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Predication of Photosynthetic Leaf Gas Exchange of Sugarcane (*Saccharum* spp) Leaves in Response to Leaf Positions to Foliar Spray of Potassium Salt of Active Phosphorus under Limited Water Irrigation

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ABSTRACT: Sufficient water and fertilizer inputs in agriculture play a major role in crop growth, production, and quality. In this study, the response of sugarcane to limited water irrigation and foliar application of potassium salt of active phosphorus (PSAP) for photosynthetic responses were examined, and PSAP's role in limited water irrigation management was assessed. Sugarcane plants were subjected to limited irrigation (95−90 and 45−40% FC) after three months of germination, followed by a foliar spray (0, 2, 4, 6, and 10 M) of PSAP. The obtained results indicated that limited water irrigation negatively affected sugarcane growth and reduced leaf gas exchange activities. However, the application of PSAP increased the photosynthetic activities by protecting the photosynthetic machinery during unfavorable conditions. Mathematical modeling, a Skewed model, was developed and compared with the existing Gaussian model to describe the photosynthetic responses of sugarcane leaves under the limited irrigation with and without PSAP application. The models fitted well with the observed values, and the predicted photosynthetic parameters were in close relationship with the obtained results. The Skewed model was found to be better than the Gaussian model in describing the photosynthetic parameters of plant leaves positioned over a stem of limited water irrigation and applied PSAP application and is recommended for further application.
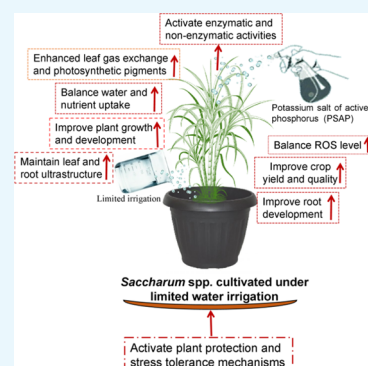
1. INTRODUCTION

Sugarcane (*Saccharum* spp.) is one of the major cash crops in the globe, mainly cultivated in dry and semidry regions.[1] China is the third largest cane producer worldwide,[2,3] and the Guangxi province is the leading sugarcane producer, which produces 6−9 million tons of cane sugar, amounting to over 60% of the total production of sugarcane in the country,[3] mainly for sugar and ethanol production. Cane production has rapidly enhanced and gained attention as a feedstock for 2-G ethanol, considered as a source of cleaner energy as relative to fossil fuels.[4]

Limited water is one of the main limiting factors for agricultural crop production. The loss of yield by limited irrigation of crops exceeds about 60% for a variety of plants/crops.[4−6] Limited water which inhibits plant leaf gas exchange and growth traits[1,7,8] is responsible for the loss in crop production.[9,10] However, the impacts of limited water supply vary according to the growth phases.

Photosynthetic capacity is the main physiological process for crop growth and productivity.[11,12] Other related studies have reported that the leaf photosynthetic performance in C_4 crops is very sensitive to fluctuations in soil moisture capacity.[13−18] The inhibitory impacts of insufficient water supply on photosynthetic

performance can be linked with low CO_2 levels in the stroma of chloroplasts caused by diffusion limitations through the stomata and the mesophyll,[19] the variation of enzymatic carbon assimilation, and phloem transport limitations.[17,20,21] The closure of stomatal openings is an initial effect to limited irrigation and an efficient way to decrease the loss of water when stress is not too severe; however, it limits carbon dioxide diffusion in the plant leaves for photosynthetic capacity.[18,22,23] The requirement of water under field conditions has been a serious issue since most agricultural areas suffer from seasonal water stress conditions.[4,10,24]

Potassium (K) plays an important role in plant development.[25] The research evidence indicated that the plants subjected to limited irrigation have a more internal requirement for K element,[26,27] and crop productivity-limiting effects of

Table 1. Influence of PSAP on Leaf Area Expansion (cm²) in Sugarcane Plants Subjected to Limited Water Irrigation[a]

irrigation level (% FC)	PSAP (M)	leaf position vs leaf area expansion (cm²)					
		1	2	3	4	5	6
95−90%	0	235.25	251.66	268.32	316.33	317.31	317.39
	2	246.89	263.19	279.19	319.09	320.13	320.98
	4	251.05	273.98	293.01	321.12	323.79	325.02
	6	270.21	298.36	317.61	324.08	325.18	326.61
	10	278.74	302.13	327.31	339.91	342.67	346.09
45−40%	0	172.52	187.8	201.38	206.41	211.02	213.15
	2	184.02	208.18	221.13	227.43	229.19	231.09
	4	185.69	217.09	232.27	239.49	241.01	244.06
	6	199.11	224.16	239.8	251.21	257.94	259.07
	10	209.05	237.96	257.11	264.13	268.09	269.17

[a]Each set of data represents mean of at least five biological replicates. FC = field capacity.

Table 2. Model Constants for the Skewed and Gaussian Models of Control (A) and Limited Irrigation (B) with Foliar Application of PSAP in Sugarcane Plants[a]

		(A)					
		control (95−90% of FC)					
		Skewed model			Gaussian model		
photosynthetic responses	PSAP (M)	α	β	γ	a	b	c
P_N	0	21.60	83.27	17.58	21.97	1.71	3.99
	2	21.97	1634.09	15.78	22.33	1.91	4.14
	4	24.14	104.69	11.92	24.22	1.46	5.05
	6	28.80	14.24	47.96	29.32	0.73	5.67
	10	28.89	34.65	92.81	29.49	0.017	6.27
gs	0	146.38	107.68	5.98	158.13	−1.79	6.43
	2	205.52	156.24	2.71	306.89	−4.09	17.33
	4	259.95	151.97	2.33	199.51	−95.63	25.83
	6	245.28	603.60	2.88	100.48	−109.31	26.79
	10	295.67	722.28	2.12	233.27	−35.47	2.07
E	0	1.98	1.48	18.94	2.03	0.47	4.60
	2	2.04	2.46	14.33	2.07	0.95	4.02
	4	2.27	47.36	8.54	2.27	0.69	4.59
	6	2.90	2.84	10.32	3.04	−0.14	4.55
	10	2.86	7.19	5.74	3.06	−0.89	5.06
		(B)					
		drought (45−40% of FC)					
		Skewed model			Gaussian model		
photosynthetic responses	PSAP (M)	α	β	γ	a	b	c
P_N	0	13.38	5.38	258.18	14.81	−1.41	6.69
	2	15.77	8.39	42.42	17.13	−0.86	5.84
	4	17.57	17.18	7.81	19.18	−1.32	5.96
	6	20.08	22.94	7.37	21.66	−1.05	5.67
	10	20.32	62.38	5.39	22.78	−2.17	6.35
gs	0	91.27	60.04	43.07	92.95	7.28	4.16
	2	97.25	64.25	59.28	98.23	1.26	3.99
	4	123.37	194.81	9.14	124.71	0.63	4.03
	6	128.98	142.99	17.43	130.95	0.99	4.09
	10	129.27	273.39	8.52	130.61	0.62	4.32
E	0	1.13	0.83	5.76	1.39	−6.78	12.41
	2	1.21	2.58	6.07	1.301	−2.84	10.14
	4	1.22	0.81	41.47	1.24	1.69	5.24
	6	1.45	10.42	7.30	1.49	−0.34	6.45
	10	1.28	30.83	11.15	1.30	0.75	6.30

[a]P_N = photosynthesis, gs = stomatal conductance to water vapor, and E = transpiration rate.

limited water supply could be overcome by enhancing K supplementation.[28−30] Under limited water supply, more K is required for the balance of photosynthetic CO_2 assimilation rates, defense of chloroplasts from oxidative damage, impair-

