EFFECT OF WATER STRESS ON GROWTH, LEAF RESISTANCE AND CANOPY TEMPERATURE IN FIELD-GROWN SUGARCANE

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Abstract

A first ratoon crop was subjected to two 55-day periods of water stress using a rainshelter. Irrigation was withheld when the crop was 146 days old (December 1984), and again at 237 days. Daylight plant extension rate (PER) dropped below potential 12 and 20 days after imposing stress for the first and second time respectively. A decrease in PER was apparent when leaf water potential. ($\psi\ell$) was $-0,2$ MPa and extension ceased when $\psi\ell$ fell below $-0,4$ to $-0,7$ MPa. Leaf resistance increased gradually when PER was reduced but it remained comparatively low for about 45 days of stress and then rose rapidly during the final 10 days of stress in each period. Canopy temperature was used to derive a stress index that was correlated with $\psi\ell$. The stress index may be used to identify drought-resistant varieties and plants in need of irrigation.

Introduction

In South Africa, sugarcane is usually grown without irrigation in a climate in which water stress frequently restricts yield. During an unusually dry period from 1980 to 1983, NCo 376, a variety that comprised about 70% of the sugarcane crop, was highly susceptible to prolonged drought and it was found that little was known about the reaction sugarcane had to water stress. Fluctuations in the water content of the soil were thought to be the main cause of variations in the performance of commercial varieties in field trials (Inman-Bamber[8]). The studies reported in this paper are an attempt to understand the adjustments that take place when sugarcane undergoes and is relieved of water stress.

Materials and Methods

Three varieties, NCo 376, N12 and N14, were established in small plots (3,7 m $\times$ 4,2 m) on a loamy sand (Hutton form, Clansthal series) near Mount Edgecombe on 31 October 1983. Four plots (W2 plots) of each variety were randomly located in an area where rain was excluded by an automatic rainshelter. The crop rows were established 1,04 m apart to obtain an even stand of cane on either side of the rails which supported the rainshelter. These rails were 70 m long and 8,5 m apart. The dome-shaped shelter covered an area 24 $\times$ 8,5 m² and was 10 m away from the sheltered area in its standby position. The sheltered area was provided with trickle irrigation. Nine emitters were placed in each m² to ensure even distribution of water. Four plots (W1 plots) of each variety were located next to the rainshelter in its standby position and they were supplied with irrigation emitters in the same way as the sheltered plots. The surrounds of the rainshelter and the experimental plots were planted to cane and were managed in the same way as the experimental plots but were not irrigated.

The plant crop was harvested on 5 July 1984 and the ratoon crop was topdressed with 147 kg N and 125 kg K ha^{-1} on 4 September. The phosphorus content of the soil was adequate for cane growth but high soil pH resulted in Fe deficiency in the early stages of the ratoon. This was corrected with three applications of a 2% solution of $FeSo_4$. Aldicarb at a rate of 3 kg ha^{-1} was applied at the time of topdressing to reduce nematode activity in the soil. Water was applied to the W1 and W2 plots when soil water deficit reached 30 to 40 mm. Daily amounts of rainfall and irrigation are shown in Figure 1 as well as climatic data obtained from a nearby meteorological station. Irrigation was withheld from W2 plots between 30 November and 22 January and again between 28 February and 23 April. The various measurements described below were taken between 11h00 and 15h00 in a W1 and W2 plot of each variety on the days shown in Figure 1. These measurements were repeated several times during the day and night on 20 to 21 December and 1 to 2 April.
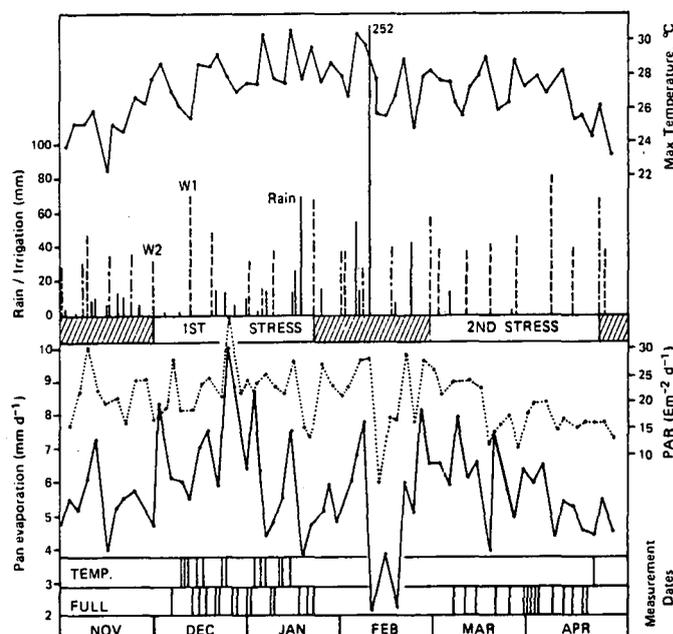

