

The adaptive significance of insect gall distribution: survivorship of species in xeric and mesic habitats

G. Wilson Fernandes* and Peter W. Price

Department of Biological Sciences, Box 5640, Northern Arizona University, Flagstaff, AZ 86011, USA

Received November 12, 1990 / Accepted in revised form December 9, 1991

Summary. We studied the relationship between habitat moisture and gall-forming insect populations. Population sizes for most galling taxa were significantly larger in xeric habitats compared with mesic habitats. Our results indicate that the differential abundance of galling insects in these habitats is due primarily to differential mortality and survivorship. Mortality factors acting upon eight insect galling species (belonging to eight genera and four families) were measured on six species (five genera and five families) of host plants. Survival was significantly higher for galling populations inhabiting xeric habitats compared with mesic habitats. Parasitism was higher in mesic habitats in seven of eight habitats and fungus-induced diseases were higher in five of seven habitats. Mortality due to predation and other (unknown) factors showed no clear trends. Overall, there was a tendency towards lower mortality and consequently higher survival for populations inhabiting xeric habitats. We hypothesize that reduced mortality caused by natural enemies and endophytic fungi has contributed to the speciation and radiation of galling insects in apparently harsh environments.

Key words: Adaptations – Habitat selection – Herbivore survivorship – Insect distribution – Insect galls

Geographical patterns of distributions of many species have been described, but the underlying mechanisms are often poorly understood. For many plants and animals differential mortality at distributional edges versus range centers is difficult to evaluate, and so at least one explanatory component of distribution is generally unavailable. Gall-forming insect herbivores, however, offer a particularly simple system for identifying geographical patterns and for evaluating the possible mechanisms

* *Current address and address for offprint requests:* Departamento de Biologia Geral, CP 2486, ICB/Universidade Federal de Minas Gerais. 30161 – Belo Horizonte, MG, Brazil

producing the pattern. Galls are conspicuous, and relatively rapid and accurate surveys of their distribution can be made; survivorship curves and sources of mortality can usually be evaluated by dissecting galls at the end of each generation.

Richness of insect galls appears to increase with increasing hygrothermal stress, and this pattern may be global. Many studies have described patterns of galling insect distribution (e.g., Cornell 1985, 1986; Leather 1986; Taper and Case 1987), and strong biogeographical patterns in the distribution of gall-forming insects were reported by Fernandes and Price (1988, 1991; see also Waring and Price 1990; Price 1991).

However, the processes and mechanisms that influence these patterns remain largely unknown and untested. We tested the hypothesis that galls suffer from lower mortality rates in xeric habitats compared to mesic habitats. We developed survivorship data for galling insects in xeric and mesic habitats, in an attempt to unravel the proximate factors influencing their success in drier habitats. Eight galling species (eight genera belonging to four families) on six species (five genera belonging to five families) of host plants were studied to test for generalities in mortality factors and survivorship.

Study sites and study species

Tephritid galler

Aciurina trixa (Diptera: Tephritidae) induces bud galls on several subspecies of *Chrysothamnus nauseosus* (Compositae) (Foot and Blanc 1963; Wasbauer 1972; McArthur et al. 1979; Wangberg 1981; Dodson and George 1986; Dodson 1987a, b). The galls are green, spheroid, glabrous, one-chambered, and have one larva per chamber. A resin layer covers the external gall walls. Galls were sampled near the Weber Power Plant (Highway I-84, 1 km east of State Route 89), Ogden, Utah during the summer of 1989. Xeric sites were located between 50 and 200 m from the river bed, adjacent to Highway I-84, whereas mesic sites were located in riparian habitats.

Psyllid galler

Pachypsylla venusta (Homoptera: Psyllidae) induces leaf petiole galls on *Celtis reticulata* (Ulmaceae) (Riemann 1954; see also Moser 1965). The galls are bright green, globoid, multi-chambered, and have up to 12 nymphs per gall. Many parasites are known to attack *P. venusta* galls (Moser 1956; Bugbee 1957; Delucchi 1962; see also Moser 1965). Galls were sampled in Sycamore Canyon, Arizona, during the summer of 1987. Xeric sites were located at distances no less than 50 m from the river bed, in sunny areas. Mesic sites were along the river bed, near shading trees.

