

## Photosynthetic response to water stress in *Themeda triandra* and *Eragrostis lehmanniana*

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The influence of water stress on the photosynthetic rate of the C<sub>4</sub> grasses *Themeda triandra* Forsk. and *Eragrostis lehmanniana* Nees was determined for the vegetative and reproductive phases. Gas exchange was determined with an infra-red gas analyser, while leaf water potential was used to quantify water stress. An open system of gas flow was used. The rate of photosynthesis was 0.3131 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> and 0.6287 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> respectively for *T. triandra* and *E. lehmanniana* ( $P \leq 0.001$ ) if water was not limiting. The rate of photosynthesis began to decline at a leaf water potential of -1 927 kPa and -1 625 kPa for *T. triandra* and *E. lehmanniana* respectively. This decline in rate of photosynthesis was significantly ( $P \leq 0.001$ ) correlated with leaf water potential, and linear relationships with correlation coefficients of 0.936 and 0.938 were obtained for *T. triandra* and *E. lehmanniana* respectively.

**Keywords:** Drought stress; leaf water potential; Lehmann's love grass; Red grass; water use efficiency.

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### Introduction

South Africa is predominantly a dry country with two thirds of the land receiving less than 500 mm of rain per annum (Schulze 1979). In these arid and semi-arid regions, feed production is limited as a result of a shortage of available water and suitable soil while animal production is largely dependent on the condition of the veld (Snyman & Fouché 1993). In stock-farming areas, the veld is frequently subject to seasonal and extreme droughts, leading to instability in farming (Snyman & Fouché 1991). Pre- and mid-summer droughts are a normal phenomenon in semi-arid regions (Snyman 1993).

To measure the productivity of pasture plants under favourable conditions, it is necessary to determine the water use efficiency under optimal conditions. It is well known that the rates of photosynthesis and plant production decline under water stress (Ashton 1956; Stålfelt 1956; Moss *et al.* 1961; Hsiao 1973; Boyer 1968; Busso & Richards 1995), but this has not been quantified for most pasture plants, and parameters to identify water stress quickly and accurately justify further investigation. According to Hsiao (1973), Turner (1981) and Venter (1988), leaf water potential is the plant characteristic most used to describe plant water status. If the leaf water potential can accurately be determined where the rate of photosynthesis and transpiration in grasses begins to decline, it can be used to identify the actual stress point. The accuracy of this parameter will depend on how well plant characteristics can be correlated with leaf water potential (Snyman *et al.* 1987; Venter 1988). Sensitivity to drought stress also depends on the phenological or growth stage of the grass plant (Moolman *et al.* 1996a & b; Sieling *et al.* 1994).

The purpose of this study was to determine the rate of photosynthesis of *Themeda triandra* and *Eragrostis lehmanniana* in the vegetative and reproductive phases under optimal soil water and water-stress conditions. The pathway of photosynthetic CO<sub>2</sub> assimilation in both grass species is via C<sub>4</sub> metabolism. Leaf water potential was investigated as a parameter to identify and quantify water stress in grasses. The quantification of the reaction of grasses to different water conditions can be used to explain changes in plant growth and refine existing mathematical simulation models. By using such a model, the probability of feed shortages at the end of the growing season can be deter-

mined and stock numbers adapted in good time. Therefore for arid and semi-arid regions, quantitative determination of the influences of water stress is a necessity.

### Study area

The study was conducted in asbestos pots (540 mm deep with a diameter of 210 mm) in a greenhouse under controlled climatological conditions. The pots were painted beforehand to counter a possible increase in pH of the soil as a result of the asbestos. A 14-h photoperiod with day and night temperatures respectively of 30–32°C and 18°C was applied. The relative humidity ranged from 41% to 58%.

Soil of the Shorrocks Series (Hutton Form) (Macvicar *et al.* 1977) or, according to the new soil classification system (Soil Classification Working Group 1991), a fine sandy loam soil of the Bloemdal Form (Roodeplaat family – 3 200), sampled to a depth of 600 mm, was used as the growth medium. The first horizon (A: 0–200 mm) contained 10.6% and 2.7%, and the second horizon (B2: 200–600 mm) 19.0% and 5.1% clay and silt respectively. The respective bulk densities for each horizon were 1 484 and 1 563 kg m<sup>-3</sup>.

