Effects of soil water stress on stomatal diffusion conductance and leaf water potential in maize (*Zea mays* L.) at flowering stage

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Abstract

Comparative studies on stomatal conductance and leaf water potentials of maize were conducted on well-watered plots and plots of which the soil water content was at "first material stress', the lower limit of "profile available water capacity". On well-watered plots early morning and midday stomatal conductance showed a strong response to early morning environmental conditions, especially air temperature. At low soil water levels (around first material stress) stomatal conductance did not respond to environmental conditions and was probably determined by soil-root conductances. Late afternoon stomatal conductances were low and did not differ between unstressed and stressed plots. These afternoon reductions in stomatal conductance facilitate recovery in leaf water status, to the benefit of the plant. Stomatal conductance and leaf water potential trends indicate that "first material stress" does represent the onset of soil-induced water stress, as it was intended to do.

Introduction

In irrigated agriculture the main objective is to avoid yield losses due to soil-induced water stress. In many semi-arid areas water is increasingly becoming a limiting factor in irrigated agriculture, *inter alia* due to increased competition from urban and industrial development. It therefore becomes imperative to maximise irrigation water-use efficiencies.

Hensley and De Jager (1982) developed a definition for plant available soil water that would meet the demands for maximum water-use efficiencies in an irrigation situation. They defined the "profile available water capacity" (PAWC) of a specific soil for a specific crop (cultivar, growth stage) under a certain evaporative demand as the amount of water which is held in the effective root zone between field capacity (FC) and first material stress (FS). The lower limit (FS) was defined as the quantity of water in the soil profile at the degree of crop water stress at which the next irrigation should be applied to avoid significant yield losses due to soil-induced water stress. The concept of PAWC is very similar to the "allowable depletion" concept of Buchheim and Ploss (1977).

A major difference in approach between "allowable depletion" and PAWC is that the former is determined empirically for each site whereas models, based on simple routine soil analysis data, have been developed to estimate PAWC for unknown sites. The first simple model of Laker (1982) was expanded by Boedt and Laker (1985). The "allowable depletion" concept has been utilised very effectively in practical irrigation scheduling by the United States Bureau of Reclamation. Likewise PAWC has been implemented very effectively in irrigation scheduling by means of the BEWAB computer model developed by the Department of Soil Science of the University of the Orange Free State (Bennie, 1988).

Hensley and De Jager (1982) and Boedt and Laker (1985) studied PAWC intensively and initially found both visual symptoms and predawn leaf water potentials to be useful indicators of FS for crops such as wheat and maize. However, when working under conditions of high evaporative demand, visual symptoms failed as indicator of FS and predawn leaf water potential trends became very difficult to interpret as FS indicators (Boedt and Laker, 1985; Vanassche and Laker, 1989). Maize plants wilted early in the morning (by 09:00) even in soils at field capacity. Under these extreme conditions predawn leaf water potentials fluctuated sharply at soil water contents in the FS range (Boedt and Laker, 1985; Laker et al., 1987). During this period very low predawn leaf water potentials (indicating stress) and relatively high values (indicating unstressed conditions) would succeed each other alternately.

Boedt and Laker (1985) devised an interpretation system for identifying FS under conditions of fluctuating predawn leaf water potentials (See also Laker et al., 1987). However, in the case of maize, an explanation for this type of behaviour was still required. It was suggested that stomatal closure may be the factor determining recovery of leaf water potentials on following days. In subsequent studies it was shown that under extreme conditions maize reaches high photosynthesis rates and very high stomatal conductance very early in the morning, after which both drop dramatically and stay very low during the afternoon (Laker et al., 1987; Ceulemans et al., 1988a; b). Recently Bunce (1990a; b) also found that the photosynthesis rate of maize drops to low levels on the afternoons of hot, dry days. A USDA News Feature (issued on 2 May, 1990) indicated that the latter was "the first report of such an afternoon drop in photosynthesis in the C4 family of plants, to which maize belongs." Bunce gives an excellent outline of the practical implications of these findings.

