Effects of Elevated Temperature and CO₂ on Biomass and Sucrose Accumulation of Selected Sugarcane Genotypes

A.L.C. De Silva, W.A.J.M. De Costa and L.D.B. Suriyagoda

1Postgraduate Institute of Agriculture, University of Peradeniya, Peradeniya, Sri Lanka
2Department of Crop Science, Faculty of Agriculture, University of Peradeniya, Peradeniya, Sri Lanka

ABSTRACT

Global warming caused by increasing atmospheric CO₂ concentration, and the resulting increase in air temperature is a considerable challenge in crop production. Hence, the objectives of this study were to determine: (a) responses of biomass and sucrose accumulation of sugarcane to elevated CO₂ (ECO₂) and elevated temperature (ETₐ), both individually and together, and (b) genotypic variation of these responses. A three-factor factorial experiment considering the combination of CO₂ concentrations and temperatures as the main-plot factor and eight sugarcane varieties as the sub-plot factor arranged in a split-plot design in open-top chambers. Plots in open field conditions were the negative control. The main plot factor had four levels, combinations of ambient/elevated CO₂ concentrations (344-351/777-779 ppm) and ambient/elevated temperatures (34.9-35.6/36.6-38.4 °C). Significant treatment × variety interaction effects observed on the number of shoots per hill, sucrose% (Pol), and pure obtainable cane sugar (POCS) in cane juice. Genotypic variations were significant in all variables measured. Elevated Tₐ increased the number of shoots per hill in 4 out of 8 varieties. Biomass accumulation of sugarcane on the dry weight basis did not respond clearly to the simulated future climatic conditions. The response of Pol and POCS to ECO₂ and the combination of ECO₂ and ETₐ varied depending on varieties with decreased, increased, or no response. Notably, Pol and POCS in the variety SL88116, which had higher respective values at ambient and simulated future climatic conditions, were not affected by either ECO₂ or ETₐ individually or in combination. The responses and the significant genotypic variation observed in sucrose accumulation to ECO₂ and ETₐ, both individually and together, demonstrate considerable scope in sugarcane to breed varieties to maintain the stability of sugar recovery in CO₂-rich warm climates.
INTRODUCTION

Increasing atmospheric CO₂ concentration and resulting increase of air temperature (Tₐ) has variable impacts on the productivity of sugarcane depending on varieties and growing conditions (Marin et al., 2013, 2014). Therefore, determining the impacts of climate change on the growth and productivity of sugarcane is vital to sustaining an adequate supply of sugar and its by-products to meet their increasing demand in the future. Biomass and sucrose accumulation of sugarcane shows variable responses to elevated CO₂ (ECO₂) and temperature (ETₐ) depending on the specific growing conditions. For example, several studies conducted using potted plants grown in open-top chambers (OTCs) under well-watered conditions show that biomass accumulation of sugarcane increases at ECO₂ (Vu et al., 2006; De Souza et al., 2008; Vu and Allen, 2009; Allen et al., 2011; Marin et al., 2013). Vu et al. (2006) has shown ECO₂ increases sucrose accumulation as well. In contrast, Stokes and colleagues did not observe a stimulation of biomass accumulation in ECO₂ under well-watered conditions (Stokes et al. (2016), which agrees with the majority of research findings on C₄ species (Lawlor and Mitchell, 1991; Bowes, 1993; Kimball et al., 2002; Kim et al., 2006; Leakey et al., 2006, 2009). Elevated CO₂ has been shown to induce shifts in the carbon and nitrogen dynamics, and consequently, changes in the source-sink interactions within crops (Wolfe et al., 1998). Furthermore, the interactive effects of ECO₂ and ETₐ on the physiology and growth of plants differ depending on their genetic make-up and ecological adaptation (Eller et al., 2013). Therefore, it is likely that the magnitude of the impacts of increasing atmospheric CO₂ could be different on different crops grown under varying environmental and management conditions (Chaves and Pereira, 1992; Leakey et al., 2006).

Vu and Allen (2009) show significant increases and genotypic variation in biomass accumulation of sugarcane in response to ETₐ. In addition, they observe amplification of the stimulation of biomass accumulation of sugarcane when ECO₂ is combined with ETₐ. In contrast, Allen et al. (2011) show that the increasing trend of biomass and sucrose accumulation in sugarcane at ECO₂ is down-regulated when ECO₂ is combined with ETₐ. Only limited work reported on the response of sugarcane growth and yields to climate change (Vu et al., 2006; De Souza et al., 2008; Vu and Allen, 2009; Allen et al., 2011; Stokes et al., 2016). Even such experiments have been conducted at the lower temperature range, where the daily mean temperature did not exceed 29 °C while being less than 25 °C for most of the crops’ duration. The net assimilation rate of sugarcane shows a positive correlation with air and soil temperature (Venkataramana et al., 1984). However, increasing temperatures increase respiration rates (Atkin and Tjoelker, 2003) resulting in a decrease in growth and sucrose accumulation. Therefore, even though growth and sucrose accumulation may increase with ETₐ up to an optimum temperature, further temperature increases are likely to reverse this response. Accordingly, the objectives of this study were to determine responses, and genotypic variations of biomass and sucrose accumulation of sugarcane to ECO₂ and ETₐ expected in the future.