*Themeda triandra* Forsk. and *Eragrostis lehmanniana* Nees plants were obtained from Sydenham, the experimental farm of the University of the Orange Free State, 5 km west of Bloemfontein (29°06'S, 26°57'E: 1 350 m.a.s.l), and is situated in a semi-arid summer-rainfall region (annual mean 560 mm, 55% of which falls during the period January to April). In the central grassveld region, *Themeda triandra* (decreaser species: Foran *et al.* 1978) is the dominant grass species of veld which is in a good condition, while *Eragrostis lehmanniana* (increaser species: Fourie & Visagie 1985) dominates veld in a moderate condition (Snyman & Fouché 1993). The experiment was conducted on *T. triandra* between October and December 1987 and during the same time of year in 1988 on *E. lehmanniana*.

### Methods

#### Treatments

The plants were allowed to establish well in the greenhouse before samples of *T. triandra* and *E. lehmanniana* were randomly divided into control plants and those to be subjected to water stress. Plants

were randomly allocated to cuvettes in the same greenhouse for the determination of rate of gas exchange. The vegetative phase was first investigated, followed by the reproductive phase. Six replicates per treatment were used. After allocating a plant to a certain cuvette, it was always placed under the same cuvette for the duration of the experiment to exclude the possible effect of cuvette variation. The control plants were kept above wilting point as far as possible by regular watering. The amount of water held by the soil in the pot at field capacity was determined gravimetrically (Graven 1968). Pots were weighed every second day and the amount of water needed to obtain a mass corresponding to 85% of field capacity was added.

The plants subjected to water stress were not watered until the leaf water potential decreased to less than  $-6\ 000$  kPa. The leaf water potential of randomly selected leaves from every tuft was determined daily with a Scholander pressure bomb (Scholander *et al.* 1965) after the plants began to show stress symptoms (Snyman *et al.* 1987). Care was taken that the length of leaf protruding above the rubber seal was shorter than 20 mm (Waring & Cleary 1967) in order to minimize transpiration of that part of the leaf above the pressure bomb and to exclude unnecessary variation. The pressure at which water was observed at the top of the vascular bundles was taken as the potential of the water just before the leaf was removed (Waring & Cleary 1967). The leaf water potential was determined immediately after measuring gas exchange.

#### Relationship between linear measurements and real area

The relationship between linear measurements and real area of leaves and stems of other *T. triandra* and *E. lehmanniana* plants was established on plants grown under the same conditions as those subjected to water stress. The length and total breadth of leaves and stems were determined, as discussed by Kvet *et al.* (1971), and these values of every leaf and stem were multiplied to calculate surface area, after which the leaves and stems were removed and the area determined with a Licor LI 3 000 planimeter. A linear regression between calculated area and the determined area was applied. The mass of leaves and stems was also determined, after which the relationship between real area and mass was calculated in the same way. These relationships were determined for both the vegetative and reproductive growth stages.

#### Plotting a growth curve by means of regression relationships

Two to three parts of every grass tuft were separated from the rest of the tuft with a wire marker in order to ensure sampling within a reasonable time. To monitor the growth of the plant, the length and breadth of all green leaves, vegetative and reproductive stems in the marked plant parts were measured and noted separately at regular intervals for the duration of the experiment. After the experiment, the whole plant was cut off and dried at 70°C for a period of 24 h. The mass of the marked parts was determined separately.

The real areas of leaves, vegetative and reproductive stems respectively in the marked plant parts were multiplied with the relation between the total above-ground dry mass and the dry mass of the marked plant parts. This was done to extrapolate the real areas of the respective plant parts to the total plant. The ratio between mass of the total above-ground part of the plant and the marked plant parts was used after obtaining good relationships between dry mass and real determined areas. It was assumed that the measured plant part in relation to its end mass increased the same as the whole plant, if the sample taken in the beginning was representative of the whole plant.

In the case of plants subjected to water stress, the leaf area was only determined until visible wilting occurred. With *T. triandra*, this was done as the leaves began to close, and with *E. lehmanniana*, when they began to curl up (the turgor pressure in the leaves decreases due to low leaf water potential). At this point, the leaf area cannot be accurately determined as the regression equations are no longer valid.