The wisdom of Hensley (1976), father of the PAWC concept, when he insisted that all these studies should be conducted under field conditions, is clear from the above and also from the following statements by Kramer (1988):

> "In most of the experiments cited, root systems or parts of root systems were stressed while the shoots were kept turgid. This is the reverse of the situation usually existing in the field and forest where during hot sunny weather temporary midday water deficits often occur in leaves and shoots even when the roots are in moist soil. Certainly, this is true of crop plants in the central and south-eastern United States and Laker et al. (1987) reported that in South Africa maize leaves often show visual symptoms of water stress in soil near field capacity."

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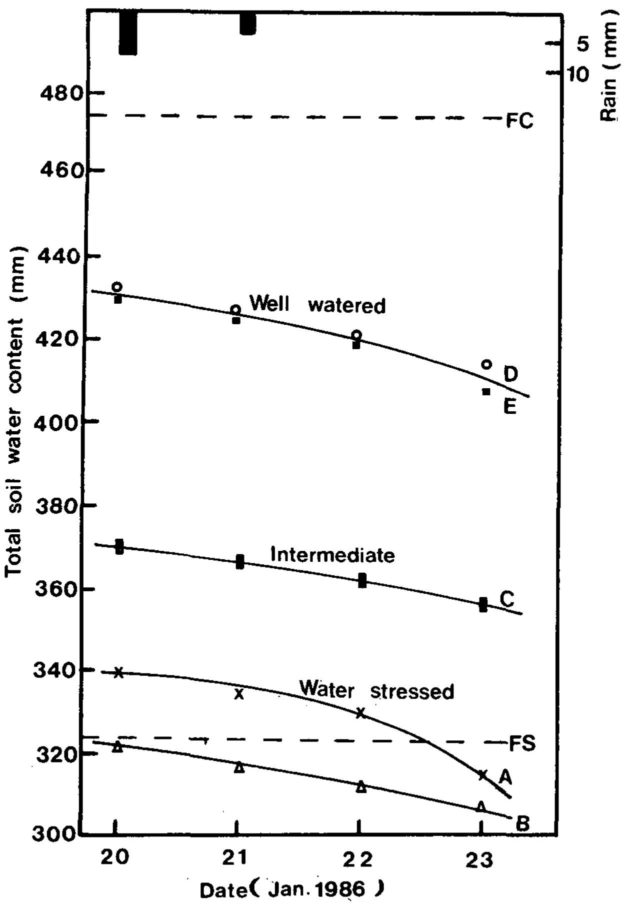

Figure 1
Soil water contents (to a depth of 1,5 m) for five irrigation plots (A,B,C,D,E). Soil water contents at field capacity (FC) and first material stress (FS) are included for reference purposes (Lines eye-fitted)

Ceulemans et al. (1988a) studied diurnal trends in photosynthesis by maize under hot semi-arid conditions, while Ceulemans et al. (1988b) studied diurnal trends in stomatal conductance by maize under these conditions. Because of the large number of measurements involved in these studies, only one soil water level could be studied on any specific day. The small study reported here was conducted to compare stomatal conductance of maize under different soil water levels at the same times on the same days. The three times chosen were early morning, midday and mid-afternoon.

List of symbols

FC — field capacity
FS — first material stress
g_s — stomatal diffusion conductance
LWP — leaf water potential
PAWC — profile available water capacity
PPFD — photosynthetic photon flux density
r_s — stomatal resistance
T_l — leaf temperature
VSD — vapour saturation deficits

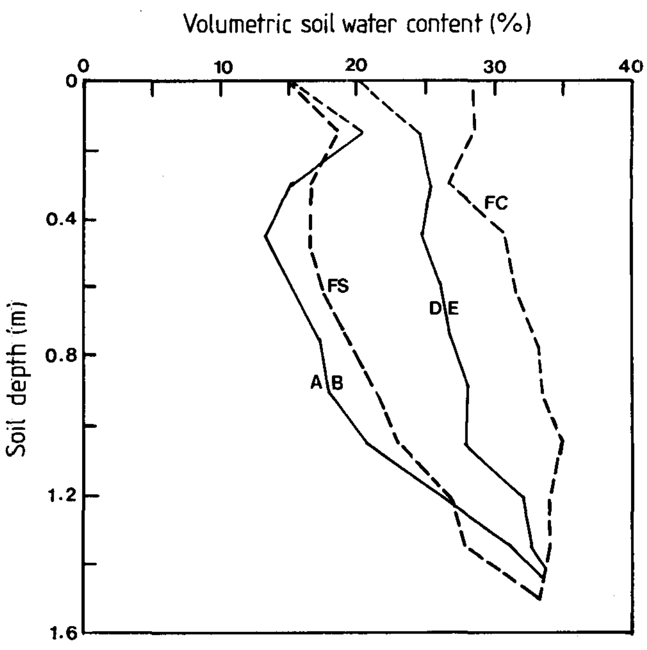

Figure 2
Soil water profiles for unstressed (D,E) and stressed (A,B) plots on 23 January, 1986. Soil water profile lines at field capacity (FC) and first material stress (FS) are included for reference purposes (Lines eye-fitted)

