

## Gall-inducing insects and biological control of *Parthenium hysterophorus* L. (Asteraceae)

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### Summary

Weeds invade agricultural ecosystems and degrade productive land. *Parthenium hysterophorus*, introduced accidentally into Australia from the United States of America, not only affects productive land, but also causes severe health problems to humans. Since gall-inducing arthropods are increasingly becoming useful in weed management campaigns, we discuss in this paper the benefits of using gall-inducing insects in the biological control of weeds, targeting *P. hysterophorus* which is a major problem weed in Queensland. We evaluate the capability of two gall-inducing insects against *P. hysterophorus*. The gall-inducing moth, *Epiblema strenuana* and the gall-inducing weevil, *Conotrachelus albocinereus* display significant morphological and physiological impacts on *P. hysterophorus* indicating them to be effective organisms for use in biological control in Australia.

### Introduction

*Parthenium hysterophorus* L. (parthenium weed, white top, false ragweed) was accidentally introduced into Australia from the United States of America. It was first recorded in Queensland in the 1950s (Everist 1976). At present it is reported throughout much of Queensland and occurs in small pockets along roadsides in northern New South Wales (McFadyen 1995) and in the Northern Territory (Navie *et al.* 1996). In the last two decades, this species has caused severe economic and ecological impacts in Queensland. It has spread to nearly 170 000 km<sup>2</sup> in Queensland with an estimated loss of farm productivity up to 40% (Chippendale and Panetta 1994). It is a serious health hazard and induces allergic dermatitis, hay fever and asthma in more than 20% of the exposed population (McFadyen 1995, Cheney 1998). Management of this species is expensive (Chippendale and Panetta 1994) and control programs from 1977 to 1992 have cost nearly \$3.5 m in Australia (McFadyen 1992). Severe economic and health

problems due to parthenium also occur in several parts of Asia, Africa and the Caribbean (Navie *et al.* 1996, Mahadevappa 1997).

*Parthenium hysterophorus* is a vigorous and fast-growing annual plant that produces nearly 60 000 florets, each bearing one seed (K. Dhileepan, unpublished observations). The seeds persist in the soil for a long time, with nearly 50% of the seed bank remaining viable up to six years (Navie *et al.* 1998).

Different chemical, biological and cultural methods have been adopted to manage this weed in Australia and in other parts of the world. Use of herbicides has proved uneconomic (Holman and Dale 1981). Biological control offers great potential to minimize and manage *P. hysterophorus*, especially in the heavily-infested areas of Central Queensland (McFadyen 1992).

As an effort towards biological control, nine insect species and one pathogenic rust fungus from Central America were released in Queensland between 1980 and 1999 (Table 1). Among these, a gall-inducing moth, *Epiblema strenuana* Walker (Lepidoptera: Tortricidae) and a gall-inducing weevil, *Conotrachelus albocinereus* Fiedler (Coleoptera: Curculionidae) appear to have the potential for controlling *P. hysterophorus* (McFadyen 1992, Dhileepan *et al.* 1996, Raman and Dhileepan 1999, Treviño *et al.* 1999, McFadyen 2000). This paper discusses the strengths and advantages of using the gall moth and the gall weevil for the management of *P. hysterophorus*, as well as summarizes the benefits in using galling arthropods in weed management and the