Table 3. Calculated Values of the Photosynthetic Parameters, That Is, Net Photosynthetic Rate (P_N), Stomatal Conductance to Water Vapor (gs), and Transpiration Rate (E) by the Skewed and Gaussian Models for Different Leaf Positions under Normal Growth Conditions with Foliar Application of PSAP in Sugarcane Plants

| | Skewed model | | | | | Gaussian model | | | | |
| | PSAP (M) | | | | | PSAP (M) | | | | |
leaf position	0	2	4	6	10	0	2	4	6	10
	P_N (μmol CO_2 m^{-2} s^{-1})									
1	21.601	21.975	24.141	28.803	28.802	21.623	21.795	24.121	29.287	29.166
2	21.567	21.920	23.996	28.796	28.415	21.908	22.320	24.078	28.592	28.125
3	20.955	21.440	23.141	27.753	26.616	20.847	21.563	23.110	27.058	26.440
4	19.009	20.006	21.378	24.582	24.081	18.632	19.654	21.328	24.822	24.232
5	15.845	17.308	18.940	21.536	21.455	15.641	16.899	18.925	22.074	21.650
6	11.981	13.282	16.112	19.397	19.018	12.331	13.709	16.147	19.029	18.858
	gs (mmol H_2O m^{-2} s^{-1})									
1	143.66	168.671	187.230	211.566	209.307	143.85	165.301	182.529	209.025	206.113
2	133.35	141.335	154.428	177.398	169.841	132.82	143.547	157.801	179.119	173.372
3	119.65	121.407	132.394	151.068	143.751	119.71	124.242	136.220	153.278	145.650
4	104.97	105.716	115.650	129.946	124.170	105.32	107.176	117.413	130.982	123.301
5	90.294	92.773	102.103	112.401	108.487	90.453	92.146	101.052	111.774	106.611
6	76.011	81.762	90.712	97.445	95.410	75.824	78.962	86.840	95.249	95.793
	E (mmol H_2O m^{-2} s^{-1})									
1	1.985	2.042	2.265	2.903	2.839	2.013	2.067	2.267	2.945	2.851
2	1.968	2.020	2.179	2.803	2.621	1.918	1.998	2.182	2.720	2.597
3	1.763	1.838	2.001	2.401	2.272	1.743	1.816	2.002	2.394	2.275
4	1.461	1.532	1.756	1.943	1.899	1.511	1.551	1.752	2.007	1.916
5	1.211	1.226	1.470	1.567	1.546	1.249	1.246	1.462	1.604	1.552
6	1.033	0.964	1.158	1.281	1.224	0.985	0.941	1.164	1.221	1.209

Table 4. Calculated Values of the Photosynthetic Parameters, That Is, Net Photosynthetic Rate (P_N), Stomatal Conductance to Water Vapor (gs), and Transpiration Rate (E) by the Skewed and Gaussian Models for Different Leaf Positions during Limited Water Irrigation with Foliar Application of PSAP in Sugarcane Plants

| | Skewed model | | | | | Gaussian model | | | | |
| | PSAP (M) | | | | | PSAP (M) | | | | |
leaf position	0	2	4	6	10	0	2	4	6	10
	P_N (μmol CO_2 m^{-2} s^{-1})									
1	13.382	15.775	17.564	20.069	20.040	13.883	16.283	17.776	20.293	20.110
2	13.382	15.740	16.808	19.140	18.493	13.010	15.193	16.418	18.748	18.360
3	12.569	14.179	14.783	16.837	16.348	11.922	13.767	14.743	16.791	16.351
4	10.187	11.650	12.606	14.321	14.123	10.685	12.113	12.871	14.579	14.206
5	8.940	9.963	10.747	12.097	11.998	9.364	10.351	10.925	12.271	12.041
6	8.437	9.001	9.249	10.245	10.025	8.026	8.588	9.016	10.012	9.955
	gs (mmol H_2O m^{-2} s^{-1})									
1	91.275	97.256	123.354	128.989	129.225	92.749	98.018	124.207	130.959	130.112
2	91.117	97.234	119.442	128.222	125.263	88.697	96.556	117.753	127.067	124.123
3	81.961	91.825	105.198	118.202	112.618	80.054	89.327	104.959	116.142	112.239
4	64.798	75.326	86.551	99.170	95.464	68.191	77.611	87.959	100.000	96.203
5	52.320	60.691	68.478	79.633	77.651	54.820	63.329	69.306	81.109	78.160
6	44.836	51.186	52.596	63.104	60.878	41.594	48.530	51.342	61.972	60.192
	E (mmol H_2O m^{-2} s^{-1})									
1	1.135	1.207	1.225	1.452	1.287	1.140	1.210	1.225	1.456	1.301
2	1.092	1.166	1.225	1.399	1.274	1.080	1.160	1.233	1.393	1.276
3	1.018	1.103	1.208	1.303	1.231	1.017	1.101	1.198	1.301	1.221
4	0.944	1.032	1.124	1.183	1.152	0.952	1.035	1.121	1.186	1.139
5	0.879	0.961	1.001	1.053	1.042	0.884	0.964	1.012	1.056	1.036
6	0.824	0.892	0.885	0.975	0.908	0.817	0.889	0.880	0.917	0.919

ment of related disruption in carbohydrate metabolism, regulation of stomatal openings, and relations of water status.[31]

