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SHORT COMMUNICATION

Impacts of saline stress on the physiology of *Saccharum* complex genotypes

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Abstract

Knowledge of the physiological mechanisms in saline environment may boost sugarcane breeding programmes targeting abiotic stresses. Our hypothesis is that the physiology of *Saccharum* genotypes responds differently under salt stress. Thus, the objective of the study was to evaluate the physiological performance of *Saccharum* complex genotypes grown under presence and absence of saline stress. The experimental design used was randomized blocks arranged in a 32 × 2 factorial scheme (32 genotypes × 2 salinity levels). The presence of salinity provided higher mean values for photosynthetic rate in genotypes G4, G18, G22, G25 and G29 compared with the environment without salinity, with mean values (17.26, 21.49, 24.22 and 26.19 μmol $CO_2 m^{-2} s^{-1}$), respectively, for internal CO_2 concentration in G2, G6, G9, G14, G17, G19, G23 and G29, with mean values (323.45, 399.64, 386.88, 412.14, 366.31, 250.48, 379.10 and 380.75 μmol CO_2 mol air^{-1}), respectively, for transpiration in G18, G24, G25 and G29, with mean values (5.05, 3.30, 4.39 and 4.01 mmol H_2O $m^{-2} s^{-1}$), respectively, and for chlorophyll content in G3, G5, G6, G8, G10, G13, G20, G22, G23, G25, G31 and G32, with mean values (34.18, 43.01, 38.08, 32.38, 37.09, 37.18, 32.47, 38.38, 38.04, 36.95 and 33.32 SPAD units) respectively. Genotypes that under salt stress increase their physiological performance demonstrate superiority over others and should be considered in breeding programmes. Photosynthesis and transpiration is the most adequate combination for screening, but the spad index is the most viable tool because of its ease of determination and cost.

KEYWORDS
abiotic stress, chlorophyll, photosynthesis, salinity tolerance, transpiration

1 | INTRODUCTION

Sugarcane (*Saccharum officinarum L*) is the main raw material for sugar production worldwide and is a commercially viable source in bioenergy production (Ferreira et al., 2017). Sugarcane has stood out in Brazil by the large planted areas and the favourable soil and climate conditions for cultivation, making Brazil the largest world producer and a highly competitive participant in global marketing (Conab, 2020). Na safra 2020, o cultivo da cana no Brasil ocupou uma área de 9,74 milhões de hectares, correspondendo a uma produtividade média de 76,61 kg/ha (IBGE, 2020).

However, sugarcane cultivation in regions with great production potential may be compromised due to soil degradation by salinity and sodicity (Asfaw et al., 2018). Increased soil salinity may result

from anthropogenic activities, including irrigation with saline water and poorly conducted irrigation and drainage practices, especially in regions with low rainfall associated with shallow soils (Castro and Santos, 2020).

In plants, salt stress leads to physiological disorders due to the increase in salts in the root zone, reducing the osmotic potential of the soil and water uptake (Taiz et al., 2017; Zuffo et al., 2020). The salinity effect on sugarcane varies and can promote reduced stomatal conductance and, consequently, decreased photosynthetic rates (Simoes et al., 2018; Simões et al., 2019) as well as negatively compromise growth with increasing salinity (Simões et al., 2016).

As stress resistance, plants of the same species can develop mechanisms to adjust to adverse stress situations making their identification important. Chiconato et al. (2019) found that gas exchange is a more sensitive indicator of the salinity effects on photosynthesis in sugarcane cultivars. Simoes et al. (2020) reported that higher chlorophyll indices favour gas exchange and may contribute to the adaptation of sugarcane cultivars to salt stress conditions.

