The effect of CO_2 enrichment on the growth of a C_3 weed (*Parthenium hysterophorus* L.) and its competitive interaction with a C_4 grass (*Cenchrus ciliaris* L.)

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Summary
The growth of parthenium weed (*Parthenium hysterophorus* L.), an introduced annual weed species with a C_3 photosynthesis mechanism, was stimulated when the atmospheric CO_2 concentration was increased from 360 (ambient) to 480 (enriched) ppmv, regardless of whether competition from buffel grass (*Cenchrus ciliaris* L.) was present or absent. Seventy days after sowing a significant increase in the height, stem base diameter, above-ground biomass, capitula production and seed production was observed in *P. hysterophorus* plants grown at the higher CO_2 concentration. In addition, these plants showed greater phenological development than those grown at the ambient CO_2 concentration. The large magnitude of the increases detected is probably due to the time period over which the experiment was conducted, the fact that this weed is a C_3 broad-leaf species, and the highly adaptable nature of this aggressive weed. The growth of *C. ciliaris*, a perennial pasture species with a C_4 photosynthesis mechanism, was not significantly affected by elevated CO_2 concentration, but some differences in its growth were detected (i.e. reduced tiller production and changes in its appearance). When *P. hysterophorus* was grown in competition with *C. ciliaris*, the ratio of *C. ciliaris* to *P. hysterophorus* above-ground biomass was much lower in the pots from the enriched CO_2 cabinet. This is an indication that the C_3 weed species gained a competitive advantage over the C_4 pasture species at the higher CO_2 concentration. The stimulation of growth, and increased competitiveness, of *P. hysterophorus* at an elevated CO_2 concentration indicates that this weed could become more aggressive in the future if atmospheric CO_2 levels continue to rise, especially in areas dominated by C_4 species such as the semi-arid subtropical and tropical pastures of northern Australia.

Keywords: parthenium weed, buffel grass, carbon dioxide, competition.

Introduction
The concentration of carbon dioxide (CO_2) in the atmosphere is increasing, and has been increasing for many years (Houghton *et al*. 1990). This increase in atmospheric CO_2 has been attributed to industrialization and the clearing and burning of large areas of forest. In 1990 the atmospheric CO_2 concentration was approximately 360 ppmv, and increasing at about 1.8 ppmv each year (Houghton *et al*. 1990).

It has been demonstrated, in many experiments, that the growth of plants is accelerated when the concentration of CO_2 is increased (Kimball 1983, Cure and Acock 1986). This is because a higher CO_2 concentration stimulates photosynthesis, suppresses photorespiration and reduces water loss by reducing stomatal aperture size (Gifford 1988). These experiments are often conducted at twice the present concentration of CO_2 (about 670 to 720 ppmv), have usually involved crop species, and generally report an increase in growth of 30 to 40% (Kimball 1983, Gifford 1988). More recently, experiments have been conducted which examine the effects of elevated CO_2 concentration on weed performance and on competition between weeds and crops (Patterson and Flint 1980, O'Donnell and Adkins 1996). Some of the most recent of these experiments have been conducted at 480 ppmv CO_2 (O'Donnell and Adkins 1996), a level that will be reached in about 65 years if the current annual rate of CO_2 increase is maintained.

The type of photosynthetic pathway that a species possesses (i.e. whether it is a C_3 or C_4 plant) has been found to influence its performance when CO_2 concentration is increased. In general the growth of C_3 species is increased to a greater degree than that of C_4 species (Ghannoum *et al*. 1997), and there is also an improvement in the relative fitness of C_3 species when grown in competition with C_4 species (Patterson and Flint 1980). Cure and Acock (1986) reviewed many prior experiments and reported, on average, a 28% increase in the growth of C_3 grasses when the CO_2 concentration was doubled, while in C_4 grasses such as maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* (L.) Moench) the increase was only 9% and 3% respectively. Plants exhibiting a C_4 photosynthesis pathway utilize CO_2 more efficiently, and their leaf anatomy concentrates CO_2 internally, hence an increase in atmospheric CO_2 is not as beneficial to such species (Patterson and Flint 1980).