FIGURE 1 Rainfall, irrigation and three-day means of maximum temperature, photosynthetically active radiation (PAR), and pan evaporation at the rainshelter site. Dates of the first and second stress periods and of plant stress measurements. Canopy temperature was measured more frequently than other stress indicators.

Total leaf water potential was determined between 12h00 and 13h00 on six to eight leaf strips per treatment. A section of the third leaf was covered with wet cloth, cut from the margin to the midrib and then stripped from the remainder of the leaf, and placed in a Scholander pressure chamber so that the cut end protruded through a hard rubber seal. The chamber was pressurised with compressed air until xylem water returned to the cut end. The pressure at this stage was recorded as the total leaf water potential. Resistance to gaseous diffusion by the abaxial surface of the leaf was measured between 11h00 and 12h00 with a Delta T Mk3 dynamic porometer (Stiles *et al*[17]) which was calibrated in a germination cabinet and in the field. Temperature gradients between leaf surface and porometer cup were corrected according to the manufacturer's manual.

Plant elongation rate (PER) was determined by measuring the height above a marker on the stalk of the spindle leaf before and after the other readings were taken. Six stalks per plot were observed in this way. Canopy temperature (Tc) was measured with a Teletemp Ag-42 infra-red thermometer (IRT). The instrument was checked periodically on a black body reference plate and was accurate to 0,5°C and had a resolution of 0,1°C. The IRT was held about 0,5 m above the canopy at an angle of about 30° from the horizontal in line with the crop row. Readings of each of two rows were obtained over periods of up to 60 s depending on how the wind affected the fluctuation in Tc. The difference between Tc and screen temperature (Ta) was regarded as the canopy temperature differential (Tc-Ta). The data used here are the means of up to 32 Tc-Ta readings per plot.

Results and Discussion

Leaf water potential (ψℓ)

