Effects of gall induction by *Epiblema strenuana* on gas exchange, nutrients, and energetics in *Parthenium hysterophorus*

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Abstract. Gall induction by arthropods results in a range of morphological and physiological changes in their host plants. We examined changes in gas exchange, nutrients, and energetics related to the presence of stem galls on *Parthenium hys terophorus* L. (Asteraceae) induced by the moth, *Epiblema strenuana* Walker (Lepi doptera: Tortricidae). We compared the effects of galls on *P. hysterophorus* in the rosette (young), pre flowering (mature), and flowering (old) stages. Gall induction reduced the leaf water potential, especially in flowering stage plants. In young and mature stage plants, galling reduced photosynthetic rates considerably. Gall induction reduced the transpiration rate mostly in mature plants, and this also diminished stomatal conductance. Energy levels in most galls and in shoot tissue immediately below the galls were significantly higher than the energy levels in stem tissue imme diately above the galls, indicating that the gall acts as a mobilizing sink for the moth. Galling had significant effects on concentrations of minerals such as boron, chloride, magnesium, and zinc. In galled plants, reduced leaf water potential and reduced rates of photosynthesis, transpiration, and stomatal conductance may have altered mineral element levels. These observed effects demonstrate that *E. strenuana* has the potential to regulate *P. hysterophorus*.

Key words: Asteraceae, biological control, changes in mineral contents, energetics, *Epiblema strenuana*, *Parthenium hysterophorus*, stem galling moth, Tortricidae

Introduction

Gall-inducing insects have highly specialized and intimate nutritional relationships with their host plants because such insects spend a major part of their life within the gall (Shorthouse and Rohfritsch, 1992; Raman, 1996). Galls arise from modification of the structure and

metabolism of plants. Modifications, from simple removal of tissue (Dreger-Jauffret and Shorthouse, 1992) or physical damage to vascular tissue (Raman and Dhileepan, 1999), to complex manipulation of synthesis and transportation of host-plant nutrients (Rohfritsch, 1988; Bronner, 1992) affect the life history performance of host plants (Abrahamson and Weis, 1987). Gall induction by insects reduces photosynthetic and transpiration efficiencies, stomatal conductance, and water potential in plants (Flinn et al., 1990; Larson, 1998), eventually leaving the host plant stressed (Abrahamson and Weis, 1987; Raman, 1994; Florentine et al., 2001). The gall becomes a sink for nutrients (Kirst and Rapp, 1974; Larson and Whitham, 1991; Fay et al., 1993), which would otherwise be used by the plant for its growth and reproduction (Lalonde and Shorthouse, 1984; Raman and Abrahamson, 1995). Galls not only capture photoassimilates, but also mineral nutrients such as Ca, Cu, Fe, Mg, Mn, Ni, and Zn (Abrahamson and Weis, 1987; Bagatto and Shorthouse, 1991, 1994, 1997; Paquette et al., 1992).

Parthenium hysterophorus L. (Asteraceae) is a weed of national significance in Australia. Therefore, the biology and ecology of *P. hysterophorus* and of several arthropods that might prove useful as biological control agents are currently being investigated (McFadyen, 1992; Navie et al., 1996; Dhileepan and McFadyen, 1997). Two gall-inducing insects, *Epiblema strenuana* Walker (Lepidoptera: Tortricidae) and *Conotrachelus albocinereus* Fiedler (Coleoptera: Curculionidae) are considered the most promising candidates likely to have a role in *P. hysterophorus* management (Florentine et al., 2001, 2002). Gall induction by *E. strenuana* reduces main shoot height, flower and leaf production, and shoot and root biomass in *P. hysterophorus* (Navie et al., 1998; Dhileepan and McFadyen, 2001). The galls also alter shoot structure and metabolic pathways of the plant (Raman and Dhileepan, 1999).

Parthenium hysterophorus is an annual herb with a deeply penetrating taproot and an erect shoot. As it grows, it branches profusely, and can reach heights up to 2 m. Young plants form a rosette of leaves close to the soil surface. This plant grows vigorously, particularly during warmer months. Flowering usually commences 6 8 weeks after germination and a fully-grown plant can produce more than 25,000 florets in its lifetime, with each inflorescence bearing 4 5 seeds (Navie et al., 1996; Dhileepan et al., 2000).