Cynipid gallers

a. *Andricus tecturnarum* (Hymenoptera: Cynipidae) induces leaf galls on *Quercus turbinella* (Fagaceae) (Weld 1960). The galls are reddish, spheroid, hairy, one-chambered, have one larva per chamber, and occur in clusters on the abaxial leaf surfaces. Galls were sampled in Oak Creek, Sedona, Arizona during the fall of 1987. Xeric sites were located in sunny areas, 30–50 m from the river bed, whereas mesic sites were located in riparian habitats, near shading trees.

b. *Neuroterus lamellae* forms leaf galls on *Q. turbinella* (Weld 1960). The galls are on the leaf midrib, are yellowish, globoid, one-chambered, have one larva per chamber, and have short hairs over the external gall walls. Galls were sampled at Grasshopper Point, near Sedona, Arizona, along Oak Creek during the fall of 1987. Xeric sites were located at least 100 m from the river bed, in sunny habitats, and mesic sites were located in riparian habitats.

Cecidomyiid gallers (Diptera: Cecidomyiidae)

Four species were studied, including two tropical and two temperate species.

a. *Contarinia* sp. induces galls on the compound leaves of *Copaifera langsdorffii* (Leguminosae) (Fernandes et al. 1988). The galls are brownish, button-like, dehiscent, one-chambered, and have one larva per chamber. Galls were sampled in Macacos (near Belo Horizonte), Minas Gerais, Brazil during the summer of 1988. Xeric sites were located at least 300 m from the river, in sunny habitats, whereas mesic sites were in riparian habitats, near shading trees.

b. *Unidentified cecidomyiid* induces leaf galls on *Bauhinia* sp. (Leguminosae). The galls are reddish, spheroid, hairy, one-chambered, have one larva per chamber, and generally occur in clusters on the adaxial leaf surface (G.W. Fernandes, unpublished). Galls were sampled in the Estação Ecológica de Parapitinga, Três Marias, Minas Gerais, Brazil during the summer of 1988. Xeric sites were located in sunny habitats, away from water sources, and mesic sites were located adjacent to the margins of the Três Marias Lake.

c. *Asphondylia garryae* forms bud galls on *Garrya flavescens* (Cornaceae) (R.J. Gagné, pers. comm.; see also Gagné 1989). The galls are green, globoid, one-chambered, and have one larva per chamber. Coalescent galls occur frequently. Galls were sampled in Oak Creek, Sedona, Arizona during the summer of 1987. Xeric sites were located 10–15 m from the river bed, whereas mesic sites were located in riparian habitats.

d. *Rhopalomyia chrysothamni* produces stem galls on several subspecies of *Chrysothamnus nauseosus* (e.g. Felt 1940; Gagné 1989); we studied *C. n. consimilis*. The galls are green, conical, one-chambered, have one larva per chamber, and have hairs that cover the gall portal area, from which the galling insect and most of its parasitoids emerge. Galls were collected near Flagstaff, Arizona, during the summer and fall of 1987. Xeric sites were located along Schultz Pass Road (US Forest Service road 420), and mesic sites were located along the shore of a small pond (Schultz Tank).

Materials and methods

Population sizes were quantified as the number of galls per stem or leaf depending on the location of the gall. Ten stems or leaves were randomly selected from each plant and the number of galls counted. We tried to collect at least 10 plants per site. Table 1 shows how many plants were collected for each galling species in xeric and mesic habitats. For gregarious gallers, we counted the number of larvae or nymphs per chamber also.

Samples of galls were taken for taxa present in both xeric and mesic sites at a single elevation. We measured plant xylem water potential using a Scholander Pressure Bomb, as an indicator of plant physiological status (e.g., Mason 1969; Ritchie and Hinckley 1975), for *C. nauseosus*, *Q. turbinella*, and *C. n. consimilis*. We were unable to measure the water potential for all specimens of the species measured because of difficulties in reaching individuals located in inaccessible cliffs.

Mortality factors and survivorship

Ten randomly selected galled stems or leaves were collected from each plant, and 10 plants constituted a sample at a site. Sample sizes varied according to the number of galls per plant organ. The smallest sample ($n=5$) was for the cynipid *Andricus tecturnarum* on *Q. turbinella* in mesic sites. All galls on each stem or leaf were counted, measured and opened after adult emergency for the identification of mortality factors. Overall, we dissected 5,653 galls.

