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The additive effect of a stem galling moth and a competitive plant on parthenium weed under CO_2 enrichment

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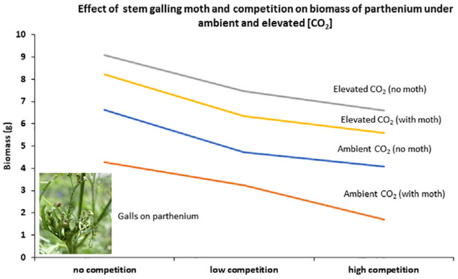
GRAPHICAL ABSTRACT



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ABSTRACT

Parthenium weed (*Parthenium hysterophorus*) is a highly invasive plant that has invaded many parts of world including Australia. The present study reports on the effects of rising [CO_2] on the performance of one of its biological control agents, stem-galling moth (*Epiblema strenuana*) when combined with a competitive plant, buffel grass (*Cenchrus cilliaris*). The study was carried out under controlled environment facilities during 2010–11. *P. hysterophorus* when grown under elevated [CO_2] of 550 µmol mol^{-1}, produced a greater biomass (27%), attained greater stature (31%), produced more branches (45%) and seeds plant^{-1} (20%), than those grown at ambient [CO_2] of 380 µmol mol^{-1}. Buffel grass reduced the biomass and seed production of *P. hysterophorus* plants by 33% and 22% under ambient [CO_2] and by 19% and 17% under elevated [CO_2], respectively. The combined effect of buffel grass and *E. strenuana* reduced dry biomass and seed production by 42% and 72% under ambient [CO_2] and 29% and 37% elevated [CO_2], respectively. Although the suppressive effect was different between ambient and elevated [CO_2], the effect is likely to be retained. Stem gall formation by *E. strenuana* significantly enhanced the lateral branch production in plants grown under both [CO_2]. *Epiblema strenuana* did not reduce the seed production of *P. hysterophorus* under the elevated [CO_2] nevertheless, our earlier study had confirmed that many of the seeds produced under such conditions are not filled. This study has highlighted that the additive suppressive effect of *E. strenuana* and buffel grass on *P. hysterophorus* growth would be retained under future atmospheric CO_2 enrichment.

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1. Introduction

Parthenium weed, *Parthenium hysterophorus* L. (Asteraceae) is a highly problematic invasive weed of natural and agricultural ecosystems across many countries (Adkins and Shabbir, 2014; Shabbir et al., 2019a). A native of Mexico and southern United States of America, *P. hysterophorus* has now invaded *c.* 50 countries in Asia, Africa and Oceania (Shabbir et al., 2019a). In its introduced range, this plant has become a serious weed of crop and pasture lands, forests and national parks (Adkins and Shabbir, 2014). The negative effects of *P. hysterophorus* are not limited to environment and agriculture, it is reported to be a significant allergen in both humans and domestic animals (Ahmed et al., 1988; McFadyen, 1995).

In Australia, biological control is the underlying approach used to manage *P. hysterophorus* supplemented by other strategies (Dhileepan and McFadyen, 2012). *Epiblema strenuana* Walker, a stem-galling moth, was introduced into Australia from Mexico as a biological control agent of *P. hysterophorus* in 1982 (McClay, 1987; McFadyen, 1992). It is now widespread and effective as a biological control agent. (Dhileepan and McFadyen, 2012). *Epiblema strenuana* is active throughout the growing season and can complete its life cycle within 4–6 weeks, with an average of 6 to 7 generations per season in central and north Queensland (McFadyen, 1987). Galling by *E. strenuana* can significantly suppress the vegetative and reproductive growth of *P. heterophorias*, with the impact being more pronounced if the plants are young when initially attacked (Dhileepan, 2001), or if competitive pasture plants, such as buffel grass (*Cenchrus cilliaris* L.) are sown within *P. hysterophorus* infestations (Navie et al., 1998).

Sowing competitive pasture plants in *P. hysterophorus* invaded pastures had shown potential to suppress the growth of *P. hysterophorus* under field conditions (Shabbir et al., 2020), and when tested under simulated grazing (Khan et al., 2019). Further, this strategy worked additively with biological control agents to suppress the weed growth and seed production (Navie et al., 1998; Shabbir et al., 2013, 2015, 2018, 2020). For instance, two competitive plants, *Astrebla squarrosa* C.E. Hubb. and *Clitoria ternatea* L. additively act with *E. strenuana* to suppress seed production of *P. hysterophorus* by up to 73 and 81%, respectively under ambient [CO_2] (Shabbir et al., 2020).

