

Impact of late-season drought on water relations in a sparse canopy of millet (*Pennisetum glaucum* (L.) R. Br.)

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Abstract

Although millet is known to be adapted to very dry conditions, little is known about its canopy water relations. The control of water loss and dehydration tolerance were studied during the grain filling for two cultivars presumed resistant and sensitive to moisture deficit at this stage. Two experiments were conducted in the dry hot season at Niamey, using crops based on the traditional system of hill sowing at low density: a preliminary trial with low leaf area (index of 0.7 at flowering); and a main trial with higher leaf area (index of 1.8) induced by tillering where parameters were recorded at a short time scale.

The preliminary trial with small initial leaf area revealed a less apparent leaf water deficit according to leaf water potential and stomatal regulation but the main results were in agreement with those of the main trial. The cultivars were similar in their water relations. During drought, water losses declined quickly due essentially to a large decrease in the green leaf area through senescence. The potential effect of stomatal regulation was reduced by a natural decline of 50% after earing. The water deficit was relatively small and osmotic adjustment was absent in the upper leaves of eared shoots, which stayed green. These results reveal for millet, that rapid control of leaf area by senescence is the predominant mechanism at this stage, inducing long-term avoidance of dehydration of the upper leaves on eared shoots. The quick adjustment of canopy conductance to the reduction of soil water availability is an hypothesis advanced.

Keywords: Drought resistance; *Pennisetum glaucum*; Canopy conductance; Leaf senescence; Osmotic adjustment

1. Introduction

In Sahelian countries, the improvement of millet yields in the best growing areas represents one way

of easing food dependency and the imbalance of agro-pastoral systems (Ryan and Van Oppen, 1984; Van Keulen and Veeneklaas, 1993). But the intensification of agriculture, in raising farmer initial investments and water requirements, increases risks related to uncertain precipitation. These uncertainties are high in the Sahelian zone (300–600 mm annual rainfall), particularly at the end of the growing season during the crucial grain-filling phase (Sivakumar, 1991). At that stage of development, possibili-

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ties of increasing soil water availability are limited as the root system essentially completes its development at flowering (Chopart, 1983). Millet does escape the effects of drought to some extent through early flowering, (Bidinger et al., 1987a,b; Mahalakshmi et al., 1987; Fussel et al., 1991) and asynchronous development of tillers (Siband, 1983, Mahalakshmi and Bidinger, 1986).

Even though the adaptation of millet to the driest areas is recognized (Kumar, 1989), its responses in terms of canopy water relations in the face of drought at the end of the growing season have not been clearly defined. The published literature is contradictory on the importance and nature of mechanisms controlling water losses and tolerance of leaf tissue to dehydration (Winkel and Do, 1992). Henson et al. (1983a), Henson et al. (1983b), Henson and Mahalakshmi (1985) and Squire et al. (1984) considered that stomatal regulation plays a predominant role while Azam-Ali (1983) and Wallace et al. (1993) noted that such regulation is secondary to changes in green leaf area. Bidinger et al. (1982) suggested that osmotic adjustment is not important in millet while others underlined its existence and the possibilities for discrimination of genotypes that it offers (Blum and Sullivan, 1986; Bala Subramanian and Maheshwari, 1989; Conover and Sovonick-Dunford, 1989).

In a more general approach, Jansen and Gosseye (1986) studied the possibilities of simulating millet response to a water deficit with the SUCROS model and concluded that a special effort needs to be made to clarify relationships between the level of water stress and physiological behaviour, particularly during flowering and grain-filling phases. The construction of a simplified, mechanistic, model of crop response, simulating the final yield reduction, is an underlying long-term objective. It represents a means of analyzing directly the relative importance of factors identified as affecting yield stability (Ludlow and Muchow, 1988; McCree and Fernandez, 1989).

The aim of the present work is to characterize, in an end-of-season drought situation, the responses of canopies of a low-density millet (as in the farmer fields of the Sahel) with regards to: the control of water losses by stomatal conductance and total leaf area; and the increase of dehydration tolerance of leaf tissues by osmotic adjustment. The study focused on the 15 days after mid-flowering, which

correspond to the crucial phase of grain initiation and growth, preceding the maturation phase (Siband, 1981; Bieler, 1992). Two cultivars presumed resistant and sensitive were used with the purpose of maximizing the variability of potential responses. This paper is based on two experiments: a preliminary trial with low leaf area (index of 0.7 at flowering) where parameters were recorded at a large time scale; and a main experiment with higher leaf area (index of 1.8) induced by tillering where parameters were recorded at a short time scale and in a more complete way. The preliminary observations provided complementary information on the persistence of responses in relation to a lower leaf area.

