

## Drought resistance by six Senegalese local strains of *Andropogon gayanus* var. *bisquamulatus* through osmoregulation

P. GEERTS<sup>1</sup>, A. BULDGEN<sup>1</sup>, T. DIALLO<sup>2</sup> and A. DIENG<sup>2</sup>

<sup>1</sup>Unité de Zootechnie, Faculté Universitaire des Sciences Agronomiques, Gembloux, Belgium

<sup>2</sup>Département des Productions Animales, Ecole Nationale Supérieure d'Agriculture, Thiès, Senegal

### Abstract

Leaf water potential ( $\Psi$ ) and osmotic potential ( $\pi$ ) in 6 Senegalese local strains of *Andropogon gayanus* var. *bisquamulatus* were studied during the rainy season of 1995 (July–September) under the Sahelo-Sudanese climate (Thiès, Senegal). Strains were chosen according to their phenotypic diversity and vigour. During the experiment, soil volumetric water content (SVWC, % volume) decreased from 22% to 8%. Each day of measurements, 3 replicates of 9 plants per strain were studied. At the end of the experiment, leaf hairiness, length and width of leaves, length of stems, number of tillers and height and diameter of plants were measured, using 3 replicates, on each strain at the 5–6 leaf stage.

No significant difference ( $P > 0.05$ ) appeared between the strains in  $\Psi$  and  $\pi$  when the SVWC was higher than 15%. During a drying cycle, at the end of July, mean values of  $\Psi$  and  $\pi$  decreased in a 13-day lag, respectively, from  $-0.5$  MPa and  $-1.5$  MPa to  $-1.5$  MPa and  $-2$  MPa. Logarithmic models were fitted for the hydric parameters of each strain and the constants of the models were subjected to a one-way analysis of variance. Significant differences ( $P < 0.05$ ) were observed between strains and 3 groups were identified according to their capacity for osmotic adjustment. The  $\pi$  adjustment (expressed at full turgor) was correlated with: a drought resistance index (DRI), involving DM concentration and sap osmolality of the leaves; and morphological

characteristics of the strains (higher osmotic adjustment was related to narrower leaves and abundant pilosity).

This study confirms the capability of active osmoregulation in the var. *bisquamulatus* and underlines the high intravarietal variability of the Senegalese ecotypes. The capacity for osmotic adjustment may be used as a criterion when selecting for drought resistance. In this perspective, a selection strategy, which combines measurements of leaf width and a DRI, is proposed.

### Introduction

The general degradation of the environment accentuated by episodes of drought, which have occurred since 1970 in the Senegalese Groundnut Basin (Buldgen *et al.* 1994), requires the modification of the traditional farming systems. In this context, it is necessary to develop productive fodder crops adapted to the local climatic and soil conditions, with the aim of creating a real synergy between agricultural and breeding activities. A number of studies have shown that the perennial fodder crop *Andropogon gayanus* var. *bisquamulatus* is, without any doubt, the species best suited for this function (Boyer 1977; Toledo *et al.* 1990; Dieng 1991; Buldgen *et al.* 1994). However, drought episodes occurring in the Sahelo-Sudanese region between 400 and 800 mm rainfall necessitate the selection of adapted ecotypes.

Previous studies have highlighted the ability of *Andropogon gayanus* to survive during persistent drought episodes, thanks to an osmotic adjustment (A. Buldgen, unpublished data). The purpose of this study was: (i) to analyse different ecotypes of the var. *bisquamulatus* for their capability to perform osmotic adjustment, which improves survival of the grass or photosynthesis and growth during a mild drought period (Barlow 1986); (ii) to identify a relationship between osmotic adjustment and criteria easily measurable in the field, such as grass morphological characteristics, which are highly variable in the var. *bisquamulatus* (Dieng 1991).

Correspondence: Dr A. Buldgen, Unité de Zootechnie, Faculté Universitaire des Sciences Agronomiques, Passage des Déportés 2, 5030 Gembloux, Belgique. e-mail: zootechnie@fsagx.ac.be

## Materials and methods

### Plant materials and growth conditions

The experiment was carried out between July 7 and September 28, 1995 at the Ecole Nationale Supérieure d'Agriculture (ENSA, Thiès, Senegal). From a collection of strains of *A. gayanus* var. *bisquamulatus* maintained since 1989, 6 strains were selected according to plant vigour and, mainly, their phenotypic differences: hairiness of leaves, length and width of leaves, length of stems, tillering, height and diameter of tussocks. The experimental design used 12 plants (replicates) per strain (1 m between plants; 1.5 m between lines or strains). It was achieved on a typically sandy soil of the Senegalese Groundnut Basin (Buldgen *et al.* 1995). The plants subjected to drought (9 plants per strain, plot P1) were separated from those growing at field capacity (3 plants per strain, plot P2), which were irrigated every 3 days, except during rainy periods. On each day of measurement, 3 plants per strain from P1 were chosen at random so that all 9 droughted plants were measured over 3 days. During the experiment, the measurements were performed regularly on the 3 control plants (plot P2).

