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RESEARCH ARTICLE

Effect of co-occurrence of high night temperature and low moisture stress in sugarcane

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Abstract

Sugarcane is an important crop, essential for sugar and bioenergy and makes a substantial contribution to India's Gross Domestic Product. Global warming and climate change result in increased frequency and intensity of combined water deficit and high temperature stress episodes, which ultimately limits worldwide sugarcane productivity. In reality, global night temperatures are rising more rapidly than daytime temperatures, demonstrating the sensitivity of plants to warmer nights. From 1991 to 2024, which covers a period of 34 years, the night temperature of Coimbatore, Tamil Nadu during March (R^2= 0.402) and April (R^2= 0.232) showed significantly increasing trend, notably, there has been a significant rise since the beginning of the 21st century. During an investigation (January-December 2024) to study the responses of sugarcane variety Co 86032 to drought stress during formative phase, an episode of high night temperature was observed during March and April (25.48 °C and 27.90 °C, respectively), which was significantly higher than the night temperature observed during the past 34 years (21.26 °C and 23.37 °C, respectively). This episode of combined high night temperature along with water deficit condition caused drying of leaves starting from the tips and later spreading to the entire leaf lamina. Membrane stability, photosynthetic pigments and proline content were significantly suppressed, whereas alterations in leaf water status resulted in higher canopy temperature under stress. Although the crop recovered during the grand growth phase due to the southwest monsoon (June-September 2024), the number of millable canes, cane weight and juice weight showed significant reduction of 52.0 %, 51.9 % and 21.0 %, as compared to irrigated control. However, the biochemical parameters viz., total soluble sugars (Brix %) and sucrose content in juice (Pol %) did not show significant variation due to stress. Increment in the global night temperature indicated through historical data analysis, along with the present experimental results, revealed an important concern for the scientific community to study in detail the magnitude of high night temperature. It is also crucial to identify suitable physiological traits for combating climate change, thus paving the way for climate resilient sugarcane production.

Keywords: climate change; high night temperature; physiology; sugarcane; water stress; yield

Introduction

The Intergovernmental Panel on Climate Change (IPCC) has projected that in the last twenty years, the global temperature has increased by 1.09 °C (1). The production of sugarcane is mainly influenced by changes in weather and climate related events (2). The average ambient temperatures have been steadily increasing in the past 40 years and are predicted to increase further with frequent occurrences of heat waves and elevated night temperatures (3). India's average temperature has risen by around 0.7 °C during 1901 to 2018. By the end of the twenty-first century, average temperature over India is projected to rise by approximately 4.4 °C relative to the recent past (4). Between 1985 and 2014, Tamil Nadu had 107 days of discomfort every year and it has increased by 41.5 % since 2014. From 2024 to 2050, it will average at 150 days. A temperature increase of as little as 1 °C over the optimal range is defined as heat shock (5). Discomfort days refer to those when the mean temperature is above 29 °C and relative humidity below 30 %, the ideal relative humidity being 30 % to 60 % (6). There may be an increase of 3.30 °C during daytime and 3.55 °C during night-time, along with a decrease in rainfall of 3.24 % by the end of the 21st century in Tamil Nadu (7). The minimum temperature projections consistently show higher values when compared to maximum temperature with a difference ranging from 0.2 °C to 0.5 °C. The trends of night-time Land Surface Temperature (LST) change over the years (2003 to 2023) showed significant increase in Coimbatore during monsoon (3 °C) and post monsoon (2.5 °C) (8). LST decreases the surface water availability by increasing evaporation rate and crop water demand which leads to wilting, in turn affecting crop yield.

The area affected by drought has increased by 1.3 % per decade over the period 1901 to 2018 (9). Water stress affects sugarcane yield particularly when the summer months coincides with the formative phase of the crop, which affects millable canes, weight and girth of cane, yield and juice quality in sugarcane (10-12). High temperature negatively affects germination and especially high night temperature ceases growth of internodes and leaves, with drastic decline in cane and sugar yield (13, 14). Recent studies demonstrated that future crop yields will be directly impacted by complex interactions between the frequent episodes of water deficit and heat stress, driven by global warming and climate change (15). Although the individual effects of high temperature and water deficit stresses have been studied in detail, their combined effect on sugarcane has not received significant attention. Understanding combined impact of high night temperature episodes and water deficit condition on growth, physiology and yield in sugarcane is critical to develop climate change-resilient crops. Under these circumstances, an investigation was carried out to identify the trend in long term temperature data of Coimbatore district and to study the effect of high night temperature on physiology, yield and quality of sugarcane crop under water deficit condition.

Materials and Methods

Experimental design and treatments

A field experiment was conducted during 2024 at ICAR-Sugarcane Breeding Institute, Coimbatore, (11°0' N 76°55' E; 475 m above mean sea level) Tamil Nadu, India. The sugarcane variety Co 86032 was sown during January 2024, by following the recommended package of practices. The design adopted was RBD with three replications, wherein each replication consisted of five rows (10 × 4 feet). The control plots were irrigated as per the recommended irrigation schedule, while treatment plots were maintained under unirrigated condition during the formative phase (critical period for sugarcane) i.e., 90 to 160 days after planting (DAP). During the stress period (110-120 DAP), morphological, physiological and biochemical parameters were recorded.

Growth characteristics

Growth parameters such as plant height (cm), total leaf area (cm^2 $plant^{-1}$), canopy biomass (leaf and sheath fresh weight in g $plant^{-1}$) were collected at 360 DAP. Plant height (cm) was measured from the base of the stem to the tip of the topmost leaf using a measuring tape. Total leaf area was recorded by using leaf area meter (LI-COR) and expressed in $cm^2 plant^{-1}$. Canopy biomass (g $fwplant^{-1}$) was recorded by weighing the fresh leaves and sheaths in a weighing balance.

Physiological and biochemical parameters

The samples were collected from physiologically active leaf for analysing the physiological and biochemical parameters. The canopy temperature was measured with a thermal imaging infrared camera (FLIR E6) during 11:00 a.m. and 12:00 noon on clear sky days. The captured image was processed through FLIR software. Each canopy temperature measurement was the average of fifteen readings taken in different plants within each treatment. Relative water content (%) and membrane stability index (%) was measured following the procedure from previous studies (16, 17).

