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RESEARCH ARTICLE

Root growth responses of parthenium weed and different pasture plants under elevated atmospheric carbon dioxide

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Abstract: Parthenium weed (*Parthenium hysterophorus* L.) is an alien invasive species reducing pasture productivity and livestock production in Australia and other countries around the world. Three C_4 pasture grasses (*Setaria incrassata*, *Astrebla squarrosa* and *Bothriochloa decipiens*) and one C_3 pasture legume species (*Clitoria ternatea*), all previously known to be suppressive of the growth of parthenium weed under ambient CO_2 (390 µmolmol^{-1}), were re-tested under an elevated atmospheric CO_2 (550 µmolmol^{-1}) level in a controlled environment growth chamber. When grown alone and under elevated atmospheric CO_2 level, the root dry biomass of *S. incrassata* and *A. squarrosa* did not get affected significantly, whereas that of *B. decipiens*, *C. ternatea* and *P. hysterophorus* significantly increased by 10, 34 and 26 %, respectively. When *S. incrassata* and *A. squarrosa* were grown together with parthenium weed under the same conditions, their root dry biomass reduced by 20 and 16 %, while that of *B. decipiens* and *C. ternatea* was increased by 7 and 28 %, respectively. The root to shoot ratio of *S. incrassata* and *A. squarrosa* decreased significantly by 24 and 16 %, while that of *B. decipiens*, *C. ternatea* and parthenium weed increased by 6, 17 and 12 %, respectively, under the same conditions. These results have important implications for the management of parthenium weed in future climate scenarios involving elevated atmospheric CO_2 levels. Our results suggest that some pasture species with the potential to suppress the growth of parthenium weed under the present climate will remain an important tool in managing pastures invaded by parthenium weed in the future.

Keywords: C_3 or C_4 pasture species, elevated atmospheric CO_2, parthenium weed, root systems growth.

INTRODUCTION

Atmospheric carbon dioxide (CO_2) concentration, which is an important climate change variable has been rising from *c*. 315 µmolmol^{-1} in the 1960s to *c*. 403 µmolmol^{-1} at present (Mauna-Loa Observatory, 2017) with a further predicted rise to *c*. 550 µmolmol^{-1} by 2050 (IPCC, 2007). Under elevated atmospheric CO_2 levels, shoot and root growth of C_3 plant species will generally increase more than that of the C_4 species (Wand *et al*., 1999; Poorter & Navas, 2003; Ainsworth & Long, 2005; Long *et al*., 2006). This differing responses of C_3 compared to C_4 plants (Devi & Raghavendra, 1994) may have significant effects on the distribution and abundance of invasive weeds (Poorter & Navas, 2003) with changes in the species compositions in plant communities.

Parthenium weed (*Parthenium hysterophorus* L.) being an invasive member of the Asteraceae family and originated from the tropical and subtropical America, has now invaded *c*. 35 countries including Australia (Adkins & Shabbir, 2014). In Australia, it currently infests large areas of pastoral land (*c*. 60 million ha; DAFF, 2011)

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and has the ability to further spread due to its large seed production (Navie *et al*., 2004), rapid growth and allelopathic effects (Adkins & Sowerby, 1996). Parthenium weed can greatly decrease plant biodiversity in native ecosystems (Belgeri, 2013) and reduce pasture fodder production (Khan *et al*., 2014), which can result in a 40 to 80 % decline in the cattle carrying capacity of pastoral areas (McFadyen, 1992).

A large area (> 70 %) of Queensland, Australia comprises rangelands having mainly C_4 grass species, such as pitted bluegrass - *Bothriochloa decipiens* (Hack.) C.E. Hubb., buffel grass - *Cenchrus ciliaris* L. and purple pigeon grass - *Setaria incrassata* Hochst. (Tothill & Hacker, 1996). These rangelands are widely invaded by C_3 (Navie *et al*., 2004) or $C_3 – C_4$ intermediate (Devi & Raghavendra, 1994) parthenium weed. The progressively elevating atmospheric CO_2 levels are likely to have a significant effect on the growth and interactions that take place between plants in communities (Ziska, 2008). A number of plant species have been shown to respond positively to elevated atmospheric CO_2 when grown alone, while their growth is decreased when grown in the presence of companion plants (Poorter & Navas, 2003) with effects seen both in terms of their root and shoot growth (Wand *et al*., 1999). The differential responses of plants in the absence or presence of companion plants under elevated atmospheric CO_2 may be due to the absence or presence of the suppressive effects by the companion plants. Being a C_3 or $C_3 – C_4$ intermediate plant, parthenium weed has been shown to grow more rapidly under elevated atmospheric CO_2 than many other C_4 pasture plants (Navie *et al*., 2005; Khan *et al*., 2015).