Mortality was caused by: parasitoids of the galling larva, predation on the gall tissue and/or galling larva, fungus-caused diseases, and other factors probably including plant resistance, and death caused by parasitoids during feeding or oviposition. For the galling tephritid, *Aciurina trixa*, the mortality factor of "resinosis" was also applicable. Here, plant resins cover the gall's external surface and punctures during oviposition by parasitoids may cause droplets of resin to be produced. In this category, we grouped all dead larvae that were yellowish and dry, with a resinous appearance. Larvae were perhaps killed directly, or plant resins may cover and damage the feeding larva. Furthermore, the host *C. nauseosus* is known for its stem and leaf resin contents (e.g. Hegerhorst et al. 1985, 1987). Deaths of galling larvae in galls opened by predators, but with fungus invasion, were considered as death by predation; those of galling larvae in closed galls with fungus invasion were considered as death by fungal disease.

Table 1. Population size of tropical (southeast Brazil) and temperate (southwest United States) galling insect species in xeric and mesic habitats at different dates between 1987 and 1989

Galling species	Plant organ galled	Habitat	Galls per stem or leaf (\pm SE)	Number of plants (<i>n</i>)	<i>t</i> -test	<i>P</i>
<i>Aciurina trixa</i>	Buds	Xeric	0.600 \pm 0.06	25	1.758	<0.05
		Mesic	0.433 \pm 0.07	20		
<i>Pachypsylla venusta</i>	Leaves	Xeric	0.364 \pm 0.05	25	5.386	<0.0001
		Mesic	0.064 \pm 0.01	20		
<i>Andricus tecturnarum</i>	Leaves	Xeric	14.49 \pm 0.27	10	3.058	<0.005
		Mesic	0.244 \pm 0.12	5		
<i>Neuroterus lamellae</i>	Leaves	Xeric	0.396 \pm 0.05	20	4.365	<0.0001
		Mesic	0.080 \pm 0.03	11		
<i>Contarinia</i> sp.	Leaves	Xeric	0.711 \pm 0.29	14	4.203	<0.0001
		Mesic	0.194 \pm 0.04	10		
Unidentified sp.	Leaves	Xeric	0.541 \pm 0.14	14	2.307	<0.02
		Mesic	0.182 \pm 0.08	17		
<i>Asphondylia garryae</i>	Buds	Xeric	95.07 \pm 25.7*	14	0.69	>0.05
		Mesic	98.00 \pm 33.3*	8		
<i>Rhopalomyia chrysothamni</i>	Stems	Xeric	0.728 \pm 0.25	10	0.937	>0.05
		Mesic	0.435 \pm 0.18	10		

* Galls per plant

Differences in population size between habitats were analyzed by two-sample *t*-tests (see Zar 1984)

Table 2. Temperate host plant xylem water potential estimates based on Scholander Pressure Bomb measurements (in bars)

Host plant species	Galling species	Habitat	Plant water potential (\bar{x} \pm SE)	Number of plants (<i>n</i>)	<i>t</i> -test	<i>P</i>
<i>Chrysothamnus nauseosus</i>	<i>A. trixa</i>	Xeric	19.92 \pm 0.85	10	7.000	<0.0001
		Mesic	12.52 \pm 0.63	10		
<i>Quercus turbinella</i>	<i>A. tecturnarum</i>	Xeric	18.31 \pm 0.87	10	9.627	<0.0001
		Mesic	5.64 \pm 0.56	56		
<i>Q. turbinella</i>	<i>N. lamellae</i>	Xeric	34.51 \pm 1.21	20	12.793	<0.0001
		Mesic	11.29 \pm 1.06	11		
<i>C. n. consimilis</i>	<i>R. chrysothamni</i>	Xeric	12.17 \pm 0.57	20	5.285	<0.0001
		Mesic	9.54 \pm 0.19	35		

Measurements were taken between 12:00 a.m. and 6:00 a.m. Differences in plant xylem water potential between habitats were analyzed by two-sample *t*-tests (see Zar 1984)

Statistical analysis

Two-sample *t*-tests were used to test for differences in population size between xeric and mesic habitats (Zar 1984) (Table 1). Due to differences in gall density within and among sites, mortality data were transformed into proportions (percent mortality) to allow weighted comparisons. We used Hotelling-Lawley Trace multivariate statistics (Morrison 1976) to test for differences in percent mortality of gallers per plant between the two habitat types studied.