Materials and methods

Maize (*Zea mays* L., cultivar Pioneer PNR 542) was planted in November 1985 in 5 field plots (Plots A to E) at the Cradock Experimental Farm (Republic of South Africa; 32°08'S, 25°38'E; 660 m above sea level). It is situated at the eastern edge of the Great Karoo, a large semi-desert, and has an average annual rainfall of 341 mm. The Thornthwaite water budget shows a deficit throughout the year. The biggest deficits occur during the mid-summer months, viz. December and January (Ceulemans et al., 1988b). Each plot consisted of 5 rows of 10 m length each. Spacings between rows were c. 1,0 m and between plants in rows c. 0,2 m, giving a plant density of c. 50 000 plants·ha^{-1}, the optimum for irrigated maize in this area.

The soil of the experimental site was a deep medium-textured Inceptisol of alluvial origin. It had a field capacity of 475 mm and a PAWC of 151 mm to 1,5 m depth (Figs. 1 and 2). This study was not done at the same site as that reported by Ceulemans et al. (1988a; b), but on a similar soil nearby.

All plots were kept well watered until early January 1986, whereafter drying cycles were started at different dates to give different soil water levels at the stage when this study was to be conducted. Soil water content was measured daily by means of a neutron hydroprobe (Campbell Pacific Nuclear, model CPN503) at 0,15 m depth intervals to a depth of 1,5 m. The maize plants were at the flowering stage at the time of the measurements.

Stomatal diffusion conductance (g_s), leaf temperature (T_l), leaf water potential and photosynthetic photon flux density (PPFD) were determined under natural field conditions three times daily, i.e. during early morning (08:00 to 09:00), at midday (12:00 to 13:00) and mid-afternoon (16:00 to 17:00) on three consecutive days during mid-summer (January 21 to 23, 1986).

Stomatal resistance, r_s, was measured in 5 replications for each plot at each time on the abaxial side of mature, fully expanded upper canopy leaves with an automatic, ventilated diffusion porometer as described by Ceulemans et al. (1988b). Conversion from stomatal resistance to stomatal conductance, g_s, was done as outlined by Ceulemans et al. (1988b).

Simultaneously with porometer measurements, T_l was measured with thin copper-constantan thermocouples (Omega Inc., USA) mounted in aluminium hairclips and clamped to the abaxial leaf suface. Measurements were done in 5 replicates on different leaves. Leaf water potentials were measured with a modified pressure chamber, described originally by Scholander et al. (1965). Measurements in 5 replicates, using different leaves, were done on small pieces cut from the centre of the leaf next to the midvein. Only youngest mature leaves were used. Vanassche and Laker (1989) carefully standardised and tested this sampling procedure, originally developed by Boedt and Laker (1985). The importance of choosing a standard type of leaf (with a standard position on the plant) and a standard position on the leaf was stressed by Vanassche and Laker (1989).

Immediately prior to the porometer and pressure chamber measurements, PPFD incident on the sampled leaf was determined with a Lambda LI-190S quantum sensor (LiCor Inc., USA). Dry bulb temperature and relative atmospheric humidity were monitored continuously with a calibrated thermohygrograph at a meteorological station about 300 m from the experimental site. Vapour saturation deficits (VSD) were calculated from these readings. Some meteorological data from the same station for the 3 days on which the measurements were conducted are presented in Table 1.