On the contrary, the genetic breeding programme of the crop has prospected, within the *Saccharum* complex, genes related to resistance to biotic and abiotic stresses. Considering that this complex is composed of the genera *Erianthus*, *Sclerostachya*, *Miscanthuse* and *Narenga*, these are phylogenetically close to *Saccharum* and capable of being used in gene introgression programmes (Oliveira et al., 2017; Todd et al., 2014). Simões et al. (2021) found that some accessions of *E. arundinaceus* have higher photosynthetic rate and transpiration rate, these being adaptability characteristics of these accessions to salt stress.

Our hypothesis is that the physiology of *Saccharum* complex genotypes respond differently to salt stress. Thus, the knowledge of the physiological mechanisms developed by *Saccharum* genotypes to thrive under salt stress is an essential source of information for sugarcane breeders in identifying potential salinity-tolerant genotypes. Therefore, the objective of this research was to evaluate the physiological performance of *Saccharum* genotypes grown in the presence and absence of saline stress.

2 | MATERIAL AND METHODS

2.1 | Experiment conduction

The study was carried out in a greenhouse at EmbrapaSemiarido, located in Petrolina, PE, Brazil. The climate of the region is the semiarid BSWh type, characterized by scarce and irregular rainfall and high evaporation. The average annual total rainfall is about 560 mm, with rainfall concentrated between January and April. The relative humidity varies from 55% to 72%; the air temperature presents average variations between 21°C and 32°C and 3,000 hours of sunshine.

The experiment was carried out in a 32 × 2 factorial scheme in a randomized block design with three replicates. The first factor consisted of 32 *Saccharum* genotypes (Table 1), and the second factor consisted of the presence and absence of salinity.

To subject the sugarcane genotypes to salt stress, a salt solution containing NaCl, $CaCl_2.2H_2O$ and $MgSO_4.7H_2O$ was used, obtaining an equivalent proportion between Na:Ca:Mg of 7:2:1 (Aquino et al., 2007).

The plants were grown in plastic pots with a capacity of 10 litres, perforated at the base and connected to collecting hoses for conducting the leaching water. They were filled with a layer of gravel of approximately two centimetres, and the volume was completed with soil classified as medium-texture QuartzarenicNeosol, collected at a depth of 0 to 0.2 m, whose electrical conductivity (EC) was 0.6 dS m^{-1}.

Each pot corresponded to an experimental unit. Two buds of each genotype were planted in each pot. The genotypes were acquired from the Embrapa Tabuleiros Costeiros Germplasm Bank and multiplied in the experimental field of Mandacaru, belonging to Embrapa Semiarido, in Petrolina-PE. The irrigation of the units was performed every two days to maintain the soil at field capacity (FC). To avoid the accumulation of salts in the soil profile, a water volume higher than the necessary to bring the soil to field capacity was applied, obtaining a leaching fraction of approximately 15%.

2.2 | Traits evaluated

Physiological variables of the three plants that comprised the replicates were analysed 90 days after being submitted to salt stress. The traits evaluated were photosynthesis rate (A), internal CO_2 concentration (Ci) and transpiration (E), obtained through a portable infrared gas analyser (IRGA), model Li-6400, using artificial light fixed at 2,000 μmol $m^{-2}s^{-1}$. Leaf chlorophyll content (SPAD index) was also determined from measurements taken at three points on the +3 leaf, using a commercial chlorophyll metre CFL 1030.

2.3 | Statistical analysis

The data were submitted to variance analysis and clustering of means by the Scott-Knott test at 5% probability. Afterwards, a scatterplot was constructed containing the dispersion and correlation between the variables evaluated in the presence and absence of salt stress. The analyses were performed on R software (R Core Team, 2021) with the packages 'ExpDes.pt' and 'GGally'.