Rising [CO_2] levels may affect the growth of plants, and performance of their biological control agents (Johns and Hughes 2002; Stiling and Cornelissen, 2007; Robinson et al., 2012). Our earlier study demonstrated that *E. strenuana*, can significantly suppress *P. hysterophorus* biomass and seed fill under elevated [CO_2] (Shabbir et al., 2019b). However, it is unknown how *E. strenuana* might interact with a competitive plant under a changing climate, involving [CO_2] enrichment.

The aim of this study was to investigate if there could be any interaction between the biological control agent, *E. strenuana* and a competitive plant, *C. cilliaris*, in suppressing *P. hysterophorus* growth and reproduction under elevated [CO_2].

2. Materials and methods

2.1. Plant husbandry

Seeds of *P. hysterophorus* and buffel grass were obtained from the University of Queensland seed bank and were sown into four seedling trays (35 × 30 × 6 cm; l × w × h) containing a commercial potting mix moistened to field capacity with tap water. The trays were placed in a controlled environment room (CER) set at a temperature regime of 30/18 ± 2 °C (day/night), with 60% relative humidity (RH). Newly emerged seedlings (10 d old) of both species were removed and transplanted into plastic pots (6 L, 18 cm diameter; 24 cm high) each containing 5 L of a commercial potting mix. Plants were grown in the following combinations; one *P. hysterophorus* seedling alone (control), one *P. hysterophorus* seedling with one buffel grass seedling (low competition), one *P. hysterophorus* seedling with two buffel grass seedlings (high competition), and one buffel grass seedling alone (control) with four replicates per treatment. Eight pots were set up for each treatment and the controls. All plants were watered daily with a hand-held sprinkler.

2.2. *Epiblema strenuana*

Galls of *E. strenuana* were harvested randomly from ragweed (*Ambrosia artimissifolia* L.) or *P. hysterophorus* plants growing in a pasture near Kilcoy, south east Queensland in November 2010. Upon harvest, the stem galls were packed (six per bag) into ziplock plastic bags and brought back to the plant processing laboratory at the University of Queensland. When the *P. hysterophorus* plants growing alone or in combination with buffel grass were 6 weeks old, two 2nd instar larvae were carefully removed by hand from the galls and transferred to the middle of the leaf rosette of the *P. hysterophorus* plants, using a fine paint brush. Observations of transferred larvae showed that all entered the growing tips of the rosette within 24 h.

2.3. Experimental approach and facilities

The effect of *E. strenuana*, in the presence or absence of buffel grass (*C. ciliaris*) upon the vegetative and reproductive capacity of *P. hysterophorus* growing under an ambient or elevated [CO_2] was assessed. Half of the pots (32), were distributed onto the surface of three steel benches in a completely randomized fashion (1.0 × 1.0 × 1.5 m; l × w × h) and placed inside a CER with an ambient CO_2 concentration (380 μmol mol^{-1}) and the other half distributed in the manner onto three benches in an identical CER where the [CO_2] concentration had been elevated (550 ± 10 μmol mol^{-1}). The ambient [CO_2] of 380 μmol mol^{-1} represent the atmospheric [CO_2] of 2010–11 while elevated [CO_2] 550 μmol mol^{-1} is predicted [CO_2] for 2050 (Anonymous, 2012). The CO_2 levels were set and maintained by an ADC CO_2 monitor (ANRI Instruments and controls, Victoria) attached to a G size CO_2 cylinder containing food grade gas (for details see Shabbir et al., 2014). The temperature inside both CERs was set to 30 ± 2/18 ± 2 °C (day/night) each with a thermoperiod of 12 h day and 12 h night (7:00 pm to 7:00 am) and a RH of 65 ± 5%. The day light intensity inside each of the CERs was *c.* 400 μmol m^{-2} s^{-1} at the level of the plant canopy. The climatic parameters set inside the CERs provided favourable growing conditions for *P. hysterophorus* (Navie et al., 1996). The environmental conditions in each CER room were controlled through a centrally located and hanging sensor, monitoring temperature and relative humidity, attached to a computer. In addition, the light, RH and temperature levels were also manually measured fortnightly to double check the maintenance of uniformity of the conditions inside each CER. The location of each pot upon the benches was randomly rearranged every 14 days to minimize location effects. The developing plants were watered daily with tap water and using a hand-held sprinkler.

