

A QUANTITATIVE STUDY OF WATER STRESS EFFECT ON SUGARCANE PHOTOSYNTHESIS

KOONJAH S S¹, WALKER S², SINGELS A³, VAN ANTWERPEN R³
and NAYAMUTH A R¹

¹*Mauritius Sugar Industry Research Institute, Réduit, Mauritius*

²*University of Free State, Bloemfontein, South Africa*

³*South African Sugarcane Research Institute, Private Bag X02,
Mount Edgecombe, 4300, South Africa*

skoonjah@msiri.intnet.mu walker.sci@mail.uovs.ac.za abraham.singels@sugar.org.za

Abstract

Water scarcity is often the most common limiting factor to sugarcane production. With the on-going climate change, the occurrence and duration of drought periods is expected to increase in the future. Water stress affects many processes linked to growth and development, among which is photosynthesis. If such effects were to be incorporated into models, it would lead to more accurate cane and sugar yield prediction. In this context, a trial was established under a rainshelter facility at Mount Edgecombe with well-watered and water-stressed sugarcane variety NCo376. The rate of photosynthesis (PN), light interception (LI), plant extension rate (PER), leaf temperature (Φ_T) and leaf water potential (Ψ_L) were measured, together with the soil water potential.

Mild water stress affected PER to a relatively greater extent than LI and PN. Difference in PN between the well-watered and water-stressed sugarcane were observed when the Ψ_L of the latter reached -0.7 MPa. At this stage the PN which was at $20.0 \mu\text{mol}/\text{m}^2/\text{s}$ started to decline, reaching the lowest level of $2.2 \mu\text{mol}/\text{m}^2/\text{s}$ at a Ψ_L of -1.6 MPa. A strong correlation ($R^2=0.97$) was obtained when regressing PN with Ψ_L so that for every 0.1 MPa decrease in Ψ_L there was a linear reduction in PN of $1.6 \mu\text{mol}/\text{m}^2/\text{s}$. The Φ_T of the stressed cane was higher due to the poorer cooling effect from higher stomatal resistance and accompanying reduction in transpiration rate. Regressing the values of PN against that of Φ_T in the range of 25 to 40°C showed that PN in the stressed crop decreased linearly by $0.4 \mu\text{mol}/\text{m}^2/\text{s}$ for every one-degree rise in temperature. The diurnal pattern of PN in the well-watered crop followed closely the daily trend of incoming solar radiation, whereas in the stressed cane (-1.6 Mpa Ψ_L) PN was reduced to almost zero after midday. Hence, the photosynthetic efficiency of the stressed cane at -1.6 MPa was 0.22% compared with 1.09% for the unstressed crop. The lower biomass accumulation in the water stressed cane was attributed to reduced LI, PER and PN.

Keywords: water stress, photosynthesis, leaf water potential, leaf temperature, light interception, efficiency

Introduction

Plants are frequently exposed to a variety of environmental stresses that may occur simultaneously, such as drought and high temperatures. With the ongoing climate change, the occurrence and duration of drought periods is expected to increase in the future, accentuating the risk of yield reduction and crop failure due to water stress. Water deficit can trigger a variety of plant responses. One of the more immediate responses is a reduction in the water

potential of plant tissues leading to diminished stomatal aperture (Yordanov *et al*, 2000; Meinzer and Grantz, 1989) and consequent reduction in transpiration rate and photosynthesis, as well as longer term responses such as growth inhibition, and accumulation of osmolytes (Serraj and Sinclair, 2002). Besides these physiological responses, plants also undergo morphological changes.

The sensitivity of photosynthesis to water stress varies in different species. Studies on sugarcane have shown that photosynthesis (PN) starts to be affected by water stress when the leaf water potential (Ψ_L) goes below -0.37 MPa (Du *et al*, 1996) and that, with further reduction in Ψ_L , there is a linear decrease in PN. In maize and wheat, the initial inhibition of photosynthesis was observed at ψ_L of -0.3 MPa (Beadle *et al*, 1973) and -1.0 MPa (Johnson *et al.*, 1974) respectively. In soybeans, 80% reduction in PN was reported when ψ_L decreased from -0.32 to -0.39 MPa. (Ohashi *et al*, 2000).

Apart from lack of water, photosynthesis is also affected by high temperatures during a drought period. Elevated temperatures increase respiration and therefore require greater carbon fixation for sustained growth and tissue maintenance. Limited transpirational cooling exacerbates the effects of the already high air temperatures by causing leaf temperature to rise above the air temperature, thus making a plant susceptible to photo-inhibition. Hence, the combined effects of water stress and high temperature have both additive and interactive effects on plant growth (Griffin *et al*, 2004).

Few studies have quantified the reduction in PN due to water stress in sugarcane. An improved understanding would be useful for crop growth models to refine yield prediction in sugarcane and to develop strategies to sustain high yields in the tropics.