**Table 1. Biological control agents released in *P. hysterophorus*-infested areas in Australia.**

Biological control agents	Country of origin	Year of release	Year of establishment	Biology on host	Impact	References
<i>Bucculatrix parthenica</i> (Lepidoptera: Bucculatricidae)	Mexico	1984–85	na	Leaf mining	+	McClay <i>et al.</i> (1990)
<i>Conotrachelus albocinereus</i> (Coleoptera: Curculionidae)	Argentina	1995–97	2000	Stem galling	na	McFadyen (2000)
<i>Carmenta ithacae</i> (Lepidoptera: Sesiidae)	Mexico	1998–99	2000	Root boring	na	Dhileepan (pers. obs.)
<i>Epiblema strenuana</i> (Lepidoptera: Tortricidae)	Mexico	1982–85	1983	Stem galling	+++	McFadyen (1989)
<i>Listronotus setosipennis</i> (Coleoptera: Curculionidae)	Brazil and Argentina	1982–86	1983	Stem boring	++	Wild <i>et al.</i> (1992)
<i>Platphalonida mystica</i> (Lepidoptera: Tortricidae)	Argentina	1992–96	na	na	na	Dhileepan and McFadyen (1997)
<i>Smicronyx lutulentus</i> (Coleoptera: Curculionidae)	Mexico	1981–83	1996	Seed feeding	+	McFadyen and McClay (1981)
<i>Stobaera concinna</i> (Hemiptera: Delphacidae)	Mexico	1983–85	1992	Sap sucking	Nil	Dhileepan and McFadyen (1997)
<i>Zygomma bicolorata</i> (Coleoptera: Chrysomelidae)	Mexico	1981–83	1990	Leaf feeding	+++	Dhileepan and McFadyen (1997)
<i>Puccinia abrupta</i> var. <i>parthenicola</i> (Fungi: Uredinales)	Mexico	1992	1994	Pustule forming on leaves	na	Dhileepan and McFadyen (1997)

+ = low. ++ = moderate. +++ = high. na = data unavailable.

nature of physical and physiological damage caused by these arthropods.

### Why gall-inducing insects hold promise in weed control?

Use of plant-feeding arthropods and pathogenic fungi is preferred in weed management programs, because such a practice is ecologically sound and economically viable (Shepherd 1993). Gall-inducing insects have played a key role in biological weed control activities throughout the world (Julien and Griffiths 1998). Among plant-feeding insects, only those belonging to 20 Families classified under seven Orders have the ability to induce galls on their host plants. Within the broad context of insects used in weed biological control, only 2% of them are gall inducers (Meyer 1987). Gall-inducing insects have a narrow host range and they severely impair the growth and development of the host plant (Harris and Shorthouse 1996). They induce structural (Lalonde and Shorthouse 1984, Raman and Dhileepan 1999) and metabolic changes (Daley and McNeil 1987, Paquette *et al.* 1992, Raman 1994) in the host plant. Their ability to significantly affect host-plant growth and metabolism, and their narrow host range indicate that they could be an ideal group for the biological control of weeds. The gall weevil, *Rhinocyllus conicus* (Coleoptera: Curculionidae) on the thistles (*Carduus nutans* and *C. acanthoides*) (Shorthouse and Lalonde 1984); the seed-fly, *Urophora cardui* (Diptera: Tephritidae) on *Cirsium arvense*; the fly, *Pegomya cutricornis* (Diptera: Anthomyiidae) on *Euphorbia virgata* and *E. esula* (Shorthouse and Gassmann 1994); the stem-gall fly, *Procecidochares utilis* (Tephritidae: Diptera) on *Eupatorium adenophorum* (Swaminthan and Raman 1981) are some of the well documented examples of gall inducers used in weed management practice.

Larvae of gall-inducing arthropods feed actively on flower heads (Lalonde and Shorthouse 1984), stems (Gassmann and Shorthouse 1990, Raman and Dhileepan 1999), leaves (West and Shorthouse 1981) and roots (Shorthouse and Gassmann 1994). This process creates a nutrient sink (Jankiewicz *et al.* 1970) in the galled region and thus weakens the host-plant metabolism. Gall-inducing arthropods exist in adverse environmental conditions such as deserts and saline marshes, since they are better adapted and acclimatized to those conditions than are their free-living relatives (Fernandes and Price 1991, Tscharrntke 1988). The gall being a 'concealed' habitat, made of several layers of host-plant tissue, protects the inducers from extreme environmental situations (Martel 1995). Summarizing the impact of gall inducers on the management of noxious plants, Harris and Shorthouse

(1996) indicate the vulnerability of the host plant to moisture stress and the gall acting as a metabolic sink as the key strengths in using gall insects in weed management.

