Photosynthesis response in elicited tomato (*Solanum lycopersicum*) plants to identify eustress or distress: first approach

Respuesta en la fotosíntesis de jitomate (*Solanum lycopersicum*) elicitado para distinguir eustrés-distrés: primer acercamiento

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Resumen
La elicitación en plantas induce producción de metabolitos secundarios. Dependiendo de la dosis, las plantas manifiestan eustrés o distrés. Al respecto, se presenta una primera aproximación para estudiar el efecto de la elicitación sobre la fotosíntesis en plantas de jitomate y usarla como indicador de estrés. Ácido salicílico y peróxido de hidrógeno se aplicaron en tres dosis, vías foliar y radicular. La fotosíntesis se midió mediante una cámara hermética colocando una planta de jitomate a la vez y midiendo el consumo de CO_2 en el tiempo. El consumo de CO_2 presentó una tendencia lineal y los cambios de pendiente indicaron baja o alta actividad fotosintética. La fotosíntesis podría usarse como indicador del estrés en plantas en la agricultura de precisión.

Palabras clave: hormesis, consumo-de-CO_2, clima, dosis-elicitor, tendencia-lineal-fotosíntesis.

Abstract
Elicitor application to plants has been used to induce them to produce secondary metabolites. Depending on elicitor dosing plants may present eustress or distress. In this study we presented a first approach to study the effect of elicitors on photosynthesis of tomato plants and used it as an indicator of stress. Salicylic acid and hydrogen peroxide were used in three doses via foliar and radicular

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pathways. Photosynthesis was evaluated using a chamber where a whole plant was enclosed, and CO_2 consumption was measured over time. CO_2 consumption curves showed a linear behavior, changes in the slope indicated low or high photosynthetic plant activity. Photosynthesis may be used as a plant stress indicator in precision agriculture.

Keywords: hormesis, CO_2-consumption-curves, climatic-conditions, elicitor-dose, photosynthesis -linear-behavior.

Introduction

Photosynthesis (PS) literally means synthesis using light. Photosynthetic organisms use solar energy to synthesize complex carbon compounds. Light energy drives the synthesis of carbohydrates and generation of oxygen from carbon dioxide and water (Taiz & Zeiger, 2010). PS estimation could be achieved by invasive methods, interfere with the natural processes of the plant; or non-invasive methods, which do not interfere with the plant processes (García-Rodríguez *et al*., 2022). PS indicates how well plants are growing (García-Rodríguez *et al*., 2022) and has been evaluated as a plant response to stress caused by drought (Roig-Oliver *et al*., 2021; Zeroual *et al*., 2023) and heat (Ru *et al*., 2022; Zahra *et al*., 2023), which are considered to be the major abiotic stresses in the current climate change scenario. However, sources can vary and include: chemical, mechanical, drought, light, climatic conditions, among others. Elicitors in plants are used to intentionally induce stress. Today, the application of elicitors to plants is more relevant than ever for humans (Hassini *et al*., 2019). However, their effects on plants are not well understood (Zheng *et al*., 2020) and often cannot be seen immediately. The application of elicitors has the potential to induce plants to produce secondary metabolites of interest, so overproduction through natural synthesis of secondary metabolites in plants cannot be neglected, as this may reduce the use of chemical extraction (Vazquez-Hernandez *et al*., 2019; Ali, 2021; Hashim *et al*., 2021; Kantayos *et al*., 2021; Guru *et al*., 2022). These secondary metabolites are economically important for humans and are used in pharmaceuticals, nutraceuticals, food additives, and agrochemicals (Hassini *et al*., 2019; Singh 2023). Salicylic acid (SA) and hydrogen peroxide (H_2O_2) are of great interest in plants. SA is one of the most important plant phenolics that affects seed germination, stomatal movements, pigment accumulation, PS, enzyme activities, abscission reversal, nutrient uptake, flower induction, membrane functions, metabolic activities and overall growth and development of plants (Ali, 2021). H_2O_2 is a molecule generated by plant cells during vital processes such as PS and photorespiration. This molecule is required for plant development and growth, as well as for coordinating appropriate responses to survive in a changing climate (Mhamdi, 2023). On the other hand, depending on the elicitor dose, plants may present eustress or distress effects. Eustress is a beneficial stress, while the latter is non-beneficial and can damage or even kill plants. In other words, plants can benefit from low doses of stress but can be damage by high doses of stress, affecting basic plant functions (Jalal *et al*., 2021). Therefore, the goal should be reaching the peak of the hormesis curve where plants are not in distress and only an eustressor effect is induced in plants (figure 1). This is not a simple matter as the peak is a movable point and its location depends on many factors: climatic conditions, plant development stage, plant nutritional stage, elicitor dose, and plant plasticity, among others (Calabrese, 2008). Similarly, PS is modified. Flood (2019) explained how PS can vary according to natural events (climate) and local adaptation and the genetic basis of this variation and concluded that we need to understand how plants adapt to fast changing environments (water, CO_2 concentration, temperature, etc.) to improve agricultural productivity and how photosynthetic variation can help us complete this task (Roig-Oliver *et al*., 2021; Zahra *et al*., 2023). Agathokleous & Calabrese (2019) pointed out that hormesis is the key to increasing agricultural sustainability in a changing environment and growing population. According to this evidence, we posed the hypothesis that the changes in PS are a key plant mechanism for identifying eustress or distress, avoiding long periods of harmful stress and plant damage. The goal of our research was to evaluate the effect of elicitation on tomato plant PS, by identifying changes in the rate of CO_2 consumption to develop a first approach for identifying eustress or distress in elicited plants.

