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## SPECIALTY SECTION

This article was submitted to  
Plant Abiotic Stress,  
a section of the journal  
Frontiers in Plant Science

RECEIVED 26 April 2022

ACCEPTED 20 September 2022

PUBLISHED 26 October 2022

## CITATION

Javaid MM, Florentine S, Mahmood A,  
Wasaya A, Javed T, Sattar A, Sarwar N,  
Kalaji HM, Ahmad HB, Worbel J,  
Ahmed MAA, Telesiński A and Mojski J  
(2022) Interactive effect of elevated  
CO<sub>2</sub> and drought on physiological  
traits of *Datura stramonium*.  
*Front. Plant Sci.* 13:929378.  
doi: 10.3389/fpls.2022.929378

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# Interactive effect of elevated CO<sub>2</sub> and drought on physiological traits of *Datura stramonium*

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Rising atmospheric CO<sub>2</sub> concentrations are known to influence the response of many plants under drought. This paper aimed to measure the leaf gas exchange, water use efficiency, carboxylation efficiency, and photosystem II (PS II) activity of *Datura stramonium* under progressive drought conditions, along with ambient conditions of 400 ppm (aCO<sub>2</sub>) and elevated conditions of 700 ppm (eCO<sub>2</sub>). Plants of *D. stramonium* were grown at 400 ppm and 700 ppm under 100 and 60% field capacity in a laboratory growth chamber. For 10 days at two-day intervals, photosynthesis rate, stomatal conductance, transpiration rate, intercellular CO<sub>2</sub> concentration, water use efficiency, intrinsic water use efficiency, instantaneous carboxylation efficiency, PSII activity, electron transport rate, and photochemical quenching were measured. While drought stress had generally negative effects on the aforementioned physiological traits of *D. stramonium*, it was found that eCO<sub>2</sub> concentration mitigated the adverse effects of drought and most of the physiological parameters were sustained with increasing drought duration when compared to that with aCO<sub>2</sub>. *D. stramonium*, which was grown under drought conditions, was re-watered on day 8 and indicated a partial recovery in all the parameters except maximum fluorescence, with this recovery being higher with eCO<sub>2</sub> compared to aCO<sub>2</sub>. These results suggest that elevated CO<sub>2</sub> mitigates the adverse growth effects of drought, thereby enhancing the

adaptive mechanism of this weed by improving its water use efficiency. It is concluded that this weed has the potential to take advantage of climate change by increasing its competitiveness with other plants in drought-prone areas, suggesting that it could expand into new localities.

#### KEYWORDS

gas exchange, photosystem II activity, fluorescence, water use efficiency, electron transport rate

## Introduction

Since the Industrial Revolution, atmospheric CO<sub>2</sub> has been increasing and is predicted to reach 800 ppm at the end of this century (Valone, 2021). Elevated CO<sub>2</sub> (eCO<sub>2</sub>) stimulates global warming, causing rapid changes in the climate of the earth, affecting variations in temperature, precipitation amounts and intensity patterns (Skendžić et al., 2021). Moreover, it has been reported that global warming acts to cause deficits in atmospheric vapor pressure, resulting in drought stress in plants (Song et al., 2021). This rapid climate change may also alter the geographical ranges of species (Skendžić et al., 2021), and it is, therefore, predicted that species that can tolerate warmer and drier weather will have competitive benefits over non-tolerant species (Karimizadeh et al., 2021). Changes in precipitation patterns will also affect the success of species invasion and the nature of ecosystems in general. It has been reported that crop species under eCO<sub>2</sub> act to enhance photosynthesis when other factors like light, water, and nutrients are not limiting (Boucher et al., 2009; AbdElgawad et al., 2015; AbdElgawad et al., 2016; Cruz et al., 2018; Alba et al., 2019). Dusenget al. (2019) concluded that the current ambient CO<sub>2</sub> concentration is a limiting factor to growth, so an increase in CO<sub>2</sub> concentration clearly has the potential to increase the growth and yield of plants.

Elevated CO<sub>2</sub> increases the activity rate of Rubisco, which results in increased plant growth (López-Calcagno et al., 2020). This will be beneficial for agriculture because of greater crop productivity, but the growth of weeds, especially invasive species, will also be enhanced (Wu et al., 2017). Physiologically, elevated CO<sub>2</sub> increases biomass production by reducing water loss through the stomata, in conjunction with an increase in root growth and improved root structure (Li et al., 2020). Stomatal conductance is based on CO<sub>2</sub>, which reduces the transpiration rate of crop species grown under elevated CO<sub>2</sub> with ample water supplies (Kimball, 2016). However, the response of stomata to eCO<sub>2</sub> is dependent on the interactive effect of elevated CO<sub>2</sub> and soil water content (Xu et al., 2016). It is well documented that an increase in CO<sub>2</sub> concentration causes partial stomatal closure, which reduces leaf transpiration and increases net carbon

assimilation (Dai, 2013; AbdElgawad et al., 2015; Cruz et al., 2018).

Elevated CO<sub>2</sub> increases the net assimilation rate by up to 30%, which can lead to a significant increase in dry matter and yield of crops (Robredo et al., 2007; Cruz et al., 2018; Pan et al., 2018). Wheat crops grown under 550 ppm CO<sub>2</sub> concentration have been shown to increase their yield by 15%, the canopy temperature by 0.85°C, and have reduced their evapotranspiration by 13%, consequently increasing the water use efficiency by 18%. Rising levels of CO<sub>2</sub> have, therefore, potential beneficial effects on the growth and yield of plants, especially in areas where drought causes crop failure (Jin et al., 2019). According to AbdElgawad et al. (2016), eCO<sub>2</sub> has been shown to mitigate the stress impact of drought, and they quoted examples of barley and alfalfa crop growth reduction under drought stress (Zeid and Shedeed, 2006; Robredo et al., 2007). However, despite these beneficial effects on crops, the rising level of atmospheric CO<sub>2</sub> may have negative consequences for yield losses due to weed-crop competition (Ziska et al., 2019). Observations have shown that while vegetative growth of C<sub>3</sub> crops is favored over C<sub>4</sub> weeds under elevated CO<sub>2</sub> (Ziska and Caulfield, 2000), C<sub>3</sub> weeds may be favored over C<sub>3</sub> crops (Ziska et al., 2019). It has recently been suggested that the effect of drought may be overcome by some compensatory mechanism within the plants (Qi et al., 2021). Numerous reports showed that plants that were grown under eCO<sub>2</sub> dried more slowly as water was withheld due to lower stomatal conductance and transpiration rate (Yan et al., 2017; Dikšaitytė et al., 2019; Pastore et al., 2020). It is postulated that the benefit gained by weeds from eCO<sub>2</sub> under drought conditions is linked to physiological traits like chlorophyll content, gas exchange, water use efficiency, and PSII activity of plants (Li et al., 2019). Elevated CO<sub>2</sub> increased the growth and reproduction of both indigenous and non-indigenous weeds, which has resulted in an enhancement of their competitive ability. This outcome supports the hypothesis of Blossey and Notzold (1995), who hypothesized that there is an evolution of increased competitive ability in invasive plants. It is well documented that invasive species affect the growth, development, and reproduction of native species by altering the ecosystem and introducing direct competition for

essential resources (Werner et al., 2008). Although gaining an understanding of the effect of increased atmospheric CO<sub>2</sub> combined with drought on the growth and yield of crops has a priority over weed studies (Nguyen et al., 2017), weed infestation is, nevertheless, an important impediment to crop productivity and needs to be investigated in its own right.