3 | RESULTS

There was a significant effect (p-value<.05) for the effects of genotypes, salinity and the interaction between these factors for all variables evaluated. Table 2 shows the significant interaction between genotypes × salinity level for the variable photosynthesis rate. The genotypes G1, G3, G9, G14, G16, G18, G20, G22, G25 and G29 presented the highest photosynthesis rate under saline stress. For the

TABLE 1 Genus and species of the 32 *Saccharum* complex genotypes evaluated

Genotype	Genus	Species
G1, G2, G3, G4, G5 e G6, G13, G15, G16, G17, G18, G19, G20, G21, G25, G30, G31 e G32	*Saccharum*	*officinarum*
G7, G8, G9 e G10 e G29	*Erianthus*	*arundinaceus*
G11	*Saccharum*	*hibrido*
G12, G14 e G26	*Saccharum*	*spp.*
G22 e G23	*Miscanthus*	*spp.*
G24	*Saccharum*	*spontaneum*
G27 e G28	*Saccharum*	*robustum*

control condition, the genotypes G5 and G20 stood out by obtaining the highest means of this variable. Regarding the comparison of environments within genotypes, 21 of the 32 genotypes showed no differences in mean photosynthesis rates under environments with and without saline stress, except genotypes G4, G18, G22, G25 and G29, in which the saline environment obtained higher mean values, and for genotypes G5, G6, G7, G20, G21 and G28, where their mean values in the control environment exceeded those achieved under stress conditions.

The results obtained for the variable internal CO_2 concentration are shown in Table 2. Except for the genotypes G4, G5, G10, G13, G19, G21, G26, G30 and G32, the remaining genotypes were allocated in the group of the highest means for this variable in the saline stress environment. For the control condition, the genotypes G1, G3, G5, G7, G8, G10, G11, G12, G13, G15, G18, G20, G22, G24, G25, G26, G27, G30 and G31 obtained the highest means for this variable. Regardless of the genotype × salinity level interaction, the genotypes G1, G3, G7, G8, G11, G12, G15, G18, G20, G22, G24, G25, G27 and G31 stood out by belonging to the highest mean groups in both environments.

By comparing environments within genotypes, there was no difference between them for 20 of the 32 genotypes. However, some genotypes showed specific responses as a function of the environment. For G13, G21, G26 and G30, the absence of salinity stress caused higher mean internal CO_2 concentration. However, the saline environment provided mean values higher than the environment without saline stress for G2, G6, G9, G14, G17, G19, G23 and G29.

Table 3 contains the transpiration results. The genotypes G14, G18 and G25 obtained the highest mean transpiration under saline stress. For the control condition, the genotypes G5, G6, G7 and G20 stood out by obtaining the highest means of this variable. By comparing environments within the genotypes, the absence of salinity stress provided the highest mean transpiration, except for the genotypes G18, G24, G25 and G29, in which the saline stress environment provided the highest mean values.

The mean leaf chlorophyll contents (SPAD index) of the genotypes grown with and without saline stress are shown in Table 3. The genotypes G5, G6, G7, G10, G12, G13, G14, G18, G22, G23, G25, G26 and G31 stood out by obtaining the highest SPAD means under salinity stress. For the control condition, the genotypes G2, G4, G12, G23 and G24 obtained the highest means for this variable. Regarding the comparison of environments within genotypes, there was no difference between environments for most genotypes. However, some genotypes showed specific responses as a function of the environment. In the genotypes G2 and G23, the absence of salinity stress resulted in higher SPAD means. However, the genotypes G3, G5, G6, G8, G10, G13, G20, G22, G23, G25, G31 and G32 obtained higher means under salinity stress compared with control environment.

The Figure 1 demonstrates the scatterplot constructed for the physiological variables evaluated in the *Saccharum* genotypes grown in the presence (pink) and absence (blue) of salinity stress. Overall, the magnitude and direction of the correlations among variables were not affected by the salinity condition. The main correlation observed was between photosynthesis and transpiration ($r = .819^*$), which was positive and significant by t test (p-valour <.05) in both salinity conditions ($r = .781^*$ under salinity stress and $r = 0.833^*$ without salinity stress).