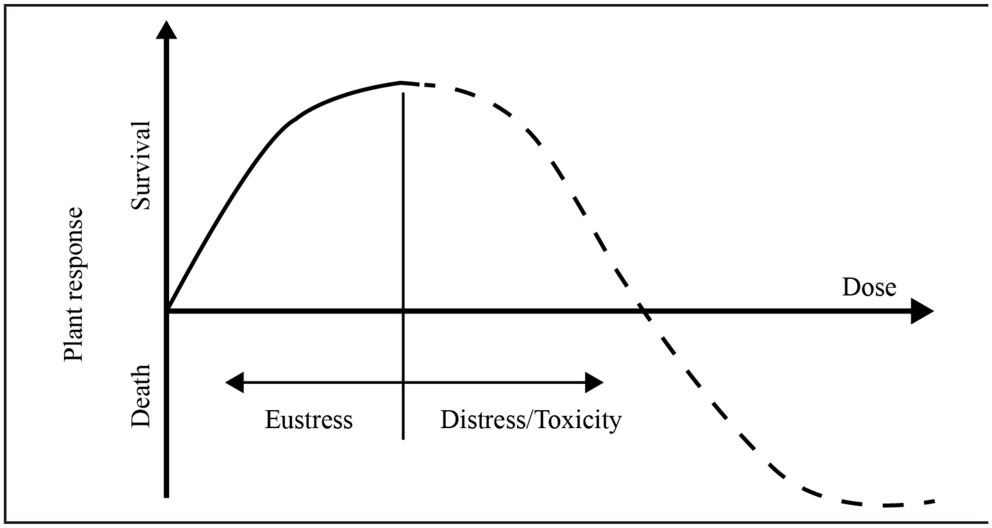

FIGURA 1
Concept of hormesis
Source: modified from Vargas-Hernández *et al*., 2017.

1. Materials and methods

1. 1. Location

The experiments were carried out at the Universidad Autónoma de Querétaro, Amazcala Campus México, latitude 20°42'20.35" N, longitude 100°15'34.92" W and altitude 1 920 m.

1. 2. Plant material and management

We used the tomato plant (*Solanum lycopersicum*) variety Torreón F1 Bejo®. The seeds were germinated in a peat-lite mix (Sunshine 3®) and transplanted after 42 days into plastic 14 L pots with a volcanic rock substrate called "tezontle" with a particle size no larger than 5 mm. Plants were cultivated with a single stem. Nutrition was made of the following fertilizers diluted in 5 000 L water: 250 ml of sulfuric acid, 2 950 g of calcium nitrate, 1 000 g of potassium sulfate, 800 g of magnesium sulfate, 650 g of potassium phosphate, 650 g of magnesium nitrate and 100 g of potassium chloride. Electric conductivity 2 dS m^{-1}. pH 6.5. Nutrients were distributed to plants through a drip irrigation system.

