

# Effectiveness of introduced biocontrol insects on the weed *Parthenium hysterophorus* (Asteraceae) in Australia

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## Abstract

Six species of insects and a rust fungus have been successfully established for biocontrol of the weed *Parthenium hysterophorus* L. in Queensland, Australia. Effectiveness of biocontrol insects was evaluated at two properties in Queensland during 1996–97 based on an exclusion experiment using insecticides. Parthenium-infested plots with and without biocontrol insects were sampled at monthly intervals and the impact of biocontrol insects on parthenium at individual plant and whole population levels monitored. Biocontrol insects were more effective at Mt Panorama (central Queensland) than at Plain Creek (north Queensland). At Mt Panorama, the leaf-feeding beetle *Zygogramma bicolorata* Pallister caused 96% defoliation and the stem-galling moth *Epiblema strenuana* Walker affected 100% of the plants, resulting in reductions of 90% in weed density, 40% in plant height, and 82% in flower production. Exclusion of biocontrol insects resulted in a 52% increase in seedling emergence and a seven-fold increase in the soil seed bank in the following season. At Plain Creek, *E. strenuana* was the only prominent agent. It affected 92% of the plants and prevented 32% of plants from producing any flowers, reduced plant height by 40% and flower production by 49%, but did not reduce the plant biomass, weed density or soil seed bank. However, exclusion of biocontrol insects resulted in an eight-fold increase in the soil seed bank in the following season.

## Introduction

The weed *Parthenium hysterophorus* L. (Asteraceae: Heliantheae), commonly known as parthenium, is native to the Gulf of Mexico and central South America, and has become widespread in North America, South America, the Caribbean and many parts of Africa, Asia and Australia (Navie *et al.*, 1996). In Australia, parthenium mainly occurs in Queensland, affecting 170,000 km<sup>2</sup> of prime grazing country and causing A\$ 16.5 million per year loss to the pasture industry (Chippendale & Panetta, 1994). Parthenium

is also known to cause human health problems such as hayfever, allergic skin problems and asthma (McFadyen, 1995).

In Australia, biological control of parthenium was initiated in 1977 and since then, nine species of insects and one rust fungus have been introduced (McFadyen & McClay, 1981; McFadyen, 1985, 1992, 2000; McClay *et al.*, 1990; Wild *et al.*, 1992; Parker *et al.*, 1994; Dhileepan & McFadyen, 1997). Among these, the stem-galling moth *Epiblema strenuana* Walker (Lepidoptera: Tortricidae), the leaf-feeding beetle *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae), the stem-boring weevil *Listronotus setosipennis* Hustache (Coleoptera: Curculionidae), the seed-feeding weevil *Smicronyx lutulentus* Dietz (Coleoptera: Curculionidae), the leaf-mining moth *Bucculatrix parthenica* Bradley (Lepidoptera: Bucculatricidae), the stem-galling weevil *Conotrachelus albocinereus* Fiedler (Coleoptera: Curculionidae) and the winter rust *Puccinia abrupta* var. *partheniicola* (Jackson)

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Parmelee (Uredinales) are known to be established in the field (McFadyen, 1992, 2000; Dhileepan *et al.*, 1996; Dhileepan & McFadyen, 1997).

Studies evaluating the effectiveness of weed biocontrol insects have mostly focused either on the performance of the biocontrol insects or on the effects at plant level (McClay, 1995). Only limited studies have been done on the effectiveness of biocontrol insects at the population level of the weed (Crawley, 1989; Moran & Hoffmann, 1989; McEvoy *et al.*, 1991; McClay, 1995; Hoffmann & Moran, 1998) and seed banks have rarely been studied in conjunction with a biocontrol programme (McEvoy *et al.*, 1991). Information on the impact of biocontrol insects on parthenium is restricted to the evaluation of effectiveness of *Z. bicolorata* (Dhileepan *et al.* 2000a), *E. strenuana* (Navie *et al.*, 1998a; Raman & Dhileepan, 1999; Dhileepan & McFadyen, 2001), *L. setosipennis* (Dhileepan *et al.*, 1996) and *C. albocinereus* (David, 1998; Florentine *et al.*, 2001) individually in greenhouses, and for *Z. bicolorata* in the field (Dhileepan *et al.*, 2000b). In this study, the combined effectiveness of biocontrol insects on parthenium at individual plant and weed population levels was evaluated along with the impact on soil seed banks.

## Materials and methods

### Study areas

The trial was conducted from July 1996 to June 1997 on two cattle properties; Mt Panorama (24°31'S, 148°34'E) in central Queensland and Plain Creek (21°49'S, 146°67'E) in north Queensland. Mt Panorama and Plain Creek are in the southern and northern regions of the core parthenium infestations in Queensland and both locations have had severe parthenium infestation since the mid-1970s. Mt Panorama in central Queensland represents an area with high and reliable rainfall where all six insect species and the rust fungus are present. Plain Creek in north Queensland represents an area with erratic rainfall pattern where only three of the insect species are known to occur. Parthenium germinates in response to rain, usually in spring (September–November) in central Queensland and in summer (December–January) in northern Queensland. Flowering begins six to eight weeks after germination and continues until frost (March–April) in central Queensland or until the end of the wet season (April–May) in northern Queensland. From July 1996 to June 1997, Mt Panorama and Plain Creek properties received 635 mm and 265 mm rainfall, respectively. In Mt Panorama the rainfall was well distributed throughout the year, including the winter months. In Plain Creek around 70% of the rainfall was received in the summer months (December–February).