Phosphorus (P) is an essential element for optimum plant growth and development, but its slow mobility in soil results in poor uptake by plant roots, which consequently hinders the growth and metabolism activities.[32,33] Previous studies indicated that P contributes to the enlargement of root morphology, and P deficiency will exacerbate limited water irrigation.[34,35] The
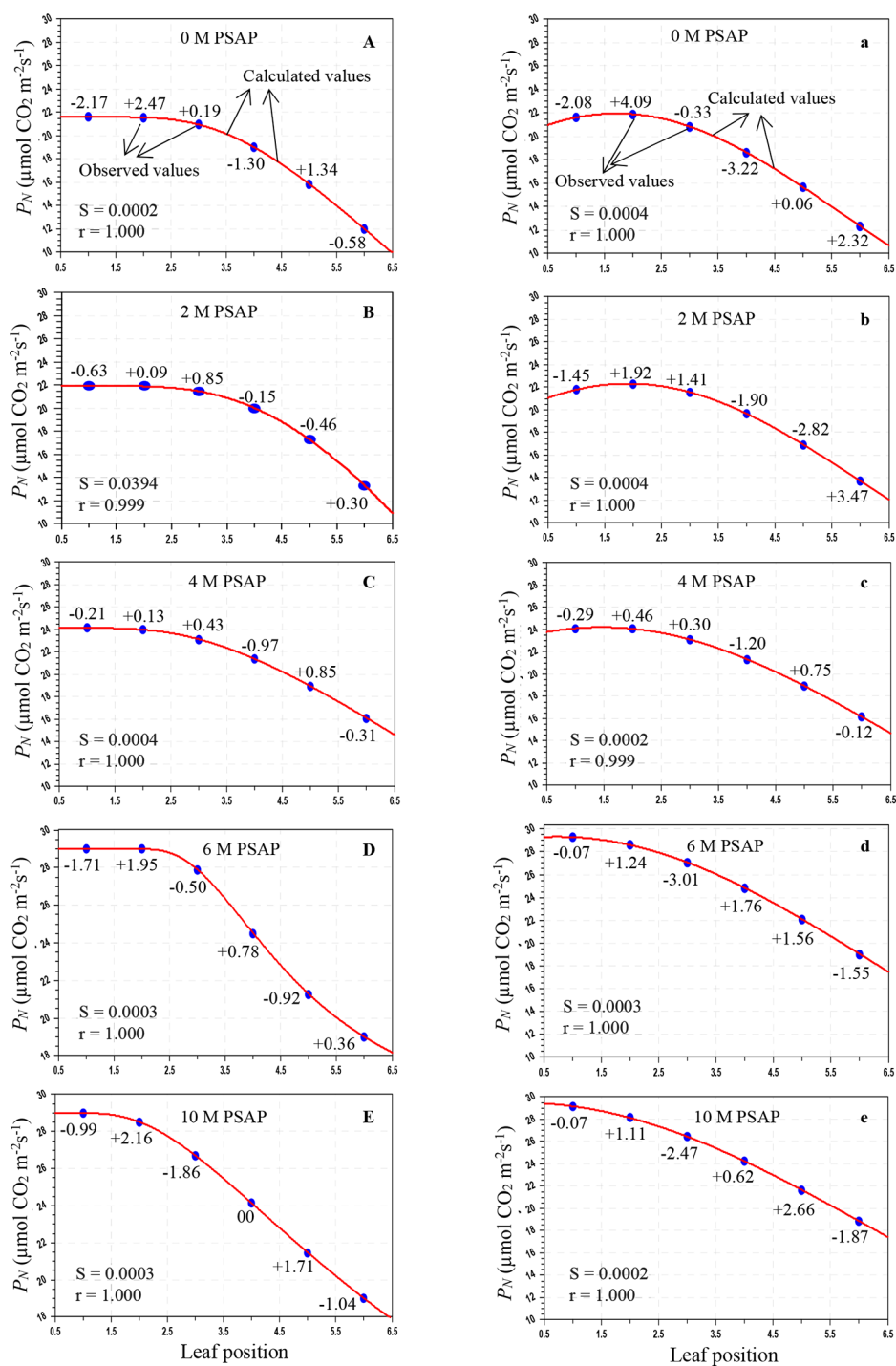
Figure 1. Variation of photosynthesis (P_N; μmol CO_2 m^{-2} s^{-1}) in sugarcane leaves after the application of PSAP (0, 2, 4, 6, and 10 M) under normal irrigation in the Skewed and Gaussian models. Data are represented as the arithmetic mean ($n = 3$). Blue ovals denote the observed values and red lines show the calculated values. Parenthesis values indicate percent deviation. (A−E) Skewed model, (a−e) Gaussian model, S = standard error, and r = correlation coefficient.

application of P decreases its deficiency in soil, enhances the stress-tolerance mechanism of plants,[36] and results in adaptations of morpho-physiological and biochemical activities that upregulate plant performance.[33,37−41]

However, knowledge about how potassium salt of active phosphorus (PSAP) regulates the photosynthetic variation in sugarcane plants subjected to limited water irrigation remains elusive. In addition, available information concerning the specific dose of PSAP for its application method in sugarcane

crops is very limited and thus warrants an in-depth assessment. Exposure to severe water stress may affect the photosynthetic capacity of sugarcane plants with the effects on the leaves varying with leaf position (+1−6th, top to bottom). The plant performance/productivity is actually associated with the accumulated photosynthetic activities and hence with the cumulative photosynthesis, so the response of sugarcane plants to limited irrigation in relation to plant leaf position should be better understood. This study was devoted to develop a
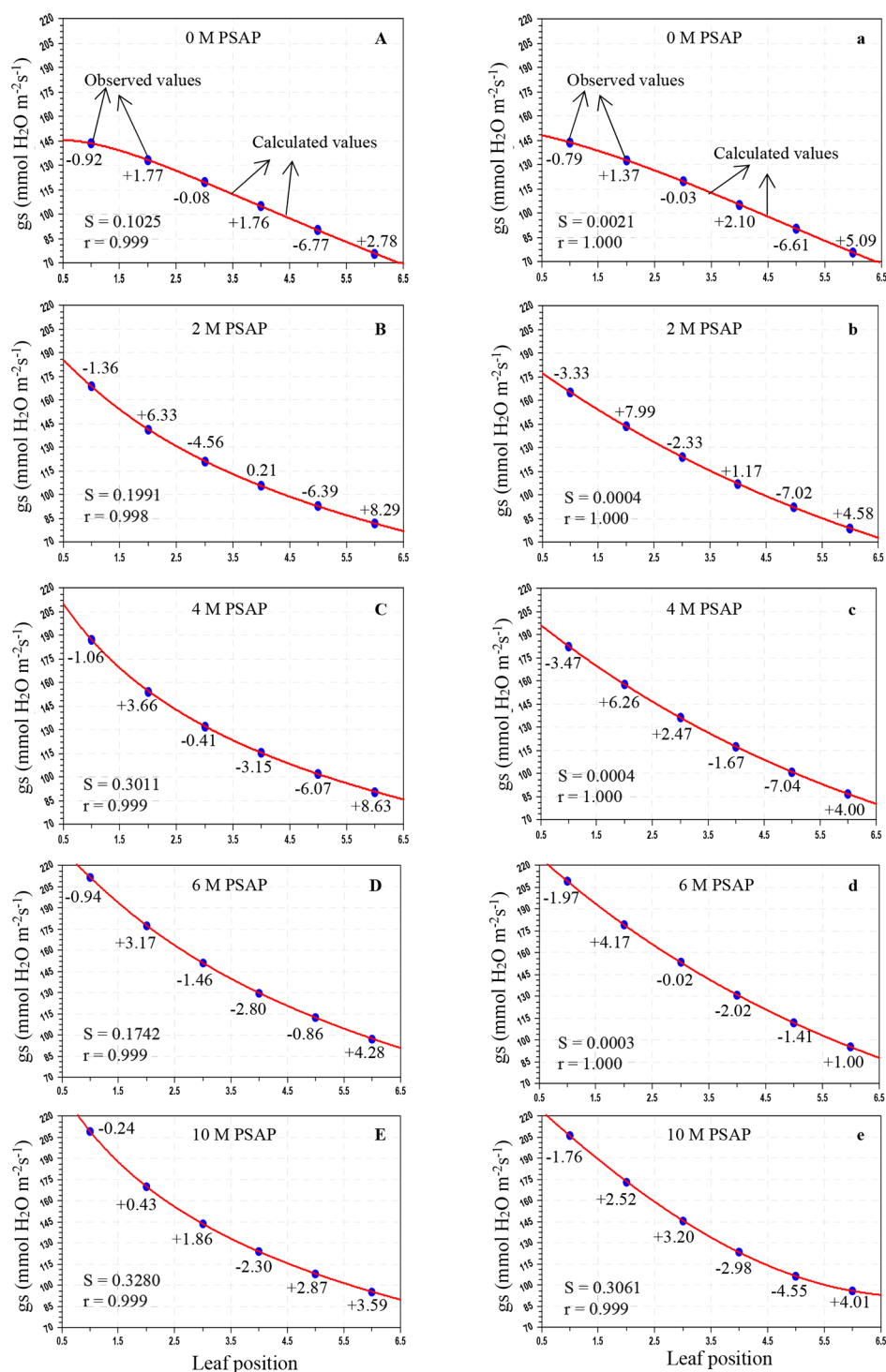
Figure 2. Variation of stomatal conductance to water vapor (gs; mmol H_2O m^{-2} s^{-1}) in sugarcane leaves after application of PSAP (0, 2, 4, 6, and 10 M) under normal irrigation in the Skewed and Gaussian models. Data are represented as the arithmetic mean ($n = 3$). Blue ovals denote the observed values and red lines show the calculated values. Parenthesis values indicate percent deviation. (A–E) Skewed model, (a–e) Gaussian model, S = standard error, and r = correlation coefficient.

mathematical modeling for correlating the photosynthetic activities against leaf position over the main stem that could be helpful in integrating the photosynthetic parameters in each leaf of the main stem.

