with more water than the other stations throughout the year and buffered the variation in shrub water status. The intensity and the age of past exploitations were not significant (Table 1).
2. For *stations 2 and 5*, most of the models indicate a part of explained variability just above the values of the previous group. The two stations can be grouped as having intermediate temporal variability explained, as well as the intermediate total variance (around 0.2, Table 3). The two stations of this group 2 also have intermediate ranges of variation (0.019–0.032 for station 2 and 0.017–0.034 for station 5).
3. Most of the models explain a greater part of the total variability for those stations where the data have a high dynamic range: *stations 1 and 4* is where there are large variations in Ψ values between seasons (low in dry and high in wet) and between shrubs.

Table 3
Part of the total variance accounted for by the model (%), residual mean square (between brackets), for each model and each station

Models	Number of parameters	Stations					
		1	2	3	4	5	6
		Observations number					
		1012	2038	2532	1414	1792	2226
		Total variance					
		0.375	0.200	0.130	0.405	0.220	0.139
1: reference	n/2	98.5% (0.0056)	97.9% (0.0041)	95.5% (0.0058)	99.0% (0.0042)	97.4% (0.0058)	95.1% (0.0067)
2: Shrub* P(16, 5, 9, 4)	174	95.2% (0.018)	90.3% (0.019)	82.0% (0.023)	96.6% (0.014)	92.1% (0.017)	84.8% (0.021)
3: Shrub* P(9, 4, 9, 4)	150	91.8% (0.031)	88.7% (0.023)	78.7% (0.028)	94.0% (0.024)	88.4% (0.025)	82.3% (0.025)
5: Shrub* P(16, 5, 0, 0)	66	92.2% (0.029)	86.8% (0.027)	78.5% (0.028)	95.3% (0.018)	87.1% (0.028)	79.3% (0.029)
5: Shrub + P(16, 5, 9, 4)	60	89.4% (0.040)	87.5% (0.025)	79.1% (0.027)	89.9% (0.041)	89.2% (0.023)	83.5% (0.023)
6: Shrub + P(9, 4, 9, 4)	52	87.9% (0.045)	86.1% (0.028)	76.4% (0.031)	88.2% (0.048)	85.9% (0.031)	81.2% (0.026)
7: Shrub + P(16, 5, 0, 0)	24	87.0% (0.049)	84.2% (0.032)	75.9% (0.031)	88.7% (0.046)	84.7% (0.034)	78.2% (0.030)
8: P(16, 5, 9, 4)	58	88.6% (0.043)	87.1% (0.026)	78.8% (0.027)	84.5% (0.063)	89.0% (0.024)	83.4% (0.023)
9: P(9, 4, 9, 4)	50	87.1% (0.048)	85.6% (0.029)	76.1% (0.031)	82.7% (0.070)	85.7% (0.032)	81.1% (0.026)
10: P(16, 5, 0, 0)	22	86.2% (0.052)	83.8% (0.032)	75.7% (0.032)	83.5% (0.067)	84.5% (0.034)	78.1% (0.030)