METHODOLOGY

Experimental location and period

The experiment was conducted in open top chambers (OTCs) installed in the research farm of the Sugarcane Research Institute (SRI), Uda Walawe, Sri Lanka (6°24′40″N latitude, 80°50′17″E longitude and 76 m altitude) from 12th September 2017 to 25th September 2018. The experimental site has an average annual rainfall of 1450 mm with a distinctly bimodal distribution. The average annual minimum and maximum temperatures and daily pan evaporation rates were 22 °C and 32 °C and 5 mm/day, respectively (Panabokke, 1996). The soil has been classified as Walawe Series of Reddish Brown Earth (RBE), in the great group of Rhodustalfs (order Alfisols, suborder Ustalfs) soils and has a sandy clay loam texture (De Silva and Dassanayake, 2010).

Design and construction of open top chambers

Twelve OTCs were constructed with ion bars covered with UV-treated 200-gauge polythene (Figure 1). The frame of OTCs was approximately circular (3 m in diameter) with 12 sides fitted together. Its total height was 3 m and had an open-top (1.5 m in diameter). The vertical beams were bent, at a height of 2.5 m, inwards to form a frustum at the open top with a diameter of about 2 m. It maintains air temperature (Tₐ) within OTCs in near-natural conditions with a diurnal variation pattern similar to open field conditions (Norby et al., 1997; Welshofer et al., 2018).

Elevation of atmospheric CO₂ and temperature

The methodology used in elevating, maintaining, and monitoring atmospheric CO₂ and temperature is described in detail in De Silva (2021) and De Silva et al. (2021). Air blowers (0.25 kW) were used to maintain the adequate air circulation in all OTCs. The CO₂ level in designated OTCs elevated during the daylight hours (i.e. 0630 – 1800 hours).
by injecting pure CO$_2$ through a gas regulator and a hose from 31 kg CO$_2$ cylinders housed outside the chambers. The required CO$_2$ concentration in the chamber was maintained by adjusting the pressure of release of CO$_2$ from the cylinders. The pressure of CO$_2$ release from the cylinder was set at 5 bars during the daylight hours when CO$_2$ was being injected into the OTCs. The concentration of CO$_2$ within the OTCs was monitored using the IEQ Chek environmental quality monitor (Bacharach Inc.). The T$_a$ in designated OTCs elevated via heating coils installed in the air blowers. A heating unit had three 1 kW heaters. Each unit of heaters and air blower was manufactured as a single compound unit and was housed outside each chamber. The ambient or heated air was pumped to the chamber via an underground PVC pipe, connected to an adjustable polythene tube laid within the plot around the middle and perimeter of the OTC. The elevation of CO$_2$ and T$_a$ in OTCs was done daily from 0630 to 1800 h to coincide with daylight hours following globally-adopted standard methodology (Norby et al., 1997; Welshofer et al., 2018).

**Figure 1: Field view of open top chambers before (A) and after (B) planting of sugarcane**

**Experimental design and treatments**

Three experimental treatment factors, viz. CO$_2$ and T$_a$ in the growing environment and sugarcane varieties, arranged in a three-factor factorial treatment structure, laid out in a split-plot design with three replicates. Four CO$_2$ × T$_a$ treatment combinations and an open field treatment were main-plot factors while eight varieties constituted the sub-plot factor. Two levels each of CO$_2$ and T$_a$ (‘ambient’ and ‘elevated’) formed the four CO$_2$ × T$_a$ combinations in OTCs. Within each of the three
main plots in the split-plot design, the four CO$_2 \times$ T$_a$ combinations in OTCs and ambient CO$_2 \times$ T$_a$ combination in the open field were randomized. The open field plots, established in the same field but 20 m away from OTCs, also had the same dimensions as the plots within OTCs.

Eight commercial sugarcane (Saccharum hybrid spp.) varieties (i.e. Co775, SL7130, SL8306, SL88116, SL906237, SL924918, SL96128, and SL96328) were randomized separately within the two halves of each OTC and open field plots. Each variety was planted as 2 m rows spaced at 1.3 m. Therefore, each half of the OTC contained one row each from all eight varieties. As the eight varieties did not differ substantially in their plant and canopy architecture, the crop within each main plot (i.e. an OTC or an open field plot) was considered one contiguous population of sugarcane plants.

**Crop establishment and management**

Crop rows were established using single-budded seed-cane sets of the eight varieties. Each row consisted of four seed-cane sets of each variety. Hence, there were eight hills of each variety in a given OTC arranged in two rows with one row in each half of the OTC. Additional hills were established along the borders of the plots within OTCs to minimize the border effects. Crops were maintained with recommended fertilizer application and plant protection measures under well-watered conditions. Irrigation was provided at 0.15 m$^3$ of water per plot at 5-day intervals, while the soil water potential in the top 1 m was maintained above -0.05 MPa.