2. Materials and methods

2.1. Site, season and cultivars

The experiments were conducted in the field at the Institut des Radio-Isotopes of the University of Niamey (13°29'N, 2°10'E, 221 m asl), in Niger, during the hot dry season (February to May). During the grain-filling period (last 30 days of the crop cycle), air temperature varied diurnally between 25 and 41°C, mean daily incident radiation was 21 MJ m⁻², and the daily mean vapour pressure deficit (VPD) was 3.8 kPa.

Two pearl millet cultivars, non-photoperiodic and with short cycle (85–90 d) adapted to the Sahelian zone were used: HKP, a local cultivar released by the Institut National de la Recherche Agronomique of Niger; and ICMVIS-86330 (thereafter called IC30), a breeding line from the ICRISAT Sahelian Center. According to the Drought Response Index (DRI) of Bidinger et al. (1987a,b) IC30 has been described as resistant and HKP as susceptible to a drought during grain filling (L.K. Fussel, pers. comm., 1989). This ranking was observed at ICRISAT Sahelian Center (Niger) during a hot dry season (1988) with high plant density (10 plants m⁻²). A large genetic distance between the two cultivars was found using enzymatic diversity analysis (Tostain, ORSTOM internal report, 1990).

2.2. Crop management

Plants were grown on a deep sandy soil used for a long time by a farmer for millet cropping without

fertilizers. Sand and clay percentages, pH, organic matter and nitrogen were respectively 96%, 1.7%, 6.0%, 0.14%, 0.09% in the upper 0.5 m. Water storage at field capacity, estimated in situ from neutron probe data was approximately 175 mm in the upper 2.00 m, and the water storage at wilting point, estimated by pF 4.2 measurements, was 50 mm. Further characterization of the soil is given by Do (1994). The levels of fertilization were: 45 kg of N and 9.7 kg P and 19 kg K ha⁻¹ in the first trial in 1990; 10 t of manure ha⁻¹, 65 kg of N and 19 kg P and 37 kg K ha⁻¹ in the second trial in 1992.

The sowings took place 23 February in the first trial and 14 February in the second, at the traditional spacing of one hill/m² and thinned to three plants 15 days after emergence (DAE). In relation with soil fertility, the number of eared shoots at flowering were respectively of 3 (± 0.5) in the first trial in 1990 ('low-tillering trial': thereafter called LT90) and 9.5 (± 1) in the second trial in 1992 ('high-tillering trial': thereafter called HT92). Maturity was reached at 92 DAE in the LT90 trial and 84 DAE in the HT92 trial.

Treatments consisted of a well-watered control, and a dry treatment in which irrigation was withheld for 15 days beginning at 50% flowering in the LT90 trial (62 to 77 DAE) and until maturity in the HT92 trial (54 to 84 DAE). Flowering percentage was determined for the hill as a whole, as the ratio of eared shoots with stigmas to the total number of eared shoots.

Daily amount of water use was calculated using crop coefficients and 10-y means of potential ET (Doorenbos and Pruitt, 1975). In 1990, water was supplied by drippers (rate of 4 l h⁻¹) spaced 0.5 m apart on the sowing line. Irrigated soil volume corresponded approximately to a channel of 0.5 m width and 1.4 m depth. In 1992, water was supplied every 2 days by diffuser (rate of 15 l h⁻¹ m⁻²) with total cover of the soil (one diffuser/m²).

2.3. Experimental design and measurements

The experimental designs included 6 blocks in the LT90 trial and 10 blocks in the HT92 trial. Each block included two irrigation treatments as main plots with the two cultivars as sub-plots. Each sub-plot consisted of four rows, 1 m apart, 11 m long in

1990 and 18 m long in 1992. Discarding the outside rows as border, the center of each sub-plot was used for leaf area and physiological samplings.

Leaf area index was determined in each sub-plot every 15 days in the LT90 trial and twice a week in the HT92 trial. Green and senescent leaf blades were separated from harvested plants for oven drying and dry matter weighing. Data of green leaf dry matter (DM, g m⁻²) were converted to green leaf area (GLA, m² m⁻²) using the following relationship established in a previous study (Do, 1994):

$$GLA = 0.024 \text{ DM}^{0.89} \quad R^2 = 0.96 \quad n = 90$$

In addition, the number of green leaves on the main shoot was recorded every 2 to 3 days during the drought period in the LT90 trial.

