Biological Control 139 (2019) 104077

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Biological control under a changing climate: The efficacy of the parthenium weed stem-galling moth under an atmosphere enriched with CO_2

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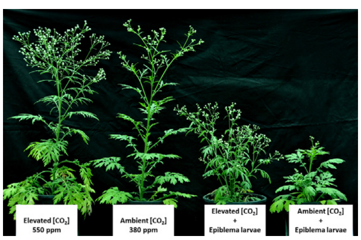
GRAPHICAL ABSTRACT

Parthenium weed plants grown under two atmospheric CO_2 concentrations, with and without the biological control agent *Epiblema strenuana*.



ARTICLE INFO

Keywords:
CO_2 enrichment
Biological weed control
Epiblema strenuana
Parthenium hysterophorus
Ecophysiology

ABSTRACT

Parthenium hysterophorus (Parthenium weed) is a highly invasive species that has become a major weed in Australia and many other parts of the world. The present study reports on the effect of atmospheric CO_2 enrichment upon the performance and effectiveness of one of its biological control agents, *Epiblema strenuana* (stem-galling moth). Parthenium weed plants, when grown under an elevated CO_2 concentration (550 µmol mol^{-1}), produced a significantly greater dry biomass (38%), produced more branches (35%) and seeds per plant (37%), than plants grown under an ambient CO_2 concentration (380 µmol mol^{-1}). Galls produced by *E. strenuana* significantly reduced the height (46%) and dry biomass (45%) of parthenium weed under the elevated CO_2 concentration. In the presence of *E. strenuana*, the total number of cypselae produced by plants was 60 or 32% less at ambient or elevated CO_2 concentrations, respectively. X-ray revealed that *E. strenuana* had a significant negative impact upon cypsela fill under elevated CO_2 concentration with about 50% not being filled. Gall induction by *E. strenuana* stimulated lateral branching and this was observed in plants grown both under elevated and ambient CO_2 concentrations. Under elevated CO_2 and in the presence of *E. strenuana*, net photosynthesis and water use efficiency were decreased by 25 and 28%, respectively. Despite parthenium weed producing more biomass and seed, this study indicates that the efficacy of *E. strenuana* as a biological control agent of parthenium weed is likely to be retained in a future climate with an elevated CO_2 concentration.

1. Introduction

Global atmospheric carbon dioxide concentrations [CO_2] have increased rapidly since pre-industrial times with this increase mainly being attributed to human activity. The current [CO_2] (410 ppm) is about 35% higher than the pre-industrial era (280 ppm) and under the

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https://doi.org/10.1016/j.biocontrol.2019.104077
Received 7 April 2019; Received in revised form 9 August 2019; Accepted 20 August 2019
Available online 21 August 2019
1049-9644/

'no mitigation' scenario, is expected to reach 600 or 1000 ppm by the end of this Century (IPCC, 2014). As a consequence of [CO_2] increase, the average global temperature is increasing, sea levels are rising and rainfall patterns are changing across many regions (IPCC, 2007). The changing atmospheric [CO_2] may be expected to affect the biology and ecology of certain organisms. For example, increased [CO_2] has a direct impact upon plant photosynthesis and other aspects of metabolism (Bowes et al., 1996; Sage et al., 1995). The different growth responses of C_3 and C_4 plant species to elevated [CO_2] (Ziska et al., 1990) will have implications for the future spread and distribution of invasive alien plant species across a range of environments (Ziska, 2003; Ziska and Dukes, 2011).

Parthenium hysterophorus L. (Asteraceae) commonly known as parthenium weed, is a highly invasive plant known to reduce crop and pasture productivity, native plant biodiversity and adversely affect human and animal health (Adkins and Shabbir, 2014). This weed has invaded more than 50 countries worldwide (Shabbir et al., 2019) and it threatens to invade more areas under current and future climates (McConnachie et al., 2011; Kriticos et al., 2015). Being either a C_3 (Navie et al., 2005) or a C_3/C_4 intermediate species (Moore et al., 1987), parthenium weed is able to harness significant growth advantages from elevated [CO_2] (Navie et al., 2005; Nguyen et al., 2017; Khan et al., 2018).

