[Now published in full after the initial publication as an Epub ahead of print on April 24, 2020, at www.fluorideresearch.online/epub/files/078.pdf]

THE EFFECT OF LEAF POSITION ON THE PHYSIOLOGICAL RESPONSES IN POPLAR LEAVES (CLONE S_7C_{15}) IRRIGATED WITH FLUORIDE-LADEN WATER

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ABSTRACT: In the present study, a Skewed model was developed and compared with the existing Gaussian model to describe the physiological parameters of poplar leaves (*Populus deltoides* L. clone S_7C_{15}) under irrigation with fresh water with no fluoride (control) and fluoride-laden (100–500 mg/L) water. The models fitted well with the experimental data and the calculated physiological responses were in close agreement with the observed values. The average root mean square deviations of the calculated photosynthetic CO_2 assimilation (P_N), the stomatal conductance (g_s), and a chlorophyll fluorescence variable per maximum yield (F_v/F_m), under fresh water irrigation, were found to be 1.92, 1.73, and 1.65%, respectively, with the Skewed model, and 4.23, 5.69 and 1.29%, respectively, with the Gaussian model. With fluoride-laden water irrigation, the corresponding values for the P_N, g_s, and F_v/F_m were 3.54, 4.09, and 1.83% with the Skewed model and 8.02, 8.46, and 2.87% with the Gaussian model. The use of the models was illustrated with a solved example by calculating the total CO_2 assimilation of a field plantation. The Skewed model was found to be superior to the Gaussian model in explaining the physiological responses of leaves positioned over a stem-branch with irrigation with both fresh and fluoride-laden water and is recommended for further application.

Key words: Chlorophyll fluorescence; Fluoride; F_v/F_m; Leaf position; Photosynthetic CO_2 assimilation; Poplar leaves; *Populus deltoides clone* S_7C_{15}; Stomatal conductance.

INTRODUCTION

Fluorine is the most reactive of the elements of the periodic table with no chemical substance being capable of freeing fluorine from any of its compounds. Fluorine is present in the form of fluorides in a number of minerals such as fluorspar, cryolite, and fluorapatite. Fluorine is the 13th most abundant element and distributed widely throughout the earth in soil, water, and food.[1] The fluoride ion (F) is present in humans and animals through the intake of air, water, and food. F may also come from pharmaceutical drugs (~20%) and through agrochemicals (~35%).[2-3] F is present in the soil and water within the range of 10–1000 and 0.5–2000 ppm, respectively.[4-6]

Fluoride toxicity, from high levels in soil and ground water, is a great concern.[7] An excessive intake of fluoride over a long period can cause serious health hazards such as dental and skeletal dysfunctions including crippling deformities. Dental fluorosis may occur when the F exposure occurs during tooth development, particularly up to the age of 6 to 8 years. In addition to dental and skeletal fluorosis, non-skeletal

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fluorosis may occur in humans with infertility, neurological and muscular dysfunction, and reduced mental ability in children.[6] Foodstuffs such as cereals, vegetables, fruit, milk, and meat may contain F if F-contaminated water was used in their production and processing. The inhalation of F-contaminated air can significantly contribute to the accumulation of F in the human body through food chains.[8-10] Agricultural production in F-contaminated soils can also significantly contribute to F-accumulation in plants and the human food chain.

The use of F-contaminated groundwater for irrigation is prevalent in endemic fluorosis areas. As well as fluorosis occuring in humans and animals, plants may be affected by F. F inhibits germination, causes ultra-structural malformations of the chloroplast and mitochondria, and impairs several metabolic pathways associated with photosynthesis, respiration, protein synthesis, carbohydrates, mineral metabolism, lipids, vitamins, and nucleotide synthesis thereby affecting plant growth-development, productivity/quality, and biomass.[1,11-14] The consumption of F -rich agricultural produce coupled with F-laden potable water may have a detrimental impact on humans.

Perennial fast growing plantations could accumulate a large quantity of F without its entering the human food chain and have a great reclamation effect on the soil and air. Plantation trees could lock up a huge amount of F without harming humans. Associated advantages would be enhanced carbon sequestration and an improvement in the quality of the environment. Popular is a fast growing plantation tree which could address the problem to a great extent. Poplar is a native of North America and was introduced to India only relatively recently during the 1950’s. It has become an important agro-forestry tree species in the Indo-Gangetic plains of North-West India[15] due to its good agronomic traits and economics in agro-forestry models.

In keeping with this view, poplar plants were subjected to irrigation with F-contaminated water to reveal the consequences of this on the physiological responses. Exposure to high doses of F may the affect the physiological responses of a poplar plantation with the effects on the leaves varying with leaf position. The productivity of a plantation is actually regulated by the accumulated physiological responses and hence by integrating the cumulative physiological responses, the response of popular plants to irrigation of F-laden water in relation to leaf position should be better understood. A mathematical modeling for relating the physiological response against leaf position over a stem or branch may be useful in integrating the physiological responses of each individual leaf of a stem-branch.[16] The present study was devoted to developing a mathematical model to describe the physiological responses of leaves located at different positions on the stem or branch under irrigation with fresh and F-laden water.

MATERIAL AND METHODS

Plant material and NaF treatment: Poplar (*Populus deltoides* L. clone S_7 C_{15}) seedlings were raised from stem cuttings by using uniform diameter and length (size 18–20 cm) brought from WIMCO Seedlings ITC, PSPD, Bagwala Kashipur Road, Rudrapur, Udham Singh Nagar, Uttarakhand, India. The cuttings were kept vertically in a bunch in a plastic tray filled with water (ca. 3 weeks) for rooting/sprouting under light exposure (200 μE, 12 hr) at room temperature with repeated changes of the tray water.[17] Afterwards, these seedlings (21 days old) were shifted to earthen pots (size 30 cm, filled with fertile soil, 8 kg pot^{-1}) for their establishment under field conditions for a period of 3 weeks (12 hr photoperiod), diurnal photon flux density of 500–1500 µE (30ºC/20ºC) and an average relative humidity ca. 65–70%. The soil texture was silty clay loam (pH 7.1), with levels of organic carbon, nitrogen, phosphorus, and potassium of 0.86%, 245 kg ha^{-1}, 35.5 kg ha^{-1}, and 172 kg ha^{-1}, respectively. The fully established poplar seedlings (6 weeks old) raised in the earthen pots were subjected to irrigation with F-contaminated or fresh (control) water. In both cases, the irrigation was to the level of field capacity.

The six-week-old poplar seedlings were subjected to 100–500 ppm F-contaminated irrigation water by applying F solutions weekly, to the level of field capacity (1 L), for a period of 6 weeks. The F-irrigation treatments were then terminated (82 days) and observations were made from the seedlings. The control seedlings were raised identically except for being irrigated with fresh (control) water with no F. For each treatment at least 7–10 independent replicates were taken.