Root weight ratio is the most appropriate measurement to get an idea about biomass partitioning between above and belowground systems of plants (Oechel & Strain, 1985). An increased biomass allocation to plant roots has been reported under elevated atmospheric CO_2 (Rogers *et al*., 1994; Yue *et al*., 2009), which allows plants to spread further and penetrate roots deeper (Idso *et al*., 1987). The differential shoot biomass responses of some C_4 pasture species in the absence or presence of the C_3 or $C_3 – C_4$ intermediate parthenium weed under elevated atmospheric CO_2 may be due to the absence or presence of the suppressive effects of the weed plants on the pasture plants (Khan *et al*., 2015). However, the response of root systems of C_4 and C_3 or $C_3 – C_4$ intermediate plants under elevated atmospheric CO_2 has not been described before. The belowground interactions among C_4 pasture species and a C_3 or $C_3 – C_4$ intermediate parthenium weed under different atmospheric CO_2 concentrations could help in selecting suppressive plants to be used in long-term management interventions of invasive C_3 weeds.

The aims of the present study were to determine: (a) the root growth responses and suppressive abilities of three selected suppressive C_4 pasture grass species (*S. incrassata*, *A. squarrosa* and *B. decipiens*) and a C_3 pasture legume species [*Clitoria ternatea* L. (O'Donnell & Adkins, 2005; Khan *et al*., 2013)] on the growth of the C_3 or $C_3 – C_4$ intermediate invasive parthenium weed, (b) their biomass allocation patterns, and to verify how these results may help to develop long-term management interventions against invasive C_3 weeds.

METHODOLOGY

Plant materials

Three C_4 perennial grass species (*S. incrassata*, *A. squarrosa* and *B. decipiens*) and a C_3 perennial legume (*C. ternatea*) were selected on the basis of previously shown strong suppressive abilities against the growth of parthenium weed (O'Donnel & Adkins, 2005; Khan *et al*., 2013; Table 1). Seeds of all species were obtained from registered seed suppliers in Queensland, Australia, while seeds of parthenium weed were collected from a pastoral area near Injune, Queensland, Australia (S 25° 46' 18"; E 148° 21' 06").

The trial environment

Two identical growth chambers (200 × 180 × 100 cm^3 indicating length, width and height as internal dimensions) made from a translucent plastic (Kirby Pty Ltd., Brisbane, Queensland, Australia) were positioned inside a glasshouse (31/15 ± 3 °C day/night thermoperiod; and a 14/10 h day/night photoperiod and *c*. 1400 µmol $m^{-2}s^{-1}$ light intensity) at the University of Queensland, Brisbane, Australia. The relative humidity inside each of the two growth chambers was maintained at 85 ± 5 % with the help of relative humidity regulators (Weather Proof Model IP-53, Clipsal). The temperature regime (controlled through Model UHI 24 temperature regulators) and the relative humidity inside each growth chamber were regularly checked with data loggers (T-Tec 7-IC, Temperature Technology). One growth chamber was attached to a G-size CO_2 gas cylinder to provide an elevated atmospheric CO_2 concentration (550 µmolmol^{-1}). The CO_2 inflow to the growth chamber was controlled and monitored by an ADC-2000 CO_2 monitor (ANRI Instruments and Controls Pty. Ltd., Melbourne, Victoria, Australia) equipped with an automatic switching solenoid valve. The other growth chamber was provided with an ambient CO_2 concentration maintained by daily ventilating with air.