Parthenium weed (*Parthenium hysterophorus* L.) is a major pasture weed of Queensland (Chippendale and Panetta 1994, Navie *et al*. 1996). This introduced annual weed reduces the productivity of pastures (Haseler 1976), affect the well-being of livestock (Narasimhan *et al*. 1980, Navie *et al*. 1996), causes serious human health problems (Towers and Mitchell 1983, McFadyen 1995), and is a significant weed of crops (Hammerton 1981). The worst infestations of *P. hysterophorus* occur in areas that have been cleared of native vegetation or where there has been continued disturbance, particularly from heavy grazing (Haseler 1976, McFadyen 1992). The most common pasture grass in the heavily affected areas of Queensland is buffel grass (*Cenchrus ciliaris* L.), which is also an introduced species. In fact, in many parts of inland Australia *C. ciliaris* is regarded as a serious environmental weed.

The aim of this experiment was to ascertain if the growth of *P. hysterophorus*, a broad-leaf C_3 species, is significantly enhanced by a moderate increase in the concentration of atmospheric CO_2. This was studied in the presence and absence of competition from *C. ciliaris*, a perennial C_4 pasture grass, to examine any effect of increased CO_2 concentration on the competition balance of these two species. These two species are very common in the semi-arid pastoral areas of central Queensland and are often found growing in competition with each other. It is hoped that the results of these experiments will indicate whether there could be any change in the aggressiveness and competitiveness of *P. hysterophorus* in the future, as a result of the continuing increase in atmospheric CO_2 concentration.

Materials and methods
Plant husbandry
Parthenium hysterophorus seeds were collected from plants growing at the Alan Fletcher Research Station (QDNRM, Brisbane) and stored at room temperature for 12 months prior to use. Seeds were then placed in mesh bags and buried in damp soil for two weeks. This burial process was employed because it had previously been found to overcome any innate dormancy in the seeds of this species and

hence ensure rapid and even germination of the weed upon sowing (Navie 2003). After the bags were exhumed, the seeds were recovered and sown into standard 20 cm diameter spots containing a mixture of equal parts (v/v) heavy black soil and sand (seeds were covered with a thin layer of soil during sowing). The soil was then watered to field capacity.

Cenchrus ciliaris seed was obtained from Redland Bay Research Farm (University of Queensland, Brisbane) and stored at room temperature for about 18 months prior to use. These seeds were sown with *P. hysterophorus* seeds in the competition treatments only. Emergence of both species occurred within a couple of days of sowing, and two weeks after sowing the plants were thinned to one *P. hysterophorus* seedling and either one (light competition), or three (heavy competition), *C. ciliaris* seedlings per pot.

Experimental design

One *P. hysterophorus* plant was grown in each of sixteen pots in each of three competition treatments (i.e. no competition, light competition, and heavy competition). Within each of these three treatments, half of the pots were distributed randomly in a growth chamber with ambient CO_2 concentration (360 ppmv) and the remaining half were distributed randomly in an identical growth chamber in which the CO_2 concentration had been increased to 480 ppmv CO_2. The growth chambers (1.0 × 2.4 × 1.5 m) were constructed of Lexan (Cadillac Plastics, Brisbane), a transparent plastic material that allowed for a very high level of light transmission. These chambers were positioned within a glasshouse so as to avoid shading and to ensure that similar quantities of solar radiation were intercepted during the course of each day. The experiment was conducted during winter (from April to June 1996). The temperature inside the chambers during the day often reached 35 to 40°C and glasshouse heaters maintained the temperature above 15°C during the night, while a relative humidity exceeding 90% was maintained. This temperature regime is similar to that which occurs in central Queensland during summer, however the humidity was significantly higher than would usually be expected in the field. An ADC 2000 CO_2 monitor (ANRI Instruments and Controls, Victoria) was attached to one of the growth chambers in order to maintain the concentration of CO_2 in the chamber at 480 ppmv. Soil moisture in all pots was maintained at field capacity and the plants were fertilized once a month with 200 mL of a soluble fertilizer solution (1.6 g L^{-1}; Aquasol™, Hortico, Melbourne).

Data collection

The experiment ran for 70 days from the time of sowing. At harvest, the height of each *P. hysterophorus* plant was measured (i.e. resting height). The number of capitula that had reached anthesis was recorded, and the total number of seeds produced by each plant determined. Total seed production was taken to be equal to five times the number of mature capitula produced, as five seeds are generally produced in each capitulum. The diameter of the base of the stem was also measured at soil level for each of the plants.