1. 3. PS measurements

PS was measured as illustrated in the scheme (figure 2). This method for measuring PS is based on CO_2 depletion in a closed chamber, where it is assumed that CO_2 is taken up by the plant due to PS activity (García-Rodríguez *et al*., 2022) and the whole plant PS is measured. Our system is similar to the one described in Song *et al*. (2016); the difference is that we used a second chamber to control temperature and light while they used it on the open field. A C1 PS measurement chamber of 0.6 × 0.6 × 1.2 m (length, width and height) was equipped with two infrared CO_2 sensors with a range of measurement from 0 to 9 999 ppm and accuracy ± 100 ppm + 5% of measured value (ALMEMO®, type FY A600-CO_2H) and two digital sensors for temperature and atmospheric humidity with accuracy ± 0.4 k at +10 to + 40 °C and ± 1.8% RH in the range 10 to 90 RH, respectively (ALMEMO® D FH0D462). This equipment was connected to a datalogger (ALMEMO® 2590-4S). Light was supplied using high-pressure sodium

(HPS) lamps hanging 70 cm above chamber C1, providing a total radiation of 800 W at the level of the internal radiation sensor of chamber C1. This sensor and datalogger were from Spectrum Technologies. A 2-inch fan was placed inside the chamber to homogenize air and CO_2. Initial temperature and humidity were controlled using a larger climatic chamber C2 with approximate dimensions of 3 × 3 × 2.5 m (length, width and height). The chamber was thermally isolated with polyurethane foam covering walls and ceilings. This set up allowed us to measure CO_2 consumption for 20 min while avoiding humidity saturation due to plant transpiration inside chamber C1, and data were taken every second (Arellano-Beltrán *et al*., 2017). Before running the experiments with plants and to ensure that chamber C1 was hermetically sealed, we injected CO_2 into chamber C1 at a level of 740 ppm without plants inside and confirmed that there was not significant CO_2 depletion for at least 15 min.

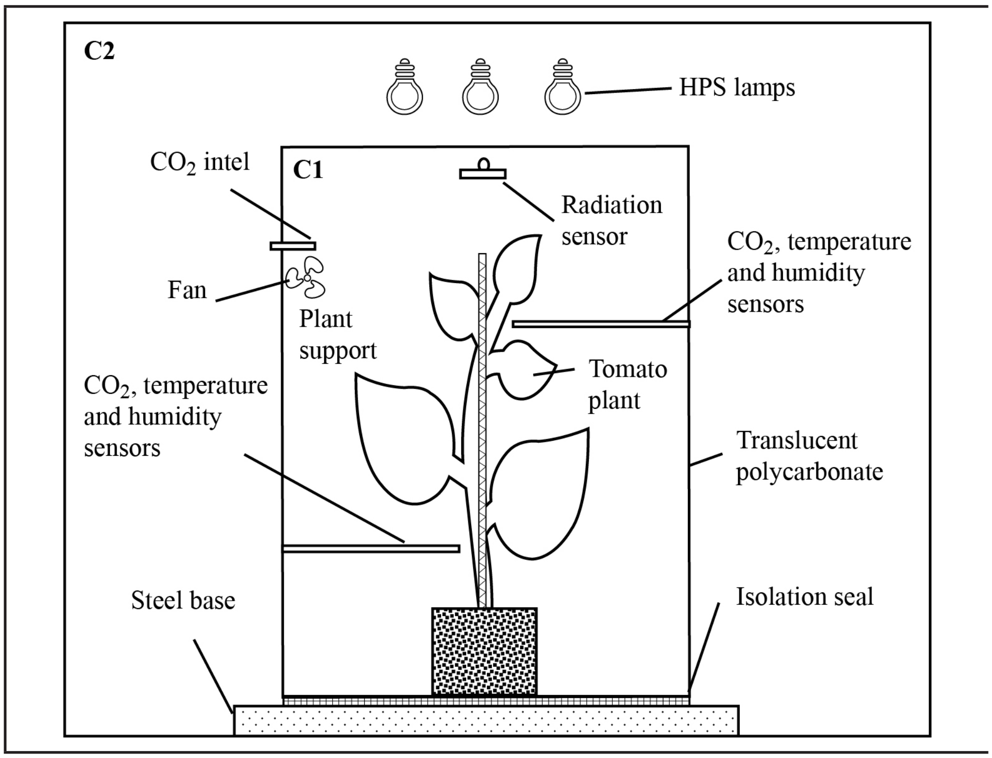

FIGURA 2
Chamber layout for PS measurements
Source: own elaboration.

1. 4. Experimental set up

Two sets of experiments were carried out, and the lap of time between them was approximately two months. The second set of experiments was tested to try to generate less erratic results than for the first set of experiments, controlling leaf area and increasing air temperature in chamber C2.

All plants were grown in a plastic greenhouse until the time of the experiments. Plants to be tested were taken from the greenhouse and placed inside chamber C2 for at least 20 minutes before being placed inside chamber C1 to allow for acclimation (20 °C and 60% relative humidity).