Experimental procedures

The seeds of four pasture species and those of the parthenium weed were individually sown in germination trays (30 × 30 × 4 cm) filled with a moist University of California potting mixture and placed in a glasshouse to germinate (14/10 day/night thermoperiod of 30/20 ± 4 °C with a 14/10 h day/night photoperiod and a constant relative humidity of 55 ± 5 %) for *c*. 6 ds. Seedlings of uniform size were then transplanted individually into 40 plastic pots (each 25 cm diameter) and each pot was filled with *c*. 9 kg black cracking clay soil. All the pots were uniformly watered to field capacity throughout the duration of the trial (40 ds). Seedling transplantation was made as described below. In order to differentiate the transplanted seedlings from any self-emerged seedlings, tooth picks were placed alongside all transplanted seedlings and all self-emerging seedlings were removed on a daily basis. A total of 40 pots (20 pots assigned to the 4 plants per pot planting density and 20 pots assigned to the 6 plants per pot density) were set randomly within each growth chamber. To guarantee evenness of the experiment, the pots and the CO_2 maintaining equipment were exchanged between the two growth chambers on a weekly basis. The pots inside the growth chambers were also re-randomised on a weekly basis. As the internal floor area of the growth chambers was not large enough to test all the 4 pasture species in one phase, the trial was run in 4 consecutive phases (i.e., October 2009 - March 2010) and in each phase one pasture species was tested.

After 40 ds of growth, all pots were removed from the chambers and all individual plants were carefully removed from the soil, the roots washed and the plants were individually separated into roots and shoots. Any debris found attached to the roots were removed carefully with forceps. All samples were then put into marked brown paper bags, oven dried for *c*. 50 h (72 ± 4 °C) and the dry biomass was determined.

Planting pattern and data analysis

Each phase of the experiment was carried out in a completely randomised design and by the application of addition series approach (Spitters, 1983). The seedlings were sown at a planting density of either 4 or 6 plants per pot with five planting arrangements of parthenium weed-to-pasture species (i.e., for four plants per pot 4 : 0, 3 : 1, 2 : 2, 1 : 3 and 0 : 4; and for six plants per pot 6 : 0, 4 : 2, 3 : 3, 2 : 4 and 0 : 6). Each planting density was replicated 4 times in each growth chamber accordingly. The aboveground biomass of all species was harvested after 40 ds growth and measured (Khan *et al*., 2015) as was the ground biomass (this study). In addition, the root to shoot dry biomass ratio (R/S) for all species was calculated in each treatment by dividing the root dry biomass by the shoot dry biomass. The root dry biomass data and the R/S recorded under ambient and elevated atmospheric CO_2 levels were analysed by analysis of variance in MINITAB 16 statistical programme. The means were separated by LSD test at 5 % level of significance (Steel & Torrie, 1980).

RESULTS AND DISCUSSION

Root growth

When grown alone, the root growth of two C_4 pasture species (*S. incrassata* and *A. squarrosa*) did not change significantly, while that of the other C_4 species (*B. decipiens*), the C_3 legume species (*C. ternatea*) and parthenium weed increased significantly ($p < 0.04$, 0.002 and 0.01, respectively) under elevated atmospheric CO_2 level compared to the ambient (Figure 1). When *S. incrassata* and *A. squarrosa* were grown with parthenium weed, their root dry biomass significantly decreased ($p < 0.001$) in both treatments by 20 and 16 %, respectively, while that of *B. decipiens* and *C. ternatea* significantly ($p < 0.002$) increased by 7 and 28 %, respectively under elevated atmospheric CO_2 level compared to ambient (Figure 1; Table 1). The reduction of root dry biomass noted in *S. incrassata* and *A. squarrosa* in the presence of parthenium weed, and under elevated CO_2 can be explained by the differential growth responses of the two plant types to elevated atmospheric CO_2 concentration. The root growth of pasture species *B. decipiens* and *C. ternatea* and parthenium weed increased under elevated CO_2 conditions; however, growth of the pasture species increased comparatively more than that of the weed and hence suppressing the growth of parthenium weed. The increase in root dry biomass observed in *B. decipiens* and *C. ternatea* may be due to their higher growth under the same elevated CO_2 concentration (Figure 1). Previous studies have shown similar responses under elevated CO_2 for C_3 plants at the cost of C_4 plants (Ainsworth & Long, 2005) due to their increased photosynthetic rate (Nowak *et al*., 2004), which in turn increases the flow of photosynthates from the shoots to roots, thereby promoting the root growth (Rogers *et al*., 1994). The differential root growth response of one C_4 species, *B. decipiens* than the other two C_4 species (*S. incrassata* and *A. squarrosa*) under elevated atmospheric CO_2 showed species specific responses indicating that some C_4 species may incur suppressive ability over parthenium weed in the future.