### Insect exclusion

Within each property, eight 2.25 m<sup>2</sup> plots were maintained free of biocontrol insects using insecticides and eight plots of similar size were left exposed to biocontrol insects. As both properties run beef cattle destined for the export market, all eight plots to be kept free of biocontrol insects were selected within a 100 m<sup>2</sup> area at one end of the properties and fenced off to prevent cattle grazing. This was necessary to restrict insecticide application to one area of the properties in order to avoid any potential pesticide residue problems. Monocrotophos (400 g/l EC), a systemic

organophosphate as a foliar spray (600 g ai ha<sup>-1</sup>) and carbofuran (100 g/kg G), a broad-spectrum carbamate as granules in soil (3 kg ai ha<sup>-1</sup>) were applied within the fenced 100 m<sup>2</sup> area at monthly intervals. All eight plots within the fenced biocontrol insect-excluded area had a minimum of one metre of insecticide sprayed border buffer area. During the periods of peak insect activities (January–March), both insecticides were applied at fortnightly intervals. In both trial sites, there was no rust activity and fungicide application was not required. Two 40 m<sup>2</sup> areas, selected on either side of the biocontrol insect excluded area were also fenced to prevent grazing. Within each 40 m<sup>2</sup> area, four 2.25 m<sup>2</sup> plots were selected and left exposed to biocontrol insects. To minimize the impact of competition from grass on parthenium due to lack of grazing, in all plots with and without biocontrol insects, manual grazing using a lawn mower was imposed at the beginning and at the end of the season. At the beginning of the trial, within each property, the soil seed bank and the number of seedlings emerged did not differ significantly between plots selected for biocontrol insect exclusion and the plots to be left exposed to biocontrol insects (t test, *P* > 0.05).

### Impact assessment

At both trial sites the density of seedlings, rosettes, pre-flowering and flowering plants, plant height and flower production were recorded in all plots at monthly intervals. The percentage of plants with *E. strenuana* gall damage, defoliation by *Z. bicolorata* and oviposition by *L. setosipennis* along with the number of *Z. bicolorata* adults, larvae and eggs were also recorded at monthly intervals in all plots exposed to biocontrol insects. From plots with biocontrol insects, ten randomly selected plants were removed from the soil without damaging the tap root and the following parameters recorded: number of *E. strenuana* galls per plant, number of leaves defoliated and levels of defoliation by *Z. bicolorata* (0–100% using visual scores) and the number of *L. setosipennis* larval feeding sites. Incidence of other biocontrol agents was also recorded at monthly intervals. Plots sprayed with insecticides were sampled at monthly intervals to confirm that the plants were free of insect damage.

Soil samples (16 cm<sup>2</sup> area, 2 cm depth) were collected at random from ten sites each in plots with and without biocontrol insects at the beginning (July 1996) and the end (June 1997) of the season for soil seed banks estimation. The soil samples were spread uniformly on the top of plastic trays (18 cm × 12 cm × 5 cm) filled with potting mix, watered twice a week and the number of germinated seeds recorded at weekly intervals for three months. All plants from plots with and without biocontrol insects were removed at the end of the season (March 1997 in Mt Panorama and May 1997 in Plain Creek) and the following parameters measured: plant height, root length, plant biomass, number of flowers, number of leaves, *E. strenuana* gall incidence, *Z. bicolorata* defoliation level and *L. setosipennis* larval damage intensity. Soil seed banks and seedling emergence in plots with and without biocontrol insects were recorded in the following season (1997–98) also.

### Data analysis

Impact of biocontrol insects and location on plant height, root length, plant biomass, flower production and plant

Table 1. Impact of biocontrol (biocontrol  $\times$  no biocontrol) on plant height, root length, plant biomass, flower production and plant density of *Parthenium hysterophorus* in relation to location (Mt Panorama  $\times$  Plain Creek) in 1996–97.

Source of Variation	df	Plant height		Root length		Plant biomass		Flowers/plant		Plant density	
		F	P	F	P	F	P	F	P	F	P
Biocontrol	1	40.447	<0.0001	0.840	0.366	0.723	0.401	7.100	0.012	43.285	<0.001
Location	1	0.118	0.733	9.820	0.004	6.811	0.014	9.292	0.005	243.461	<0.001
Biocontrol $\times$ Location	1	0.003	0.956	0.121	0.730	0.225	0.639	0.123	0.728	53.299	<0.001
Residual	33										

density was analysed using two-way ANOVA with means separated using Tukey test. Incidence and intensity of gall damage by *E. strenuana* in relation to plant growth stage, as well as the impact plant growth stage at which the *E. strenuana* gall damage was initiated on flowering were analysed using one-way ANOVA with means separated using Tukey test. Differences in root length, number of branches, seedling establishment, percentage of plants producing flowers and total parthenium biomass between plots with and without *E. strenuana* gall damage at Plain Creek were compared using paired t-test.

## Results

### Abundance of biocontrol agents

All six biocontrol insects occurred at Mt Panorama and among them, *Z. bicolorata*, *E. strenuana* and *L. setosipennis* were the prominent agents. *Epiblema strenuana* activity in the field became evident in the middle of spring with 20% of plants showing gall damage (fig. 1a). At the end of the season, 100% of the plants had gall damage (fig. 1a) with an average of  $4.8 \pm 1.6$  galls per plant. *Zygogramma bicolorata* adults appeared in late spring and remained active till late summer (fig. 1b), but oviposition by *Z. bicolorata* was noticed only till early summer. *Zygogramma bicolorata* larvae that emerged in early summer reached peak population in the middle of summer, but declined subsequently with no larval activity evident from early autumn (fig. 1b). Oviposition by *L. setosipennis* was evident in 45% of plants in the summer, but at the end of the season none of the plants ( $n = 1010$ ) showed any larval feeding damage. *Smicronyx lutulentus* was prevalent in the middle of spring and again in the middle of summer, with no adult weevil activity recorded during the main flowering time. Evidence of leaf-mining by *B. parthenica* was noticed occasionally and the rust *P. a. parthenicola* was not recorded.