For the first set of experiments, PS measurements were carried out between the blooming and fruiting stages; that is, plants had flowers and small fruits and were approximately 50-70 cm in height with 23 to 30 leaves 50 to 54 days after transplanting. Thirteen sets of three plants each were established according to elicitor—SA and H_2O_2—, way of elicitation—foliar and radicular—and control (table 1). As we only used one measurement chamber (C1), treatments T1 to T3 were tested on the first day, T4 to T6 on the second day, T7 to T9 on the third day, T10 to T12 on the fourth day and the control group on the fifth day. For these experiments, a constant air temperature of 20 °C was maintained (C2), the initial CO_2 concentration was set between 600 and 700, and initial relative humidity was set between 60% and 70% (C1).

TABLE 1
Foliar and radicular elicitation of SA and H_2O_2

Treatment	SA (µM)	H_2O_2 (mM)
T1	0.1 F	
T2	0.5 F	
T3	1.0 F	
T4	0.1 R	
T5	0.5 R	
T6	1.0 R	
T7		2 F
T8		20 F
T9		200 F
T10		2 R
T11		20 R
T12		200 R
Control	Without elicitation	

Source: own elaboration.
Note: F and R mean foliar and radicular elicitation, respectively. For foliar elicitation leaves were sprayed up to obtain a uniformly wet leaf surface. For radicular elicitation, 300 ml was poured into the 14 L pot substrate where plants were grown. $n = 3$ for each treatment.

For the second set of experiments, the air temperature (C2) was set at 24 °C, the initial level of CO_2 was maintained as close as possible to 1 200 ppm, and the initial relative humidity was set between 60% and 70% for each single plant in chamber C1. This time, only SA was applied via the foliar route. Foliar and substrate temperatures were also measured (table 2). Plants were grown the same way as in the first experiment, but this time plants were measured at the developmental stage before flowering, 35 days after transplant. To improve consistency, we chose plants with similar leaf areas (visual qualitative inspection).

TABLE 2
SA, foliar elicitation

Treatment	SA (µM)	Foliar temperature (°C ± SD)	Substrate temperature (°C ± SD)	Amount
T1	0.1	23.2 ± 0.87	20.7 ± 1.15	Up to get a uniformly wet leaf surface
T2	0.5	23.2 ± 0.26	20.7 ± 1.15	
T3	1.0	22.9 ± 0.06	21.2 ± 0.76	
Control	Without elicitation	23.3 ± 0.50	21.0 ± 0.71	

Source: own elaboration.
Note: SD standard deviation. $n = 3$, for each treatment.

1. 5. Determination of leaf area

After every single plant PS measurement, the leaf area of each plant was determined via digital image processing. The tomato leaves were cut from the plant and placed on a white surface. A set of pictures was taken with a digital camera at a fixed distance to allow for calibration with a known area. Leaf area analysis was carried out with MATLAB software—correlating the number of pixels with the reference area—to compute the leaf area value (Rico-García *et al*., 2009).

1. 6. Statistical analysis

Statistical analysis was carried out using OriginPro (version 8, OriginLab, Northampton, MA, USA). One-way analysis of variance (ANOVA). Mean comparisons were carried out by the Tukey test ($p < 0.05$).

2. Results and discussion

Chamber lay out disposition, C1 and C2 allowed CO_2 consumption measurements for 20 min before chamber C1 air was saturated with humidity from plant transpiration. However, a longer period is desired to study the effect of elicitation on plants over time. This method for measuring PS has a clear advantage over equipment that measures over a small leaf portion. Our method allowed for whole plant PS measurements and blocked external influences that can modify PS during measurements. In addition, controlling light and external temperature with the help of external chamber C2 allowed measurements to be taken up to 10 times longer than in open field chambers, in which solar radiation causes a rapid temperature increase in the chamber, reducing the measurement time to two to three minutes (Song *et al*., 2016). Measuring whole plant PS also allowed for a better evaluation of plant performance at the canopy scale, as the growth and development of plants are more closely related to canopy photosynthetic capacity (Li *et al*., 2022).

2. 1. Leaf area

For the leaf area, our results showed high variability. However, plants with similar leaf areas are desired (figure 3). Similar leaf area is important as we measured the PS of the whole plant under similar conditions. Only for the second experiment was the leaf area statistically similar (figure 3e).