Measurement of the physiological responses: An infrared gas analyzer (IRGA-6400, portable photosynthesis system, USA) was used for monitoring the photosynthetic CO_2 assimilation (P_N), stomatal conductance (g_s), and the chlorophyll fluorescence variable per maximum yield (F_v/F_m) in the F-irrigated poplar seedlings after the withdrawal of the treatment. These seedlings (82 days old) were used for obtaining all physiological responses. The physiologically mature leaves (6–8th) were selected and placed in the leaf chamber carefully for all the photosynthetic measurements under open environmental conditions under a saturating natural photosynthetic photon flux density (PPFD) without changing the leaf angle. The F_v/F_m was measured by using a Plant Efficiency Analyzer (PEA, Hansatech, UK) to assess the functionality of the phytosynthetic complex PS II to correlate with photosynthetic CO_2 assimilation.[18]

Hypothesis: As a stem of poplar grows, new leaves come out. The very first leaf has a low leaf area expansion and chlorophyll content so that consequently the physiological responses, such as the photosynthesis rate, transpiration, stomatal conductance, and other interrelated biochemical and enzymatic activities within the leaf, are also low. As the leaf grows, the leaf area expansion, chlorophyll content, and physiological responses also increase. A new leaf may then be added at the apex of the stem whose physiological responses will grow over time as occurred with the first leaf but still be lower in magnitude than those of the first leaf. With the passage of time, another leaf may get added to the stem whose physiological responses and manner of growth will be similar to that of the previous leaves, and so on. When a large number of leaves have emerged over the stem, the last leaf growing at the top of the stem (the apical one) and the first leaf positioned at the bottom of the stem, may both have a similar lower level of physiological responses due to the small size of the apical leaf and to the aging of the bottom leaf with the associated reduction in its chlorophyll activity, in spite of the bottom leaf having a higher leaf area expansion and chlorophyll content. The leaves which are well grown and positioned in the middle of the stem will be having their maximum physiological response rates.

The physiological responses in the stem increase from the bottom to the middle of the stem, and then decrease from the middle to top of the stem. Verma et al. [19]

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developed a model to describe the physiological response of *Jatropha* leaves over a stem/twig which followed the normal distribution pattern. The experimental data shows that unlike the physiological response rates of *Jatropha* leaves with respect to leaf position, the trend of the physiological responses in the case of poplar leaves over a well developed stem is skewed. The following hypothesis was developed:

The rate of change of the physiological response with respect to leaf position (dp/dn) is directly proportional to the physiological response (p). This means, if the physiological response rate of the leaf is high or potentially high, changes occur accordingly to Equation 1:

$$\frac{dp}{dn} \propto p \qquad \text{.....................Equation 1}$$

Where:

dp	=	Incremental physiological response
dn	=	Incremental leaf position
p	=	Physiological response

The rate of change of the physiological response with respect to leaf position is directly proportional to the physiological response and inversely proportional to the leaf position (Equation 2):

$$\frac{dp}{dn} \propto \frac{p}{n} \qquad \text{.....................Equation 2}$$

Where:

dp	=	Incremental physiological response
dn	=	Incremental leaf position
p	=	Physiological response
n	=	Leaf position

Equation (1) can be written in the following form by introducing a proportionality constant (λ) as Equation 3:

$$\frac{dp}{dn} = \lambda p \qquad \text{.....................Equation 3}$$

Where:

dp	=	Incremental physiological response
dn	=	Incremental leaf position
p	=	Physiological response
n	=	Leaf position
λ	=	Proportionality constant

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Similarly, Equation 2 may written after introducing a proportionality constant (μ) as Equation 4:

$$\frac{dp}{dn} = \mu \frac{p}{n} \qquad \text{.....................Equation 4}$$

Where:

dp	=	Incremental physiological response
dn	=	Incremental leaf position
p	=	Physiological response
n	=	Leaf position
μ	=	Proportionality constant

Equations 3 and 4 can be combined to develop a combined hypothesis as Equation 5:

$$\frac{dp}{dn} = \lambda p + \mu \frac{p}{n} \qquad \text{.....................Equation 5}$$

Where:

dp	=	Incremental physiological response
dn	=	Incremental leaf position
p	=	Physiological response
n	=	Leaf position
λ	=	Proportionality constant
μ	=	Proportionality constant

By separating the variables and integrating one will obtains Equations 6–10:

$$\frac{dp}{dn} = (\lambda + \frac{\mu}{n}) p \qquad \text{.....................Equation 6}$$

$$\frac{dp}{p} = (\lambda + \frac{\mu}{n}) dn \qquad \text{.....................Equation 7}$$

$$\frac{dp}{p} = \lambda dn + \mu \frac{dn}{n} \qquad \text{.....................Equation 8}$$

$$\log_e p = \lambda n + \mu \log_e n + C \qquad \text{.....................Equation 9}$$

$$p_n = e^{\lambda n + \mu \log_e n + C} \qquad \text{.....................Equation 10}$$

Where:

p_n	=	Physiological response of leaf located at position n
CX	=	Integration constant

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Equation 10 can be rewritten as Equations 11 and 12:

$$p_n = e^C . e^{\lambda n} . e^{\mu \log_e n} \quad \text{.....................Equation 11}$$

$$p_n = \gamma . e^{n \log_e \omega} . e^{\mu \log_e n} \quad \text{.....................Equation 12}$$

Where:

λ = $.\log_e \omega$
γ = e^c

The derived model will hereafter be called the Skewed model.

Model validations and comparison with the existing model: The measured values of CO_2 assimilation (P_N), stomatal conductance (g_s), and a chlorophyll fluorescence variable per maximum yield (Fv/Fm) of poplar leaves with respect to their position were fitted to the derived "Skewed model" for validation. The same data were also fitted in the Gaussian model of Verma et al.[19] for the purpose of comparison. The Gaussian model is written as Equation 13.

$$p_n = p_m e^{-\frac{1}{2}\left(\frac{n-b}{c}\right)^2} \quad \text{.....................Equation 13}$$

Where:

b = A constant
c = A constant
p_n = Physiological response with respect to the leaf position n
p_m = Maximal physiological response of the middle leaf

RESULTS

The measured position-wise leaf areas are given in Tables 1A and 1B.

Table 1A. Influence of fluoride-contaminated irrigation water on leaf area (cm^2) in poplar seedlings. Each data point represents an average of at least ten independent observations. SD is within 7 %.

Irrigation water	Leaf area (cm^2) for the leaves in different positions on the stem (Leaf 1 was at the tip and leaf 12 at the base of the stem)					
	Leaf position (n)					
	1	2	3	4	5	6
Fresh (control)	1.35	2.01	2.21	2.45	2.89	3.18
F-laden (100–500 mg/L)	0.71	1.19	1.42	2.45	3.81	4.41

Table 1B. Influence of fluoride-contaminated irrigation water on leaf area (cm^2) in poplar seedlings. Each data point represents an average of at least ten independent observations. SD is within 7 %.

Irrigation water	Leaf area (cm^2) for the leaves in different positions on the stem (Leaf 1 was at the tip and leaf 12 at the base of the stem)					
	Leaf position (n)					
	7	8	9	10	11	12
Fresh (control)	3.41	3.42	5.21	8.12	8.2	7.41
F-laden (100–500 mg/L)	4.92	6.13	6.53	8.13	8.4	8.61

The model parameters (regression coefficients) for both the Skewed model (namely γ, ω, and μ) and for the Gaussian model (a, b, and c) with irrigation with fresh (control) and F-laden (100–500 mg/L) irrigation water are presented in Table 2.

Table 2. Model parameters for the Skewed and Gaussian models with irrigation with fresh (control) and fluoride-laden water. (PP: physiological parameter, P_N: photosynthetic CO_2 assimilation (μmol m^{-2} s^{-1}), g_s: stomatal conductance (mmol m^{-2} s^{-1}), and Fv/Fm : chlorophyll fluorescence variable per maximum yield)

PP	Parameters for the Skewed and Gaussian models with irrigation with fresh (control) and fluoride-laden (100–500 mg/L) water					
	Fresh water (control) irrigation			Fluoride-laden water irrigation		
	Skewed model			Skewed model		
	γ	ω	μ	a	b	c
P_N	4.97867520	0.87019991	1.0945493	3.02205940	0.828467620	1.16605030
g_s	0.21952945	0.83223391	0.99741385	0.08094801	0.817706240	1.06781170
Fv/Fm	0.47343839	0.96501017	0.27236320	0.41487500	0.939255210	0.38029882
	Gaussian Model			Gaussian Model		
P_N	16.459319	8.5005702	5.8241861	7.85107490	7.2454762	5.6915785
g_s	0.43011674	6.4446864	5.8955872	0.16059299	6.2732904	5.8008732
Fv/Fm	0.63588642	8.2659864	10.798474	0.56487310	7.1831953	9.4766191

The calculated values of the physiological responses with the Skewed and Gaussian models with irrigation with fresh (control) normal water irrigation are presented in Table 3 and Figures 1A–1F, and those with irrigation with F-laden (100–500 mg/L) water in Table 4 and Figures 2A–2F.

