The response of glyphosate-resistant and glyphosate-susceptible biotypes of *Echinochloa colona* to carbon dioxide, soil moisture and glyphosate

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Physiological and growth responses of two Australian *Echinochloa colona* biotypes (glyphosate-resistant and susceptible, produced from a single population) to different concentrations of carbon dioxide (CO2) (ambient ~450 ppm and elevated ~750 ppm) and soil moisture (well-watered and water-stressed) were analyzed. Elevated CO2 and well-watered conditions resulted in *E. colona* plants with greater biomass, height and numbers of tillers and leaves in both biotypes; however, no significant response was observed for seed production or the amount of photosynthesis pigments with increasing CO2 at both soil moisture levels. In addition, water availability was more influential for growth than CO2 concentration. The mean shoot biomass of the susceptible biotype under elevated CO2 and well-watered conditions was significantly greater than the resistant biotype. Although the susceptible biotype showed more vegetative and reproductive growth than the resistant biotype, no significant difference was observed for seed production between the biotypes in the water-stressed condition. In a second experiment, different doses of glyphosate (0, 180, 360, 720 and 1440 g a.e ha−1) were applied to both biotypes grown at two soil moisture levels (well-watered and water-stressed). In the water-stressed condition, glyphosate efficacy was decreased in both biotypes. The resistant biotype in the well-watered condition had only 19% survival at 1440 g ha−1 glyphosate (double the recommended rate), but this value increased in the water-stressed condition by 62%. Our study suggests that future climate change can affect the physiological and growth processes of weeds and their responses to herbicides. Knowledge of their adapting behaviors will be critical to weed management strategies.

Climate components such as radiation, temperature and precipitation have a direct impact on the agriculture industry. Therefore, climate change could affect plant biophysiological processes and productivity1. An increase in the emission of greenhouse gases (carbon dioxide-CO2, methane-CH4 and nitrous oxide-N2O), aerosols, temperature and evaporation, as well as a decrease in precipitation will be important factors of future climate change2. These factors will influence other variables, such as different stresses (drought, salinity, etc), changes in pests’ life cycles and soils quality3–6.

The current atmospheric CO2 concentration, recorded at Mauna Loa Observatory, Hawaii, is 411 ppm7. Some studies have quantified a difference of 80 ppm in the CO2 concentration between urban and suburban areas8,9. According to emission scenarios on climate change as reported by the Intergovernmental Panel on Climate Change (IPCC), CO2 concentrations are predicted to be in the range between 600 to 1000 ppm at the end of the 21st century10.

Increased levels of CO2 in C4 weeds have less beneficial photosynthetic effects compared with C3 weeds because they already have a pathway for inhibiting photorespiration11. Different studies assessed that under current temperature conditions, elevated CO2 can increase aboveground biomass and productivity of some weeds through greater carbon availability and increases in photosynthesis12,13. However, increases in temperature,

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Floods and drought can change the effect of elevated CO₂ because plants respond to all environmental factors and one factor can influence the other factors\(^1\). Some studies predicted a shift in the precipitation pattern and soil moisture deficiency\(^{15-20}\). For example, the amount of rainfall is expected to decrease in central Queensland, Australia, by 10–20% of the current rainfall by 2070\(^{16}\) and an average decrease of 2–5% is expected in all areas of Australia except the far north of Queensland by 2030\(^{21}\).

The change in the pattern of rainfall and temperature as a result of climate change can lead to the growth of C₄ and thermophile weeds\(^4,22\). Some grass weeds, such as Echinochloa spp., Setaria spp., Digitaria spp., and Sorghum halepense, have expanded their distribution range because of climate change over past decades\(^23\). E. colona is highly sensitive to water stress\(^24,25\). Early stomata closing and reductions in CO₂ assimilation and photosynthetic enzyme activities are the main responses of water deficit in plants\(^26\). Plants have different pigments for absorbing light at different wavelengths, allowing a greater efficiency in light absorption in the photosynthetic process\(^27\). The number of photosynthetic pigments may change with environmental factors\(^28-31\). The effect of drought, CO₂ concentration and temperature on different physiological processes in canola (Brassica napus) were studied and significant differences were reported between temperatures, CO₂ concentrations and soil moistures for photosynthetic pigments content\(^31\).

Weeds are always among the problematic components in cropping systems. Therefore, understanding of weeds’ responses to climate change is essential for developing weed management strategies. Climate change can induce transformations and shifts in the weed flora and consequently changes their distribution and traits.