#### Lay-out of the system for determination of gas exchange

An open system of air flow was used (Jarvis & Catský 1971). The six cuvettes consisted of a cylindrical framework of aluminium (height 1.5 m and diameter 500 mm) covered by polyethylene film. Inside the cuvette, the air was evenly distributed over the plant with an electric fan. An air sample was taken before entering the cuvette and at the outlet of each of the six cuvettes. The CO<sub>2</sub> concentration and vapour pressure of both samples were analysed by an ADC 225 MK II infra-red gas analyser according to the absolute method for every cuvette (Catský *et al.* 1971). Temperature was controlled by a separate system of air flow (Venter 1988) and maintained in the cuvettes at 32–36°C, which is the optimal range for growth of C<sub>4</sub> plants (Lawlor 1976).

The soil around the plants in the pots, in which the rate of gas exchange was measured, was sealed with plastic film. This was pasted to the bottom of the cuvette once the pot was placed in the cuvette, in order to obtain an airtight seal. An adaptation period of 45 min was allowed after placing the plants in the cuvettes, and measurements of gas exchange were done on the total above-ground part of the plants.

#### Determination of the rate of photosynthesis

The equation, described by Catský *et al.* (1971) for the determination of CO<sub>2</sub> exchange, and adapted by Venter (1988), was used in this study. Measurements to determine rate of gas exchange were only taken in full sunlight so that light intensity would not be a limiting factor. A Licor quantum light sensor was used. Inside the cuvettes, values of 1 100–1 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  were found. The rate of air flow was controlled in such a way that the change in CO<sub>2</sub> compensation point with water stress would not affect the measurement (Meidner 1967; Shearman *et al.* 1972; Lawlor 1976).

In the case of plants subjected to water stress, the rate of gas exchange was expressed as mg CO<sub>2</sub> plant<sup>-1</sup> s<sup>-1</sup> and not per m<sup>2</sup>, which is justified as the leaf area will not increase after permanent wilting (Cleland 1959; Probine & Preston 1962; Boyer 1968; Kramer 1969; Green *et al.* 1971; Sharp *et al.* 1979). Measurements were always taken between 11:00 and 12:00, so that the angle of incidence of the sun on the plants would not differ for the duration of the experiment.

#### Processing of data

After calculating the rates of photosynthesis, the data was processed to characterize the reaction of every species to water stress. In calculating the mean rate of photosynthesis, the reading of the control plants was used together with that of the rest of the plants before stress. The leaf water potential, at which a continual decrease in rate of photosynthesis was observed per plant, was taken as the onset of water stress regarding rate of photosynthesis. To characterize the decrease in rate of photosynthesis with increasing water stress, the rate of gas exchange per plant and the corresponding leaf water potential were used. After withdrawing water from the plants subject to water stress, the rate of photosynthesis of the total plant increased initially. These highest values of photosynthesis, just before a steady decrease in both the rate of gas exchange and leaf water potential occurred, were taken as the reference values for each plant. These rates of gas exchange with increasing water stress were then expressed as a percentage of the reference values. The relative values of photosynthesis obtained in this way were related to the absolute values of the corresponding leaf water potentials and expressed as a relationship per species. The plants were compared with each other according to the analysis of variance technique for a complete randomized design. The *F*-test was used for the comparisons.

## Results

#### Relationships between plant measurements and area

The calculated areas of the stems and leaves of both species were related to the real determined areas by means of a linear regres-

sion ( $y = a + bx$ ) (Table 1) where  $y$  is the real area and both  $a$  and  $b$  the constants, with  $x$  the calculated area in  $\text{mm}^2$ .

### Rate of photosynthesis

*Eragrostis lehmanniana* developed very quickly from vegetative to reproductive phase and therefore rates of photosynthesis of only the reproductive phase were determined. *Themeda triandra* plants differed very little in the vegetative and flowering stages ( $p > 0.05$ ) regarding rates of photosynthesis. In *Themeda triandra* the rate for both vegetative and reproductive phases was nearly half ( $p \leq 0.01$ ) that of *E. lehmanniana* in the reproductive phase if water was not limiting (Table 2). The leaf water potential, where the first signs of a decrease in rate of photosynthesis was observed, was  $-1\ 927$  kPa in *Themeda triandra* and  $-1\ 625$  kPa in *E. lehmanniana* ( $p > 0.05$ ). *T. triandra* plants in the vegetative and flowering stages did not differ significantly ( $p > 0.05$ ) regarding leaf water potential when the first signs of a decrease in rate of photosynthesis were observed.