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Table 3. Calculated values of the physiological parameters by the Skewed and Gaussian models for different leaf positions under the control conditions with fresh water irrigation. (LP=leaf position)

LP (n)	Physiological parameter					
	Skewed model			Gaussian model		
	P_N (µmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	*F*v/Fm	P_N (µmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	*F*v/*F*m
2	8.051	0.304	0.533	8.829	0.324	0.538
4	13.019	0.420	0.599	12.211	0.395	0.588
6	15.366	0.436	0.623	15.010	0.429	0.622
8	15.942	0.402	0.727	16.399	0.414	0.736
10	15.412	0.348	0.721	15.923	0.359	0.728
12	14.248	0.289	0.708	13.741	0.279	0.700

Table 4. Calculated values of the physiological parameters by the Skewed and Gaussian models for different leaf positions under irrigation with F-laden (100–500 mg/L) water irrigation. (LP=leaf position)

LP (n)	Physiological parameter					
	Skewed model			Gaussian model		
	P_N (µmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	*F*v/Fm	P_N (µmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	*F*v/*F*m
2	4.655	0.114	0.476	5.134	0.122	0.486
4	7.169	0.159	0.547	6.673	0.149	0.533
6	7.894	0.164	0.563	7.665	0.160	0.560
8	7.578	0.149	0.554	7.782	0.154	0.562
10	6.747	0.127	0.532	6.983	0.131	0.540
12	5.728	0.103	0.503	5.539	0.099	0.496

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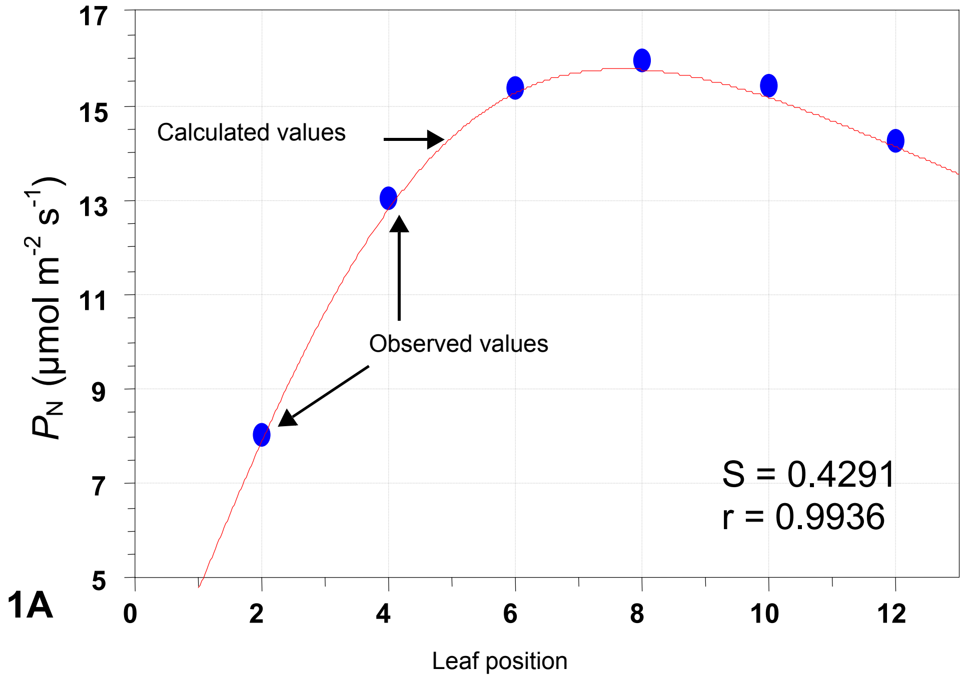
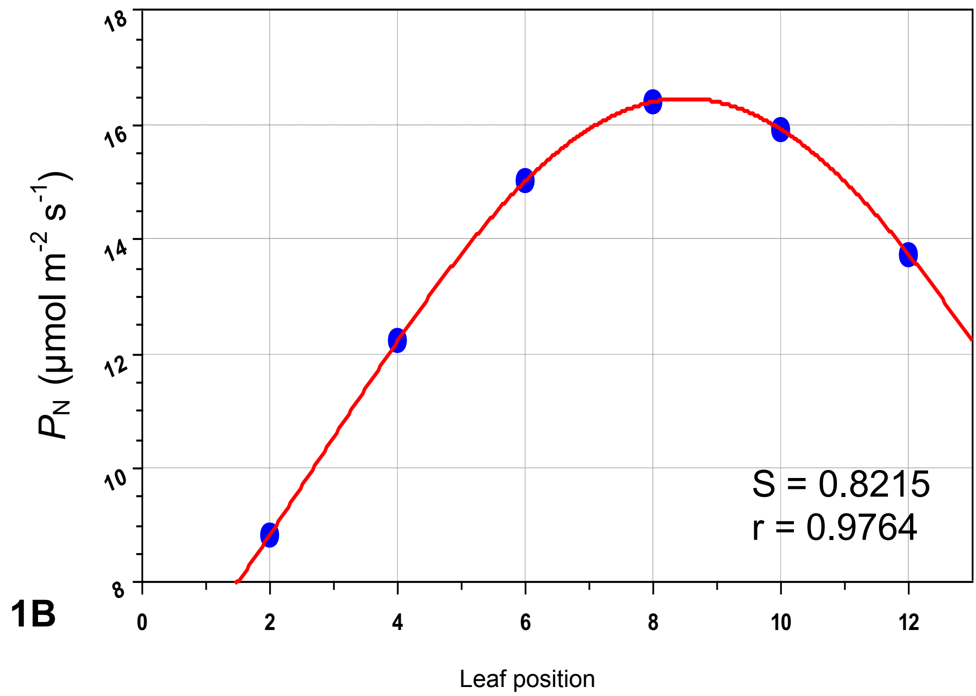
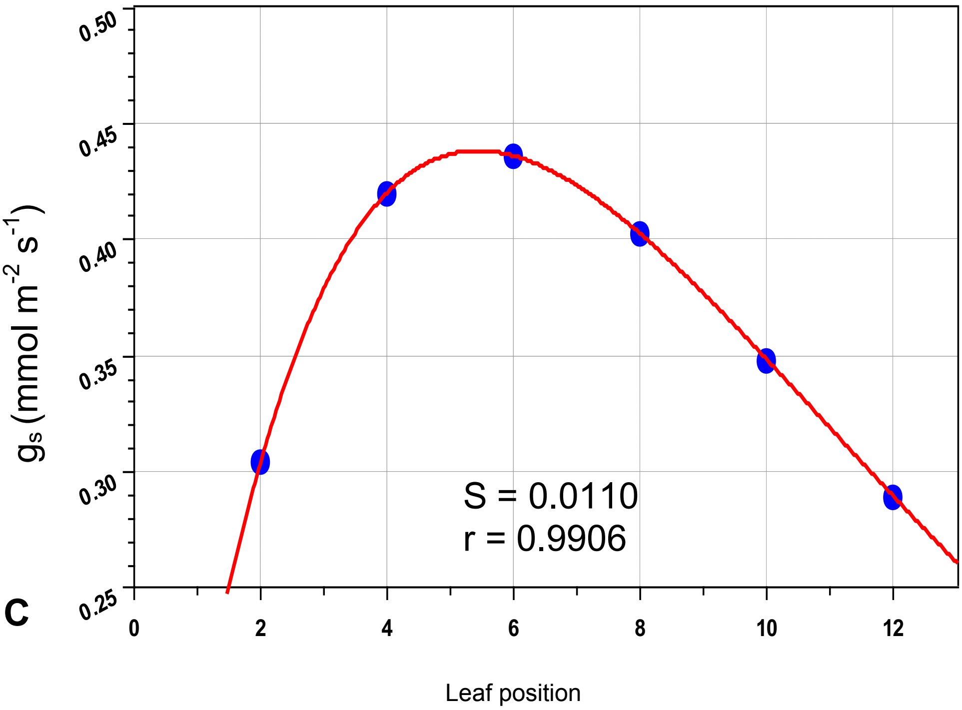
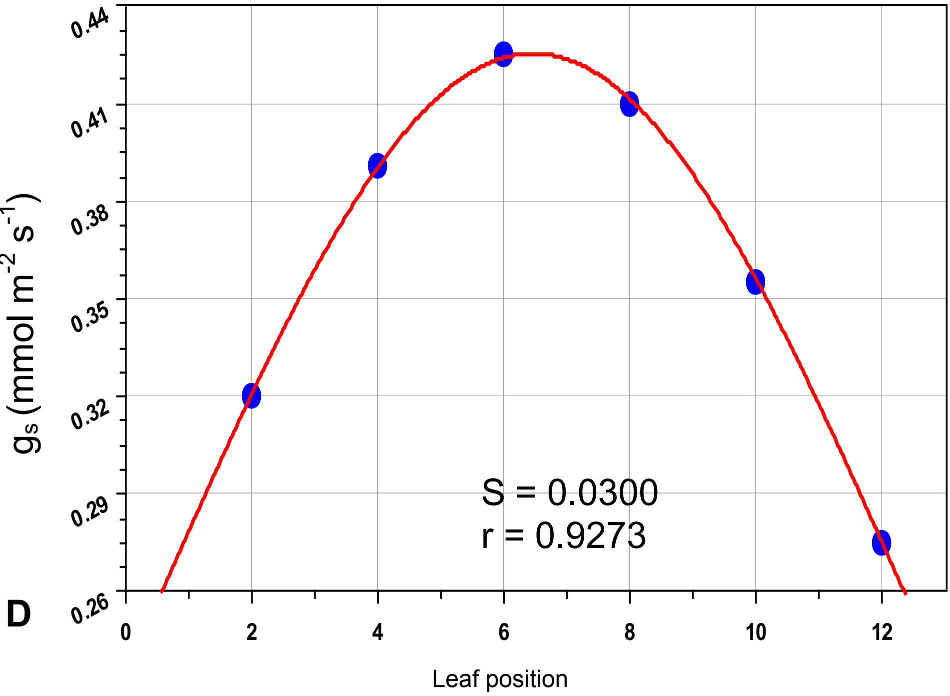