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**Figure 1.** Effect of different CO₂ concentrations and soil moisture on the height of susceptible (S) and resistant (R) biotypes of Echinochloa colona. (A) first experimental run (B) second experimental run. High CO₂ and Low CO₂ denote 750 ppm and 450 ppm CO₂ concentration, respectively. 50% water represents water-stress treatment and 100% water represents well-water treatment. Modeled with the use of equation \( f = a/(1 + \exp(-(x - x_{50})/b)) \). In this equation \( f \) represents height at time \( x \), \( a \) is the maximum height at a given time, \( x_{50} \) is the time (days) required for 50% height and \( b \) indicates the slope. Estimated parameters are given in Table 1. Vertical bars represent the standard error of means (Experiment I).
making some of the opportunistic weeds invasive\textsuperscript{32}. Response to climate change may vary, depending on the weed, region, latitude or soil\textsuperscript{33}. Echinochloa colona (L.) Link is a C\textsubscript{4} annual summer grass native to Europe and India. It is a problematic weed in more than 60 countries and 35 crops\textsuperscript{34}. In Australia, it has become problematic in summer fallows and crops such as maize (Zea mays L.), rice (Oryza sativa L.), cotton (Gossypium hirsutum L.), sugarcane (Saccharum officinarum L.) and sorghum (Sorghum bicolor L.)\textsuperscript{35,36}. E. colona is an invasive weed with its vigorous growth traits and high seed production\textsuperscript{37}. Each E. colona plant is capable of producing up to 42,000 seeds. Seeds can germinate at different ranges of soil temperature and moisture conditions\textsuperscript{38}. The excessive use of glyphosate for high seed production\textsuperscript{37} makes some of the opportunistic weeds invasive\textsuperscript{32}. Response to climate change may vary, depending on the weed, region, latitude or soil\textsuperscript{33}.

### Materials and Methods

#### Seed collection and development of glyphosate-resistant and susceptible biotypes.

A suspected glyphosate-resistant biotype was collected from the research farm of the University of Queensland at Gatton, QLD, Australia (latitude 27.33°S, longitude 152.16°E and altitude 94 m.a.s.l.) in 2016. Resistance was confirmed in a screen-house study, in which plants were sprayed with different doses of glyphosate. Resistant and susceptible biotypes were developed through the cloning method as described by Mutti et al. (in press)\textsuperscript{42}.

#### Seedling preparation.

Two experiments with two experimental runs/repeat (details given below) were conducted: one in growth chambers and the other in the screen-house. Seeds of both resistant and susceptible biotypes of E. colona were planted in plastic trays filled with a commercial potting mix and placed in the screen-house at the Gatton Campus of the University of Queensland, Australia, during the winter and autumn seasons of 2018. After one week, 2-leaf seedlings were transplanted into 15-cm-diameter plastic pots that were filled with a soil mix (potting mix and field soil at 1:1). Only one plant per pot was maintained. The pots were well watered and kept for 2 weeks in the screen-house with average minimum and maximum temperatures of 13.3–15.7 °C and 35.0–35.7 °C, respectively, for the two experimental runs. Two soil moisture conditions were applied after the three-leaf stage through the weighing method\textsuperscript{45}. The 100% and 50% water holding capacity (WHC) were considered as well-watered and water-stressed conditions, respectively.

### Table 1. Effect of different CO\textsubscript{2} concentrations and soil moisture on the height of the glyphosate-resistant (R) and glyphosate-susceptible (S) biotypes of Echinochloa colona (Experiment I).

| Treatments                        | Parameters   | a          | b          | X\textsubscript{50} | R\textsuperscript{2} |
|-----------------------------------|--------------|------------|------------|---------------------|----------------------|
| R- 100% Water- High CO\textsubscript{2} | Model could not fit |
| S- 100% Water- High CO\textsubscript{2} | 63.5 ± 4.4  | 5.4 ± 3.3  | 17.5 ± 5.0  | 0.94                |
| S- 50% Water- Low CO\textsubscript{2} | 50.4 ± 0.3  | 0.5 ± 0.2  | 23.3 ± 4.8  | 0.99                |
| S- 100% Water- Low CO\textsubscript{2} | 54.6 ± 3.6  | 6.1 ± 2.9  | 18.6 ± 3.7  | 0.97                |
| R- 50% Water- High CO\textsubscript{2} | 61.8 ± 2.2  | 5.5 ± 1.8  | 19.3 ± 2.1  | 0.99                |
| R- 50% Water- Low CO\textsubscript{2} | 45.9 ± 0.6  | 0.4 ± 0.0  | 24.1 ± 0.0  | 0.99                |
| R- 100% Water- Low CO\textsubscript{2} | 62.0 ± 3.8  | 6.8 ± 2.6  | 20.1 ± 2.7  | 0.98                |