Total leaf chlorophyll content was determined through the method outlined in earlier research (18). Proline in the leaf extract was measured following procedures described in previous studies, with minor modifications (19). The total soluble protein content was measured according to the method described earlier, using bovine serum albumin as standard (20). Total sugar was estimated using the Anthrone method (21). The total phenolic content in the leaf extract was determined by Folin-Ciocalteu method (22). Sucrose synthase (SS) activity was quantified according to methods reported in previous work and expressed as µM g fresh $weight^{-1}$ $hour^{-1}$ (23). The nitrate reductase enzyme (NRase) activity in leaves was performed based on an established procedure and expressed in mM nitrate produced g^{-1} fwh^{-1} (24).

For antioxidant enzyme analysis, protein extracts were obtained by homogenizing the leaf tissue in phosphate buffer. The catalase (CAT) activity was determined using a method reported in earlier studies and the results were expressed in U mg^{-1} protein min^{-1} (25). Peroxidase (POX) activity was measured spectrophotometrically by monitoring the oxidation rate of *O*-dianisidine following procedures described in previous research and the results were expressed in U mg^{-1} protein min^{-1} (26). Superoxide dismutase (SOD) activity was determined according to protocols outlined in earlier work and the activity was expressed in U mg^{-1} protein h^{-1} (27).

Yield and quality characters

Yield and juice quality parameters were recorded at 360 DAP. Number of millable canes, single cane weight, cane height, cane girth, internodal length were recorded in entire 10 feet row at harvest and expressed in unit area (m^2). Cane yield per plot was recorded and expressed as t ha^{-1}. Juice quality parameters such as total soluble sugars (Brix %) and sucrose content (Pol %) were recorded by using sugar analysis system (SUCROLYSER) at temperature of 24.2 ± 0.2 °C. Commercial cane sugar (CCS) was calculated and expressed in percentage and t ha^{-1} by using the formula (28).

CCS% = [Sucrose content x 1.022)/TSS x 0.292)] (Eqn. 1)

$$CCS\left(\frac{t}{ha}\right) = (CCS\% \times Yield)/100 \quad \text{(Eqn. 2)}$$

Soil and weather parameters

Soil moisture content was recorded at an interval of 75, 120 and 150 DAP using the gravimetric method at the soil depths of 15 to 30 cm. The collected soil samples were oven-dried at 105 °C for 72 hr. The soil moisture percentage was determined from the weights of both wet and dry soils and was calculated as follows:

Soil moisture content =

$$\left[\frac{(weight\ of\ moist\ soil - weight\ of\ dry\ soil)}{weight\ of\ dry\ soil}\right] \times 100 \quad \text{(Eqn. 3)}$$

Temperature data of the experimental region (1991-2024) was collected from ICAR-SBI, Coimbatore and trend analysis using linear regression where a straight line is fitted to the weather dataset 1991 to 2024 to identify the overall direction (upward, downward or stable) of a trend, was performed by using JMP software version 9.0. Linear regression calculates the slope (rate of change) and intercept (starting point) of the trend line and to visualize and quantify the trend. Also, the distribution analysis was performed to observe the nature of the data. Statistical analysis of the data was performed using the software WASP 2.0 and analysis of variance and the treatment means were compared using least significant differences (LSD) at $P < 0.05$.

Results

Trend analysis of temperature

Through the regression analysis during the period 1991-2024, the minimum temperature (T_{min}) of March and April month showed a significantly increasing trend. The β value in the regression for March and April months are +0.106 (R^2= 0.402) and +0.059 (R^2= 0.232), which indicates that every year there is an increase of 0.106 °C and 0.059 °C in T_{min}, respectively (Fig. 1). The distribution statistics of T_{min} during March, depicted as histogram revealed that 26 % of the data falls between 22 °C-23 °C and 3 % of the data falls in 25 °C-26 °C, while for April 64 % falls between 22 °C-26 °C and 3 % of the data falls in 27 °C-28 °C. The 3 % of data during March and April was mainly observed after the year 2010 (Fig. 2). On comparison of the base line data during 1940 to 1990, the present scenario shows an increasing trend of T_{min} during March month (29).

The regression analysis during the period 1991-2024 revealed that the Maximum temperature (T_{max}) of March showed a significantly decreasing trend, whereas it significantly increased during April (Fig. 1). The β value in the regression for the March and April month are -0.017 and +0.042, which confirms that every year there is a decrease of T_{max} by 0.017 °C during March and an increment of 0.042 °C during April (Fig. 1). The distribution statistics of T_{max} during March depicted by a histogram revealed that 56 % of the data falls between 35 °C-36 °C and 3% of the data falls in 36 °C-37 °C and 30 °C-31 °C, while for the April 26 % falls between 35 °C-36 °C and 6 % of the data falls in 38 °C-39 °C. Thus 6 % of T_{max} during March and April was mainly observed in the after 2010 (Fig. 2). Comparing the baseline data during 1940-1990, the present scenario shows an increasing trend in T_{max} during March and April months (29).

The β value in the regression analysis for T_{mean} and T_{DTR} for the same period (1991-2024) indicated that every year T_{mean} increased significantly 0.044 °C and 0.049 °C during March and April, respectively, while T_{DTR} showed significant decrease of 0.123 °C and 0.017 °C during March and April, respectively (Fig. 1). The distribution statistics of the T_{mean} during March revealed that 52 % falls between 27.5 °C-28.0 °C and 28 °C-29.5 °C, while 39 % falls between 29 °C-30 °C during April. In respect of T_{DTR} during March, 47 % distributed between 12 °C-14 °C, while in April 29 % distributed between 12 °C-13 °C (Fig. 2).

Soil moisture depletion

The weather data during the experimental period of 2024 showed there was no precipitation in the experimental plot for 115 days (i.e., 6th to 120th DAP) with highest open pan evaporation (6.0 mm/day) on 120th DAP, resulting in prolonged atmospheric drought. Data on soil moisture recorded during 75, 120 and 150 DAP indicated that there was a severe decline in soil moisture in the Unirrigated control (UIC) plot (4.4 %) than the Irrigated control (IC) plot (10.7 %) during 120 DAP, which is a critical phase of the crop (Fig. 3a).

Growth characters

Growth characters like plant height (cm), showed a significant reduction (30.2 %) under UIC at 360 DAP. On the contrary, total leaf area (cm^2 $plant^{-1}$) and canopy biomass (leaf and sheath fw $plant^{-1}$ and t ha^{-1}) did not show a significant reduction under UIC and the observed total leaf area (cm^2 $plant^{-1}$) 1022.4 and 906.9 (Fig. 3b); leaf biomass (g $fwplant^{-1}$)–85.8 and 66.0; sheath biomass (g $fwplant^{-1}$) 75.7 and 52.8 under IC and UIC, respectively (Table 1).