Biological control plays an important role in the strategy for the integrated management of parthenium weed in Australia and to date, two rust and nine insect species have been released (Dhileepan and McFadyen, 2012). Some of the 11 agents are well established and considered as effective against parthenium weed (Shabbir et al., 2013, 2018). *Epiblema strenuana* Walker (Tortricidae: Lepidoptera), a stem galling moth, is one of the more damaging and effective biological control agents released to-date to control parthenium weed in Australia (McFadyen, 1992; Dhileepan, 2003). This insect has dispersed widely throughout the current invaded range of weed. The moth is active throughout the summer season in northern and central Queensland where parthenium weed has invaded significant areas. It can complete its life cycle within 4–6 weeks, with an average of 6–7 generations per year (McFadyen, 1987). Galls produced by the moth significantly affect the vegetative and reproductive growth of parthenium weed, with enhanced impact observed for young plants (Dhileepan and McFadyen, 2001; Dhileepan, 2003).

Elevated atmospheric [CO_2] does not often directly affect insect behaviour but may act indirectly by changing the quality of the plant tissue on which the herbivorous insects feed (Johnson and Lincoln, 1991; Lincoln et al., 1984; Stiling and Cornelissen, 2007 but see Akbar et al., 2015). Certain plants when grown under elevated [CO_2] environments produce nitrogen-deficient foliage, with an increased carbon to nitrogen ratio (Johnson and Lincoln, 1991; Taub et al., 2008). The reduced foliar N content results in reductions in its nutritional quality which may intern result in increased consumption of the plant tissues (Whittaker, 1999; Hunter, 2001). Further, in elevated [CO_2] atmospheres, some insects may encounter host plants with reduced defences (Coviella and Trumble, 1998; Zavala et al., 2008).

The life cycle, biology and performance of weed biological control agents is also expected to be affected by enriched atmospheric [CO_2] enrichment (Thomson et al., 2010). For example, the winter rust (*Puccinia abrupta* var. partheniicola Jackson parmelee), a classical biological control agent released against parthenium weed in Australia, reduced the weed biomass 13% more under elevated compared to ambient [CO_2] (Shabbir et al., 2014). Although there is limited information available for the responses of insect biological control agents of weeds to [CO_2] enrichment (Shabbir et al., 2014; Stange, 1997), it is expected that such responses may be species-specific and depend on individual insect-plant systems.

In this study, we explored the efficacy of *E. strenuana* on parthenium weed under enriched [CO_2] (550 μmol mol^{-1}). We hypothesized that the performance of *E. strenuana* would be enhanced under elevated [CO_2]. It was further hypothesized that under elevated [CO_2], the growth and reproductive capacity of parthenium weed would also be enhanced through increased rates of photosynthesis and enhanced physiology.

2. Materials and methods

2.1. The plant growth facility

Two identical temperature-controlled growth chambers (200 × 180 × 100 cm; w × l × h; Kirby Ltd., Sydney, New South Wales), were placed into two separate glasshouses with natural light supply (*ca.* 900 μmol m^{-2} s^{-1}; 9 to 10 h day^{-1}) for the duration of the experiment. The chamber effect was likely to be small as both chambers were comparably constructed and the experiment was repeated in opposing chambers. The temperature inside each chamber was set to 30/15 ± 2 °C (day/night) with a relative humidity of *ca.* 70 ± 5%.

To study the effects of enriched [CO_2], the gaseous atmosphere inside one of the growth chambers was controlled. To regulate the gaseous flow inside the chamber, a solenoid valve switch was connected between a CO_2 monitor (ADC 2000, ANRI Instruments and Controls, Victoria) and a G size gas cylinder filled with food grade CO_2 (Shabbir et al., 2014). This set-up allowed the maintenance of a constant concentration of 550 ± 10 μmol mol^{-1} inside one of the growth chambers. The other growth chamber was maintained at an ambient [CO_2] (380 μmol mol^{-1}) by circulating fresh air through it and measuring the [CO_2] with another ADC monitor.

2.2. Preparation of plant and insect cultures

Parthenium weed seeds were collected from Injune, central Queensland and stored in a cold room (4 °C) for 6 months before the commencement of this study. Seed was sown into plastic trays (30 × 30 × 6 cm) filled with a commercial potting material (UC mix) and then incubated in a glasshouse at 30/20 ± 2 °C (day/night) for a week until maximum seed germination had been achieved. Seedlings of uniform size were then selected and transplanted individually into 32 plastic pots (8 L, 25 cm diameter) filled with a commercial potting mix and watered. Half of the pots were randomly distributed into one growth chamber (380 μmol mol^{-1}) while the remainder were placed into the other (550 μmol mol^{-1}). The developing plants were watered daily using a hand-held sprinkler. The location of each pot within the chamber was randomized every 14 days to minimize any location effects.