#### Experimental run 1

| Treatments                        | Parameters   | a          | b          | X\textsubscript{50} | R\textsuperscript{2} |
|-----------------------------------|--------------|------------|------------|---------------------|----------------------|
| S- 50% Water- High CO\textsubscript{2} | 45.4 ± 0.2  | 3.0 ± 0.9  | 17.2 ± 2.4  | 0.99                |
| S- 100% Water- High CO\textsubscript{2} | 65.2 ± 3.5  | 10.2 ± 6.7 | 23.0 ± 7.2  | 0.92                |
| S- 50% Water- Low CO\textsubscript{2} | 44.1 ± 0.4  | 2.4 ± 6.0  | 18.3 ± 6.4  | 0.99                |
| S- 100% Water- Low CO\textsubscript{2} | 53.1 ± 5.7  | 7.5 ± 4.2  | 19.7 ± 4.8  | 0.95                |
| R- 50% Water- High CO\textsubscript{2} | 45.9 ± 1.4  | 3.2 ± 2.9  | 15.7 ± 8.4  | 0.99                |
| R- 100% Water- High CO\textsubscript{2} | 65.2 ± 6.5  | 8.4 ± 3.6  | 23.2 ± 3.5  | 0.99                |
| R- 50% Water- Low CO\textsubscript{2} | 45.5 ± 0.7  | 3.6 ± 1.7  | 17.3 ± 3.6  | 0.99                |
| R- 100% Water- Low CO\textsubscript{2} | 62.4 ± 11.5 | 9.9 ± 6.1  | 22.9 ± 6.4  | 0.93                |

#### Experimental run 2

| Treatments                        | Parameters   | a          | b          | X\textsubscript{50} | R\textsuperscript{2} |
|-----------------------------------|--------------|------------|------------|---------------------|----------------------|
| S- 50% Water- High CO\textsubscript{2} | 52.6 ± 0.8  | 0.5 ± 0.0  | 21.6 ± 8.4  | 0.99                |
| S- 100% Water- High CO\textsubscript{2} | 63.5 ± 4.4  | 5.4 ± 3.3  | 17.5 ± 5.0  | 0.94                |
| S- 50% Water- Low CO\textsubscript{2} | 50.4 ± 0.3  | 0.5 ± 0.2  | 23.3 ± 4.8  | 0.99                |
| S- 100% Water- Low CO\textsubscript{2} | 54.6 ± 3.6  | 6.1 ± 2.9  | 18.6 ± 3.7  | 0.97                |
| R- 50% Water- High CO\textsubscript{2} | 61.8 ± 2.2  | 5.5 ± 1.8  | 19.3 ± 2.1  | 0.99                |
| R- 50% Water- Low CO\textsubscript{2} | 45.9 ± 0.6  | 0.4 ± 0.0  | 24.1 ± 0.0  | 0.99                |
| R- 100% Water- Low CO\textsubscript{2} | 62.0 ± 3.8  | 6.8 ± 2.6  | 20.1 ± 2.7  | 0.98                |

Effect of different CO\textsubscript{2} concentrations and soil moisture on the height of the glyphosate-resistant (R) and glyphosate-susceptible (S) biotypes of Echinochloa colona (Experiment I). High CO\textsubscript{2} and Low CO\textsubscript{2} denote 750 ppm and 450 ppm CO\textsubscript{2} concentration, respectively. 50% water represents water-stress treatment and 100% water represents well-water treatment.
Experiment I. CO₂ and soil moisture: A growth chamber study. The resistant and susceptible biotypes of *E. colona* were grown in pots placed in two growth chambers set at ambient CO₂ (450 ppm) and elevated CO₂ (750 ppm) under well-watered and water-stressed conditions. The temperature in both growth chambers was set at 30/20 °C (12 h light/12 h dark), optimum conditions for *E. colona*⁴². This experiment was conducted in a completely randomized design with six replications. Physiological and growth characteristics such as plant height, dry biomass, number of leaves, tillers and inflorescences per plant were measured at an interval of 10 days. Number of seeds per plant and photosynthetic pigments were measured at the end of the experiment.

Photosynthetic pigment content was measured with a portable meter and an extractable chlorophyll method⁴⁴. Two middle leaves of each plant were marked and the relative chlorophyll content was measured using a SPAD meter. At the end of the experiment, the same leaves were used for measuring the amount of chlorophyll *a*, *b* and carotenoids using the extractable method proposed by Hiscox and Israelstam⁴⁵. For each sample, around 0.05 g of fresh leaves were weighed and after adding 5 ml dimethylsulfoxide (DMSO), all samples were placed in a water bath at 65 °C for 45 minutes⁴⁵. The final solution of samples was measured with a spectrophotometer (Shimadzu, visible spectrophotometer, UV-2550) for detecting the amount of pigments using the wavelengths of 470, 645 and 663 nm for carotenoids, chlorophyll *b* and chlorophyll *a*, respectively⁴⁶. Chlorophyll content was estimated by measuring the correlation of the extractable method and the portable meter value⁴⁷.