The linear relationship ( $P \leq 0.01$ ) between the absolute leaf water potential values and the relative rate of photosynthesis for the range of  $-1\ 350$  kPa to  $-5\ 850$  kPa for *T. triandra* and *E. lehmanniana* are presented in Figure 1. As much as 88% of the variation in photosynthetic rates for both species may be attributed to differences in leaf water potential. *Eragrostis lehmanniana* differed significantly ( $p \leq 0.01$ ) from *T. triandra* regarding rate of photosynthesis with increasing water stress (Figure 1).

### Discussion

The rate of photosynthesis of *T. triandra* and *E. lehmanniana*, if water was not limiting, was similar to the values obtained by Beadle *et al.* (1973) on leaves of *Zea mays* and *Sorghum vulgare*. Sawada and Sugai (1984), in complete plants of the genus *Plantago* and Knapp (1993) in other  $C_4$  grasses, determined the rate of photosynthesis and obtained results which correspond to those of this study. Stomata play an important role according to John-

**Table 2** Photosynthesis rate ( $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) of *Themeda triandra* (vegetative and reproductive phases) and *Eragrostis lehmanniana* (reproductive phase) if water is not limiting

	Photosynthesis	Sx	Vx	VI
<i>Themeda triandra</i>	0.3131	0.0757	24.1787	0.0451
<i>Eragrostis lehmanniana</i>	0.6287	0.0698	11.0950	0.0697

Sx: Standard deviation

Vx: Coefficient of variation

VI: Deviation from average at  $p \leq 0.05$

son *et al.* (1987), Polley *et al.* (1992) and Baruch and Fernandez (1993) in explaining differences in rate of photosynthesis between species where both species follow the same photosynthetic pathway.

The leaf water potential, where the rate of photosynthesis of *T. triandra* and *E. lehmanniana* decreases, did not differ significantly. Beadle *et al.* (1973) and Melzack *et al.* (1985) however obtained different values for *Zea mays*, *Sorghum vulgare* and *Pinus halepensis*. This indicates that leaf water potential, once the rate of photosynthesis begins to decrease, is a plant characteristic which may differ between species. The leaf water potential in *T. triandra* and *E. lehmanniana*, where the rate of photosynthesis decreases, was respectively  $-1\ 927$  kPa and  $-1\ 625$  kPa in our study, but Snyman *et al.* (1987) found that these two species first show visible signs of wilting at  $-2\ 450$  kPa and  $-2\ 050$  kPa respectively. The process of photosynthesis therefore undergoes water stress before the plants show visible signs of wilting.

Below the threshold value of total leaf water potential in *T. triandra* and *E. lehmanniana* the rate of photosynthesis decreased

**Table 1** Relationships between plant dimensions and area of *Themeda triandra* and *Eragrostis lehmanniana*

	$a$	$b$	$r^2$	$r$	$n$
<i>Themeda triandra</i>					
Leaves (A)	696.5008	0.9099	0.8865	0.9415 ***	20
Vegetative stems (B)	427.1123	0.6695	0.8562	0.9253 ***	16
Reproductive stems (C)	-982.9526	2.7207	0.7470	0.8643 *	16
<i>Eragrostis lehmanniana</i>					
Leaves (D)	-39.4374	0.6366	0.8998	0.9486 ***	19
Reproductive stems (E)	13.6868	0.9544	0.9088	0.9533 ***	17

A: The regression was determined with groups of four leaves for the range of  $2\ 280 \text{ mm}^2 - 5\ 970 \text{ mm}^2$

B: The regression was determined with groups of four vegetative stems for the range of  $1\ 078 \text{ mm}^2 - 2\ 035 \text{ mm}^2$

C: The regression was determined with groups of three reproductive stems for the range of  $1\ 532 \text{ mm}^2 - 2\ 044 \text{ mm}^2$