Figures 1A and 1B. Photosynthetic CO_2 assimilation (P_N) with irrigation with fresh (control, fluoride-free) water with the Skewed and Gaussian models. 1A: P_N with the Skewed model, 1B: P_N with the Gaussian model. Blue ovals: observed values, Red line: calculated values.

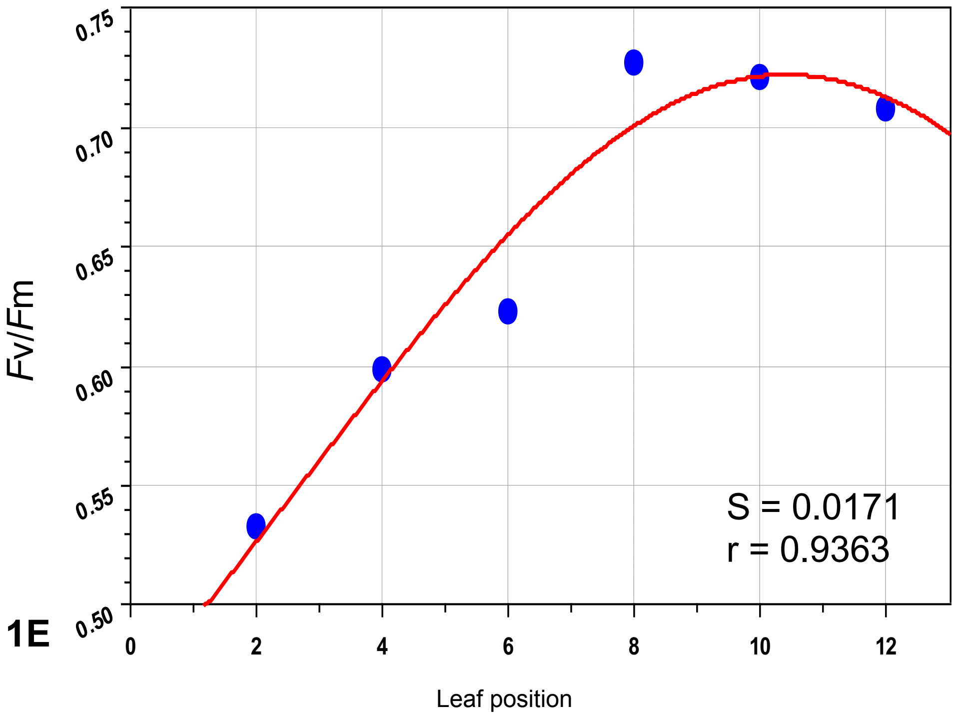


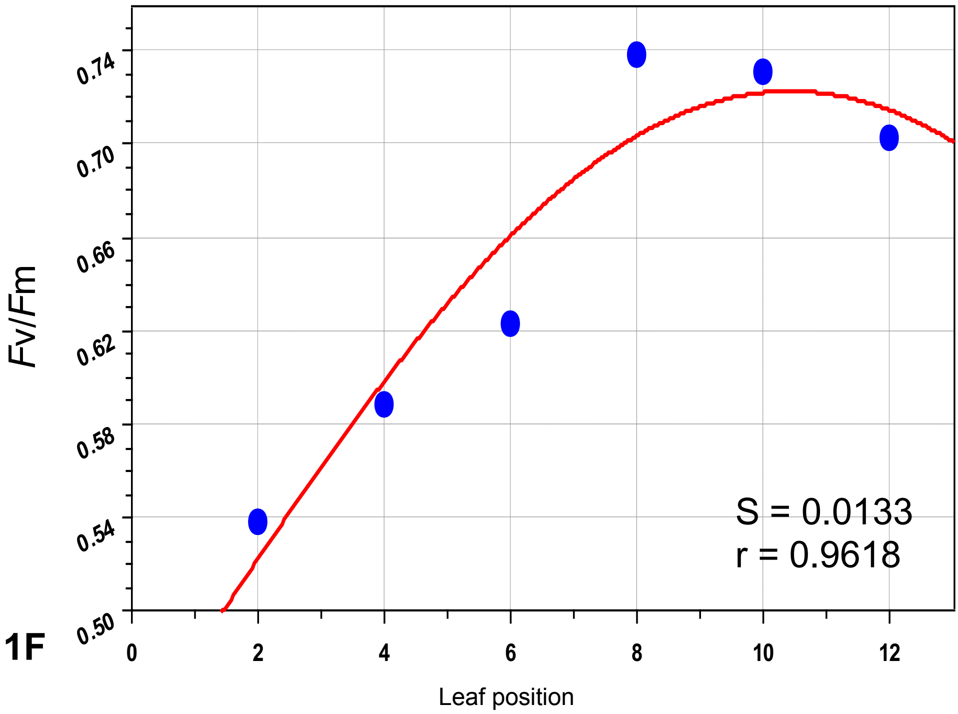
1C



1D

Figures 1C and 1D. Stomal conductance (g_s) with irrigation with fresh (control, fluoride-free) water with the Skewed and Gaussian models. 1C: g_s with the Skewed model, 1D: g_s with the Gaussian model. Blue ovals: observed values, Red line: calculated values.