The climatic conditions prevailing during the experiment remained fairly constant. They may be summarised as follows: mean temperature about 27 °C; radiation of  $520 \pm 91.4 \mu\text{E}/\text{m}^2/\text{s}$ ; windy period at the end of July; high relative humidity (about 90%); and abundant rain (more than 500 mm). However, a drought period occurred between July 15–28, 1995. During this period, the soil volumetric water content (SVWC) declined from 20% to 8%. The mean SVWC in the upper layer of the soil was estimated every day with a Trime System (Trime MUX 6, IMKO GMBH, Ettlingen, Germany). Five tube access of the MUX 6 probe were positioned randomly in plot P1 (droughted plants). The probe measurements were made every 10 cm in each tube down to 60 cm depth. Each daily mean value of SVWC was established by calculating the mean of the 30 measurements (5 tubes  $\times$  6 depths). A sixth tube placed in plot P2 (control plants) enabled the SVWC to be maintained close to field capacity during the whole experiment.

During the experimental period, the growing phase of the plants was interrupted by cutting the biomass on July 31 and August 30, 1995. On the following days, the plots were fertilised with the equivalent of 50 N, 60 P and 75 K per hectare.

### Leaf water-status measurements

Daily measurements were chosen according to the SVWC, because previous work showed a strong correlation between plant water-status and this parameter (Buldgen and François 1998). Leaf water potential ( $\Psi_l$ ) was measured on the most recent fully expanded leaf of tillers which were chosen at random. The same leaves were used to determine the relative water content (RWC). The penultimate fully expanded leaf of each tiller was used for osmotic potential ( $\pi$ ) measurements.

The leaves were sampled between 700–800 h (1 h after dawn), packed in plastic bags and placed in a frigo box maintained at a temperature between 19–21 °C. They were transferred rapidly to the laboratory in order to avoid evaporation losses.  $\Psi_l$  was measured in a pressure chamber PMS 650 (PMS Instruments Co., Corvallis, Oregon, USA). RWC at full turgor was established using the pressure-volume technique (Wilson *et al.* 1980). Each leaf was weighed quickly to 0.0001 g (FW, initial fresh weight) and sealed in the pressure chamber to determine the initial leaf water potential ( $\Psi_l$ , pressure balance). Then, the chamber was pressurised slowly above the previous balance point (+0.3 MPa) and the resulting exudate was collected with a soft tissue. Afterwards, the chamber pressure was reduced slowly until sap exudation ceased. Then, a new balance pressure was determined and the leaf was reweighed. The procedure was repeated until 3  $\Psi_l$ -weight values were obtained. Turgid weight (TW) was calculated at  $\Psi_l = 0$  using a linear weight-pressure regression. Leaf dry weight (DW) was determined after drying in a forced air circulating oven at 105 °C for 24 h. RWC at full turgor was calculated as:  $\text{RWC} = [(\text{FW} - \text{DW})/(\text{TW} - \text{DW})] \times 100$ .

The set of data giving the relationship between  $\Psi_l$  and RWC (plot of  $-1/\Psi_l$  against RWC) was used to estimate the percentage of symplasmic water (F) (Percy *et al.* 1989), which was evaluated at 40%.

The osmolality of the leaf sap (N/V in moles per litre water), extracted by using a manual press, was measured with a Fiske ONE-TEN osmometer (Cryoscopic method, Fiske Associates, Massachusetts, USA). Osmotic potential ( $\pi$  in MPa) of the symplasmic water was calculated as follows:  $\pi = -0.1 \times (\text{N}/\text{V} \times \text{R} \times \text{T})/\text{F}$ , where 0.1 = conversion factor from bar to MPa; R = the universal gas constant = 8.314 J/Kelvin/mole; and

$T$  = Kelvin temperature during the measurement period (300 K). The osmotic potential expressed at full turgor ( $\pi_{\text{turg.}}$ ) was established using the following formula:  $\pi_{\text{turg.}} = \pi \times \text{RWC}$ . Turgor potential ( $\tau$  in MPa) was determined as follows:  $\tau = \Psi - \pi$ . For each strain, the osmotic adjustment ( $\Delta\pi_{\text{turg.}}$ ) and the loss of turgor ( $\Delta\tau$ ) were determined respectively as the difference between the values of  $\pi_{\text{turg.}}$  and  $\tau$  recorded at field capacity in P2 (control plot) and those registered at the lowest SVWC in P1 (plot submitted to drought).