2. 2. CO_2 consumption

For CO_2 consumption, the correlation coefficient (R^2) shows that the behavior fits a linear model accurately (table 3); this behavior is observed in all curves in figure 4. Our results for CO_2 consumption by intact tomato plants confirmed those from Ming-yang *et al*. (2021), who reported a linear relationship between the quantum yield of photosystem II and CO_2 exchange for superhigh-yielding and high-yielding wheat cultivations. Choudhury (1986) reported a linear correlation between leaf net PS and crop water stress index. Our results showed a linear trend for CO_2 consumption for different elicitor concentrations and air temperatures. Interestingly, the slope for these curves changed but remained linear, suggesting that a change in slope represented differences by elicitation. Ahmed *et al*. (2022) reported a positive correlation between the photosynthetic rate, in lettuce plant, and the CO_2 concentration. This could overcome the disadvantage of evaluating elicitor effects at the end of the growing cycle of plants, as PS presented a linear behavior, and any change in the slope may indicate eustress or distress in plants throughout production (growth and development). This idea was reinforced by Mahajan *et al*. (2020), as they indicated that primary metabolites are precursors for secondary metabolites in plants, but the latter rarely participate in building block processes, so the production of secondary metabolites may demand an increase in PS for a eustressor effect and a decline in PS for a distress effect. The highest R^2 values were found for SA elicitation—radicular or foliar—(table 3), which may indicate that foliar elicitation with SA is more homogeneous than H_2O_2 elicitation. Ali (2021) points out that SA is an efficient elicitor of secondary metabolite production in plants acting from basic plant functions; however, H_2O_2 R^2 values still indicate good correlation. Additional experiments are needed to elucidate differences between foliar and radicular elicitation.

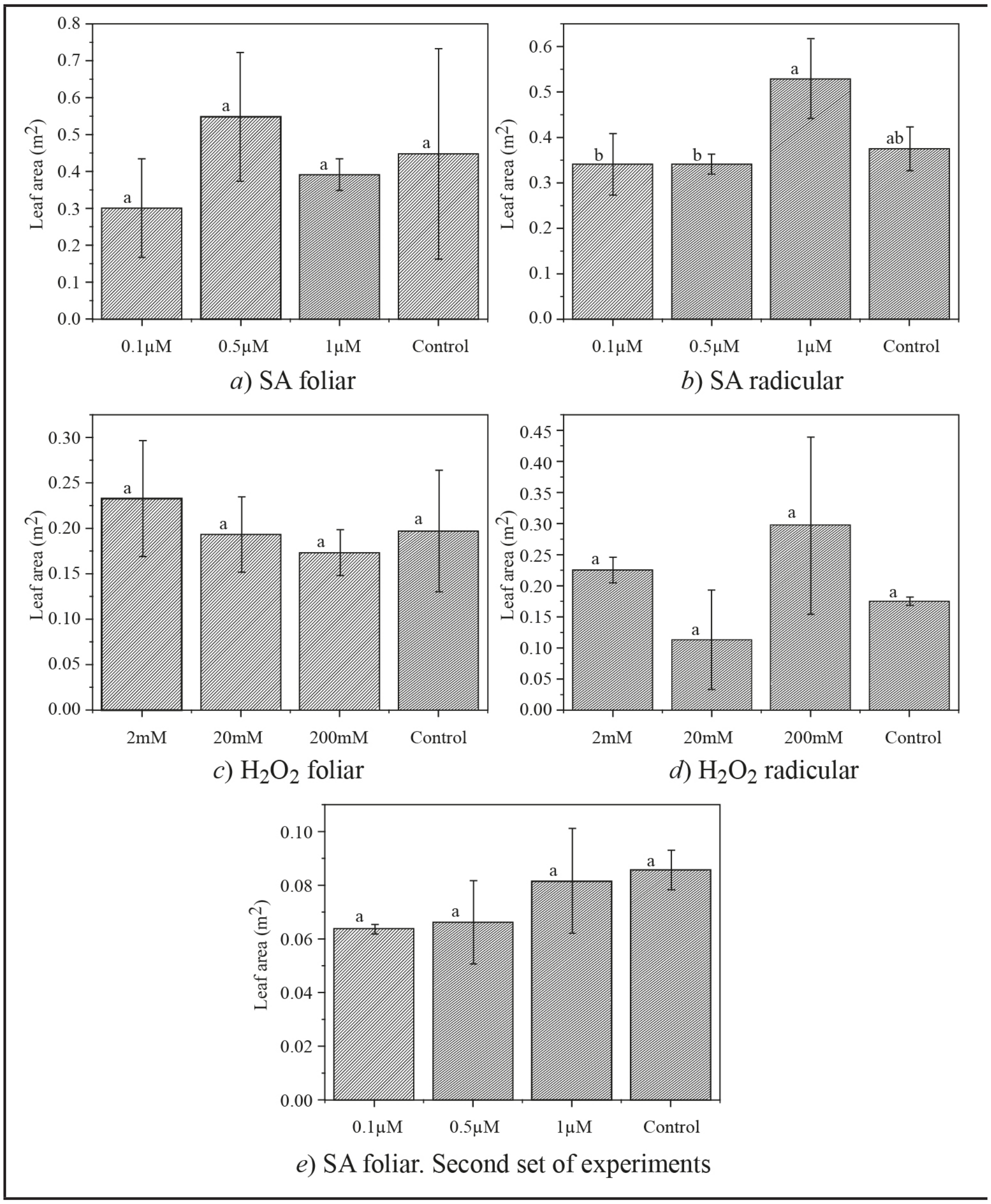

FIGURA 3
Leaf area

Source: own elaboration. Note: values are expressed as the mean of three replicates ± SD. $p < 0.05$.