2.4. Data collection

The experiment was harvested 120 days (Nov 2010–March 2011) after its start. Upon harvest, the height (from soil level to the tip of the tallest leaf) and basal stem diameter (taken at soil level with a set of Vernier callipers) of each of the *P. hysterophorus* plants. The numbers of flowers and branches produced by each plant were counted, then the plants were cut at soil level and all of the aerial parts were placed individually in brown paper bags. They were then oven dried at 80 ± 2 °C for 72 h for dry biomass determination. During the experiment, the number of mature capitula (those that had reached anthesis) were harvested and placed into paper bags (one bag per plant). At the termination of the experiment, all the remaining immature capitula were counted. Seed production was estimated by multiplying the number of mature capitula produced by five as there are five seeds in each capitulum.

2.5. Statistical analysis

All planting combinations (four) were replicated four times and grown in both ambient and elevated CO_2 concentration, with and without *E. strenuana* (64 pots). Data on plant height, biomass, branches, basal stem diameter and seed production were analysed using a three-way analysis of variance with three main factors (CO_2, biological control and competition). The factors were coded into categorical variables for statistical analysis, two CO_2 concentrations (ambient or elevated), three competition levels (no competition, low competition or high competition) and two levels of biological control (with and without *E. strenuana*). Interaction among these factors was also explored using GenStat (18th edition) statistical package.

3. Results

3.1. Height

Regardless of competition or presence of *E. strenuana*, *P. hysterophorus* grew 31% taller ($F_{1,3} = 83.8$, $p < 0.001$) under the elevated $[CO_2]$ as compared with the ambient $[CO_2]$ (Fig. 1A). Buffel grass, across both competition levels, individually reduced *P. hysterophorus* height ($F_{1,3} = 21.6$, $p < 0.001$) by 26% and 24% under ambient and elevated $[CO_2]$, respectively (Fig. 1A). *Epiblema strenuana* interactively reduced ($F_{1,3} = 150$, $p < 0.001$) *P. hysterophorus* plant height by 36% and 17% under ambient and elevated $[CO_2]$, respectively (Fig. 1A; Table 1). The combined effect of buffel grass and *E. strenuana* further suppressed *P. hysterophorus* height by 57% and 44%, respectively.

3.2. Biomass

In the absence of competition or biological control, *P. hysterophorus* produced 27% more biomass ($F_{1,3} = 179$, $p < 0.001$) under elevated than ambient $[CO_2]$ (Fig. 1B). Buffel grass independently reduced *P. hysterophorus* biomass by 34% and 24% ($F_{1,3} = 35.1$, $p < 0.001$) under ambient and elevated $[CO_2]$, respectively (Fig. 1B). *Epiblemma strenuana* independently reduced the biomass of weed ($F_{1,3} = 44.5$, $p < 0.001$) by 35% and 10% at ambient and elevated $[CO_2]$, respectively. The combined effect of buffel grass and *E. strenuana* further suppressed *P. hysterophorus* biomass by 42% and 28%, respectively under ambient and elevated $[CO_2]$ (Fig. 1B; Table 1).

3.3. Branches

In the absence of buffel grass and *E. strenuana*, *P. hysterophorus* grown under elevated $[CO_2]$ produced 45% more branches ($F_{1,3} = 27.2$, $p < 0.001$) as compared to those plants grown under ambient concentration (Fig. 1C). *Parthenium hysterophorus* branch production was significantly ($F_{1,3} = 26.3$, $p < 0.001$) reduced by the presence of buffel grass. Under elevated CO_2 there were 33% fewer branches compared to ambient $[CO_2]$. There was a significant interaction ($F_{1,3} = 4.0$, $p < 0.02$) between $[CO_2]$ and buffel grass. *Epiblema strenuana* stimulated more branching of *P. hysterophorus* plants both under elevated and ambient $[CO_2]$. In the absence of buffel grass, the average number of branches produced by *P. hysterophorus* increased by 65% and 54% respectively in the presence of *E. strenuana*, both under ambient and elevated $[CO_2]$ (Fig. 1C). The combined effect of buffel grass and *E. strenuana* resulted in a 29% and 42% respectively reduction in weed branches plant^{-1} under ambient and elevated $[CO_2]$ (Fig. 1C) There was a positive interaction between the buffel grass and *E. strenuana* ($F_{2,\ 47} = 9.4$, $p < 0.001$) (Fig. 1C; Table 1).