**Monitoring environmental conditions**

Micro-climatic conditions in OTCs were monitored continuously by installing sensors and data loggers (WatchDog1000 series micro stations model 1400, Spectrum Technologies, Inc. USA). Four temperature sensors (A, B, C, and D) were placed outside the OTC (A), and within it at 30 cm soil depth (B), at the soil surface (C), and in the air 2 m above the soil surface (D). The sensors monitored T$_a$ continuously and recorded at 5-minute intervals. In addition, CO$_2$, relative humidity (RH%), and T$_a$ in the chambers were monitored using the IEQ Chek environmental quality monitor (Bacharach Inc., USA) while taking physiological measurements. During the experimental period, daily meteorological conditions in the experimental site, i.e. rainfall, minimum and maximum T$_a$ and, relative humidity (RH%), were recorded at the SRI weather station located near the experimental field.

**Estimation of biomass and sucrose accumulations**

One sugarcane bush in each sub-plot was uprooted for biomass estimation on 77, 121, 156, 187 and 370 days after planting (DAP). Roots, stems, leaves with the immature top of canes, and trash separated and oven-dried at 105 °C to a constant weight. The biomass of each portion of canes was estimated. The number of shoots, stem diameter, the height of all shoots at the leaf of a top visible dewlap (TVD), and the number of leaves in each sub-plot taken, and above-ground total biomass per stalk and bush, was estimated. Biochemical analysis of juice quality parameters such as Brix, pol, purity, pure obtainable cane sugar (POCS), and fiber percentages in all stalks in the subplots, was done in the laboratory after harvesting sugarcane at the end of the experiment i.e 370 DAP.

**Statistical analysis**

The significance of treatment effects on measured variables was tested by analysis of variance (ANOVA) in the general linear models procedure (SAS® Studio, SAS Institute Inc. 2021). When the CO$_2 \times$ T$_a$ × variety interaction was significant (p<0.05), the effects of CO$_2$ and T$_a$ on tested variables were evaluated for each variety separately. The following pre-planned mean contrasts were used to separately test the significance of the effects of elevated CO$_2$ (ECO$_2$), elevated T$_a$ (ET$_a$) and the combination of ECO$_2$ and ET$_a$ in each variety:

Effect of ECO$_2$ = XCeTa - XCaTa

Effect of ET$_a$ = XCaTe - XCaTa

Combined effect of ECO$_2$ and ET$_a$ = XCeTe = XCaTa

where, XCeTa, XCaTa, XCaTe and XCeTe were the respective means of treatment combinations, elevated CO$_2$ + ambient T$_a$ (C$_a$T$_a$), ambient CO$_2$ + ambient T$_a$ (C$_a$T$_a$), ambient CO$_2$ + elevated T$_a$ (C$_a$T$_e$), elevated CO$_2$ + elevated T$_a$ (C$_e$T$_e$). The ‘chamber effect’ (i.e. effect of the presence of the chamber) was estimated as the difference between the respective variable means of the C$_i$T$_a$ and the open field treatment.

**RESULTS AND DISCUSSION**

**Environmental conditions in the treatments**

During the daylight hours, CO$_2$ enrichment increased CO$_2$ in OTCs having the ECO$_2$ treatment by 433 ± 2.6 and 435 ± 3.4 ppm, respectively in C$_i$T$_a$.
and C.Tₐ relative to C.Tₑ (Table 1). During the night time, all five treatments had their respective CO₂ within a very narrow range (mean CO₂ 363 – 405 ppm). The open field treatment showed a slightly higher CO₂ compared to C.Tₐ and C.Tₑ during the day and in comparison, to all treatments during the night (Night time data are not shown).

Open top chambers containing ECO₂ and ETₐ treatments, both individually and in combination, had higher air temperatures than the OTCs consist of the C.Tₑ treatment during the daylight hours (Table 1). Mean temperature elevation was the highest in CₑTₑ with 3.46 ± 0.03 °C. The corresponding temperature elevations in CₑTₐ and CₑTₑ were 1.72 ± 0.03 °C and 0.70 ± 0.02 °C, respectively. Air temperatures within OTCs having elevated ECO₂ and ETₐ treatments were higher than C.Tₑ during the night as well (Night time data not shown). Notably, Tₑ in the OTCs containing CₑTₑ was higher than in the open field plots, with mean temperature elevations of 1.63 ± 0.04 °C and 1.46 ± 0.03 °C during the day and night, respectively.

Relative humidity (RH%) inside all OTCs was greater than that in the open field throughout the day (Table 1). Compared to CₑTₑ, ECO₂ and ETₐ both individually and in combination, RH% decreased within the OTCs. The highest depletion of RH% was in CₑTₑ whereas the lowest was in CₑTₐ during the day and in CₑTₑ during the night. The reduction of RH% was lower in the two ECO₂ treatments compared to the C.Tₑ treatment because the ECO₂ retained more water vapor than ambient CO₂. This data agrees with the atmospheric processes taking place on a global scale (Houghton, 2009).