Soil water content was monitored with a neutron probe (Solo 25, Nardeux S.A., Les Ulis, France) every 15 days in the LT90 trial and every 2 or 3 days in the HT92 trial. Access tubes were installed in 4 blocks for each cultivar in both irrigation treatments. Measurements collected at 0.10-m intervals up to 2.20 m depth were field-calibrated using the gravimetric method. The potential root extraction zone was considered up to 2.00 m depth as water was extracted up to 1.70 m and roots were collected from soil cores taken at depths of between 1.80 and 2.00 m (Daouda Ousmane, unpublished data). Relative soil water availability (SWA) was calculated up to 2.00 m depth as the ratio of actual water storage above wilting point to the potential soil water availability between wilting point and field capacity (125 mm). The method of estimating the evapotranspiration treated water drainage below -2.00 m as negligible as long as water content at this depth was low and did not vary. In the absence of runoff, evapotranspiration (ET) between time t and $t + dt$ was taken as: $ET = I - dS$, where dS is the variation of total water supply obtained by the integration of water profiles between 0 and 2.00 m and I is accumulated irrigation.

Physiological measurements were made on the second, third and fourth green leaves below the panicle of eared-shoots. Samplings included eight shoots of each cultivar in both treatments. Stomatal conductance (g_s , sum of adaxial and abaxial conductances) was measured on the third leaf at 09:00, 11:00 and 13:00 (solar time) every 2 or 3 days with

Mk2 automatic porometers (Delta-T Device, Cambridge, UK) in the LT90 trial and with LCA2 porometers (Analytical Development Corp., Hoddeson, Herts., UK) in the HT92 trial. Daily canopy conductances (g_c) was calculated as the product of the green leaf area and g_s integrated between 07:00 and 18:00 assuming zero values at those hours.

The same shoots were sampled for leaf water potential (Ψ_1) on the second leaf using a J14 leaf press (Decagon Device, Pullman, WA, USA). In a previous study, calibration of this press with a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) provided a good linear relation for leaf water potentials lower than -0.5 MPa ($R^2 = 0.96$), but with an underestimation of 0.15 MPa (Do, unpublished data).

Osmotic potentials at zero and full turgor were obtained using the pressure–volume (P – V) technique (Ladiges, 1975) on a subsample of four leaves of rank 2 taken at 14:00. After rehydration over night, samples were cut from the leaves and enclosed in the press. Paired measurements of water potential and fresh weight of the leaf samples were made by 0.2 MPa steps down to -2.0 MPa (Lougnet and Laffray, 1988). Saturated weight was determined using linear regression for leaf water potentials higher than -1.0 MPa. Relative water content of the sample (RWC) then was plotted versus $1/\Psi_1$. VOYONS software (Thiéry, 1991) was used to fit the relation to the sum of power and linear functions and to calculate osmotic potentials at zero and full turgor (Ψ_π^0 , Ψ_π^{100}), relative water content at zero turgor (RWC_0), and mean modulus of cell wall elasticity (ϵ) calculated as $[\Delta \text{turgor potential} / \Delta \text{RWC}] \times 100$, over the RWC range from full hydration to zero turgor (Henson et al., 1983a).

3. Results

3.1. Water deficit and evapotranspiration

The leaf water potential (Ψ_1) measured at midday is presented versus the soil water availability in Fig. 1, from the stopping of water supply up to maturity. With the control plants, where soil water availability fluctuated slowly between 70% and 100%, Ψ_1 was similar for both trials and was not influenced by age

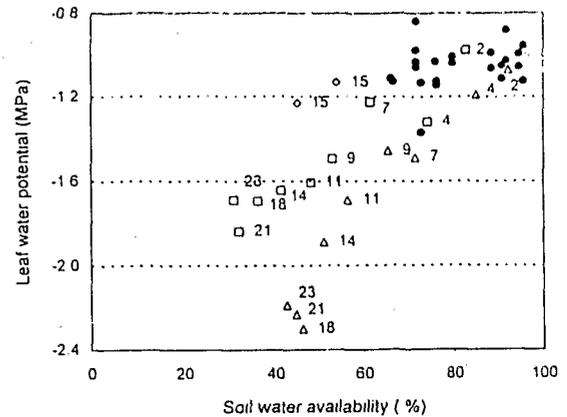


Fig. 1. Midday leaf water potential versus soil water availability in control and stressed plants. Closed circles represent control plants in high-tillering and low-tillering trials (●: for both IC30 and HKP). Open symbols represent stressed plants in the low-tillering (○: IC30 and HKP) and high-tillering trials (□: IC30, △: HKP). Labels indicate the number of days without irrigation on stressed plots.

or by the cultivar: it varied between -0.9 and -1.2 MPa.