Experiment II. Glyphosate efficacy and soil moisture: A screen-house study. Plants of both biotypes were grown in the screen-house at two soil moisture conditions: well-watered (irrigated daily) and water-stressed (irrigation stopped 2 weeks before glyphosate application). Plants were treated with different glyphosate doses (0, 180, 360, 720 and 1440 g a.e. ha⁻¹) at the 3–4 leaf stage with a Research Track Sprayer (using 108 L water solution/ha). Flat fan nozzles were used in the sprayer. After 24 hours of spraying, all plants were well watered daily. At 2 weeks after spraying, plant survival data were taken with the criterion of survival being at least one green leaf. Surviving plants were cut from the soil surface, placed in paper bags and dried in an oven at 70 °C for 48 h for measuring dry biomass. The experiment was conducted in a randomized complete block design with eight replications.

Figure 2. Effect of different CO₂ concentrations and soil moisture on the number of leaves per plant in susceptible (S) and resistant (R) biotypes of *Echinochloa colona* (A) first experimental run (B) second experimental run. High CO₂ and Low CO₂ denote 750 ppm and 450 ppm CO₂ concentration, respectively. 50% water represents water-stress treatment and 100% water represents well-water treatment. Modeled with the use of equation \( f = a \cdot \exp(b \cdot x) \). In this equation \( f \) represents the number of leaves per plant at time \( x \), \( a \) is a constant amount and \( b \) indicates the slope. Estimated parameters are given in Table 2. Vertical bars represent the standard error of means (Experiment I).
Statistical analyses. Both experiments were conducted twice (experimental runs). In the experiments, whenever no significant interaction was observed between experimental runs and treatments, data from both runs were pooled for analysis of variance (ANOVA). Results were reported separately when the interaction of experimental run × treatment was significant. SAS (version 9.0.3) was used for ANOVA. Data from both experiments met the assumptions of homogeneity of variance and normality, and did not need transformation.

In experiment I, a three-parameter sigmoidal model was fitted to the height data:

\[ f = a / (1 + \exp(- (x - x_{50})/b)) \]  

In this equation, \( f \) represents height at time \( x \), \( a \) is the maximum height at a given time, \( x_{50} \) is the time (days) required to attain 50% height of the maximum height and \( b \) indicates the slope.

Leaf, tiller, and inflorescence numbers per plant were modeled using a two-parameter exponential growth equation:

\[ f = a \times \exp(b \times x) \]  

In this equation, \( f \) represents the number of leaves, tillers or inflorescences at time \( x \), \( a \) is the intercept and \( b \) indicates the slope.

Results

Experiment 1. CO₂ and soil moisture: A growth chamber study. Plant height. Soil moisture and elevated CO₂ affected the plant height of both resistant and susceptible biotypes. Plants grown in the well-watered treatment were taller than those grown in the water-stressed treatment at both CO₂ concentrations (Fig. 1a,b). In the well-watered treatment, 55 days after planting, the height of the susceptible biotype at elevated CO₂ was increased by ~16% (means of experimental runs) compared to plants grown at ambient CO₂ but there was no significant increase in the resistant biotype. In the water-stressed treatment, no significant difference was observed between the height of the resistant and susceptible biotypes at both CO₂ concentrations. Compared with the well-watered treatment, the height of both resistant and susceptible plants was decreased by ~29% in the water-stressed treatment at elevated CO₂ (Fig. 1a,b). The maximum height was observed for the susceptible biotype in the well-watered treatment at elevated CO₂.

The comparison of the slope (\( b \) parameter) of the curves shows that in the water-stressed treatment, plant height was mostly constant from 25 days after planting to weed maturity and this was true at both CO₂ concentrations (Fig. 1a,b; Table 1).

Number of leaves per plant. At elevated CO₂, the number of leaves per plant in the well-watered treatment was significantly higher than in the water-stressed treatment at 55 days after planting; 55% and 58% greater for susceptible and resistant biotypes, respectively (Fig. 2a,b). In the water-stressed condition, the susceptible biotype at ambient and elevated CO₂ produced 7% and 28% greater number of leaves, respectively, than the resistant