Leaf water potential at midday of irrigated plants generally remained above −0,3 MPa during both measurement periods and although readings were discontinued, it was assumed that these plants were not stressed much beyond this. Leaf water potential of the crop in the sheltered area fell below −0,5 MPa 12 days after irrigation was withheld for the first time. Leaf water potential dropped rapidly to −1,3 MPa during the following week and then fell gradually to about −1,5 MPa in NCo 376 and to about −1,7 MPa in N14 (Figure 2a). N12 appeared to recover its leaf water status to some exent after the period of rapid desiccation possibly as a result of a rapid increase in its leaf resistance at this stage. Leaf water potential of stressed N12 gradually declined but was generally greater than in NCo 376. Midday ψℓ of N14 was significantly lower (P < 0,25) than that of NCo 376 and N12 from 27 December to 10 January. During the second period of stress, ψℓ of stressed plants dropped below that of irrigated plants about 20 days after the last irrigation and it declined more gradually than in the first period to a minimum of −1,8 MPa 18 days later (Figure 2b). Leaf water potential of N14 reached the minimum value (−1,8 MPa) about 7 days earlier than ψℓ of the other varieties. The delay in the development of stress in the second stress period compared with the first could be attributed to fewer leaves per plot and lower evaporation, radiation and air temperature (Figure 1).
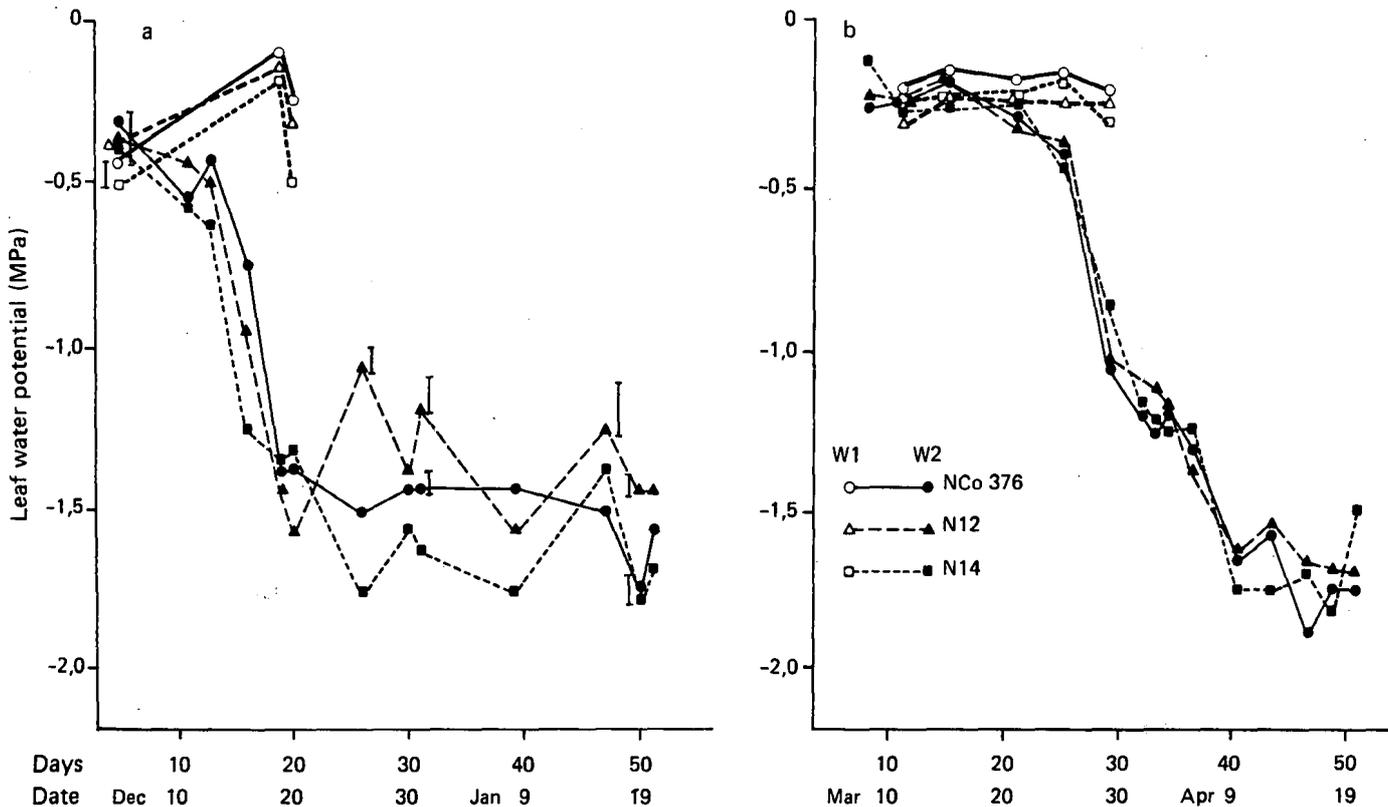
FIGURES 2a and 2b Midday leaf water potential (ψℓ) of well watered (W1) and stressed (W2) plants during the first stress period in December 1984/January 1985 (A) and during the second stress period during March/April 1985 (B). Bars denote standard errors larger than symbols.
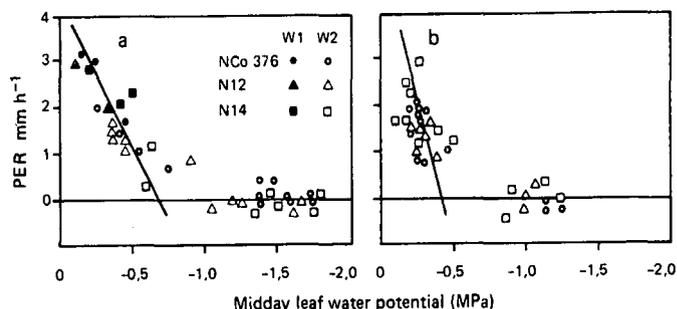
Plant extension rate (PER)