TABLE 3
CO_2 consumption slope and correlation coefficients (R^2) for a linear model

Concentration	SA Foliar		SA Foliar*		SA Radicular	
µM	m	R^2	m	R^2	m	R^2
0.1	−0.054 ±0.022	0.955 ±0.039	−0.208 ±0.002	0.995 ±0.003	−0.043 ±0.004	0.961 ±0.014
0.5	−0.066 ±0.012	0.975 ±0.010	−0.116 ±0.089	0.995 ±0.002	−0.074 ±0.012	0.986 ±0.007
1.0	−0.058 ±0.007	0.969 ±0.004	−0.141 ±0.017	0.990 ±0.006	0.060 ±0.003	0.978 ±0.007
Control	−0.060 ±0.004	0.974 ±0.008	−0.161 ±0.046	0.985 ±0.001	−0.055 ±0.007	0.969 ±0.011

TABLE 3 (continúa)

CO_2 consumption slope and correlation coefficients (R^2) for a linear model

Concentration	H_2O_2 Foliar		H_2O_2 Radicular	
mM	m	R^2	m	R^2
2	−0.050 ±0.022	0.930 ±0.029	−0.019 ±0.007	0.808 ±0.113
20	−0.041 ±0.009	0.943 ±0.027	−0.012 ±0.045	0.950 ±0.018
200	−0.043 ±0.040	0.871 ±0.095	−0.038 ±0.008	0.932 ±0.027
Control	−0.017 ±0.004	0.768 ±0.132	−0.025 ±0.004	0.910 ±0.046

Source: own elaboration.

Note: *These values correspond to the second experiment for T = 24 °C and CO_2 = 1 200 ppm. Values are expressed as the mean of three replicates ±SD.