*Datura stramonium*, commonly known as thorn apple or Jimson weed, is an invasive C<sub>3</sub> weed species belonging to the family Solanaceae (Chadha et al., 2020). It is grown in subtropical and temperate regions worldwide (Chadha et al., 2020). It has fast seedling growth with a short vegetative stage and is characterized by indeterminate growth habits. Broad leaves and sympodial branches allow this weed to shade the surrounding areas and increase its competitive ability. It is a common weed found in soybean, potato, tomato, and tobacco crops. *D. stramonium* has narcotic properties and contains tropane alkaloids, mainly scopolamine, hyoscyamine, and atropine chemicals, which are known to be poisonous for humans, cattle, and horses (Baloch et al., 2017). These characters restrict the agricultural use of this species, but some studies have shown the potential of *D. stramonium* for bio-oil production (Aysu and Durak, 2015; Durak and Aysu, 2016). Therefore, it is important to develop a good understanding of how *D. stramonium* is likely to respond to changing environments, indicating that the lack of scientific literature regarding the effect of eCO<sub>2</sub> concentration on the physiological processes of *D. stramonium* is a significant problem. The current study focuses on an understanding of the regulation of gas exchange, photosynthetic efficiency of PSII, and water use efficiency of *D. stramonium* at 400 and 700 ppm CO<sub>2</sub> grown under normal irrigation and drought conditions, and reflects on the implications of these results for their growth and invasive characteristics.

## Materials and methods

### Seed collection

Seeds of *D. stramonium* were obtained by removing the heads from mature plants, and subsequently drying and threshing them to remove extraneous material. These heads were collected from more than 100 different plants in Ballarat, Victoria, Australia. The cleaned seeds were stored in a dried amber glass bottle at 19°C in the seed ecology laboratory of Federation University, Mt. Helen, Australia, until used in the experiment.

### Condition of the experiment

Experiments were conducted at Federation University (37° 37.39'S, 143°53.27'E) in two CO<sub>2</sub> chambers (2.1 m length, 2.1

width, and 2.0 m height) (Steridium Pty. Ltd., Brendale, Qld, Australia). One CO<sub>2</sub> chamber was set at 400 ppm CO<sub>2</sub> concentration (aCO<sub>2</sub>), while the other was set at 700 ppm CO<sub>2</sub> concentration (eCO<sub>2</sub>). The average chamber temperature was maintained at 22/18°C day/night alternating temperature with 60% humidity. Twenty plastic pots (13 cm wide and 14 cm high) were filled, each with 1.2 kg of a 2:1 mixture of garden soil and a commercially available potting mixture. Three seeds of *D. stramonium* were sown in the center of each pot. Out of the twenty pots, 10 randomly selected samples were kept in the cabinet maintained at an ambient CO<sub>2</sub> level (400 ppm), and the remaining 10 pots were kept in the second cabinet maintained at an elevated CO<sub>2</sub> level (700 ppm). The pots were watered daily, and seedlings were thinned at the four-leaf stage, leaving one seedling in each pot. Two moisture levels (well-watered and drought) were also maintained in each CO<sub>2</sub> chamber. The well-watered treatments were maintained at 100% field capacity and drought treatments at 60% field capacity. Drought treatment commenced 25 days after sowing. These water regimes were selected as different plant species showed variable responses to eCO<sub>2</sub> concentrations under drought conditions. Water holding capacity was determined according to Bajwa et al. (2019). Briefly, 10 kg of the soil was placed into three pots and saturated with tap water. The pot surface was covered with black plastic, and the pots were allowed to drain for 48 h to determine the water hole. After this time, the plastic sheet was removed and three soil samples (each weighing 300 g) were taken from the mid position of each pot. These samples were weighed (wet weight of soil, A) before being oven-dried (90°C for 72 h) and reweighed (dry weight of soil, B). The field capacity was then calculated by the formula  $(A - B) \times 100/B$ . The 60% field capacity was determined based on that fraction of the water holding capacity.

Of the 10 pots in each chamber, half were subjected to well-watered conditions and the remaining half were subjected to a drought regime. The pots were weighed to maintain an accurate amount of water field capacity levels, noting that the weight of the growing plant was much smaller than that of the soil in the pot. There were five replications (one pot for each replication) for each treatment and each replication consisted of one plant. In drought treatments, water was withheld until Day 8 in both CO<sub>2</sub> chambers, after which drought treatment pots were re-watered to investigate the recovery response of the *D. stramonium* plants. The amount of water added was calculated based on pot weight, and 60% field capacity was maintained till Day 10. In the well-watered treatments, water was added on alternate days.

### Gas exchange and fluorescence

To evaluate the effect of CO<sub>2</sub> and drought on physiological parameters, the LI-COR portable infrared CO<sub>2</sub> gas analyzer was

used (LI-6400 XT portable photosynthesis system, LI-COR, Biosciences, Lincoln, Nebraska, USA). Measurements were recorded with the following adjustments by LI-COR: The block temperature was set at 20°C, the photosynthetic photon flux density (PPFD) was 1,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  with a red-blue light source, the leaf cuvette area was set at 2  $\text{cm}^2$  and the flow rate was adjusted to 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The light conditions in the chamber were set for 12 h and 12 h dark. The mean value of VPD in the leaf cuvette was  $1.75 \pm 0.03$  kPa. The  $\text{CO}_2$  concentration in the chamber was noted before each measurement, and adjusted to within  $\pm 10$  ppm of the stated level. On alternate days, net photosynthesis rate, stomatal conductance, transpiration rate, and intercellular  $\text{CO}_2$  concentration were measured and the parameters were started to measure at 9:30 am. Water use efficiency was calculated by dividing the net photosynthesis rate with the transpiration rate; intrinsic water use efficiency was calculated by dividing the net photosynthesis rate with stomatal conductance; and instantaneous carboxylation efficiency was calculated by dividing the net photosynthesis rate by the intercellular  $\text{CO}_2$  concentration. Photosystem II (PSII) activity, such as minimum fluorescence, maximum fluorescence, the effective quantum efficiency of PSII, photochemical efficiency of PSII, photochemical quenching, and photosynthetic electron transport rate, were calculated according to the methods described by Maxwell and Johnson (2000). Maximum fluorescence was determined by applying a saturating light pulse of 7,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The effective quantum efficiency of PSII was measured under actinic light of 180  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

The effective quantum efficiency of PSII was calculated as

$$\Phi_{\text{PSII}} = \frac{(F'_m - F_s)}{F'_m} \quad (1)$$

Where  $\Phi_{\text{PSII}}$  is the effective quantum efficiency of PSII,  $F'_m$  is the maximum fluorescence and  $F_s$  is the steady state fluorescence prior to the flash.

Photochemical efficiency of PSII ( $F'_v/F'_m$ ) was determined in terms of efficiency of energy harvesting by oxidized PSII using the following equation

$$\frac{F'_v}{F'_m} = \frac{F'_m - F'_0}{F'_m} \quad (2)$$

Where  $F'_m$  is the maximum fluorescence and  $F'_0$  is the minimum fluorescence.

The photochemical quenching was computed from

$$qp = \frac{F'_m - F_s}{F'_m - F'_0} \quad (3)$$

Where  $F_s$  is the steady-state fluorescence and  $F'_0$  is the minimum fluorescence.