4 | DISCUSSION

Genotypes that showed higher photosynthetic rates under saline environment when compared to the environment without salinity (Table 3) reveal to have lower sensitivity to saline stress. This result reveals the superior behaviour of these genotypes compared with the others. In this aspect, higher photosynthetic rates may be an adaptive response to stress. Considering that differential expression of genotypes is indicative of response to abiotic stress conditions.

According to Jackson et al. (2016) and Li et al. (2017), significant genetic variability in different *Saccharum* complex genotypes (*Saccharum* spp., *Erianthus* spp. and *Miscanthus* spp.) is associated with the photosynthetic activity. Thus, the magnitude of the photosynthesis values is related to the genetic characteristics of each genotype.

Chiconato et al. (2019), when comparing the performance of genetically distinct sugarcane cultivars under different salinity levels, found that the most salinity-tolerant cultivar was the one that maintained its photosynthetic rate under saline environment. According to these authors, the high tolerance to salinity is caused by the higher accumulation of proline, lower lipid peroxidation and the ability to exclude Na^+ while withdrawing water from the soil.

On the contrary, the behaviour of the internal CO_2 concentration is related to the activity of the ribulose-1,5-bisphosphate carboxylase-oxygenase enzyme which, under favourable conditions, increases

TABLE 2 Unfolding the significant interaction between *Saccharum* genotypes and the presence and absence of salinity stress for photosynthesis rate (A, μmol $CO_2 m^{-2} s^{-1}$) and internal CO_2 concentration (Ci, μmol $CO_{2\ mol}$ air^{-1})

	A		Ci	
Genotype	Presence	Absence	Presence	Absence
G1	23.30 aA	17.97 cA	395.32 aA	356.19 aA
G2	11.76 cA	13.89 dA	323.45 aA	245.02 bB
G3	18.32 aA	19.63 cA	375.35 aA	388.85 aA
G4	17.26 bA	10.99 dB	264.62 bA	274.10 bA
G5	15.90 bB	35.12 aA	296.28 bA	326.21 aA
G6	14.79 bB	28.15 bA	399.64 aA	296.51 bB
G7	12.48 cB	27.54 bA	352.42 aA	362.79 aA
G8	11.09 cA	9.55 dA	400.69 aA	393.34 aA
G9	24.12 aA	28.98 bA	386.88 aA	251.95 bB
G10	12.17 cA	14.34 dA	313.29 bA	340.43 aA
G11	10.28 Ac	10.31 dA	391.48 aA	367.49 aA
G12	17.18 bA	20.32 cA	374.21 aA	327.82 aA
G13	6.94 cA	11.09 dA	243.75 cB	362.64 aA
G14	23.41 aA	20.63 cA	412.14 aA	273.07 bB
G15	14.76 bA	15.76 cA	384.74 aA	358.15 aA
G16	19.33 aA	19.19 cA	335.21 aA	313.63 bA
G17	10.77 cA	14.17 dA	366.31 aA	273.24 bB
G18	21.49 aA	10.28 dB	412.16 aA	355.09 aA
G19	12.52 cA	11.82 dA	250.48 cA	96.79 cB
G20	19.90 aB	32.01 aA	396.14 aA	413.66 aA
G21	15.46 bB	29.47 bA	181.04 cB	293.49 bA
G22	24.22 aA	16.31 cB	370.30 aA	339.12 aA
G23	15.02 bA	20.62 cA	379.10 aA	285.79 bB
G24	14.84 bA	13.81 dA	392.35 aA	394.77 aA
G25	24.93 aA	17.94 cB	412.35 aA	401.15 aA
G26	16.57 bA	19.23 cA	245.70 cB	396.35 aA
G27	10.42 cA	16.28 cA	334.41 aA	334.97 aA
G28	11.97 cB	23.11 bA	343.37 aA	314.38 bA
G29	26.19 aA	17.55 cB	380.75 aA	283.29 bB
G30	12.14 cA	18.28 cA	214.31 cB	387.48 aA
G31	15.67 bA	17.87 cA	416.24 aA	393.89 aA
G32	11.81 cA	15.89 cA	279.47 bA	271.81 bA

Note: Means followed by equal lowercase letters in the same column and equal uppercase letters in the same row do not differ by the Scott-Knott test and *F* test at 5% probability.