In the dry treatments, a decrease of Ψ_1 did not appear in the trial with low tillering and it developed slowly in the trial with high tillering (Fig. 1). In this last trial, Ψ_1 began to decrease significantly ($P < 0.05$) after 7 to 9 days without irrigation, when it had reached -1.5 MPa. Afterwards, the decrease was much more marked with the cultivar HKP where Ψ_1 reached -2.3 MPa after 19 days of drought as opposed to -1.7 MPa with IC30. In the LT90 trial, Ψ_1 had not decreased during the 15 days of drought; it remained equivalent to that of the control plants, around -1.2 MPa.

The ET of the control treatments of the HT92 trial reached more than 10 mm d^{-1} when leaf area was at its maximum, underlining the intensity of the atmospheric demand in the hot dry season in Niamey (Fig. 2). Before the specific period of study, ET decreased between 40 and 50 DAE due to an underestimation of the crop water requirements. At 54 DAE, when the soil water availability was close to 100%, the arrest of irrigation in the dry treatment caused a large reduction in ET. In these sandy soils, the drying of the surface is very rapid and by 2 days after the last rain or irrigation, soil evaporation becomes negligible (Wallace et al., 1993) so that ET

values of the dry treatments can be taken as transpiration. They were on average 4.7 mm d^{-1} for the first period (54–68 DAE) and 1.5 mm d^{-1} for the second period (68–84 DAE), without significant differences between cultivars. Because of the non-uniform moistening of the soil in the LT90 trial, the estimation of ET from neutron probe data was only possible during soil drying and remains approximate. During the period of 15 days without water, average transpiration was then estimated at 2.2 mm d^{-1} , with no difference between cultivars. This is a very low rate but plausible compared to the values measured during drought in the high-tillering trial.

3.2. Green leaf area

Maximal leaf area indices were logically much larger in the HT92 trial (1.8) than in LT90 (0.7) (Fig. 3 and Fig. 4). In both trials, drought caused a large reduction in leaf area index through an arrest of late growth (from 54 to 61 DAE in HT92, Fig. 3a and Fig. 3b) and an acceleration of the leaf senescence (from 61 DAE in HT92 and 67 DAE in LT90, Fig. 4 and Fig. 5). After 15 days without irrigation, the leaf area of stressed plants was less than 30 to 50% of that of control plants. The response occurred quickly and was noticeable 4 to 5 days after the arrest of irrigation (Fig. 3 and Fig. 5). It occurred even though

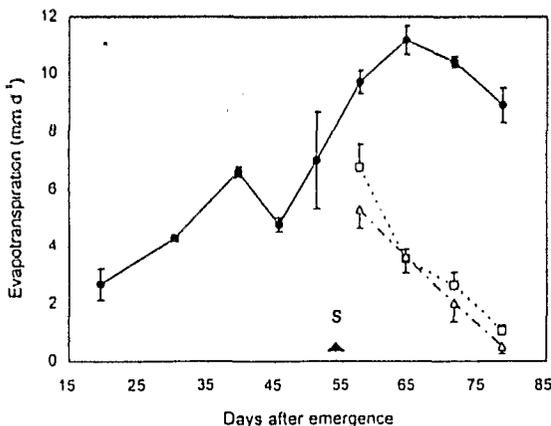


Fig. 2. Seasonal changes in daily crop evapotranspiration in the high-tillering trial for control (●: IC30 and HKP) and stressed treatments (□: IC30, Δ: HKP). The S arrow indicates the date of the last irrigation of the dry treatment. Points are means \pm SE ($n = 4$) and the arrow indicates the stop of irrigation.