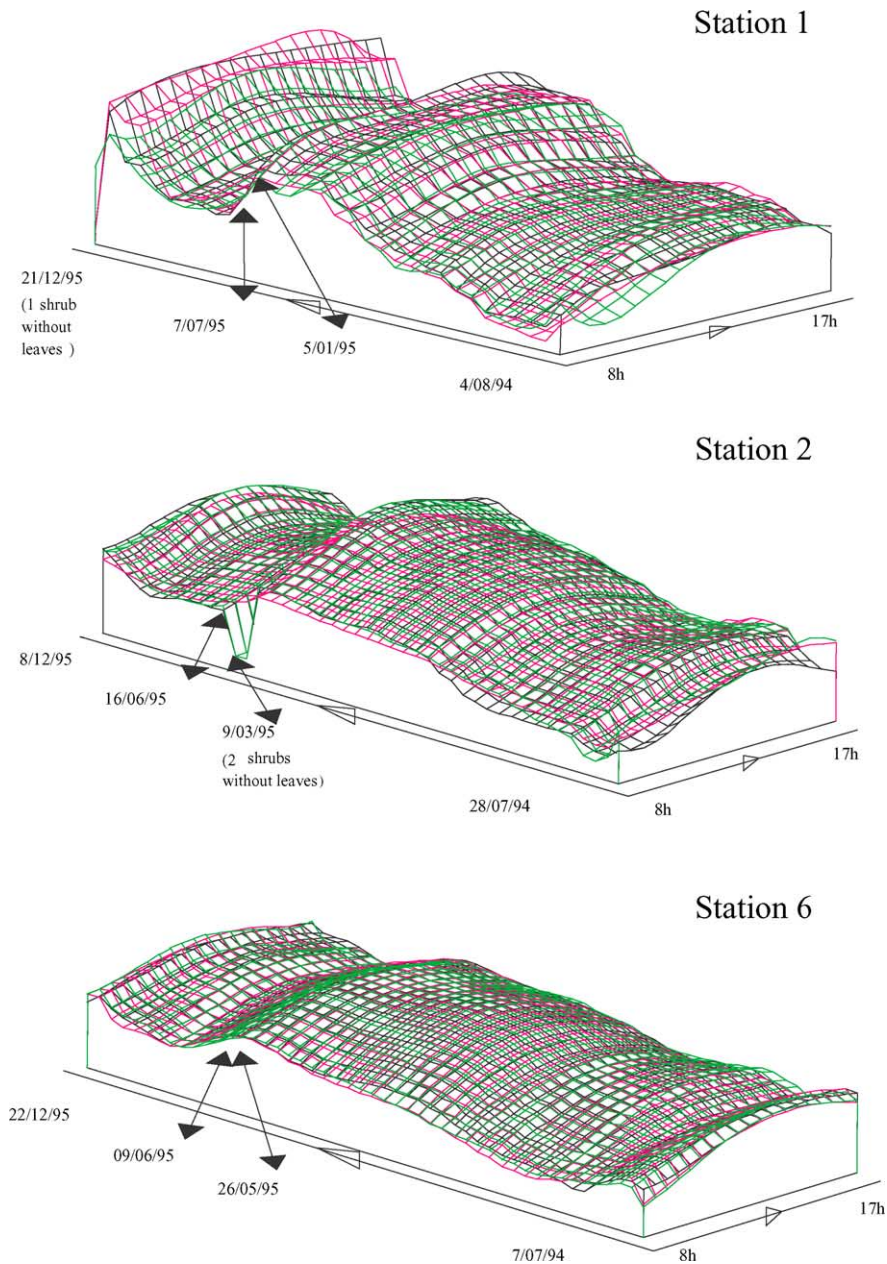
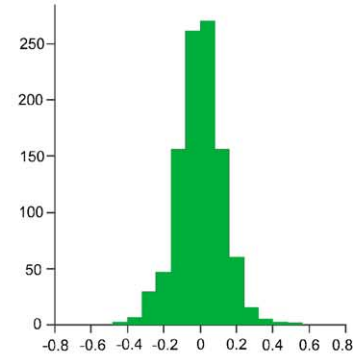
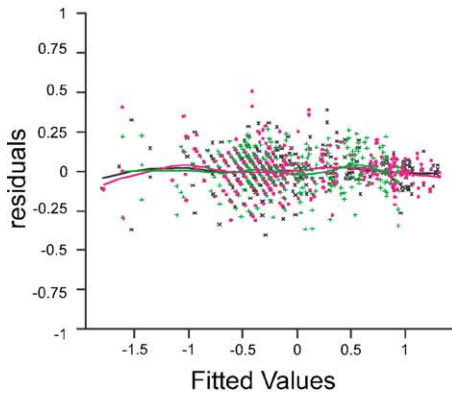


Fig. 1. Surface responses for each shrub from model 2 [Shrub* $P(16, 5, 9, 4)$] in stations 1, 2 and 6. The scales of the three graphs are the same.

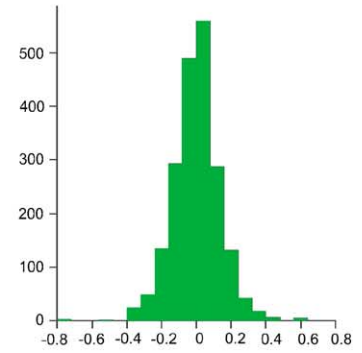
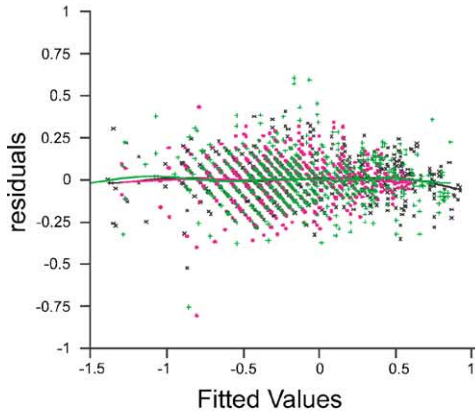
The characteristics displayed for each group in terms of Ψ variability remain true for model 2, (see Table 3). As an illustration, the trend surfaces presented in Fig. 1 shows the difference of shrub effects between the groups of stations. The three “trend sur-

face responses” are quite distinct for station 1, and almost indistinguishable for the two others (Fig. 1). The spline regression lines of those residuals on the fitted values (Fig. 2) show that the model may be considered as unbiased. For stations 1 and 2, the range of