The length of the longest *C. ciliaris* tiller was measured, and the total number of tillers counted, in each of the pots that contained *C. ciliaris* plants (i.e. the light and heavy competition treatments). The above-ground biomass of the *P. hysterophorus* and *C. ciliaris* plants was determined following dehydration at 80°C for five days. For each of these pots, the ratio of *C. ciliaris* biomass to *P. hysterophorus* biomass was determined and the average ratio calculated for each of the treatments.

Statistical analysis

Data were evaluated statistically using two-way Analysis of Variance (ANOVA) with the two factors being CO_2 concentration (two levels) and competition (three levels), followed by a LSD test for significance. In addition, t-tests were carried out on the total above-ground biomass data and on the *C. ciliaris* to *P. hysterophorus* above-ground biomass ratios.

Results

Growth of Parthenium hysterophorus

The *P. hysterophorus* plants grown at elevated CO_2 (480 ppmv) were much taller than those grown at ambient CO_2 (360 ppmv), while competition had little effect on the height of *P. hysterophorus* plants (Figure 1). Statistical analysis confirmed that *P. hysterophorus* height was increased at the elevated CO_2 concentration (Table 1), and slightly decreased by the level of competition (Table 2). Across the three competition treatments, the height of *P. hysterophorus* plants grown under 480 ppmv CO_2 was nearly five times that of plants grown under 360 ppmv CO_2 (Table 1).

The stem base diameter of *P. hysterophorus* plants was greater at 480 ppmv CO_2 than at 360 ppmv CO_2, while competition with *C. ciliaris* reduced stem base diameter – especially in plants from the enhanced CO_2 treatment (Figure 2). Across the three competition treatments, there was a large (110%) increase in the stem base diameter

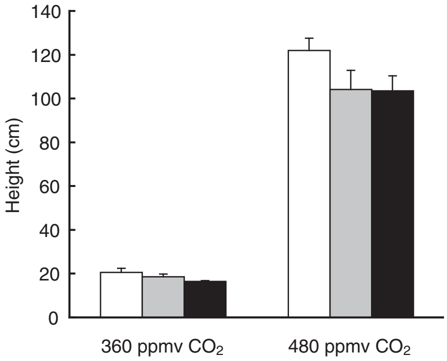

Figure 1. Effect of increased atmospheric CO_2 concentration and competition from *Cenchrus ciliaris* plants (□ no competition; ▒ light competition; and ■ heavy competition) on the mean height of *Parthenium hysterophorus* plants.

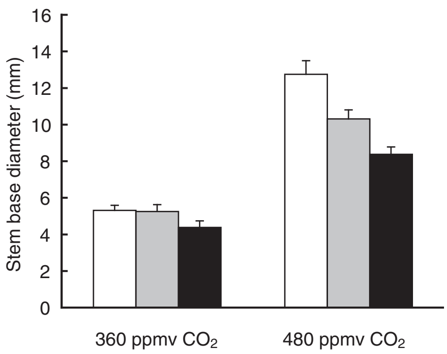

Figure 2. Effect of increased atmospheric CO_2 concentration and competition from *Cenchrus ciliaris* plants (□ no competition; ▒ light competition; and ■ heavy competition) on the mean stem base diameter of *Parthenium hysterophorus* plants.

Table 1. Effect of CO_2 concentration on some growth parameters of *Parthenium hysterophorus*. Values given are the means across the three competition treatments and those in parentheses are the percentage difference from the control (i.e. ambient CO_2 concentration, 360 ppmv). P values in italics signify a statistically significant difference (P <0.05).

	CO_2 Concentration		ANOVA	
Character	360 ppmv	480 ppmv	F_{1df}	P
Plant height (cm)	18.48	109.85 (+494%)	95.22	*0.0001*
Stem base diameter (mm)	4.98	10.48 (+110%)	50.99	*0.0001*
Above-ground biomass (g $plant^{-1}$)	0.88	9.27 (+953%)	44.45	*0.0001*
Capitula produced per plant	0.04	516.37 (+ >1000%)	28.10	*0.0001*
Seed production per plant	0.00	694.58 (+ >1000%)	14.61	*0.0004*

Table 2. Effect of level of competition from *Cenchrus ciliaris* on growth parameters of *Parthenium hysterophorus*. Values are the means across both CO_2 treatments and those in the same row followed by the same letter are not significantly different (LSD). Values in parentheses represent the percentage difference from the control (i.e. No competition). P values in italics signify a statistically significant difference (P <0.05).