Results

Galling population densities in the field

Galling insect populations were significantly larger in xeric habitats compared with mesic habitats for six out of eight species (Table 1). In addition to higher gall

density per plant, there were more *Pachypsylla venusta* nymphs per gall in xeric habitats than in mesic habitats (xeric = 3.987, SE \pm 0.287 nymphs; mesic n = 2.953, SE \pm 0.089 nymphs; Student's $t_{1,598}$ = 3.439; P < 0.0005). Only two species, *Asphondylia garryae* and *Rhopalomyia chrysothamni*, did not show significant differences in population sizes between the two habitats studied.

Host plant xylem water deficits

Plants in xeric habitats experienced significantly higher water deficits compared with plants in mesic habitats. Host xylem water potential estimates based on pre-dawn Scholander Pressure Bomb measurements were higher in xeric than in mesic habitats for all species measured (Table 2).

Table 3. Gallling insect taxa differer habitats

Species	Habitat	Parasitism	Predation	Diseases	Other	Resinosis	Survivorship
<i>Acutirina trixa</i>	Xeric	11.27 ± 1.37*	2.16 ± 0.78****		4.06 ± 0.96**	12.20 ± 1.77*	67.87 ± 2.75****
	Mesic	16.05 ± 2.18	19.45 ± 3.26		7.83 ± 1.32	17.47 ± 2.61	19.75 ± 1.96
<i>Pachypsylla venusta</i>	Xeric	29.58 ± 3.09****	3.04 ± 1.34**		0.63 ± 0.37 ^{ns}		60.64 ± 2.89****
	Mesic	49.96 ± 3.01	0.11 ± 0.11		0		34.62 ± 3.11
<i>Andricus tecturnarum</i>	Xeric	11.67 ± 2.02****	2.00 ± 1.33 ^{ns}				85.83 ± 2.10****
	Mesic	24.66 ± 2.43	4.00 ± 1.87				47.68 ± 3.11
<i>Leuroterus lamellae</i>	Xeric	0.77 ± 0.50****	3.39 ± 0.86**				81.50 ± 1.91****
	Mesic	9.70 ± 3.68	7.76 ± 2.34				59.66 ± 5.81
<i>Contarinia</i> sp.	Xeric	20.71 ± 3.99****	0.71 ± 0.71 ^{ns}				77.14 ± 4.12****
	Mesic	48.00 ± 6.63	1.00 ± 1.00				35.00 ± 7.34
Unidentified sp.	Xeric	10.71 ± 2.45 ^{ns}	7.14 ± 1.94 ^{ns}				77.86 ± 3.00****
	Mesic	18.82 ± 3.73	8.82 ± 3.08				29.41 ± 3.26
<i>Asphondylia garryae</i>	Xeric	0.46 ± 0.32**					93.38 ± 2.96*
	Mesic	20.00 ± 7.56					80.00 ± 7.56
<i>R. chrysothamni</i>	Xeric	12.00 ± 2.91**	2.00 ± 1.33 ^{ns}	30.00 ± 7.75 ^{ns}			56.00 ± 8.33 ^{ns}
	Mesic	22.00 ± 3.59	1.00 ± 1.00	28.00 ± 5.54			49.00 ± 5.04

Statistically significant differences between mortality factors, and survivorship in xeric and mesic habitats. * $P < 0.05$; ** $P < 0.02$; *** $P < 0.002$; **** $P < 0.0001$; ns, not statistically significant at $\alpha = 0.05$; -, not observed for the gallling insect in question. Differences in mortality and survivorship between habitats were tested through multivariate analysis of variance (Hotelling-Lawley Trace test) (see Morrison 1976)

Discussion

General trends in gallling insect populations in xeric and mesic habitats

Six gallling species were significantly more abundant in xeric habitats than in mesic habitats. One species, *R. chrysothamni*, showed the same pattern of greater abundance in xeric habitats but the differences in population size was not statistically significant, and another species, *Asphondylia garryae*, showed the opposite trend. Larger population sizes of gallers in harsh environments have been reported for some gallers (e.g. Tschardtke 1988; Waring and Price 1990; see also Fernandes and Price 1991). This phenomenon may be widespread and the result of differential preference by ovipositing female and survival of larval gallers in these two distinct environments (discussed in the next section).