TABLE 1
ENVIRONMENTAL AND METEOROLOGICAL CONDITIONS ON THE DIFFERENT SAMPLING DAYS AT THE EXPERIMENTAL FIELD SITE OF CRADOCK EXPERIMENTAL FARM (REPUBLIC OF SOUTH AFRICA) IN MIDSUMMER (JANUARY 1986)

January 1986	21	22	23
Max. temp. (°C)	34,0	22,5	30,4
Min. temp. (°C)	18,6	12,0	7,5
Grass temp. at 08:00 (°C)	14,5	6,8	1,8
Wind speed (m·s^{-1})	4,64	3,09	2,49
Pan A evaporation (mm)	7,0	9,5	9,0
Sunshine duration (h)	7,1	11,8	11,0
Rainfall (mm)	3,0	0,0	0,0

Results

During the study period Plots A and B were slightly water stressed, having soil water contents in the order of FS (Fig. 1). Plots D and E were well-watered, unstressed plots in which soil water extraction during the measuring period never exceeded 50% of PAWC. Plot C was intermediate. In terms of PAWC 100, 110, 75, 40 and 45% of PAWC were extracted from Plots A, B, C, D, and E respectively on 23 January 1986, the last day on which measurements were made. A typical example of soil water profiles with depth, representing these extractions on 23 January 1986, is given in Fig. 2. Mean water extraction for the stressed plots (A and B) and unstressed plots (D and E) respectively is given. Maize roots effectively extracted water to 1,5 m depth in this soil. For reference purposes the soil water profiles at FC and FS are also indicated in Figs. 1 and 2.

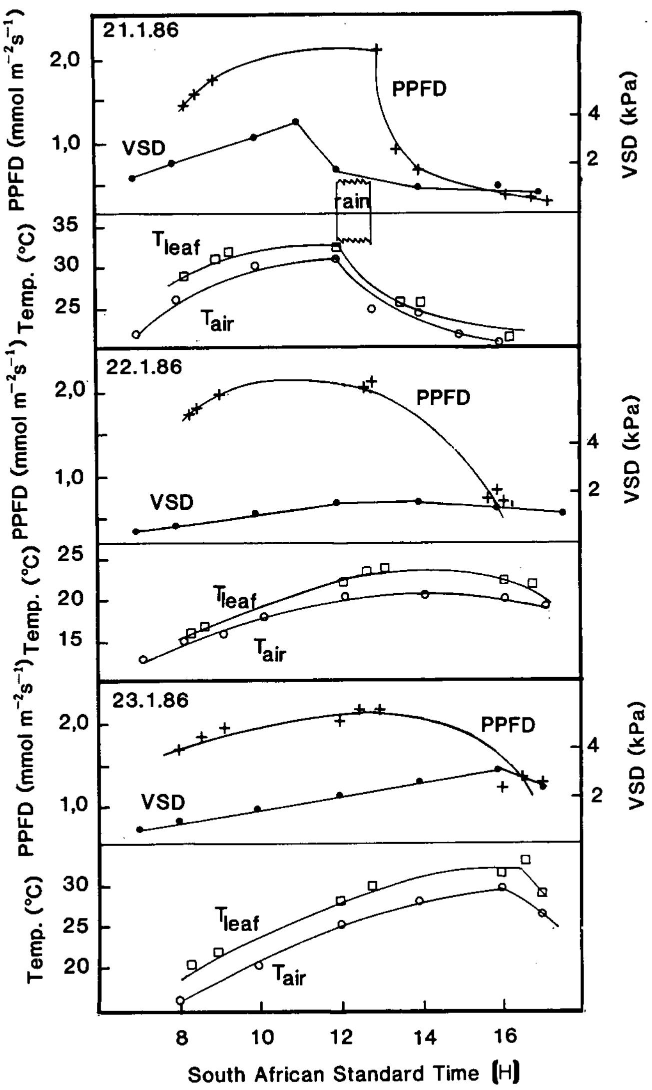

Figure 3
Diurnal courses of photosynthetic photon flux density (PPFD), air vapour saturation deficit (VSD), atmospheric temperature above the canopy (T_{air}) and leaf temperature (T_{leaf}) on the three measuring days (Lines eye-fitted)

Diurnal marches in atmospheric and leaf temperatures, air VSD and PPFD during the measuring period are presented in Fig. 3. While trends in PPFD and VSD on 22 and 23 January reflect normal daily patterns, the cloudy, cool and humid conditions, associated with a light rain shower, strongly modified the afternoon pattern for 21 January. On the latter day open pan evaporation was also significantly lower than on the other two days (Table 1) and there was no direct sunshine between 11:30 and 12:30 and after 14:30. It should be noted that 22 January was an abnormally cool day, with a maximum temperature of only 22°C (compared with the average maximum temperature of 30,6°C for the month). Although 23 January had a maximum temperature of 30,4°C it had an extremely low minimum temperature of only 8,0°C (the lowest for the month). In contrast 21 January had a very high minimum temperature of 18,6°C (third highest for the month).