Character	No competition	Light competition	Heavy competition	ANOVA F_{2df}	ANOVA P
Plant height (cm)	71.26 a	61.31 (-14%) ab	59.92 (-16%) b	2.85	0.0689
Stem base diameter (mm)	9.03 a	7.78 (-14%) b	6.37 (-29%) c	16.21	*0.0001*
Above-ground biomass (g plant^{-1})	7.03 a	4.94 (-30%) b	3.26 (-54%) c	12.17	*0.0001*
Capitula produced per plant	283.30 a	323.80 (+14%) a	167.60 (-41%) a	0.92	0.4050
Seed production per plant	297.80 a	448.40 (+51%) a	295.60 (-1%) a	0.31	0.7352

of plants grown at the higher CO_2 concentration (Table 1), and the stem base diameters of plants in the three competition treatments were also significantly different from each other (Table 2).

Similar trends were observed for *P. hysterophorus* above-ground biomass, however the effect of *C. ciliaris* competition was even more apparent (Figure 3). Two-way analysis demonstrated that *P. hysterophorus* plants grown in elevated CO_2 had an increased above-ground biomass, and plants grown in these conditions produced over 10 times the above-ground biomass of plants grown at ambient CO_2 (Table 1). Competition reduced the above-ground biomass of *P. hysterophorus* plants, regardless of CO_2 concentration, with the 'heavy competition' treatment reducing above-ground biomass by 54% (Table 2).

There were a larger number of capitula produced by plants at 480 ppmv CO_2 (516 capitula per plant) than at 360 ppmv CO_2 (Table 1), with only one plant producing a single capitulum at the ambient CO_2 concentration. Capitulum production varied among competition treatments (295 to 448 capitula per plant), however the variability within treatments (e.g. 0 to 1848 capitula per plant in the 'no competition' treatment) was so high that these differences were not statistically significant (Table 2). This was reflected in similar statistical findings in the seed production data (Tables 1 and 2). At the termination of the experiment numerous seeds had been produced by the plants grown at elevated CO_2, while no seed had yet been produced by any of the plants grown at ambient CO_2 (Figure 4).

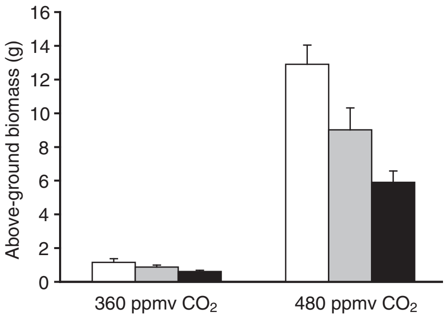

Figure 3. Effect of increased atmospheric CO_2 concentration and competition from *Cenchrus ciliaris* plants (□ no competition; ▒ light competition; and ■ heavy competition) on the mean above-ground biomass of *Parthenium hysterophorus* plants.

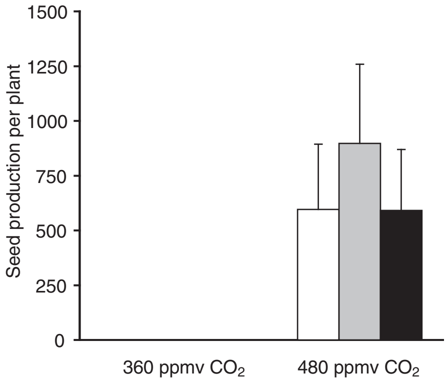

Figure 4. Effect of increased atmospheric CO_2 concentration and competition from *Cenchrus ciliaris* plants (□ no competition; ▒ light competition; and ■ heavy competition) on the mean seed production of *Parthenium hysterophorus* plants.

Table 3. Effect of CO_2 concentration on various growth parameters of *Cenchrus ciliaris* grown in competition with *Parthenium hysterophorus*. Values given are the means across two competition treatments and those in parentheses represent the percentage difference from the control (i.e. ambient CO_2 concentration, 360 ppmv). P values in italics signify a statistically significant difference (P <0.05).