## Statistical analysis

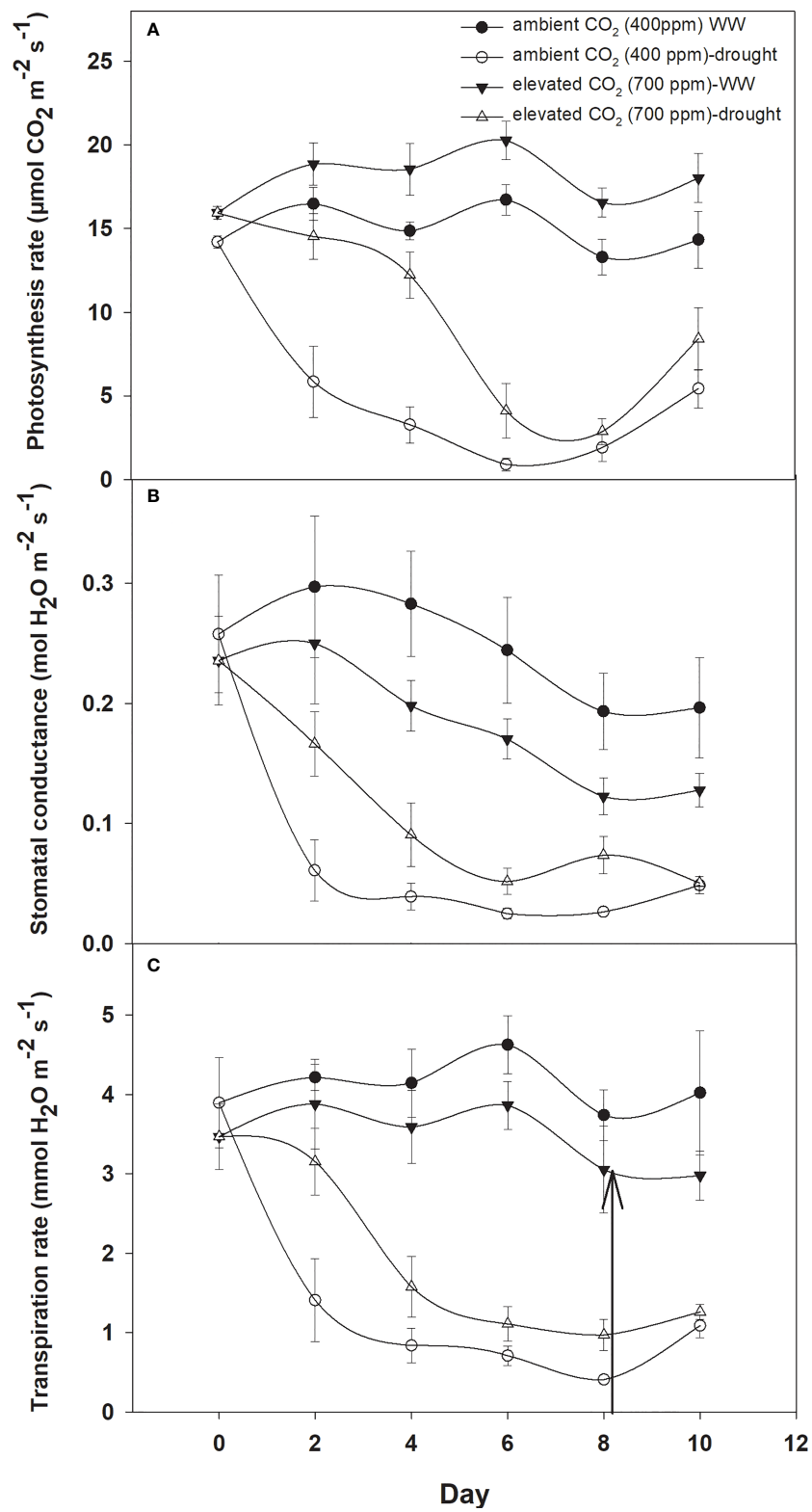
Data for gas exchange parameters were presented in graphs along with the standard error of each mean, and the graphs were prepared using the SigmaPlot 11 software. Regression analysis was performed on the data of photosynthesis rate, stomatal conductance, and transpiration rate under 8 days of drought conditions. To investigate the effects of time of observation (time), water conditions (water), and  $\text{CO}_2$  levels ( $\text{CO}_2$ ), physiological parameters were analyzed with Statistix 8.1 using three-factor ANOVA. All the main effects and two- and three-way interactions were examined using Tukey's HSD test at a 5% probability level.

## Results

### Gas exchange parameters

Photosynthesis activities were recorded for *D. stramonium* under two moisture conditions (well-watered and drought) at 400 ppm and 700 ppm  $\text{CO}_2$  concentrations (Figure 1A). These measurements were recorded for 10 days at two-day intervals. It is depicted in Figure 1A that elevated  $\text{CO}_2$  increased the photosynthesis rate by 2–3  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  when compared to that with ambient  $\text{CO}_2$ . However, the photosynthesis rate was variable under drought conditions with the two  $\text{CO}_2$  concentrations. Under drought conditions, the photosynthesis rate under a $\text{CO}_2$  decreased from 14 to 1  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at Day 8, while with e $\text{CO}_2$  this reduction was less, being 2.8  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  photosynthesis rate at Day 8. This clearly indicates that e $\text{CO}_2$  mitigated the adverse effects of drought on *D. stramonium*. After the measurement, water was added to the drought-treated plants to investigate the recovery response. The photosynthesis rate was seen to recover, showing a higher rate with e $\text{CO}_2$  compared to that under a $\text{CO}_2$ . Figure 1 showed that the photosynthesis rate increased from 2.86 to 8.4  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  with e $\text{CO}_2$ , while the corresponding recovery under a $\text{CO}_2$  was 5.4  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . The ANOVA table indicated that  $\text{CO}_2$  ( $p < 0.001$ ), time ( $p < 0.001$ ), water ( $p < 0.001$ ),  $\text{CO}_2 \times \text{time}$  ( $p < 0.001$ ), and time  $\times$  water ( $p < 0.001$ ) interactions were significant for photosynthesis rate, while the interactions of  $\text{CO}_2 \times \text{water}$  and  $\text{CO}_2 \times \text{time} \times \text{water}$  were non-significant for this parameter.

When *D. stramonium* was grown under well-watered conditions, the stomatal conductance was higher with a $\text{CO}_2$  compared to that with e $\text{CO}_2$  (Figure 1B). Moreover, the stomatal conductance under drought conditions showed variable responses to both  $\text{CO}_2$  concentrations (400 ppm and 700 ppm). The decline in stomatal conductance due to drought conditions was higher with a $\text{CO}_2$  and reached 0.03  $\text{mol H}_2\text{O}$



**FIGURE 1**  
 Effect of CO<sub>2</sub> concentrations and moisture conditions on (A) photosynthesis rate, (B) stomatal conductance, and (C) transpiration rate, of *Datura stramonium*. The vertical line on the data point represents the standard error of the mean and the vertical arrow line after Day 8 represents the addition of water in the drought treatments. WW, well-watered.

$m^{-2} s^{-1}$  on Day 8. Stomatal conductance with  $eCO_2$  on Day 8 was  $0.07 \text{ mol H}_2\text{O m}^{-2} s^{-1}$ . Re-watering the *D. stramonium* sample after the Day 8 measurement did not significantly improve the stomatal conductance and recorded only  $0.05 \text{ mol H}_2\text{O m}^{-2} s^{-1}$  conductance. The ANOVA results in Table 1 showed that time ( $p < 0.001$ ), water ( $p < 0.001$ ),  $CO_2 \times$  water ( $p < 0.001$ ), and time  $\times$  water ( $p < 0.001$ ) were all significant for stomatal conductance. The rest of the effects were non-significant for this parameter.

*D. stramonium* exhibited a significant difference in transpiration rate under  $eCO_2$  and  $aCO_2$  when grown under well-watered or drought conditions (Figure 1C). Elevated  $CO_2$  reduced the transpiration rate compared to that with  $aCO_2$  under well-watered conditions. Under this water regime, transpiration rate with  $aCO_2$  was recorded up to  $4.6 \text{ mmol H}_2\text{O m}^{-2} s^{-1}$  while it was  $3.8 \text{ mmol H}_2\text{O m}^{-2} s^{-1}$  with  $eCO_2$ . Drought stress resulted in a progressive decline in transpiration rate under both concentrations of  $CO_2$  until Day 8, but this

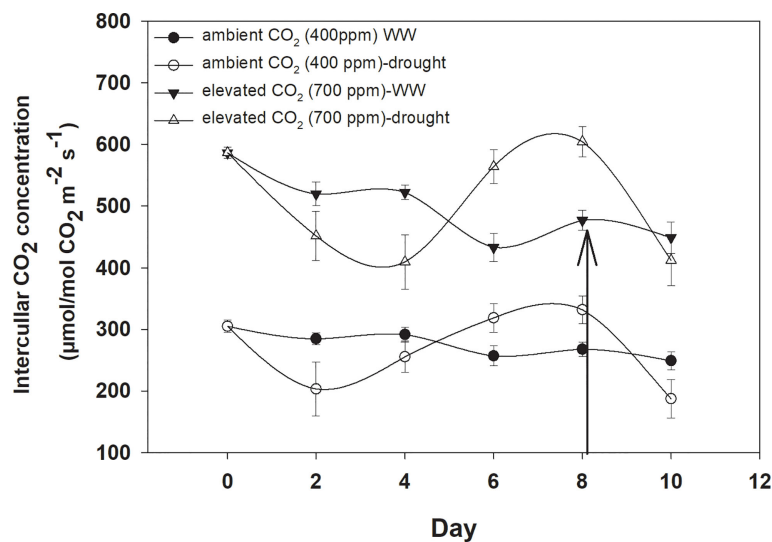
decline was significantly less with  $eCO_2$ . The transpiration rate was  $0.97 \text{ mmol H}_2\text{O m}^{-2} s^{-1}$  at Day 8 with  $eCO_2$ , whereas it was  $0.41 \text{ mmol H}_2\text{O m}^{-2} s^{-1}$  with  $aCO_2$ . Moreover, recovery in transpiration was higher with  $eCO_2$  upon re-instating the water to drought treatments (Figure 1C). The main effects of time ( $p < 0.001$ ) and water ( $p < 0.001$ ) and the interaction of  $CO_2 \times$  water ( $p < 0.001$ ) and time  $\times$  water ( $p < 0.001$ ) were significant for the transpiration rate.