Because the soil water status of the stressed plots (A and B) and

TABLE 2
STOMATAL CONDUCTANCE OF MAIZE UNDER TWO SOIL WATER REGIMES AT 3 TIMES OF THE DAY

Date (Day)	Time of day	Stomatal conductance (mmol·mm^{-2}·s^{-1}) Unstressed	Stressed
21.1.86	Early morning	625,3	607,9
(1)	Midday	852,6	338,2
	Late afternoon	108,4	103,4
22.1.86	Early morning	210,3	302,5
(2)	Midday	423,3	354,3
	Late afternoon	160,0	190,7
23.1.86	Early morning	476,5	425,3
(3)	Midday	657,8	445,5
	Late afternoon	297,8	279,9

Statistically significant differences in pair-wise comparisons (according to the Tukey test at P = 0,05):
Day (1) midday: Unstressed > Stressed
Day (2) early morning: Stressed > Unstressed
Day (3) midday: Unstressed > Stressed

unstressed plots (D and E) respectively was very similar, as was expected, it was decided to pool the data of each pair for statistical analysis. Thus 10 replicates per pair were obtained. This increased number of replicates was especially important for stomatal conductance data since these had a very high variability between measurements. Different sets of variance analyses were conducted, using the Tukey test (at P = 0,05) to determine the significance of differences.

Early morning g_s values for both unstressed and stressed plots responded sharply to differences in air temperature at the time of measurement (Table 2 and Fig. 3). This response is in agreement with the findings of Ceulemans et al. (1988b). Early morning conditions, furthermore, determined g_s values and trends during the course of each day. In the unstressed plants g_s values increased by values of about the same order from early morning to noon on all 3 days (Table 2 and Fig. 4). The noon g_s value for each day was, therefore, a function of the early morning value for that day. In the case of stressed plots midday g_s values did not differ significantly from the corresponding early morning values on the days which had moderate early morning values, viz. 22 and 23 January (Table 2 and Fig. 4). On the day with moderately high early morning g_s values (21 January) the midday value for the stressed plots was nearly 50% lower than the early morning value.

It is concluded that in the stressed plots low soil water content and soil water conductance are limiting factors, causing failure of the system to maintain a high g_s after a high early morning start. In the unstressed plots soil water conductance was adequate to cope with even the highest g_s demands until midday under the conditions prevailing on these 3 days. No very high early morning g_s values, such as the values of 700 to 800 mmol·m^{-2}·s^{-1} observed at 08:00 in a complementary study (Ceulemans et al., 1988b), occured during the period of this study. Consequently situations where well-watered systems failed to cope with evaporative demand, as were found by Ceulemans et al. (1988b), did not occur during this study. On any particular day of the present study g_s in unstressed plants responded in a classical way to increasing PPFD (Fig. 5) and a rectangular hyperbola could be fitted to describe the conductance-PPFD response curve (Whale, 1983). All points in Fig. 5 are mean values of 5 replications on different leaves.

The sharp daily fluctuations in midday g_s in unstressed plants (i.e. where only a small fraction of the plant available water has been extracted), in response to differences in early morning environmental conditions, gives scenario A of Fig. 6. In contrast day-to-day fluctuations in midday g_s for stressed plants in soil from which larger proportions of the plant-available water have been extracted are very small and not statistically significant, giving scenario B of Fig. 6. In other words, in the drier soil water range midday g_s was not significantly affected by atmospheric conditions, possibly because soil-root resistances became the limiting factors in this soil water range. This provides a possible explanation for the findings of Hensley and De Jager (1982) that the soil water contents at which "first material stress" occurred was not affected by environmental conditions, contrary to what they had anticipated.