| Treatments               | Parameters | \( a \)  | \( b \)  | \( R^2 \) |
|--------------------------|------------|---------|---------|---------|
| **Experiment 1**         |            |         |         |         |
| S- 50% Water- High CO₂   | 5.70 ± 2.40 | 0.02 ± 0.009 | 0.84    |
| S- 100% Water- High CO₂  | 4.70 ± 1.30 | 0.04 ± 0.005 | 0.98    |
| S- 50% Water- Low CO₂    | 3.82 ± 1.30 | 0.03 ± 0.007 | 0.92    |
| S- 100% Water- Low CO₂   | 2.57 ± 1.05 | 0.04 ± 0.008 | 0.96    |
| R- 50% Water- High CO₂   | 2.62 ± 1.11 | 0.03 ± 0.008 | 0.92    |
| R- 100% Water- High CO₂  | 3.55 ± 1.49 | 0.04 ± 0.008 | 0.95    |
| R- 50% Water- Low CO₂    | 2.03 ± 0.73 | 0.04 ± 0.007 | 0.96    |
| R- 100% Water- Low CO₂   | 3.29 ± 1.40 | 0.04 ± 0.009 | 0.92    |
| **Experiment 2**         |            |         |         |         |
| S- 50% Water- High CO₂   | 1.35 ± 0.39 | 0.06 ± 0.005 | 0.98    |
| S- 100% Water- High CO₂  | 2.17 ± 0.54 | 0.06 ± 0.004 | 0.99    |
| S- 50% Water- Low CO₂    | 1.65 ± 0.36 | 0.05 ± 0.004 | 0.99    |
| S- 100% Water- Low CO₂   | 1.98 ± 0.42 | 0.06 ± 0.004 | 0.99    |
| R- 50% Water- High CO₂   | 1.35 ± 0.39 | 0.05 ± 0.005 | 0.98    |
| R- 100% Water- High CO₂  | 1.48 ± 0.34 | 0.07 ± 0.004 | 0.99    |
| R- 50% Water- Low CO₂    | 1.43 ± 0.26 | 0.05 ± 0.003 | 0.99    |
| R- 100% Water- Low CO₂   | 2.37 ± 0.71 | 0.05 ± 0.005 | 0.98    |

Table 2. Effect of different CO₂ concentrations and soil moisture on the number of leaves per plant in the glyphosate-resistant (R) and glyphosate-susceptible (S) biotypes of Echinochloa colona (Experiment I). High CO₂ and Low CO₂ denote 750 ppm and 450 ppm CO₂ concentration, respectively. 50% water represents water-stress treatment and 100% water represents well-water treatment.
The comparison of the slope (b parameter) shows that the increase in the number of leaves in the well-watered treatment was faster than in the water-stressed treatment (Table 2).

**Number of tillers per plant.** Regardless of moisture condition, elevated CO₂ increased the number of tillers in both biotypes; however, this increase was more obvious in the well-watered treatment than in the water-stressed treatment (Fig. 3a,b, Table 3). At elevated CO₂, the susceptible biotype produced 23% more tillers than the resistant biotype in the well-watered treatment (Fig. 3a,b).

**Number of inflorescences per plant.** In both biotypes, the increase in soil moisture and CO₂ resulted in a significant increase in the number of inflorescences per plant; however, the comparison of the slope (b parameter) of the curves shows that water availability had a more pronounced effect on the number of inflorescences per plant (Table 4). The susceptible biotype produced more inflorescence numbers than the resistant biotype at both CO₂ concentrations in the well-watered condition (Fig. 4a,b). At both CO₂ concentrations, the lowest number of inflorescences was observed in the resistant biotype under water-stressed conditions (Fig. 4a,b).

**Number of seeds per plant.** In the well-watered treatment, the susceptible biotype produced more seeds than the resistant one under both CO₂ concentrations (Table 5). However, no significant difference was observed between their seed production in the water-stressed condition. The decrease in water availability (by 50%) led to a decrease in seed production in the resistant and susceptible biotypes by 67% and 88% at 450 ppm and 45% and 72% at 750 ppm CO₂, respectively. Increasing the CO₂ concentration did not significantly change the number of seeds per plant in both biotypes.

Figure 3. Effect of different CO₂ concentrations and soil moisture on the number of tillers per plant of susceptible (S) and resistant (R) biotype of *Echinohcloa colonia*. (A) first experimental run (B) second experimental run. High CO₂ and Low CO₂ denote 750 ppm and 450 ppm CO₂ concentration, respectively. 50% water represents water-stress treatment and 100% water represents well-water treatment. Modeled with the use of equation \( f = a \exp(b \cdot x) \). In this equation, \( f \) represents the number of tillers per plant at time \( x \), \( a \) is a constant amount and \( b \) indicates the slope. Estimated parameters are given in Table 3. Vertical bars represent the standard error of means (Experiment I).
Total dry shoot biomass. An increase in water availability and CO₂ concentration resulted in an increase in shoot biomass of both biotypes but the effect of water availability was more than CO₂ concentration (Table 6). The highest amount of shoot biomass was observed for the susceptible biotype in the well-watered treatment under elevated CO₂ and the lowest biomass was observed in the water-stressed treatment under ambient CO₂ concentration in the susceptible biotype. In the well-watered condition, the biomass of the resistant and susceptible biotypes increased by 12% and 47%, respectively, at elevated CO₂ compared with the ambient CO₂ concentration. Water stress reduced the biomass of the resistant and susceptible biotypes by 73% and 77%, respectively.
at elevated CO₂. Under ambient CO₂, water stress decreased the total dry biomass of the resistant and susceptible biotypes by 70% and 64%, respectively. The response of the susceptible biotypes was more evident compared with the resistant biotypes in both soil moisture levels and CO₂ concentrations.