Figures 1E and 1F. Chlorophyll fluorescence variable (F_v/F_m) with irrigation with fresh (control, fluoride-free) water with the Skewed and Gaussian models. 1E: F_v/F_m with the Skewed model, 1F: F_v/F_m with the Gaussian model. Blue ovals: observed values, Red line: calculated values.

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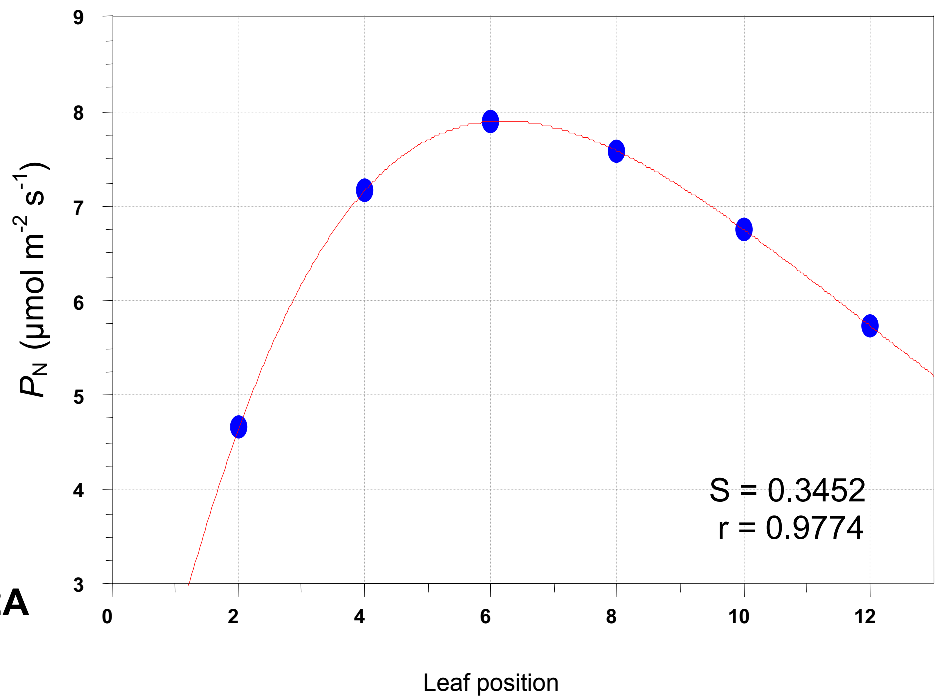
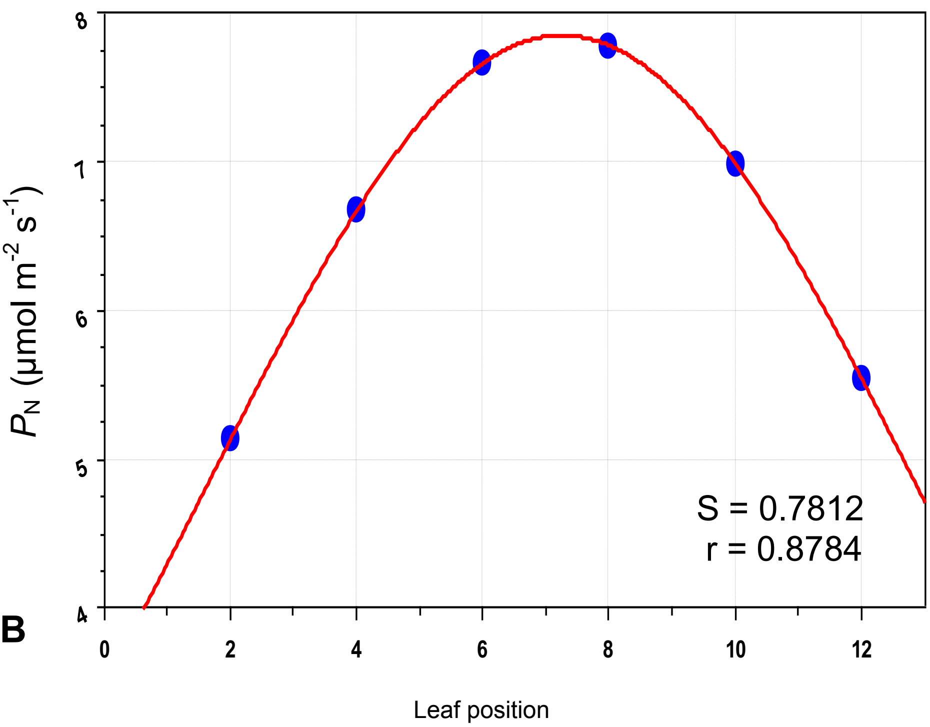


2A



2B

Figures 2A and 2B. Photosynthetic CO_2 assimilation P_N with irrigation with fluoride-laden water (100–500 mg/L) with the Skewed and Gaussian models. 2A: P_N with the Skewed model, 2B: P_N with the Gaussian model. Blue ovals: observed values, Red line: calculated values.