PER of fully irrigated plants ranged between 2,0 and 3,0 mm h^{-1} in both measurement periods. PER of irrigated N12 tended to be lower than PER of NCo 376 or N14. PER was apparently reduced when midday $\psi\ell$ fell below −0,2 MPa in the first stress period (Figure 3a). No plant extension occurred when $\psi\ell$ fell below −1,0 MPa but by regressing PER on $\psi\ell$ above this value it was evident that plant extension stopped when $\psi\ell$ reached −0,7 ± 0,05 MPa. PER of stressed plants recorded overnight in December (Figure 4) was well below that of irrigated plants even when $\psi\ell$ rose to values which were not markedly restrictive for irrigated plants. PER of stressed plants nevertheless dropped below this limited rate when $\psi\ell$ decreased slightly at 06h00. Plant extension ceased when $\psi\ell$ was between −0,5 and −1,0 MPa on 21 December and there was contraction of the growing portion of the stalk when $\psi\ell$ fell below −1,0 MPa at about 07h00. Plant extension in the second stress cycle reduced to zero at a higher $\psi\ell$ (−0,4 ± 0,05 MPa) than in the first stress period (Figure 3b) and was thus at least as sensitive to leaf water potential as in the first stress period. When measured overnight on 1 and 2 April 1985, PER was positive only while $\psi\ell$ was more than −0,5 MPa (Figure 5). Although $\psi\ell$ recovered almost completely overnight PER of stressed plants recovered to less than half the extension rate of irrigated plants. There appeared to be a considerable degree of hysteresis in the relationship between these two expressions of water stress and the threshold values mentioned above apply to increasing rather than decreasing stress. The initial rapid decline in PER was possibly due to a reduction in the elongation of young cells and the effect of water stress may be fully reversible. This could explain the daily fluctuations in PER of W1 plants (Figure 5) and the low extension rates of these plants early in the morning were probably due to low temperatures. Cell division or cell wall synthesis was possibly reduced when stress was prolonged in W2 plants and the recovery in PER overnight may have been limited by the number of cells capable of expansion (Hsaio[6]).

Sugarcane leaf extension occurs largely in the undifferentiated tissue 40 to 100 mm above the apical meristem and stalk extension occurs most rapidly about 40 mm below the meristem (van Dillewijn[19]). The water potential of the xylem in this region was probably similar to that measured in the expanded leaf blades since pressure gradients in the xylem are generally smaller than 0,05 MPa m^{-1} even when transpiration is rapid (Slayter[16]). The osmotic potential of cells in the elongating region may be considerably lower than that of the cells of the expanded blade (Michelena and Boyer[13]) and turgor pressure of the expanding cells would be greater than that of the cells of expanded blade. Cell turgor is thought to be directly involved in the mechanism of cell elongation (Boyer[1]; Green[3]; Green and Cummins[4]) but some experiments have shown that turgor pressure may not always be important for elongation (King and Bush[11]; Michelena and Boyer[13]).

Leaf resistance (rs)

Diffusive resistance of leaves from irrigated plants remained at about 0,25 s mm^{-1} during December but rose as high as 0,5 s mm^{-1} during April (Figure 6). Kortschak and Forbes[12] found that photosynthetic capacity of unstressed sugarcane leaves of the same age decreased as the crop aged. This may have resulted from an increased stomatal resistance such as that observed in this experiment. Leaf resistances of plants stressed for the first time rose above these minimum values when plants had been without irrigation for 10 days and continued to rise for a further 10 days. After

a slight recovery, rs rose to the limit of the porometer's range (3,5 s mm^{-1}) 40 to 50 days after irrigation had ceased (Figure 6a). The increase in rs was most rapid in N12 and least rapid in N14. When irrigation water was withheld for the second time diffusion resistance remained low for 20 days and then rose gradually to maximum values after a further 30 days (Figure 6b). Leaf resistances of N12 were significantly greater than those of the other varieties undergoing water stress for the second time. The comparatively rapid change in rs of N12 was also evident in the data shown in Figure 5. Leaf resistances of stressed plants were as low as those of irrigated plants at 08h00 and they rose steadily until 14h00 when $\psi\ell$