### Number of shoots per hill (Nₐh)

Significant (p<0.05) effects of treatment, variety, and treatment × variety interaction on the number of shoots per hill (number of shoots emerged from a one-budded sett planted) were observed at 121, 156, and 187 DAP (Table 2, Figure 2).

Separate analyses of variance for different varieties showed significant (p<0.05) treatment effects on Nₐh in some of the varieties. In comparison to the ambient (CₑTₑ), elevated Tₑ increased Nₐh in the majority of varieties (e.g. Co775, SL7130, SL924918, and SL96328) at 121, 156, and 187 DAP. As such, the data suggest higher temperatures stimulated tillering and the population density of sugarcane. Similarly, Inman-Bamber (1994) showed that temperature is a major factor influencing the tiller and leaf appearance of sugarcane, and it is more important for efficient canopy light interception of sugarcane.

Elevated CO₂ and the combination ECO₂ and ETₐ increased Nₐh relative to C.Tₑ in a minority of varieties (Figure 2). It showed that when elevated Tₑ combined with ECO₂, the observed stimulation of tillering and population density have been further enhanced in some varieties (ex SL7130 and SL96128) but not in others. However, encouraging good tillering is vital to building an adequate plant population in the field (Robertson et al., 1996; van Heerden et al., 2010), and it provides the crop with the sufficient number of stalks required for a good plant and ratoon cane yields (Vasantha et al., 2010; Matsuoka and Stolf, 2012; Bonnett, 2014).

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**Table 1: The average air temperatures, air CO₂ concentration ([CO₂]) and relative humidity (RH%) in the main treatments from 07:00 to 17:00 hours in open top chambers and open field conditions**

| Environmental variables | CₑTₐ | CₑTₐ | CₑTₑ | CₑTₑ | Open |
|-------------------------|------|------|------|------|------|
| Air [CO₂] ppm           | 344  | 777  | 352  | 779  | 368  |
| Air temperature (°C)    | 34.9 | 35.6 | 36.6 | 38.3 | 33.3 |
| RH%                     | 55.9 | 53.3 | 50.5 | 52.4 | 47.9 |
| VPD (kPa)               | 2.47 | 2.72 | 3.05 | 3.21 | 2.67 |

**Note:** CₑTₑ: ambient CO₂ + ambient Tₑ; CₑTₐ: elevated CO₂ + ambient Tₑ; CₑTₑ: ambient CO₂ + elevated Tₑ; CₑTₑ: elevated CO₂ + elevated Tₑ. Open: open field conditions under the sugarcane canopy; RH%: relative humidity; VPD: Vapour Pressure Deficit
Table 2: Statistical significance of variety, treatment and variety × treatment interaction on number of shoots per hill at different stages

| Source               | 121 DAP | 156 DAP | 187 DAP |
|----------------------|---------|---------|---------|
| Variety              | 0.0001  | 0.0001  | 0.0065  |
| Treatment            | 0.0004  | 0.0126  | 0.0020  |
| Variety × treatment  | 0.0579  | 0.0007  | 0.0054  |

Note: DAP: days after planting

Figure 2: Number of shoots per hill (Nsh) in different sugarcane varieties at ambient CO₂ and ambient temperature (CaTa), ambient CO₂ and elevated temperature (CaTe), elevated CO₂ and ambient temperature (CeTa), elevated CO₂ and elevated temperature (CeTe) and in open field conditions (Open) at 121, 156 and 187 DAP. Each bar represents a mean of 6 data points. Error bars denote standard errors of mean
Biomass accumulation of sugarcane

Biomass in the individual stalks (\(W_{st}\))

Biomass per stalk (dry weight basis) showed significant (\(p<0.05\)) treatment effects at 121, 156, and 370 DAP (Figure 3). The variety × treatment interaction effect on \(W_{st}\) was not significant (\(p>0.05\)). Elevated CO\(_2\) increased \(W_{st}\) by 27% relative to C\(_{aT_a}\) at 156 DAP. However, at 370 DAP, \(W_{st}\) was decreased by 7% and 6%, respectively, in ET\(_a\) and the combination of ECO\(_2\) and ET\(_a\) in comparison to C\(_aT_a\). Elevated CO\(_2\) did not show significant (\(p>0.05\)) effects on \(W_{st}\) at 370 DAP. It could be due to the low response of C\(_4\) photosynthetic process to ECO\(_2\) (Long, 1999; Ghannoum et al., 2000; von Caemmerer and Furbank, 2003; Long et al., 2004; Leakey et al., 2009; Stokes et al., 2016; De Silva et al., 2021).

Significant (\(p<0.05\)) genotypic variation was observed in the variation of \(W_{st}\) of sugarcane at different growth stages (Figure 4). Varieties Co775, SL7130, and SL8306 recorded higher values, and SL88116 and SL906237 recorded lower values of \(W_{st}\) on a majority of measurement days. Inman-Bamber et al. (2011) revealed that increasing biomass content in stalks through breeding and selection may not necessarily result in reduced sucrose content and increased fiber content.