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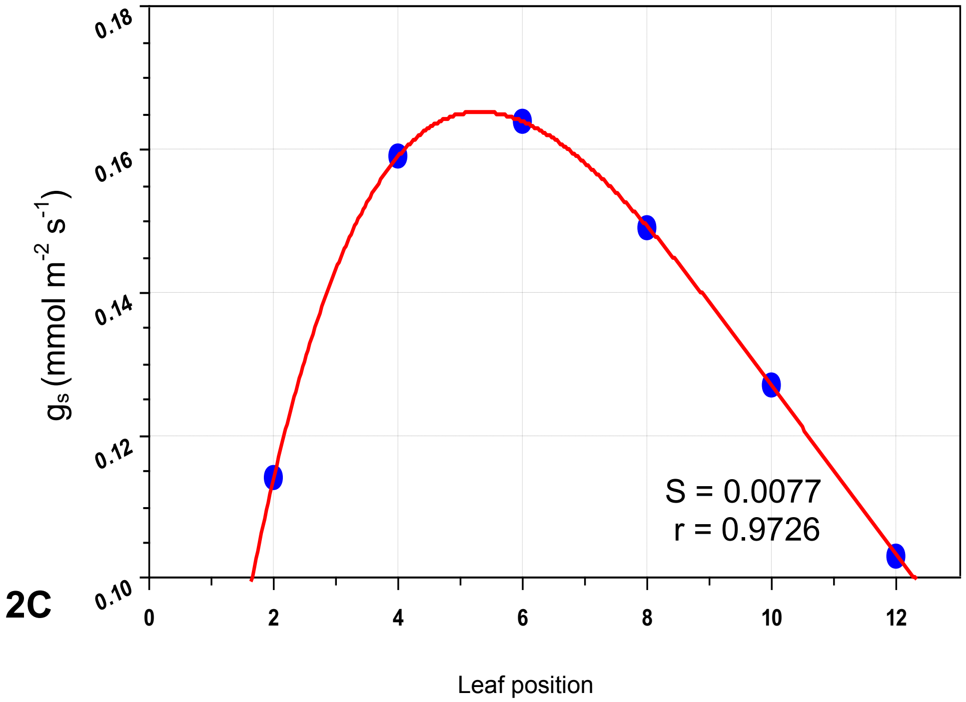
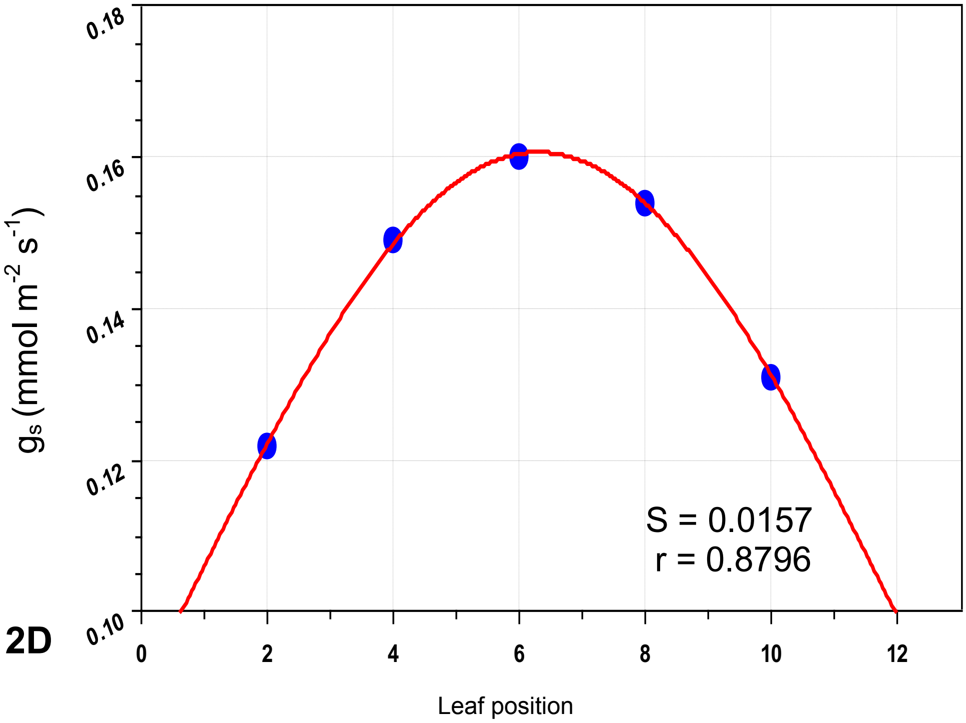
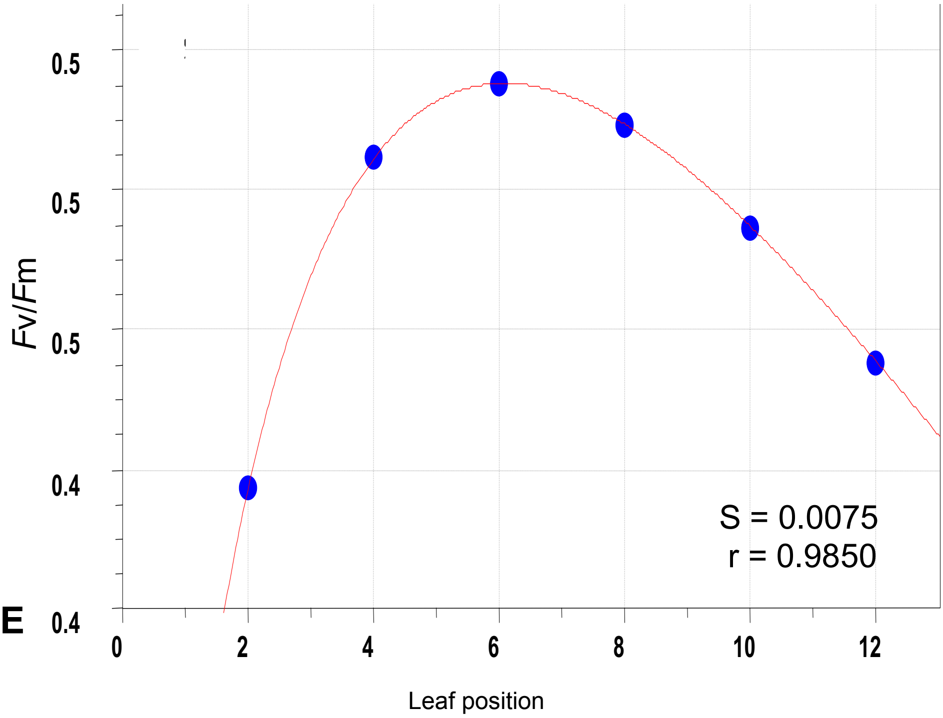


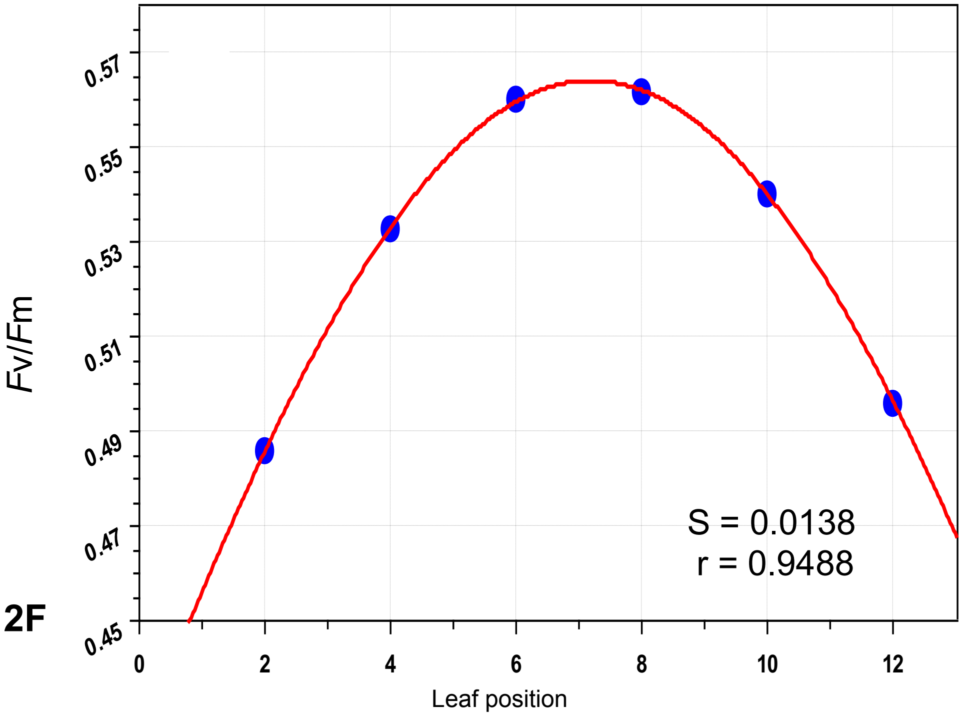


Figures 2C and 2D. Stomal conductance (g_s) with irrigation with fluoride-laden water (100–500 mg/L) with the Skewed and Gaussian models. 2C: g_s with the Skewed model, 2D: g_s with the Gaussian model. Blue ovals: observed values, Red line: calculated values.

2E



2F



Figures 2E and 2F. Chlorophyll fluorescence variable (F_v/F_m) with irrigation with fluoride-laden water (100–500 mg/L) with the Skewed and Gaussian models. 2E: F_v/F_m with the Skewed model, 2F: F_v/F_m with the Gaussian model. Blue ovals: observed values, Red line: calculated values.