The differential responses of the three C_4 pasture species under similar conditions could be due to their differential ability to withstand allelo-chemicals that may have been released by parthenium weed (Adkins & Sowerby, 1996).

Table 1: The percentage (%) change in pooled mean root dry biomass formed by the four pasture species and parthenium weed when grown alone and together at either four or six plants per pot and at five planting arrangements for 40 days under ambient CO_2 (390 µmolmol^{-1}) and elevated atmospheric CO_2 (550 µmolmol^{-1}) conditions

Species used	Photosynthetic pathway	Dry root biomass per plant (g) when grown alone		Change in biomass (%)	Dry root biomass per plant (g) when grown together		Change in biomass (%)
		390 µmolmol^{-1}	550 µmolmol^{-1}		390 µmolmol^{-1}	550 µmolmol^{-1}	
S. incrassata	C_4	2.00 ± 0.2	1.98 ± 0.3^{NS}	- 1	4.12 ± 0.3	3.30 ± 0.5*	- 20
A. squarrosa	C_4	1.55 ± 0.3	1.60 ± 0.1^{NS}	+ 3	2.50 ± 0.1	2.10 ± 0.2*	- 16
B. decipiens	C_4	1.70 ± 0.1	1.87 ± 0.4*	+ 10	2.90 ± 0.2	3.14 ± 0.3*	+ 7
C. ternatea	C_3	2.70 ± 0.4	3.6 ± 0.5*	+ 34	3.20 ± 0.5	4.12 ± 0.8*	+ 28
P. hysterophorus	C_3/C_3 to C_4	2.00 ± 0.2	2.52 ± 0.2*	+ 26	2.80 ± 0.1	3.32 ± 0.4*	+ 19

^{NS} = non-significant difference; * = significant difference ($p < 0.05$)

The C_3 legume *C. ternatea* was more responsive (28 % increase in root dry biomass) than the C_4 pasture grass, *B. decipiens* (7 % increase in root dry biomass). The comparatively greater root growth response of the legume *C. ternatea* under elevated CO_2 level (Figure 1) may be due to its greater photosynthetic rate compared to the other species under similar conditions. C_3 legume species have similar responses in previous studies (Hebeisen *et al*., 1997; Rogers *et al*., 2009). The increased growth of parthenium weed might have been arrested by the relatively superior growth of *C. ternatea* under elevated CO_2. It can be assumed that *C. ternatea* and other C_3 legume plants could be useful for the competitive management of parthenium weed in the future for predicted elevated levels of atmospheric CO_2. However, pasture species and parthenium weed may show different growth responses under field conditions due to the influences of other climatic variables such as reduced soil moisture, high temperature, presence of methane gas and high N deposition (Belgeri, 2013). Future studies will be useful to examine these species under elevated CO_2 and potential interactions with other climatic variables.

The greater root growth of parthenium weed under elevated CO_2 level (Figure 1) may be inter-related to the enhanced shoot growth of the weed under similar conditions (Belgeri, 2013; Shabbir *et al*., 2014). The increased root growth of parthenium weed under elevated atmospheric CO_2 may have caused reduction in root dry biomass of the two C_4 pasture species (*S. incrassata* and *A. squarrosa*). However, the exact mechanism behind how weeds can suppress the growth of neighbouring pasture plants under elevated levels of CO_2 is not fully understood. Nevertheless, the growth of parthenium weed was comparatively rapid than many other plant species under elevated atmospheric CO_2 (Nguyen *et al*., 2012). Navie *et al*. (2005) have shown a slower growth for the C_4 species, *C. ciliaris* in the presence of parthenium weed under elevated CO_2.