On all 3 days later afternoon g_s values were low (Table 2). The values for 21 January, the day with high early morning g_s values, were particularly low. These results agree with those of Ceulemans et al. (1988b). In contrast Bunce (1990a; b) found that stomatal conductance of maize in his studies did not decline during the afternoon inhibition of photosynthesis. He points out that this might have been a cultivar effect, since he did find that in some other maize cultivars afternoon inhibition of photosynthesis was accompanied by partial stomatal closure. In his USDA press release Bunce indicated that it may be important to keep this in mind during maize breeding and cultivar selection programmes.

No significant differences were found between the late afternoon g_s values of unstressed and stressed plants on any of these days (Table 2). On 22 January, which followed upon 3 days during which both maximum temperatures were high, the early morning g_s values of stressed plants were significantly higher than those of unstressed plants (Table 2). This is contrary to all logical expectations. Scrutiny of g_s trends during the previous day and leaf water potential (LWP) data for the previous afternoon and that morning, and taking into account the environmental data for the previous 3 days does provide a possible explanation: Both stressed and unstressed plots started with high g_s values the previous morning (21 January). Thereafter g_s for the stressed plots dropped sharply to midday, while that for the unstressed plots increased. Maintenance of this much higher g_s in the unstressed plants caused midday LWP values for these plants to drop to values which did not differ statistically significantly from those for the stressed plants (Table 3). By late afternoon LWP values for the unstressed plants were even significantly lower than those for the stressed plants. (On the other days LWP for the unstressed plants was significantly higher than that for the stressed plants at all times of day, as would be expected). It would seem that maintenance of a high g_s in the unstressed plants for a major part of the day reduced the leaf water status of these plants (relative to the stressed plants) later in the afternoon to such a degree that it negatively affected stomatal response the next morning.

Figure 7 clearly illustrates a negative linear relationship between midday stomatal conductance and midday leaf water potential for the unstressed plants. This further supports the above discussion on the effect of high stomatal conductance on leaf water potentials in unstressed plants. In the plants growing in soil with water contents at first stress, the pattern seems to indicate a positive relationship between midday stomatal conductance and midday leaf water potential. The latter again supports the findings that high evaporative demand did not reduce PAWC in the previous research. The opposing patterns also illustrate basic differences between atmospherically controlled situations (unstressed plants) and soil controlled situations (stressed plants), as Kramer (1988) highlighted.

Early morning leaf water potentials for the unstressed plots were very consistent and were always significantly higher than the values for the stressed plots, despite the fluctuation of the latter. This supports the conclusion of Boedt and Laker (1985) and Vanassche and Laker (1989) that predawn leaf water potential is a good indicator of first material stress. An advantage of leaf water