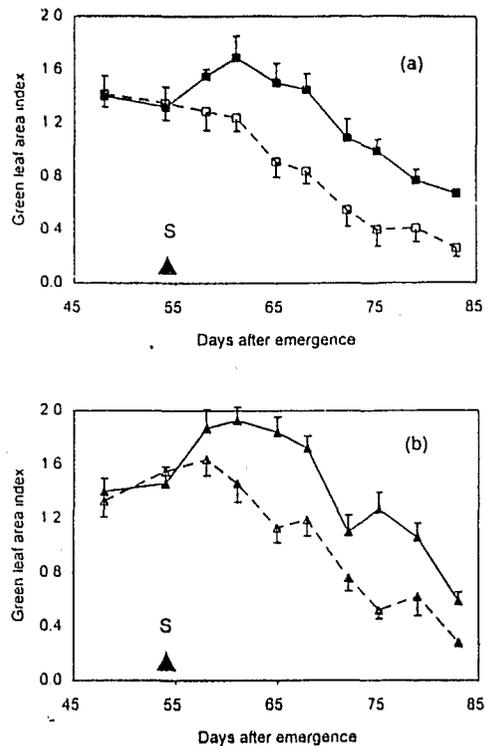


Fig. 3. Changes in green leaf area index in the high-tillering trial for control (closed symbols) and stressed treatments (open symbols) for IC30 (a) and HKP (b). The S arrow indicates the date of the last irrigation of the dry treatment. Points are means \pm SE ($n = 10$) and the arrow indicates the stop of irrigation.

the leaf water potential had not declined and the availability of water still appeared to be high (SWA $> 70\%$, Fig. 1). Observations revealed that senescence had affected the non-eared tillers and the basal leaves of eared shoots. After 15 days without irrigation, only three or four of the higher leaves of the eared stems were still green (Fig. 5, LT90).

3.3. Stomatal regulation

Study of the impact of the drought on stomatal conductance is complicated by the high instantaneous variability of this parameter and a strong influence of phenological stage of the eared stem. Fig. 6a illustrates conductances measured on the control plants in the middle of the day between earing and maturity. Conductance decreased by 50% between earing and the end of flowering and then

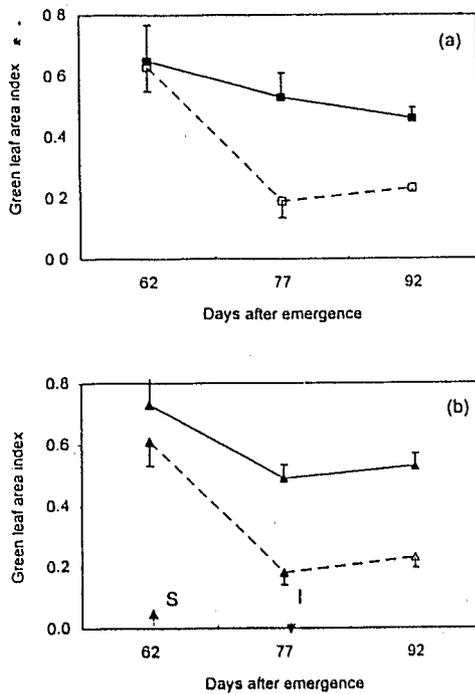


Fig. 4. Changes in green leaf area index in the low-tillering trial for control (closed symbols) and stressed treatments (open symbols) for IC30 (a) and HKP (b). Points are means \pm SE ($n = 6$). The arrows indicate the stop and the return of irrigation.

oscillated around an average value of 7 mm s^{-1} up to maturity.

Stomatal conductances of droughted plants are

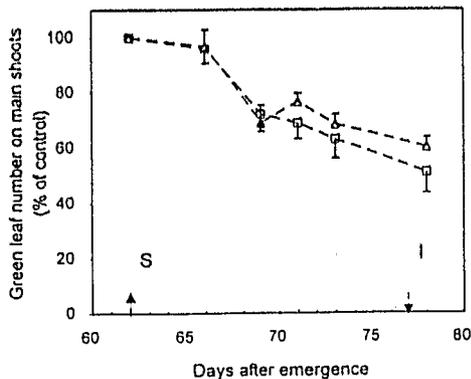


Fig. 5. Green leaf number on main shoots of stressed plants relative to controls in the low-tillering trial (\square : IC30, Δ : HKP). The 100% is the mean value of control plants, which was stable between 60 and 80 DAE and equal to $6.5 (\pm 0.3)$. Points are means \pm SE ($n = 6$).