TABLE 3 Unfolding the significant interaction between *Saccharum* genotypes and the presence and absence of salinity stress for of transpiration means (E, mmol H_2O $m^{-2} s^{-1}$) and leaf chlorophyll content (SPAD index)

	E		SPAD Index	
Genotype	Presence	Absence	Presence	Absence
G1	3.68 bA	3.62 cA	30.10 bA	34.03 bA
G2	1.61 dA	2.31 dA	34.69 bB	43.00 aA
G3	3.58 bA	3.73 cA	34.18 bA	17.70 eB
G4	3.04 bA	2.04 dA	34.77 bA	38.31 aA
G5	2.93 dB	5.07 aA	43.01 aA	30.97 cB
G6	3.78 bB	5.08 aA	38.08 aA	32.52 bB
G7	2.23 dB	5.60 aA	36.71 aA	34.35 bA
G8	2.65 cA	1.74 dA	32.38 bA	25.61 dB
G9	4.00 bA	4.77 bA	32.96 bA	36.62 bA
G10	1.52 dB	3.05 cA	37.09 aA	27.17 cB
G11	2.58 cA	2.22 dA	34.65 bA	34.61 bA
G12	3.04 cA	3.99 bA	36.12 aA	39.18 aA
G13	1.95 dB	3.56 cA	37.18 aA	29.60 cB
G14	4.74 aA	4.32 bA	35.37 aA	31.87 cA
G15	3.75 bA	3.48 cA	31.62 bA	31.53 cA
G16	4.12 bA	4.56 bA	25.81 bA	23.64 dA
G17	2.24 dB	3.33 cA	31.40 bA	35.80 bA
G18	5.05 aA	2.43 dB	38.92 aA	36.94 bA
G19	1.49 dA	1.91 dA	33.08 bA	35.29 bA
G20	3.50 bB	5.86 aA	32.47 bA	24.40 dB
G21	2.80 cB	4.78 bA	32.23 bA	28.64 cA
G22	3.94 bA	3.01 cA	38.38 aA	26.97 cB
G23	2.55 cA	3.33 cA	35.16 aB	40.78 aA
G24	3.30 bA	2.23 dB	32.33 bA	37.62 aA
G25	4.39 aA	3.43 cB	38.04 aA	25.99 dB
G26	2.69 cB	3.99 bA	35.37 aA	32.72 bA
G27	1.94 dA	2.69 dA	33.63 bA	28.87 cA
G28	2.27 dB	4.03 bA	33.71 bA	29.98 cA
G29	4.01 bA	2.25 dB	33.65 bA	30.55 cA
G30	1.93 dA	2.44 dA	34.07 bA	31.05 cA
G31	2.96 cA	3.15 cA	36.95 aA	28.42 cB
G32	2.14 cA	2.91 cA	33.32 bA	27.75 cB

Note: Means followed by equal lowercase letters in the same column and equal uppercase letters in the same row do not differ by the Scott-Knott test and *F* test at 5% probability.

carboxylation and reduces the oxygenation of the photosynthetic process, resulting in better CO_2 use (Lima et al., 2021). The higher internal CO_2 concentration in the genotypes (Table 4) can be attributed to the high photosynthetic activity of sugarcane. In *Saccharum*, the increase in CO_2 concentration at the Rubisco active site, with consequent reduction in photorespiration, occurs due to the C4 photosynthetic metabolism (Von Caemmerer and Furbank, 2016).

When present in the soil, Na^+ and Cl^- alter the osmotic potential causing a reduction in water uptake (Pereira et al., 2020). Thus, plants under salt stress partially close the stomata to prevent water loss and, consequently, have lower transpiration and CO_2 assimilation rates (Taiz et al., 2017). Reducing transpiration is a plant strategy to minimize water loss and is therefore considered a mechanism of resistance to saline stress (Ferreira et al., 2017).