Character	CO_2 Concentration 360 ppmv	CO_2 Concentration 480 ppmv	ANOVA F_{1df}	ANOVA P
Length of longest tiller (cm)	173.99	188.58 (+8%)	2.89	0.1004
Number of tillers per pot	10.25	7.31 (-29%)	17.71	*0.0002*
Above-ground biomass (g pot^{-1})	12.11	12.59 (+4%)	0.15	0.6988

Growth of Cenchrus ciliaris

Elevated CO_2 had no effect on the above-ground biomass and length of the longest tiller of *C. ciliaris* plants, but fewer tillers were produced by plants grown at 480 ppmv CO_2 (Table 3). The above-ground biomass of *C. ciliaris* plants from the heavier competition treatment (16.3 g pot^{-1}) was about twice that of *C. ciliaris* plants from the lighter competition treatment (8.4 g pot^{-1}). Hence, each individual plant in the heavier competition treatment produced about two-thirds the above-ground biomass (5.4 g plant^{-1}) of those in the lighter competition treatment (8.4 g plant^{-1}). Similar trends were also observed in the numbers of tillers produced by *C. ciliaris* plants (i.e. heavier competition, 11.2 tillers pot^{-1} or 3.7 tillers plant^{-1}; lighter competition, 6.4 tillers pot^{-1} and plant).

Competition and biomass production

A comparison of the total above-ground biomass production of both *P. hysterophorus* and *C. ciliaris*, in each of the CO_2 and competition treatments, shows that above-ground biomass production was significantly higher at 480 ppmv CO_2 (light competition, t_{14df} = 4.32, P = 0.0007; heavy competition, t_{14df} = 3.20, P = 0.0065) than at 360 ppmv CO_2. This increase in total biomass can be attributed to the increase in *P. hysterophorus* biomass mentioned earlier (Figure 5).

The average above-ground biomass ratio of *C. ciliaris* to *P. hysterophorus* in the lighter competition treatment was 10.9 at ambient CO_2 and 1.2 at elevated CO_2

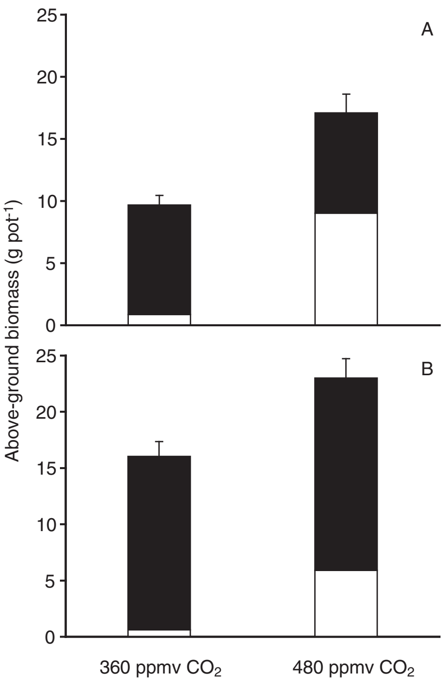

Figure 5. Effect of increased atmospheric CO_2 concentration on the above-ground biomass of *Parthenium hysterophorus* (□) and *Cenchrus ciliaris* (■) plants grown in competition with each other, under two separate regimes; (A) 1:1, and (B) 1:3, *Parthenium hysterophorus* plants to *Cenchrus ciliaris* plants per pot respectively.

(Figure 5). In the heavier competition treatment, where there were more *C. ciliaris* plants, the average ratio was 26.9 at ambient CO_2 and 3.1 at elevated CO_2. These results demonstrate that an increase in the concentration of CO_2 led to a significant decrease in the *C. ciliaris* to *P. hysterophorus* above-ground biomass ratio in both the lighter (t_{14df} = 7.51, P <0.0001) and heavier (t_{14df} = 6.51, P <0.0001) competition treatments.

Discussion

Growth of Parthenium hysterophorus

The growth of *P. hysterophorus* in the first 70 days after sowing was greatly enhanced by a moderate increase (33%) in atmospheric CO_2 concentration. In plants grown at 480 ppmv CO_2, dramatically greater values were recorded in all characters measured (Table 1). The greatest percentage difference was observed in the height and biomass of the weed, and while the percentage difference in stem base diameter was not quite as large, it was equivalent to a 343% increase in stem base area.