Physiological and biochemical traits

Physiological parameters like canopy temperature (°C), membrane stability (%) and relative water content (%) significantly affected under UIC (Fig. 4a-c). Similar trends were noted in biochemical parameters like total chlorophyll (mg g^{-1} fw) and soluble protein content (mg g^{-1} fw) (Fig. 5a, b). Further, the compatible osmolyte proline (μmol g^{-1} fw) and total phenol content (%) did not show any significant change under UIC (Fig. 5 c, d). Total sugar content (%) followed a similar trend (Fig. 5e). A substantial decline in sucrose synthase (SS) activity was noted under UIC (Fig. 5f). Nitrate reductase (NRase) activity (mM nitrate produced g^{-1} fw h^{-1}) was also reduced under UIC (Fig. 6a). SOD (U mg^{-1} protein h^{-1}) and POX (U mg^{-1} protein min^{-1}) activities showed no significant increases under UIC, whereas antioxidant enzyme CAT (U mg^{-1} protein min^{-1}) activity significantly increased (Fig. 6b-d). Overall, the data indicated that water deficit stress along with high night temperature condition during formative stage negatively influenced physiological and biochemical traits in sugarcane crop.

Cane yield and juice quality

Sugarcane plants showed a significant reduction in yield attributes (Table 1) such as cane girth (cm) 2.856 and 2.30; single cane weight (g) 670.1 and 298.3, which led to a significant reduction in cane yield (t ha^{-1}) under UIC (Fig. 7a). However, no significant reduction was observed in brix (%), sucrose content (Pol %) and CCS % under combined stress (Fig. 7b, c, d). Commercial cane sugar (CCS, t ha^{-1}) was also reduced by 51.7 % under UIC (Fig. 7e).

Discussion

High temperature and water stress are crucial factors affecting sugarcane, as they can lead to substantial adverse effects during germination, early growth stage and flowering and maturity stages (30, 31). In tropical India, sugarcane planted during January generally faces hot summer induced soil water depletion during March-May at the grand growth stage which is significant for cane formation, elongation and yield increase. Subsequently, the crop starts recovering to some extent during the arrival of south-west monsoon (SWM). However, water deficit during the early stage especially at formative stage is a major factor which can limit cane growth (32) and reduce cane and sugar yield by over 36 % and 40 %, respectively (33). Meanwhile, temperature above 32 °C reduces internodal length and sugar yield. Further, high night temperature affects internode development, in turn resulting in significant decline in cane and sugar yield (13, 34). Increase in temperature during formative stage alter the daily evaporation, intensifies water stress, warranting frequent irrigation cycles to meet the demand of crop evaporation.

The weather data during the experimental period of 2024 showed there was no precipitation in the experimental plot for 115 days (i.e., 6th DAP to 120th DAP) with highest open pan evaporation during March-April, 2024 (Average 5.594 mm/day) which leads to prevailed atmospheric drought. This substantiates present reports that the sugarcane under water deficit stress during formative stage coincide with high day and night temperature during March-April, 2024 (37.16 °C and 26.52 °C, respectively) compared to the long-term average for the period 1991-2024 (34.85 °C and 22.15 °C, respectively). Excessive heat stress adversely influences the accessibility of water for plant utilization by increasing the rate of evapotranspiration (35).