Stem galls produced by *E. strenuana*, were collected from parthenium weed or ragweed (*Ambrosia artimissifolia* L.) plants growing in Kilcoy, South east Queensland or Fig Tree Pocket, Brisbane. The galls were cut from the plants, placed into plastic bags and transported back to the laboratory. They were then transferred to plastic trays lined with moistened paper towel and kept for 2 days before the larvae (2nd instar) were isolated and used in the experiments. Some of the galls were viewed with an X-ray machine (Model: Faxitron MX-20 Radiography System) to confirm the presence of suitable second-instar larvae (Fig. 1).

2.3. Experimental measurements design and statistical analysis

When the parthenium weed plants to be inoculated with stem-galling moth were 6-weeks old, larvae (2nd instar) were removed from their galls with the aid of a scalpel blade and placed with a fine paint brush into the middle of the parthenium weed rosettes. This took place in a random manner for half of the pots (eight) in each chamber, at a rate of two larvae per plant. Following the application, all larvae were observed to enter the plant rosette growing tips. An insect net was used to regularly remove any newly-emerged adult moths from the cages to prevent them from laying any eggs on the plants.

Fig. 1. An X-ray image of two stem galls collected from field growing ragweed plants showing the presence (upper, coloured) and the absence (lower, empty) of *Epiblema strenuana* larvae.

When plants were about 8–9 weeks old, leaf gas exchange was measured for each treatment using a portable gas exchange system (Li-6400, Li-Cor, Lincoln, NE, USA). The net photosynthetic rate (P_n), transpiration rate (T_r) and stomatal conductance (g_s) were measured on one recently expanded leaf (three per treatment) in the day time (between 10:00 am to 1:00 pm) to capture the peak photosynthetic rate over a period of one week. Photosynthetic responses to intercellular CO_2 concentration (C_i) was measured and a P_n-C_i curve developed using a series of [CO_2] (*viz.* 50 to 1,200 μmol mol^{-1}) at 28 °C with a constant light intensity (1,500 μmol m^{-2} s^{-1}) produced by a red/blue LED source mounted to top of the leaf chamber.

After 120 days of growth in the chambers, the inflow of CO_2 was stopped and remaining mature cypselae (dry, single-seeded fruits) from each plant were collected. The cypselae were placed into separate brown paper bags and transferred to a laboratory where they were examined with an X-ray machine (Model: Faxitron MX-20 Radiography