Station 1



Station 2



Station 6

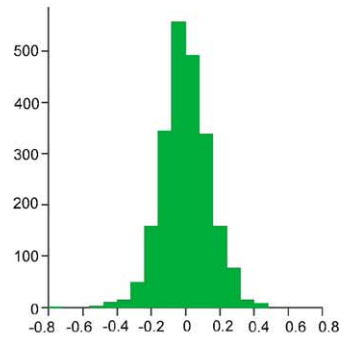
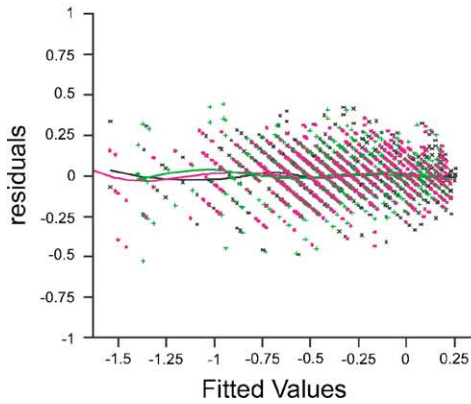


Fig. 2. Left: graphs of residuals (points) and spline regressions of residuals on fitted values (lines) vs. fitted values from model 2 [Shrub*P(16, 5, 9, 4)] for each shrub in stations 1, 2 and 6. Right: histograms of those residuals.

the residuals is slightly lower if the fitted values are greater than 0.25. For station 6, for which fitted values do not exceed 0.25, the range of the residuals is stable. This indicates a larger shrinkage effect of the log transformation for the high values. Histograms of the residual indicate near normal distributions.

Again, for the group consisting of stations 2 and 3, the intensity and the time since the last crop do not appear to be significant factors of physiological seasonal variation and intra-station heterogeneity (Table 1). However, this does not mean that the second group of stations (2 and 5), with intermediate variability of Ψ , supply shrubs with higher soil moisture than the third group of stations (1 and 4) with the highest Ψ variation. Indeed, exceptions appear in the relative rank of the accounted-for variability for each model among these four stations (Table 3). In addition, phenology recorded at the population scale by Seghieri and Simier (2002) was much more disturbed for stations 2 and 5 than for stations 1 and 4, which supports the hypothesis of adverse conditions. This confirms, first that the intensity of past exploitation per se is not a good indicator of the vegetation disturbance when considered alone, and second that the relationships between *G. senegalensis* phenology in dry and disturbed conditions and its water status are more complex than what be shown by a simple correlation.

To go further in the analysis, we compared the linear models to each other.

4.3. Comparison between models

We recall that, as for the reference model, when a given model explains more variability for one station than another (Table 3), it does not mean that the model fits the data better in absolute terms. As residual mean squares are of the same order of magnitude (0.008–0.044, Table 3), a greater part of explained variation only means that there is more temporal variability to be explained.

Linear models are made according to three groups of shrub effects. For all stations, the range of the residual mean square increases from the first (no. 2–4) to the third (no. 8–10) group of models (0.014–0.029 to 0.026–0.067, respectively). But the magnitude of this increase depends on the station group. It is much more important for the third group (stations

1 and 4) than for the other two. For station 1, we observed an important effect of interactions involving shrubs, with a low additive effect (residual mean squares are analogous for models groups 2 and 3). For station 4, the additive and interaction effects are important.

4.4. Conclusion

For sites where the water seems to be non-limiting, models of the dynamics of vegetation water status can be based on just a few field observations and could be simplified regarding the shrub effect influence. However, models or any other estimation method must take into account the inter-shrub variability at the station scale. We clearly showed the magnitude of the possible variability at the population scale (intra-station differences), and the even more significant values at the meta-population scale (inter-stations comparison) of the leaf water potential daily course in the study species in Sahelian conditions. In terms of plasticity, the large range of water status to which *G. senegalensis* can survive should largely contribute to the species sustainability in its dominance area even after disturbances have stopped (Poupon, 1979; Devineau, 1999; Seghieri and Simier, 2002).

This makes a natural regeneration of the other original native species doubtful. After a serious disturbance, there are a number of ecological niches available for colonization, and plants with the most plastic environmental requirements get a window of opportunity that gives them a decisive competitive advantage. *G. senegalensis* behaves in this way and our results have showed its physiological advantages under the overall shifting hydrologic performance of the landscape. The value of the water reserve globally alters with degradation (Casenave and Valentin, 1992; Seghieri et al., 1994, 1995; Walker and Langridge, 1997), so that most of the ecological niches of the original species could disappear. This is also probably why, when following human transformation of ecosystems, plants from more xeric habitats, since they are pre-adapted to a large range of conditions, tend to invade more mesic ones rather than the reverse (Blondel and Aronson, 1999, pp. 38–39, 121, Seghieri and Simier, 2002).

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