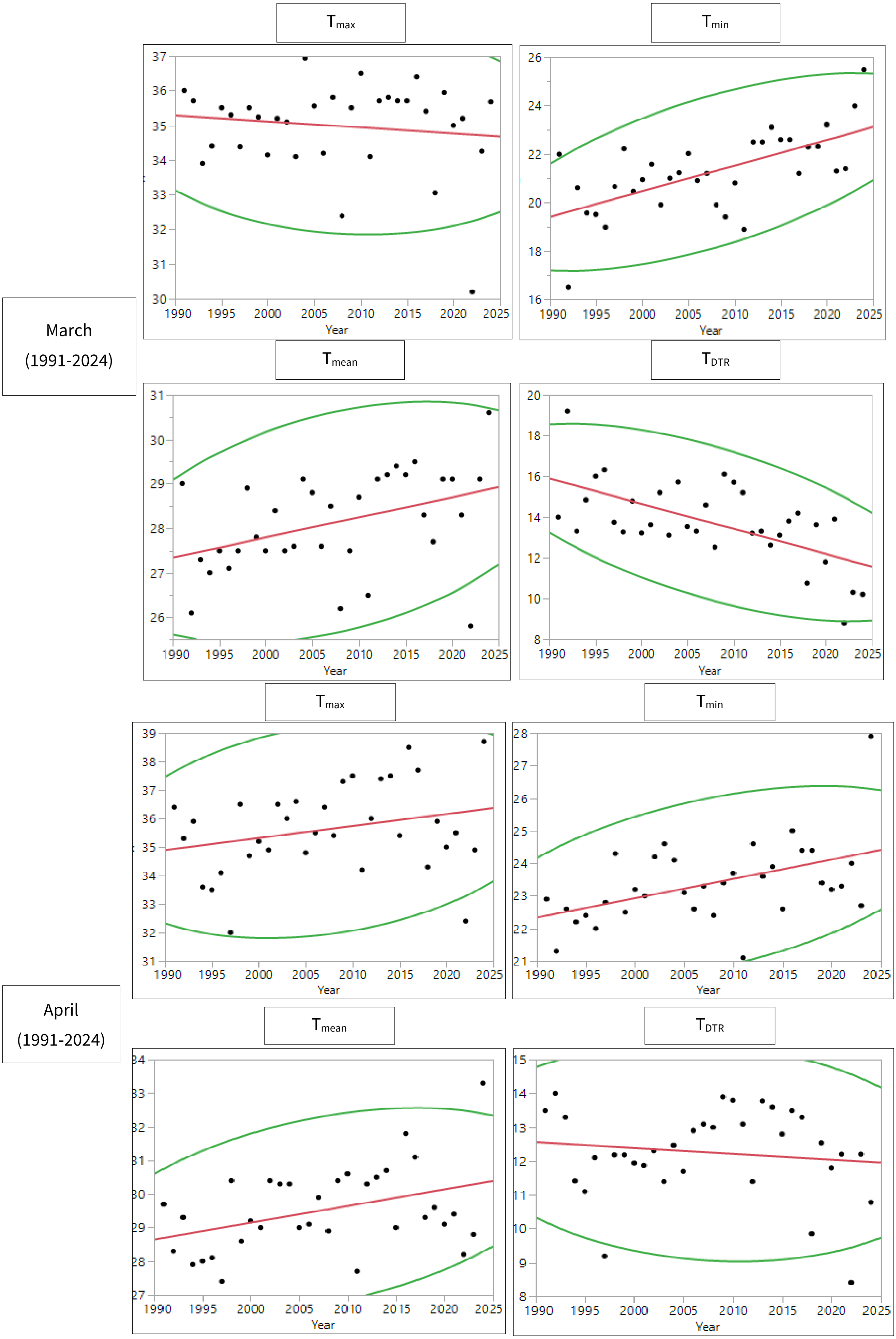

Fig. 1. Regression statistics of T_{max}, T_{min}, T_{mean} and T_{DTR} during the period of 1991-2024.

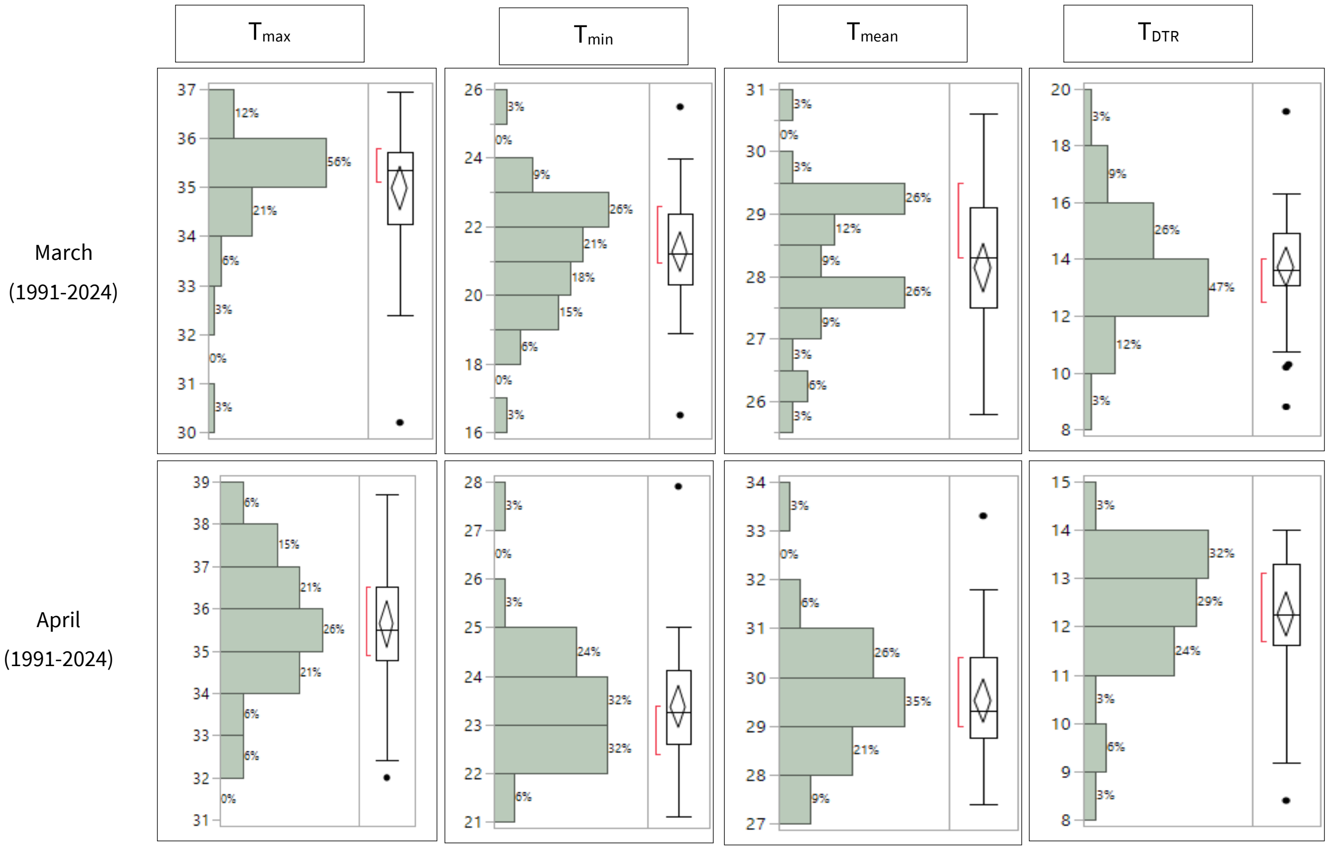

Fig. 2. Distribution statistics of T_{max}, T_{min}, T_{mean} and T_{DTR} during the period of 1991-2024.