### Mechanism of damage by gall-inducing insects

Gall-inducing insects play a major role in redirecting photo-assimilates from the active meristems of the host to the gall site (Abrahamson and Weis 1987). An active gall performs as a metabolic sink trapping the nutrients and transporting them to tissues lying close to larva, through localized cellular modifications (Raman 1987, Rohfritsch 1988). Galls act as sinks of energy as well, to subserve the nutritional needs of the parasitic galler (Stinner and Abrahamson 1979, Raman and Abrahamson 1995). High levels of soluble nutrients such as the sugars and amino acids exist in the feeding layers of tissues in galls (Raman 1994). In the galls induced by *Phanacis taraxaci* on the common dandelion (*Taraxacum officinale*), up to 70% of carbon was redirected to the gall, to provide nutrition to the growing larva (Bagatto *et al.* 1996). In addition to photo-assimilates, galls accumulate mineral nutrients in their specialized nutritive tissue (Abrahamson and McCrear 1985, Shorthouse and Gassmann 1994). During early stages of development of galls induced by *Hemadas nubilipennis* on *Vaccinium angustifolium*, minerals such as copper, nickel, iron and zinc remained higher in the galled tissue than in the ungalled tissue (Bagatto and Shorthouse 1994, Shorthouse *et al.* 1986). Early developmental pressure of galls acting as the nutrient sinks for the inhabiting insect increases energy allocation from the storage reserves of the plant organ; in some instances, the development of the insect progeny depends on the resources mobilized at the galled organ (e.g. leaf) and from the immediate neighbourhood. Such an activity of drawing resources from the neighbourhood represents active manipulation of the normal host-transport mechanisms by the gall inducer (Larson and Whitham 1991).

### *Epiblema strenuana*/*C. albocinereus* and *P. hysterothorus* interactions Natural history of *E. strenuana* and *C. albocinereus*

*Epiblema strenuana* lays eggs on young leaves of *P. hysterothorus*. Emerging larvae mine the leaf briefly, then move to the closest vegetative axillary meristems. They enter the stem and their feeding action induces a gall. After considerable movement down the stem, the larvae turn by 180° and commence feeding in an upward direction (Figure 1). When larvae stop feeding, cells in that area degenerate and die. Pupal stage ranges between four and six days, and adult moths emerge



**Figure 1.** *Epiblema strenuana*-induced gall on *P. hysterothorus*, cut open longitudinally to show the mature larva (scale bar: 1 mm).

through a window cut by the mature larva before pupation (McFadyen 1986, Raman and Dhileepan 1999).

The weevil, *C. albocinereus* is active at night and feeds on the stems and leaves of *P. hysterothorus*. Adults live for up to three months. The female weevil chews the epidermal and outer cortical tissue of the shoot. She lays eggs singly in the feeding scar sites and sometimes on leaf axils and covers them with frass. A neonate larva bores directly into the stem (Figure 2). The larvae remain inside the gall until mature, and then move to the soil for pupation (McFadyen 2000).

### Impact of *E. strenuana* and *C. albocinereus* on *P. hysterothorus*

Trial infestations of *E. strenuana* on about 50 plant species belonging to 28 families indicate that this moth caused a powerful impact on *P. hysterothorus* in particular (Jayanth 1987). *E. strenuana* only attacks related species such as the annual ragweed (*Ambrosia artemisiifolia*), perennial ragweed (*A. psilostachya*) and noogoora burr (*Xanthium pungens*) (McClay 1987). *E. strenuana* attacks different developmental stages of *P. hysterothorus* (rosette, pre-flowering and flowering stages) and induces galls of different morphologies; younger shoots respond with vigorous, spherical galls and older shoots with weaker, fusiform galls (Raman and Dhileepan 1999). Field investigations on the impact of *E. strenuana* on parthenium,

demonstrate that rates of infestation range between 7 and 55, 43 and 90, 85 and 95% on the rosette, pre-flowering, and flowering stages, respectively. The average number of galls per plant increased with age. Further, *E. strenuana*, reduced the number of plants attaining the flowering stage by 45% and reduced flower production by 38% (Dhileepan and McFadyen 1997). Presence of *E. strenuana* larvae on *P. hysterophorus* reduced plant height, mature capitula, and viable seeds by 34, 74, and 74%, respectively (Navie *et al.* 1998).