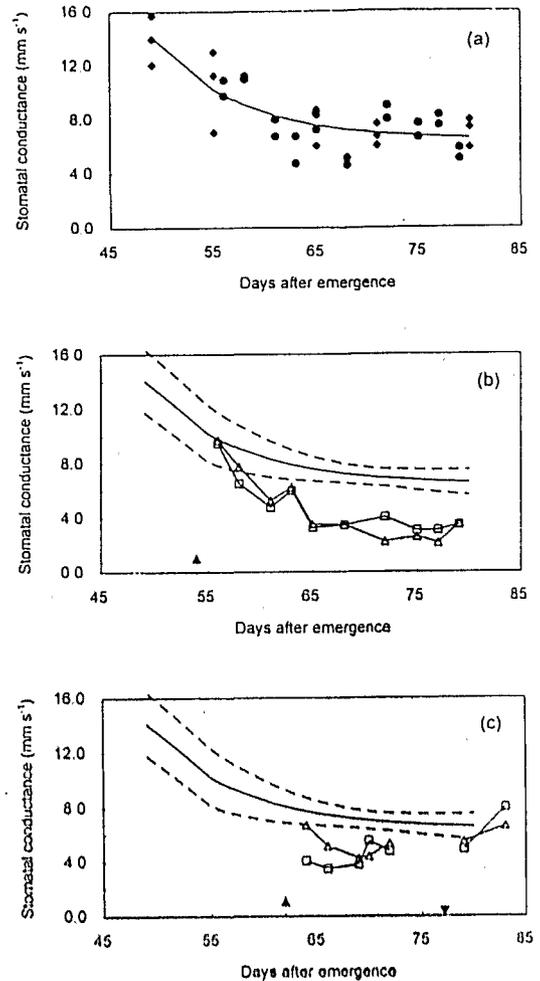


Fig. 6. Midday stomatal conductance from the beginning of flowering to maturity, flowering being spread over approximately 20 days between 50 and 70 DAE. (a) Control plants in high-tillering (\bullet : IC30 and HKP) and low-tillering (\blacklozenge : IC30 and HKP) trials; the regression line is $y = 6.36 + 2231.44 e^{-0.1156x}$, $R^2 = 0.66$. (b) Stressed plants in high-tillering trial (\square : IC30, Δ : HKP) compared to the regression line of control plants and its confidence interval at $P < 0.05$. (c) Stressed plants in low-tillering trial (same legend as for (b)). The arrows indicate the stop and return of irrigation.

described relative to the average values of the controls and a minimal value of 2 mm s^{-1} corresponding to complete stomatal closure (Henson et al., 1983a). Stomatal regulation appeared in both trials after about 4 days without irrigation, a length of time similar to that observed for reductions of leaf area

(Fig. 6b and Fig. 6c). The intensities of regulation $[100(g_s - 2)/(g_s \text{ control} - 2)]$ fluctuated over time. After 7 days without irrigation, the values were equivalent for both trials at around 50% (Fig. 6b and Fig. 6c). After 10 to 11 days, regulation became much more marked in the HT92 trial with 80% as opposed to 40%. In the HT92 trial, conductance rose on the ninth day following a rainfall of 6 mm. In the LT90 trial, rehydration after 15 days of drought caused a rise in the conductance to the level of the control treatment.

To sum up, the strong reduction of canopy transpiration is explained in these trials by the combined effects of the reduction of the green-leaf surface and stomatal regulation in leaves that were still green.

3.4. Canopy conductance

The effect of the soil drought on transpiration control can be analyzed by representing the conductance of the canopy (product of the leaf area index and the stomatal conductance) versus soil water availability, these data being available with a short time scale in the HT92 trial (Fig. 7a). This calculation assumes homogeneous canopy relations by comparison with the sampling carried out on the upper leaves of the eared shoots.

The evolution of canopy conductance was influenced independently of water conditions, at first by the decrease in the stomatal conductance after ear formation and second, by leaf senescence preceding

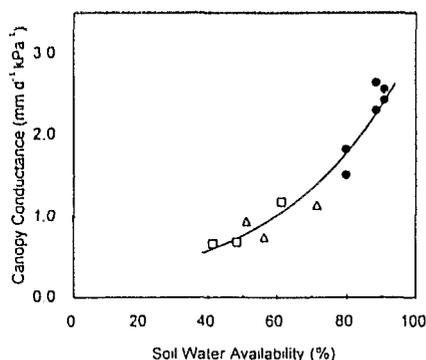


Fig. 7. Daily canopy conductance of crops in the high-tillering trial versus soil water availability from 61 to 65 DAE, in control plots (●: IC30 and HKP) and in stressed plots (□: IC30, Δ: HKP). Regression line is $y = 0.186 e^{0.0282x}$, $R^2 = 0.94$.