Materials and Methods

The experiment was carried out under a rainshelter at the South African Sugarcane Research Institute (SASRI), Mount Edgecombe ($29^{\circ}43'20''S$, $31^{\circ}04'29''E$, elevation 96 m). The purpose of using the rainshelter was to ensure that no rain interfered with the treatments during the water stressed period. Sugarcane variety NCo376 was grown on a soil with an orthic topsoil (24% clay content and a rooting depth of 950 mm). The drained upper and lower limits of plant available water capacity were 26% and 13% (w/w) respectively.

The experiment plot consisted of 24 rows of sugarcane, each 6.5 m long. The interrow spacing was 1.2 m. After harvest of the plant cane in August 2000 the whole field was drip-irrigated. The crop showed no sign of any nutrient deficiencies or attack by pests and diseases at the start of the trial. From 8 January 2001 water was withheld from half of the trial and this constituted the dry plot. The other half, known as the wet plot, was irrigated at regular time intervals so that the plant available water capacity never fell below 21%. Two equitensiometers were permanently buried at depths of 250 and 500 mm in each plot and hourly measurements of soil water potential (Ψ_s) were automatically recorded on a CR10X datalogger.

During the trial, midday Ψ_L was destructively determined on the topmost, fully expanded leaf using a Scholander pressure chamber. This was carried out on five leaves per plot between 12h00 and 14h00 on a daily basis. Plant extension rate was measured by means of growth transducers as designed by Inman-Bamber (1995), and the CR10X datalogger was used to record the data hourly. The amount of total radiant flux intercepted by the canopy in the water-stressed and well-watered plots was measured by placing a 1 m tube solarimeter just

below the lowest green leaves between two rows, and another tube solarimeter placed above the canopy to measure incoming radiant flux. All the readings were logged in the CR10X datalogger hourly.

A portable LCA-3 infrared gas analyser (IRGA Analytical Development Company, England) was used to measure the rate of photosynthesis, together with incoming photosynthetically active radiation (PAR) and leaf temperature. The measurements were made on portions of leaves exposed directly to the sunlight, and the leaves were maintained at right angles to incident solar radiation. The IRGA readings were taken on five plants in each plot. Diurnal readings with the IRGA were also carried out at three-hour intervals when there was full sunshine.

Results and Discussions

Leaf water potential (Ψ_L)

During the period of the trial the midday Ψ_L of the irrigated cane was generally above -0.5 MPa (Figure 1). From eight days after water stress, significant difference in midday Ψ_L existed between the stressed and irrigated cane (Figure 1). During this period, the soil water potential (Ψ_S) of the stressed cane was -52 kPa. Up to 16 days without water, the water stress could have been categorised as mild, with a difference of 0.27 MPa existing between the stressed and well-watered cane. By this time the Ψ_L of the stressed cane was -0.82 MPa and the Ψ_S in the dry plot dropped to -140 kPa. Inman-Bamber and de Jager (1986) got a Ψ_L below -0.5 MPa 12 days after irrigation was withheld. This level of water deficit will impact negatively on the normal growth of the crop by reducing the rate of plant growth rate and related physiological processes.

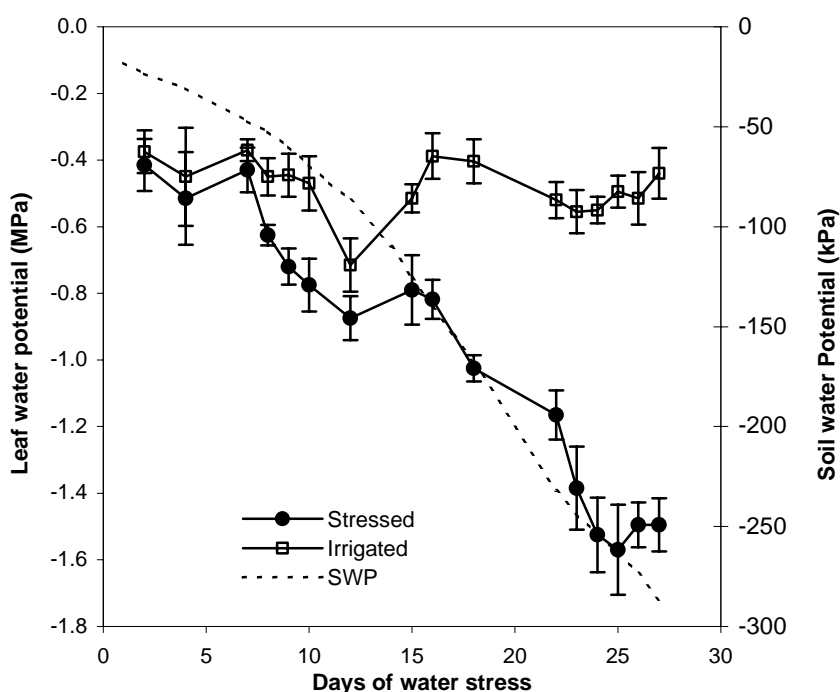


Figure 1. Midday leaf water potential in water-stressed and well-irrigated sugarcane leaf blades, and soil water potential (SWP) in the dry plot.