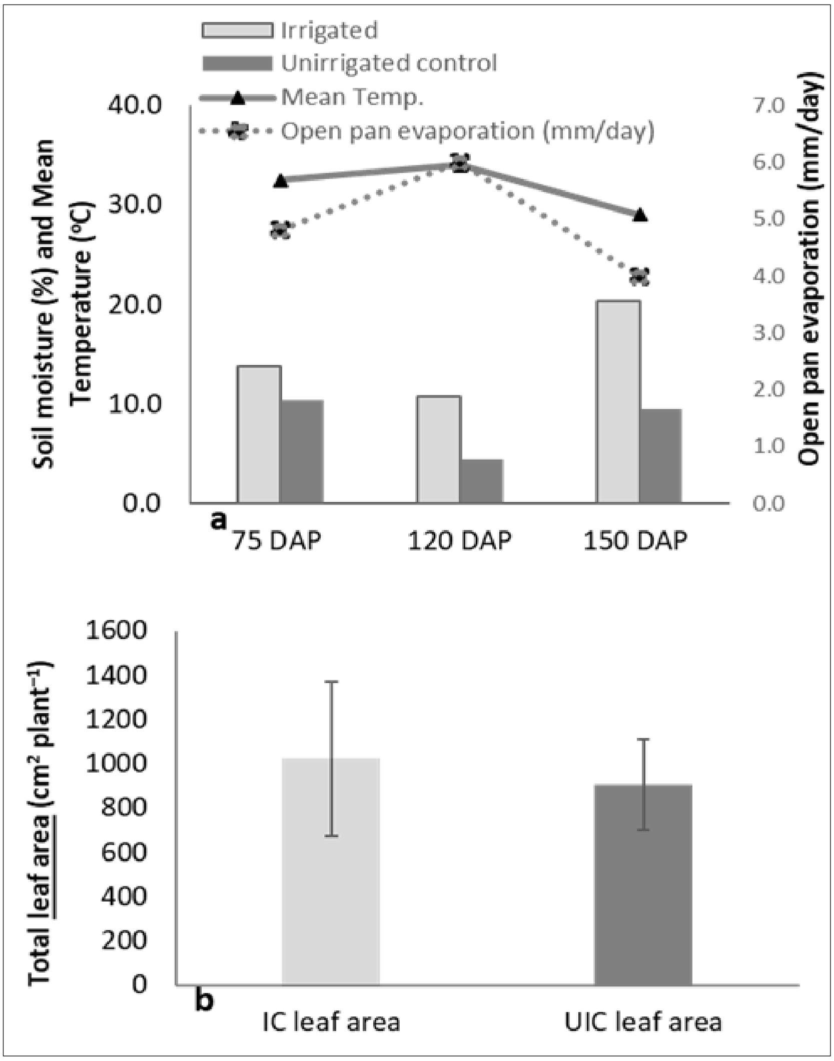

Fig. 3 (a) Soil moisture depletion, Mean temperature and Open pan evaporation during different stages of stress treatment; (b) total leaf area under high night temperature with water deficit.

Table 1. Effect of high night temperature on morphological and yield characters in sugarcane under water deficit condition

	Plant height (cm)	Cane girth (cm)	Single cane weight plant^{-1} (g)	Leaf fresh weight plant^{-1} (g)	Sheath fresh weight plant^{-1} (g)	Leaf number plant^{-1}	No. of internodes plant^{-1}	No. of Millable canes plant^{-1}	No. of water shoots plant^{-1}	Internodal length (cm)
Irrigated control (IC)	122.0^{a}	2.856^{a}	670.1^{a}	85.89	75.78	7.889	19.56	4.302	2.133	6.375
Unirrigated control (UIC)	85.0^{b}	2.300^{b}	298.3^{b}	66.00	52.89	9.889	21.11	2.041	2.151	4.292
Mean	103.5	2.578	484.2	75.94	64.33	8.88	20.33	3.171	2.142	5.333
CV%	15.55	13.72	20.16	54.2	53.24	24.83	36.10	36.02	34.70	32.80
CD (0.05)	17.50	0.385	106.1	ns	ns	ns	ns	0.895	ns	1.045

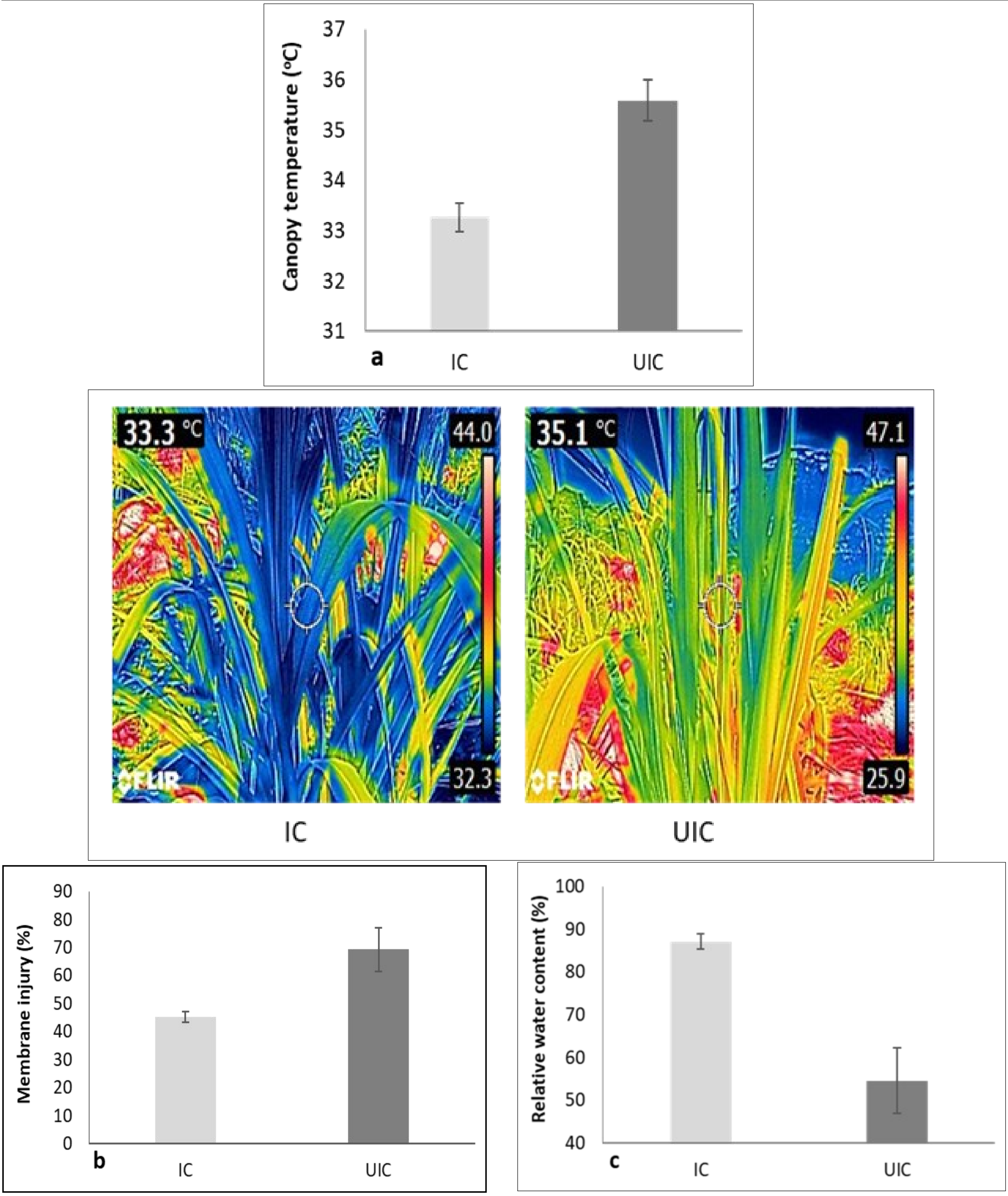

Fig. 4. Combined stress effect of high night temperature with water deficit on (a) canopy temperature; (b) membrane injury (%); (c) relative water content (%) in sugarcane crop.