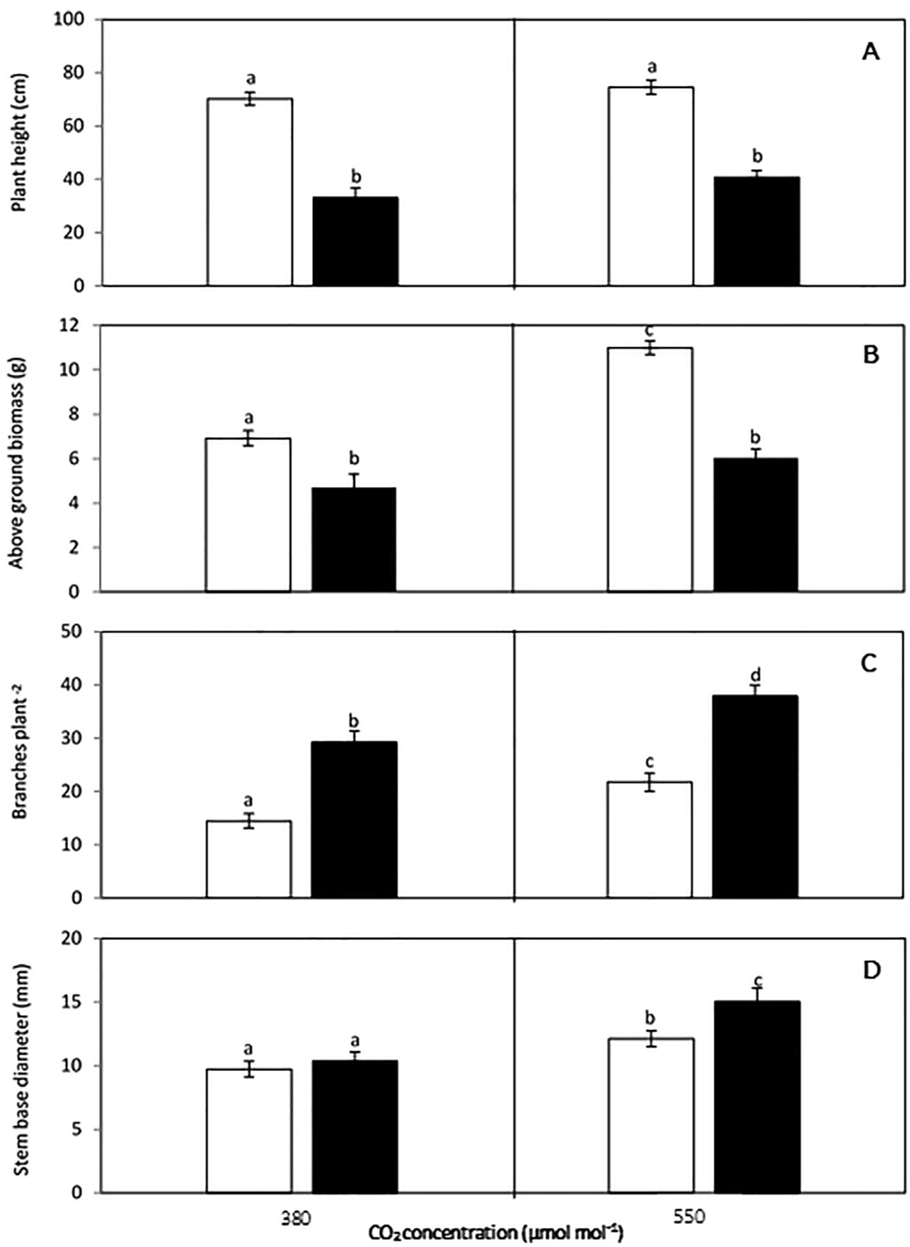

Fig. 2. The effect of elevated [CO_2] and *Epiblema strenuana* larvae (no moth larvae □; with moth larvae ■) on (A) plant height, (B) dry biomass, (C) branches per plant and (D) stem base diameter of parthenium weed. Each bar is the mean ± SE taken from eight replicated pots. Different letters above the bars indicate values that are statistically different ($p < 0.05$).

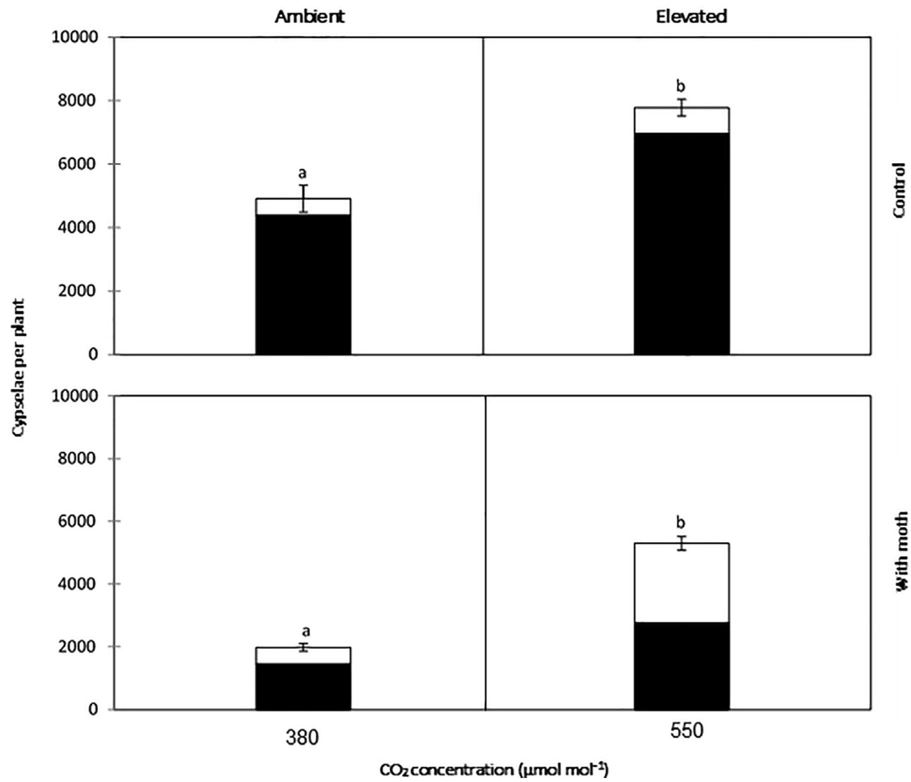

Fig. 3. The effect of elevated [CO_2] and *Epiblema strenuana* on filled (■) and unfilled (□) seed production of parthenium weed. Each bar is the mean ± SE taken from eight replicated pots; different letters above the bars indicate values that are statistically different (p < 0.05).