**Photosynthetic pigments.** In both experimental runs, significant differences were found between soil moisture treatments for the content of photosynthetic pigments, while no significant differences were observed between CO₂ concentrations (Table 7). The well-watered condition significantly increased the amount of total chlorophyll by 23% and 25% in the resistant and susceptible biotypes, respectively, in the ambient CO₂ condition.
Experiment II. Glyphosate efficacy and soil moisture: A screen-house study. Biomass data showed that glyphosate efficacy was significantly decreased in the water-stressed condition at all glyphosate doses (Table 8). The resistant biotype in the well-watered treatment had 19% survival at 1440 g ha\(^{-1}\) glyphosate (twice of the recommended dose), but this survival degree increased in the water-stressed treatment by 62% (Table 8). For the susceptible biotype, plant biomass decreased by 62% and 92% at 720 and 1440 g ha\(^{-1}\) glyphosate, respectively, in the water-stressed condition, while at the same herbicide doses, no plant survived in the well-water condition (Table 9).

**Table 6.** Effect of carbon dioxide (CO\(_2\)) concentrations and soil moisture on dry biomass of the glyphosate-resistant and glyphosate-susceptible biotypes of *Echinochloa colona* (Experiment I).

| CO\(_2\) concentration | Well water | Water stress |
|------------------------|------------|--------------|
|                        | Susceptible | Resistant    | Susceptible | Resistant    |
| Experimental run 1     |             |              |             |              |
| 450 ppm                | 1.09        | 1.56         | 0.47        | 0.51         |
| 750 ppm                | 2.71        | 1.93         | 0.61        | 0.52         |
| LSD (0.05%) = 0.48     |             |              |             |              |
| Experimental run 2     |             |              |             |              |
| 450 ppm                | 2.93        | 3.58         | 0.81        | 0.95         |
| 750 ppm                | 4.45        | 3.77         | 1.07        | 1.01         |
| LSD (0.05%) = 0.67     |             |              |             |              |

**Table 7.** Content of photosynthetic pigment of the glyphosate-resistant and glyphosate-susceptible biotypes of *Echinochloa colona* grown at different carbon dioxide (CO\(_2\)) concentrations and soil moisture in growth chambers (Experiment I).

| Photosynthetic pigments content (mg g\(^{-1}\) dry weight) | Well water | Water stress |
|-----------------------------------------------------------|------------|--------------|
|                                                           | Susceptible | Resistant    | Susceptible | Resistant    |
|                                                           |             |              |             |              |
| Carotenoids                                               |             |              |             |              |
| 450 ppm                                                   | 1.77        | 1.77         | 1.44        | 1.43         |
| 750 ppm                                                   | 1.81        | 1.79         | 1.47        | 1.44         |
| LSD (0.05%) = 0.07                                        |             |              |             |              |
| Chlorophyll a                                             |             |              |             |              |
| 450 ppm                                                   | 30.55       | 30.53        | 24.94       | 24.69        |
| 750 ppm                                                   | 31.34       | 30.88        | 25.36       | 24.86        |
| LSD (0.01%) = 1.30                                       |             |              |             |              |
| Chlorophyll b                                             |             |              |             |              |
| 450 ppm                                                   | 6.76        | 6.76         | 5.21        | 5.14         |
| 750 ppm                                                   | 6.96        | 6.86         | 5.33        | 5.19         |
| LSD (0.05%) = 0.36                                       |             |              |             |              |
| Chlorophyll total                                         |             |              |             |              |
| 450 ppm                                                   | 37.32       | 37.3         | 30.16       | 29.84        |
| 750 ppm                                                   | 38.2        | 37.75        | 30.7        | 30.06        |
| LSD (0.05%) = 1.66                                       |             |              |             |              |
| Experimental run 2                                         |             |              |             |              |
| Carotenoids                                               |             |              |             |              |
| 450 ppm                                                   | 2.42        | 2.39         | 1.71        | 1.8          |
| 750 ppm                                                   | 2.41        | 2.46         | 1.71        | 1.8          |
| LSD (0.05%) = 0.19                                       |             |              |             |              |
| Chlorophyll a                                             |             |              |             |              |
| 450 ppm                                                   | 41.87       | 41.35        | 29.49       | 31.09        |
| 750 ppm                                                   | 41.69       | 42.54        | 29.6        | 31.03        |
| LSD (0.01%) = 3.32                                       |             |              |             |              |
| Chlorophyll b                                             |             |              |             |              |
| 450 ppm                                                   | 9.9         | 9.76         | 6.47        | 6.9          |
| 750 ppm                                                   | 9.85        | 10.09        | 6.5         | 6.9          |
| LSD (0.05%) = 0.92                                       |             |              |             |              |
| Chlorophyll total                                         |             |              |             |              |
| 450 ppm                                                   | 51.78       | 51.11        | 35.97       | 38.01        |
| 750 ppm                                                   | 51.55       | 52.63        | 36.11       | 37.93        |
| LSD (0.05%) = 4.25                                       |             |              |             |              |