As the Ψ_S level dropped further to -240 kPa, the sugarcane plants were under major water stressed condition. The lowest Ψ_L was -1.57 MPa and it occurred 25 days after water was withheld. This value was close to that obtained by Inman-Bamber and de Jager (1986) but at a longer period of 31 days without water. The difference in Ψ_L between the two treatments during the major water stressed condition was 0.83 ± 0.24 MPa and was significantly different at the 5% level. At the lowest recorded Ψ_L , the observed plant extension rate of the stressed plant was zero and each stalk had less than five green leaves. A good correlation ($R^2=0.94$) was obtained when regressing the Ψ_L of sugarcane with the Ψ_S . Hence, these values could be taken into consideration for irrigation scheduling in sugarcane fields during the dry period in order to limit yield reduction.

Plant extension rate (PER)

When compared to the growth of well-watered cane, PER of haulms in the dry plot started to be affected after withholding water for nine days (Figure 2). After this period, significant differences in PER between the well-watered and water stressed canes were recorded. The plant extension rate was reduced when the Ψ_S fell to -60 kPa and the Ψ_L to -0.7 MPa. This decline in extension rate continued to a value of almost zero when the Ψ_S was around -270 kPa and the midday Ψ_L was -1.5 MPa. The Ψ_L value was close to that obtained by Inman-Bamber and de Jager (1986) corresponding to complete cessation of PER in sugarcane grown in pots. The rapid decline in PER was due to a reduction in the elongation of young cells, as was observed in maize by Boyer (1970). Compared to sugarcane, maize is slightly more sensitive to water stress, as it was reported that leaf elongation rate stopped when midday Ψ_L was reduced to -1.1 MPa (Hsiao and Xu, 2000).

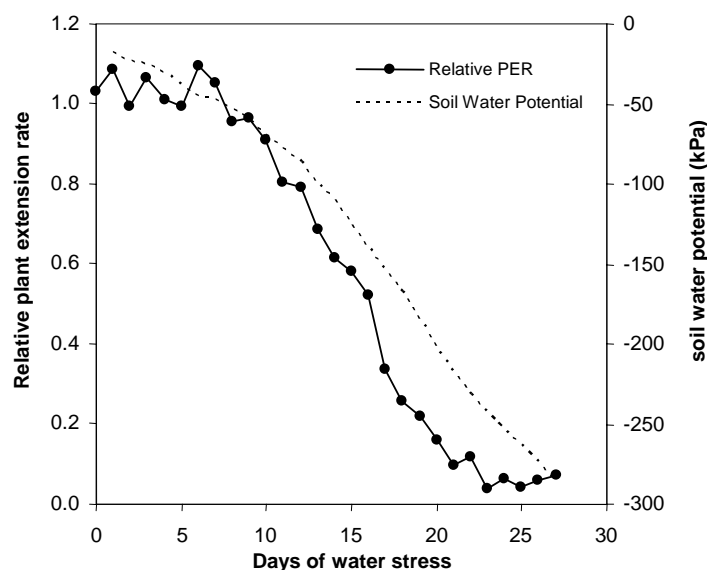


Figure 2. Plant extension rate (PER) of stressed sugarcane relative to well-irrigated sugarcane and the change in soil water potential with time in the plot without irrigation.

There was a direct relationship between Ψ_L and PER, as shown in Figure 3. PER in irrigated plants, which had the lowest Ψ_L of -0.5 MPa, ranged from 30 to 50 mm/day. The regression of PER on Ψ_L using the values from the stressed cane showed that plant extension ceased

when Ψ_L fell below -1.2 MPa. This value is much lower than that obtained by Inman-Bamber and de Jager (1986) where PER stopped when Ψ_L reached -0.7 MPa.