General trends in mortality factors and survivorship of gallling insect species in xeric and mesic habitats

Consistent with the pattern of increased population density in xeric habitats, mortality factors were also reduced

Mortality factors affecting gallling insect populations in xeric and mesic habitats

in the xeric environment. Parasitism and fungal diseases were stronger mortality factors in galling insect populations living in mesic than in xeric habitats. Galling insects suffer from some of the richest parasitoid faunas (Price et al. 1986, 1987; see also Askew 1961; Hawkins and Lawton 1987; Hawkins 1988). High parasitism rates have been commonly reported in the literature (e.g., Osgood and Gagné 1978; Washburn and Cornell 1979, 1981; Ehler 1982; Fernandes 1987a). On the other hand, the effects of fungus-caused diseases upon galling populations have only seldom been reported (Smirnov 1970; Lasota et al. 1983; Taper et al. 1986; Carroll 1988).

Gall mortality due to fungus attack may be widespread (e.g. Carroll 1988; Fernandes and Price 1991; see also Clay 1988), and thus be an important agent against some galling insect populations. Carroll (1988) reported significantly higher larval mortality of cecidomyiid species on fungus-infected host plant needles. Fungus-caused diseases were reported as the major mortality factor for the cynipid *Dryocosmus dubiosus* on two *Quercus* species (Taper et al. 1986).

In a subsequent paper, Taper and Case (1987) reported on positive correlations between leaf tannin content and cynipid galler species richness, survival, and abundance. These findings may also apply to the *Cynips divisa*-*Q. robur* system studied by Sitch et al. (1988), where fungus attack was the second major mortality factor for the galling cynipid. The effects of tannins as fungus-growth inhibitors is well known (e.g. Matta 1971; Deverall 1977; Janzen 1977; Cruickshank 1980; Agrios 1988). Tannins have been suggested to accumulate in galls (e.g., Bronner 1977) and protect the gall tissue as well as the gall former from herbivores (Janzen 1977; Cornell 1983; Taper et al. 1986; Price et al. 1987; Taper and Case 1987). Corroborating these findings, Müller et al. (1987) reported increased leaf tannin content with increasing plant water stress. These positive associations between plant stress, tannins, gall survivorship, abundance, and species richness are probably not coincidental and deserve more attention (explored in the next section; see also Fernandes and Price 1991).

The evolution of gallers in harsh environment.

The mechanisms producing the differential abundance of gall forming insects in xeric and mesic habitats are differential mortality and survivorship. Our findings are corroborated by the work by Carroll (1986, 1988) on the higher mortality of needle galling *Contarinia* species on endophyte-infected needles, and by the work of Tscharrntke (1988, 1989) on the mortality and abundance of the galling midge, *Giraudiella inclusa*, on *Phragmites australis* plants in dry and wet sites. Furthermore, studies by Taper et al. (1986) and Taper and Case (1987) on the positive correlations between oak leaf tannin content and cynipid gall survival, abundance, and richness also support our findings on the proximal factors influencing galling distribution. The ultimate factor influencing distribution of gallers may then be an evolved positive

female response to xeric habitats in preference to mesic habitats (Fernandes and Price 1991).

Galling insects may have speciated and radiated in harsh environments. Fernandes and Price (1988, 1991; see also Price 1991) noted that galls were commonly associated with sclerophyllous plants. They also observed that sclerophylly is associated with long-lived leaves, reduced probability of leaf abscission, high phenol contents, and low-nutrient status (especially phosphorus). Interestingly, the majority of all galls in all biogeographical regions are on leaves (see Felt 1940; Mani 1964). Correlations between sclerophylly, low nutrient status, resource stability and predictability, and high chemical defense may all be part of a syndrome of plant traits favoring galling species.