3.4. Basal stem diameter

In the absence of *E. strenuana* and buffel grass, the stem base diameter of *P. hysterophorus* grown under elevated $[CO_2]$ was 28% greater ($F_{1,3} = 27.1$, $p < 0.001$) as compared to those plants grown under ambient $[CO_2]$ (Fig. 1D). However, with buffel grass, the basal stem diameter of *P. hysterophorus* plants was reduced by 21% and 30%, respectively under ambient and elevated $[CO_2]$ ($F_{1,3} = 20.6$, $p < 0.001$) (Fig. 1D). The combined effect of *E. strenuana* and buffel grass reduced the basal stem diameter by 34% and 37% under ambient and elevated $[CO_2]$, respectively (Fig. 1D).

3.5. Seed production

In the absence of buffel grass and *E. strenuana*, *P. hysterophorus* grown under elevated $[CO_2]$ produced 20% more seeds ($F_{1,3} = 101$, $p < 0.001$) as compared to those grown under ambient $[CO_2]$ (Fig. 2). Buffel grass alone significantly decreased ($F_{1,3} = 395$, $p < 0.001$) seed production by 20% and 17%, respectively under ambient and elevated $[CO_2]$ (Fig. 2). When *E. strenuana* was present, some inconsistent differences between the seed production under both levels of $[CO_2]$ were noticed. *Epiblema strenuana* significantly reduced ($F_{1,3} = 27.1$, $p < 0.001$) total *P. hysterophorus* seed production by 54% under ambient $[CO_2]$ but, there was no difference in seed production at elevated $[CO_2]$ (Fig. 2). *Epiblema strenuana* and buffel grass combinedly reduced seed production by 72% and 36%, respectively under an ambient and an elevated $[CO_2]$. No interaction was found between biological control and buffel grass under both levels of $[CO_2]$.

4. Discussion

Our earlier work had demonstrated that *E. strenuana* is an effective biological control agent that retained its suppressive effect on *P. hysterophorus* under elevated $[CO_2]$ (Shabbir et al., 2019b). The present study further investigated how the interactive effect of *E. strenuana* and a competitive plant, buffel grass, will affect the growth and seed production of *P. hysterophorus* under elevated $[CO_2]$. This study has demonstrated that the combined effect of biological control and plant competition was more pronounced under ambient than elevated $[CO_2]$. Here, we investigated the effect of one biological control agent, *E. strenuana* combined with buffel grass under controlled environmental conditions, nonetheless, under field conditions, there would be additional biological control agents present that target different parts of the weed. For instance, in Australia, the leaf-feeding beetle, *Zygogramma bicolorata* Pallister, the stem-boring weevil, *Listronotus setosipennis* Hustache and the seed-feeding weevil, *Smicronyx lutulentus* Dietz. are well established in field so, the combined impact of selected competitive plants and a suite of biological control agents, under field conditions might be expected to be greater than the effect seen under controlled environment facilities (Shabbir et al., 2013, 2015). Thus, it is likely that these strategies would work together in the field to achieve a better management of *P. hysterophorus*.

In line with previous studies (Shabbir et al., 2015, 2019b), *P. hysterophorus* plants attained greater stature, produced a greater biomass, more branches per plant, and as well as seeds under the elevated CO_2 (Figs. 1 & 2). Earlier studies have shown that the growth and reproduction of *P. hysterophorus* was significantly enhanced in a climate that involves an elevated $[CO_2]$ (Navie et al., 2005; Nguyen et al., 2017). *Parthenium hysterophorus* being either a C_3 (Navie et al., 2005) or C_3-C_4 intermediate plant species (Devi and Raghavendra, 1994) would be expected to gain a growth advantage from CO_2 enrichment, and therefore produce more biomass and height than seen under an ambient $[CO_2]$ (Fig. 1). These results suggest that *P. hysterophorus* will potentially become more effective under a future climate where CO_2 levels are elevated.