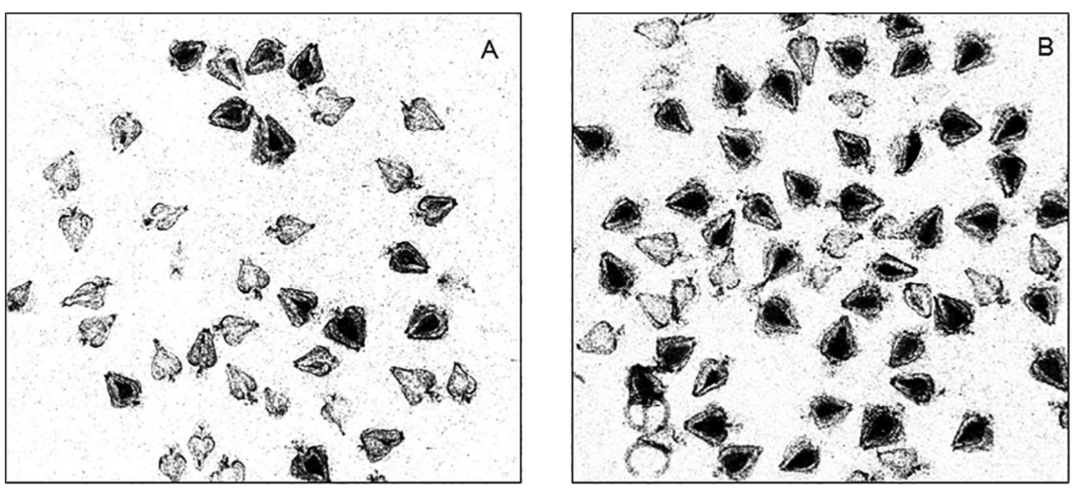

Fig. 4. Cypsela fill in parthenium weed plants grown under an elevated [CO_2] both in the presence (A) and absence (B) of *Epiblema strenuana* larvae. Cypselae with solid black centers are filled, while those light in color are empty.

System) to determine the proportion that were filled. Plant morphometrics recorded included height, basal stem diameter, above ground dry biomass, number of branches and the leaf gas exchange rate were measured.

Data sets for plant biomass, height, stomatal density, basal stem diameter, number of branches, and leaf area were analysed statistically using a two-way analysis of variance (ANOVA) with the factors being [CO_2] and biological control agent. An LSD test was performed using the Minitab −16 statistical package.

3. Results

The elevated [CO_2] had no significant effect upon parthenium weed height attainment (Fig. 2A) but *E. strenuana* significantly ($F_{1,14}$ = 154.0, $p < 0.001$) decreased the height of the plants by 53% and 46% when grown at ambient and elevated [CO_2], respectively (Fig. 2A).

Elevated [CO_2] led to a significant increase (38%; $F_{1,14}$ = 38.1, $p < 0.001$) in the above ground biomass production of parthenium weed plants (Fig. 2B). *Epiblema strenuana* reduced the above ground biomass production by 36 and 45% ($F_{1,14}$ = 67.3, $p < 0.001$), at ambient and elevated [CO_2], respectively (Fig. 2B). Moreover, there was a statistically significant interaction ($F_{1,14}$ = 9.8, $p < 0.005$) found between [CO_2] and the biological control agent, *E. strenuana*.

Parthenium weed grown at elevated [CO_2] produced 34% more branches ($F_{1,14}$ = 19.5, $p < 0.001$) per plant as compared to those

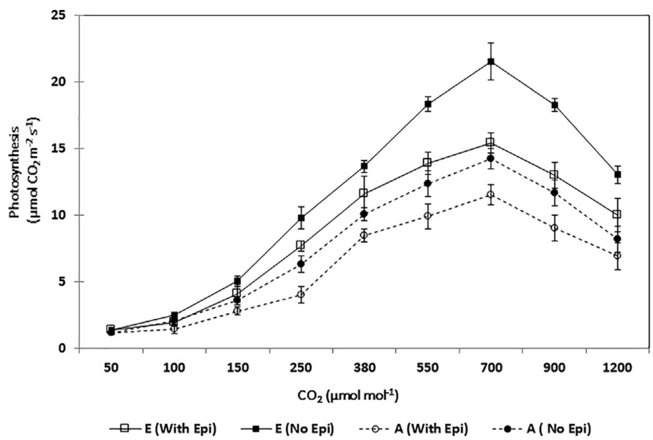

Fig. 5. The photosynthetic response of parthenium weed plants to various [CO_2] initially grown for 55 days under an ambient (A: 380 µmol mol^{-1}) or elevated (E: 550 µmol mol^{-1}) [CO_2], and with ('with Epi') or without *E. strenuana* ('No Epi'). Bars represent two standard errors of the mean.

grown under an ambient [CO_2] (Fig. 2C). *Epiblema strenuana* significantly ($F_{1,14} = 73.9$, $p < 0.001$) stimulated the production of lateral branches in plants grown both under ambient and elevated [CO_2] (Fig. 2C). The average number of lateral branches produced in the presence of the stem-galling moth was approximately twice that seen when *E. strenuana* was absent, under both [CO_2]. However, no interaction between [CO_2] and the biological control agent was observed.