In Plain Creek, *E. strenuana* was the most prevalent biocontrol insect followed by *L. setosipennis*. Evidence of *E. strenuana* activity in the field was first noticed at the end of summer, with only 10% of plants showing gall damage (fig. 1a). However, at the end of the season, 92% of the plants ( $n = 973$ ) had gall damage (fig. 1a) with an average of  $3.6 \pm 0.6$  galls per plant. The number of galls per plant was higher when gall damage was initiated at the flowering stage ( $4.3 \pm 0.4$ ) than at pre-flowering ( $2.3 \pm 0.1$ ) and rosette stages ( $1.1 \pm 0.1$ ) (one way ANOVA,  $F_{2,910} = 27.482$ ;  $P < 0.001$ ). *Listronotus setosipennis* activity in the field was first noticed only at the end of the season with 0.31% ( $n = 973$ ) of the plants showing the larval feeding damage. Evidence of *S. lutulentus* adult activity and leaf-mining by *B. parthenica* were noticed only occasionally, and *Z. bicolorata* was not recorded

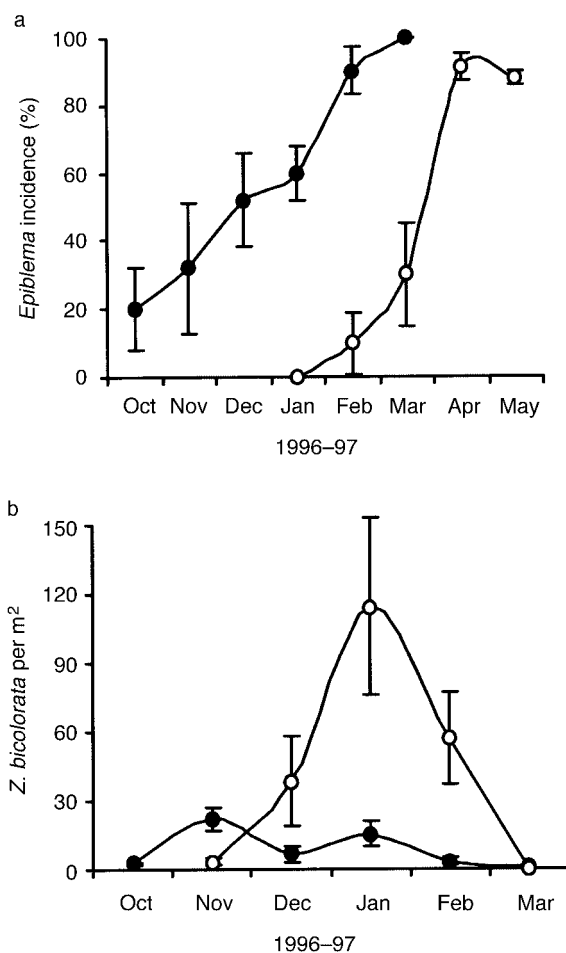


Fig. 1. Abundance of biocontrol insects in Mt Panorama and Plain Creek during 1996–97: (a) Percentage of plants with gall damage by *Epiblema strenuana* in Mt Panorama (●) and Plain Creek (○). (b) Population density of *Zygogramma bicolorata* adults (●) and larvae (○) in Mt Panorama. Vertical bars represent the standard error.

### Effect on individual plants

The biocontrol insects had a significant negative impact on plant height and flower production, but had no negative impact on root length and total plant biomass (table 1). In Mt Panorama, the rate of increase in the plant height slowed down initially in the middle of spring due to gall damage by

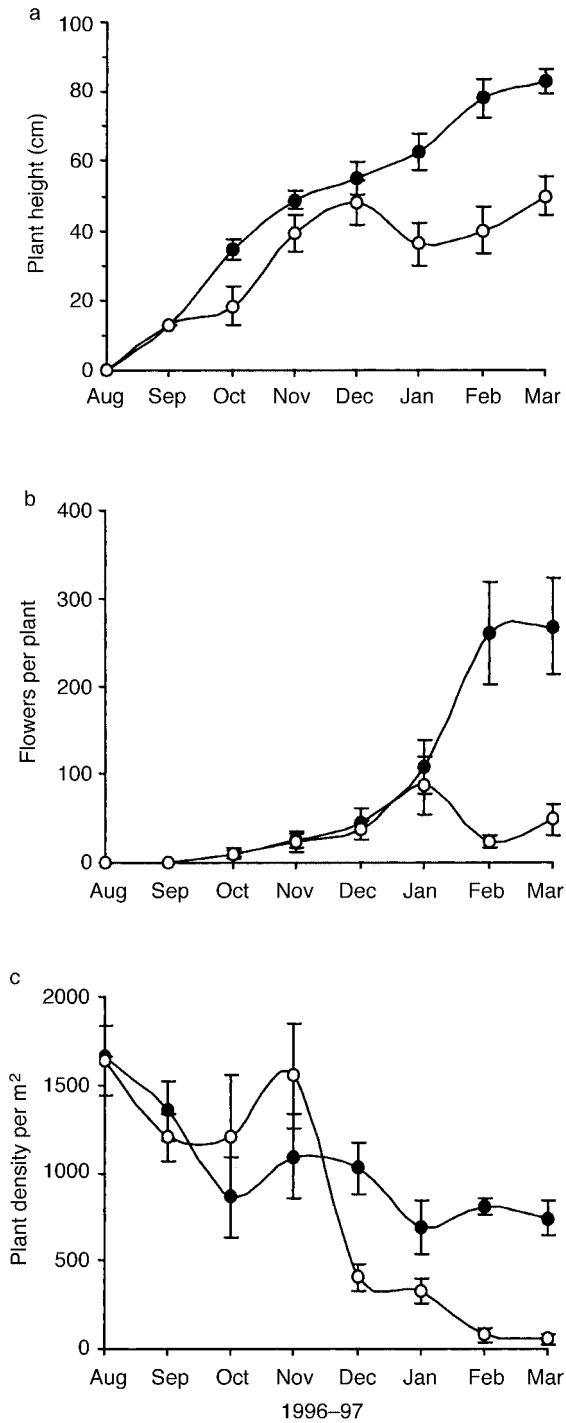


Fig. 2. Impact of biocontrol insects on (a) plant height, (b) flower production, and (c) plant density of *Parthenium hysterophorus* in Mt Panorama. ●, Plants without biocontrol insects; ○, plants with biocontrol insects. Vertical bars represent standard error.