2. RESULTS

Sugarcane plants (*Saccharum* hybrid cv. GT 42) were used to examine the photosynthetic traits to limited irrigation and

impact of PSAP by foliar application. The observed position-wise (from top to bottom since leaf + 1) leaf area expansion is given in Table 1. The model constants (regression coefficient) for the Skewed model, that is, α, β, and γ, and for the Gaussian model, that is, a, b, and c, of the control and limited irrigation (95−90 and 45−40% of FC) with PSAP (0, 2, 4, 6, and 10 M) in sugarcane plants are shown in Table 2. The calculated values of the photosynthetic parameters such as the net photosynthetic
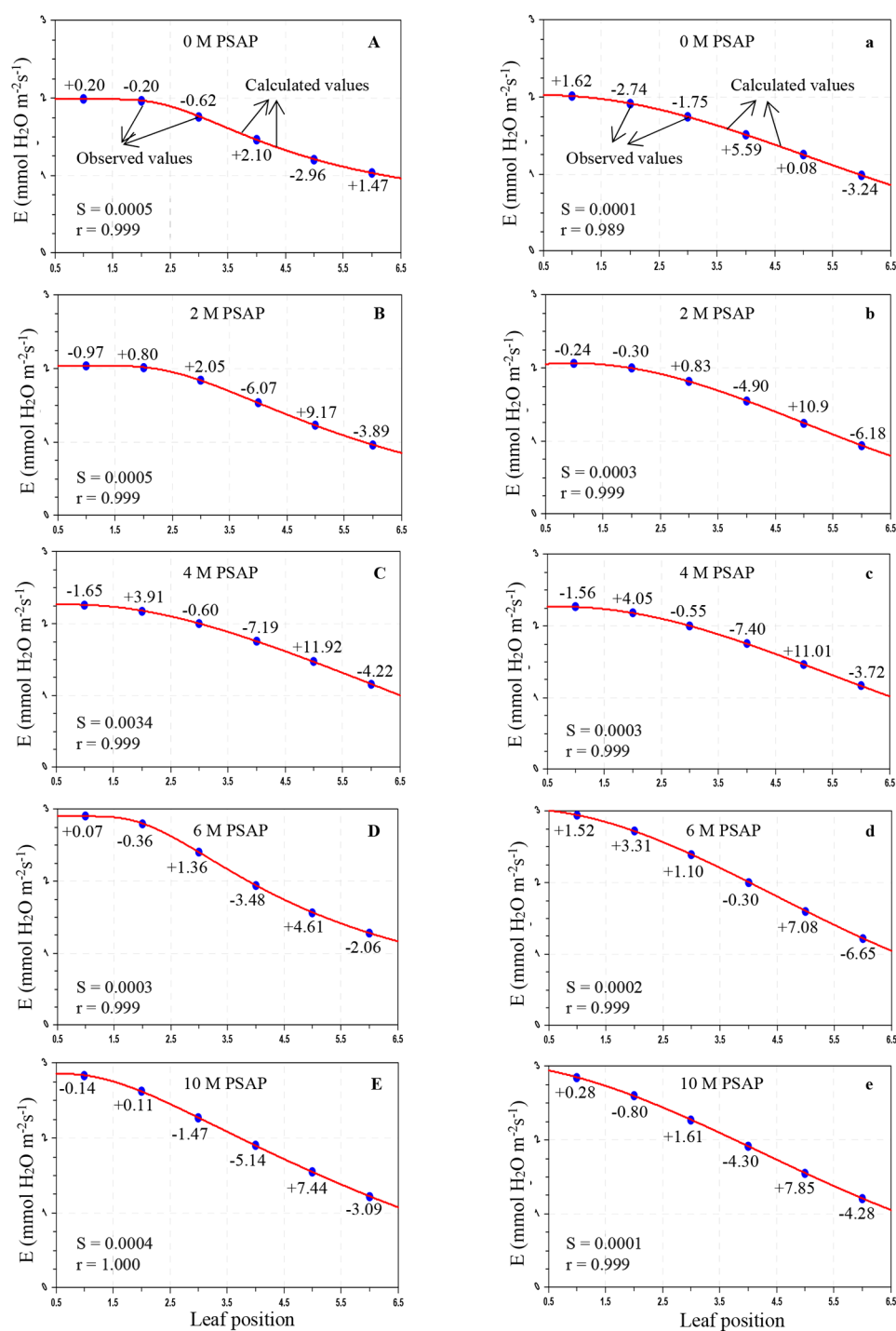
Figure 3. Variation of the transpiration rate (E; mmol H_2O m^{-2} s^{-1}) in sugarcane leaves after application of PSAP (0, 2, 4, 6, and 10 M) under normal irrigation in the Skewed and Gaussian models. Data are represented as the arithmetic mean ($n = 3$). Blue ovals denote the observed values and red lines show the calculated values. Parenthesis values indicate percent deviation. (A–E) Skewed model, (a–e) Gaussian model, S = standard error, and r = correlation coefficient.

rate (P_N), stomatal conductance to water vapor (gs), and transpiration rate (E) with the Skewed and Gaussian models of normal and treated plants with PSAP application are represented in Tables 3 and 4 and Figures 1–6.

As shown in Table 3, under normal irrigation with different concentrations of PSAP, the calculated values of the P_N for the Skewed model were in the range of 28.803−11.981 μmol CO_2 m^{-2} s^{-1}, and for the Gaussian model, the range was 29.287−12.331 μmol CO_2 m^{-2} s^{-1}; the predicted gs for the Skewed