Biomass allocation pattern

The R/S of *S. incrassata* and *A. squarrosa* did not change significantly, while the R/S of *B. decipiens*, *C. ternatea* and parthenium weed significantly increased ($p < 0.04$) when grown alone but under elevated CO_2 (Table 2). As expected, when *S. incrassata* and *A. squarrosa* were grown with parthenium weed, the R/S significantly decreased while the R/S of *B. decipiens* and *C. ternatea* increased under elevated CO_2 than that of ambient CO_2 atmosphere ($p < 0.02$; Table 2). The enhanced R/S of *B. decipiens*, *C. ternatea* and parthenium weed under elevated CO_2 may be due to the better response of roots than the shoots of these species under similar conditions. According to previous research, a significant higher amount of extra biomass accumulated in the root system than in the shoot system under an elevated CO_2 atmosphere, hence increasing the R/S (Chong *et al*., 2009). Many studies (Rogers *et al*., 1994; Pritchard *et al*., 1999) have shown an increased R/S under elevated atmospheric CO_2 levels while some studies (McMaster *et al*., 1999; Salsman *et al*., 1999) have shown a decrease.

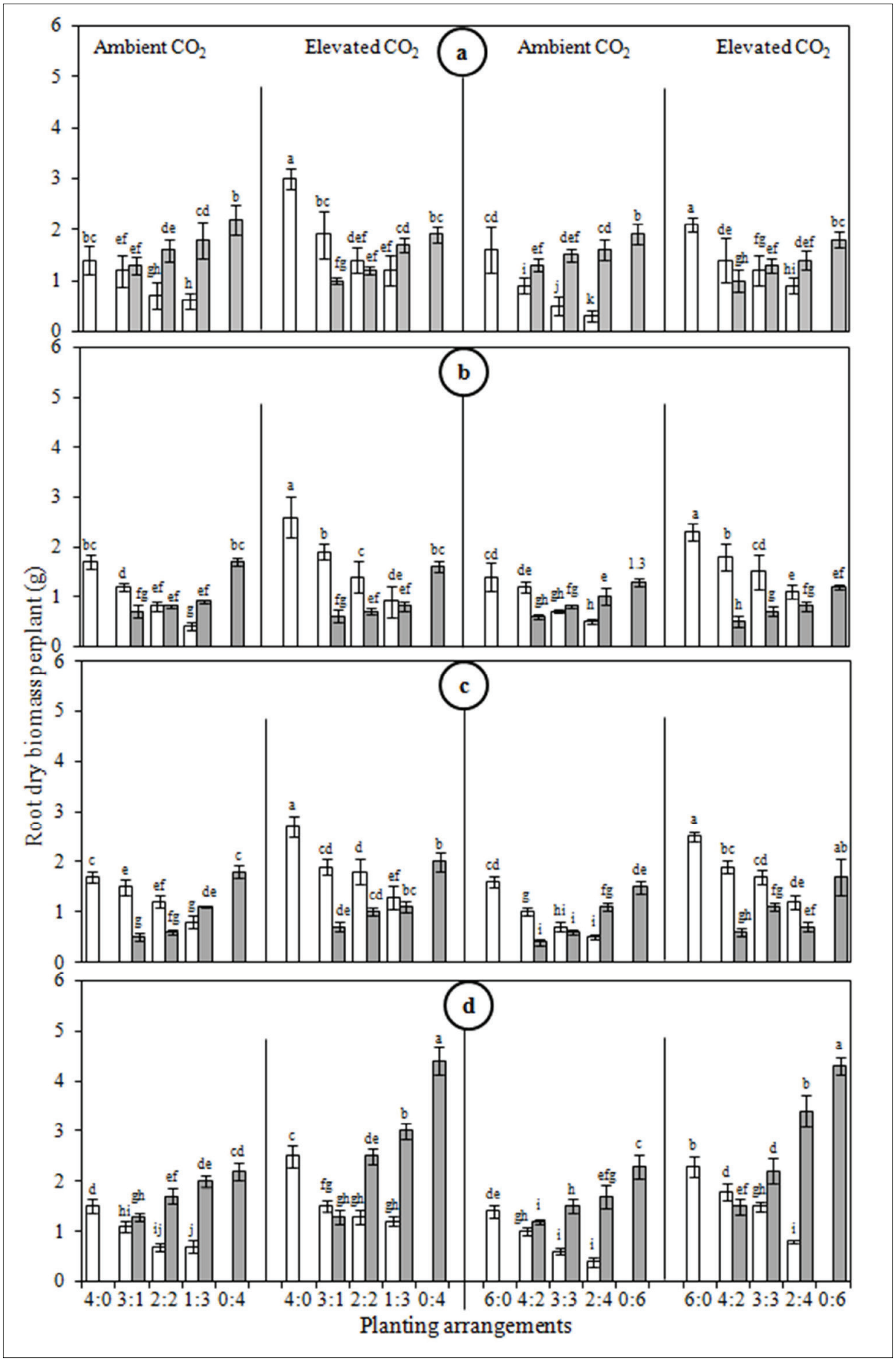

Figure 1: The root dry biomass of parthenium weed (□) and four pasture species (■): (a) *S. incrassata*; (b) *A. squarrosa*; (c) *B. decipiens* and (d) *C. ternatea* at the four or six plants pot^{-1} densities and at the five planting arrangements under the ambient (390 µmolmol^{-1}) and elevated (550 µmolmol^{-1}) CO_2. The upright bars show ± SE of means and the letters on top of the bars indicate significant differences among the root dry biomass of the parthenium weed or pasture species ($p < 0.05$)

Table 2: The percentage (%) change in root to shoot ratios (R/S) by the four pasture species and parthenium weed when grown alone and together at either four or six plants per pot and at five planting arrangements for 40 days under the ambient CO_2 (390 µmolmol^{-1}) and elevated atmospheric CO_2 (550 µmolmol^{-1}) conditions