Biomass per hill (\(W_h\))

Biomass per hill (\(W_h\)) in the majority of days of measurement was not affected by ECO\(_2\) or ET\(_a\) or their combination (Figure 5), despite the increase in the number of shoots (\(N_{sh}\)) in the majority of days of measurements, especially in ET\(_a\) (Figure 2). Therefore, the absence of a response in the biomass per stalk (Figure 3) has had a dominant influence in controlling \(W_h\) under elevated CO\(_2\) and elevated T\(_a\), which simulated future climates. In agreement with these results, previous studies of sugarcane (Stokes et al., 2016) and C\(_4\) species such as maize (Leakey et al., 2006) did not show stimulation of biomass at ECO\(_2\) under well-watered conditions. In contrast, at 156 DAP, the individual effects of both ECO\(_2\) and ET\(_a\) and their combination caused a significant (\(p<0.05\)) increase in \(W_h\) relative to C\(_{aT_a}\). In ECO\(_2\), this has occurred because of an increase in both \(N_{sh}\) and \(W_{st}\). De Souza et al. (2008) and Allen et al. (2011) observed similar patterns, where sugarcane was grown at ECO\(_2\).

Figure 3: Dry weight basis biomass per stalk (\(W_{st}\)) of sugarcane at ambient CO\(_2\) and ambient temperature (C\(_{aT_a}\)), ambient CO\(_2\) and elevated temperature (C\(_{eT_a}\)), elevated CO\(_2\) and ambient temperature (C\(_{eT_a}\)), elevated CO\(_2\) and elevated temperature (C\(_{eT_e}\)) and in open field conditions (Open) at different stages. Each bar represents a mean of 48 data points across eight varieties and six replicates. Error bars denote standard errors of mean
Figure 4: Dry weight basis biomass per stalk ($W_s$) in different sugarcane varieties at different stages. Each bar represents a mean of 30 data points across five treatments and six replicates. Error bars denote standard errors of mean.

Figure 5: Dry weight basis biomass per hill ($W_h$) of sugarcane at ambient CO$_2$ and ambient temperature (CaTa), ambient CO$_2$ and elevated temperature (CaTe), elevated CO$_2$ and ambient temperature (CeTa), elevated CO$_2$ and elevated temperature (CeTe) and in open field conditions (Open) at different stages. Each bar represents a mean of 48 data points across eight varieties and six replicates. Error bars denote standard errors of mean.
Figure 6: Dry weight basis biomass per hill (Wₜ) in different sugarcane varieties at different stages. Each bar represents a mean of 30 data points across five treatments and six replicates. Error bars denote standard errors of mean.

In response to ETₐ, the increase in Wₜ had occurred because of increased N_sh while W_st has remained unchanged. Similarly, Vu and Allen (2009) showed significant increases and genotypic variation in biomass accumulation of sugarcane in response to ETₐ. In contrast, Allen et al. (2011) showed that ETₐ caused a slight downward trend in sugarcane biomass accumulation regardless of genotypes or CO₂ elevation.

Significant (p<0.05) genotypic variation was shown in the responses of Wₜ at different growth stages (Figure 6). Varieties Co775 and SL96128 recorded higher Wₜ on a majority of measurement days. Notably, SL88116, which had higher Pol and POCS (Figure 7), recorded the lowest Wₜ than all other varieties at all measurement days (Figure 6).

Succrose accumulation and quality characters

Percentages of Pol and POCS in cane juice showed significant (p<0.05) effects of treatment, variety, and variety × treatment interactions at 370 DAP (Figure 7). Separate analyses showed significant (p<0.05) treatment effects on Pol and POCS in the majority of varieties.

SL96328 recorded the highest reduction of Pol and POCS by 20 and 25%, respectively, due to the effect of ECO₂ in Cₜₑ. On the other hand, ECO₂ increased Pol and POCS by 9 and 14%, respectively, in SL924918. While SL96328 had the highest Pol and POCS in ambient conditions (Cₜₑ), SL924918 had the lowest of the respective values in Cₜₑ. Percentages of Pol and POCS in other varieties did not show responses to ECO₂. It indicated that the effect of ECO₂ in the absence of ETₐ on sucrose accumulation varied among varieties. Previous studies using single variety have also shown that the sucrose content in sugarcane was increased by elevation of CO₂ (Vu et al., 2006; De Souza et al., 2008). They further showed that increased photosynthetic rates (+30%) and biomass accumulation (+40%) at ECO₂ enhanced biomass partitioning to sucrose. Inman-Bamber et al. (2011) and Lobo et al. (2015) showed that photosynthesis did not alter by a feedback mechanism induced by sucrose accumulation in stalks. Sink strength for sucrose storage in the upper internodes is stronger in both high fiber and high sucrose varieties. McCormick et al. (2006, 2008, and 2009) and Ribeiro et al. (2017) showed an increase in leaf photosynthetic capacity with a decrease in assimilating availability in young sink tissues.