model ranges from 211.566 to 76.011 mmol H_2O m^{-2} s^{-1} and that for the Gaussian model ranges from 209.025 to 75.824 mmol H_2O m^{-2} s^{-1}; and the E for the Skewed model ranges from 2.903 to 0.964 mmol H_2O m^{-2} s^{-1} and that for the Gaussian model ranges from 2.945 to 0.941 mmol H_2O m^{-2} s^{-1}. For drought stress (45−40% of FC) with foliar application of PSAP, the calculated values of P_N for the Skewed model range from 20.069 to 8.437 μmol CO_2 m^{-2} s^{-1} and those for the Gaussian model range from 20.293 to 8.026 μmol CO_2 m^{-2} s^{-1}; the
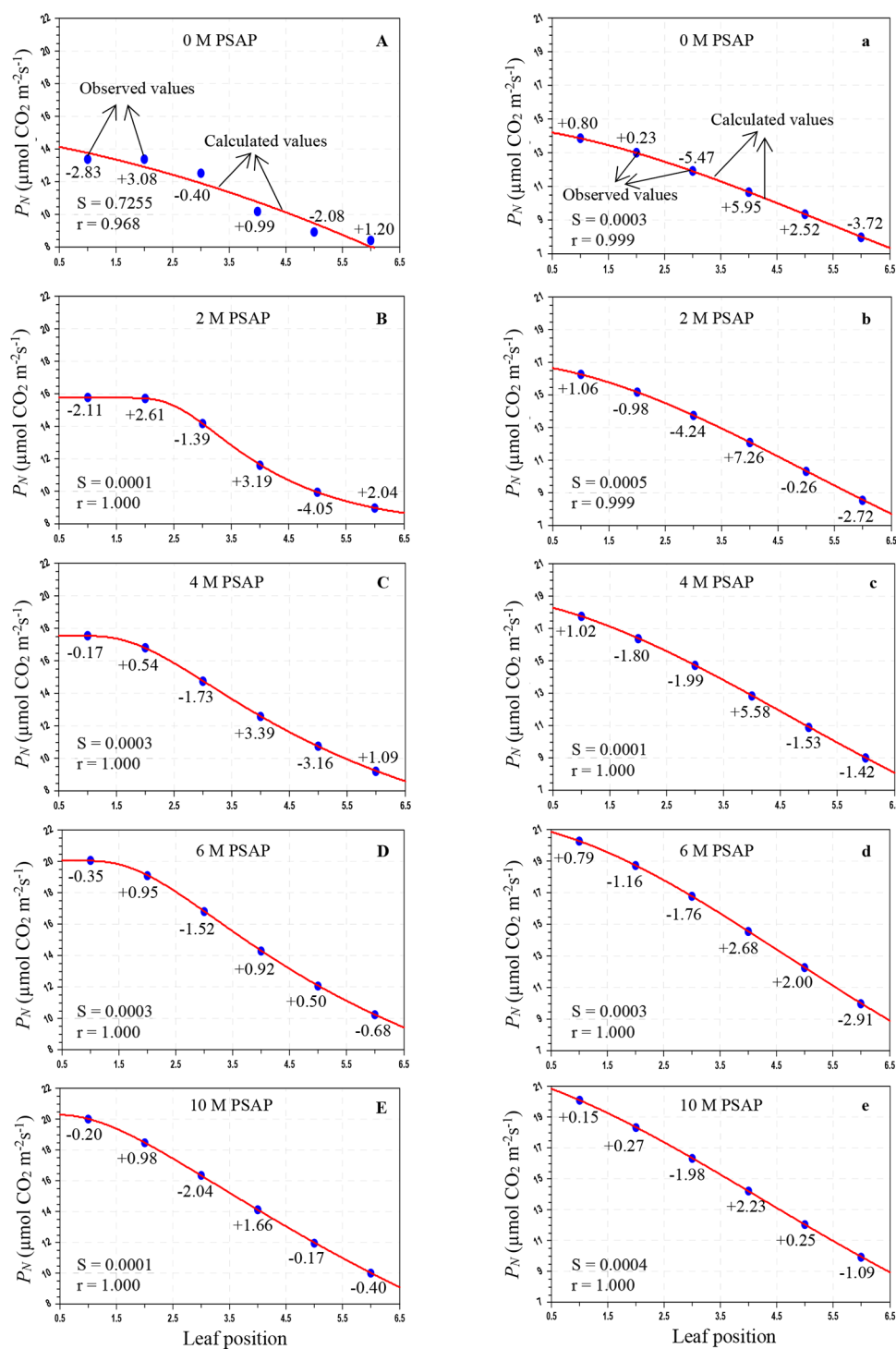
Figure 4. Variation of photosynthesis (P_N; μmol CO_2 m^{-2} s^{-1}) in sugarcane leaves after application of PSAP (0, 2, 4, 6, and 10 M) under limited water irrigation in the Skewed and Gaussian models. Data are represented as the arithmetic mean ($n = 3$). Blue ovals denote the observed values and red lines show the calculated values. Parenthesis values indicate percent deviation. (A−E) Skewed model, (a−e) Gaussian model, S = standard error, and r = correlation coefficient.

predicted g_s for the Skewed model ranges from 128.989 to 44.836 mmol H_2O m^{-2} s^{-1} and that for the Gaussian model ranges from 130.959 to 41.594 mmol H_2O m^{-2} s^{-1}; and the E for the Skewed model ranges from 1.452 to 0.824 mmol H_2O m^{-2} s^{-1} and that for the Gaussian model ranges from 1.456 to 0.817 mmol H_2O m^{-2} s^{-1}.

The average percent (%) deviation was maximum for the predicted values of the net photosynthetic rate, stomatal

conductance to water vapor, and transpiration rate by the Skewed and Gaussian models in the control and stressed plants with PSAP application (Tables 5 and 6). As may be seen from Table 5, for normal irrigation with PSAP application, the present deviations of the predicted P_N for the Skewed model range from +2.47 to −2.17% and those for the Gaussian model range from +4.09 to −3.22%, and the stomatal conductance and transpiration rate for the Skewed model range from +8.63 to
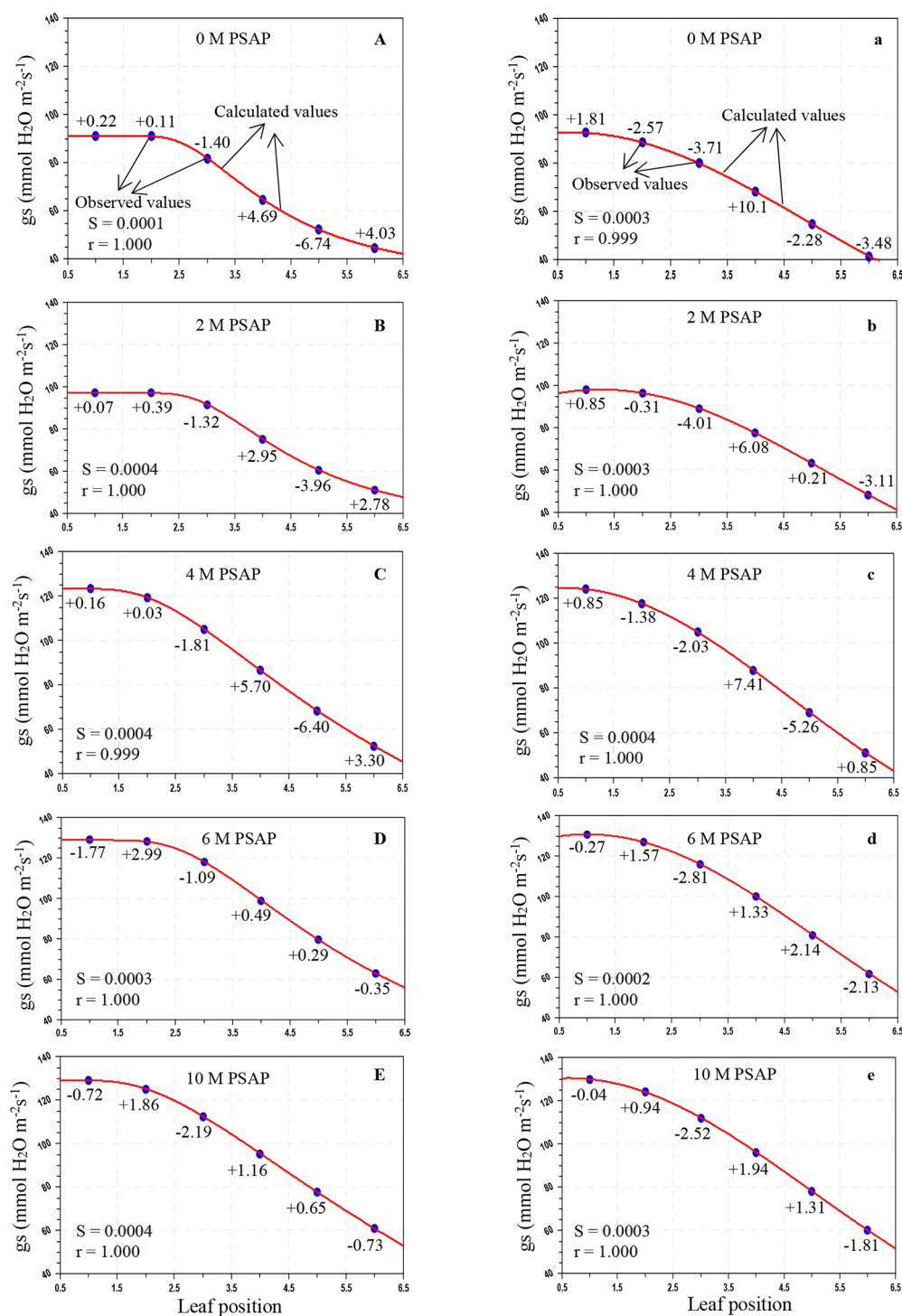
Figure 5. Variation of stomatal conductance to water vapor (gs; mmol H_2O m^{-2} s^{-1}) in sugarcane leaves after application of PSAP (0, 2, 4, 6, and 10 M) under limited water irrigation in the Skewed and Gaussian models. Data are represented as the arithmetic mean ($n = 3$). Blue ovals denote the observed values and red lines show the calculated values. Parenthesis values indicate percent deviation. (A–E) Skewed model, (a–e) Gaussian model, S = standard error, and r = correlation coefficient.