FIGURES 3a and 3b Plant extension rate (PER) and midday leaf water potential ($\psi\ell$) during the first (A) and second (B) stress periods.
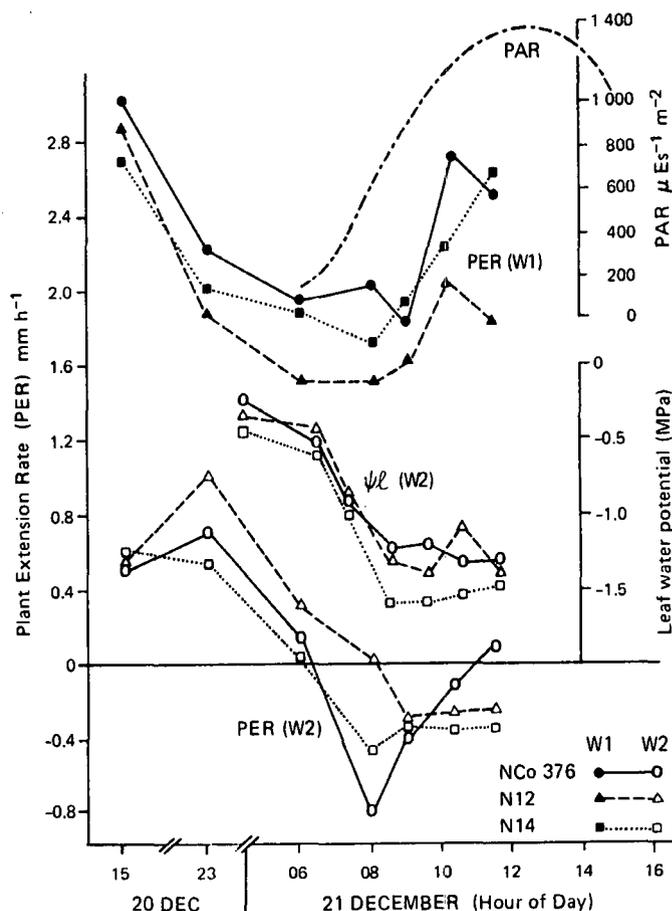

FIGURE 4 Plant extension rate (PER), leaf water potential ($\psi\ell$) and photosynthetically active radiation (PAR) above the canopy during a two-day period when W2 plants had been without irrigation or rain for 21 days (note break in abscissa).
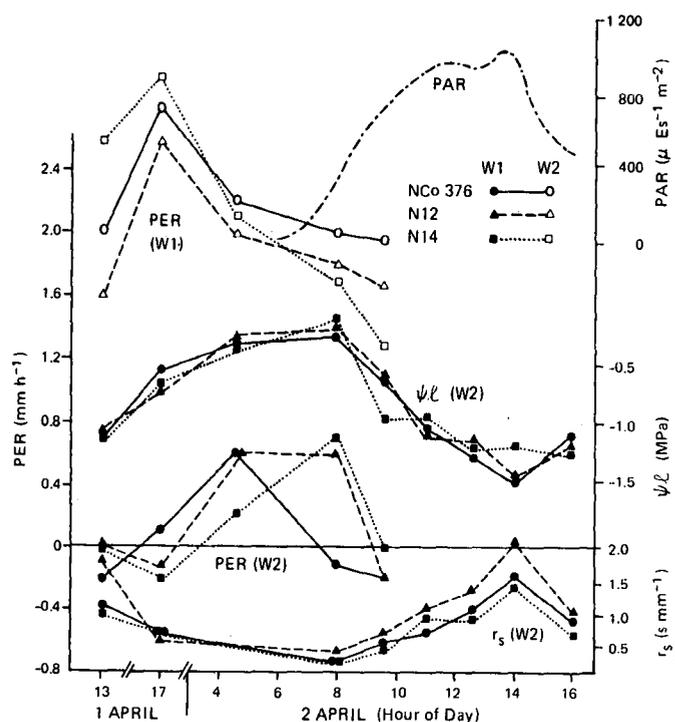
FIGURE 5 Plant extension rate (PER), leaf water potential ($\psi\ell$), leaf resistance (rs) and photosynthetically active radiation (PAR) above the canopy during a two-day period in the second stress cycle when W2 plants had been without irrigation or rain for 31 days (note break in abscissa).