Elevated  $CO_2$  concentration increased the intercellular  $CO_2$  concentration compared to that with  $aCO_2$  (Figure 2). *D. stramonium* grown under well-water conditions recorded about  $430\text{--}586 \mu\text{mol mol}^{-1}$  intercellular  $CO_2$  concentration with  $aCO_2$  compared with  $eCO_2$ , where it was  $249\text{--}304 \mu\text{mol mol}^{-1}$ . Drought conditions were seen to have drastic effects on intercellular  $CO_2$  concentration, and this was increased with an increase in drought duration. The ANOVA values in Table 1 showed that the main effects ( $CO_2$  and time) and interaction of time  $\times$  water were significant for intercellular  $CO_2$  concentration ( $p < 0.009$ ).

TABLE 1 Summary of the analysis variance for physiological parameters of *Datura stramonium* in response to  $CO_2$  levels, water condition and time of observation.

| Parameter  | $CO_2$  |             | Time    |             | Water   |             | $CO_2 \times$ Time |             | $CO_2 \times$ Water |             | Time $\times$ Water |             | $CO_2 \times$ Time $\times$ Water |             |
|--|---------|-------------|---------|-------------|---------|-------------|--------------------|-------------|---------------------|-------------|---------------------|-------------|-----------------------------------|-------------|
|  | p-value | HSD at 0.05 | p-value | HSD at 0.05 | p-value | HSD at 0.05 | p-value            | HSD at 0.05 | p-value             | HSD at 0.05 | p-value             | HSD at 0.05 | p-value                           | HSD at 0.05 |
| Photosynthesis rate $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$                       | 0.000   | 0.95        | 0.000   | 2.42        | 0.000   | 0.95        | 0.040              | 3.94        | 0.158               | 1.77        | 0.000               | 3.94        | 0.057                             | 6.23        |
| Stomatal conductance $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$                          | 0.312   | 0.03        | 0.000   | 0.06        | 0.000   | 0.03        | 0.788              | 0.10        | 0.000               | 0.47        | 0.001               | 0.10        | 0.579                             | 0.17        |
| Transpiration rate $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$                           | 0.752   | 0.32        | 0.000   | 0.82        | 0.000   | 0.32        | 0.352              | 1.33        | 0.000               | 0.60        | 0.000               | 1.33        | 0.629                             | 2.11        |
| Intercellular $CO_2$ concentration $\mu\text{mol mol}^{-1}$                                  | 0.000   | 19.87       | 0.005   | 50.44       | 0.711   | 19.87       | 0.165              | 82.14       | 0.140               | 37.03       | 0.008               | 82.14       | 0.105                             | 129.86      |
| Water use efficiency $\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$                 | 0.001   | 0.93        | 0.110   | 2.37        | 0.024   | 0.93        | 0.322              | 3.86        | 0.580               | 1.74        | 0.216               | 3.86        | 0.172                             | 6.10        |
| Intrinsic water use efficiency $\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$       | 0.000   | 16.88       | 0.000   | 42.86       | 0.000   | 16.88       | 0.107              | 69.76       | 0.006               | 31.45       | 0.000               | 69.76       | 0.240                             | 110.28      |
| Instantaneous carboxylation efficiency $\mu\text{mol m}^{-2} \text{ s}^{-1} \text{ Pa}^{-1}$ | 0.000   | 0.04        | 0.000   | 0.01        | 0.917   | 0.04        | 0.150              | 0.02        | 0.433               | 0.07        | 0.000               | 0.02        | 0.330                             | 0.03        |
| Minimum fluorescence (F0)  | 0.106   | 16.60       | 0.093   | 42.13       | 0.522   | 16.60       | 0.033              | 68.60       | 0.339               | 30.93       | 0.126               | 68.60       | 0.362                             | 108.45      |
| Maximum fluorescence (F)   | 0.000   | 30.84       | 0.000   | 78.27       | 0.000   | 30.84       | 0.000              | 127.46      | 0.280               | 57.46       | 0.000               | 127.46      | 0.977                             | 201.50      |
| Quantum yield of PSII  | 0.970   | 0.02        | 0.000   | 0.05        | 0.000   | 0.02        | 0.060              | 0.07        | 0.080               | 0.03        | 0.000               | 0.07        | 0.419                             | 0.11        |
| Photochemical efficiency of PSII (Fv/Fm)   | 0.000   | 0.02        | 0.000   | 0.02        | 0.000   | 0.02        | 0.031              | 0.09        | 0.400               | 0.04        | 0.001               | 0.09        | 0.040                             | 0.14        |
| Photochemical quenching (qP)   | 0.148   | 0.03        | 0.000   | 0.08        | 0.000   | 0.03        | 0.422              | 1.33        | 0.167               | 0.06        | 0.000               | 1.33        | 0.676                             | 0.21        |
| Photosynthetic electron transport rate $\mu\text{mole}^{-1} \text{ m}^{-2} \text{ s}^{-1}$   | 0.980   | 7.76        | 0.000   | 19.23       | 0.000   | 7.76        | 0.626              | 31.32       | 0.822               | 14.12       | 0.000               | 31.32       | 0.413                             | 49.51       |

$CO_2$  was 400 and 700 ppm; water condition was 100 and 60% field capacity; time of observations was 0 to 10 days at two days intervals from the start of drought conditions.



**FIGURE 2**  
Effect of CO<sub>2</sub> concentrations and moisture conditions on intercellular CO<sub>2</sub> concentration of *Datura stramonium*. The vertical line on the data point represents the standard error of the mean and the vertical arrow line after Day 8 represents the addition of water in the drought treatments. WW, well-watered.