−6.77 and +11.62 to −7.19%, respectively, and those for the Gaussian model range from +7.99 to −7.04 and +11.01 to −7.40%, respectively. When PSAP was supplied as foliar application with limited water irrigation of sugarcane plants, the deviations of the predicted photosynthetic capacity were enhanced for both models. With the Skewed model, the % deviations of the ranges of the calculated P_N, gs, and E were +3.36 to −4.05, +5.70 to −6.74, and +7.50 to −3.52%,

respectively. Similarly, with the Gaussian model, the ranges of the percent deviations of the predicted values of P_N, gs, and E were +7.26 to −5.47, +10.18 to −5.26, and +3.91 to −4.61%, respectively.

Overall mean percent deviations of the Skewed and Gaussian models were 0.913, 2.978, and 2.968% and 1.539, 3.231, and 3.526%, respectively, for P_N, gs, and E of PSAP application under control conditions, and 1.546, 1.995, and 1.536% and 2.195,
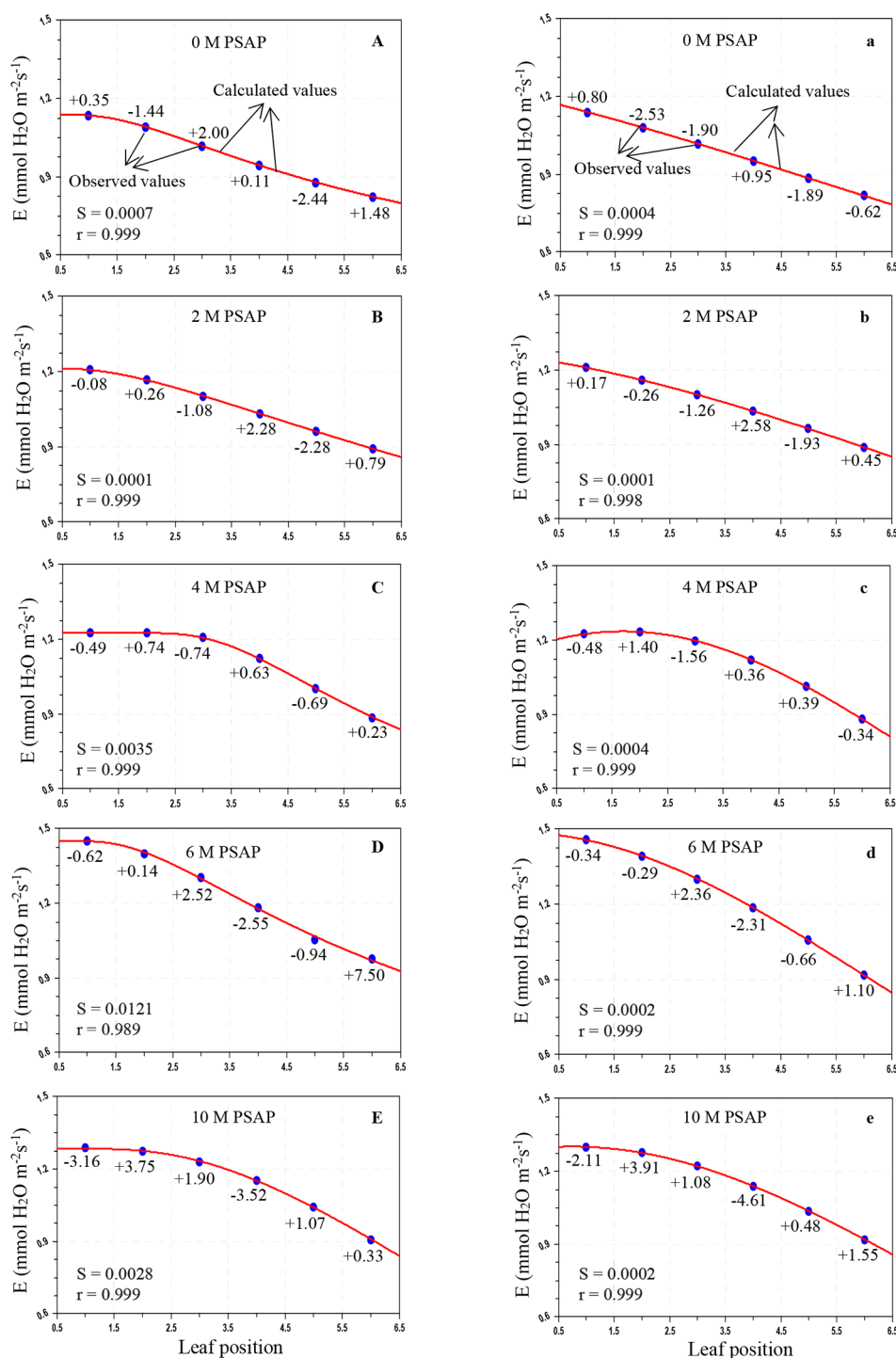
Figure 6. Variation of transpiration rate (E; mmol H_2O m^{-2} s^{-1}) in sugarcane leaves after application of PSAP (0, 2, 4, 6, and 10 M) under limited water irrigation in the Skewed and Gaussian models. Data are represented as the arithmetic mean ($n = 3$). Blue ovals denote the observed values and red lines show the calculated values. Parenthesis values indicate percent deviation. (A–E) Skewed model, (a–e) Gaussian model, S = standard error, and r = correlation coefficient.

2.506, and 1.356%, respectively, under limited water with PSAP. The Skewed model should be used for future studies for modeling the photosynthetic responses of sugarcane against leaf positions.

Under control conditions with foliar application of PSAP, the correlation coefficients (r) for P_N, gs, and E in the Skewed model were found to be 0.999–1.000, 0.998–0.0999, and 0.999–1.000, respectively and those in the Gaussian model were found

to be 0.999–1.000, 0.999–1.000, and 0.989–0.999, respectively. Under limited water irrigation with PSAP application, the r values for P_N, gs, and E were found to be 0.968–1.000, 0.999–1.000, and 0.989–0.999, respectively, in the Skewed model, and 0.999–1.000, 0.999–1.000, and 0.998–0.999, respectively, in the Gaussian model. The "r" values were higher in the Skewed model than in the Gaussian model for control and stressed plants with different levels of PSAP. The Skewed model is superior to

Table 5. The Percentage Deviations (±) of the Calculated Values of Photosynthetic Responses by the Skewed and Gaussian Models for Different Leaf Positions under Control Conditions (95−90% FC) with PSAP Application in Sugarcane Plants