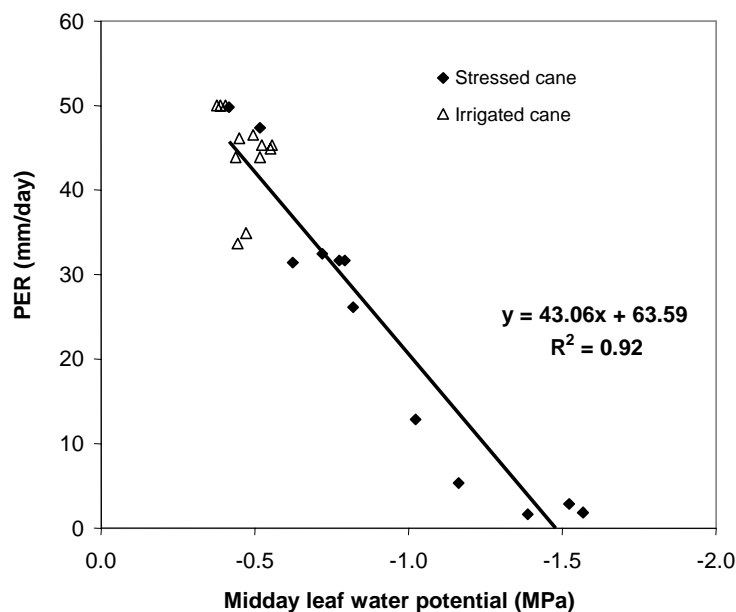


Figure 3. Plant extension rate and midday leaf water potential during the trial. Regression line based on data obtained from stressed cane only.

Light interception

The fractional total radiant flux intercepted by the fully irrigated crop ranged from 0.79 to 0.85. Each haulm had about nine fully expanded green leaves. When the crop was under mild water stress (up to 20 days without water), the decrease in radiation interception compared to irrigated cane was of the order of 10% (Figure 4).

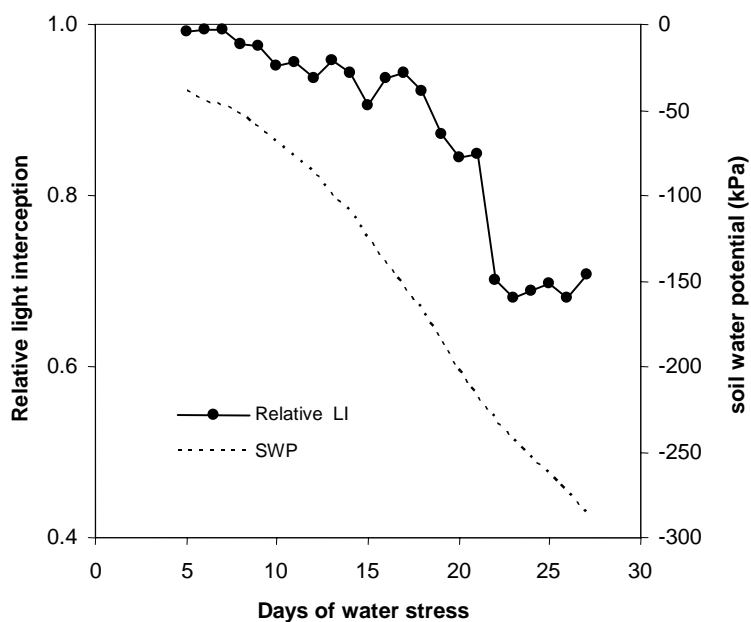


Figure 4. Light interception of stressed sugarcane relative to irrigated sugarcane and the change in soil water potential (SWP) with time in the plot without irrigation.

Beyond 20 days without water, the crop intercepted 25% less solar radiation than the well-watered crop. At this stage the soil water potential was just below -140 kPa.

The stressed plants had on average only four to five green leaves at this stage, which, due to loss in leaf turgidity, remained rolled during the day, and most of the lower leaves were dead. Thus the stressed crop had a reduced leaf area, which intercepted less solar radiation than the fully irrigated crop. Monteith (1972) associated lower radiation interception due to water deficit with a reduction in crop biomass and yield.

Rate of photosynthesis

Time course of the effect on photosynthetic gas exchange

During the trial, the well-watered plants had more than eight green leaves and the measured photosynthetic rate (PN) was $18.4 \pm 1.8 \mu\text{mol}/\text{m}^2/\text{s}$. The Ψ_L of the unstressed crop was above -0.5 MPa. The response of leaf blade PN to water stress could be divided into three parts: no detectable effect for the first nine days, a progressive decrease from the 9th to the 13th day, and a sudden decrease to zero thereafter (Figure 5). When PN started to be affected after nine days of water restriction, the Ψ_S was around -60 kPa and Ψ_L was -0.72 MPa. There was significant difference in PN between the stressed and well-watered canes 16 days after water stress, and the Ψ_L of the stressed cane was -0.82 MPa. The rate of photosynthesis decreased significantly to an average value of $2.2 \mu\text{mol}/\text{m}^2/\text{s}$ after 25 days without water, when the Ψ_S reached -260 kPa and Ψ_L fell to -1.57 MPa.