Epiblema strenuana lays eggs on young leaves of *P. hysterophorus*. The gall-inducing larval stage specifically feeds on *P. hysterophorus* and the annual common ragweed (*Ambrosia artemisiifolia* L.). Emerging larvae mine the leaves briefly, and then move to the closest axillary

vegetative buds. They enter stems by chewing the vegetative bud tissue, and this action induces galls. When the larvae cease to feed, the nutritive cells degenerate. Larvae pupate within the gall and the pupal stage ranges from 4 to 6 days. Adult moths emerge from the galls through a 'window' cut by the mature larvae before pupation (Raman and Dhileepan, 1999).

In this paper, we report our evaluation of the subtle effects of galling by the moth on *P. hysterophorus* by measuring gas exchange, mineral concentrations, and energy levels within galled shoots on different-aged plants; we examined the developmental stage of the host plant in which gas exchange is most affected and examined whether gall induction affects mineral nutrient concentration and energetics in the host plant.

Materials and methods

Experimental procedures

Seeds of *P. hysterophorus* were collected from the Plain Creek property (21°29′S, 146°40′E) in northern Queensland in March 1999. They were air-dried and stored at room temperature (21 °C) in labelled airtight containers until use. Seeds were sown in seedling trays ($35 \times 29 \times 5.5$ cm^3) containing sterilized coarse sand. The trays were maintained in a greenhouse, and were placed in larger trays ($43 \times 30 \times 6$ cm^3) to enable watering from below and to ensure minimal disturbance of the seedlings. Newly emerged seedlings bearing 2 3 leaves were transplanted into plastic pots (20×20 cm^2) containing commercial soil mixture. To obtain different developmental stages of the host plant, seedlings were transplanted on different dates. Gall-bearing host plants in the rosette stage (3 4 weeks old, with galls immediately above the root collar), pre-flowering stage (5 6 weeks old, obtained shortly before the commencement of flowering), and flowering stage (7 8 weeks old, bearing flowers) were used in the experiments. About 250 mature galls also were obtained from Cardigan Station (146°38.3′S, 20°13.5′E) located approximately 25 km northeast of the Tropical Weeds Research Centre (TWRC) at Charters Towers, North Queensland. Gall samples were immediately placed in plastic containers covered with wet muslin cloth (to avoid desiccation), and transported to TWRC. On the same day, galls containing *E. strenuana* larvae and pupae were transferred to insect-proof cages that were maintained in greenhouses for rearing adults. Newly emerged adult moths were used for initiating galls.

Sixty similar-sized and single-stem, unbranched plants at the rosette, pre-flowering, and flowering stages (180 total) were randomly selected, labelled, maintained in the greenhouse and watered twice daily. Among the 60 plants of each stage, 30 randomly selected plants were placed in three insect-proof cages (10 plants/cage) and exposed to 10 pairs of *E. strenuana* adults/cage. A similar number of plants (30 each of the rosette, pre-flowering, and flowering stages) were maintained free of *E. strenuana* in separate insect-proof cages (10 plants/cage). Plants exposed to *E. strenuana* were monitored daily for signs of gall initiation. Plants on which frass appeared close to vegetative buds were considered gall-initiated plants and were transferred to new insect-proof cages.

Gas exchange

Gas exchange measurements were carried out on day 7, following exposure to *E. strenuana* (to coincide with larval entry into stem tissue) and day 12 (when the shoot showed signs of swelling, i.e., the gall). On each of these days ambient temperature was recorded (min. 29 °C; max. 31 °C). Five fully expanded leaves selected below the gall region from each of the three stages from galled plants and similar sized leaves from ungalled plants were selected randomly, and the photosynthetic rate, rate of transpiration, stomatal conductance, photosynthetically active radiation (PAR > 500 μmol m^{-2} s^{-1}), chamber temperature, and ambient humidity were measured. Recordings were made between 1200 and 1300 h using an open gas exchange system (LCA-3, Analytical Development Co., Hoddesdon, England) attached to the leaf chamber (PLC-301(3B)). Leaf water potential of excised leaves was determined using a pressure chamber (Model No. Mk 3005, Soil Moisture Equipment Co., Santa Barbara, California, USA) following Scholander et al. (1965). Dividing the actual measurement by the sum of measurements and multiplying by 100 provided percentage values.