was minimum for the day. Unlike plant extension, rs recovered almost completely overnight as the $\psi\ell$ approached zero. The differences between PER and rs in relation to water stress may have the following consequences for sugarcane:

- sucrose storage is enhanced as photosynthesis proceeds throughout the day, at least at moderate rates, for several days after growth has stopped because of water stress

- as stress becomes more severe, photosynthesis but not growth will occur for a limited time in the morning after $\psi\ell$ has recovered overnight. This will also favour sucrose storage.

Canopy temperature and crop water stress index

Canopy temperature (Tc) was used to compute a crop water stress index (CWSI) which was first described by Idso *et al*[7] and has been used by several authors including Mottram *et al*[14]. Jackson[11] provided a theoretical basis for a CWSI in terms of net radiation (Rn), aerodynamic resistance (ra), canopy temperature (Tc), air temperature (Ta) and vapour pressure deficit (VPD). CWSI at constant Rn and ra are represented graphically (Figure 7). The line X-Y represents the leaf to temperature differential (Tc-Ta) of the canopy with a minimum resistance (0,05 s mm^{-1}) and the line P-Q represents the (Tc-Ta) of the canopy with infinite resistance. The line X'-Y' (baseline) was obtained empirically from (Tc-Ta) of well-watered plants of sugarcane on days with more than five hours of sun and when the run of the wind was less than 150 km d^{-1}. The line described below fitted the data reasonably well, and the small range in VPD (kPa) is characteristic for the coastal cane belt. Standard errors for the intercept and slope were 0,61 and 0,52°C respectively.