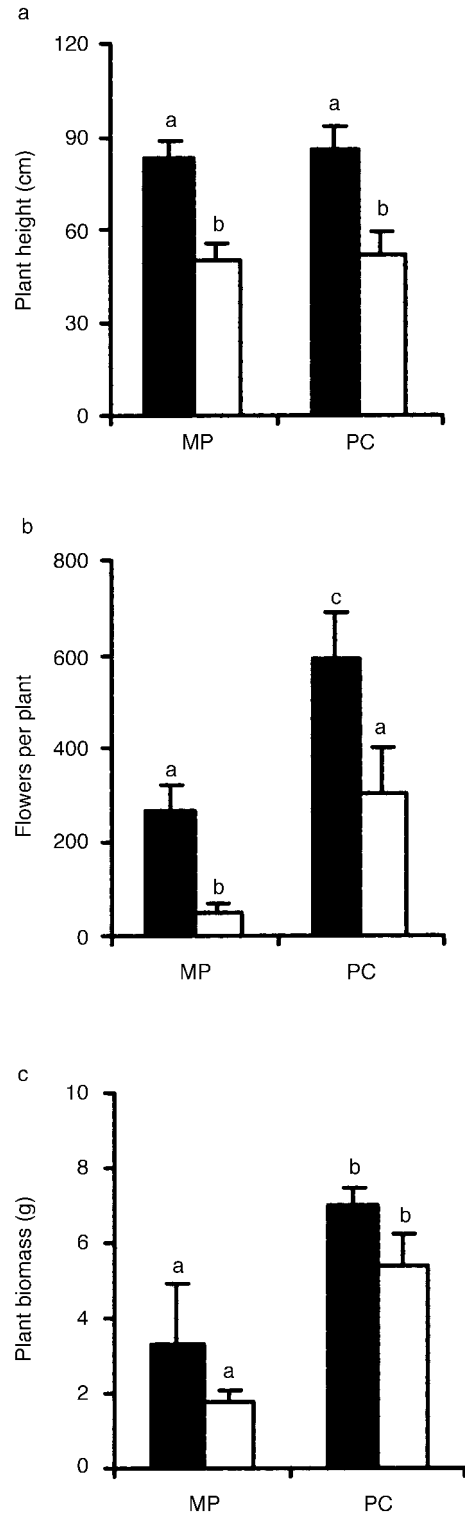


Fig. 3. Impact of biocontrol insects on (a) plant height, (b) flower production and (c) plant biomass of *Parthenium hysterophorus* in Mt Panorama (MP) and Plain Creek (PC) during 1996-97. ■, Plants without biocontrol insects; □, plants with biocontrol insects. Vertical bars represent standard error. Tukey Test: for each plant parameter, means followed by the same letter are not significantly different ( $P > 0.05$ ).

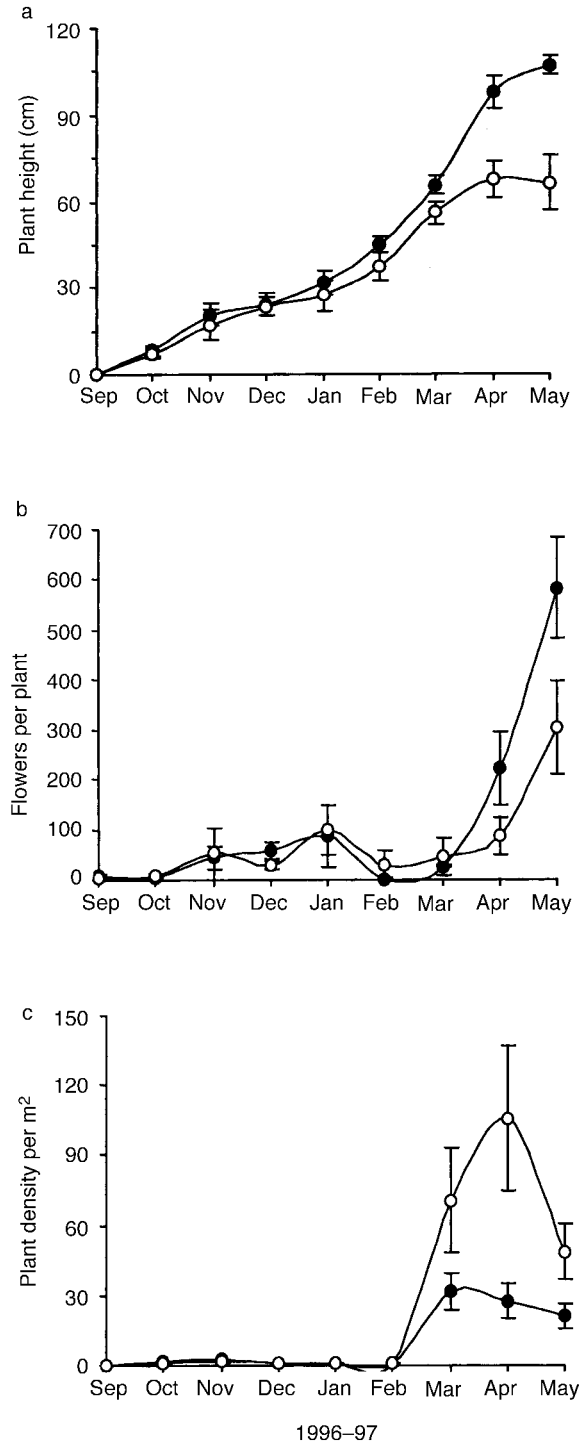


Fig. 4. Impact of biocontrol insects on (a) plant height, (b) flower production and (c) plant density of *Parthenium hysterophorus* in Plain Creek during 1996–97. ●, Plants without biocontrol; ○, plants with biocontrol. Vertical bars represent standard error.