Mineral content

In total, 427 galled plants and 891 ungalled plants were obtained from the Plain Creek property in April 1999. On the basis of morphology, the plants were categorized into rosette, pre-flowering, and flowering stages. From similar categories of plants, the leaves, stems, and roots (just below the root collar), were pooled in separately labelled plastic bags. Samples were dried in an oven at 80 °C for 24 h. They were ground in an electric grinder (Retsch GmbH WRS 80c/29). From the ground samples, subsamples (approximately 5 g) were taken and used in the mineral nutrient

analysis. Nitrogen was assayed using the method of Sweeney and Rexroad (1987), minerals such as Ca, Cu, Fe, K, Mg, Mn, Na, P, S, and Zn according to the method of McQuacker et al. (1979), chloride and nitrate according to Zall et al. (1959), and B following Wolf (1974).

Energetics

To examine energy levels, plants were collected from the Plain Creek property in April 1999, and transported to TWRC in a dry-ice chest (2 to 4 °C). At TWRC, these plants were segregated into rosette, pre-flowering, and flowering stages. Galls, shoot tissue 1 cm above galls, and shoot tissue 1 cm below galls (except the rosette stage plants that bear galls only immediately above the root collar, therefore only the tissue l cm above galls was available) were trimmed and dried at room temperature (21 °C). The samples were packed in labelled aluminium foil and dried in an oven at 45 50 °C for 24 h. Samples were ground individually in the electric grinder. The ground samples were then packed in fresh, labelled aluminium foil for energy estimation. Calorific values were estimated using a semimicro Gallenkamp ballistic bomb calorimeter (CBB 330; 500 & THP-520 series; jacket thermometer 130 070) following the technique used by Raman and Abrahamson (1995).

Data analysis

Data were analyzed using the Super ANOVA software program (Abacus Concepts, Berkeley, California, USA) for obtaining two-way ANOVA and all pairwise multiple comparison procedures. Residual plots of each ANOVA were obtained to examine homogeneity of the variance.

Results

Gas exchange

Gall induction significantly reduced all measures of gas exchange by the host plant, although the effect of galling varied with the plant stage (Figure 1; Table 1). Effect of galling on all but leaf-water potential also varied according to gall age. The difference in responses of different plant stages to galling also varied with gall age for transpiration rate and stomatal conductance.