Table 1

Main parameters of pressure–volume curves on leaf samples in high-tillering (HT92) and low-tillering (LT90) trials for control and stressed plants of pearl millet cvs. IC30 and HKP

		Ψ_{π}^0 (MPa)	Ψ_{π}^{100} (MPa)	RWC ₀ (%)	ϵ (MPa)
<i>HT92 trial</i>					
Control	-IC30	-1.43	-0.98	80	5.3
	-HKP	-1.49	-1.01	81	5.7
Stressed	-IC30	-1.50	-0.96	81	5.6
	-HKP	-1.42	-0.93	82	5.7
<i>LT90 trial</i>					
Control	-IC30	-1.59	-1.16	79	5.6
	-HKP	-1.59	-1.11	82	5.7
Stressed	-IC30	-1.48	-1.02	70 ^a	3.6 ^b
	-HKP	-1.48	-0.99	74	4.6

The parameters include leaf osmotic potentials at zero and full turgor (Ψ_{π}^0 and Ψ_{π}^{100}); relative water content at zero turgor (RWC₀) and the mean modulus of cell wall elasticity (ϵ). For HT92 trial $n = 9$ and for LT90 trial $n = 4$. Significant differences between the means of the control and stressed treatments are shown by:

^a $P \leq 0.001$.

^b $P \leq 0.01$.

maturity. Therefore, Fig. 7 illustrates only the points corresponding to the phase from 61 to 68 DAE during which the two terms of canopy conductance were approximately stable on control plants (Fig. 3 and Fig. 6). Canopy conductance versus water availability fits an exponential decay independently of cultivars ($R^2 = 0.94$). The relationship needs further investigation but it indicates a regulation of the canopy conductance as function of an equilibrium value of water availability.

3.5. Osmotic adjustment of leaf tissues

With the control plants, the characteristic parameters of the pressure–volume curves were of the same size between the two trials and without any significant differences between cultivars (Table 1). The osmotic potential at zero turgor was around -1.5 MPa (± 0.1), the osmotic potential at maximum turgor around -1.0 MPa (± 0.1), the relative water content at zero turgor around 80% (± 1) and the modulus of cell wall elasticity varied between 5.0 and 6.0 MPa.

In both trials, the water deficit well illustrated by leaf senescence was not followed by a lowering of standard osmotic potentials that could be called osmotic adjustment. Only in the LT90 trial were tendencies noted for decline in the relative water content at zero turgor and the modulus of elasticity, particularly for the IC30 variety. The importance of these phenomena may be doubtful, but it seemed to be going in the direction of a decrease in the impact of dehydration on turgor.

4. Discussion

4.1. Regulation of water losses

The preliminary trial with lower initial leaf area (LT90) had a less apparent leaf water deficit, according to leaf water potential and stomatal regulation, but the main results were in agreement with those of the major trial (HT92). The water loss regulation mechanisms were revealed to be important. The main mechanism was the control of the green leaf area by the arrest of growth and the acceleration of senescence. That was accompanied by a stomatal regulation whose potential effect was reduced by the strong decline of stomatal conductance after heading. These responses occurred early by comparison with the small decrease in soil water availability and the stability of leaf water potential at this time.

By comparison with the end of the rainy season, the conditions of the hot dry season amplify water constraints by increasing the transpiration as a result of greater radiation load and greater VPD of the atmosphere (more than doubled on average from 1.8 to 3.8 kPa). High values of VPD and temperature values particularly in the middle of the day (6.5 kPa and 41°C), could also directly decrease stomatal conductance. We did not observe stomatal closure in the middle of the day with the control plants, however. Squire (1979) and Black and Squire (1979) observed in the field, contrary to the laboratory, that stomatal conductance of pearl millet was insensitive to large variations in the saturation deficit.

In other respects, the natural decrease of the stomatal conductance after the earing–flowering stage has already been described (Henson et al., 1983b; Squire et al., 1984; Henson and Mahalak-

shmi, 1985). And, the conductances measured in the middle of the day are equivalent to values in the literature collected during the rainy season (Wallace et al., 1990, 1993) and during the dry season (Azam-Ali, 1983; Henson et al., 1983a; Azam-Ali et al., 1984a,b; Squire et al., 1984) on leaves of a comparable age.

If the high VPD of the hot dry season does not obviously modify stomatal conductances, it does raise transpiration. This explains the rapidity of the response of the canopy, 4 days after the arrest of irrigation. In the rainy season, periods of 4 days without rain are relatively common and without impact on the canopy. Compared with the average air saturation deficits, 4 days of transpiration in the hot dry season would correspond to 8 or 9 days of transpiration at the end of the rainy season, which is closer to a period of significant drought in its impact on the canopy.