**Experiment II. Glyphosate efficacy and soil moisture: A screen-house study.** Biomass data showed that glyphosate efficacy was significantly decreased in the water-stressed condition at all glyphosate doses (Table 8). The resistant biotype in the well-watered treatment had 19% survival at 1440 g ha\(^{-1}\) glyphosate (twice of the recommended dose), but this survival degree increased in the water-stressed treatment by 62% (Table 8). For the susceptible biotype, plant biomass decreased by 62% and 92% at 720 and 1440 g ha\(^{-1}\) glyphosate, respectively, in the water-stressed condition, while at the same herbicide doses, no plant survived in the well-water condition (Table 9).

**Discussion** Elevated CO\(_2\) resulted in taller plants of both susceptible and resistant *E. colona* biotypes with more tillers, leaves, and biomass, but seed production was not affected by the increased CO\(_2\) concentration. Generally, elevated CO\(_2\), when considered alone, leads to increased numbers of leaves and inflorescences, height and total biomass, which could be attributed to increased photosynthesis and water use efficiency and decreased transpiration through
increasing under rising CO₂ and temperature. Plants in water stress conditions cannot properly use high CO₂ concentrations, but it should not be assumed that C₄ plants do not have the ability to use high CO₂ amounts.

Increase in the growth potential of C₄ plants by elevated CO₂ depends on the decrease in water use and reduction of stomatal conductance. While some studies reported an increase in seed production by elevated CO₂, our study found no significant difference. In C₄ species, because of their ability to concentrate CO₂ via their photosynthesis pathway, increasing the external CO₂ concentration has little effect on net photosynthesis, but it should not be assumed that C₄ plants do not have the ability to use high CO₂ amounts.

Water deficit is one of the most concerning issues surrounding climate change and may interfere with plant growth and development. The current study observed that water deficit resulted in the reduction of growth parameters and consequently seed production, especially for the susceptible biotype. Other studies also considered the importance of water deficiency on weed growth. The amount of photosynthetic pigments was significantly decreased by the reduction in water availability. Water stress can affect the synthesis of chlorophyll, the electron transport chain and consequently seed production, especially for the susceptible biotype. Other studies also considered the importance of water deficiency on weed growth. The amount of photosynthetic pigments was significantly decreased by the reduction in water availability. Water stress can affect the synthesis of chlorophyll, the electron transport chain and consequently seed production, especially for the susceptible biotype.

The interaction effect of soil moisture and CO₂ concentration significantly influenced all measured growth parameters and seed production. The effect of elevated CO₂ in increasing plant growth is likely to happen at the optimum temperature for growth and sufficient water availability. In the current study, the effect of soil moisture and CO₂ concentration was examined at the optimum temperature for Echinochloa colona. Water availability was found to affect weed growth more than CO₂ concentration. Elevated CO₂ can be helpful for the vegetative growth of plants but cannot compensate for the adverse effect of water stress on them. Leakey et al. suggested that the increase in the growth potential of C₄ plants by elevated CO₂ depends on the decrease in water use and reduction in drought stress, and not by the direct effect of increased photosynthesis. The water requirement of weeds will increase under rising CO₂ and temperature. Plants in water stress conditions cannot properly use high CO₂ concentration as much as those that are well watered, due to the lower stomatal conductance caused by less guard cell turgescence. Therefore, CO₂ uptake will decrease in these plants. The difference in seed production between the resistant and susceptible biotypes was not significant in the water-stressed condition at both CO₂ concentrations. In the water-stressed condition, increasing CO₂ concentration via decreasing stomatal conductance and increasing water use efficiency may allow plants to produce more seeds, but total biomass may always be lower compared with plants grown in well-watered conditions.