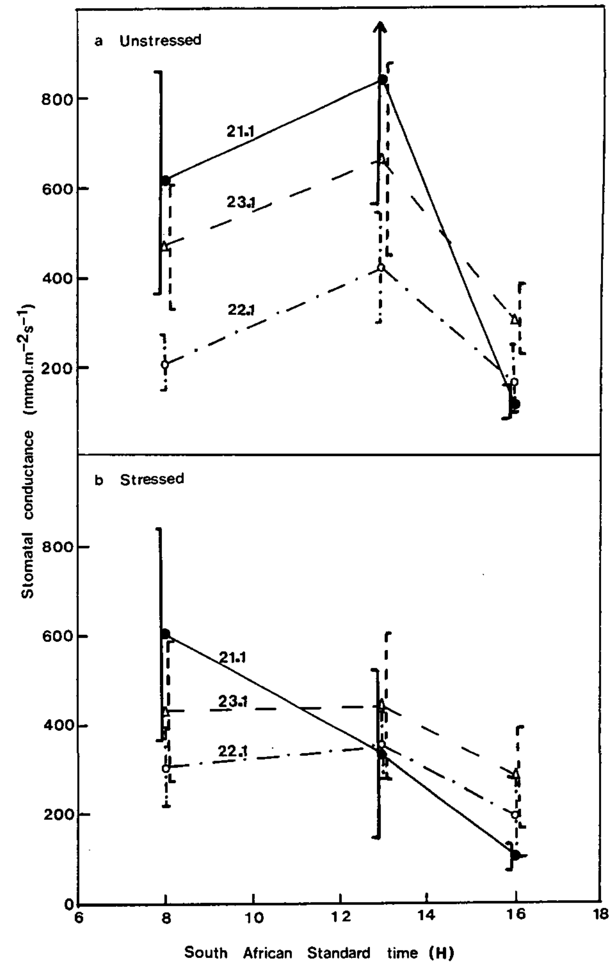

Figure 4
Stomatal conductance trends during the day on 3 consecutive days

TABLE 3
LEAF WATER POTENTIAL OF MAIZE UNDER TWO SOIL WATER REGIMES AT 3 TIMES OF THE DAY

Date (Day)	**Time of day**	**Leaf water potential (MPa) Unstressed**	**Stressed**
21.1.86 (1)	Early morning	-1,135	-1,460
	Midday	-1,685	-1,805
	Late afternoon	-1,180	-0,970
22.1.86 (2)	Early morning	-1,050	-1,240
	Midday	-1,330	-1,840
	Late afternoon	-1,180	-1,630
23.1.86 (3)	Early morning	-1,070	-1,500
	Midday	-1,600	-1,730
	Late afternoon	-1,405	-1,615

Statistically significant differences in pair-wise comparisons (according to Tukey test at P=0,05):
On all days at all times Unstressed>Stressed, except
Day (1) midday: No significant difference
Day (1) late afternoon: Stressed>Unstressed

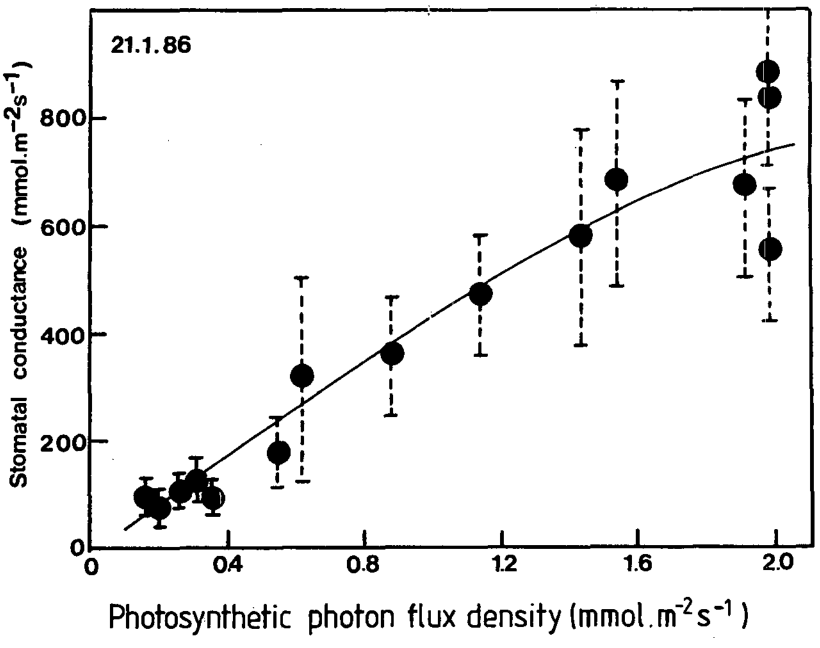

Figure 5
Response of stomatal conductance of unstressed maize plants to photosynthetic flux density on a specific measuring day (21 January 1986) (Each data point is the mean value of 5 replications. Vertical bars represent standard error of the mean)