While the plants grown at 480 ppmv CO_2 displayed significant seed production, the plants grown at 360 ppmv CO_2 were much less developed. In fact, all of the plants grown at the higher CO_2 concentration had started flowering 53 days into the experiment, whereas only one of the plants grown at ambient CO_2 concentration had produced a flower 70 days after sowing. In the field, in Queensland, soil moisture is often limiting as soils dry out rapidly. This experiment demonstrates that if the atmospheric CO_2 concentration were to increase to 480 ppmv, *P. hysterophorus* would be able to attain reproductive maturity more quickly. This, combined with the fact that enhanced CO_2 concentration usually increases the drought tolerance of plants (Patterson 1995, Saralabai *et al*. 1997), suggests that the weed would be able to take advantage of smaller rainfall events and inhabit drier areas, thereby increasing the magnitude of the problems it causes.

The enhanced growth of *P. hysterophorus* plants in this experiment was very large in comparison to previous experiments with other species, especially considering that the CO_2 concentration in the present experiment was only increased by 33%, and not doubled as in most of these other experiments (Patterson and Flint 1980, Cure and Acock 1986). The differences reported here, especially for above-ground biomass and height, might have been reduced if the experiment had run slightly longer as the plants grown at the ambient CO_2 were just entering the stem elongation phase of growth (i.e. bolting). Other studies on *P. hysterophorus* suggest that plants at this stage of the life-cycle have a much larger below-ground biomass (Navie 2003), a feature that was not measured in these experiments.

Kendall *et al*. (1985) and Cure and Acock (1986) have reported greater responses to increased CO_2 concentration in experiments conducted at higher temperatures and/or at higher light intensities. In addition, Ghannoum *et al*. (1997) demonstrated that the stimulatory effect of CO_2 enrichment is greater in natural sunlight than in artificial light of greater intensity. The temperatures apparent during the present experiment were high compared to most studies, the light intensity very similar to that of the incoming solar radiation, and the light source natural sunlight. Therefore, these conditions may have contributed to the large response to enriched CO_2 observed in this experiment (as compared to other earlier experiments). The experimental conditions were also more representative of conditions in the field, especially those in central Queensland. Kendall *et al*. (1985) and Cure and Acock (1986) have also reported that broad-leaf C_3 species gave more erratic, but generally higher, growth responses to elevated CO_2 than C_3 grasses.

While *P. hysterophorus* is considered to be a C_3 species, and therefore is most likely to benefit from an increase in atmospheric CO_2 concentration, research in India has identified *P. hysterophorus* as a C_3–C_4 intermediate species (Patil and Hegde 1983, Prasada Rao and Rajendrudu 1989, Devi and Raghavendra 1993). Such species have been shown to have a reduced rate of photorespiration in spite of the predominance of the Calvin cycle in the photosynthetic process (Devi and Raghavendra 1994). *Parthenium hysterophorus* plants also possess leaf anatomical characteristics and photosynthetic rates that are intermediate to those of C_3 and C_4 photosynthetic types (Prasada Rao and Rajendrudu 1989), although these characters are generally closer to C_3 species than C_4 species.

It has been determined that *P. hysterophorus* leaves possess moderately developed Kranz anatomy and reduced photorespiration, but have little or no biochemical capacity for C_4 photosynthesis (Moore *et al*. 1987). Patil and Hegde (1983) reported that Kranz anatomy was not discernible in juvenile leaves and that the differentiation of Kranz anatomy progresses with leaf age. *Parthenium hysterophorus* is a very physiologically adaptable weed (Doley 1977, Hegde and Patil 1980) and this body of research suggests it may possess a certain degree of plasticity in its photosynthetic mechanisms as well. This adaptability may be another reason why *P. hysterophorus* was able to respond so effectively to an increase in atmospheric CO_2 concentration.

Growth of Cenchrus ciliaris

The fact that the biomass of *C. ciliaris* did not increase significantly in the elevated CO_2 treatment is not surprising since this species possesses a C_4 photosynthetic pathway. However, there might have been a large increase in *C. ciliaris* growth if it had not been grown in competition with *P. hysterophorus*. The large increase in weed biomass at 480 ppmv CO_2 could have enhanced its competitive effect on *C. ciliaris*, and suppressed any potential increase in grass biomass due to elevated CO_2 concentration. Aqueous leachates of *P. hysterophorus* leaves have been observed to inhibit the seedling growth of *C. ciliaris* (Adkins and Sowerby 1996). This allelopathic effect, if present, is highly likely to have been greater in the elevated CO_2 cabinet as a result of the larger above-ground biomass of *P. hysterophorus* in these pots.