## Water use efficiency

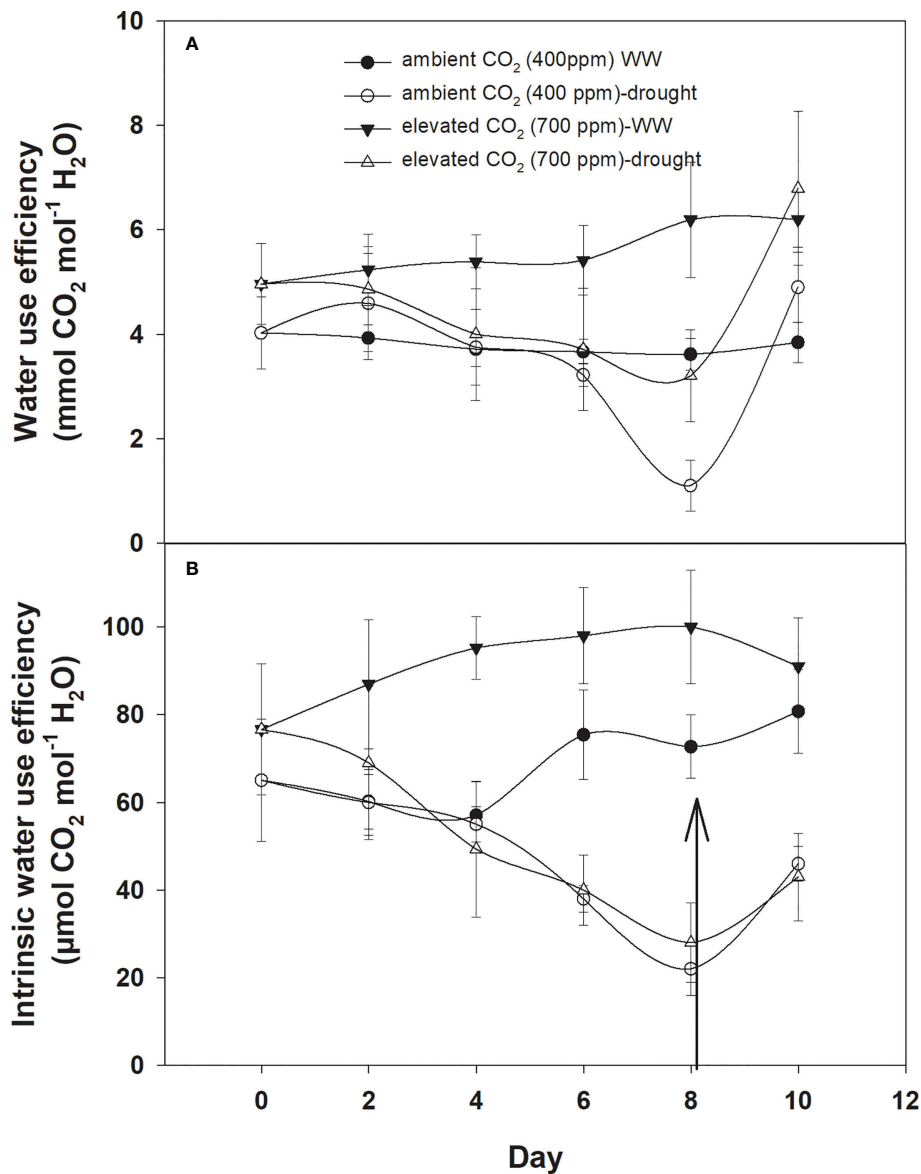
Under well-watered conditions, water use efficiency was 5–6 with eCO<sub>2</sub> compared to that of aCO<sub>2</sub>, which recorded 3–4 mmol CO<sub>2</sub> mol<sup>-1</sup> H<sub>2</sub>O (Figure 3A). The response of *D. stramonium* towards water use efficiency under drought conditions was variable, with water use efficiency decreasing with an increase in drought duration until Day 8. The decline in water use efficiency with eCO<sub>2</sub>, was lower than that with aCO<sub>2</sub>. Water use efficiency was reduced from 4 to 1.6 mmol CO<sub>2</sub> per mol of water under eCO<sub>2</sub> whereas this decline was up to 2.1 mmol CO<sub>2</sub> per mol of water with aCO<sub>2</sub> concentration under drought conditions. The re-instatement of water in drought treatment at Day 8 led to a significant recovery in water use efficiency, reaching 4.8 mmol CO<sub>2</sub> mol<sup>-1</sup> H<sub>2</sub>O in the treatment where a 400 ppm CO<sub>2</sub> concentration was maintained. By comparison, water use efficiency reached 5.7 mmol CO<sub>2</sub> mol<sup>-1</sup> H<sub>2</sub>O when the CO<sub>2</sub> concentration was maintained at 700 ppm. Statistical analysis of water use efficiency in Table 1 showed that the main effects of CO<sub>2</sub> ( $p < 0.001$ ) and water ( $p < 0.024$ ) were significant, whereas the main effects of time and all interactions were non-significant.

Similar to water use efficiency, the intrinsic water use efficiency of *D. stramonium* was higher with eCO<sub>2</sub> compared to that with aCO<sub>2</sub> under well-watered conditions (Figure 3B), while the intrinsic water use efficiency under drought conditions with aCO<sub>2</sub> or eCO<sub>2</sub> was reduced at variable rates. A progressive decline in intrinsic water use efficiency under eCO<sub>2</sub> in drought treatment conditions started at Day 6 and reached a minimum (49 mmol CO<sub>2</sub> per mol of water) at Day 8. With aCO<sub>2</sub> in

drought conditions, the progressive decline started on Day 4 and reached 31 mmol CO<sub>2</sub> per mol of water on Day 8. The addition of water at this date significantly recovered intrinsic water use efficiency. Elevated CO<sub>2</sub> and aCO<sub>2</sub> resulted in 162.2 and 110.5 mmol CO<sub>2</sub> per mol of water as their intrinsic water use efficiency, respectively. Data from ANOVA showed that the main effects of CO<sub>2</sub> ( $p < 0.001$ ), time ( $p < 0.001$ ), and water ( $p < 0.0001$ ), plus interaction of CO<sub>2</sub> × water ( $p = 0.006$ ), and time × water ( $p < 0.001$ ), were significant for the intrinsic water use efficiency of *D. stramonium*. The three-way interaction was non-significant for this parameter.

## Carboxylation efficiency

Under well-watered conditions, elevated CO<sub>2</sub> caused a significant reduction in instantaneous carboxylation efficiency when compared with aCO<sub>2</sub> (Figure 5). The instantaneous carboxylation efficiency values were between 0.05 and 0.07  $\mu\text{mol m}^{-2} \text{s}^{-1} \text{Pa}^{-1}$  under eCO<sub>2</sub>, whereas it was 0.03–0.04  $\mu\text{mol m}^{-2} \text{s}^{-1} \text{Pa}^{-1}$  under aCO<sub>2</sub>. Drought conditions resulted in a variable response for instantaneous carboxylation efficiency for *D. stramonium*. Drought caused reductions in instantaneous carboxylation efficiency with an increase in the duration of drought, but this decline was much more progressive under aCO<sub>2</sub> compared to that with eCO<sub>2</sub>. Figure 4 shows that the instantaneous carboxylation efficiency decline started at the second day of drought stress, compared with the decline starting at Day 4 with eCO<sub>2</sub> under drought conditions. The



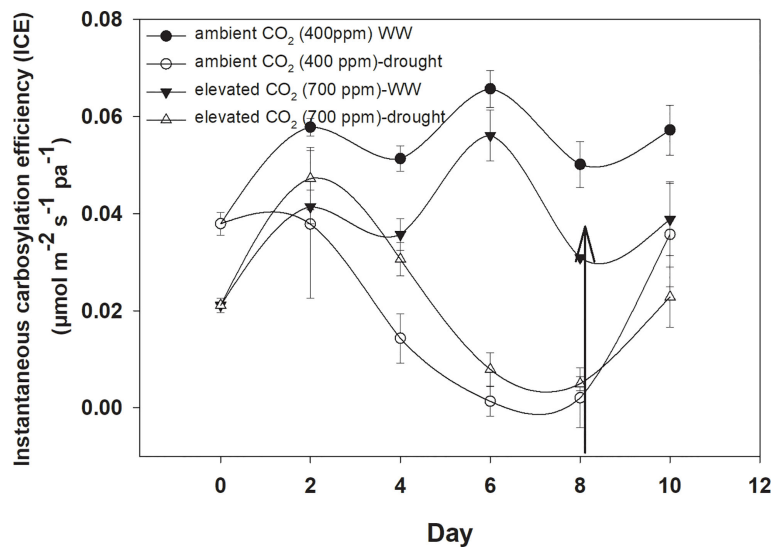
**FIGURE 3**  
 Effect of CO<sub>2</sub> concentrations and moisture conditions on (A) water use efficiency and (B) intrinsic water use efficiency of *Datura stramonium*. The vertical line on the data point represents the standard error of the mean and the vertical arrow line after Day 8 represents the addition of water in the drought treatments. WW, well-watered.

addition of water at Day 8 to drought treatments increased the instantaneous carboxylation efficiency under both CO<sub>2</sub> concentrations but instantaneous carboxylation efficiency reached 0.04 μmol m<sup>-2</sup> s<sup>-1</sup> Pa<sup>-1</sup> with aCO<sub>2</sub> after water addition to the drought treatment. The ANOVA results presented in Table 1 showed that the main effects of CO<sub>2</sub> (p<0.001), time (p<0.000), water (p<0.000), and interaction of time × water (p<0.000) were significant for instantaneous carboxylation efficiency of *D. stramonium*, whereas the rest of the interactions were non-significant.