Galls had a significant effect on leaf-water potential ($p < 0.001$) (Figure 1; Table 1). Reduction in leaf-water potential due to gall
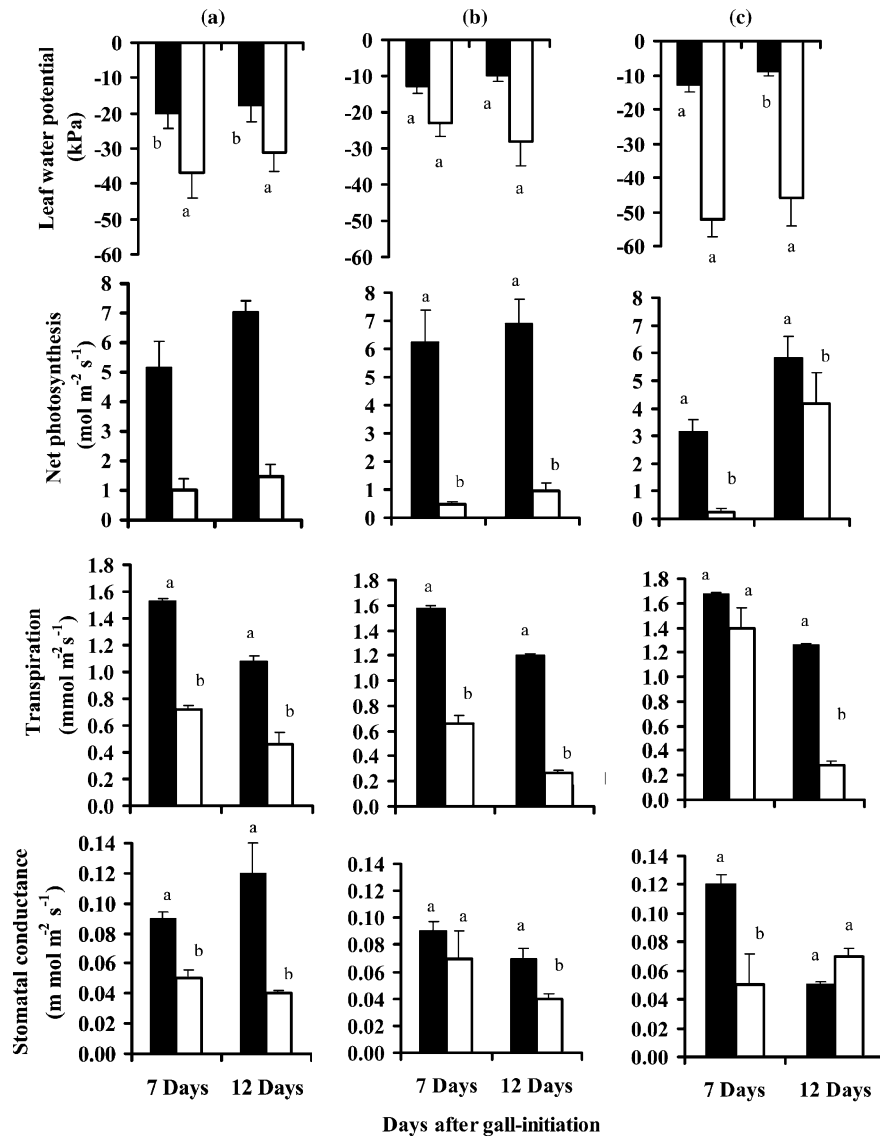
Figure 1. Leaf water potential, net photosynthesis, transpiration, and stomatal con ductance of ungalled (solid) and galled (open) rosette (a), pre flowering (b), and flow ering (c) stages of *P. hysterophorus*. Values are means. Same letters indicate means are not statistically different when tested with Tukey's HSD test. Vertical bars indicate standard errors.

induction was greater (71 78%) in the flowering stage than in the rosette (41 45%) and pre-flowering stages (42 67%) (Figure 1). However, no difference in the reduction in leaf-water potential

Table 1. Effect of galling, plant growth stage and gall age on leaf water potential, photosynthesis, transpiration, and stomatal conductance

Source	df	Leaf water potential		Photosynthetic rate		Transpirational rate		Stomatal conductance	
		F	p	F	p	F	p	F	p
Galling (G)	1	65.1	***	120.5	***	603.6	***	36.6	***
Plant stage (P)	2	6.04	**	0.25	ns	20.01	***	0.75	ns
Gall age (A)	1	0.92	ns	18.14	***	268.12	***	6.04	*
G × P	2	8.01	**	7.23	**	7.39	**	3.51	*
G × A	2	0.44	ns	4.33	*	19.61	***	4.13	*
P × A	1	0.01	ns	0.02	ns	8.56	**	0.73	ns
G × P × A	2	0.45	ns	0.96	ns	20.06	***	9.48	***
Residual	48								

G galled vs. ungalled plants; P rosette vs. pre flowering vs. flowering plants; A early stage (7 days) vs. mature stage (12 days) galls.
*Indicates samples are significantly different. *$p < 0.01$, **$p < 0.001$, ***$p < 0.0001$, ns not significant, and (n 5).