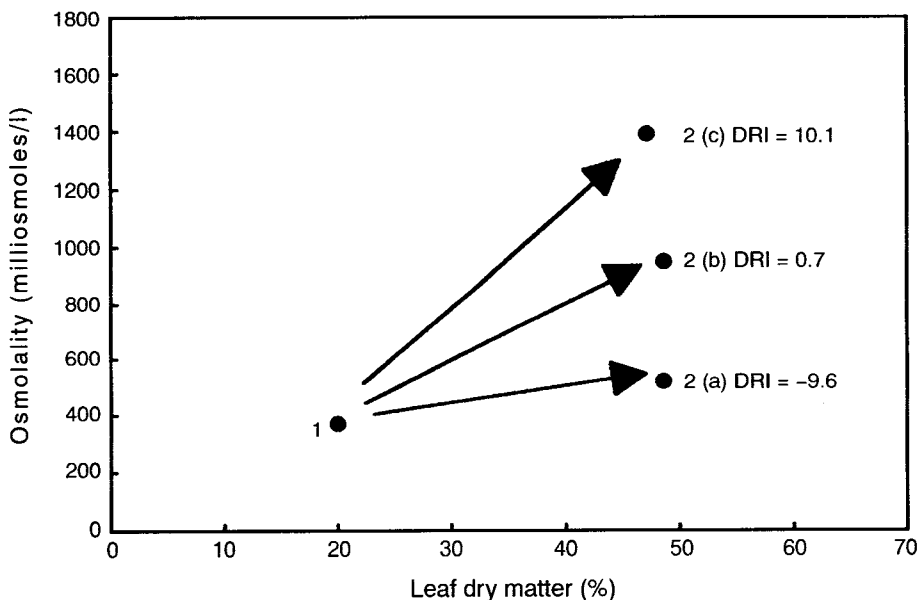
#### Definition of a drought resistance index (DRI)

The effects of osmotic adjustment on dry matter (DM) production of drought-resistant plants (in relation to their maintenance of turgor) led us to define a drought-resistance index (DRI). This index was based on the ratio between the osmolality of the leaf sap and the DM concentration in the leaves before (State 1) and at the end (State 2) of the drying cycle (mean of 9 repetitions per strain). The ratio was defined as follows:  $\text{DRI} = \text{O}(2)/\text{DM}(2) - \text{O}(1)/\text{DM}(1)$ , where  $\text{O}$  = the osmolality of leaf sap (mosm/kg  $\text{H}_2\text{O}$ ). The DRI was established in order to partition the increase of leaf DM due to the growth of plants during the

13 days of the drying cycle, from that due to the dehydration of leaves. The theoretical relations between the osmolality of the leaf sap and its DM concentration during a drying cycle and the resulting values of the DRI are presented in Figure 1.

Plants exhibit 3 behaviours during a drying cycle:

1. lowest DRI (Case "a" in Figure 1) represents plants without any osmotic adjustment; the  $\text{O}(2)/\text{DM}(2)$  ratio is relatively low at the end of the drying cycle; the plant is dehydrated;  $\text{DM}(2)$  is much higher than  $\text{DM}(1)$  whereas  $\text{O}(2)$  is similar to  $\text{O}(1)$ ; in this case, leaf DM increases rapidly in response to a rapid drop of RWC during drought;
2. intermediate DRI (Case "b" in Figure 1) occurs in plants with relatively low osmotic adjustment capacity; the plant continues its development for a short period, but becomes completely dehydrated when  $\Psi$  drops;
3. highest DRI (Case "c" in Figure 1) represents plants with the highest capacity for osmotic adjustment and production; with limited dehydration of the leaves during the drying cycle, leaf DM increases regularly during the plant growth; the  $\text{O}(2)/\text{DM}(2)$  ratio is high at the end of the drying cycle;  $\text{DM}(2)$  and  $\text{O}(2)$  are both greater than  $\text{DM}(1)$  and  $\text{O}(1)$ , respectively;



**Figure 1.** Theoretical relationships between osmolality of the leaf sap and its dry matter content. Arrows describe a drying cycle during which leaves evolve from Status 1 to Status 2 (DRI = drought-resistance index).

these plants resist longer drying cycles, provided that they can maintain their turgor potential at lower SVWC (Wilson and Ludlow 1983; Barlow 1986).