	Skewed model						Gaussian model					
	PSAP (M)						PSAP (M)					
leaf position	0	2	4	6	10	average	0	2	4	6	10	average
P_N (μmol CO_2 m^{-2} s^{-1})												
1	−2.17	−0.63	−0.21	−1.71	−0.99	1.142	−2.08	−1.45	−0.29	−0.07	−0.07	0.792
2	+2.47	+0.09	+0.13	+1.95	+2.16	1.36	+4.09	+1.92	+0.46	+1.24	+1.11	1.764
3	+0.19	+0.85	+0.43	−0.50	−1.84	0.762	−0.33	+1.41	+0.30	−3.01	−2.47	1.504
4	−1.30	−0.15	−0.97	+0.78		0.8	−3.22	−1.90	−1.20	+1.76	+0.62	1.74
5	+1.34	−0.46	+0.85	−0.92	+1.71	1.056	+0.06	−2.82	+0.75	+1.56	+2.66	1.57
6	−0.58	+0.30	−0.31	+0.36	−1.04	0.518	+2.32	+3.47	−0.12	−1.55	−1.87	1.866
average	1.342	0.413	0.483	1.037	1.29	0.913	2.017	2.162	0.52	1.532	1.467	1.539
gs (mmol H_2O m^{-2} s^{-1})												
1	−0.92	−1.36	−1.06	−0.94	−0.24	0.904	−0.79	−3.33	−3.47	−1.97	−1.76	2.264
2	+1.77	+6.33	+3.99	+3.17	+0.43	3.318	+1.37	+7.99	+6.26	+4.17	+2.52	4.462
3	−0.08	−4.56	−0.41	−1.46	+1.86	1.674	−0.03	−2.33	+2.47	−0.02	+3.20	1.61
4	+1.76	−0.21	−3.15	−2.80	−2.30	2.044	+2.10	+1.17	−1.67	−2.02	−2.98	1.988
5	−6.77	−6.39	−6.07	−0.86	−2.87	4.592	−6.61	−7.02	−7.04	−1.41	−4.55	5.326
6	+2.78	+8.29	+8.63	+4.28	+3.59	5.514	+5.09	+4.58	+4.00	+1.00	+4.01	3.736
average	2.347	4.523	3.885	2.252	1.882	2.978	2.665	4.403	4.152	1.765	3.17	3.231
E (mmol H_2O m^{-2} s^{-1})												
1	+0.20	−0.97	−1.65	+0.07	−0.14	0.606	+1.62	−0.24	−1.56	+1.52	+0.28	1.044
2	−0.20	+0.80	+3.91	−0.36	+0.11	1.076	−2.74	−0.30	+4.05	+3.31	−0.80	2.24
3	−0.62	+2.05	−0.60	+1.39	+1.47	1.226	−1.75	+0.83	−0.55	+1.10	+1.61	1.168
4	+2.10	−6.07	−7.19	−3.48	−5.14	4.796	+5.59	−4.90	−7.40	−0.30	−4.30	4.498
5	−2.96	+9.17	+11.62	+4.61	+7.44	7.16	+0.08	+10.95	+11.01	+7.08	+7.85	7.394
6	+1.47	−3.89	−4.22	−2.06	−3.09	2.946	−3.24	−6.18	−3.72	−6.65	−4.28	4.814
average	1.258	3.825	4.865	1.995	2.898	2.968	2.503	3.9	4.715	3.327	3.187	3.526

Table 6. Percentage Deviations (±) of the Calculated Values of Photosynthetic Parameters by the Skewed and Gaussian Models for Different Leaf Positions during Limited Irrigation (45−40% FC) with PSAP Application in Sugarcane Plants

	Skewed model						Gaussian model					
	PSAP (M)						PSAP (M)					
leaf position	0	2	4	6	10	average	0	2	4	6	10	average
P_N (μmol CO_2 m^{-2} s^{-1})												
1	−2.83	−2.11	−0.17	−0.35	−0.20	1.132	+0.80	+1.06	+1.02	+0.79	+0.15	0.764
2	+3.08	+2.61	+0.54	+0.95	+0.98	1.632	+0.23	−0.98	−1.80	−1.16	+0.27	0.888
3	−0.40	−1.39	−1.73	−1.52	−2.04	1.416	−5.47	−4.24	−1.99	−1.76	−1.98	3.088
4	+0.99	+3.19	+3.36	+0.92	+1.66	2.024	+5.95	+7.26	+5.58	+2.68	+2.23	4.74
5	−2.08	−4.05	−3.16	+0.50	−0.17	1.992	+2.52	−0.29	−1.53	+2.00	+0.25	1.318
6	+1.20	+2.04	+1.09	−0.68	−0.40	1.082	−3.72	−2.72	−1.42	−2.91	−1.09	2.372
average	1.763	2.565	1.675	0.82	0.908	1.546	3.115	2.758	2.223	1.883	0.995	2.195
gs (mmol H_2O m^{-2} s^{-1})												
1	+0.22	+0.07	+0.16	−1.77	−0.72	0.588	+1.81	+0.85	+0.85	−0.27	−0.04	0.764
2	+0.11	+0.39	+0.03	+2.49	+1.86	0.976	−2.57	−0.31	−1.38	+1.57	+0.94	1.354
3	−1.40	−1.32	−1.81	−1.09	−2.19	1.562	−3.71	−4.01	−2.03	−2.81	−2.52	3.016
4	+4.69	+2.95	+5.70	+0.49	+1.16	2.998	+10.18	+6.08	+7.41	+1.33	+1.94	5.388
5	−6.74	−3.96	−6.40	+0.29	+0.65	3.608	−2.28	+0.21	−5.26	+2.14	+1.31	2.24
6	+4.03	+2.78	+3.30	−0.35	−0.73	2.238	−3.48	−3.11	+0.85	−2.13	−1.81	2.276
average	2.865	1.911	2.9	1.08	1.218	1.995	4.005	2.428	2.963	1.708	1.427	2.506
E (mmol H_2O m^{-2} s^{-1})												
1	+0.35	−0.08	−0.49	−0.62	−3.16	0.94	+0.80	+0.17	−0.48	−0.34	−2.11	0.78
2	−1.44	+0.26	+0.74	+0.14	+3.75	1.266	−2.53	−0.26	+1.40	−0.29	+3.91	1.678
3	+2.00	−1.08	−0.74	+2.52	+1.90	1.648	+1.90	−1.26	−1.56	+2.36	+1.08	1.632
4	+0.11	+2.28	+0.63	−2.55	−3.52	1.818	+0.95	+2.58	+0.36	−2.31	−4.61	2.162
5	−2.44	−2.24	−0.69	−0.94	+1.07	1.476	−1.89	−1.93	+0.39	−0.66	+0.48	1.07
6	+1.48	+0.79	+0.23	+7.50	+0.33	2.066	−0.62	+0.45	−0.34	+1.10	+1.55	0.812
average	1.303	1.122	0.587	2.378	2.288	1.536	1.448	1.108	0.755	1.177	2.29	1.356

the Gaussian model. The Skewed model predicted more closely, the values of the photosynthetic traits of control and limited irrigation with PSAP application and may hence be recommended for further application.

3. DISCUSSION

Insufficient water irrigation is well-known for its inhibitory effects. It reduces crop growth, development, and ultimately productivity.[42−44] Limited water irrigation decreases photosynthetic responses due to the reduction in leaf area expansion and linked damage to the photosynthetic apparatus.[45] Plants have developed numerous types of adaptive mechanisms to respond to stresses. In this experiment, the protective role of the PSAP fertilizer was assessed in sugarcane plants subjected to limited water irrigation. However, the application of PSAP as foliar spraying decreased the severity of limited irrigation-induced growth inhibition. It increased sugarcane tolerance to limited irrigation in terms of maintaining and/or improving the photosynthetic responses. During limited irrigation, stomatal closure is one of the initial plant responses to reduce the loss of water, accompanied by a remarkable reduction in stomatal conductance to water vapor and consequently, stomatal limitation of photosynthetic CO_2 assimilation rates.[18,43,46,47] The PSAP application also resulted in an enhanced rate of transpiration, possibly driven by the increased gs to improve a steady state of P_N subjected to limited irrigation (Figures 1−6).