between early (7 days old) and mature galls (12 days old) in all growth stages existed (Table 1). The galls alone, as well as gall age had a significant effect on net photosynthetic rate ($p < 0.001$), but the effect of plant-growth stage on net photosynthetic rate was not significant (Figure 1; Table 1). No significant relationship was evident among galling, plant development stage, and gall age on photosynthetic rate (Table 1). In both rosette and pre-flowering stages, galling reduced the net photosynthetic rate by 80 and 87%, respectively, but the interaction between plant stage and gall age was not significant (Figure 1; Table 1). In flowering plants, the reduction in net photosynthetic rate was significantly greater (92%) in mature galls (12 days old) than in young galls (7 days old) (Figure 1). Galling significantly reduced (57%) the transpiration rate and the reduction was greater in the pre-flowering stage (68%) than in the rosette stage (55%), and flowering stage (48%) (Figure 1; Table 1). The reduction in transpiration rate was statistically higher in mature (71%) than in young galls (43%) (Figure 1; Table 1). Effect of plant-growth stage on the reduction in stomatal conductance due to galling was not significant (Table 1). Gall showed stomatal conductance reduced by 50% and the reduction was more in old galls (12 days) (61%) than in young galls (7 days) (39%) (Figure 1; Table 1). The effect of plant-growth

stage on reduction in stomatal conductance due to gall damage was not significant (Table 1).

Mineral concentrations

Gall incidence significantly increased chloride concentrations in leaves, but had no effect on other minerals tested (Table 2). Interaction between plant-growth stage and plant part had a significant effect on the total chloride, K, Mg, Mn, N, P, S, and Zn. Concentrations of B, Ca, and Na were affected by plant part only, whereas nitrate was affected by the plant stage (Table 2).

Galling resulted in a 17% increase in B concentration in leaves of pre-flowering plants. In flowering plants, chloride concentrations in leaves and stems of galled plants were 42 and 63% higher, respectively, than in ungalled plants. In pre-flowering plants there were 26 and 44% increases in chloride concentration in the leaves and stems, respectively, due to galling. In galled flowering plants Mg concentrations were 32% higher in leaves, and 30 and 32% lower in stems and roots, respectively, than in ungalled plants. Mg content in galled pre-flowering plants was 15% higher in leaves and 16% lower in stems than in ungalled pre-flowering plants. In pre-flowering plants, Zn content was 33 and 26% higher in leaf and root, respectively, in galled than ungalled plants. In contrast, in pre-flowering plants, Zn content of galled stems was 38% lower than in ungalled stems. Effect of galling by *E. strenuana* on concentrations of Ca, Cu, Fe, K, Mn, total nitrate, N, Na, P, and S were not significant.

Energetics

In the pre-flowering and flowering stages of *P. hysterophorus*, stem tissue from above the gall had significantly lower energy than tissue from below the gall (Figure 2a c). Energy levels of the galls of pre-flowering stages were not statistically different from adjacent tissues, but galls of flowering plants had higher energy levels than tissue below them and were not statistically different from the tissue above. In rosette-stage plants, there was significantly less energy in tissue above the gall than in the gall itself (Figure 2a).

Discussion

Galling by *E. strenuana* had negative effects on leaf-water potential, photosynthetic and transpiration rates, stomatal conductance, and also

Table 2. Impact of galling on the concentration of 14 minerals in relation to various plant parts and growth stages