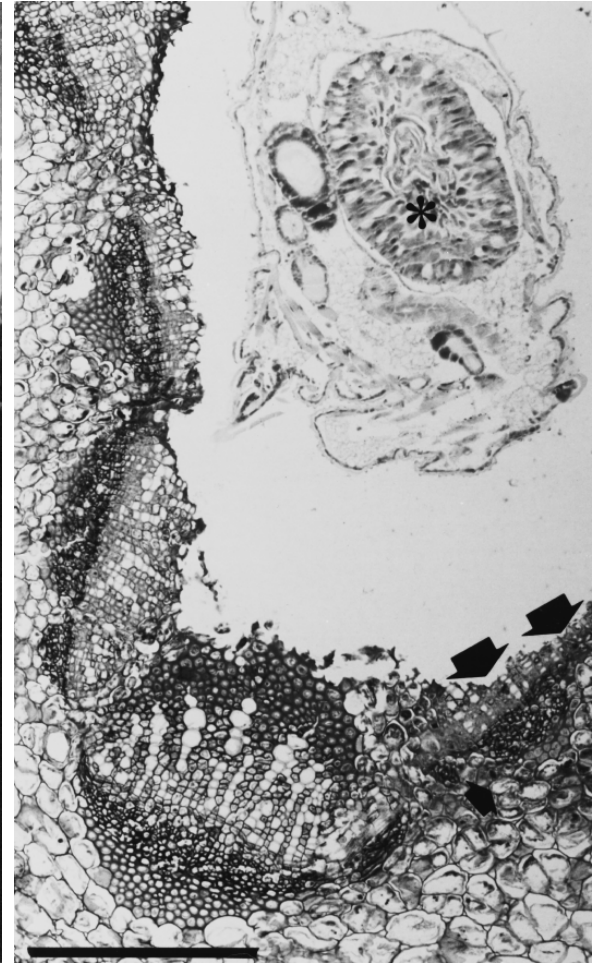
Host specificity studies on *C. albocinereus* prior to their release in Australia gave the following results. Of 36 genera of Asteraceae tested, *C. albocinereus* fed only on *P. hysterophorus* and its close relative, *Ambrosia artemisiifolia* (McFadyen 1993). Under controlled, glasshouse conditions, the release of 10 *C. albocinereus* larvae per plant reduced the plant height by 34%, root biomass by 41%, number of mature capitula by 21%, and viable seed set by 18%. There was also a strong impact on the pre-flowering stage of *P. hysterophorus* by reducing the formation of mature capitula and viable seeds by 46 and 47%, respectively (David 1998).

Both *E. strenuana* and *C. albocinereus* induce single-chambered galls 1–2 cm long and 1 cm wide. Galls are initiated by larval feeding on the central cortical callus parenchyma and such a stimulus induces the stem to enlarge and grow into galls (Figure 3).

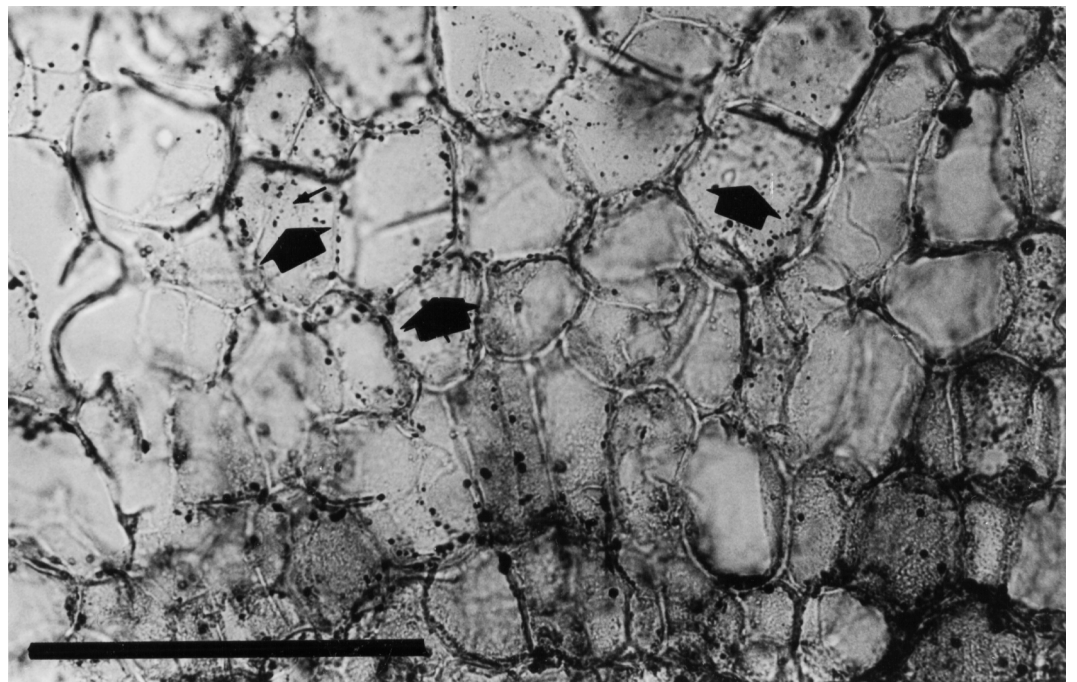
Larval feeding activity of *E. strenuana* impacts on *P. hysterophorus* by rendering the phloem and associated vascular parenchyma inactive. Intense feeding fractures the vascular traces and consequently plant parts above the gall suffered vigour loss due to disruption of fluid movement. Organic nutrients (e.g. starches and lipids) synthesized by the host plant are mobilized rapidly at the gall sites (Figure 4) to provide nutrition for the developing larvae. The active metabolic response of the host plant by synthesizing and accumulating secondary metabolites in the galled region and the physical action of