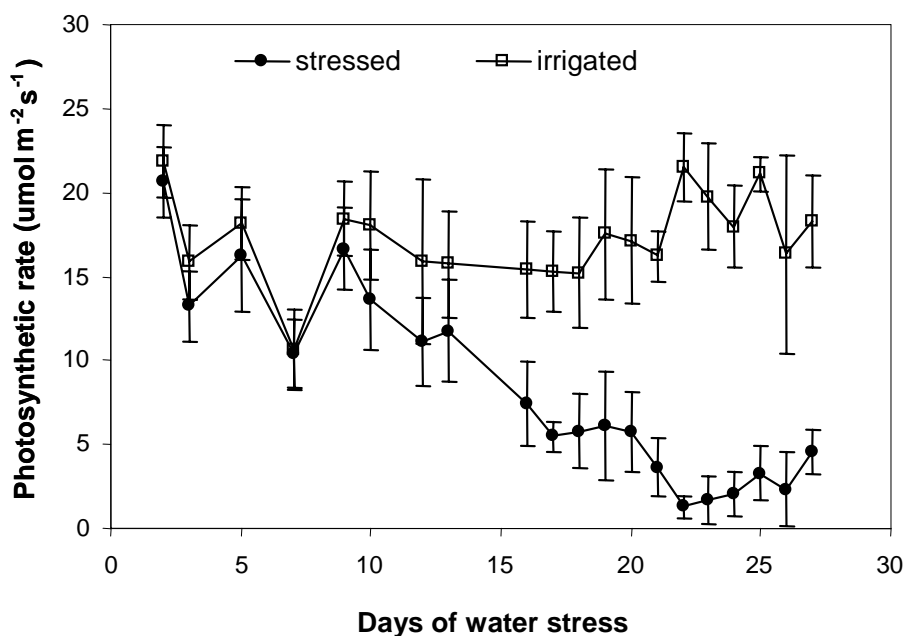


Figure 5. Time course of photosynthetic rate in water-stressed and well-irrigated sugarcane.

The initial decrease in PN of the stressed plant was likely due to the closure of stomata, which reduced the amount of carbon dioxide necessary for photosynthesis. In the severe stage of water stress, the plants had at most five green leaves, which were rolled during the day due to loss of turgidity. The decrease in PN to the very low level could be attributed to both

stomatal and non-stomatal limitations (Du *et al.*, 1996; Lawlor, 2002). Similar reduction in PN was observed in maize, but in the latter crop PN was affected much earlier, when the Ψ_L fell to below -1.0 MPa (Pelleschi *et al.*, 1997).

Diurnal variation

Diurnal variation in net photosynthesis for the stressed and irrigated plants was measured 20 and 25 days after the withdrawal of water (Figure 6). Twenty days after withholding water from the stressed plot, the PN measured before noon was $7.5 \mu\text{mol}/\text{m}^2/\text{s}$ as compared to $18.0 \mu\text{mol}/\text{m}^2/\text{s}$ in the well-watered crop. In the stressed plants, low photosynthetic rate was recorded at high solar radiation, whereas in irrigated plants, PN increased with higher solar radiation. The response of net photosynthesis to increasing PAR was significantly higher in the irrigated canes than in the stressed plants, suggesting that the stomata in the latter may be partially closed at relatively lower PAR.

Twenty-five days without water, it was observed that the rate of photosynthesis in the stressed plant increased to $8 \mu\text{mol}/\text{m}^2/\text{s}$, and then decreased to almost zero by noon. In response to the severe water stress conditions, the stomata in the stressed sugarcane plant appeared to be closed at high PAR, thus limiting any flux of carbon dioxide into the leaf and reducing considerably the rate of photosynthesis.

The amount of carbon dioxide fixed per m^2 green leaf area, together with the photosynthetic efficiency during these two days, was estimated by integrating the area under the curves shown in Figure 6. The values obtained for daily total CO_2 fixation and photosynthetic efficiency by the irrigated and water stressed plants are shown in Table 1. Twenty days after water stress, the sugarcane plant was able to fix only $10.91 \text{ mg CO}_2/\text{m}^2$ representing about 43% of its potential amount under non-limiting water conditions. This amount decreased further during 25 days without water and represented only 20% of the potential of the fully-irrigated crop. The low leaf area index measured in the stressed canes was responsible for the inferior carbon dioxide fixation as compared to the crop without water stress.

Photosynthetic efficiency (PE) was computed as a percentage of total amount of carbon dioxide fixed over total amount of incoming PAR. In stressed cane, PE of 0.44 and 0.22% was obtained at 20 and 25 days after withholding water, respectively. The PE in the well-watered cane was around the 1% level.

Table 1. Leaf area index, daily carbon dioxide fixation and photosynthetic efficiency (%) in irrigated and water-stressed sugarcane plants.