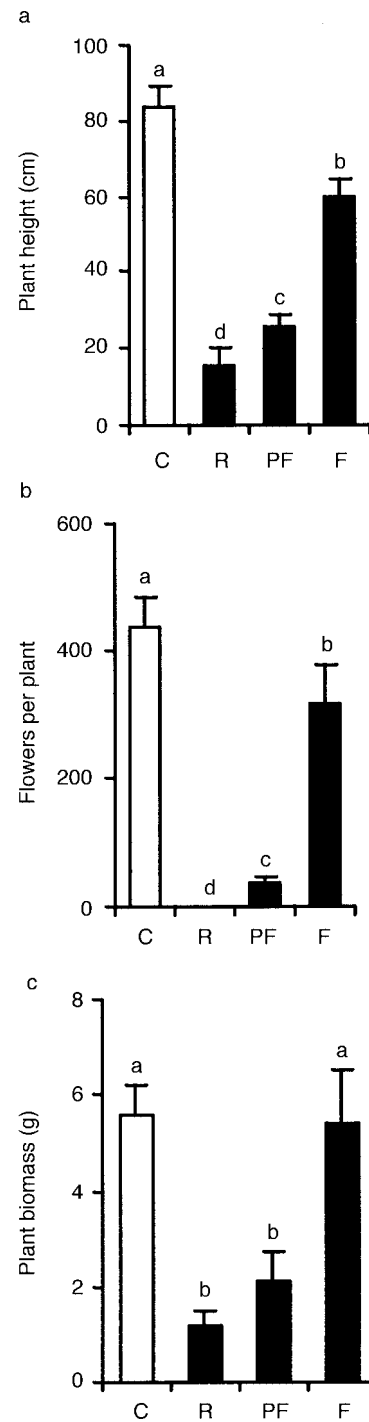


Fig. 5. Impact of gall damage by *Epiblema strenuana* at rosette (R), preflowering (PF) and flowering (F) stages of *Parthenium hysterophorus* on (a) plant height, (b) flower production and (c) plant biomass in Plain Creek during 1996–97. □, Ungalloled control (C) plants; ■, plants with gall damage. Vertical bars represent standard error. One-way ANOVA: for plant height,  $F_{3,1337} = 589.27$ ,  $P < 0.001$ ; for flower production,  $F_{3,1320} = 17.526$ ,  $P < 0.001$ ; for plant biomass,  $F_{3,1320} = 8.679$ ,  $P < 0.001$ . Tukey Test: for each plant parameter, means followed by the same letter are not significantly different ( $P > 0.05$ ).

*E. strenuana*, and again from late summer due to defoliation by *Z. bicolorata* (fig. 2a). Gall damage by *E. strenuana* did not have an immediate effect on flower production in early spring, but in combination with defoliation by *Z. bicolorata* reduced the flower production from late summer (fig. 2b). At the end of the season, gall damage by *E. strenuana* and defoliation by *Z. bicolorata* were noticed in all plants ( $n = 1041$ ), with an average of  $4.8 \pm 1.6$  galls and  $96 \pm 1\%$  defoliation in each plant. As a result, the combined effect of *Z. bicolorata*, *E. strenuana* and *L. setosipennis* at Mt Panorama reduced plant height by 40% (fig. 3a) and flower production by 82% (fig. 3b), but the impact on plant biomass was not significant (fig. 3c). Difference in the root length between galled ( $5.5 \pm 0.9$  cm) and ungalled ( $6.0 \pm 0.8$  cm) plants was also not significant (t test,  $P > 0.05$ ).

In Plain Creek, gall damage by *E. strenuana* slowed down the increase in plant height (fig. 4a) and the number of flowers produced (fig. 4b) from early autumn. By the end of the season, gall damage by *E. strenuana* reduced the plant height by 40% (fig. 3a) and flower production by 49% (fig. 3b), but the impact on plant biomass was not significant (fig. 3c). The reductions in plant height (69 and 81%), plant biomass (80 and 82%) and flower production (88 and 99%) were greater when gall damage was initiated at rosette and pre-flowering stages than at the flowering stage (fig. 5). There was also a reduction in the number of branches in galled plants ( $2.9 \pm 0.7$ ) compared to ungalled plants ( $5.2 \pm 0.5$ ) ( $t = 2.74$ ;  $df = 1391$ ;  $P = 0.015$ ). In plots with biocontrol insects, fewer plants produced flowers ( $64 \pm 10\%$ ) than in plots excluded from biocontrol insects ( $96 \pm 1.5\%$ ) ( $t = 3.12$ ;  $df = 15$ ;  $P = 0.007$ ). Among plants with gall damage initiated after flowering, 99  $\pm$  0.6% of the plants continued to produce flowers, whereas in plants with gall damage initiated at rosette and pre-flowering stages, only 28% and 65% of the plants respectively produced any flowers (one way ANOVA,  $F_{2,23} = 14.817$ ;  $P < 0.001$ ).

#### Effect on weed population

In Mt Panorama at the beginning of the trial there was no difference in the number of seedlings emerged (fig. 6a) and the soil seed bank (fig. 6b) between plots with and without biocontrol insects. However, in plots with biocontrol insects the proportion of seedlings established by early summer (19%;  $n = 3256$ ) was significantly lower ( $t = 3.71$ ;  $P = 0.002$ ) than in plots without biocontrol insects (63%;  $n = 8216$ ) (fig. 3c). Only 3% ( $n = 448$ ) of the seedlings in plots with biocontrol insects survived till the end of the season and produced flowers, as against 45% ( $n = 5936$ ) of seedlings in plots without biocontrol insects (fig. 2c). As a result of biocontrol insects, the density (fig. 7a) and total biomass (fig. 7b) of parthenium were reduced by 90% and 78%, respectively. In plots excluded from biocontrol insects, the number of seedlings emerged (fig. 6a) and the soil seed bank (fig. 6b) in the following season (1997–98) were 76% and 36% higher respectively than in plots with biocontrol insects. In plots with biocontrol insects, there was no increase in the number of seedlings emerged (fig. 6a) and the soil seed bank (fig. 6b) between the 1996–97 and 1997–98 seasons.