Species	R/S when grown alone		Change in R/S (%)	R/S when grown together		Change in R/S (%)
	390 µmolmol^{-1}	550 µmolmol^{-1}		390 µmolmol^{-1}	550 µmolmol^{-1}	
S. incrassata	0.30 ± 0.02	0.31 ± 0.01^{NS}	+ 3	0.50 ± 0.03	0.38 ± 0.02*	- 24
A. squarrosa	0.41 ± 0.01	0.42 ± 0.02^{NS}	+ 2	0.36 ± 0.02	0.30 ± 0.01*	- 16
B. decipiens	0.32 ± 0.01	0.35 ± 0.01*	+ 9	0.63 ± 0.02	0.67 ± 0.02*	+ 6
C. ternatea	0.61 ± 0.05	0.77 ± 0.03*	+ 26	0.70 ± 0.01	0.82 ± 0.04*	+ 17
P. hysterophorus	0.42 ± 0.02	0.50 ± 0.01*	+ 19	0.50 ± 0.04	0.56 ± 0.01*	+ 12

^{NS} = non-significant difference; * = significant difference ($p < 0.05$)

CONCLUSION

Out of the four pasture species tested, two C_4 grasses *S. incrassata* and *A. squarrosa* may possibly not be as suppressive against the growth of the C_3 or $C_3 – C_4$ intermediate parthenium weed in a future increased atmospheric CO_2 concentration, however, one C_4 grass *B. decipiens* and a C_3 legume *C. ternatea* both have increased root dry biomasses and R/S ratios under an elevated atmospheric CO_2 concentration. From the above findings, it can be concluded that some of the tested suppressive pasture species will continue to provide better suppression of parthenium weed in the future. Unless emissions are not reduced, the problem of invasive plants such as the parthenium weed is expected to get worse; however, adapting to such challenges would be a key to mitigate the effects of a changing climate of elevated CO_2. Selection of C_3 or C_4 pasture plants that have the ability to suppress the growth of parthenium weed under a future atmosphere of elevated CO_2 would be an important strategy that holds promise for the integrated management of invasive parthenium weed. This research investigated a single climatic variable (atmospheric CO_2 concentration) and future studies will be useful to examine the potential interactions of this variable with other climatic variables, especially increased temperature.

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