The lower mortality caused by endophytic fungi and natural enemies in xeric sites appears to reinforce galling in those habitats, fostering speciation and radiation in harsh environments. Plant pathogens are more active in moist environments but relatively inactive in dry environments (e.g. Preece and Dickinson 1971). Thus gall-forming insects have lower probability of surviving in humid habitats. Gallers may also suffer higher rates of parasitism, as well as predation, in humid habitats because of longer maturation and hardening of the gall, although more studies would be needed to substantiate this concept. Overall, in xeric sites, gallers occupy a niche relatively free of diseases and with relatively reduced incidence of enemies (especially parasitoids and, possibly, herbivores which eat the gall because of its concentrated nutrients).

The scenario we envisaged (see Fernandes and Price 1991) for the evolution of galling insects was reinforced by our present findings. Nevertheless, more work is needed on the ultimate factors that shape galling distribution. In addition, more work is needed on the different aspects of galler distribution to strengthen our two-level view (xeric vs. mesic) of selection pressures and survivorship for galling insects. Forthcoming papers will report on experimental and behavioral studies on insect galling responses to plant resources which generally support the patterns found in this field study.

Acknowledgments. We are very grateful for the field and laboratory aid of A. Fernandes and R.L. Souza throughout the development of this project. We also would like to thank three anonymous reviewers, J. Lawton, T.G. Whitham, C.N. Slobodchikoff, C. Grier, R. Preszler, and C. Tobin for reading and commenting on several drafts of this manuscript, and G. Bell, Department of Mathematics, NAU for expert statistical advice. Identification of the galling insects was kindly provided by B.L. Blanc, R.J. Gagné, and J.G. Riemann. Facilities were provided by Departamento de Biologia Geral of the Universidade Federal de Minas Gerais, Northern Arizona University, T.G. Whitham's logistical support during our collecting at Ogden, Utah, and the United States Forest Service. We gratefully acknowledge a scholarship of the Conselho Nacional de Pesquisas (CNPq) n. 200.747/84-3-ZO, and a Sigma-Xi Grants-in-Aid to GWF. This project was supported by the National Science Foundation Grants BSR: 8314594, and BSR: 8705302. This study was in partial fulfillment of requirements for the PhD degree at Northern Arizona University.