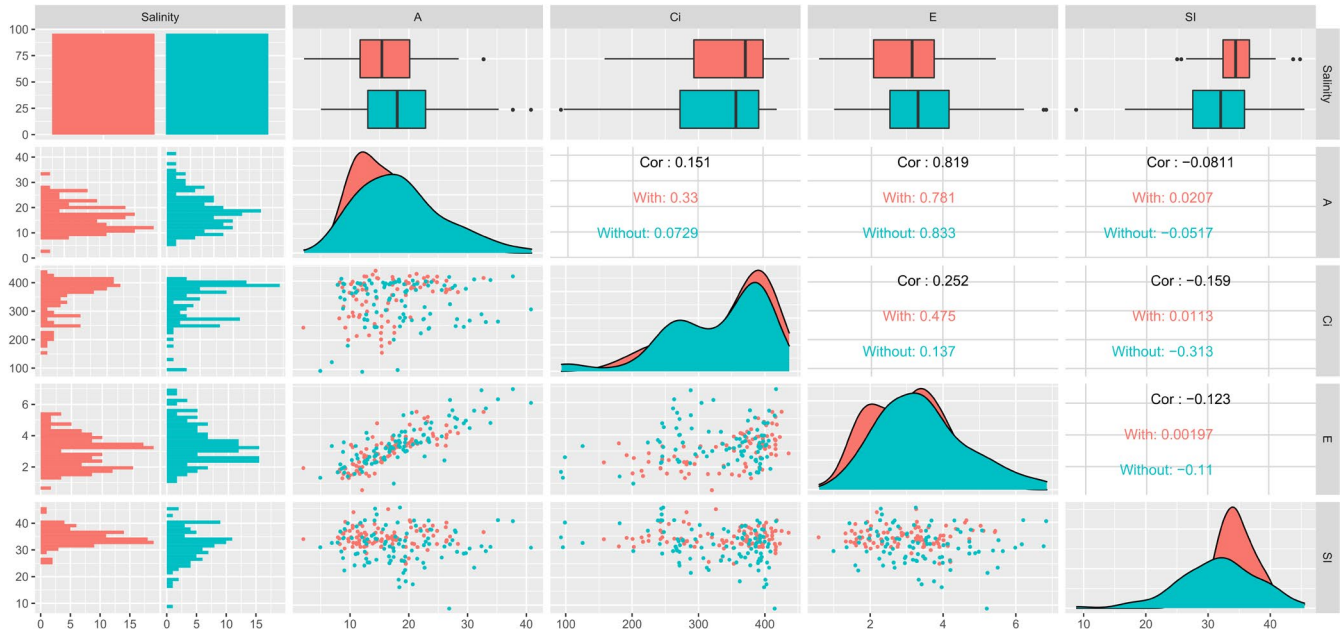

FIGURE 1 Scatterplot and Pearson's correlation between the variables photosynthesis (A), internal CO_2 concentration (Ci), transpiration (E) and SPAD index (SI) evaluated in 32 *Saccharum* genotypes grown in the presence (pink) and absence (blue) of saline stress

However, genotypes G18, G24, G25 and G29 obtained higher mean transpiration in saline environment than in no saline environment (Table 5). Simoes et al. (2020) evaluated the physiological and biochemical responses of sugarcane varieties subjected to salinity and also observed a significant increase in transpiration as a function of increasing electrical conductivity in one of the varieties.

Thus, increased transpiration can also be considered a mechanism of resistance to saline stress. The physiological response of plants to salinity is complex, depending on several factors such as the salt concentration in the soil and the duration of stress, thereby varying the symptoms and consequences (Chaves et al., 2009). Differences in physiological behaviour also occur within species with high genetic variability, as in sugarcane, and therefore may not undergo selection pressure on individual traits for salinity tolerance (Chiconato et al., 2019).