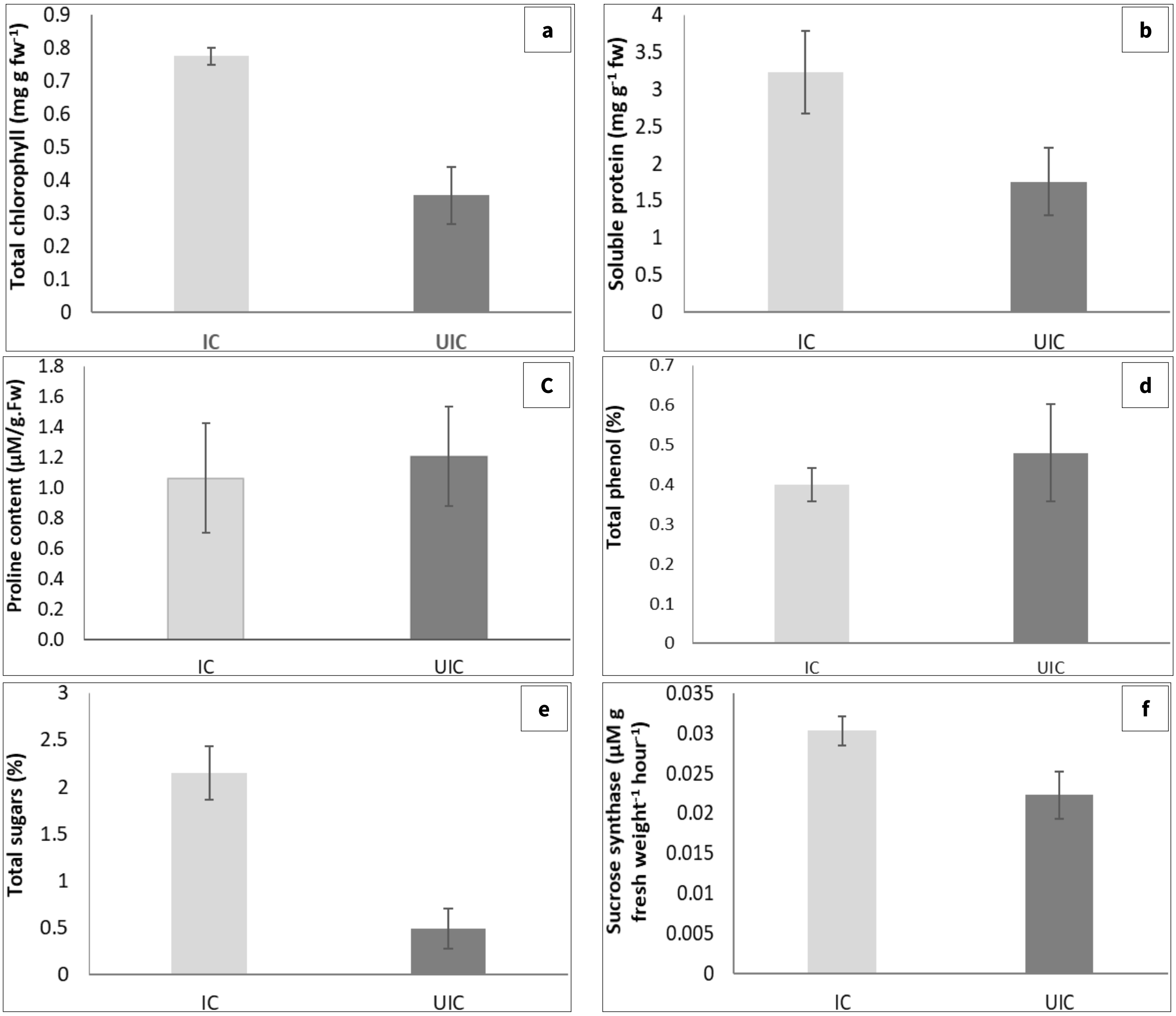

Fig. 5. Combined effect of high night temperature with water deficit on (a) total chlorophyll (mg g^{-1} fw); (b) soluble protein (mg g^{-1} fw); (c) proline content (µM g^{-1} fw); (d) total phenol (%); (e) total sugar (%); (f) sucrose synthase (µM g^{-1} fw h^{-1}) in sugarcane crop.