References

- Agrios GN (1988) Plant pathology. (3rd edn). Academic, New York
- Askew RR (1961) On the biology of the inhabitants of oak galls of the Cynipidae in Britain. *Trans Br Soc Entomol* 14: 237–268
- Bronner R (1977) Contribution à l'étude histoquimique des tissus nourriciers des zoocécidies. *Marcellia* 40: 1–34
- Bugbee RE (1957) Four new species of the genus *Eurytoma* from galls on hackberry (Chalcidoidea, Hymenoptera). *J Kans Entomol Soc* 30: 45–50
- Carroll G (1986) The biology of endophytism in plants with particular reference to woody perennials. In: Fokkema NJ, van den Heuvel J (eds) *Microbiology of the phylloplane*, Cambridge, University Press, Cambridge, England, pp 205–222
- Carroll G (1988) Fungal endophytes in stems and leaves: from latent pathogen to mutualistic symbiont. *Ecology* 69: 2–9
- Clay K (1988) Fungal endophytes of grasses: a defensive mutualism between plants and fungi. *Ecology* 69: 10–16
- Cornell HV (1983) The secondary chemistry and complex morphology of galls formed by the Cynipinae (Hymenoptera): why and how? *Am Midl Nat* 110: 225–234
- Cornell HV (1985) Local and regional richness of cynipine gall wasps on California oaks. *Ecology* 66: 1247–1260
- Cornell HV (1986) Oak species attributes and host size influence cynipine wasp species richness. *Ecology* 67: 1582–1592
- Cruickshank IAM (1980) Defenses triggered by the invader: chemical defenses. In: Horsfall J, Cowling EB (eds) *Plant diseases*, Volume V, Academic Press, New York, pp 247–267
- Delucchi VL (1962) *Moserina maculata* gen. et sp. nov. (Hymenoptera: Chalcidoidea: Eulophidae), parasite of *Pachypsylla* (Hemiptera: Psyllidae) on *Celtis*. *J Kans Entomol Soc* 35: 389–392
- Deverall BJ (1977) *Defense mechanisms of plants*. Cambridge University Press, Cambridge, England
- Dodson G (1987a) Biological observations on *Aciurina trixa* and *Valentibulla dodsoni* (Diptera: Tephritidae) in New Mexico. *Ann Entomol Soc Am* 80: 494–500
- Dodson G (1987b) Host-Plant records and life history notes on New Mexico Tephritidae (Diptera). *Proc Entomol Soc Wash* 89: 607–615
- Dodson G, George SB (1986) Examination of two morphs of gall-forming *Aciurina* (Diptera: Tephritidae): ecological and genetic evidence for species. *Biol J Linn Soc* 29: 63–79
- Ehler LE (1982) Ecology of *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae) and its parasites in an urban environment. *Hilgardia* 50: 1–32
- Felt EP (1940) *Plant galls and gall makers*. Comstock, Ithaca, New York
- Fernandes GW (1987a) Gall forming insects: their economic importance and control. *Rev Bras Entomol* 31: 379–398
- Fernandes GW (1987b) Tropical and temperate altitudinal gradients in galling species richness. MSc thesis, Northern Arizona University, Flagstaff, Arizona
- Fernandes GW (1990) Hypersensitivity: a neglected plant resistance mechanism against insect herbivores. *Environ Entomol* 19: 1173–1182
- Fernandes GW, Price PW (1988) Biogeographical gradients in galling species richness: tests of hypotheses. *Oecologia* 76: 161–167
- Fernandes GW, Price PW (1991) Comparisons of tropical and temperate galling species richness: the roles of environmental harshness and plant nutrient status. In: Price PW, Lewinsohn TM, Fernandes GW, Benson WW (eds), *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. Wiley, New York, pp 91–115
- Fernandes GW, Tameirão-Neto E, Martins RP (1988) Ocorrência e caracterização de galhas entomógenas na vegetação do Campus Pampulha da Universidade Federal de Minas Gerais. *Rev Bras Zool* 5: 11–29
- Footo RH, Blanc FL (1963) The fruit flies or Tephritidae of California. *Bull Calif Insect Surv* 7: 1–117
- Gagné RJ (1989) *The plant-feeding gall midges of North America*. Cornell University Press, Ithaca, New York
- Hawkins BA (1988) Do galls protect endophytic herbivore from parasitoids? A comparison of galling and non-galling Diptera. *Ecol Entomol* 13: 473–477
- Hawkins BA, Lawton JH (1987) Species richness for parasitoids of British phytophagous insects. *Nature* 326: 788–790
- Hegerhorst D, Weber DW, McArthur ED (1985) Resin and rubber content in *Chrysothamnus*. *Southwest Nat* 32: 475–482
- Hegerhorst D, Weber DW, McArthur ED, Khan AJ (1987) Chemical analysis and comparison of subspecies of *Chrysothamnus nauseosus* and other related species. *Biochem Syst Ecol* 15: 201–208
- Janzen DH (1977) Why fruits rot, seeds mold, and meat spoils. *Am Nat* 111: 691–713
- Lasota JA, Waldvogel MG, Shetlar DJ (1983) Fungus found in galls of *Adelges abietis* (L.) (Homoptera: Adelgidae): identification, within-tree distribution, and possible impact on insect survival. *Environ Entomol* 12: 245–246
- Leather SR (1986) Insect species richness of the British Rosaceae: the importance of host range, plant architecture, age of establishment, taxonomic isolation and species-area relationships. *J Anim Ecol* 55: 841–860
- Mani MS (1964) *Ecology of plant galls*. Dr. W Junk, The Hague
- Mason RS (1969) A simple technique for measuring oleoresin exudation flow in pine. *For Sci* 15: 56–57
- Matta A (1971) Microbial penetration and immunization of uncogonial host plants. *Annu Rev Phytopathol* 9: 387–410
- McArthur ED, Tiernan CF, Welch BL (1979) Subspecies specificity of gall forms on *Chrysothamnus nauseosus*. *Great Basin Nat* 39: 81–87
- Morrison DF (1976) *Multivariate statistical methods*. McGraw-Hill, New York
- Moser JC (1956) A new species of *Torymus* (Hymenoptera: Torymidae) parasitic on *Pachypsylla celtidis-vesicula* Riley (Chermidae) with notes on its biology and other parasitoids attacking the same host at Columbus, Ohio. *J Kans Entomol Soc* 29: 57–62
- Moser JC (1965) The interrelationships of three gall makers and their natural enemies, on hackberry (*Celtis occidentalis* L.). *Bull NY State Mus Sci Serv* 402: 1–95
- Müller RN, Kalisz PJ, Kimmerer TW (1987) Intraspecific variation in production of astringent phenolics over a vegetation-resource availability gradient. *Oecologia* 72: 211–215
- Osgood EA, Gagné RJ (1978) Biology and taxonomy of two gall midges (Diptera: Cecidomyiidae) found on balsam fir needles with description of a new species of *Paradiplosis*. *Ann Entomol Soc Amer* 71: 85–91
- Preece TF, Dickinson CH (1971) *Ecology of leaf surface microorganisms* (eds). Academic Press, New York
- Price PW (1991) Patterns in communities along latitudinal gradients. In: Price PW, Lewinsohn TM, Fernandes GW, Benson WW (eds), *Plant-animal interactions: tropical and temperate regions*, Wiley, New York, pp 51–69
- Price PW, Waring GL, Fernandes GW (1986) Hypotheses on the adaptive nature of galls. *Proc Entomol Soc Wash* 88: 361–363
- Price PW, Fernandes GW, Waring GL (1987) Adaptive nature of insect galls. *Environ Entomol* 16: 15–24
- Riemann JG (1954) The interrelationships of some insects found in the hackberry petiole galls of *Pachypsylla venusta* (O.S.) with observations on their biology. Unpublished M.A. thesis, University of Texas, Texas
- Ritchie GA, Hinckley TM (1975) The pressure chamber as an instrument for ecological research. *Adv Ecol Res* 9: 165–254
- Sitch TA, Grewcock DA, Gilbert FS (1988) Factors affecting components of fitness in a gall-making wasp (*Cynips divisa* Hartig). *Oecologia* 76: 371–375
- Smirnoff WA (1970) Fungus diseases affecting *Adelges piceae* in the fir forest of the Gaspé Peninsula, Quebec. *Can Entomol* 102: 799–805