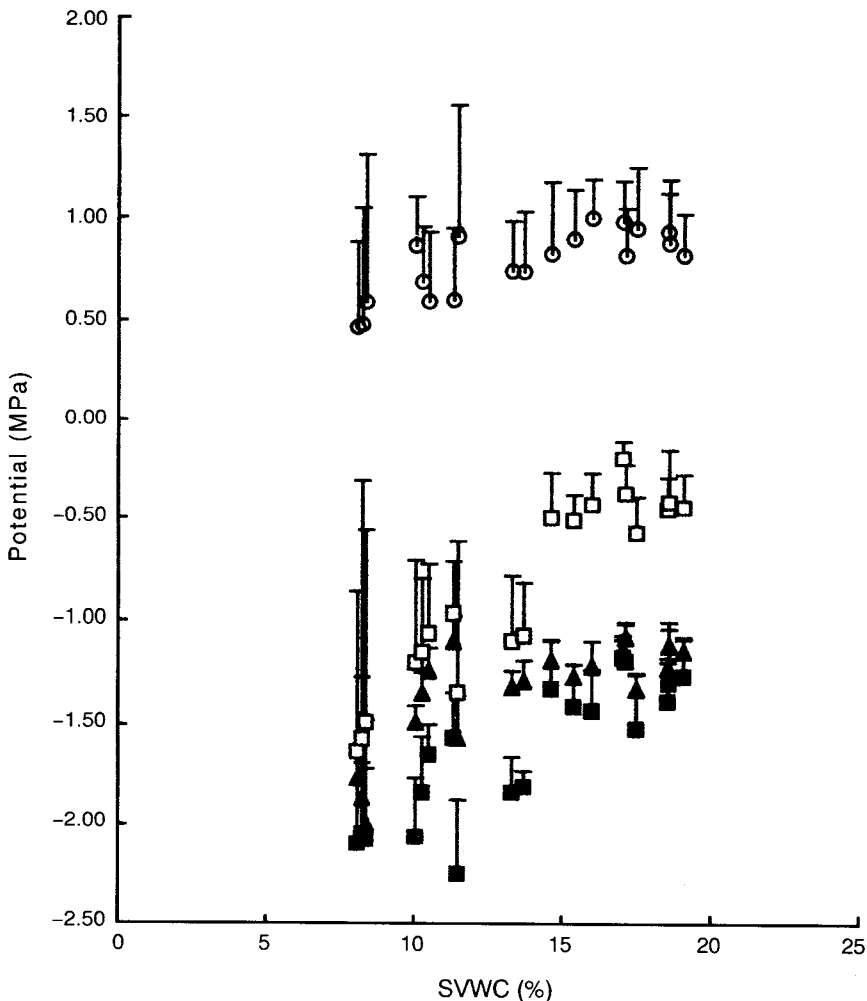
*Morphological characteristics*

Morphological characteristics were measured at the 5–6 leaves per tiller stage at the end of the second growing cycle (between August 1–30, 1995). For each plant, the following characteristics were recorded on 3 replicates per strain: number of tillers; hairiness of the leaves (3 subjective levels were noted); length of stem; width and length of leaves; height; and diameter of plants.

*Statistical analyses*

Figure 2 presents the mean changes in the various water parameters of the 6 strains, and shows a rapid change of plant water status as the SVWC decreased from 15% to 8%. The high standard deviations observed with this range of SVWC partly arise from different patterns of behaviour of the strains.

A linear relationship ( $y = c$ , with  $y =$  the water parameter considered and  $c =$  mean value of all the measurements made during the humid period) provided a significant ( $P < 0.05$ ) fit for each strain when the SVWC was higher than 15%, for the control and water-stressed treatments. In contrast,



**Figure 2.** Changes in leaf water parameters with decrease in soil volumetric water content (SVWC). Means of the 6 strains  $\pm$  standard deviations (T) for leaf water potential ( $\square$ ), osmotic potential ( $\blacksquare$ ), osmotic potential at full turgor ( $\blacktriangle$ ) and turgor potential ( $\circ$ ).

an exponential model was fitted when SVWC was lower than 15% for data from the water-stressed treatment. The model corresponded with the following formula:  $y = a \times (SVWC^b)$ , where  $y$  = the water parameter considered and “a” and “b” are constants. The constant “a” represents the value of SVWC when  $\Psi_l$ ,  $\pi$  or  $\pi_{turg}$  is equal to  $-\infty$ , while the constant “b” represents the rate of decrease in these parameters.

The statistical analyses were based on the constants “c” and “b” for each water parameter, by using a one-way analysis of variance (Minitab 10 Xtra Release, Minitab Inc., State College, PA, USA). The constant “a” was not considered because it was highly correlated with “b” ( $r^2 = 0.99$ ). The data concerning  $\Delta\tau$ ,  $\Delta\pi_{turg}$ , DRI and the morphological characteristics of the strains were also subjected to a one-way analysis of variance.