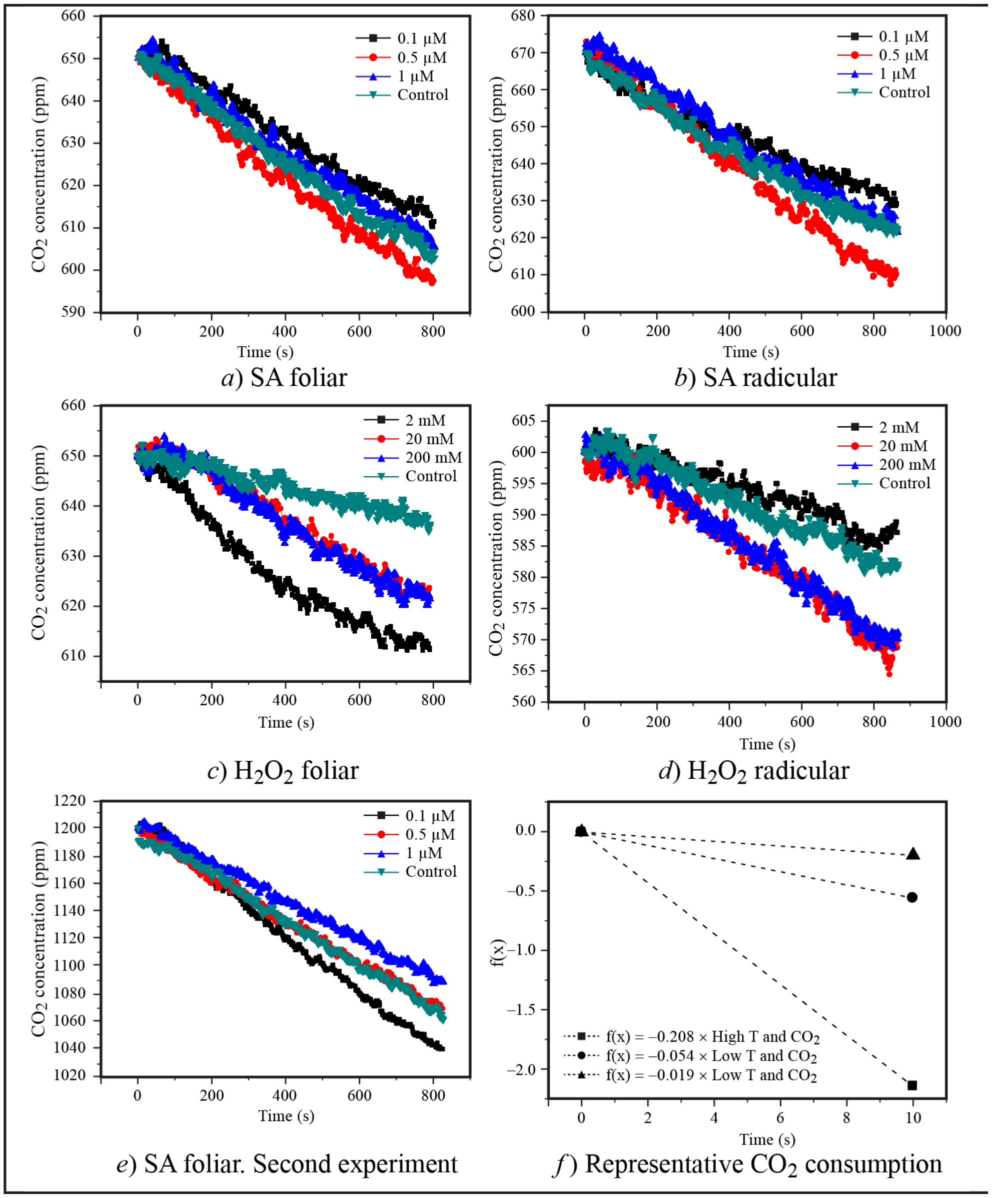

FIGURA 4

CO_2 consumption curves

Source: own elaboration.

2. 3. Photosynthesis results

For the first set of experiments, high variability was found, and unexpected behavior was observed (figures 5a, 5b, 5c, 5d). The results for the first testing group showed high variability in photosynthetic rates induced by differences in leaf area. In this regard, Calzadilla *et al*. (2022) indicated that the efficiency of photosynthesis depends on several plant characteristics in addition to its interaction with the environment. Different factors have a direct impact on CO_2 assimilation measurements. In our study, as we controlled light intensity, air temperature, initial CO_2 concentration and initial relative humidity, we assumed that variation in photosynthetic rates was due to differences in leaf area. This was supported by the results for the second set of experiments where less variation was observed, as plants with similar values were chosen (figure 5e). A J-shaped hormesis curve is observed, as suggested by Calabrese (2008). This result indicates that PS could differentiate eustress or distress in plants caused by elicitation, considering that PS is the basis for the production of carbohydrates that depending on external signals, induce stress, plants derived carbohydrates on different metabolic routes to produce secondary metabolites. This causes an increase, eustress, or decrease, distress, in PS. This is represented in the hormesis curve. Roig-Oliver *et al*. (2021) reported that water shortage reduced PS in *Hordeum vulgare* and *Triticum aestivum*, mainly due to stomatal conductance declines, being accompanied by reduced osmotic potential at full turgor and increased bulk modulus of elasticity. Roig-Oliver *et al*. (2021) did not report whether this stress was eustress or distress. We know that stress in plants could potentiate plant growth and development, and the new issue is not to surpass the peak of the hormesis curve to reach distress.

Prospective

The information developed in this study will be part of precision agriculture in the near future to induce eustress in commercial agricultural cultivars to produce functional foods without reducing productivity or even increasing productivity. On the other hand, considering that as living beings, plants can get used to elicitors, so elicitation in plants needs further research to indagate dose, time gap between elicitation, and method of elicitation. Therefore, we proposed focusing on plant PS to evaluate the effects of elicitation.

Conclusion and future work

According to our results we concluded that plant PS may be used as a plant stress indicator and stablish the basis for developing an innovative methodology for identifying eustress or distress in elicited plants. Since PS presents a linear behavior any change in the slope may indicate eustress or distress in plants and could be used as an immediate indicator to identify changes in plant physiology. This approach could overcome the disadvantage of evaluating elicitor effects until the end of the growing cycle of plants. Of course, as we mention in the title, this is just a first approach, and our results need to be corroborated using different methodologies to evaluate photosynthetic activity in plants. Calzadilla *et al*. (2022) indicated that scientists have been assessing photosynthetic activity under different conditions and in different plant species to understand the mechanisms that plants use to cope with changing environments, ranging from photoprotective mechanisms to adaptive processes striving towards acclimation.