Table 3 shows that for irrigation with fresh water, the calculated values of P_N for the Skewed model ranged from 8.051 to 15.942 µmol m^{-2}s^{-1} and for the Gaussian model the range was 8.829 to 16.399 µmol m^{-2}s^{-1}; the predicted g_s for the Skewed model ranged from 0.304 to 0.436 and for the Gaussian model the range was 0.324 to 0.429; and the *F*v/*F*m for the Skewed model ranged from 0.533 to 0.627 and for the Gaussian model the range was 0.538 to 0.636. For irrigation with F-laden (100–500 mg/L) water, the calculated values of P_N for the Skewed model ranged from 4.655 to 7.894 µmol m^{-2}s^{-1} and for the Gaussian model the range was 5.134 to 7.782 µmol m^{-2}s^{-1}; the predicted g_s for the Skewed model ranged from 0.114 to 0.164 and for the Gaussian model the range was 0.122 to 0.160; and the *F*v/*F*m for the Skewed model ranged from 0.476 to 0.563 and for the Gaussian model the range was 0.486 to 0.562. The average percent deviation or root mean square deviations (RMSD) were higher for the calculated values of photosynthesis, stomatal conductance, and *F*v/*F*m by the Gaussian model with irrigation with both fresh water and F-laden water.

The percent deviations of the calculated values of the physiological responses with the Skewed and Gaussian models are presented in Table 5 with the fresh water irrigation, and in Table 6 with the F-laden water irrigation.

Table 5. The percent deviations (±) of the calculated values of the physiological parameters by the Skewed and Gaussian models for different leaf positions under the control conditions with fresh water irrigation. (LP=leaf position)

LP (n)	Physiological parameter					
	Skewed model			Gaussian model		
	P_N (µmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	*F*v/*F*m	P_N (µmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	*F*v/*F*m
2	+2.53	–0.66	+1.30	–6.89	–7.28	+0.37
4	–4.15	0.00	–3.99	+2.31	+5.95	–2.08
6	+2.75	+1.36	+2.35	+5.00	+2.94	+2.51
8	+0.36	–0.50	+1.10	–2.49	–3.50	–0.32
10	–1.395	–4.19	–0.49	–4.76	–7.49	–1.62
12	+0.36	+3.67	–0.66	+3.91	+7.00	+0.83
Mean	1.92	1.73	1.65	4.23	5.69	1.29

As may be seen from Table 5, for irrigation with fresh water, the percent deviations of the calculated photosynthesis (P_N) for the Skewed model ranged from +0.36 to –4.15%, with an average deviation of 1.92 and for the Gaussian model the range was +2.31 to –6.89% with an average deviation of 4.23%; the percent deviations of the calculated stomatal conductance (g_s) for the Skewed model ranged from –0.00 to –4.19%, with an average deviation of 1.73% and for the Gaussian model the range was +2.94 to –7.49% with an average deviation of 5.69%; and the percent deviations of the calculated chlorophyll fluorescence variable per maximum yield (*F*v/*F*m) for the Skewed model ranged from –0.49 to –3.99%, with an average deviation of 1.65% and for the Gaussian model the range was +0.37 to +2.51% with an average deviation of 1.29%.

Table 6. The percent deviations (±) of the calculated values of the physiological parameters by the Skewed and Gaussian models for different leaf positions with irrigation with fluoride-laden (100–500 mg/L) water. (LP=leaf position)

LP (n)	Physiological parameter					
	Skewed model			Gaussian model		
	P_N (µmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	*F*v/*F*m	P_N (µmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	*F*v/*F*m
2	–4.84	–2.70	+0.42	–15.63	–9.91	–1.67
4	+5.30	+1.85	–1.30	+11.85	+8.02	+1.30
6	–1.47	+2.96	+1.75	+1.48	+5.33	+2.27
8	–2.27	–5.67	–7.16	–5.02	–9.22	–8.70
10	–2.85	–4.96	–0.19	–6.45	–8.26	–1.69
12	+4.53	+6.36	+0.20	+7.68	+10.00	+1.59
Mean	3.54	4.09	1.83	8.02	8.46	2.87

When F-laden water was applied, the deviations of the calculated physiological responses increased for both the models. With the Skewed model, the percent deviations of the ranges of the calculated P_N, g_S, and *F*v/*F*m were –1.47 to +5.30%, +1.85 to +6.36%, and –0.19 to –7.16%, respectively, with corresponding average deviations of 3.54, 4.09, and 1.83%, respectively. Similarly, with the Gaussian model, ranges of the percent deviations of the calculated P_N, g_S, and *F*v/*F*m were +1.48 to –15.63%, +5.33 to +10.00%, and +1.30 to –8.70%, respectively, with corresponding average deviations of 8.02, 8.46, and 2.87%, respectively.

With fresh water irrigation, the correlation coefficient (r) for P_N, g_S, and *F*v/*F*m, were found with the Skewed model to be 0.994, 0.991, and 0.936, respectively, and with the Gaussian model to be 0.976, 0.927, and 0.962, respectively. With F-laden water irrigation, the correlation coefficient (r) for P_N, g_S, and *F*v/*F*m, were found with the Skewed model to be 0.977, 0.973, and 0.985, respectively, and with the Gaussian model to be 0.876, 0.880, and 0.949, respectively. The values of ‘r’ were higher for the Skewed model than for the Gaussian model for both types of irrigation, further indicating the superiority of the Skewed model over the Gaussian model. The Skewed model predicted more closely the values of the physiological responses with irrigation with both fresh water and F-laden irrigation water, and may hence be recommended for further application.

Example: Poplar was planted over an area of one hectare at a spacing of 2 m × 2 m. Nearly 40% of the area was irrigated with pumped ground water with a F concentration of 100–500 ppm while 60% of the area was irrigated with pumped fresh water with no F from a pond. The average plant height of those irrigated with F-laden water was 1.00 m whereas the plants irrigated with pond water had an average height of 1.25 m. The average number of leaves on the plants were found to be 12. For the plants irrigated with fresh water, the values obtained were C=1.593, ω=0.870, and μ=1.095 while for the plants irrigated with F-laden ground water from the Indo-Gangetic plain the values were C= 1.106, ω=0.829, and μ=1.166. The measured position-wise leaf areas are given in Table 1. The total photosynthesis from the whole field for a period of one week was calculated considering 12 hr as the effective daily sunshine period.

Solution:

$$\text{Area under fresh water irrigation (ha)} = \frac{100 - 40}{100} \times 1.0$$

$$= 0.60 \text{ ha}$$

$$\text{Area under F-laden water irrigation (ha)} = \frac{40}{100} \times 1.0$$

$$= 0.40 \text{ ha}$$

$$\text{Number of popular plants under fresh water irrigation} = \frac{0.60 \times 10{,}000 \text{ m}^2}{2\text{m} \times 2\text{m}}$$

$$= 1{,}500$$

$$\text{Number of popular plants under F-laden water irrigation} = \frac{0.40 \times 10{,}000 \text{ m}^2}{2\text{m} \times 2\text{m}}$$

$$= 1{,}000$$

The calculation of the photosynthetic rates are presented in Tables 7A and 7B.