The stomatal regulation was present in this study, but did not appear to be predominant over the large reduction of leaf area that occurred under stress in both experiments. The divergences in the literature may originate from experimental conditions where the phenological stage and the rate at which water deficit develops would be discriminating factors. The rare results, corresponding to progressive stress in the field (low leaf area and moderate atmospheric demand), the condition closest to the reality of pearl millet farming in the Sahel, underline the absence of stomatal regulation and the response of the total leaf area (Azam-Ali, 1983; Wallace et al., 1993). These interpretations assume an early response of the leaf area of pearl millet in the face of a decrease in water availability, as observed here, and an interaction with stomatal conductance as shown by Black and Squire (1979) with pearl millet and Meinzer and Grantz (1990) with sugarcane. The precocity of reaction assumes that the canopy 'feels' the drying of the soil in the uppermost horizons. The intervention of chemical mediators originating from the root system in concert with drying as described by Sharp and Davies (1989) can be considered as one hypothesis.

4.2. Leaf tissue tolerance of dehydration

Concerning the upper green leaves of the eared shoots, neither osmotic adjustment nor a modifica-

tion of values characteristic of the pressure–volume curves were observed.

The osmotic potentials at full and zero turgor were similar to those found by Henson et al. (1983a) in field conditions with, in particular, Ψ_{π}^0 around -1.5 MPa. But, in apparent opposition with our results, the studies of Henson et al. (1983a) as well as other work carried out in controlled conditions mention an osmotic adjustment of 0.2 to 0.6 MPa (Henson, 1982; Henson et al., 1982; Blum and Sullivan, 1986; Dassa-Girard, 1987; Conover and Sovonick-Dunford, 1989). Interpretation of these results is influenced by differences in the cultivars studied, the physiological stage of the plants and, above all, by the intensity of the leaf water deficit. The experiment of Henson et al. (1983a) was also conducted in field conditions and in the hot season but with a high planting density (20 plants m^{-2}), which leaves us to suppose a particularly large maximum leaf area. In the present study, the leaf water deficit was probably too small or developed too slowly to induce an osmotic adjustment of an equivalent size. Our experimental conditions in the hot dry season already constitute, particularly in the trial with high tillering, a situation of relatively extreme drought by comparison with the drought conditions encountered at the end of the rainy season. Hence, one can doubt the importance of the leaf osmotic adjustment in the adaptation of pearl millet to a drought at the end of the season.

4.3. Comparison of cultivars

The cultivars presumed 'resistant' and 'sensitive' were similar in amounts of water transpired, the relationship between the canopy conductance and soil water availability, and as well as in pressure–volume relationships of the leaf tissues. In the high-tillering trial, a marked decline of Ψ_1 occurred with the cultivar HKP. Being very late (after 14 days of drought) by comparison with changes in leaf area and conductance, its direct influence over canopy responses is doubtful. The difference in the decline of leaf water potential appears to be more as a result of adjustment possibilities and it may have been the consequence of a slightly larger initial leaf area for HKP.

The comparison of the water relations for of the

two cultivars, even though they appear to be genetically distant, do not permit extrapolation of these conclusions for all short-season pearl millet. But, one can notice that studies showing differences among cultivars in responses to water deficits concern populations from extreme pluviometric zones (e.g., 300 as opposed to 700 mm annually; Blum and Sullivan, 1986; Dassa-Girard, 1987). These populations probably have very different growth durations. Furthermore, the screening trial of Blum and Sullivan (1986) was carried out in conditions of extreme stress on the same hypothesis as the screening tests for yield stability of Fussel et al. (1991). One assumes here that the extreme conditions permit an amplification of drought responses and facilitate, in turn, the discrimination of cultivars. The risk is that in being too far from normal conditions of crop structure and water deficit establishment, the amplified responses differ from those that occur in the real situation. In this way, the work of Azam-Ali et al. (1984a,b) revealed that the best possibilities for regulation of water losses and final yield were obtained with the traditional low plant density ensuring, by tillering, a progressive control of the leaf area.

Finally, when the water relations were similar for these two cultivars, grain yield in drought situations was higher with the cultivar presumed 'resistant' in the high tillering trial. The explanation of this result was sought and found in the partitioning of assimilates to the grains (Do, 1994).

5. Conclusion

This study permitted an analysis of the effect of an end-of-season drought on the water relations of pearl millet. It has demonstrated that rapid control of leaf area by senescence is the predominant mechanism during this phenological stage, inducing avoidance of dehydration on the upper leaves of the eared shoots. The hypothesis of an adjustment of the canopy conductance to reductions in soil water availability has been advanced also.

The control of the leaf area in relation with the level of soil water is in a general way a mechanism mentioned long ago (Begg and Turner, 1976) but, paradoxically, physiological studies have tended to focus on the mechanisms at the level of the green

leaf unit. On this point, Jones and Corlett (1992) underline the need of a deeper analysis of the processes that really determine productivity in drought conditions.

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