As a principle source of carbon for photosynthesis, elevated $[CO_2]$

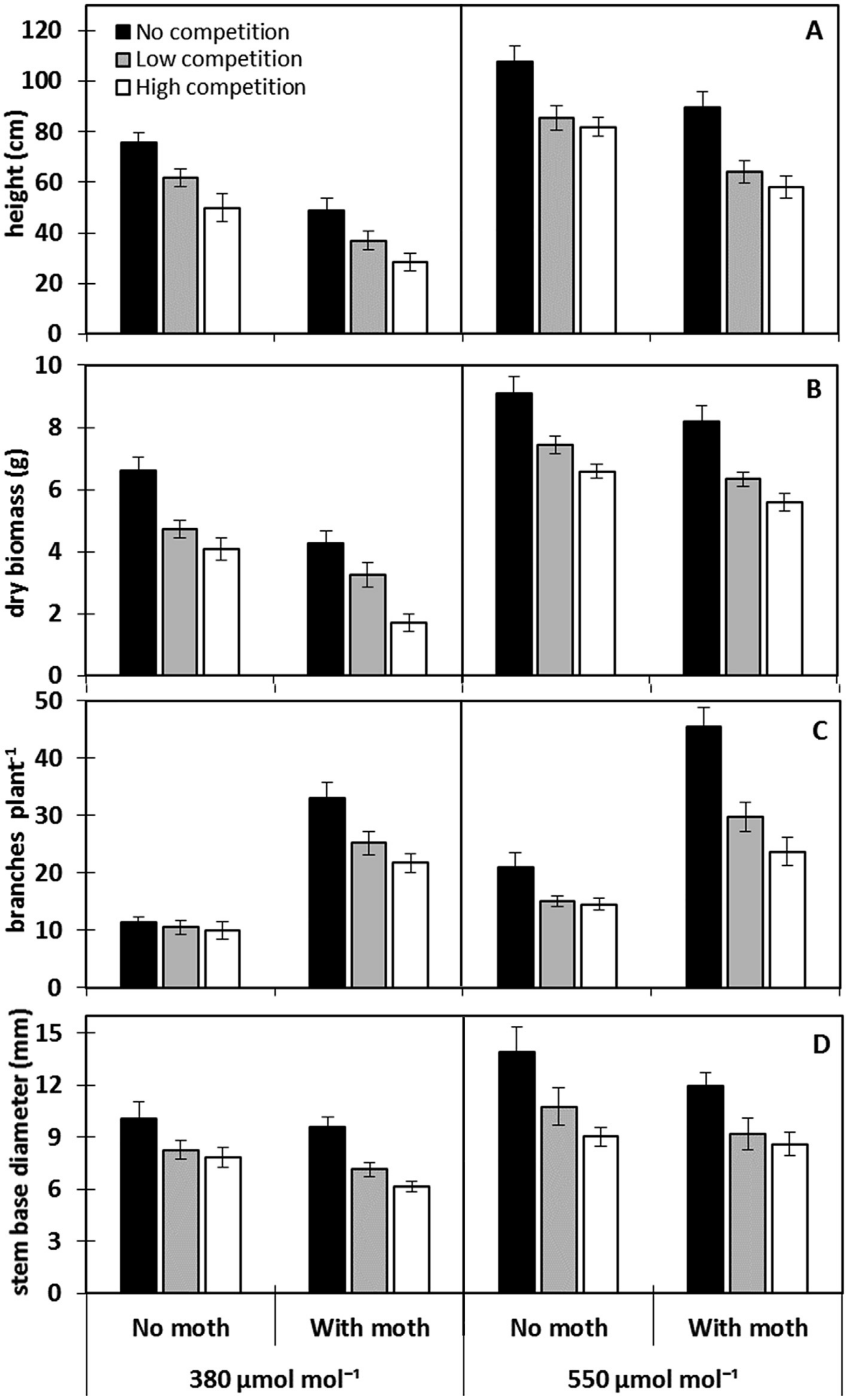

Fig. 1. The effect of ambient or an elevated [CO_2], and plant suppression from buffel grass upon (A) plant height development, (B) above ground biomass, (C) branch production and (D) stem base diameter of 120-day old *P. hysterophorus* plants growing in pots both in presence and absence of the biological control agent, the stem-galling moth. The bars represent two standard errors of the mean.