Stomatal closure is considered a major factor in reducing the photosynthetic CO_2 assimilation rate subjected to limited irrigation.[18,43,48] Stomatal closure in response to limited soil moisture occurs because roots release higher abscisic acid (ABA) concentration to the xylem, and as a result, the enhanced pH of the xylem sap promotes ABA loading and subsequent uptake to the shoots.[49] The loss of gs limits leaf gas exchange activities and reduces C_i levels and photosynthetic rates due to downregulation of Rubisco activity.[50] The present findings are consistent with previous observations that have demonstrated increased photosynthetic responses in various plant varieties/cultivars treated with P application subjected to stress conditions.[33,41,51,52]

Plant leaves are the most important factors for the photosynthetic activities, and the area of leaves depends on light harvesting, which affects gas exchange activities and the accumulation of photosynthetic products.[12,18,53] The present study noted that on all limited irrigation levels, photosynthetic capacity with PSAP was higher than that without PSAP application (Figures 4−6). The photosynthetic CO_2 assimilation rate reflects leaf gas exchange characteristics of plants and is the important factor to achieve the maximum crop productivity.[6,12,54] Limited water irrigation levels could significantly downregulate sugarcane photosynthesis and productivity.[18,55]

Soil irrigation is a common technique for the application of essential nutrients to plants. However, plants can also absorb mineral nutrients when supplied as a foliar spray in the required dose.[27,56] The foliar application facilitates the continued absorption of mineral elements, and it can be performed throughout the growth period, particularly during the apex phase of nutrient requirement without the interaction with soil particles.[57] There are limited studies on the impact of foliar application of K to correct deficiency signs and upgrade plant performance and production.[58] The status of water in plant leaves depends on stomatal regulation and supply of water from the vasculature to internal plant organs.[27,59]

Modeling of photosynthetic responses of plants is essentially required for assessing overall growth and productivity of agricultural crops. Photosynthetic responses can be integrated in terms of productivity of the leaf area expansion, and temporal variations of photoassimilation are known in response to leaf positions. The Gaussian and Skewed models have been used for explaining variations of physiological responses against leaf positions. The best performing model was the Skewed model, which explained the variations of physiological responses against leaf positions of sugarcane under normal and limited water irrigation with PSAP application. The model may be quite useful for future studies in relating crop responses against any type of nutrient and water treatment.

In conclusion, overall, the present results revealed that the PSAP application might be an efficient technique for improving the tolerance of sugarcane plants subjected to limited water irrigation. It also upregulated the photosynthetic capacity by protecting the negative impacts of sugarcane plants during limited irrigation. Taken together, PSAP has a significant role in sugarcane cultivation under insufficient water availability for irrigation and its optimum dose will be supportive in mitigation of limited irrigation in a variety of crops for sugar and bioenergy sectors. This combination also greatly improved the photosynthetic activities and plant growth. However, to suggest an optimum dose of PSAP concentration, a large-scale demonstration under field conditions should be assessed in later studies.

4. EXPERIMENTAL SECTION

4.1. Plant Material, Experimental Site, and Design. The sugarcane (*Saccharum* spp. cv. GT 42) plants were provided by Sugarcane Research Institute, Guangxi Academy of Agricultural Sciences, Nanning, Guangxi, China (22°49′ N, 108°18′ E, 800−1731 masl), and the experiment was conducted in an open greenhouse during 2020 with three replications of each treatment as a completely randomized block design. The soil of the experiment was silty clay soil. One-bud cane sets were planted in the month of mid-March 2020, following the farmer's standard practices. Row-to-row spacing was maintained (about 75 cm). Recommended basal dose of fertilizers (N/P/K) was applied. Plants were raised with a standard dose of fertilizer for three months and then exposed to limited water irrigation (drought stress) by withholding irrigation, while control plants were watered regularly and manually. Uniform plants were selected and maintained for each treatment (control and limited irrigation), and the solution of PSAP (0, 2, 4, 6, and 10 M) was applied on the upper parts (canopies) of the plant manually using a sprayer. The spraying was done only with distilled water (without PSAP) over control and stressed plants. The water treatment included normal water irrigation (95−90% of field capacity) and limited water irrigation (45−40% of FC). Soil field capacity (moisture level, %) was measured using a soil moisture meter (0−10 cm soil depth) during experiment. The PSAP source was 85% salt of potassium and phosphorus and 15% other nutrients. The PSAP solution was prepared by dissolving the appropriate concentration of PSAP in distilled water. PSAP was applied once at one-month intervals up to three months during limited irrigation. PSAP is non-poisonous and environment friendly. This salt is manufactured by the Isha Agro-Sciences Private Limited, Pune, India.

4.2. Leaf Gas Exchange. Plant leaf gas exchange characteristics such as the net photosynthetic rate (P_N), stomatal conductance to water vapor (gs), and transpiration rate (E)

were observed on 90 days subjected to limited water irrigation with foliar application of PSAP in sugarcane plants using an Li-6800 portable photosynthesis system (Li-COR Biosciences, Lincoln, NE, US). For each treatment, leaf photosynthetic parameters were recorded between 09:30 and 11:00 h on both treated and non-treated plants (three replicates). In each treatment, position-wise leaves (+1 to +6 from the top to middle part of the leaf) were used for photosynthetic responses without changing the leaf angle. The photosynthetic photon flux density, air temperature, and CO_2 concentration were set at 1200 μmol m^{-2} s^{-1}, 25 °C, and 400 ppm, respectively, inside the leaf chamber. As photosynthetic response rates change linearly along the length of the leaf, observing at the middle of the leaf provides an estimate of the integrated whole photosynthetic rate.

4.3. Models. Verma et al.[60] developed the first model to describe physiological responses of plant leaves over a stem/twig, which followed the normal distribution pattern. Measured values of the CO_2 assimilation (P_N), stomatal conductance to water vapor (g_s), and transpiration rate (E) of sugarcane leaves with respect to their positions fitted best in the model. The Gaussian model given by Verma et al.[61] is written as below.

$$p_n = p_m e^{-1/2 \left(\frac{n-b}{c} \right)^2} \tag{1}$$

where b and c = constants, p_n = the physiological response against the leaf position, n, and p_m = the maximum physiological response.

Verma et al.[61] developed the second model by combining the following hypotheses: (a) the rate of change of physiological responses with respect to the leaf position (dp/dn) is directly proportional to the physiological response (p) and (b) the rate of change of physiological responses with respect to the leaf position is directly proportional to the physiological response and inversely proportional to the leaf position. The following governing equation was developed.

$$\frac{dp}{dn} = \lambda p + \mu \frac{p}{n} \tag{2}$$

where, p = physiological response, n = leaf position, and μ and λ are the model constants.

They solved the above equation and obtained the following solution.

$$p_n = e^C \cdot e^{\lambda n} \cdot e^{\mu \log_e n}$$
$$p_n = \gamma \cdot e^{n \log_e \omega} \cdot e^{\mu \log_e n} \tag{3}$$

where, $\lambda = \log_e \omega$ and $\gamma = e^C$. The derived model was called as the Skewed model.

Both the models were fitted in the present study for a comparative study to find the best one.

4.4. Model Validations and Comparison with the Existing Model. Measured values of CO_2 assimilation (P_N), stomatal conductance to water vapor (g_s), and transpiration rate (E) of sugarcane leaves with respect to their position were fitted in the derived "Skewed model" for validation. The same data were also fitted in the Gaussian model of Verma et al.[61] for comparison purposes.

4.5. Statistical Analyses. Statistical analyses were performed between or within limited water irrigations, depending on parameters using CurveExpert 1.4 software.

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Notes

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