## Results

The mean values for “b” and “c” established for the different leaf water parameters of each strain are presented in Table 1. The analysis of variance for “c” values showed no significant differences ( $P > 0.05$ ) between strains, indicating that the

same water status was observed for all strains under wetter soil conditions (over 15% SVWC). A mean decrease of 13% was observed for RWC during the drying cycle and the values of “b” registered for this parameter presented no significant difference ( $P > 0.05$ ) between strains, indicating that the rate of drying was the same in the 6 strains during the drought period. In all plants, a decrease of  $\Psi_l$ ,  $\pi$ ,  $\pi_{turg}$  and  $\tau$  was observed during drying, between 15% and 8% SVWC. In some strains,  $\Psi_l$  and  $\pi$  decreased more rapidly (see constant “b” in Table 1), but these strains maintained a higher turgor at the end of the drying cycle (lower  $\Delta\tau$ , Table 1) according to a greater osmotic adjustment (higher  $\Delta\pi_{turg}$ , Table 1). Statistical comparison of  $\Delta\tau$  and  $\Delta\pi_{turg}$  underlined a similar behaviour in the following strains: TH 84 and TA 104 with a lower osmotic adjustment; TH 12 and TH 19 which had an intermediate behaviour; and TH 17 and TH 24 with the highest osmotic adjustment. These different behavioural patterns and our field observations were confirmed by the calculation of the DRI (higher DRI in the drought-resistant strains). A high correlation ( $r^2 = 0.99$ ) was found between the osmotic adjustment in the strains and their value of DRI (Figure 3).

**Table 1.** Mean values of constants “c” and “b” for the different leaf water parameters in each strain of the var. *bisquamulatus*, the loss of turgor ( $-\Delta\tau$ ), the osmotic adjustment ( $\Delta\pi_{turg}$ ), the drought-resistance indices (DRI) and conclusions about the drought resistance of each strain (means  $\pm$  standard deviations of 9 replicates).

Strains	TA 104	TH 84	TH 19	TH 12	TH 17	TH 24
	“c” values					
RWC (%)	91.6 $\pm$ 7.8 a <sup>1</sup>	89.3 $\pm$ 7.1 a	86.8 $\pm$ 8.5 a	91.7 $\pm$ 5.6 a	89.9 $\pm$ 9.0 a	90.8 $\pm$ 6.5 a
$\Psi_l$ (MPa)	-0.37 $\pm$ 0.28 a	-0.51 $\pm$ 0.29 a	-0.51 $\pm$ 0.25 a	-0.39 $\pm$ 0.21 a	-0.41 $\pm$ 0.25 a	-0.42 $\pm$ 0.28 a
$\pi$ (MPa)	-1.53 $\pm$ 0.21 a	-1.56 $\pm$ 0.16 a	-1.45 $\pm$ 0.21 a	-1.44 $\pm$ 0.20 a	-1.37 $\pm$ 0.23 a	-1.43 $\pm$ 0.40 a
$\pi_{turg}$ (MPa)	-1.40 $\pm$ 0.23 a	-1.39 $\pm$ 0.14 a	-1.24 $\pm$ 0.21 a	-1.31 $\pm$ 0.17 a	-1.30 $\pm$ 0.51 a	-1.28 $\pm$ 0.29 a
	“b” values					
RWC (%)	0.23 $\pm$ 0.09 a	0.21 $\pm$ 0.11 a	0.26 $\pm$ 0.04 a	0.30 $\pm$ 0.05 a	0.35 $\pm$ 0.12 a	0.27 $\pm$ 0.07 a
$\Psi_l$ (MPa)	-1.58 $\pm$ 0.70 ab	-1.30 $\pm$ 0.59 a	-1.69 $\pm$ 0.68 abc	-2.03 $\pm$ 0.54 bcd	-2.23 $\pm$ 0.47 cd	-2.47 $\pm$ 0.82 d
$\pi$ (MPa)	-0.41 $\pm$ 0.16 a	-0.44 $\pm$ 0.21 a	-0.78 $\pm$ 0.43 b	-0.85 $\pm$ 0.26 bc	-1.15 $\pm$ 0.26 cd	-1.23 $\pm$ 0.53 d
$\pi_{turg}$ (MPa)	-0.17 $\pm$ 0.17 a	-0.36 $\pm$ 0.46 ab	-0.53 $\pm$ 0.37 b	-0.60 $\pm$ 0.22 bc	-0.86 $\pm$ 0.49 cd	-0.90 $\pm$ 0.23 d
	Loss of turgor, osmotic adjustment and drought-resistance index					
$\Delta\tau$ (MPa)	-0.56 $\pm$ 0.22 a	-0.50 $\pm$ 0.30 ab	-0.41 $\pm$ 0.24 b	-0.33 $\pm$ 0.22 c	-0.33 $\pm$ 0.26 c	-0.19 $\pm$ 0.31 cd
$\Delta\pi_{turg}$ (MPa)	-0.25 $\pm$ 0.22 a	-0.35 $\pm$ 0.16 ab	-0.41 $\pm$ 0.23 bc	-0.51 $\pm$ 0.20 c	-0.62 $\pm$ 0.47 cd	-0.80 $\pm$ 0.29 d
DRI	1.77 $\pm$ 0.77 a	2.83 $\pm$ 1.09 b	3.00 $\pm$ 3.34 bc	4.85 $\pm$ 2.30 c	6.73 $\pm$ 1.74 cd	9.16 $\pm$ 6.42 d
	Conclusions					
Drought resistance	Low	Low	Medium	Medium	High	High

<sup>1</sup>In each row, values followed by different letters are significantly different ( $P < 0.05$ ).