In both biotypes, growth and seed production were enhanced by increasing CO₂ concentration and water availability. In the well-watered treatment, the stimulation of photosynthesis from increased CO₂ concentration in our study was more evident in the susceptible than in the resistant biotype. Despite higher vegetative growth of the susceptible biotype, no difference was observed in seed production between biotypes in the water-stressed treatment. It can be concluded that the resistant biotype allocated more photosynthetic resources to seed production compared with vegetative growth in the stressed condition. Potvin (1986) mentioned a strategy of investing more resources into inflorescence development (versus leaves) in E. crus-galli plants due to the importance and

| Dose (g a.e. ha⁻¹) | Dry biomass (g plant⁻¹) | Well-water | Water-stress |
|-------------------|-------------------------|------------|--------------|
|                   | Susceptible | Resistant  | Susceptible | Resistant  |
| control           | 100.0       | 100.0      | 100.0       | 100.0      |
| 180               | 93.8        | 100.0      | 93.8        | 100.0      |
| 360               | 93.8        | 93.8       | 93.8        | 100.0      |
| 720               | 0           | 75.0       | 87.5        | 100.0      |
| 1440              | 0           | 18.8       | 25.0        | 81.2       |

LSD (0.05) = 16.43

Table 8. The effect of different doses of glyphosate and soil moisture on plant survival of the glyphosate-resistant and glyphosate-susceptible biotypes of Echinochloa colona (Experiment II). Well-water represents daily irrigation, in water-stress irrigation stopped 2 weeks before glyphosate application.

| Dose (g a.e. ha⁻¹) | Dry biomass (g plant⁻¹) | Well-water | Water-stress |
|-------------------|-------------------------|------------|--------------|
|                   | Susceptible | Resistant  | Susceptible | Resistant  |
| 0                 | 0.47        | 0.40       | 0.32        | 0.30       |
| 180               | 0.24 (48%)  | 0.32 (24%) | 0.16 (50%)  | 0.29 (5%)  |
| 360               | 0.17 (63%)  | 0.19 (54%) | 0.13 (58%)  | 0.20 (35%) |
| 720               | 0 (100%)    | 0.11 (71%) | 0.12 (62%)  | 0.14 (52%) |
| 1440              | 0 (100%)    | 0.030 (93%)| 0.02 (92%)  | 0.06 (80%) |

LSD = 0.09

Table 9. The effect of different doses of glyphosate and soil moisture on total biomass of the glyphosate-resistant and glyphosate-susceptible biotypes of Echinochloa colona (Experiment II). The reduction (%) was presented in parenthesis. Well-water represents daily irrigation, in water-stress irrigation stopped 2 weeks before glyphosate application.
critical role of seed production in population dynamics61. The link between plant size and evolutionary fitness is the ability of plants to allocate resources to reproduction.

In Experiment II, reducing soil moisture content resulted in a decrease in the efficacy of glyphosate. This response could be caused by less absorption and translocation of glyphosate as the herbicide is mainly translocated by vascular transportation62. Tanpipat et al. also claimed that water stress via reducing leaf area can affect glyphosate uptake63. The requirement of high doses of glyphosate in the water-stressed condition may be related to the increase in the concentration gradient across the cuticle, consequently leading to more glyphosate uptake63. Using high glyphosate rates in water stress conditions may cause a high risk of producing resistant biotypes.

It is predicted that climate change will have a significant impact on weed management strategies in the future64. The latest studies on climate change in regards to weeds suggest that focusing on drought-resistant weed biotypes seems to be a more logical resolution than other biotypes. Understanding weed fitness could help to predict the dynamics of herbicide-resistant weeds and their management65. Species that showed adaptation to drought conditions were less adversely affected by climate change and were able to compete better in dry soil rather than species which adapted to wet soil moisture conditions65. In addition, the current study observed that herbicide efficacy was reduced by decreasing water availability. Therefore, more studies on herbicide efficacy in climate change conditions should be considered.

Conclusions

Environmental changes can affect the physiological and growth processes of weeds and their responses to herbicides. E. colona biotypes used in this study showed greater vegetative growth in response to elevated CO2. In both biotypes, seed production and photosynthesis pigments were not affected by the increased CO2 concentration. However, the water-stress condition caused a significant decrease in growth parameters, seed production and glyphosate efficacy in both biotypes. The results of this study suggest that the predicted climate change can make this weed more noxious and competitiveness. It is possible that increased vegetative growth of weeds combined with water deficiency caused by climate change reduces the herbicide uptake and translocation and consequently, decrease herbicide efficacy. More studies based on different climate change factors need to be conducted to elucidate the role of environmental parameters and nutrition on opportunistic weeds’ responses. A better understanding of how weeds respond to climate change based on known tolerance ranges and climatic selection pressures is suggested for developing effective weed management strategies.

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**Competing interests**

The authors declare no competing interests.

**Additional information**

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