At elevated [CO_2], the stem base diameter of parthenium weed plants was 26% greater ($F_{1,14} = 20.0$, $p < 0.001$) as compared to that of plants grown under ambient [CO_2] (Fig. 2D). No differences were found in the stem base diameter of parthenium weed plants grown with or without the biological control agent under an ambient [CO_2], however stem diameter was 20% ($F_{1,14} = 20.0$, $p < 0.001$) greater under elevated [CO_2] (Fig. 2D). In the presence of *E. strenuana,* parthenium weed produced 20% greater ($F_{1,14} = 5.1$, $p = 0.03$) stem base diameter under elevated [CO_2] (Fig. 4D).

A significantly greater number of cypselae (37%; $F_{1,14} = 89.3$, $p < 0.001$) were produced on parthenium weed plants grown under elevated [CO_2] as compared to those on plants grown under ambient [CO_2] (Fig. 3). However, in the presence of *E. strenuana*, the total number of cypselae per plant significantly ($F_{1,14} = 135.8$, $p < 0.001$) dropped by 60 and 32% under ambient and elevated [CO_2], respectively (Fig. 3). Since parthenium weed plants produced significantly more branches under elevated [CO_2] and in response to gall induction, there were significantly more flowers (and consequently more seed) produced on those plants as compared to those grown in absence of *E. strenuana* or under ambient [CO_2]. However, when these seeds were analysed under an X-ray machine, about 45% ($F_{1,14} = 25.5$, $p < 0.001$) were found not to be filled (Fig. 4). A significant interaction ($F_{1,7} = 24.8$, $p < 0.001$) was found between the [CO_2] and biological control agent in seed fill.

A comparison of the $P_n - C_i$ response of parthenium weed plants grown at the two [CO_2] showed that net photosynthesis was greater in plants that had been raised under elevated [CO_2], compared with those raised under ambient [CO_2] (Fig. 5). However, in the presence of *E. strenuana*, the net photosynthesis rate was decreased both in ambient and elevated CO_2-raised plants. The net photosynthetic rate steadily increased in all treatments as the [CO_2] was increased until it reached a peak at 700 µmol mol^{-1} CO_2, and from there it dropped sharply (Fig. 5).

Under elevated [CO_2], the net photosynthesis (P_n) and water use efficiency (WUE) of parthenium weed plants were significantly increased by 46% ($F_{1,14} = 112.2$, $p < 0.001$) and 76% ($F_{1,14} = 482.4$, $p < 0.001$), respectively as compared to those grown at ambient [CO_2] (Fig. 6 A and B). Under elevated [CO_2] and in the presence of *E. strenuana*, P_n and WUE were decreased to 25% ($F_{1,14} = 21.8$, $p = 0.002$) and 28% ($F_{1,14} = 27.8$, $p < 0.001$), respectively (Fig. 6 A and B). Elevated [CO_2] reduced stomatal conductance (g_s) by 32% ($F_{1,14} = 4.8$, $p < 0.05$), which led to a 55% ($F_{1,14} = 27.7$, $p < 0.001$) decrease in the average transpiration rate (T_r) for parthenium weed plants (Fig. 6 C and D). The galls induced by *E. strenuana* had no effect on stomatal conductance or transpiration of parthenium weed plants under both [CO_2].

4. Discussion

Elevated [CO_2] greatly enhanced parthenium weed dry above ground biomass and cypsela production while its biological control agent, *E. strenuana* significantly suppressed both. The growth enhancement of parthenium weed in response to elevated [CO_2] has been reported in earlier studies (Shabbir et al., 2014; Khan et al., 2018). The enhanced efficacy of *E. strenuana* could be due to altered weed foliage quality produced under elevated [CO_2]. A lower N to C ratio has been reported in plants grown under elevated [CO_2], resulting in some insects eating more plant tissue (Lincoln et al., 1993). In the presented study, we did not analyse the nutritional status of parthenium weed plants grown under the two [CO_2]. Nonetheless, the above ground weed biomass suppression ability of *E. strenuana* was significantly enhanced under elevated compared to ambient [CO_2], possibly through changes in the N:C ratio of parthenium weed. Previous studies have demonstrated that insect herbivores respond positively to an atmosphere of elevated [CO_2] by enhancing their consumption rates of plant tissue as compared to that observed under ambient [CO_2] (Hamilton et al., 2005; Hunter, 2001; Lincoln et al., 1993).