levels have a marked effect upon growth and development of many plant species (Dukes, 2002; Poorter and Navas, 2003; Ziska, 2003). It has been recognized that increasing CO_2 concentration will change the balance of competition among crop and weed plants that have different photosynthetic pathways (Bunce and Ziska, 2000; Patterson, 1995). Similarly, some studies have suggested that the enhanced atmospheric [CO_2] will favour invasive plants species over non-invasive species. For example, Song et al., (2009) found a greater competitive advantage for three invasive plants over three native plant species under an elevated [CO_2]. In central Queensland, improved pastures are comprised of both native and introduced plant species, with a predominance of C_4 tropical forages being present (Ludlow, 1985). As expected, buffel grass being a C_4 species showed no response to CO_2 enrichment in this study, but it maintained its suppressive effect against *P. hysterophorus* under

Table 1
An analysis of variance undertaken upon parthenium weed height, above ground biomass, number of branches produced, basal stem diameter and seed production of 120 day old parthenium weed plants grown under an ambient or an elevated CO_2 concentration, with or without competition from buffel grass, and with or without the biological control agent, the stem-galling moth being present.

Factor (s)	DF	Height (cm)		Dry biomass (g)		Branches plant^{-1}		Basal stem diameter (mm)		Seed plant^{-1}	
		F*	P	F	P	F	P	B	P	F	P
Carbon dioxide (CO_2)	1	**83.8**	< 0.001	**179**	< 0.001	**27.2**	< 0.001	**27.1**	< 0.001	**101**	< 0.001
Biological control (BC)	1	**150**	< 0.001	**44.5**	< 0.001	**181**	< 0.001	**7.0**	0.012	**395**	< 0.001
Competitive plant (CP)	2	**21.6**	< 0.001	**35.1**	< 0.001	**26.3**	< 0.001	**20.6**	< 0.001	**27.1**	< 0.001
CO_2 × BC	1	**6.1**	0.018	1.2	0.280	0.1	0.945	0.1	0.779	0.1	0.740
CO_2 × CP	2	0.9	0.415	0.4	0.677	**4.0**	0.026	0.1	0.521	0.3	0.731
BC × CP	2	2.1	0.140	1.4	0.252	**9.4**	< 0.001	0.03	0.962	0.7	0.494
CO_2 × BC × CP	2	0.8	0.453	0.4	0.678	0.4	0.647	0.8	0.459	0.1	0.906

* The F values in bold indicate significant difference ($p = 0.05$).

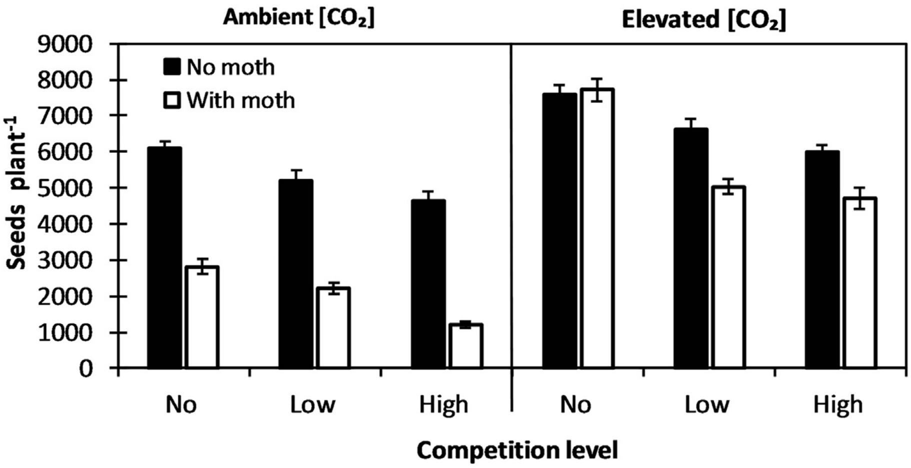

Fig. 2. The effect of an ambient or an elevated $[CO_2]$, and different levels of plant suppression from buffel grass upon seed production by 120-day old *P. hysterophorus* plants both in the presence or absence of the biological control agent, the stem-galling moth (*E. strenuana*). The bars represent two standard errors of the mean.

elevated CO_2. The idea that C_4 plants will respond less positively to CO_2 enrichment compared to C_3 plants has a long history and is supported by their physiology. However, long-term assessments have shown a reversal in typical C_3-C_4 response of plants to elevated $[CO_2]$ (Reich et al., 2018).