### Photosynthetic electron transport

Under well-watered conditions, the photosynthetic electron transport rate was higher with an eCO<sub>2</sub> concentration than with aCO<sub>2</sub> (Figure 5). Drought significantly affected the photosynthetic electron transport efficiency with every increment in the drought days and the photosynthetic electron transport rate reached a minimum value (44 μmol e<sup>-1</sup> m<sup>-2</sup> s<sup>-1</sup> for aCO<sub>2</sub> and 38 μmol e<sup>-1</sup> m<sup>-2</sup> s<sup>-1</sup> for eCO<sub>2</sub>) on Day 8 of measurement under both CO<sub>2</sub> concentrations. Water addition to drought treatments recovered



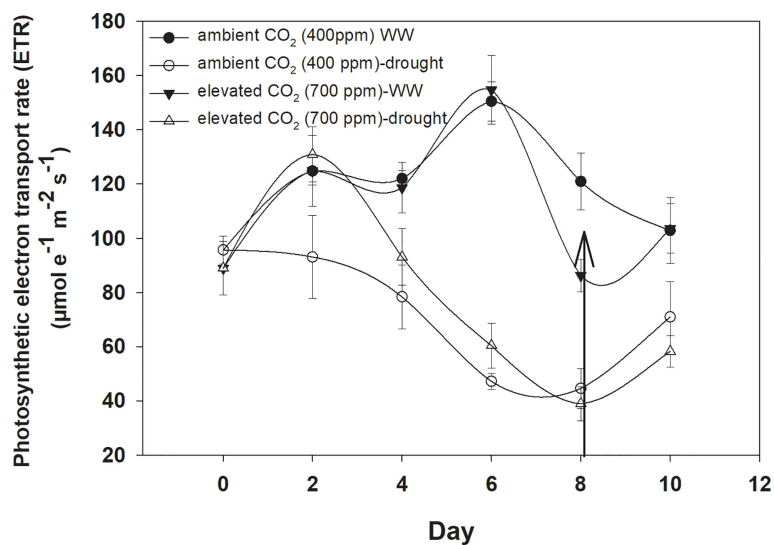


**FIGURE 4** Effect of CO<sub>2</sub> concentrations and moisture conditions on instantaneous carboxylation efficiency of *Datura stramonium*. The vertical line on the data point represents the standard error of the mean and the vertical arrow line after Day 8 represents the addition of water in the drought treatments. WW, well-watered.

the photosynthetic electron transport rate under both CO<sub>2</sub> concentrations. The photosynthetic electron transport rate of *D. stramonium* was significant in response to time and water, and the interaction time × water. The rest of the interactions were seen to be non-significant (Table 1).

### Fluorescence

The minimum and maximum fluorescence values of *D. stramonium* grown in well-watered conditions were higher with eCO<sub>2</sub> compared to with aCO<sub>2</sub> (Figures 7A, B). The effect



**FIGURE 5** Effect of CO<sub>2</sub> concentrations and moisture conditions on the photosynthetic electron transport rate of *Datura stramonium*. The vertical line on the data point represents the standard error of the mean and the vertical arrow line after Day 8 represents the addition of water in the drought treatments. WW, well-watered.

of drought was more pronounced on minimum fluorescence under aCO<sub>2</sub> as the minimum fluorescence decreased linearly until Day 8 of observation with an increase in drought duration. By comparison, eCO<sub>2</sub> under drought conditions had no effect on minimum fluorescence until Day 6, and after that, it declined to 319 (Figure 6A). Maximum fluorescence under drought conditions was higher with eCO<sub>2</sub> compared to that with aCO<sub>2</sub>, and a decline in maximum fluorescence occurred with both CO<sub>2</sub> concentrations with an increase in drought conditions until Day 8 of the observation (Figure 6B). Water addition to drought

treatment significantly recovered the minimum fluorescence under both CO<sub>2</sub> concentrations, while water addition to drought treatments slightly recovered the maximum fluorescence. The ANOVA table results showed that the interaction of CO<sub>2</sub> × time (p = 0.03) was significant for the minimum fluorescence of *D. stramonium* while the effects of CO<sub>2</sub> (p<0.001), time (p<0.001), water (p<0.001), and the interaction of CO<sub>2</sub> × time (p<0.001), and time × water (p<0.001) were significant for the maximum fluorescence of *D. stramonium*.

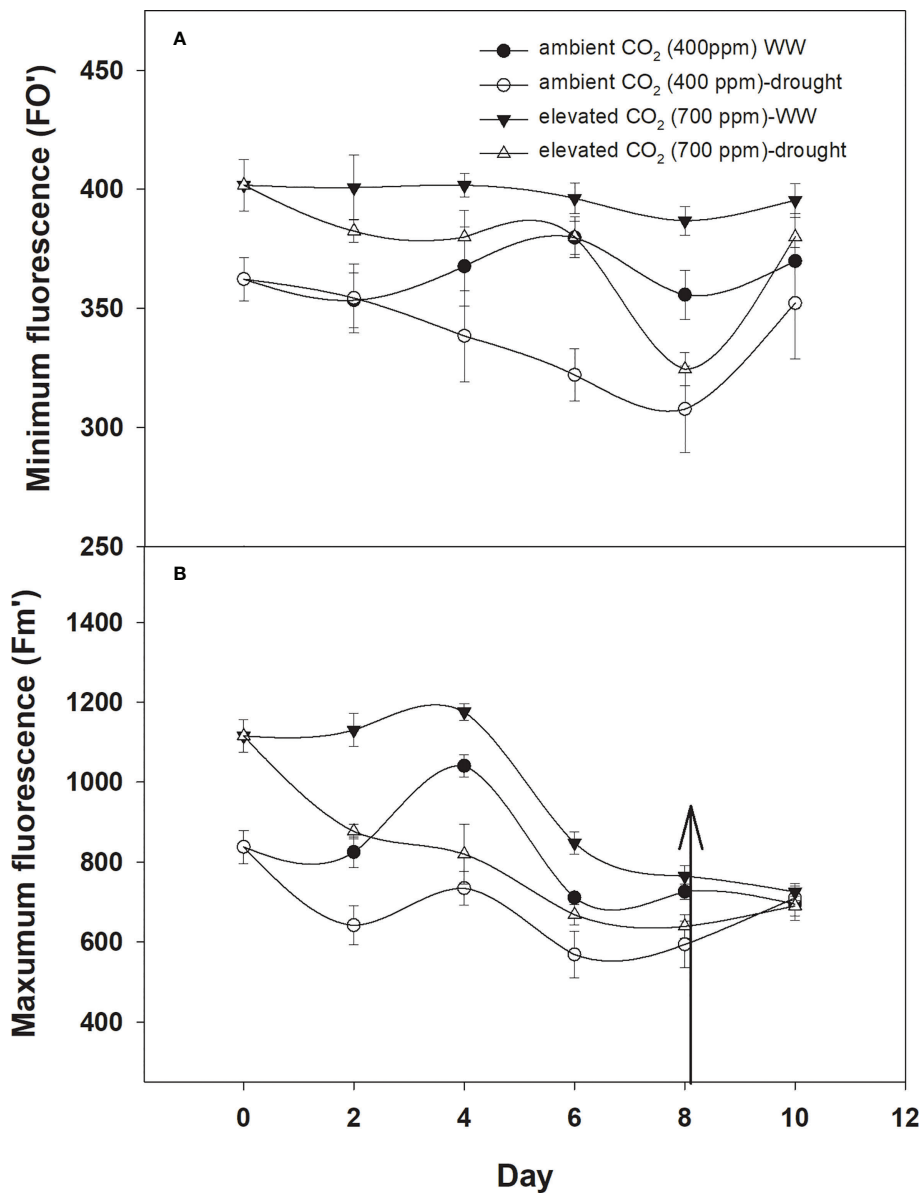


FIGURE 6 Effect of CO<sub>2</sub> concentrations and moisture conditions on (A) minimum fluorescence and (B) maximum fluorescence of *Datura stramonium*. The vertical line on the data point represents the standard error of the mean and the vertical arrow line after Day 8 represents the addition of water in the drought treatments. WW, well-watered.