- Taper ML, Case TJ (1987) Interactions between oak tannins and parasite community structure: unexpected benefits of tannins to cynipid gall-wasps. *Oecologia* 71:254–261
- Taper ML, Zimmerman EM, Case TJ (1986) Sources of mortality for a cynipid gall-wasp (*Dryocosmus dubiosus* (Hymenoptera: Cynipidae)): the importance of the tannin/fungus interaction. *Oecologia* 68:437–445
- Tscharntke T (1988) Variability of the grass *Phragmites australis* in relation to the behavior and mortality of the gall-inducing midge *Giraudiella inclusa* (Diptera: Cecidomyiidae). *Oecologia* 76:504–512
- Tscharntke T (1989) Attack by a stem-boring moth increases susceptibility of *Phragmites australis* to gall-making by a midge: mechanisms and effects on midge population dynamics. *Oikos* 54:93–100
- Wangberg JK (1981) Gall-forming habits of *Aciurina* species (Diptera: Tephritidae) on rabbitbrush (Compositae: *Chrysothamnus* spp.) in Idaho. *J Kans Entomol Soc* 54:711–732
- Waring GL, Price PW (1990) Plant water stress and gall formation (Cecidomyiidae: *Asphondylia* spp.) on creosote bush. *Ecol Entomol* 15:87–95
- Wasbauer MS (1972) An annotated host catalog of the fruit flies of America North of Mexico (Diptera: Tephritidae). California Department of Agriculture, Sacramento, California
- Washburn JO, Cornell HV (1979) Chalcid parasitoid attack on a gall wasp population on oak (*Acraspis hirta* Bassett, on *Quercus prinus*, Fagaceae). *Can Entomol* 111:391–400
- Washburn JO, Cornell HV (1981) Parasitoids, patches, and phenology: their possible role in the local extinction of a cynipid gall wasp population. *Ecology* 62:1597–1607
- Weld LH (1960) Cynipid galls of the southwest. Privately printed, Ann Arbor, Michigan
- Zar JH (1984) *Biostatistical analysis*. (2nd ed). Prentice-Hall, Englewood Cliffs, New Jersey