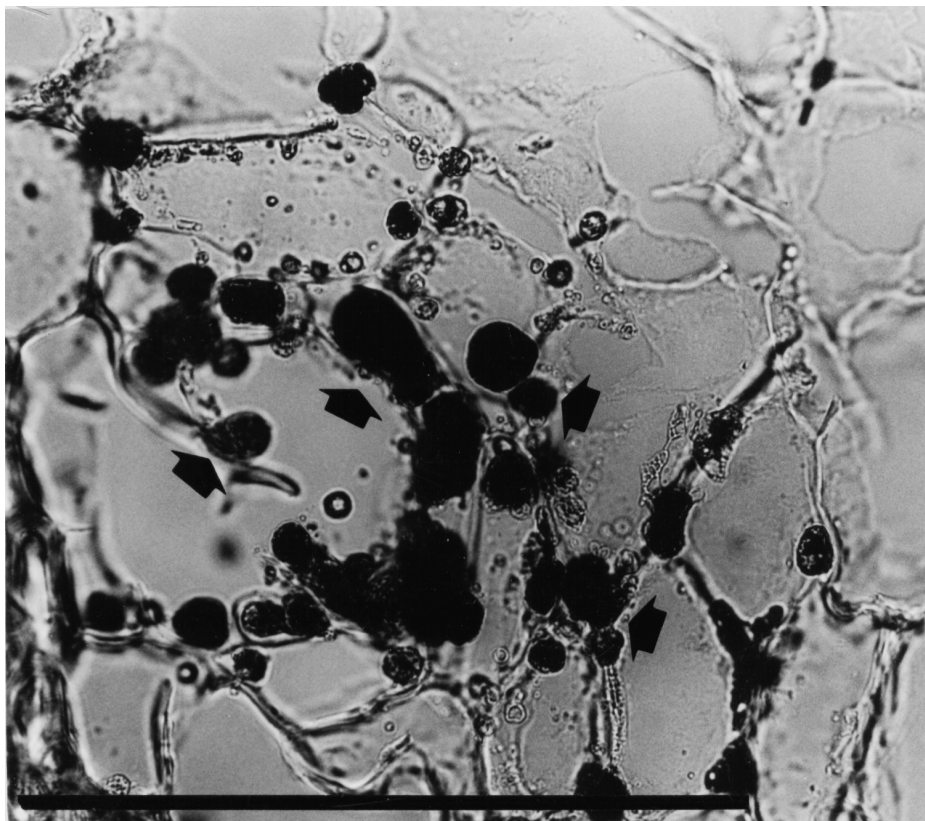
**Figure 2.** *Conotrachelus albocinereus*-induced gall on *P. hysterophorus* cut open longitudinally to show a young larva (scale bar: 1 mm).



**Figure 3.** Mature gall induced by *Epiblema strenuana* (cross sectional view), showing the feeding damage by larva (\*) disrupting the vascular cylinder and the cortical parenchyma (arrows: nutritive cells, scale bar: 100  $\mu$ m).