Sugarcane variety NCo376	Leaf area index	CO_2 fixation ($\text{mg CO}_2/\text{m}^2$)	Photosynthetic efficiency (%)
Water stressed for 20 days	2.5	10.91	0.44
Control (irrigated)	6.4	25.34	1.01
Water stressed for 25 days	2.4	6.34	0.22
Control (irrigated)	7.1	31.36	1.09

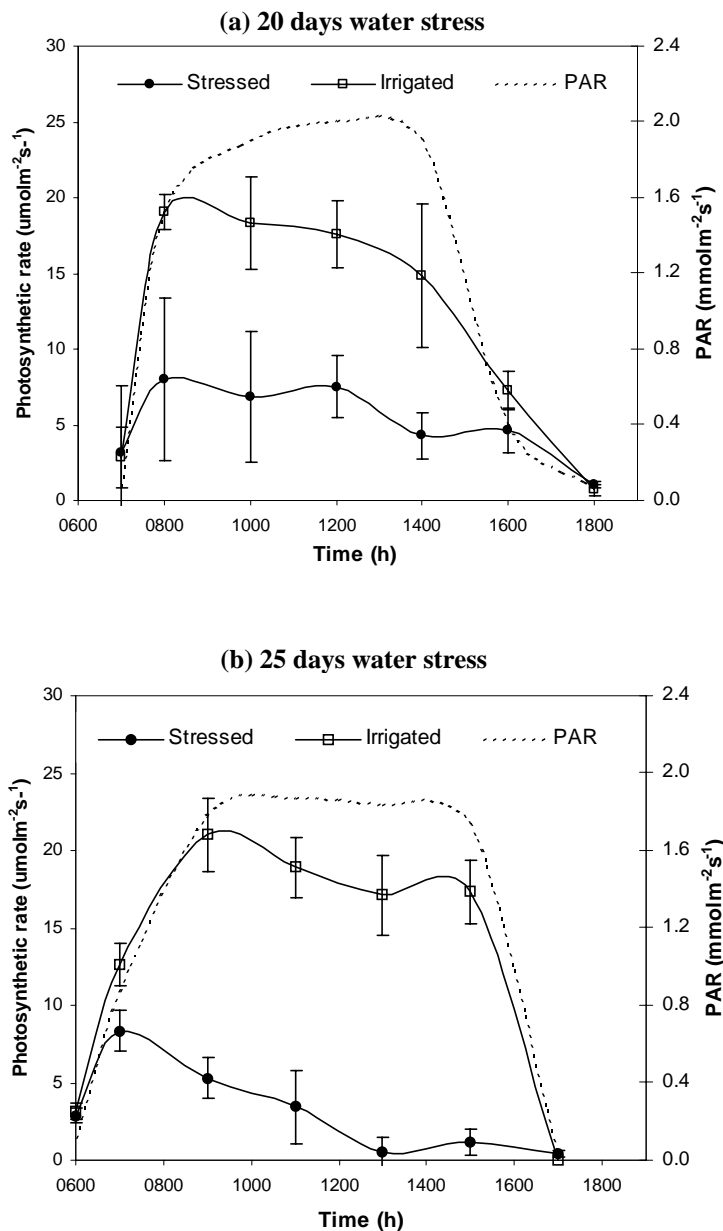


Figure 6. Diurnal variation in net photosynthesis and photosynthetically active radiation (PAR) 20 and 25 days after withholding water.

Response of PN to water stress, photosynthetically active radiation (PAR) and leaf temperature

A strong correlation was obtained when the values of PN in the stressed canes were regressed against those of Ψ_L (Figure 7). When Ψ_L decreased from -0.52 to -1.53 MPa, PN decreased almost linearly from 16.29 to 1.30 $\mu\text{mol}/\text{m}^2/\text{s}$. From the linear regression line, it could be deduced that for every 0.1 MPa decrease in Ψ_L there was a linear reduction in PN of 1.6 $\mu\text{mol}/\text{m}^2/\text{s}$. A reduction in midday Ψ_L from -0.37 to -0.85 MPa in the sugarcane plant has been reported to cause a linear decline in the carbon exchange rate from 40 to 20 $\mu\text{mol}/\text{m}^2/\text{s}$ (Du *et al*, 1996). The same authors observed that photosynthetic rate was severely affected when Ψ_L was about -1.61 MPa, which is in line with that observed in the present study.

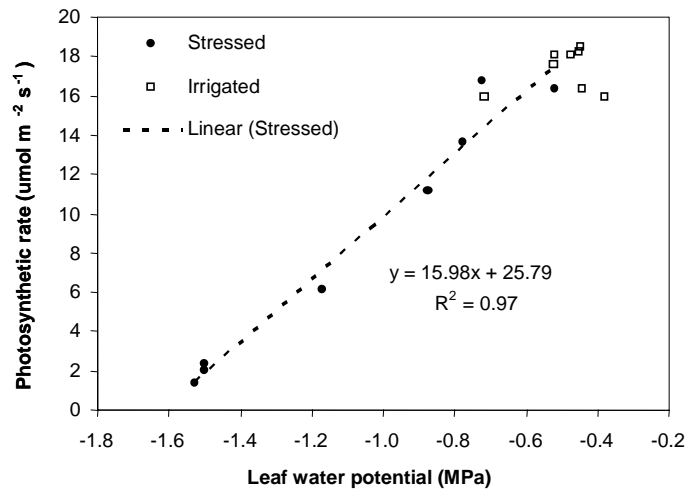


Figure 7. Regression of photosynthetic rate against the leaf water potential of water-stressed and irrigated sugarcane.