Source	df	Total N		P		K		S		Na		Mg		Ca		Cl_2		Cu		Zn		Mn		Fe		Nitrate		B	
		F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Galling (G)	1	1 73	ns	0 002	ns	3 12	ns	1 02	ns	1 22	ns	0 13	ns	0 02	ns	7 31	**	0 13	ns	0 24	ns	0 69	ns	1 85	ns	1 12	ns	1 69	ns
Plant stage (S)	1	19 25	***	21 64	***	63 11	***	16 91	***	2 92	ns	15 64	***	0 12	***	26 29	***	3 55	ns	25 49	***	2 92	ns	3 14	ns	6 88	*	0 18	ns
Plant part (P)	2	124 28	***	6 55	**	38 65	***	45 55	***	10 22	***	213 36	***	416 85	***	15 92	***	32 61	***	5 92	**	68 83	***	2 12	ns	1 10	ns	1069	***
G × S	1	2 01	ns	0 73	ns	2 32	ns	0 78	ns	2 57	ns	1 48	ns	1 68	ns	0 01	ns	0 15	ns	1 07	ns	2 26	ns	1 64	ns	0 42	ns	2 54	ns
G × P	2	0 93	ns	2 31	ns	1 01	ns	3 01	ns	0 41	ns	18 76	***	0 50	ns	1 89	ns	0 66	ns	5 31	**	0 12	ns	2 04	ns	2 84	ns	1 38	ns
S × P	2	0 10	ns	2 34	ns	2 79	ns	0 67	ns	0 13	ns	1 83	ns	1 75	ns	0 09	ns	2 07	ns	7 64	**	6 34	**	2 13	ns	0 14	ns	2 29	ns
G × S × P	2	0 66	ns	0 26	ns	0 19	ns	0 15	ns	0 92	ns	4 00	*	3 17		0 18	ns	0 86	ns	2 29	ns	0 001	ns	2 02	ns	1 98	ns	4 18	ns
Residual	49																												

Galling (G): galled vs. ungalled plants; Plant stage (S): rosette vs. pre-flowering vs. flowering plants; Plant part (P): gall/shoot vs. root vs. leaf.
*Indicates samples are statistically different. $*p < 0.01$, $**p < 0.001$, $***p < 0.0001$, ns = not significant.
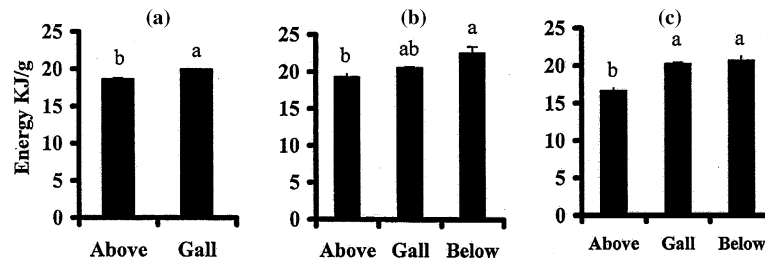
Figure 2. Mean energy levels in stem tissue 1 cm above the gall, in the gall, and stem tissue 1 cm below the gall of *P. hysterophorus* (a) rosette, (b) pre flowering, and (c) flowering stages. Same letters indicate means are not statistically different when tested with Tukey's HSD test. Because rosette stage (a) plants develop galls just above the root collar, no data for 1 cm below the gall was obtained.

increased chloride concentration. Further, leaves of gall-bearing *P. hysterophorus* plants had higher water potential rates than the ungalled plants. Energy levels in the gall and in the shoot tissue below the gall were also greater than those in the shoot tissue above the gall. All three developmental stages of galled plants showed similar patterns of water use efficiency compared with ungalled plants of similar age, because reduction in CO_2 assimilation was followed by a decline in the transpiration rates. Although a C_3 plant, metabolism of *P. hysterophorus* has characteristics of transient 'Kranz' syndrome and capabilities of evolution into a C_4 plant (Hegde and Patil, 1981). Such capabilities render *P. hysterophorus* to remain highly adaptive to non-native environments, and thus become invasive (Hegde and Patil, 1981). In this context, the role of *E. strenuana* in altering *P. hysterophorus's* physiology is noteworthy, because the moth is able to induce changes in the life history performance of the plant (Navie et al., 1998; Dhileepan and McFadyen, 2001).

The feeding action of *E. strenuana* disrupts the continuity of conductive tissue in *P. hysterophorus* resulting in reduced water movement (Raman and Dhileepan, 1999). Deposition of frass within the gall by the larva clogs the already disrupted vascular tissue. Also, toxins in the frass destroy the potentially regenerative parenchyma elements (Raman and Dhileepan, 1999). Consequently, water-transporting elements of the plant become non-functional. This effect was relatively less severe in galls on rosette and pre-flowering stages than those on the flowering stage, probably because of age-induced changes in tissues and biomass. This finding is contradictory to those reported earlier in which *E. strenuana* infestations had greater effects on galled plants of the rosette and pre-flowering stages (Dhileepan and McFayden, 1997, 2001).