In Plain Creek, at the beginning of the trial, there was no difference in the number of seedlings emerged (fig. 8a) and the soil seed bank (fig. 8b) between the plots with and without biocontrol insects. There was also no difference in

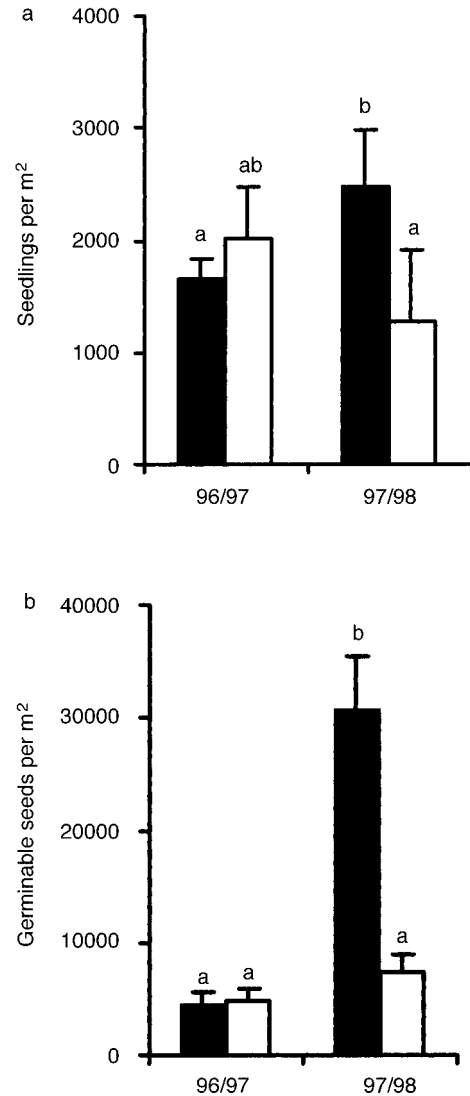


Fig. 6. Impact of biocontrol insects on (a) seedling emergence and (b) soil seed bank at the beginning (96/97) and at the end (97/98) of the trial in Mt Panorama. ■, Plots without biocontrol insects; □, plots with biocontrol insects. Vertical bars represent standard error. Two-way ANOVA for seedling emergence (a): biocontrol (with biocontrol insects  $\times$  no biocontrol insects),  $F_{1,33} = 0.781$ ,  $P = 0.383$ ; year (96/97  $\times$  97/98),  $F_{1,33} = 0.178$ ,  $P = 0.895$ ; biocontrol  $\times$  year,  $F_{1,1,33} = 4.563$ ,  $P = 0.004$ ; Two-way ANOVA for soil seed bank (b): biocontrol (with biocontrol insects  $\times$  no biocontrol insects),  $F_{1,33} = 21.00$ ,  $P < 0.001$ ; year (96/97  $\times$  97/98),  $F_{1,33} = 32.041$ ,  $P < 0.001$ ; biocontrol  $\times$  year,  $F_{1,1,33} = 21.453$ ,  $P < 0.001$ . Tukey Test: for each plant parameter, means followed by the same letter are not significantly different ( $P > 0.05$ ).

the proportion of seedlings established in plots with (26%;  $n = 3348$ ) and without (22%;  $n = 1962$ ) biocontrol insects (fig. 4c). However, only 51% ( $n = 912$ ) of the established plants in plots exposed to biocontrol insects produced flowers as against the 94% ( $n = 419$ ) of plants in plots without biocontrol insects producing flowers. This was due to gall damage initiated at early stages of plant growth, which

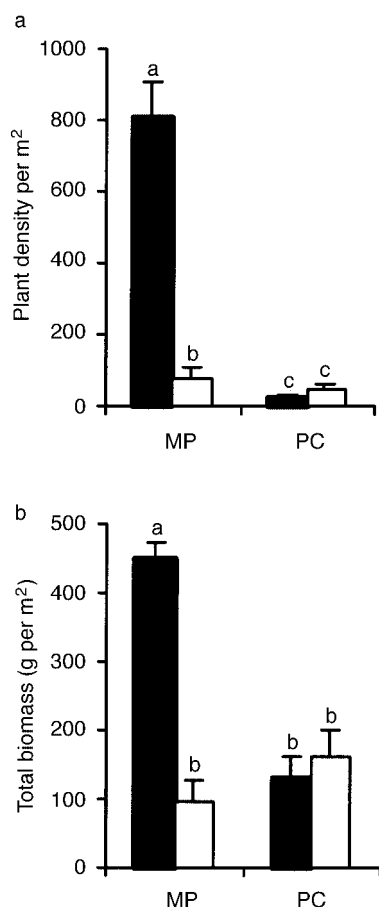


Fig. 7. Impact of biocontrol insects on (a) plant density and (b) plant biomass/m<sup>2</sup> at Mt Panorama (MP) and Plain Creek (PC) during 1996–97. ■, Plots without biocontrol insects; □, plots with biocontrol insects. Vertical bars represent standard error. Two-way ANOVA for plant density (a): biocontrol (with biocontrol insects × no biocontrol insects),  $F_{1,33} = 34.285$ ,  $P < 0.001$ ; location (Mt Panorama × Plain Creek),  $F_{1,33} = 243.461$ ,  $P < 0.001$ ; biocontrol × location,  $F_{1,1,33} = 53.290$ ,  $P < 0.001$ ; Two-way ANOVA for plant biomass per m<sup>2</sup> (b): biocontrol (with biocontrol insects × no biocontrol insects),  $F_{1,33} = 22.712$ ,  $P < 0.001$ ; location (Mt Panorama × Plain Creek),  $F_{1,33} = 36.884$ ,  $P < 0.001$ ; biocontrol × year,  $F_{1,1,33} = 59.765$ ,  $P < 0.001$ . Tukey Test: for each plant parameter, means followed by the same letter are not significantly different ( $P > 0.05$ ).