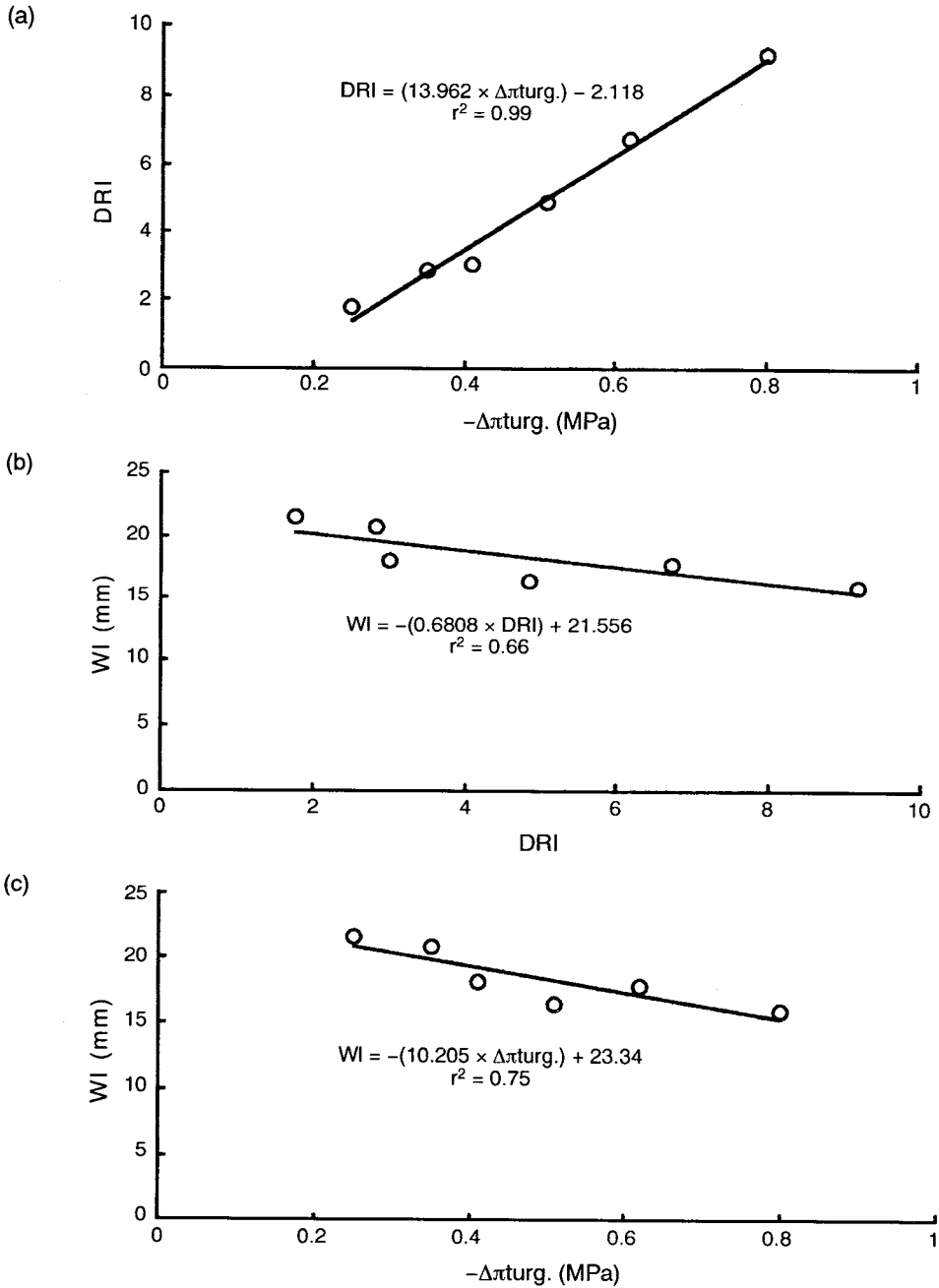


Figure 3. Relationships between: (a) the osmotic adjustment ( $\Delta\pi_{\text{urg.}}$ ) and the drought-resistance index (DRI); (b) the DRI and the width of leaf (WI); and (c)  $\Delta\pi_{\text{urg.}}$  and WI.