Elevated Tₑ in the absence of ECO₂ (Cₜₑ) reduced Pol in SL7130, SL96128, and SL96328. The highest reduction of Pol and POCS by 20 and 19%, respectively, was recorded in SL96128. The increase in Tₑ may eliminate the benefits of the projected rise in CO₂ on sugarcane as lower temperatures are essential for enhancing sucrose accumulation (Verma, 2004). Our findings agree with the previous results of Ebrahim et al. (1998) and Verma (2004), who recorded decreasing sucrose accumulation in sugarcane with increasing the Tₑ. However, Pol and POCS in SL88116, SL906237, and SL924918 did not show significant (p>0.05) responses to elevated Tₑ. Notably, sugarcane varieties in Sri Lanka grow in high-
temperature (33.3 °C) environments (Table 1). Furthermore, our study provides an indication that growth, stomatal anatomical features and photosynthesis of the variety SL88116 did not respond to the elevation of temperature up to 36.6 °C (De Silva, 2021; De Silva et al., 2021).

The combined effect of ECO₂ and ETₐ decreased Pol in Co775, SL8306, and SL96328. The highest reduction of Pol by 13% was recorded in SL8306 which had higher corresponding values in CₐTₐ. Percentages of Pol and POCS in SL7130, SL88116, SL906237, SL924918, and SL96128 did not show a significant (p>0.05) response to the combination of ECO₂ and ETₐ. Similar to these findings, Vu and Allen (2009) have observed significant varietal variation on sucrose productivity of sugarcane at ECO₂ and ETₐ. However, the increased respiration rates due to ETₐ (Hofstra and Hesketh, 1969; Atkin and Tjoelker, 2003; Heskel et al., 2016) could be the most probable reason for the reduction of sucrose accumulation in sugarcane.

Figure 7: Responses of Pol and pure obtainable cane sugar (POCS) in cane juice to elevated CO₂ at ambient temperature (A), elevated temperature at ambient CO₂ (B) and the combination of elevated CO₂ and temperature (C). CₐTa: ambient CO₂ and ambient temperature; CₐTe: elevated CO₂ and ambient temperature; CₑTa: Ambient CO₂ and elevated temperature; CₑTe: elevated CO₂ and temperature. Each bar is a mean of 6 replicate measurements. Error bars show the standard errors of means. Within each variety, significant (p<0.05) responses, based on pre-planned mean contrasts, are shown by *.

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Silva et al. (2022) Tropical Agricultural Research, 33(1): 67-79

De Silva, A.H., 2021. Tropical Agricultural Research, 33(1): 67-79.

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Notably, Pol and POCS in SL96328, which had higher respective values, were affected by the ECO2 and ETa individually and in combination. The significant (p<0.05) genotypic variation in the response of sucrose accumulation in sugarcane to ECO2 and ETa is further demonstrated by the observation of SL88116 not showing a significant (p>0.05) response in its already higher Pol and POCS to both ECO2 and ETa individually or in combination. Therefore, unresponsiveness of higher Pol and POCS in SL88116 to ECO2, ETa and the combination of ECO2 and ETa could be vital in a future climate to ensure the stability of sugar recovery of sugarcane at milling.

CONCLUSIONS

As increasing atmospheric [CO2] and the resulting increase in air temperature (T_a) are clear features of future climate change, the current results provide indications and insights into the impacts of future changes in climate on sugarcane. Biomass production of sugarcane was not affected by ECO2 or ETa or their combination. The combinations of ECO2 and ETa reduced sucrose accumulation in 3 out of 8 varieties (Co775, SL8306 and SL96328) at the end of the growing season. However, sucrose accumulation in the variety SL88116, which had higher respective values at ambient and simulated future climatic conditions, was not affected by either ECO2 or ETa individually or in combination. The responses and the significant genotypic variation observed in sucrose accumulation to ECO2 and ETa both individually and together could be utilized to maintain the stability of sugar production in CO2-rich warm climates.

ACKNOWLEDGEMENTS

This research was funded by the Sugarcane Research Institute (SRI) of Sri Lanka. Assistance given by Dr. A.P. Keerthipala (Former Director), Mr. L.M.J.R. Wijayawardhana (RO/Water Management), Mr. I.P. Manawadu (TO) and Mr. G.S. Udawatta (STO) of SRI are gratefully appreciated.

REFERENCES

Allen Jr, L.H., Vu, J.C.V., Anderson, J., & Ray, J. (2011). Impact of elevated carbon dioxide and temperature on growth and sugar yield of the C4 sugarcane. Current Topics of Plant Biology, 11, 171-178.

Atkin, O.K., & Tjoelker, M.G. (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. Trends in Plant Science, 8(7), 343-351.

Bonnett, G.D. (2014). Developmental stages (phenology). pp. 35-53. In: Moore, P.H. and Botha, F.C. (Eds.) Sugarcane physiology, biochemistry and functional biology, Iowa, USA: John Wiley and Sons, Inc.

Bowes, G. (1993). Facing the inevitable: plants and increasing atmospheric CO2. Annual Review of Plant Biology, 44(1), 309-332.