The PN response to PAR under well-watered conditions (Ψ_L -0.4 MPa) shows that PN increased rapidly with increasing amount of PAR, and that PN was fully saturated at $1.8 \text{ mmol/m}^2/\text{s}$, whereas at 20 days without water (Ψ_L -1.0 MPa), the response to change in PAR was lower than the well-watered crop and PN was saturated at about $1.2 \text{ mmol/m}^2/\text{s}$ (Figure 8). Thus, it could be deduced that stomatal closure in water-stressed cane occurred at lower PAR than in fully-irrigated cane.

The variation in PN with leaf temperature (Φ_T) in both irrigated and water-stressed sugarcane is shown in Figure 9. In well-watered canes, PN increased rapidly when leaf temperature was in the range of 26 to 32°C , after which it stabilised at about $17 \text{ } \mu\text{mol/m}^2/\text{s}$. In stressed canes, a linear decrease in PN of $0.4 \text{ } \mu\text{mol/m}^2/\text{s}$ for every degree rise in Φ_T was obtained when the values of PN were regressed against those of Φ_T in the range of 25 to 40°C . Stomatal closure was likely responsible for the reduction in PN and also decreased the rate of transpiration, which has consequences for cooling the leaves. The latter effect might explain the observed decreasing response of PN with a rise in leaf temperature of the stressed canes.

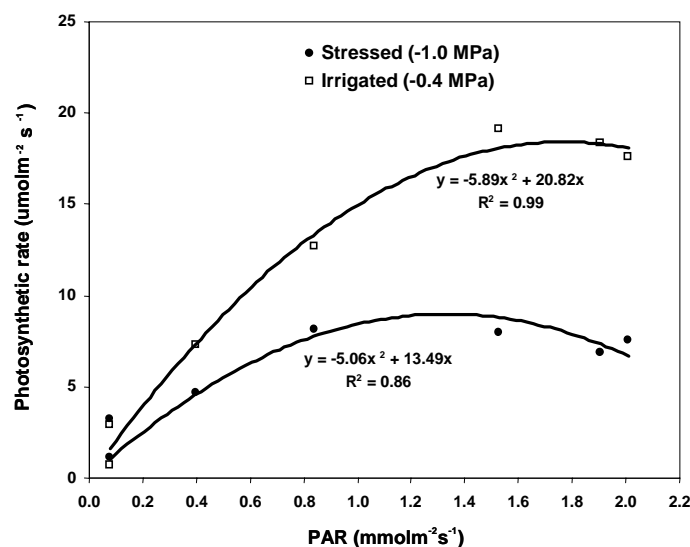


Figure 8. Photosynthetic response of irrigated and stressed (20 days without water) sugarcane to incident photosynthetically active radiation (PAR).

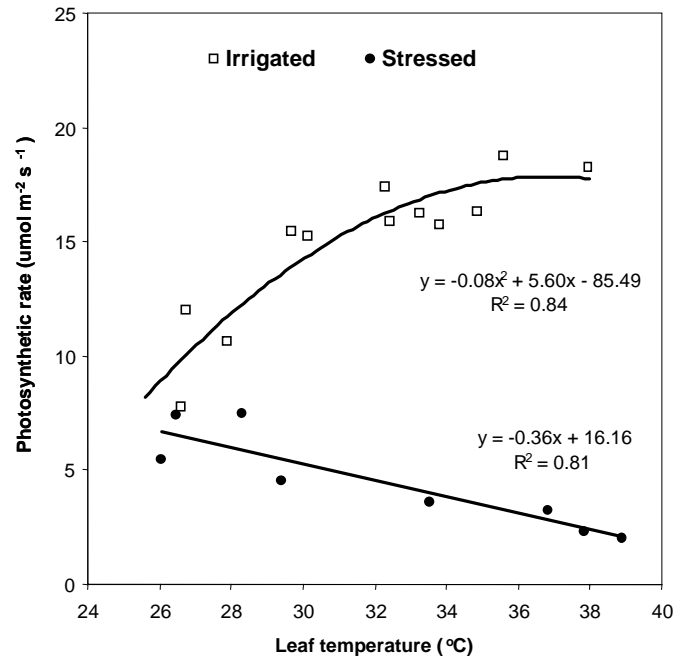


Figure 9. Regression of photosynthetic rate against the leaf temperature of water-stressed and irrigated sugarcane.