### PSII activity

The effective quantum efficiency of PSII with both CO<sub>2</sub> concentrations was similar when *D. stramonium* was grown under well-watered conditions (Figure 7A). However, drought conditions showed the variable response of the effective quantum efficiency of PSII under tested CO<sub>2</sub> concentrations. Elevated CO<sub>2</sub> concentration slightly mitigated the adverse effects

of drought, and the effective quantum efficiency of PSII was sustained up to Day 4 with an increase in drought duration. By comparison, aCO<sub>2</sub> linearly decreased the effective quantum efficiency of PSII with an increase in drought duration until Day 8. Addition of water to drought treatments recovered the effective quantum efficiency of PSII of *D. stramonium* in the same way under both CO<sub>2</sub> concentrations. The main effects of time ( $p < 0.001$ ), water ( $p < 0.001$ ), and interaction of time × water

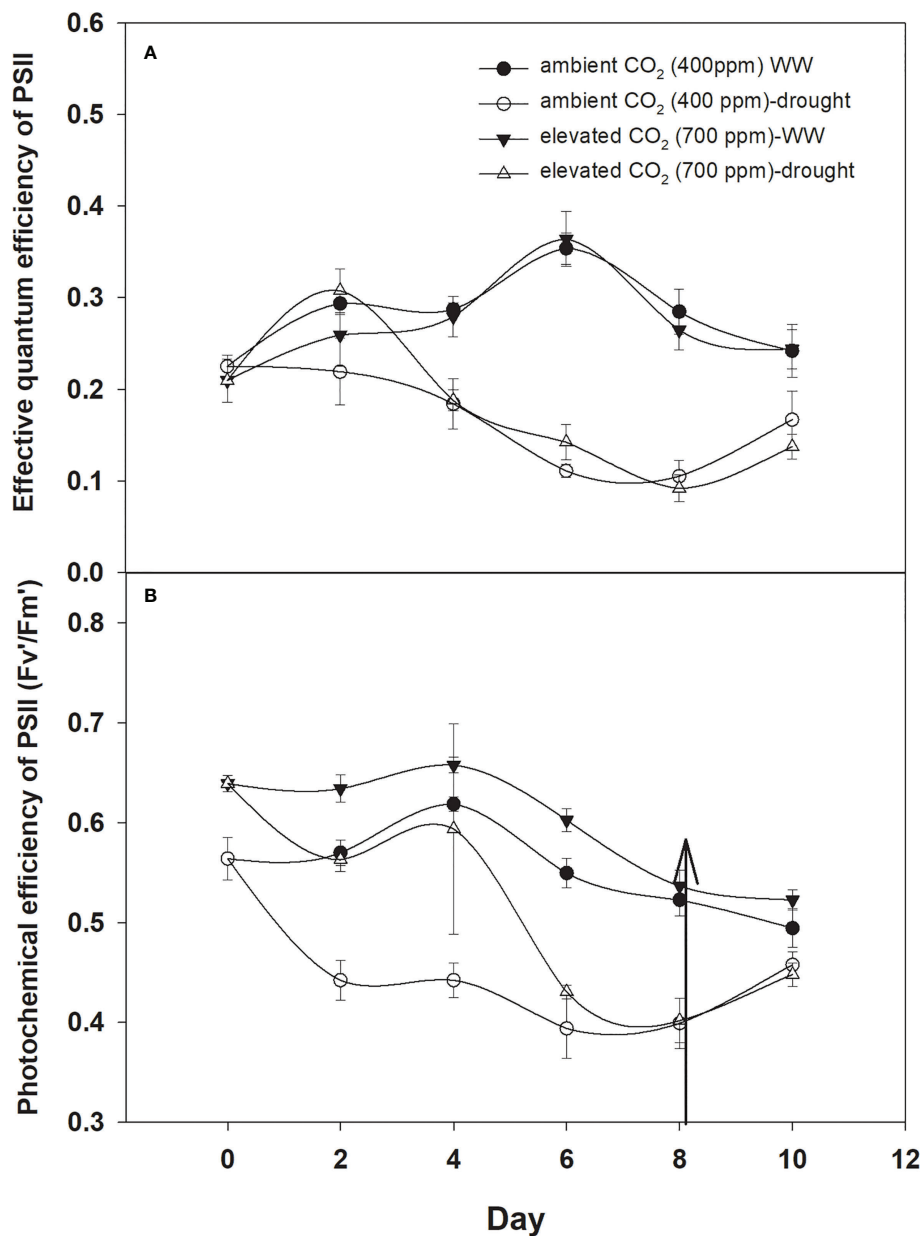


FIGURE 7 Effect of CO<sub>2</sub> concentrations and moisture conditions on (A) effective quantum efficiency of PSII and (B) photochemical efficiency of PSII of *Datura stramonium*. The vertical line on the data point represents the standard error of the mean and the vertical arrow line after Day 8 represents the addition of water in the drought treatments. WW, well-watered.

( $p < 0.001$ ) were non-significant for the effective quantum efficiency of PSII.

The photochemical efficiency of PSII was significantly higher with  $eCO_2$  compared to that with  $aCO_2$  (Figure 7B). Drought had significant effects on this parameter and effects were more pronounced on the photochemical efficiency of PSII under  $aCO_2$ , significantly decreasing with the initiation of drought and declining from 0.56 to 0.40 from drought Day 1 to Day 8. On the other hand, drought effects were slight on the photochemical efficiency of PSII until Day 4 of the drought, and after that, it declined to 0.40 at Day 8 of the drought duration. Water addition to drought treatment grown under both  $CO_2$  concentrations recovered the photochemical efficiency of PSII in the same way (Figure 7). Results of the ANOVA showed that time ( $p < 0.001$ ), water ( $p < 0.001$ ),  $CO_2$  ( $p < 0.001$ ), and time  $\times$  water ( $p = 0.001$ ) have significant effects on the photochemical efficiency of PSII (Table 1).

## Photochemical quenching

Photochemical quenching was higher with  $aCO_2$  compared to that with  $eCO_2$  when *D. stramonium* was grown under well-watered conditions (Figure 8). Drought stress significantly reduced photochemical quenching with an increase in drought duration, and this decline was in a similar way under both  $CO_2$  concentrations. The addition of water to drought treatments on Day 8 recovered photochemical quenching, with this recovery

being higher with  $aCO_2$ . The ANOVA results indicated that the effects of time ( $p < 0.001$ ), water ( $p < 0.001$ ), and time  $\times$  water ( $p < 0.001$ ) were significant for photochemical quenching of *D. stramonium* (Table 1).

## Discussion

Climate change has led to significant variation in rainfall patterns, and this, together with increased atmospheric  $CO_2$  concentrations, will increase wheat-crop competition for available resources (Ramesh et al., 2017; Bajwa et al., 2019; Chadha et al., 2020). This study revealed that atmospheric  $CO_2$  concentrations (400 ppm and 700 ppm) and limited water conditions had variable effects on gas exchange parameters, photosynthetic electron transport rate, and water use efficiency of *D. stramonium*. Drought conditions had negative effects on the photosynthesis rate of *D. stramonium*, but elevated  $CO_2$  concentrations mitigated the adverse effects of drought on the photosynthesis rate of *D. stramonium*. Moreover,  $eCO_2$  increased the photosynthetic rate under normal irrigation conditions. It is well documented that drought causes a range of responses in photosynthesis mechanisms, depending upon species and season (Alba et al., 2019; Dusenage et al., 2019). Ji et al. (2015) reported that  $eCO_2$  increased the leaf photosynthetic rate. In our study under well-watered conditions, the photosynthesis rate was increased by about 25% with  $eCO_2$  compared to that of ambient  $CO_2$  concentration. Similarly,  $eCO_2$