Parthenium hysterophorus produced more branches, and hence flowers when galled by *E. strenuana*, both under an ambient and an elevated CO_2 concentration. Although galling of growing tips (shoot meristems) on *P. hysterophorus* slowed plant growth this damage stimulated production of lateral branches, and consequently a greater number of seeds (Fig. 2). This kind of response was evident in an earlier study (Shabbir et al., 2019b) which was conducted to ascertain the impact of the same biological control agent, in the absence of plant competition, but under the same CO_2 concentration (550 μmol mol^{-1}). The increased number of branches is a compensatory response of *P. hysterophorus* to galling. Insect damaged plants are well known to undergo compensatory growth by activating dormant lateral meristems (Hendrix and Trapp, 1981; Mabry and Wayne, 1997; Nykanen and Koricheva, 2004). However, much of this additional seed was not filled, possibly due to galling not allowing enough resources to be allocated for seed fill to occur (Shabbir et al., 2019b).

Some of the other influencing factors of climate change are temperature increase and rainfall, the amount and seasonal distribution. The combined management strategy involving biological control and plant competition so far has only been tested under one climate change scenario, that of moderate CO_2 increase and under no-grazing situation. *Parthenium hysterophorus* is likely to tolerate any future drought stresses (changed rainfall pattern) through its high water use efficiency (Shabbir et al., 2014). However, in comparison, it is unknown how different pasture plants will respond to these same climate change variables, under grazing and no grazing situations. Khan et al. (2015) tested a number of different suppressive pasture plants under an elevated $[CO_2]$ in a glasshouse and found that the competition indices of most of the C_3 pasture plants increased in relation to *P. hysterophorus*, while they remained unchanged for C_4 pasture plants.

Invasive weed systems involve interacting climate, biological control, and plant competition, and this results in complex systems that are difficult to assess experimentally. One way to study this complexity is by using mechanistic modelling approaches as done for the invasive weed yellow starthistle (*Centaurea solstitialis* L) in California (Gutierrez et al., 2005). Laboratory studies like the one reported in the present manuscript are key to support modelling analyses that can in turn provide a synthesis of existing related laboratory and field studies.

Buffel grass is one of the commercially important pasture grasses in Australia. It persists under drought and heavy grazing conditions, and it is more productive species than many native plants. This grass has been reported to be a strongly competitive species against *P. hysterophorus* growth both under glasshouse and field conditions in Australia (O'Donnell and Adkins, 2005; Khan et al., 2013, 2014). Moreover, buffel grass can act in combination with other biological control agents to suppress growth of *P. hysterophorus* under field conditions (Shabbir et al., 2013). Despite being a useful pasture species, buffel grass is also considered as a serious environmental weed in some parts of Australia due to its aggressive nature and negative effects on biodiversity. The selection of buffel grass as pasture species is, therefore, needs a careful evaluation of its potential costs and benefits (Friedel et al., 2006).

The findings of this study indicate that *P. hysterophorus* could potentially benefit from the future CO_2 enrichment expected under a changing climate and produce more seeds that may intensify the impact of this weed, not only in terms of the area invaded but also in terms of spread to new locations. *Epiblema strenuana* and competitive plants such as buffel grass should together continue to suppress the growth of *P. hysterophorus* under a future climate involving CO_2 enrichment. However, the magnitude of biocontrol effectiveness on *P. hysterophorus* may decline through time under elevated CO_2 conditions. *P. hysterophorus* is likely to produce to more biomass and seeds even in the presence of *E. strenuana* under elevated CO_2 concentration but most of the seed produced is unlikely to be filled under such conditions (Shabbir et al., 2019b).

CRediT authorship contribution statement

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

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