[Now published in full after the initial publication as an Epub ahead of print on April 24, 2020, at www.fluorideresearch.online/epub/files/078.pdf]

Table 7A. Calculation of photosynthesis with irrigation with fresh water

Leaf position (n)	Fresh water irrigation				
	Physiological response of leaf located at position n (p_n) Equation 12 for the Skewed model $p_n = \gamma \cdot e^{n \log_e \omega} \cdot e^{\mu \log_e n}$ (μmol m^{-2} s^{-1})	Leaf area (cm^2)	Total leaf area, (cm^2)	Daily photosynthesis (mol day^{-1})	Weekly photosynthesis (mol $week^{-1}$)
Value 1	Value 2	Value 3	Value 4 = Value 3 ×1500	Value 5 = 12 × 60 × 60 s × Value 2 × Value 4 × 10^{-6}	Value 6 = Value 5 × 7
1	4.279530	1.35	2025	374.37	2620.59
2	7.953223	2.01	3015	1035.89	7251.23
3	10.78654	2.21	3315	1544.72	10813.04
4	12.85907	2.45	3675	2041.51	14290.57
5	14.28385	2.89	4335	2674.97	18724.79
6	15.17288	3.18	4770	3126.58	21886.06
7	15.62766	3.41	5115	3453.21	24172.47
8	15.73673	3.42	5130	3487.51	24412.57
9	15.57563	5.21	7815	5258.46	36809.22
10	15.20790	8.12	12180	8002.03	56014.21
11	14.68634	8.2	12300	7803.73	54626.11
12	14.05437	7.41	11115	6748.46	47239.22
Total for all leaf positions (1–12)				45551.44	318860.08 = 3.1886 ×10^5

[Now published in full after the initial publication as an Epub ahead of print on April 24, 2020, at www.fluorideresearch.online/epub/files/078.pdf]

Table 7B. Calculation of photosynthesis with irrigation with fluoride-laden water

Leaf position (n)	Fluoride-laden water irrigation				
	Physiological response of leaf located at position n (p_n) Equation 12 for the Skewed model $p_n = \gamma \cdot e^{n \log_e \omega} \cdot e^{\mu \log_e n}$ (μmol m-2 s-1)	Leaf area (cm^2)	Total leaf area, (cm^2)	Daily photosynthesis (mol day^{-1})	Weekly photosynthesis (mol $week^{-1}$)
Value 1	Value 7	Value 8	Value 9 = Value 8 ×1500	Value 10 = 12 × 60 × 60 s × Value 7 × Value 9 × 10^{-6}	Value 11 = Value 10 × 7
1	4.077851	0.71	710	125.08	875.56
2	7.221272	1.19	1190	371.23	2598.61
3	9.332289	1.42	1420	572.48	4007.36
4	10.60109	2.45	2450	1122.02	7854.14
5	11.22074	3.81	3810	1846.85	12927.95
6	11.35742	4.41	4410	2163.72	15146.04
7	11.14656	4.92	4920	2369.14	16583.98
8	10.69539	6.13	6130	2832.31	19826.17
9	10.08703	6.53	6530	2845.51	19918.57
10	9.384737	8.13	8130	3296.07	23072.49
11	8.635782	8.4	8400	3133.75	21936.25
12	7.874712	8.61	8610	2929.02	20503.14
Total for all leaf positions (1–12)				23607.18	165250.26 = 1.6525×10^5

[Now published in full after the initial publication as an Epub ahead of print on April 24, 2020, at www.fluorideresearch.online/epub/files/078.pdf]

DISCUSSION

The high concentration of F in the irrigation water, 100–500 mg/L, caused chlorosis and necrosis of the leaves, a reduction in the growth of roots and shoots, and ultimately a reduced biomass yield of *Populus deltoides* L. clone-S_7C_{15}. The reduction in the growth of roots and shoots with the F-laden irrigation water ultimately resulted in an impaired harvest index (HI) in poplar.[1,12] The reduction in the root growth rates with the high F concentration could be the result of a direct injury to the plasma membrane of the root system.[20-21] A loss in germination, and root and shoot growth have also been observed in other plants.[4,7,22-25] The higher values of the F found in the irrigation water affected the plant performance, productivity, and biomass by impairing the physiological responses, i.e., P_N, g_s, and Fv/Fm (Figure 1).[26-29] Fluoride affects photosynthesis by influencing the membrane permeability and integrity and the associated enzymes of the Calvin cycle essential for the carboxylation of atmospheric CO_2.[23,29]

The accumulation of F in mesophyll cells reduces mineral metabolism and chlorophyll pigments along with morphological and physiological characteristics such as plant height, the number of leaves, and the biomass yield.[29-30] A higher level of F has acute and chronic toxic effects, i.e., growth reduction and even death, on organisms such as algae, plants, fish, and marine crustaceans.[31] Hence, an acute level of F application may severely reduce g_s by limiting CO_2 diffusion from the atmosphere into the cellular system which may result in a loss in P_N due to impaired stomatal conductance, and may also down regulate the fluorescence efficiency of PS II as diagnosed through the Fv/Fm. Long-term (more than 100 days) exposure to F, by applying a high dose of the F (100–500 ppm) in irrigation water induced chlorosis, necrosis, and leaf deformations in poplar, particularly in the younger leaves,[12] similar to the findings of Elloumi et al.[25] However, the mechanism of action of F is yet to be elucidated.[32]

Fluoride-induced toxicity may be due to the break down of chlorophyll during stress or due to an inhibition of chlorophyll biosynthesis, a primary symptom of F-induced chlorosis.[33-34] The reduction in chlorophyll as leaf necrosis increases may also reflect the permanent breakdown of the membrane structure within the chloroplasts or the direct effect of F on chlorophyll biosynthesis.[35-36] The exposure the plants to high levels of F leads to F accumulation which apparently has a significant effect on the integrity of the membranes associated with an increase in the electrolyte leakage.[12] Hence, F modifies the membrane lipid-protein interactions and impairs cellular metabolic functions,[37] including the activity of enzymes, such as the H^+-ATPase,[38] leading to an increase in membrane permeability.[39]

Modeling of the physiological responses in relation to leaf position under irrigation with fresh and F-laden irrigation water can avoid a large number of time consuming and expensive experiments and provide an understanding of the various physiological responses. Therefore, a hypothesis was formulated from a basic understanding of the various physiological responses and translated to a governing equation (a first order differential equation) and then solved for deriving a model to predict the variation of the physiological responses in response to leaf position. The Skewed model we derived was compared with the Gaussian model of Verma et al.[19] When fresh water was used for the plant irrigation, a comparison of the observed and calculated physiological responses showed that average percent deviations or root mean square deviation (RMSD) of the predicted responses for CO_2 assimilation, stomatal conductance, and *F*v/*F*m with the Skewed model were 1.92, 1.73 and 1.65%, respectively, and the corresponding values when predicted by the Gaussian model were 4.23, 5.69, and 1.29%, respectively. When F-laden water was used for the plant irrigation, a comparison of the observed and calculated physiological responses showed that average percent deviations or root mean square deviation (RMSD) of the predicted responses for CO_2 assimilation, stomatal conductance, and *F*v/*F*m with the Skewed model were 3.54, 4.09, and 1.83%, respectively, and the corresponding values when predicted by the Gaussian model were 8.02, 8.46, and 2.87%, respectively. Hence, the Skewed model explains the variations in the physiological responses with respect to leaf positions quite well under both the irrigations. This illustrative example shows how the model may be used for estimating the total physiological responses and this information could be correlated with plant productivity/biomass yield under conditions of climate change.

ACKNOWLEDGEMENTS

This research work was made possible by the support of the University Grants Commission (UGC), New Delhi, by their awarding a major research project grant (F.No. 37-438/2009(SR). We extend our thanks to Professor P.K.Tandon, UGC-BSR Fellow for his kind help.

AUTHOR DISCLOSURE STATEMENT

No competing financial interests exist.

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