The mean values registered for the morphological characteristics of the strains are presented in Table 2. Statistical analysis of these values indicated a high variability between strains. Figure 3 shows the close relationships between the width of leaves and the capacity for osmotic adjustment of the strains or their DRI. Moreover, leaf hairiness clearly distinguished the strains TH 24 and TH 17 from the others (Table 2).

## Discussion

Decreases of  $\Psi$  and  $\pi$  observed during the drought period as SVWC decreased from 15% to 8%, confirm previous results in a controlled environment (Buldgen and François 1998). The decrease in  $\pi_{\text{turg}}$  observed during this experiment also confirms osmoregulation in var. *bisquamulatus* under field conditions. Some strains showed very slight active osmoregulation during the drought cycle, whereas significant changes in  $\pi_{\text{turg}}$  were observed in others.

Previous experiments (A. Buldgen, unpublished data) clearly demonstrated that the  $K^+$  ion is the major solute implicated in the *A. gayanus* osmotic adjustment. Observations on wheat and sorghum genotypes by Morgan and Condon (1986) showed that root production and soil water extraction are strongly linked to osmotic adjustment. Henson *et al.* (1989) also associated root development with the maintenance of turgor due to osmotic adjustment. Therefore, a likely reason for the differences in the osmotic adjustment of the strains may be a difference in root development, which enhances both soil water and  $K^+$  uptake. This aspect warrants investigation.

Our experiment shows that leaves with high hairiness and reduced width performed a higher

osmotic adjustment. Percy *et al.* (1989) and Kriedemann (1986) claim that these characteristics maintain the temperature of the leaf at a level which is compatible with enzyme activities, by better control of the vapour pressure deficit at the leaf surface (Norman and Campbell 1989). Our study indicates that drought-resistant strains of the var. *bisquamulatus* with these morphological characteristics had also the highest osmoregulation capacity.

The DRI appeared useful for classifying strains according to their osmotic adjustment during a drought cycle. However, it should be noted that this index has no significance in the absolute, because it depends on experimental conditions. For example, a limited drought period or, on the contrary, a severe drought, does not give the same values of osmotic adjustment or DM production. The same comment can be made about a slow versus a fast drying, because increase in leaf DM concentration due to growth can be observed only if the lag-time between 2 measures is 8–12 days (Dieng 1991). Moreover, the growing stage of the plant and its mineral nutrition before drought can also have a significant impact on DM concentration in the leaves (Dieng 1991). Therefore, the strain or plant comparisons based on DRI must be rigorously achieved in the same growing conditions and time of drying.

Briefly, our study confirms the osmotic adjustment capacity of var. *bisquamulatus* and the possibility of using this criterion for selection, because osmoregulation is a heritable trait (Ludlow and Muchow 1988). Selection may be carried out in 2 steps: (1) a population screening on plant morphological characteristics, because hairiness and width of leaves seem to be associated with osmotic adjustment in the var.

Table 2. Morphological characteristics of the 6 strains of the var. *bisquamulatus* (means  $\pm$  standard deviations of 9 replicates).

Strains	Hairiness	Height of plant	Diameter of plant	Width of leaf	Length of leaf	Length of stem	Number of tillers
		(cm)	(cm)	(mm)	(cm)	(cm)	
TA 104	Low	73.5 $\pm$ 9.6 ad <sup>1</sup>	166.3 $\pm$ 15.9 ab	21.5 $\pm$ 4.1 c	20.8 $\pm$ 2.3 a	12.2 $\pm$ 2.0 c	158.3 $\pm$ 20.1 bc
TH 84	Low	92.6 $\pm$ 28.6 bc	126.9 $\pm$ 26.3 c	20.8 $\pm$ 4.4 bc	19.6 $\pm$ 5.2 a	11.8 $\pm$ 5.4 bc	197.1 $\pm$ 68.8 c
TH 19	Medium	87.1 $\pm$ 18.2 cd	148.9 $\pm$ 7.5 a	18.0 $\pm$ 6.9 abc	17.0 $\pm$ 8.2 a	10.3 $\pm$ 4.0 ab	191.4 $\pm$ 67.5 bc
TH 12	Medium	70.6 $\pm$ 10.6 a	160.9 $\pm$ 18.1 ab	16.3 $\pm$ 6.4 ab	19.1 $\pm$ 3.7 a	9.8 $\pm$ 3.4 a	91.5 $\pm$ 21.0 a
TH 17	High	103.0 $\pm$ 13.3 b	157.8 $\pm$ 35.9 a	17.7 $\pm$ 3.7 ab	18.6 $\pm$ 3.8 a	12.4 $\pm$ 3.2 c	154.1 $\pm$ 52.9 b
TH 24	High	91.6 $\pm$ 22.2 bc	180.7 $\pm$ 23.6 b	15.8 $\pm$ 4.6 a	14.3 $\pm$ 4.2 a	12.1 $\pm$ 2.3 c	310.4 $\pm$ 56.8 d
Means	—	86.4 $\pm$ 12.3	156.9 $\pm$ 18.1	18.3 $\pm$ 2.3	18.2 $\pm$ 2.3	11.4 $\pm$ 1.1	183.8 $\pm$ 72.5

<sup>1</sup>Within columns, values followed by different letters are significantly different ( $P < 0.05$ ).