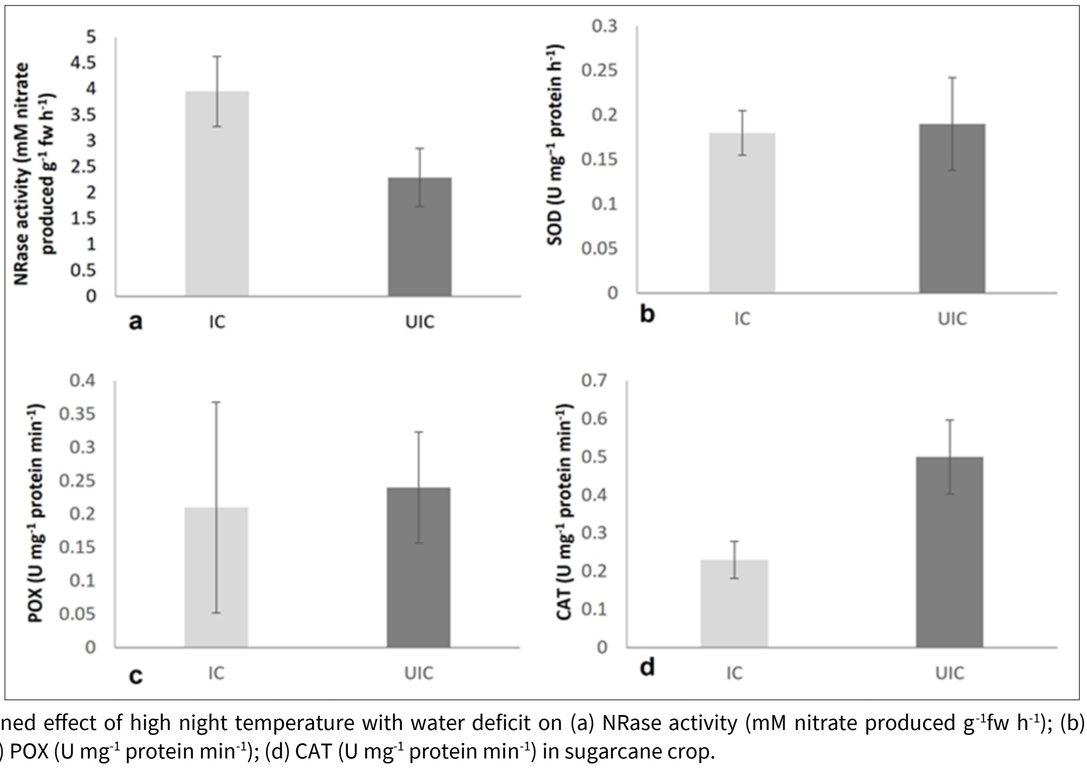

Fig. 6. Combined effect of high night temperature with water deficit on (a) NRase activity (mM nitrate produced g^{-1}fw h^{-1}); (b) SOD (U mg^{-1} protein h^{-1}); (c) POX (U mg^{-1} protein min^{-1}); (d) CAT (U mg^{-1} protein min^{-1}) in sugarcane crop.

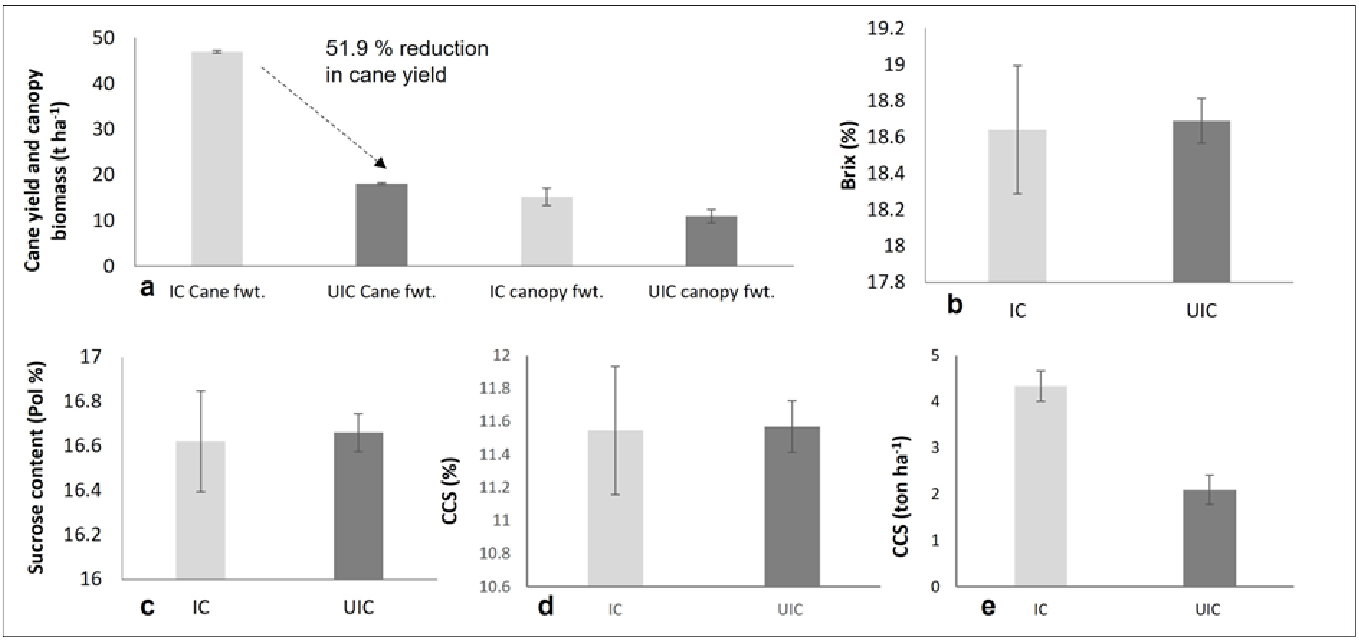

Fig. 7. Combined effect of high night temperature with water deficit on (a) cane yield and canopy biomass (t ha^{-1}); (b) Brix (%); (c) Sucrose content (Pol %); (d) CCS (%); (e) CCS (ton ha^{-1}) in sugarcane crop.

The mean maximum (38.7 °C) and minimum (27.9 °C) temperature without rainfall prevailed for a period of four weeks during April 2024, thereby causing severe sunburn in sugarcane crop as it coincided with the grand growth stage. This sunburn caused drying of leaf lamina initially on the leaf apex of top visible leaf first and then progressed towards middle of leaf lamina and the remaining portion stayed green. The young unopened leaf just above the already injured leaf gets dried irreversibly in the same way. Under the combination of prolonged high night temperature and water deficit (UIC) showed the combined symptom of stunted growth, reduced leaf size, early senescence and finally severe wilting of plants which leads to reduced plant populations (Fig. 8a, b).

Water deficit stress and heat stress occurring individually during tillering and stem elongation stage mostly affects canopy growth, stem elongation (36) and sucrose content and purity (37, 38). In the present study, the co-occurrence of extreme high night temperature and water deficit stress episode had adverse impacts on the observed growth characters such as plant height, number of millable canes and internodal length, which ultimately reduced cane yield. However, no significant effect was found on leaf area and canopy biomass (Leaf and sheath). This indicated that the transient reduction in leaf area and biomass during formative stage under water stress, recovered after the SWM. In sugarcane, the physiological activity of tillering starts from 40 DAP and may last up to 120 DAP, which determines the optimum number of millable canes required for a good yield. However, the effect of co-occurrence of high night temperature and water deficit stress on tillering during the formative stage did not recover after the SWM. Hence, the combined stress during formative stage suppressed plant growth, resulting in substantial yield loss about 51.9 %.