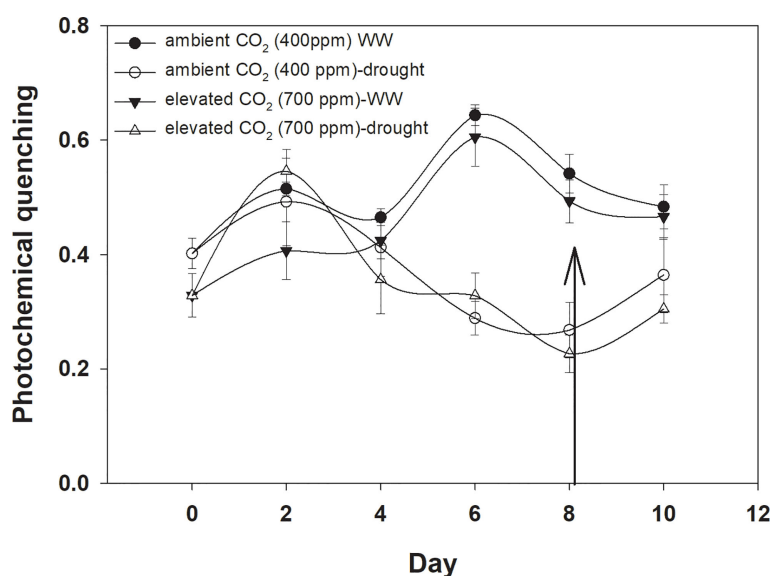


FIGURE 8

Effect of  $CO_2$  concentrations and moisture conditions on photochemical quenching of *Datura stramonium*. A nail on the data point represents the standard error of the mean and the vertical arrow line after Day 8 represents the addition of water in the drought treatments. WW, well-watered.

also mitigated the adverse effects of drought and increased the net photosynthesis rate by 12% under drought conditions, and the net photosynthesis rate was 50% higher with elevated CO<sub>2</sub> under severe drought conditions. Furthermore, it is generally believed that photosynthesis increases with eCO<sub>2</sub>, even under stressful environments (Ghahramani et al., 2019; De Kauwe et al., 2021). *D. stramonium* grown under eCO<sub>2</sub> exhibited lower stomatal conductance compared to that which was grown under aCO<sub>2</sub>. According to Habermann et al. (2019), plants grown under eCO<sub>2</sub> in drought conditions resulted in greater stomatal closure than those grown under aCO<sub>2</sub>. Stomatal conductance is considered to decrease both photosynthesis rate and CO<sub>2</sub> concentration in intercellular spaces of the leaf which inhibits metabolism (Cornic, 2000). However, the relative importance of stomatal conductance in restricting the supply of CO<sub>2</sub> to metabolism (stomatal limitation) and impairment, which decreases the potential rate, of photosynthesis rate is unclear. Moreover, metabolic limitation is often observed and correlates with loss of ATP, which stands to decrease with mild water loss (Lawlor, 2002). In our study, elevated CO<sub>2</sub> maintained stomatal functioning under water stress.

The study by Khalid et al. (2019) found that the stomatal conductors of *D. alba* decreased due to an increase in CO<sub>2</sub> concentration along roadsides. Our results showed a progressive decline in transpiration rate under both CO<sub>2</sub> concentrations, but this decline was significantly less with eCO<sub>2</sub>. The decline in transpiration rate might be due to stomatal closure, stimulated by a combination of eCO<sub>2</sub> and drought stress. A study by Walia et al. (2022) showed that elevated CO<sub>2</sub> decreased stomatal and transpiration rates by partial closure of stomata, resulting in increased water use efficiency and lower water stress in the plant. Robredo et al. (2007) found that plants grown under eCO<sub>2</sub> have more water use efficiency and developed water stress more slowly than those grown under ambient CO<sub>2</sub> concentration. Moreover, eCO<sub>2</sub> reduced the drought-induced damage in *D. stramonium*, with plant recovery being significant upon commencement of water and drought condition treatments. In previous work, it was noted that the degree of recovery depends upon species and drought duration (Duan et al., 2022). Robredo et al. (2007) also noted that barley plants were not able to recover stomatal closure upon re-watering after 16 days of drought stress. In our study, intercellular CO<sub>2</sub> concentration increased with an increase in CO<sub>2</sub> concentration, and also that drought stress has drastic effects on intercellular CO<sub>2</sub>, which increases with an increase in drought duration. Our findings are in line with those of Wang et al. (2018) and Dregulo (2022), who reported that stomatal closure and reduced transpiration rate were found under an enriched CO<sub>2</sub> environment. In another study, it was clearly shown that limitations on photosynthesis rate due to drought stress are based on the significant decrease in stomatal conductance and intercellular concentration (Salmon et al., 2020).

The water use efficiency of *D. stramonium* was 40% higher with eCO<sub>2</sub> compared to that with aCO<sub>2</sub> under well-watered

conditions, suggesting that eCO<sub>2</sub> mitigates the adverse effects of drought on the water use efficiency of *D. stramonium*. This might be due to the reduced transpiration rate as stomatal closure is seen under eCO<sub>2</sub>. Indeed, as is broadly understood from our results together with other research, water use efficiency enhancement is the result of reduced stomatal conductance and enhanced net photosynthesis rate under a CO<sub>2</sub>-enriched environmental context (Wei et al., 2022; Wu et al., 2022). Similar to water use efficiency, the intrinsic water use efficiency of *D. stramonium* shows similar trends under eCO<sub>2</sub> and drought conditions. Soil moisture conservation of many species has been reported when they are grown under elevated CO<sub>2</sub> concentrations. Our results are further supported by Hassan et al. (2022), who reported that eCO<sub>2</sub> reduced the impact of limited water conditions on the physiological traits of a number of plants. Drought conditions caused a reduction in instantaneous carboxylation efficiency with an increase in the duration of drought, but this decline was much lower with eCO<sub>2</sub> when compared to that of aCO<sub>2</sub>. Our findings are in line with those of Wang et al. (2015) and Pérez-López et al. (2013), who showed a significant decline in instantaneous carboxylation efficiency with eCO<sub>2</sub>. Under well-watered conditions, photosynthetic electron transport rate was higher with aCO<sub>2</sub>, whereas photosynthetic electron transport rate decreased with the length of drought duration. This suggests that a higher rate of electron transport occurs in drought-stress environments coupled with elevated CO<sub>2</sub> concentrations. These results are in line with the studies of the responses of Japanese white birch (*Betula platyphylla* var. *japonica*) to elevated carbon dioxide and drought, where photosynthetic electron transport rate was decreased by elevated CO<sub>2</sub> but was elevated under drought in ambient CO<sub>2</sub> conditions (Kitao et al., 2007). The minimum and maximum fluorescence values of *D. stramonium* grown in well-watered conditions were higher with eCO<sub>2</sub> compared to those with aCO<sub>2</sub>. The results are in line with those of Chadha et al. (2020) and Weller et al. (2021), who suggested that fluorescence increased with an increase in atmospheric CO<sub>2</sub>.

The effective quantum efficiency of PSII was decreased in *D. stramonium* under drought in both CO<sub>2</sub> treatments. However, elevated CO<sub>2</sub> slightly mitigated the adverse effects on the effective quantum efficiency of PSII. Such trends have been observed in previous studies (Perveen et al., 2010; Wang et al., 2018), where it was concluded that elevated CO<sub>2</sub> and drought decreased the effective quantum efficiency of PSII. However, the photochemical efficiency of PSII of *D. stramonium* was slightly increased with elevated CO<sub>2</sub>, indicating that a CO<sub>2</sub>-enriched environment reduces the risk of damage to PSII by abiotic stress. Similarly, Zhao et al. (2010) showed an increase in the photochemical efficiency of PSII in *Betula platyphylla* seedlings under 700 ppm CO<sub>2</sub>.

In conclusion, drought affects different physiological traits of *D. stramonium*. Nevertheless, eCO<sub>2</sub> generally increased the leaf gas exchange parameters, water use efficiency, and PSII activity of *D. stramonium*, by comparison with ambient CO<sub>2</sub>. This would

have contributed to maintaining a higher leaf water potential, so the improved water status of drought-treated plants at elevated CO<sub>2</sub>. As a result, plants exposed to high CO<sub>2</sub> increased their net photosynthesis rate, which, when coupled with reduced stomatal closure and transpiration rate, led to increased water use efficiency. It therefore appears that when *D. stramonium* grows under elevated CO<sub>2</sub> conditions, this mitigates or delays the effects of water stress. Therefore, under the anticipated changes in drought and rainfall patterns, this species may be found to be more competitive, thereby increasing its invasive range, which will result in its having a more serious agricultural impact in the future.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Author contributions

SF conceived and designed the study. MJ conducted the experiments. All authors were involved in writing and reviewing the manuscript. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

JM was employed by companies Twój Świat Jacek Mojski and Fundacja Zielona Infrastruktura.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2022.929378/full#supplementary-material>

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