Chaves, M.M., & Pereira, J.S. (1992). Water stress, CO2 and climate change. Journal of Experimental Botany, 43, 1131-1139.

De Silva, A.L.C. (2021). Varietal response of sugarcane to changing climate and soil conditions in Sri Lanka. Unpublished PhD thesis. Postgraduate Institute of Agriculture, University of Peradeniya, Sri Lanka.

De Silva, A.L.C., Senarathna, H.A.K.N.N., & De Costa, W.A.J.M. (2021). Genotypic variation of the interactive effects of elevated temperature and CO2 on leaf gas exchange and early growth of sugarcane. Physiologia Plantarum, 1–15. Available from: https://doi.org/10.1111/ppl.13578.

De Silva, G.G.R, & Dassanayake, A.R. (2010). Soils formed on erosional surfaces of the dry zone. pp. 79-176. In: Mapa, R.B., Somasiri, S. and Dassanayake, A.R. (Eds) Soils of the Dry Zone of Sri Lanka. Morphology, characterization and classification. Special Publication No. 7, Soil Science Society of Sri Lanka.

De Souza, A.P., Gaspar, M., Da Silva, E.A., Ulian, E.C., Wacławowski, A.J., Nishiyama Jr., M.Y., dos Santos, R.V., Teixeira, M.M., Souza, G.M., & Buckeridge, M.S. (2008). Elevated CO2 increases photosynthesis, biomass and productivity, and modifies gene expression in sugarcane. Plant, Cell and Environment, 31, 1116-1127.

Ebrahim, M.K., Zingsheim, O., El-Shourbagy, M.N., Moore, P.H., & Komor, E. (1998). Growth and sugar storage in sugarcane grown at temperatures below and above the optimum. Journal of Plant Physiology, 153, 593-602.

Eller, F., Lambertini, C., Nguyen, L.X., Achenbach, L., & Brix, H. (2013). Interactive effects of elevated temperature and CO2 on two phylogeographically distinct clones of
common reed (Phragmites australis). AoB PLANTS, 5, pls051; doi:10.1093/aobpla/pls051

Ghannoum, O., Caemmerer, S., & Ziska, L.H. (2000). The growth response of C3 plants to rising atmospheric CO2 partial pressure: a reassessment. Plant, Cell and Environment, 23, 931–942.

Heskel, M.A., O’Sullivan, O.S., Reich, P.B., Tjoelker, M.G., Weerasinghe, L.K., Penillard, A., Egerton, J.J.G., Creek, D., Bloomfield, K.J., Xiang, J., Sinca, F., Stangl, Z.R., Martinez-de la Torre, A., Griffin, K.L., Huntingford, C., Hurry, V., Meir, P., Turnbull, M.H., & Atkin, O.K. (2016). Convergence in the temperature response of leaf respiration across biomes and plant functional types. Proceeding of National Academy of Science USA 113, 3832–3837.

Hofstra, G., & Hesketh, J.D. (1969). Effects of temperature on the gas exchange of leaves in the light and dark. Planta, 85, 228–237.

Houghton, J. (2009). Global Warming: The Complete Briefing. 4th Edition. Cambridge University Press.

Inman-Bamber, N.G. (1994). Temperature and seasonal effects on canopy development and light interception of sugarcane. Field Crops Research, 36, 41-51.

Inman-Bamber, N. G., Jackson, P. A., & Hewitt, M. (2011). Sucrose accumulation in sugarcane stalks does not limit photosynthesis and biomass production. Crop and Pasture Science, 62(10), 848-858.

Kim, S. H., Sicher, R. C., Bae, H., Gitz, D. C., Baker, J. T., Timlin, D. J., & Reddy, V. R. (2006). Canopy photosynthesis, evapotranspiration, leaf nitrogen, and transcription profiles of maize in response to CO2 enrichment. Global Change Biology, 12(3), 588-600.

Kimball, B. A., Kobayashi, K., & Bindi, M. (2002). Responses of agricultural crops to free-air CO2 enrichment. Advances in Agronomy, 77, 293-368.

Lawlor, D. W., & Mitchell, R. A.C. (1991). The effects of increasing CO2 on crop photosynthesis and productivity: a review of field studies. Plant, Cell & Environment, 14(8), 807-818.

Leaky, A.D.B., Ainsworth, E.A., Bernacchi, C.J., Rogers, A., Long, S.P., & Ort, D.R. (2009). Elevated CO2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. Journal of Experimental Botany, 60(10), 2859-2876.

Leaky, A.D.B., Uribelarrea, M., Ainsworth, E.A., Naidu, S.L., Rogers, A., & Ort, D.R. (2006). Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO2 concentration in the absence of drought. Plant Physiology, 140(2), 779-790.

Lobo, A. K. M., de Oliveira Martins, M., Neto, M. C. L., Machado, E. C., Ribeiro, R. V., & Silveira, J. A. G. (2015). Exogenous sucrose supply changes sugar metabolism and reduces photosynthesis of sugarcane through the down-regulation of Rubisco abundance and activity. Journal of Plant Physiology, 179, 113-121.