$$(Tc\text{-}Ta) = 4,14 - 4,00 \times VPD°C \quad (r = 0,80 \; P < 0,0001)$$
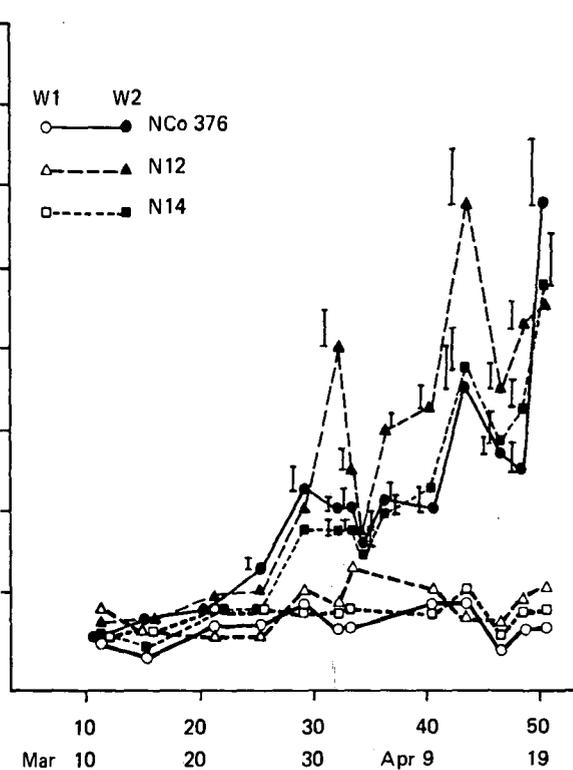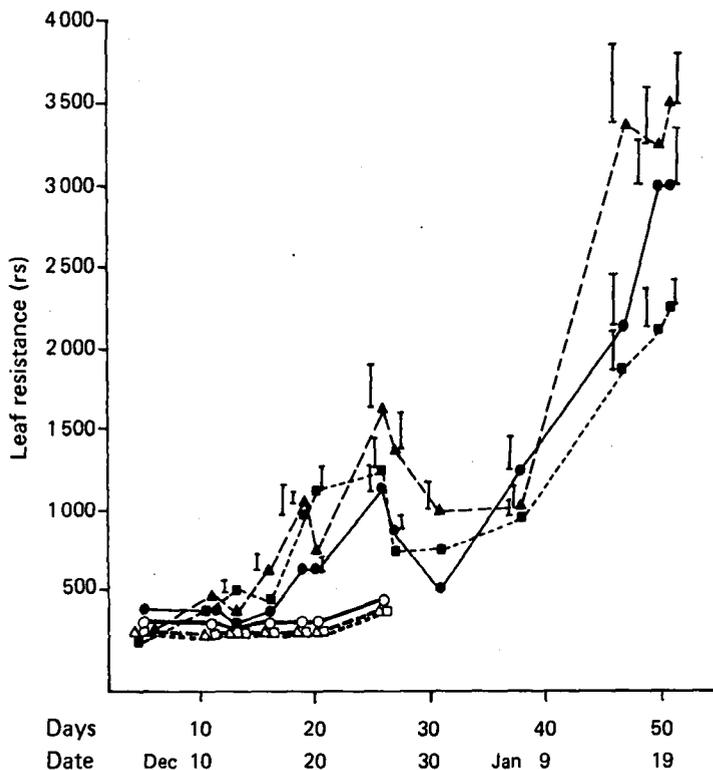
FIGURES 6, 6a and 6b Leaf resistance (rs) of well watered (W1) and stressed (W2) plants during the first stress period in December 1984/January 1985 (A) and during the second stress period during March/April 1985 (B). Bars denote standard errors larger than symbols.
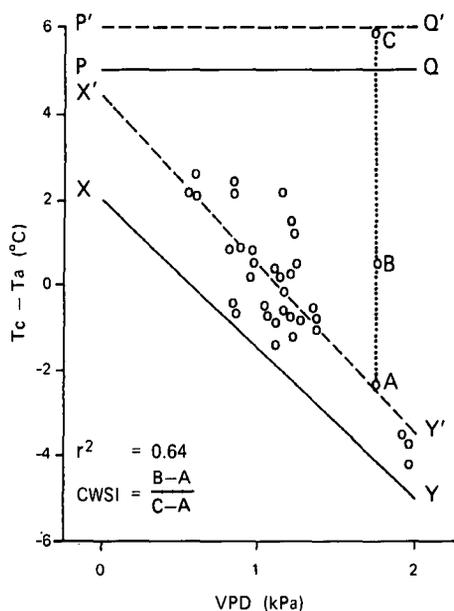
FIGURE 7 Effect of vapour pressure deficit (VPD) on the difference in temperature between air (Ta) and canopy (Tc) of unstressed (X-Y, X'-Y') and fully stressed (P-Q, P'-Q') crops. Solid lines were drawn after Jackson[10] and broken lines relate to sugarcane. Crop water stress index = (B-A) ÷ (C-A).

Table 1

Correlation and regression coefficients (r and b), intercept (a) and level of significance (P), and degrees of freedom (DF) for crop water stress index (CWSI), regressed on plant extension rate (PER), leaf water potential ($\psi\ell$) and leaf conductance (k)

Vari-able	Variety	r	b	SE(b)	a	SE(a)	p%	DF
PER	NCo 376	0,65	−0,12	0,04	0,38	0,08	0,77	14
	N12	0,70	−0,16	0,04	0,46	0,09	0,73	12
	N14	0,62	−0,17	0,04	0,51	0,12	1,44	14
	NCo 376	0,81	0,46	0,07	−0,07	0,09	0,01	20
	N12	0,94	0,48	0,07	−0,05	0,09	0,04	20
	N14	0,75	0,47	0,09	−0,11	0,12	0,01	20
k	NCo 376	0,79	−0,15	0,02	0,70	0,07	0,01	26
	N12	0,63	−0,12	0,03	0,63	0,93	0,04	26
	N14	0,70	−0,17	0,03	0,72	0,10	0,01	26