Saline stress in plants sensitive to high salinity causes swelling and rupture of the thylakoids and chloroplast layer by excess Na^+ and Cl^- ions, inhibiting the synthesis of new chlorophyll molecules (Zhang et al., 2010). However, in this study, we verified that some genotypes provided higher mean leaf chlorophyll content (SPAD index) under saline environment than genotypes under no saline stress (Table 6).

The ability to keep leaf chlorophyll content stable during stress conditions allows cells to keep the chloroplast functional, favouring the plant to maintain photosynthesis after stress (Augustine et al., 2015). Therefore, increasing total chlorophyll content may contribute to the tolerance of *Saccharum* complex genotypes to saline stress. Ferreira et al. (2017) stated that genotypes exhibiting variations in leaf chlorophyll content as well as photosynthesis rate and transpiration rate under stress conditions are considered tolerant. Simões et al. (2019) observed that varieties with higher adaptability to saline stress simultaneously increase photosynthetic rate, transpiration and chlorophyll index. On the contrary, Chiconato et al. (2019) observed that tolerant cultivar does not reduce the photosynthetic rate and does not show significant changes in Ci and chlorophyll content with increasing salinity.

Similar results were found in the present study for the genotypes G18 and G25, which simultaneously obtained higher mean values of transpiration, photosynthesis and chlorophyll index, without significant changes in Ci under saline stress environment. Thus, the salinity effect positively influences the physiology of the sugarcane genotypes G18 and G25, revealing the adaptability of these genotypes to saline stress conditions, and they should be considered in genetic breeding programmes.

We have identified genotypes that have simultaneously higher mean of transpiration, photosynthetic rate and chlorophyll index, without significant changes in Ci, under salt stress environment. This behaviour may have a significant genetic value since such measurements should not be negatively associated with growth rates (Li et al., 2017). For practical applications in breeding, investigations must now turn to establishing the narrow-sense heritability of these physiological traits.

In Figure 1, the positive correlation between photosynthesis and transpiration is expected, because variations in gas exchange can occur as a function of stomatal movement. Stomatal closure results in reduced stomatal conductance and consequently decreased transpiration and photosynthesis, just as increased stomatal opening results in increased transpiration and photosynthesis (Taiz et al., 2017).

Thus, it is possible to assume that a small number of simple leaf gas exchange measurements are sufficient to efficiently filter transpiration and distribute the variation related to the photosynthetic component (Li et al., 2017). This is important because it means that,

by breeding and selection, high levels of transpiration should be achievable without necessarily sacrificing high photosynthesis rates. This would then be a combination of traits best suited for screening. Nevertheless, these screening traits are costly.

It is important to emphasize that these results do not exclude the role of other physiological parameters, such as chlorophyll content (SPAD index), which can also help to understand the tolerance of plants to abiotic stresses since, during stress, the stability of chlorophyll content in plant tissues allows the cells to remain functional chloroplast maintaining the photosynthetic activity of the plant (Augustine et al., 2015). Thus, since the SPAD index showed a low CV and is relatively easy to determine, it is possibly the best screening tool.

In view of the above, through the physiological performance, it became evident that the genotypes of the Saccharum complex respond differently to salt stress. Higher means of photosynthetic rate, internal concentration of CO2, transpiration and chlorophyll observed in some genotypes grown in salinity environment point to a superior behaviour of these genotypes under salt conditions, as well as the importance of these variables as adaptive responses to stress. In this respect, the findings of the manuscript may contribute to sugarcane breeding programmes for abiotic stresses.

5 | CONCLUSIONS

Genotypes that under salt stress increase their physiological performance demonstrate superiority over others and should be considered in breeding programmes. Photosynthesis and transpiration is the most suitable combination for screening, but the SPAD index is the most viable screening tool because of its ease of determination and cost.

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CONFLICT OF INTERESTS

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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