prevented 87% ( $n = 308$ ) of plants with gall damage initiated at the rosette stage and 35% ( $n = 246$ ) of plants with gall damage initiated at the pre-flowering stage from producing any flowers. However, there was no reduction in the density (fig. 7a) and total biomass (fig. 7b) of parthenium due to biocontrol insects. In plots without biocontrol insects, the number of seedlings that emerged in the following season (1997–98) was 71% higher than in plots with biocontrol insects (fig. 8a). However, there was no difference in the soil seed bank in the following (1997–98) season (fig. 8b) between plots with and without biocontrol insects.

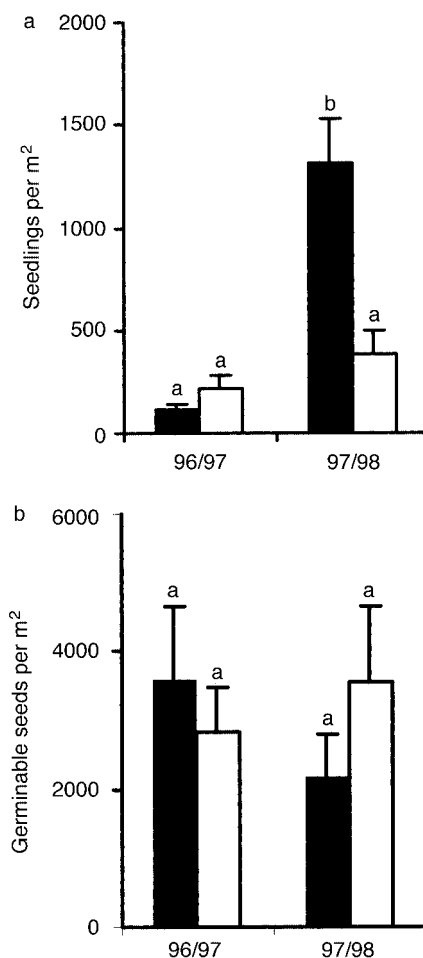


Fig. 8. Impact of biocontrol on (a) seedling emergence and (b) soil seed bank at the beginning (96/97) and at the end (97/98) of the trial in Plain Creek. ■, Plots without biocontrol insects; □, plots with biocontrol insects. Vertical bars represent standard error. Two-way ANOVA for seedling emergence (a): biocontrol (with biocontrol insects × no biocontrol insects),  $F_{1,33} = 13.883$ ,  $P < 0.001$ ; year (96/97 × 97/98),  $F_{1,33} = 41.879$ ,  $P < 0.001$ ; biocontrol × year,  $F_{1,1,33} = 16.920$ ,  $P < 0.001$ ; Two-way ANOVA for soil seed bank (b): biocontrol (biocontrol × no biocontrol),  $F_{1,33} = 0.135$ ,  $P = 0.176$ ; year (96/97 × 97/98),  $F_{1,33} = 0.003$ ,  $P = 0.959$ ; biocontrol × year,  $F_{1,1,33} = 0.794$ ,  $P = 0.380$ . Tukey Test: for each plant parameter, means followed by the same letter are not significantly different ( $P > 0.05$ ).

## Discussion

### *Measuring the success of biocontrol*

Smith & DeBach (1942) used the following three criteria as measures of the success of a biocontrol programme: (i) reduction in the pest populations; (ii) maintenance of pest populations at a low level following the establishment of natural enemies; and (iii) higher rate of survival of the pest populations when protected from the natural enemies than when exposed. Results from the current insect exclusion trial indicate that at Mt Panorama (central Queensland), the parthenium biocontrol programme meets Smith & DeBach's

first and third criteria, as evident by a significant reduction in the weed population and a high survival rate of the weed population if protected from biocontrol insects. The increased effectiveness of biocontrol insects at Mt Panorama relative to Plain Creek was primarily due to defoliation by *Z. bicolorata*, but galling by *E. strenuana* and stem and root damage by *L. setosipennis* augmented the impact of *Z. bicolorata*. Results at Plain Creek (north Queensland) did not meet any of the three criteria, as there was no reduction in the weed population, but there was a significant reduction in plant vigour. With only one year of data, the second criterion of a successful biocontrol programme, that the weed population continues to remain at a low level, could not be tested. The impact of biocontrol insects on parthenium measured in the present study suggests that the weed population would have been higher without the biocontrol insects, thus indirectly meeting Smith & DeBach's second criterion.

#### *Abundance of biocontrol agents*

At both sites, incidence of galling by *E. strenuana* when parthenium was at the rosette stage was low. This was due to lack of synchrony between parthenium germination and *E. strenuana* emergence (McFadyen, 1992; Dhileepan & McFadyen, 2001). Prevalence of gall damage increased with the plant growth, as the plant growth was positively related to survival of gall inducers (Price *et al.*, 1987; Anderson *et al.*, 1989; Craig *et al.*, 1989; Abrahamson & Weis, 1997; Prado & Vieira, 1999).

At Mt Panorama, first generation *Z. bicolorata* larvae caused complete defoliation by late summer and the first generation adults emerged in early to mid autumn migrated to adjacent areas with dense parthenium, as there was no parthenium with undamaged leaves left in the trial area. This was evident from the lack of any oviposition on the defoliated plants within the trial site. Jayanth & Visalakshi (1994) reported that in India also, *Z. bicolorata* migrated to adjacent areas after defoliating parthenium plants in a particular area. In Russia, ovipositing females of *Zygogramma suturalis* Fabricius (Coleoptera: Chrysomelidae) avoided defoliated plants of ragweed *Ambrosia artemisiifolia* L. (Asteraceae) and instead preferred undamaged plants (Reznik, 1991).