**Figure 4.** Mature gall induced by *Epiblema strenuana* (cross sectional view). Parenchymatous nutritive tissue (arrows: lipid droplets, differential staining with oil o' red, Jensen 1964) (scale bar: 100  $\mu$ m).



**Figure 5. Mature gall induced by *C. albocinereus* (cross sectional view). Parenchymatous nutritive tissue around the vascular trace (arrows: starch, differential staining with I-KI, Jensen 1964) (scale bar: 100  $\mu$ m).**

the larva by placing the frass at the fractured vascular strands stall the development of reparatory vascular bridges. In young galls, polysaccharides were mobilized through interfascicular parenchyma to cells in close proximity to the larvae (Raman and Dhileepan 1999). As in the galls induced by *E. strenuana*, the young galls of *C. albocinereus* also accumulate starches and lipids in cells close to the larval head (Figure 5). With the growth of the gall, supplementary nutrients (e.g. minerals), which would otherwise be available for the plant's growth and reproduction, are transported to the growing gall. Such a draining effect places *P. hysterophorus* under a severe physiological stress (Raman and Dhileepan 1999). In mature galls, the stem epidermal cells show active proliferation, especially around the stomata, pushing them outwards. The stomata at the summits of the elevated regions remain permanently closed.

### Discussion

Models evaluating the biological control efficiency of a few tephritids and Coleoptera that induce galls on some weedy Asteraceae are available (Harris and Shorthouse 1996). The *Sphenoptera jugoslavica* (Coleoptera: Buprestidae)–*Carduus nutans* system is similar to the *P. hysterophorus*–*E. strenuana*–*C. albocinereus* system, although *S. jugoslavica* attacks the shoot-root transition zone and induces

galls in the roots of *C. nutans* (Harris and Shorthouse 1996). However, *S. jugoslavica*, *E. strenuana* and *C. albocinereus* share a few common behavioural traits: all feed and stimulate development of callus parenchyma, rupture vascular connections and deposit frass between the disconnected vascular strands in mature galls.

As gall-inducers, *E. strenuana* and *C. albocinereus* manipulate the normal metabolic pathways of *P. hysterophorus*, to maintain a continuous supply of nutrients for their development and survival. Consequently, they place their host plant under an intense metabolic stress, particularly when attacked by large insect populations. Although both infest *P. hysterophorus* under similar temporal and spatial regimes, the gall-inducing behaviour of the two differs, especially at the time of gall initiation. The moth larva preferentially travels over a distance from tender, expanded foliage to the vegetative axillary bud. The weevil larva does not move at all; from the site of oviposition, soon after emergence, it bores through the stem tissues and places itself deeper in the cortical region. The first larval instar of the gall moth destroys the vegetative axillary meristem by its feeding action and thereby removes the potential site for further infestation by other gall moth larvae. Although this reduces competition within populations of *E. strenuana*, *P. hysterophorus* responds by producing new

vegetative axillary buds which grow into new branches; such a process creates higher numbers of sites for infestation by gall-moth populations. The result is greater opportunity for the gall-moth populations to attack and damage an individual plant.

Loss of contour of the stomatal aperture probably results in higher rates of transpiration in the galled regions, and this in turn increases importation of nitrogenous material through xylem and associated parenchyma (Zwölfer and Arnold-Reichert 1993), and eventually intensifying stress in the host tissue. Such a development becomes critical in the shoot galls of parthenium because it affects portions of shoot beyond the gall. *E. strenuana* and *C. albocinereus* place frass between the fractured vascular traces and that prevents the vascular tissues from establishing reparatory bridges. This process affects the host plant's recovery processes. Assessments of biological control agents released on *P. hysterophorus* indicate that *E. strenuana* has proliferated both extensively and vigorously causing severe impact on the rosette stages of *P. hysterophorus* in particular (McFadyen 1992).

Galls protect the larvae of *E. strenuana* and *C. albocinereus* from extremes of dry and wet environmental conditions that prevail in Queensland (McFadyen 1992, Dhileepan *et al.* 1996). This insect-plant relationship helps the concealed biological control agents, such as the gall inducers to proliferate, and provides an advantage over the biological control agents that feed externally.

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