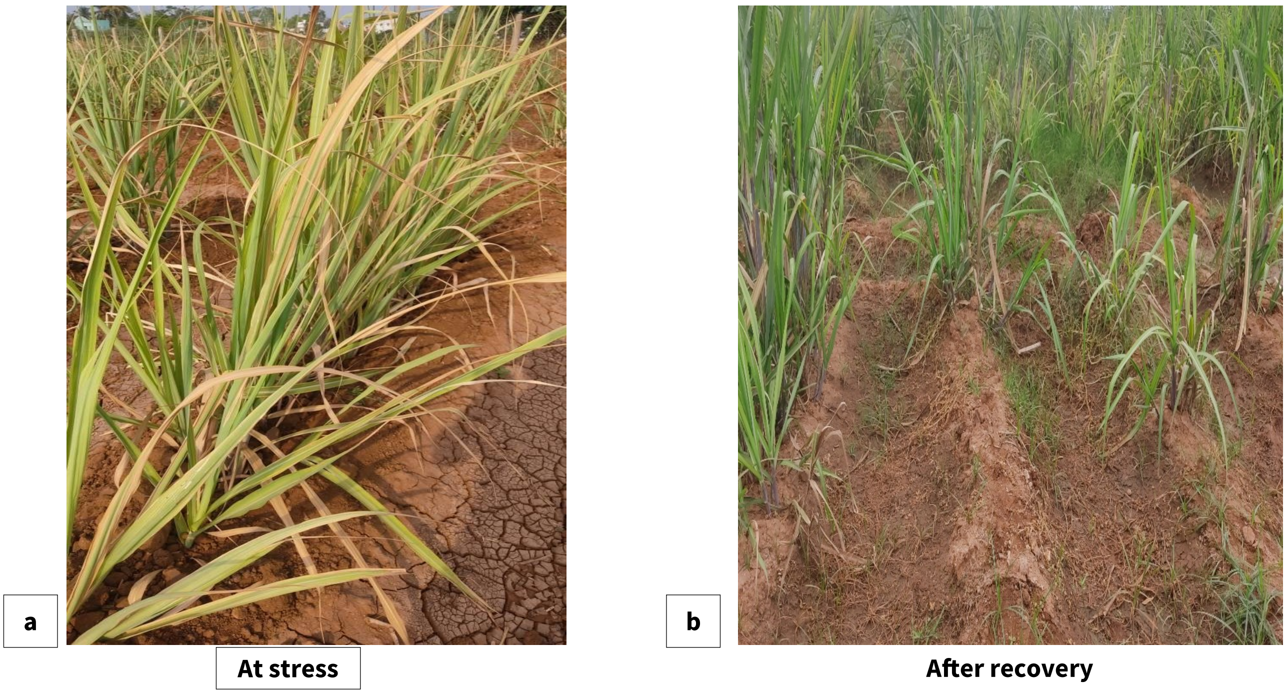

Fig. 8 (a) Affected plant symptom and (b) reduced plant population under high night temperature with water deficit.

Heat stress and water deficit stress induced differential biochemical and physiological responses in plants, through alterations in photosynthetic gas exchange, photosynthetic pigments, relative water content, oxidative balance, synthesis of protein, lipid peroxidation, membrane stability and sugar production (32, 39). Proline accumulation as a balancing source of carbon and nitrogen, maintains cytosolic pH and cell redox levels (40 -42) during drought. Proline and cell membrane stability (43, 44) are the stress damage indicators which maintain the water status of cell under heat stress. In the present study, during the co-occurrence of high night temperature under UIC, sugarcane did not show any significant trend of proline accumulation, resulting in increased cell membrane injury and reduced relative water content in the leaf tissue as compared to IC. Canopy temperature negatively affected the cane yield under drought stress (45) and our findings also corroborate the report as the plant under water deficit with high night temperature showed significantly declined cane yield. In our observation, activity of sucrose synthase enzyme and total sugar content in leaves significantly declined. These results corroborate previous findings (46), wherein the expression of sucrose synthase enzyme declined under atmospheric temperature of 42 °C.

The protective system under water deficit condition involves SOD converting superoxide to hydrogen peroxide, further reduced to H_2O by POX or CAT. In sugarcane, an increase of reactive oxygen species (ROS) induces the upregulation of SOD, POX and CAT to counteract the effect of ROS under drought stress and heat stress individually (47). Contrarily, in the present study, SOD and POX activity estimated during end of the stress period showed no significant increase in response to water deficit stress, whereas, CAT activity recorded significant increment under UIC. It could be inferred that the non-significant induction of SOD and POX under UIC aggravated the scavenging activity of free radicals in the cell associated with lipid peroxidation results in significantly higher cellular membrane injury. Results suggested that the reason for deviating from the prevailing trend could be a combined effect of high night temperature with water deficit stress.

Sugarcane plants under high temperature (above 32 °C) partitions less carbon to stored sucrose and develop shorter internodes, which are proportionately converted into more fibre in the stalk (34). On the contrary, the present results showed no significant reduction in sucrose content and CCS %, however high night temperature combined with water deficit stress during formative stage significantly reduced cane yield (51.9 %) and CCS (51.7 %).

Future direction

The earlier research reported individually about the effect of water deficit and heat stress and identified some important physiological traits for stress tolerance mechanism. In our study, long-term weather data showed an increasing trend in nighttime temperatures, which may reduce nocturnal stomatal conductance and exacerbate stress when combined with water scarcity, ultimately leading to a severe reduction in cane yield. Though sugarcane is a C4 crop which is having higher temperature optimum for photosynthesis and is inherently tolerant to drought as compared to C3 plants, there is a concern that the benefits achieved throughout the day may be diminished during the night under increasing nighttime temperature. Now is the right time to study the sensitivity of traditional heat-tolerant varieties to small increase in nighttime temperature. Identifying physiological traits responsive to high nighttime temperatures, rather than focusing solely on daytime adaptation–which is under independent genetic control, is crucial for developing climate-resilient varieties.

Conclusion

Through the trend analysis from 1991 to 2024, a notable high night temperature episode was observed during the month of March and April, 2024 coinciding with water deficit condition. As a result of this combined stress, a drastic reduction in morphological traits such plant height was observed, whereas canopy leaf area and fresh biomass (leaf and sheath) was not affected significantly. Further, a significant reduction in number of millable canes and single cane weight, along with slight changes in other yield attributes namely internodal length and cane girth, severely reduced cane yield and productivity. High night temperature significantly affected cell membrane stability, relative water content and canopy temperature. Further, biochemical parameters such as chlorophyll content, soluble protein content, total sugar content, nitrate reductase activity, catalase activity and sucrose synthase activity were significantly affected when high night temperature coincided with water deficit stress. However, other physio-biochemical parameters such as proline content, total phenol, superoxide dismutase activity and peroxidase activity did not show significant variation between IC and UIC. This study emphasises the importance of high night temperature on sugarcane production under tropical conditions.

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Authors' contributions

MA conceived the idea, carried out the experiments, observed and analysed data, and wrote the manuscript; RAK, VK, KK carried out experiments and generated data and assisted in interpretation of results; RG provided helped shape the manuscript. All authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors declare no competing interests.

Ethical issues: None

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