While there was no change in the above-ground biomass of *C. ciliaris* plants grown at elevated CO_2, there was a decrease in the number of tillers they produced (Table 2). This suggests that, at the higher CO_2 concentration, they produced a lower number of larger tillers or their tillers had a much lower water content. The first explanation is possible however there was no difference, between the two CO_2 treatments, in the length of the longest *C. ciliaris* tiller. An approximate measurement of above-ground fresh weight was taken prior to drying, and this data supports the second explanation. The above-ground fresh weight of *C. ciliaris* plants, in the lighter competition treatment, was 90 g at ambient CO_2 and 55 g at elevated CO_2 (a statistically significant difference, P = 0.0055), yet there was no significant difference between CO_2 treatments in above-ground dry weight biomass (8.1 g and 8.8 g respectively). It was noticeable that the *C. ciliaris* plants growing in the elevated CO_2 cabinet were more woody-stemmed while the *C. ciliaris* plants in the ambient CO_2 cabinet were lush with more numerous, darker green leaves.

A similar phenomenon was observed with the *P. hysterophorus* plants as well (i.e. a lower water content in the plants grown at elevated CO_2). This occurrence could have been due to a difference in the availability of soil water in the two cabinets, although an effort was made to prevent this, or it is possible that an increase in CO_2 concentration may indirectly affect the water content of plants. Unfortunately, appropriate data was not collected during the course of the experiment to reveal which one of these possible causes, if either, was the reason behind the reduction in water content of plants grown at 480 ppmv CO_2. However, it is known that changing the ambient CO_2 concentration does have an effect on the water relations and water use of plants (Patterson 1995, Saralabai *et al*. 1997).

Competition and biomass production

The above-ground biomass of *P. hysterophorus* plants grown in competition with *C. ciliaris* was greatly increased when the concentration of CO_2 was increased to 480 ppmv. However, the above-ground biomass of *C. ciliaris* grown in competition with *P. hysterophorus* was not greater at 480 ppmv CO_2. As a result, the biomass values of the two species are similar at elevated CO_2, instead of grossly favouring *C. ciliaris* as it does at ambient CO_2 (Figure 5). This represents an increase in the competitiveness of the C_3 weed, *P. hysterophorus*, over the C_4 pasture species, *C. ciliaris*. These findings are in agreement with those presented by Patterson and Flint (1980) and serve to demonstrate that C_4 pastures, as well as C_4 crops, may be affected by the enhanced competitiveness of C_3 weeds at higher atmospheric CO_2 concentrations

In the current experiment both species were germinated from seed simultaneously. Sometimes this would be the case in the field, particularly on river floodplains following a flood of extended duration, or when both species germinate after good rainfall following a prolonged drought. However, as *C. ciliaris* is a perennial tussock-forming species, *P. hysterophorus* plants would often also emerge as seedlings in the gaps between established *C. ciliaris* tussocks. In this situation the grass species should have a significant advantage. Similarly, in the field, the amount of *P. hysterophorus* seedlings emerging often greatly outnumbers the amount of grass seedlings emerging.

Conclusions

The findings of this research have implications for the potential threat that *P. hysterophorus* may pose in the future. It is likely that *P. hysterophorus* will be more aggressive, especially in the predominantly C_4 pastures of northern Australia (Hattersley 1983), and will be able to complete its life cycle more quickly. This research also highlights wider reaching implications for the pastures of northern Australia. The potential increase in the competitiveness of C_3 species, in the future, may lead to a change in the composition of the pastures of northern Australia. In particular, the dominance of C_4 pasture grasses may be reduced and they may be replaced by native or exotic tropical C_3 species, including C_3 weed species. Several authors have suggested that other climatic changes, such as global warming and an increase in the aridity of such areas, will be of advantage to C_4 species (Henderson *et al*. 1994, Patterson 1995). However, there is evidence that, even when water supply is limited, CO_2 enrichment favours C_3 plants (Patterson 1986, 1995). Therefore, studies of the interacting effect of CO_2 enrichment, water availability and temperature are needed to help predict more fully the potential changes in *P. hysterophorus* distribution due to climate change (Patterson 1995).

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