Conclusions

Water stress is one of the most important causes of decreased productivity in plants. During the onset of water stress, the various yield-determining processes in sugarcane were significantly affected in the following sequence. First, the plant extension rate (PER) was affected, followed by light interception and the rate of photosynthesis. A reduction in the effective leaf area of the stressed crop reduced radiation interception by the canopy, which in turn exacerbated the ability of the crop to convert intercepted energy to biomass by the process of photosynthesis.

A strong correlation was obtained when the values of PN in the stressed canes were regressed with those of Ψ_L and Φ_T . The diurnal pattern of PN in the well-watered crop followed closely the daily trend of incoming solar radiation whereas in the stressed cane at a midday Ψ_L of -1.6 MPa, PN was reduced to almost zero. Thus, stressed cane gave a photosynthetic efficiency of only 0.22% compared with 1.09% for the well-watered control.

This study showed that the different yield determining processes in sugarcane that are affected by water stress can be categorised according to the order in which they are affected, starting from the most sensitive to the least sensitive. This will help researchers and farmers to better understand the response of sugarcane to water stress and to develop better strategies in terms of irrigation scheduling during periods of drought. The results from this study, especially photosynthesis and radiation interception, can be used to assist in crop growth modelling to provide better estimates of yield. Many models are based on incoming radiation for the simulation of crop growth, but not all radiation received by the crop is used in crop growth. By including the photosynthesis reduction during water stress for crop models, simulation of crop growth would be more precise and yield forecasting more accurate.

The present study should be extended to other commercial sugarcane varieties in South Africa so that the results can be used to develop drought management strategies and to fine tune existing crop growth models for better prediction of sugarcane yield at the country level.

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REFERENCES

- Beadle CL, Stevenson KR, Neumann HH, Thurtell GW and King KM (1973). Diffusive resistance, transpiration, and photosynthesis in single leaves of corn and sorghum in relation to leaf water potential. *Can J Plant Sci* 53: 537-544.
- Boyer JS (1970). Leaf enlargement and metabolic rates in corn, soybean and sunflower at various leaf water potentials. *Plant Physiol* 46: 233-235.
- Du YC, Kawamitsu Y, Nose A, Hiyane S, Murayama S, Wasano K and Uchida Y (1996). Effects of water stress on carbon exchange rate and activities of photosynthetic enzymes in leaves of sugarcane (*Saccharum* sp.). *Aust J Plant Physiol* 23: 719-726.
- Griffin JJ, Ranney TG and Pharr DM (2004). Heat and drought influence photosynthesis, water relations and soluble carbohydrates of two ecotypes of redbud (*Cercis canadensis*). *J Am Soc Hort Sci* 129(4): 497-502.
- Hsiao TC and Xu LK (2000). Sensitivity of growth of roots versus leaves to water stress: Biophysical analysis and relation to water transport. *J Exp Bot*, Special issue 51(350): 1595-1616.
- Inman-Bamber NG (1995). Automatic plant extension measurement in sugarcane in relation to temperature and soil moisture. *Field Crops Res* 42: 135-142.
- Inman-Bamber NG and de Jager JM (1986). Effect of water stress on growth, leaf resistance and canopy temperature in field grown sugarcane. *Proc S Afr Sug Technol Ass* 60: 156-161.
- Johnson RR, Frey NM and Moss DN (1974). Effect of water stress on photosynthesis and transpiration of flag leaves and spikes of barley and wheat. *Crop Sci* 14: 728-731.
- Lawlor DW (2002). Limitation to photosynthesis in water-stressed leaves: Stomata vs. metabolism and the role of ATP. *Annals of Botany* 89: 871-885.
- Meinzer FC and Grantz DA (1989). Stomatal control of water use on sugarcane. *Haw Sug Technol* 47: A72-A75.
- Monteith JL (1972). Solar radiation and productivity in tropical ecosystems. *J Appl Ecol* 69: 747-766.
- Ohashi Y, Saneoka H and Fujita K (2000). Effect of water stress on growth, photosynthesis, and photoassimilate translocation in soybean and tropical pasture legume siratro. *Soil Sci Plant Nutr* 46(20): 417-425.
- Pelleschi S, Rocher JP and Prioul JL (1997). Effect of water restriction on carbohydrate metabolism and photosynthesis in mature maize leaves. *Plant Cell Evt* 20: 493-503.
- Serraj R and Sinclair TR (2002). Osmolyte accumulation: Can it really help increase crop yield under drought conditions? *Plant Cell Evt* 25: 333-341.
- Yordanov I, Velikova V and Tsonev T (2000). Plant responses to drought, acclimation and stress tolerance. *Photosynthetica* 38(1): 171-186.