Entomologists have recognized for some time that elevated concentrations of atmospheric CO_2 are likely to influence the distribution, abundance and performance of insects that feed on plants mainly through its effect on their host food quality (Fajer et al., 1989; Lincoln et al., 1984, 1986). It is likely that *E. strenuana* larvae increased their feeding activity on plants grown under elevated [CO_2]. Leaf-chewing insects have been reported to respond to elevated [CO_2] by increasing their rate of foliage consumption as compared to what would occur under ambient conditions (Osbrink et al., 1987; Whittaker, 1999). In a meta-analysis of seventy-five studies done on plant-herbivore interactions under elevated [CO_2], Stiling and Cornelissen (2007) found that herbivores increased relative consumption rate by 16.5% under CO_2 enrichment.

The parthenium weed galls that formed on shoots significantly stimulated the number of lateral branches produced by plants grown under both [CO_2] however, more branches did not translate into more cypselae per plant. These results contradict an earlier study (Dhileepan and McFadyen, 2001) which found 55% less branches being produced by parthenium weed plants when adults of *E. strenuana* were applied at rosette stage in a field cage experiment. These contrasting differences could be due to a higher number of *E. strenuana* adults (6–25) applied in the 2001 study. The larvae of *E. strenuana* have been reported to damage shoot growing points (meristems), phloem and associated parenchyma that may then induce parthenium weed plants to lose vigour (Raman and Dhileepan, 1999).

Although parthenium weed produced significantly more seeds under elevated [CO_2] and in the presence of *E. strenuana*, however, a significant proportion of that seed was not filled as compared to ambient [CO_2]. These results indicate that *E. strenuana* not only suppressed the seed quantity but also its quality and maintained its suppressive effect on the reproduction of weed under elevated [CO_2].

Stimulatory effects on the photosynthetic ability of parthenium weed (a C_3-C_4 intermediate) plants were observed in response to enriched CO_2 treatments. As compared to C_4 plants, most C_3 plants can positively respond to increased atmospheric [CO_2], which significantly enhances their photosynthetic ability (Ainsworth and Long, 2005; Ghannoum et al., 2000; Kimball et al., 1993). However, in the presence