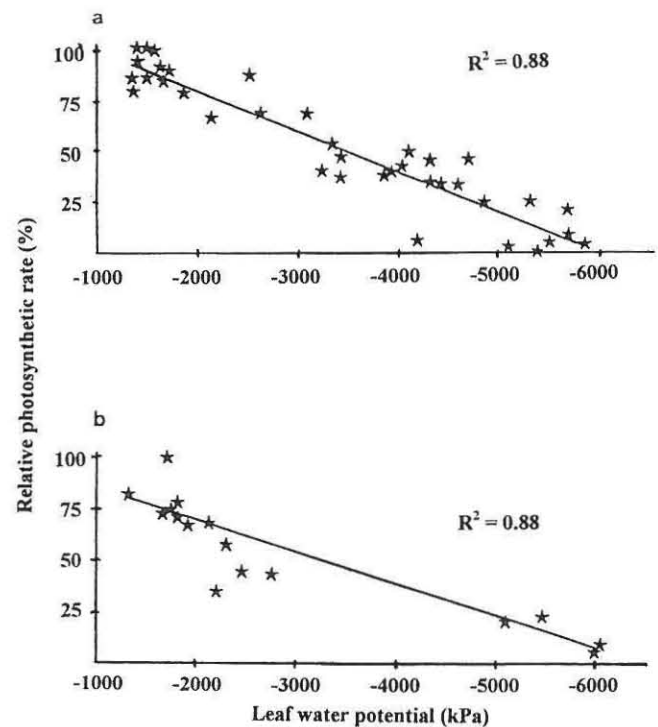
D: The regression was determined with groups of three leaves for the range of  $545 \text{ mm}^2 - 1\ 334 \text{ mm}^2$

E: The regression was determined with one reproductive stem for the range of  $216 \text{ mm}^2 - 879 \text{ mm}^2$

\* $P \leq 0.05$

\*\* $P \leq 0.01$

\*\*\* $P \leq 0.001$



**Figure 1** Change in rate of photosynthesis with increasing water stress for both vegetative and reproductive phases in *Themeda triandra* (a) and *Eragrostis lehmanniana* in the reproductive phase (b). (a):  $y = 118.9328 - 0.0199x$  ( $r = 0.94$ ;  $n = 39$ ;  $p \leq 0.001$ ) (b):  $y = 99.4151 - 0.0153x$  ( $R = 0.94$ ;  $n = 16$ ;  $p \leq 0.001$ ).

linearly with decreasing leaf water potential, which is supported by Polley *et al.* (1992) on the C<sub>4</sub> grasses *Andropogon gerardii* and *Sorghastrum nutans*. The results of Beadle *et al.* (1973), Comstock and Ehleringer (1984), McCree and Richardson (1987), Vos and Oyarzún (1987) and Nie *et al.* (1992) also clearly showed that there is a linear relationship between the rate of photosynthesis and leaf water potential below a critical leaf water potential in *Zea mays*, *Sorghum vulgare*, *Encelia frutescens*, *Beta vulgaris*, *Vigna unguiculata*, *Solanum tuberosum* and *Andropogon gerardii*.

In our study, the regression line of the relative rate of photosynthesis on water potential was purposely not lengthened to determine the leaf water potential where photosynthesis ceased. The work of Melzack *et al.* (1985) and Johnson *et al.* (1987) shows that the decrease in rate of photosynthesis can suddenly level out at a very low value of photosynthesis and then maintain a constant value. This tendency could not be determined in *T. triandra* and *E. lehmanniana* as the Scholander pressure bomb which we used could not measure such a low leaf water potential.

### Conclusion

The beginning of water stress must preferably be defined as the leaf water potential where the rate of photosynthesis begins to show a decrease. Soil water content is a misleading parameter to identify plant water stress as it does not accurately integrate both soil water content and atmospheric evaporation demand, whereas leaf water potential does (Snyman 1993). Plant water potential is a more sensitive indication of water stress than other parameters and should be used more in irrigation scheduling of cultivated pastures. A further advantage of leaf water potential as a parameter in identifying plant water stress is the ease and speed of determination in the field. We found that by measuring leaf water potential, it is possible to predict relative rates of photosynthesis without determining gas exchange of plants.

Too few research results are available to directly relate leaf water potential during water stress to production under veld conditions. Quantitative results must first be obtained on the influence of water stress on processes such as respiration (underground and above ground), cell division, cell enlargement, protein synthesis, carbohydrate metabolism, and leaf die-back, before accurate predictions of production under water stress can be done.

The physiological implementation of veld management in arid and semi-arid regions is difficult as knowledge is scant of the influence of the intensity and duration of water stress on the carbohydrate status of the plant (Venter 1988, Busso *et al.* 1990), the distribution of carbohydrates in the plant during water stress (Snyman 1993), the influence of intensity of utilization by animals on the recovery of the pasture plant after a drought (Danckwerts & Aucamp 1985; Danckwerts & Stuart-Hill 1988; Snyman & van Rensburg 1990; Snyman 1993, 1994), and the response of photosynthesis to drought (Senock *et al.* 1991; Baruch 1994). The results obtained in this study can be used to refine sound mathematical simulation models and to increase the predictive value of these in times of drought.

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