*bisquamulatus*, even though there is no clear biological link between these characteristics and osmotic adjustment; and (2) selection of plants or strains cultivated in the same conditions using a drought-resistance index (DRI), which is based on sap osmolality and dry matter concentration in leaves at the beginning and the end of relatively long drying cycles (10–15 days).

### Acknowledgements

This work was done in the frame of the project "Appui au Département des Productions Animales de l'École Nationale Supérieure d'Agriculture (ENSA) de Thiès (Sénégal)" funded by the "Administration Générale de la Coopération au Développement" in Belgium.

### References

BARLOW, E.W.R. (1986) Water relations in expanding leaves. *Australian Journal of Plant Physiology*, **13**, 45–58.

BOYER, J. (1977) Etude écophysiological de la productivité de quelques graminées fourragères cultivées au Sénégal (1re et 2ème parties). I — Influence de certains facteurs du milieu sur le comportement hydrique et la croissance. II — Consommation d'eau et production de matière sèche des parties aériennes. *Cahiers de l'O.R.S.T.O.M., Série Biologie*, Vol XII, **4**, 249–282.

BULDGEN, A. and FRANÇOIS, J. (1998) Physiological reactions to imposed water deficit by *Andropogon gayanus* Kunth var. *bisquamulatus* and *Cenchrus ciliaris* L. cv. Biloela in a mixed fodder crop. *Journal of Agricultural Science, Cambridge*, **131**, 31–38.

BULDGEN, A., PIRAUX, M. and COMPERE, R. (1994) Sécheresse dans le bassin arachidier sénégalais. Analyse SIG des nouvelles zones agro-écologiques et de certaines productions à risques. *Sécheresse*, **1**(5), 51–56.

BULDGEN, A., FRANÇOIS, J. and FALLA, J. (1995) Seedling establishment of *Andropogon gayanus* Kunth var. *bisquamulatus* under dry conditions. *Tropical Grasslands*, **29**, 248–256.

DIENG, A. (1991) In: *Introduction de la culture fourragère temporaire d'Andropogon gayanus Kunth var bisquamulatus dans la ferme intensifiée du bassin arachidier sénégalais*. Thèse de Doctorat en Sciences Agronomiques. Faculté Universitaire des Sciences Agronomiques, Gembloux, Belgique.

HENSON, I.E., JENSEN, C.R. and TURNER, N.C. (1989) Leaf gas exchange and water relations of lupins and wheat. I. Shoot responses to soil water deficits. *Australian Journal of Plant Physiology*, **16**, 401–413.

KRIEDEMANN, P.E. (1986) Stomatal and photosynthetic limitations to leaf growth. *Australian Journal of Plant Physiology*, **13**, 15–31.

LUDLOW, M.M. and MUCHOW, R.C. (1988) A critical evaluation of traits for improving crop yields in water-limited environments. *Advances in Agronomy*, **43**, 107–153.

MORGAN, J.M. and CONDON, A.G. (1986) Water use, grain yield and osmoregulation in wheat. *Australian Journal of Plant Physiology*, **13**, 523–532.

NORMAN, J.M. AND CAMPBELL, G.S. (1989) Canopy structure. *Plant Physiological Ecology*, 301–325.

PEARCY, R.W., EHLERINGER, J., MOONEY, H.A. and RUNDEL, P.W. (1989) In: *Plant Physiological Ecology. Field, Methods and Instrumentation*. pp. 162–183. (Wadsworth Publishing Company: Belmont).

TOLEDO, J.M., VERA, R., LASCANO, C. and LENNE, J.M. (1990) In: *Andropogon gayanus* Kunth. A grass for tropical acid soils. *Publication N° 90. CIAT, Cali, Colombia*.

WILSON, J.R., LUDLOW, M.M., FISHER, M.J. and SCHULZE, E.D. (1980) Adaptation to water stress of the leaf water relations of four tropical forage species. *Australian Journal of Plant Physiology*, **7**, 207–220.

WILSON, J.R. AND LUDLOW, M.M. (1983) Time trends in osmotic adjustment and water relations of leaves of *Cenchrus ciliaris* during and after water stress. *Australian Journal of Plant Physiology*, **10**, 15–24.

(Received for publication March 13, 1998; accepted July 13, 1998)