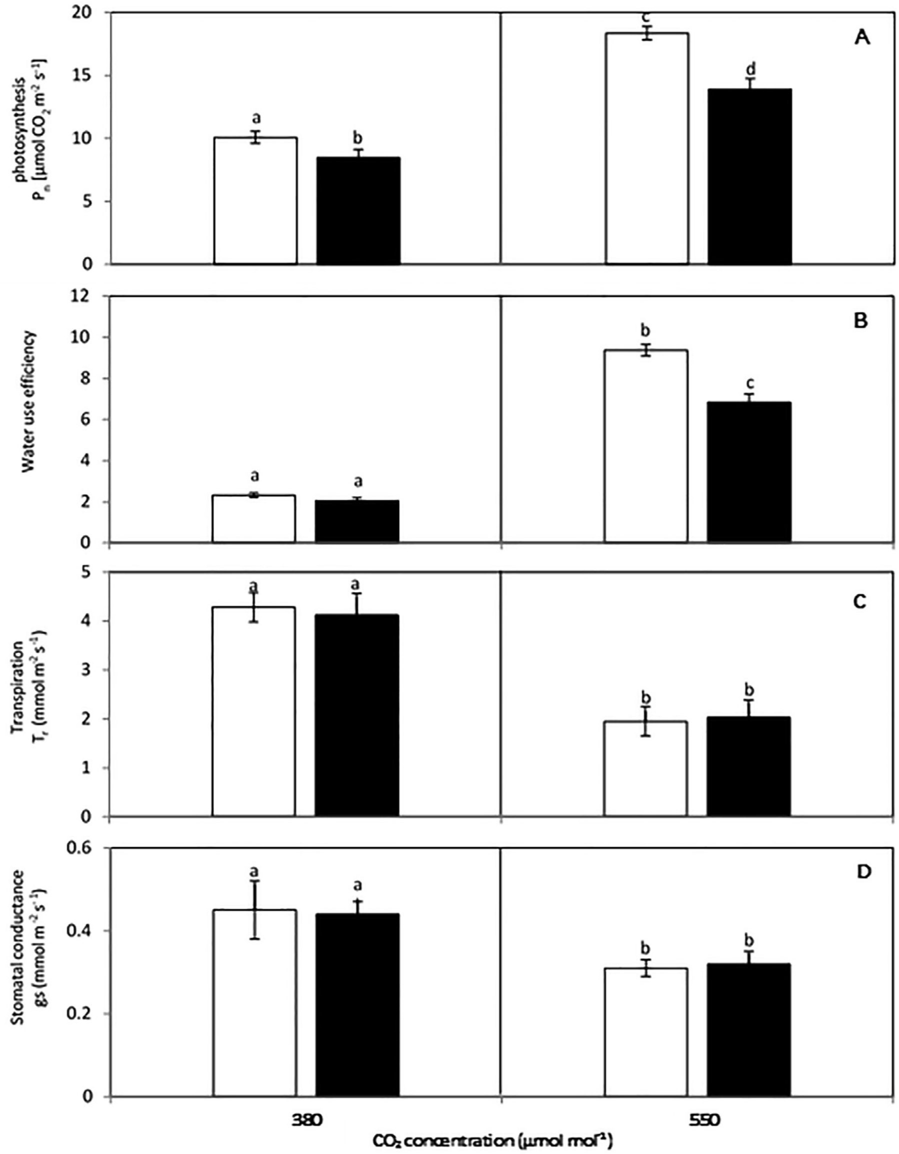

Fig. 6. The effect of an elevated [CO_2] and *Epiblema strenuana* (no moth larvae □; with moth larvae ■) on (A) net photosynthesis, (B) water use efficiency, (C) transpiration rate and (D) stomatal conductance of 60-day old parthenium weed plants growing in pots. Each bar is the mean ± SE taken from eight replicated pots; different letters above the bars indicate values that are statistically different ($p < 0.05$).

of *E. strenuana*, the net photosynthetic rate was significantly reduced under both CO_2 levels. A similar trend was also observed in the photosynthesis - CO_2 response curve under both [CO_2] (Fig. 5). Parthenium weed plants, when galled by *E. strenuana*, resulted in disrupted water movement and imobilization of nutrients that might significantly reduce the plants gaseous exchange and result in a net reduction of 80% in photosynthesis (Florentine et al., 2001, 2015). Higher rate of defoliation (tissue loss) may result in reduced plant growth due to under-compensatory photosynthesis and reduced water availability (Zhu et al., 2014).

The increased water use efficiency of parthenium weed plants grown under elevated [CO_2] has important implication for its abundance and spread under future climate change scenarios. Under the A1FI (high emissions) scenario, 20% lower precipitation has been predicted for Australia (Nakicenovic and Swart, 2000). Therefore, parthenium weed's improved water use efficiency will enable it to better tolerate any future low rainfall conditions, compared to most C_4 pasture species found in areas it has invaded. *E. strenuana* significantly decreased the water use efficiency of parthenium weed grown at elevated [CO_2] but not at ambient [CO_2]. The reasons for this suppressive effect by the biological control agent is not clear.

In this study, we examined a single climate change factor (elevated CO_2) on the performance of one of several effective biological control agents of the invasive parthenium weed. However, to better understand the impacts of climate change on insect-plant interactions, other co-variables involved in climate change (e.g. temperature mean and fluctuations, aridity etc.) would also need to be investigated.

The results of this study have shown that the growth of parthenium weed is likely to be enhanced by an atmosphere enriched in [CO_2], producing plants with a greater biomass and more seeds. These alarming changes are likely to make the weed more aggressive in the future, with enhanced spread causing new outbreaks within its introduced range. *Epiblema strenuana*¸one of the most widespread and effective biological control agents, significantly reduces the growth of parthenium weed under both current and future [CO_2] scenarios, however, it is likely that parthenium weed will also produce more flowers in response to the biological control agent. But interestingly, *E. strenuana* has a negative effect upon seed fill that will mitigate any increases in of flower production under an elevated [CO_2]. Thus, *E. strenuana* holds promise for the future management of parthenium weed under a changing climate.

CRediT authorship contribution statement

Asad Shabbir: Conceptualization, Data curation, Investigation, Methodology, Writing - review & editing. **Kunjithapatham Dhileepan:** Conceptualization, Methodology, Writing - review & editing, Supervision, Formal analysis. **Myron P. Zalucki:** Writing - review & editing, Supervision. **Steve W. Adkins:** Funding acquisition, Conceptualization, Methodology, Writing - review & editing, Supervision.

Acknowledgements

This project was financially supported by the Queensland Murray Darling Committee (Australia), a doctoral scholarship from the Islamic Development Bank (Kingdom of Saudi Arabia) and the University of Queensland (Australia).

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