Long, S.P., Ainsworth, E.A., Rogers, A., & Ort, D.R. (2004). Rising atmospheric carbon dioxide: plants FACE the future. Annual Review of Plant Biology, 55, 591–628.

Long, S.P. (1999). Environmental Responses. In: Sage, R.F. and Monson, R.K. (Eds.) C: Plant Biology. Academic Press San Diego, San Diego, pp. 215–249.

Marin, F.R., Jones, J.W., Singels, A., Royce, F., Assad, E.D., Pallegrino, G.Q., & Justino, F. (2013). Climate change impacts on sugarcane attainable yield in southern Brazil. Climatic Change, 117, 227-239.

Marin, F.R., Ribeiro, R.V., & Marchiori, P.E.R. (2014). How can crop modeling and plant physiology help to understand the plant responses to climate change? A case study with sugarcane. Theoretical Experimental Plant Physiology, DOI 10.1007/s40626-014-0006-2

Matsuoka, S., & Stolf, R. (2012). Sugarcane tillering and ratooning: key factors for a profitable cropping. Sugarcane: Production, Cultivation and Uses, 5(2), 137-157.

McCormick, A. J., Cramer, M., & Watt, D. A. (2006). Sink strength regulates photosynthesis in sugarcane. New Phytologist, 171(4), 759-770.
McCormick, A. J., Cramer, M. D., & Watt, D. A. (2008). Regulation of photosynthesis by sugars in sugarcane leaves. *Journal of Plant Physiology*, 165(17), 1817-1829.

McCormick, A. J., Watt, D. A., & Cramer, M. D. (2009). Supply and demand: sink regulation of sugar accumulation in sugarcane. *Journal of Experimental Botany*, 60(2), 357-364.

Norby, R., Edwards, N., Riggs, J., Abner, C., Wullschleger, S., & Gunderson, C. (1997). Temperature-controlled open-top chambers for global change research. *Global Change Biology*, 3(3), 259-267.

Panabokke, C. R. (1996). Soils and Agro-ecological Environments of Sri Lanka. Natural Resources, Energy and Science Authority of Sri Lanka, Colombo.

Ribeiro, R. V., Machado, E. C., Magalhães Filho, J. R., Lobo, A. K. M., Martins, M. O., Silveira, J. A., Yin, X., & Struik, P. C. (2017). Increased sink strength offsets the inhibitory effect of sucrose on sugarcane photosynthesis. *Journal of Plant Physiology*, 208, 61-69.

Robertson, M. J., Wood, A. W., & Muchow, R. C. (1996). Growth of sugarcane under high input conditions in tropical Australia. 1. Radiation use, biomass accumulation and partitioning. *Field Crops Research*, 48, 11-25.

Stokes, C. J., Inman-Bamber, N. G., Everingham, Y. L., & Sexton, J. (2016). Measuring and modelling CO₂ effects on sugarcane. *Environmental Modelling and Software*, 78, 68-78.

Van Heerden, P. D. R., Donaldson, R. A., Watt, D. A., & Singels, A. (2010). Biomass accumulation in sugarcane: unravelling the factors underpinning reduced growth phenomena. *Journal of Experimental Botany*, 61(11), 2877-2887. doi:10.1093/jxb/erq144

Vasantha, S., Esther Shekinah, D., & Gupta, C. (2010). Tiller production, regulation and senescence in sugarcane (*Saccharum species* hybrid) genotypes. *SugarTech*, 14(2), 156-160.

Venkataramana, S., Shanmugasundaram, S., & Naidu, K. M. (1984). Growth behavior of field-grown sugarcane varieties in relation to environmental parameters and soil moisture stress. *Agricultural Forest Meteorology*, 31, 251-260.

Verma, R. S. (2004). Climatic and soil conditions for sugarcane in India. Sugarcane production Technology in India. International book distributing company, Lucknow, India, pp. 23-24.

von Caemmerer, S., & Furbank, R. T. (2003). The C₄ pathway: an efficient CO₂ pump. *Photosynthesis Research*, 77, 191-207.

Vu, J. C. V., & Allen Jr., L. H. (2009). Stem juice production of the C₄ sugarcane (*Saccharum officinarum*) is enhanced by growth at double-ambient CO₂ and high temperature. *Journal of Plant Physiology*, 166, 1141-1151.

Vu, J. C. V., Allen Jr., L. H., & Gesch, R. W. (2006). Up-regulation of photosynthesis and sucrose metabolism enzymes in young expanding leaves of sugarcane under elevated growth CO₂. *Plant Science*, 171, 123-131.

Welshofer, K. B., Zarnetske, P. L., Lany, N. K., & Thompson, L. A. (2018). Open-top chambers for temperature manipulation in taller-stature plant communities. *Methods in Ecology and Evolution*, 9(2), 254-259.

Wolfe, D. W., Gifford, R. M., Hilbert, D., & Luo, Y. Q. (1998). Integration of photosynthetic acclimation to CO₂ at the whole-plant level. *Global Change Biology*, 4(8), 879-893.