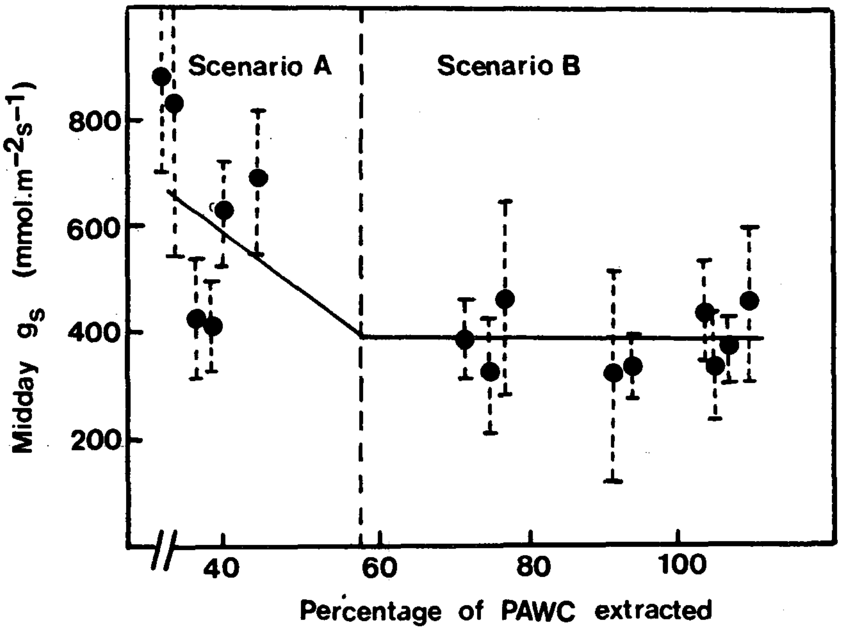

Figure 6
Effect of decreasing soil water content on stomatal conductance of mature maize leaves at midday (Each data point is the mean of 5 replications. Vertical bars indicate standard error of the mean)

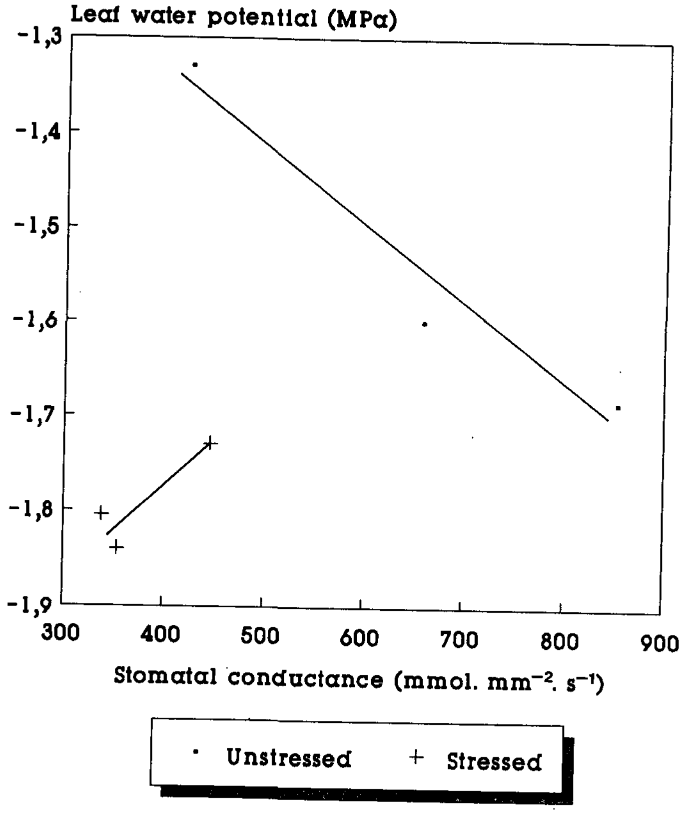

Figure 7
Relationships between midday stomatal conductance and midday leaf water potential

potentials is that the determinations are very reliable, having very small coefficients of variation if the technique is applied in a well-standardised way.

The g_s trends and LWP differences between unstressed and stressed plots indicate that FS represented soil-induced water stressed conditions. The fact that g_s for stressed plots was never lower than that of unstressed plots during early mornings or late afternoons indicates that FS represented mild stress, as it was intended to do. Since FS was estimated by means of PAWC models derived by Boedt and Laker (1985) and later confirmed by means of predawn LWP measurements by Vanassche and Laker (1989), it indicates the validity of the PAWC approach and techniques.

Conclusions

At high levels of available soil water there was strong positive response of early morning and midday stomatal conductance by maize to early morning temperature, PPFD and VSD. At low soil water levels (around first material stress) stomatal conductance did not respond to environmental conditions and was probably determined by soil-root conductances.

Afternoon reductions in r_s, due to extreme evaporative demand and/or low soil water availability, facilitate recoveries in leaf water status to the benefit of the plant. It will also improve water-use efficiencies. Bunce (1990a; b) indicated large differences between different maize cultivars in this regard and careful attention must be given to this aspect in maize breeding and selection programmes.

The importance of conducting this type of study under field conditions cannot be over-emphasised. Apart from the present study and those of Hensley and De Jager (1982) and Laker and his co-workers preceding it, this is also borne out by the papers of Kramer (1988) and Bunce (1990 a; b).

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