Except for *L. setosipennis* at Mt Panorama, the incidence of other biocontrol insects was sporadic and did not appear to have had any measurable impact on the weed population. At Mt Panorama, in spite of signs of oviposition by *L. setosipennis*, no larval feeding damage was noticed at the end of the season. Since both *E. strenuana* and *L. setosipennis* damaged the same part of the plant, it is possible that the more aggressive *E. strenuana* larvae had displaced the *L. setosipennis* larvae.

In the field, emergence of *S. lutulentus* is not perfectly synchronized with the phenology of parthenium (McClay, 1979). As a result, *S. lutulentus* activity in the field was evident either at the beginning (spring) or at the end of the season (autumn), but not consistently throughout the flowering season.

#### *Effect of biocontrol on individual plants*

Galling by *E. strenuana*, when initiated at the early stages of plant growth, damaged the meristem and reduced the

plant height (Dhileepan & McFadyen, 2001). Similar results have been reported for other galling insects also (Hartnett & Abrahamson, 1979; Fay *et al.*, 1996; Price & Louw, 1996; Abrahamson & Weis, 1997). At Mt Panorama, all galled plants produced flowers, irrespective of the plant stage at which the galling was initiated and the number of galls per plant. At Plain Creek, in more than 50% of the plants, *E. strenuana* gall damage was initiated before the plant attained the flowering phase, and as a result prevented 32% of plants from producing any flowers. Similar effects due to gall damage by *E. strenuana* at early stages of plant growth have been reported under field cage conditions (Dhileepan & McFadyen, 2001). The increased negative impact of gall damage on plant growth and survival, when initiated at early stages of plant growth is due to limited resource availability and decreased net productivity (Hartnett & Abrahamson, 1979).

Of the four species of biocontrol agents damaging parthenium in Mt Panorama, defoliation by *Z. bicolorata* from the early stages of plant growth was largely responsible for the reduction in plant vigour. Other studies have shown that extended defoliation pressure by *Z. bicolorata* on parthenium results in the reallocation of resources from the root to shoot regrowth, with significant reduction in root biomass and flower production (Dhileepan *et al.*, 2000a). Defoliation by *Z. bicolorata* damaged the primary meristem resulting in changed branching pattern and reduced plant height (Dhileepan *et al.*, 2000a,b). In India, a single adult *Z. bicolorata* per plant caused 85–100% defoliation within six to eight weeks, depending on the stage of plant growth (Jayanth & Bali, 1994). Similarly, defoliation by *Z. bicolorata* alone on parthenium in the field reduced the plant height by 18–65%, plant biomass by 55–89% and flower production by 75–100% (Dhileepan *et al.*, 2000b).

Infestation by *L. setosipennis* was negligible at both sites and had no measurable impact on parthenium plants. Parthenium can compensate for the damage by low larval densities of *L. setosipennis* and very high larval densities are required to have any significant negative impact on the weed (Dhileepan *et al.*, 1996). The very low population levels of *S. lutulentus* recorded at both trial sites appear not to have had any measurable impact on parthenium. To reduce the seed production by 50% in a parthenium plant with around 5000 flowers, a population of >20 *S. lutulentus* weevils per plant is required (Dhileepan *et al.*, 1996).

#### *Effect of biocontrol on weed population*

At Mt Panorama, defoliation by *Z. bicolorata* and gall damage by *E. strenuana*, from the early stages of plant growth, reduced the weed density by 90% and weed biomass by 78%. In India, 85–100% defoliation by *Z. bicolorata* resulted in up to 96% reduction in parthenium weed density (Jayanth & Bali, 1994; Jayanth & Visalakshi, 1996). A study of ragwort *Senecio jacobaea* L. (Asteraceae) showed that plant populations declined by more than 99% following the successful establishment of three biocontrol agents (McEvoy *et al.*, 1991). At Plain Creek, gall damage by *E. strenuana* did not reduce the weed density and weed biomass, but did prevent 32% of plants with gall damage initiated at early stages of plant growth from producing any flowers. In *S. jacobaea* also, the impact of biocontrol agents varied with the size and stage structures of the plant population, with smaller, younger plants suffering the most

(McEvoy *et al.*, 1991). At Mt Panorama and Plain Creek, in spite of the reductions in flower production due to biocontrol insects, the soil seed bank and the number of seedlings emerged in plots with biocontrol insects were not significantly different between 1996–97 and 1997–98. This was due to the very high soil seed bank accumulated over the past two decades (Dhileepan *et al.*, 2000b). However in Mt Panorama, in plots excluded from biocontrol insects, there was a significant increase in the number of seedlings emerged in 1997–98 compared to 1996–97. At Plain Creek, the number of seedlings emerged in plots excluded from biocontrol insects increased significantly in 1997–98 compared to 1996–97, but there was no significant reduction in the soil seed bank. This suggests that without biocontrol insects, more flowers would have been produced resulting in an increased soil seed bank and consequently higher weed density.

Parthenium seeds persist in the soil for a long time, with approximately 50% of the seed bank viable for up to six years (Navie *et al.*, 1998b). As the seeds persist in soil where they are unaffected by the biocontrol agents (McEvoy *et al.*, 1991), defoliation by *Z. bicolorata* in Mt Panorama would have to continue for several more years with very little or no further contribution to the soil seed bank, until the existing soil seed bank is depleted (Dhileepan *et al.*, 2000b). In Plain Creek, since the galling does not kill the plants, a reduction in the weed population could be achieved only through a reduction in contribution to the soil seed bank. To have substantial negative effects on flower production, *E. strenuana* adults need to emerge and increase their populations in synchrony with parthenium seedling emergence (Dhileepan & McFadyen, 2001).

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