Future studies should be carried out using higher temperatures (24 to 28 °C) and CO_2 concentrations of up to 1 200 ppm to better visualize PS changes. Also, it will be necessary to use other PS measuring methods as chlorophyll-a fluorescence analysis.

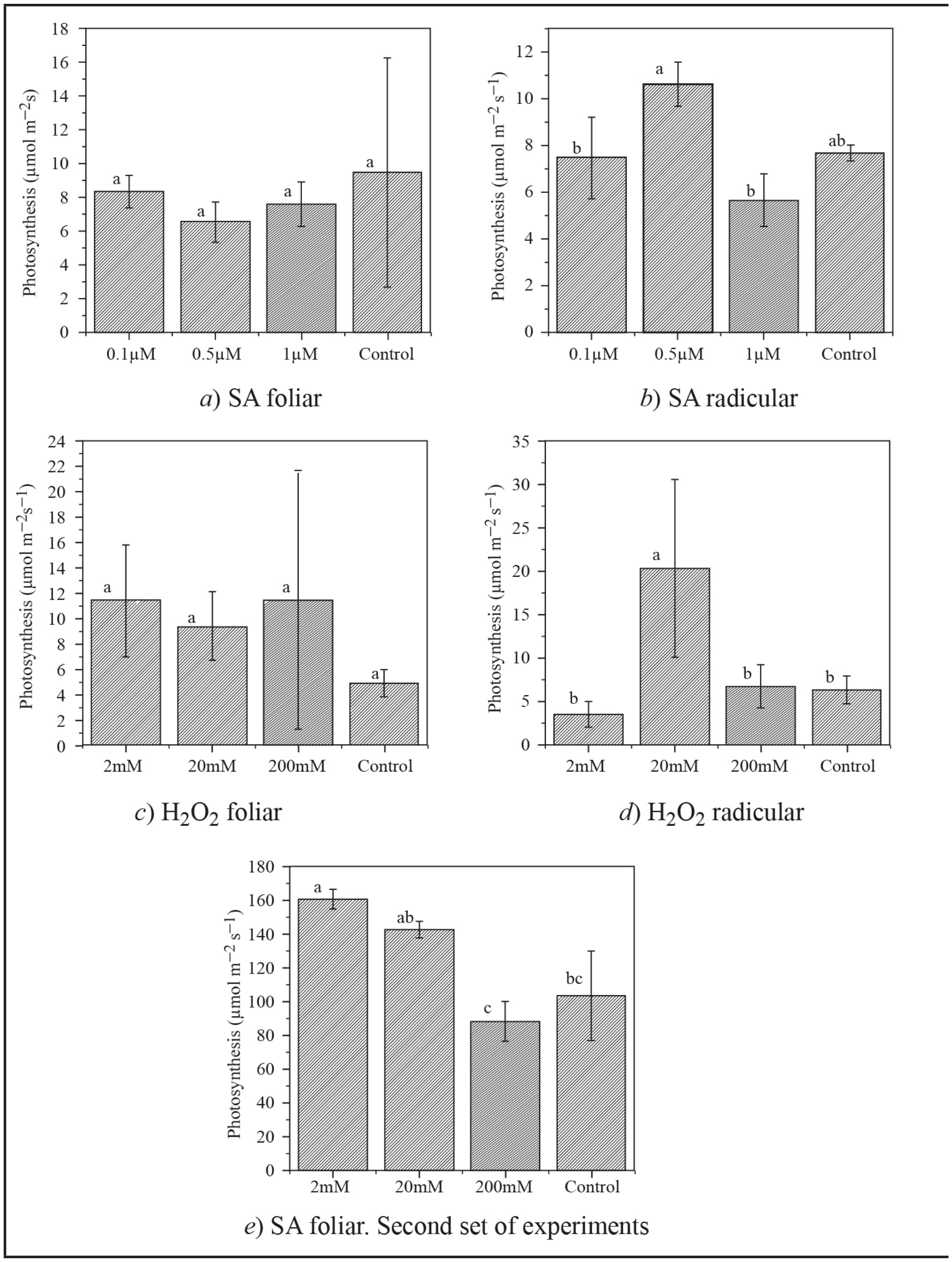

FIGURA 5

Photosynthesis results

Source: own elaboration.

Note: values are expressed as the mean of three replicates and ± SD. $p < 0.05$.

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Enrique Rico-García: conceptualización, curación de datos, análisis formal, metodología, investigación, redacción borrador original.
Adrián Esteban Ortega-Torres: metodología, redacción-revisión edición.
Sven Verlinden: conceptualización, redacción-revisión edición.
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