The maximum (Tc-Ta) values obtained from severely stressed cane were about 6,0°C and the line P'-Q' was drawn accordingly. The difference of 1 to 2°C between empirical (primed) and theoretical parameters may have been due to the difference in the height of the sugarcane canopy and the Stevenson screen where the Ta was measured. The other variables in Jackson's model (Rn and ra) may have differed as well.

CWSI was computed as the deviation from the baseline in leaf to air temperature differential (e.g. B-A) divided by the difference in Tc of canopies that were not stressed and 'fully' stressed canopies (e.g. C-A).

CWSI was well correlated with midday $\psi\ell$ which accounted for 88% of the variation in CWSI of N12 (Table 1). Ehrler et al[2] found that the Tc was not accurate when $\psi\ell$ fell below −3,0 MPa in wheat and that the two indications of water stress were not well correlated at a lower level of stress. The lowest values for midday $\psi\ell$ of sugarcane leaves were greater than −2,0 MPa and CWSI which was approaching its maximum (1,0) appeared to be linearly related to $\psi\ell$ at this stage. Jackson[10] pointed out that the large variability in $\psi\ell$ between leaves may make this the less accurate indicator of stress, at least during the early stages of stress development.

Leaf conductance was correlated with CWSI to a lesser extent than $\psi\ell$ (Table 1). This is not surprising as CWSI is more directly related to canopy resistance than it is to rs. Thom[18] outlined the factors which affect the relationship between canopy resistance and bulk stomatal resistance. The correlation between these two resistances increased with eddy velocity and this was higher in tall crops than in short crops. This correlation also depended on Ta. Wind was the only major climatic factor that was not explicit in Jackson's model. O'Toole and Hatfield[15] found that wind affected (Tc-Ta) substantially in rice, so wind which varied markedly during the experiment on the Natal coast probably affected CWSI to some extent.

Plant extension rate was not a good predictor of CWSI even though the correlation was highly significant ($P < 0.01$). Plant extension occurred only when $\psi\ell$ exceeded −1,0 MPa and at this level of stress the range in CWSI was relatively small (< 0,3). CWSI may not be sufficiently sensitive to detect a decline in PER when stress occurs but it could indicate a threshold $\psi\ell$ value of plant extension (about −0,7 MPa), which would be a useful criterion for monitoring plant water stress in an irrigation scheme or in variety evaluation trials. Growth rate would probably recover immediately after an irrigation at this point of stress but it would recover slowly if irrigation was delayed with a possible loss of efficiency in water usage (Figures 4 and 5).

The concept of estimating Tc at the same time each day from satellite transmissions to predict daily crop water requirement has been given serious consideration (Hatfield et al[5]; Wigand et al[20]) but it would be beneficial to gain more information on Tc and cane yield if this concept is to be developed further.

Conclusions

The results confirmed those previously obtained from a pot experiment (Inman-Bamber and de Jager[9]) in that the extension of sugarcane plants is highly sensitive to water stress but the stomata are not. Extension was reduced when $\psi\ell$ was less than −0,2 MPa and it ceased when $\psi\ell$ was −0,4 to −0,7 MPa. Stomatal resistance increased slightly with the onset of stress but remained relatively low until $\psi\ell$ fell below −1,2 MPa. The rapid increase in the resistance of N12 leaves and the slow response observed in N14 helped to explain why N12 is more and why N14 is less resistant to drought than NCo 376. It could not be inferred from the data that any of the varieties were rendered substantially less sensitive to water stress by the experience of the first stress. Differences in the temperature between leaf canopy and air were large enough, despite low vapour pressure deficits, to be used in the crop water stress index developed for the less humid climates. This index may be used in variety evaluation trials or in irrigation schemes to monitor crop water status since it may be obtained rapidly at some distance from the crop.

Acknowledgements

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