High negative water potential readings indicated that the host plant was under water stress. In the water-stressed state, the photosynthetic rate and stomatal conductance of *P. hysterophorus* is reduced; the plant appears to maximize conservation of the available water by reducing transpiration, by closing the stomatal apertures simultaneously (Florentine et al., 2001). Closed stomata impair CO_2 uptake resulting in further reduction in the net photosynthetic rate (Warrington et al., 1989). Difficulty in the free movement of water reduces transport of minerals. Accumulation of non-hydrolyzable crystalline starch in the galled tissue (Raman and Dhileepan, 1999) also contributes to a reduction of the host plant's photosynthetic rate (Travis and Prendergast, 1987). Accumulation of crystalline starch in the galled tissue is a unique stress symptom, since Patil and Hegde (1983) have not reported any such accumulation in ungalled *P. hysterophorus* plants. CO_2 assimilation generation pattern and water vapour exchange, and gas exchange factors measured as water potential, net photosynthetic rate, stomatal conductance, and transpiration rate have been implicated as critical in the altered metabolism of stressed plants (Evans and von Caemmerer, 1996). Reduction in the rates of transpiration and stomatal conductance in *E. strenuana*-infested plants was greater than the reduction in net CO_2 assimilation, indicating that conductance was a more intensive limiting factor to water vapour exchange than CO_2 exchange (Schaffer and Mason, 1990).

Because larvae in galls manipulate the metabolism of the host plant to redirect mineral nutrients required for their growth towards the gall, differences in mineral nutrient concentrations between galled and ungalled plants and within galled plants vary significantly. Gall-inducing insects belonging to different groups seem to require different types and levels of mineral nutrients, and as a result, host plants respond differently to different gall-inducing insects (Bagatto and Shorthouse, 1997). In the galls induced by a pteromalid wasp (*Hemadas nubilipennis* Ashmead, Hymenoptera), concentrations of Ca, Cu, Mg, Mn, Ni, and Zn are different from those in non-galled tissue. The galls act as sinks for Ca, Fe, Mg, Mn, and Zn, in particular (Bagatto and Shorthouse, 1991, 1994; Paquette et al., 1992; St. John and Shorthouse, 2000). Elevated levels of minerals in the gall could be due to either partial blocking of nutrient translocation within the gall (the galls acting as non-mobilizing sinks) or due to active drawing of nutrients and minerals from other parts of the plant (the galls acting as mobilizing sinks) (McCrea et al., 1985). In the *E. strenuana*-induced galls of *P. hysterophorus*, galling has a major effect only on chloride and Mg in the galls, Mg and Zn in the leaves and roots of galled plants, and chloride in the leaves of galled

plants. Varied patterns of change in the concentrations of minerals suggest that the galls induced by *E. strenuana* act as mobilizing sinks. Such a feature is common in single chamber galls (Paquette et al., 1992), similar to those of *E. strenuana* because vascular strands occur in close proximity to the nutritive tissue (Raman and Dhileepan, 1999). Absence of any statistical difference in the values of minerals among the three developmental stages suggests that the host plant responds to galling in a similar way irrespective of the developmental stage.

During the early stages of gall development, newly emerged larvae manipulate host plant metabolic pathways and redirect carbohydrates and lipids close to their feeding tissues (Raman and Dhileepan, 1999). The influence of *E. strenuana* on *P. hysterophorus* could be seen in the greater concentrations of energy in the gall and stem tissue immediately below the gall than in stem tissue above the gall. These findings are similar to those found in the cecidomyiid-induced galls (*Rhopalomyia solidaginis* Lw., Diptera) on another asteraceous species (the tall goldenrod, *Solidago altissima* L.) (Raman and Abrahamson, 1995).

In conclusion, *E. strenuana* disrupted water movement; induced necrosis in the gall system retarded the mobilization of nutrients beyond the gall, and significantly reduced the gas exchange in *P. hysterophorus*. These effects demonstrate that the gall moth has potential to regulate the populations of *P. hysterophorus* in Australia.

Acknowledgements

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