

Distribution and abundance of two gall-makers on the euphorbiaceous shrub *Colliguaja odorifera*

Distribución y abundancia de dos formadores de agallas en el arbusto euforbiáceo *Colliguaja odorifera*

ENRIQUE MARTINEZ¹, GLORIA MONTENEGRO¹
and MARIO ELGUETA²

¹ Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.

² Museo Nacional de Historia Natural, Sección Entomología, Casilla 787, Santiago, Chile.

ABSTRACT

Previous studies on the interaction between the two inflorescence gall-maker insects of the euphorbiaceous shrub *Colliguaja odorifera* postulated a parasitoid relationship, while effects on shrub reproduction were not addressed.

In this study, we show a significant ($P < 0.001$) segregation of the insect attack on two different shrub organs, with a low incidence of co-occurrence (2.3%). *Exurus colliguayae* (Eulophidae, Hymenoptera) attacks mainly aments at bud stage, and *Torymus laetus* (Torymidae, Hymenoptera) attacks mainly vegetative buds. It is shown that both insects attack the plant directly and that they are not hyperparasites. The infection on aments induces 100% inhibition of the female function, this, in addition to a quantitatively important natural inhibition of female flower production. The infection on vegetative buds inhibits stem development, then affecting future production of new stems and fruits.

The intensity of attack is randomly distributed within each canopy (variance/mean index ca. 1.0), but it is aggregated between shrubs (variance/mean index > 5.5). Both, the partial infection of shrub aments, and the apparent inhibition of the female function only, make this plant-insect interaction to result in a partial shrub castration. Probably, this partial effect allowed between years 1987 and 1988 a high persistence (100%) and high prevalence (76%) of the infection, compared to other parasitic interactions where resultant castration is total.

Key words: Chalcidoid-insects, herbivory, plant-castration.

RESUMEN

Estudios anteriores sobre la interacción entre los dos insectos formadores de agallas en inflorescencias del arbusto euforbiáceo *Colliguaja odorifera* postulaban una relación de parasitoidismo, mientras que no se analizaba el efecto sobre la reproducción del arbusto.

En este estudio mostramos que existe una segregación significativa ($P < 0.001$) del ataque de los insectos en dos órganos diferentes del arbusto, con una baja incidencia de co-ocurrencia (2.3%). *Exurus colliguayae* (Eulophidae, Hymenoptera) ataca principalmente los amentos al estado de yema, y *Torymus laetus* (Torymidae, Hymenoptera) ataca principalmente las yemas vegetativas. Se muestra que ambos insectos atacan directamente a la planta y que no son hiperparásitos. La infección sobre los amentos se suma a una inhibición natural, cuantitativamente importante, de la producción de flores femeninas. La infección sobre las yemas vegetativas inhibe el desarrollo de la rama, afectando la producción futura de nuevas ramas y frutos.

Se muestra que la intensidad del ataque se distribuye aleatoriamente dentro de cada dosel (índice varianza/promedio ca. 1,0), pero está agregada entre arbustos (índice varianza/promedio $> 5,5$). Tanto la infección parcial de los amentos en los arbustos, como la aparente inhibición sólo de la función femenina hace que esta interacción insecto-planta resulte en una castración parcial del arbusto. Probablemente, este efecto parcial permitió, entre 1987 y 1988, una alta persistencia (100%) y alta prevalencia (76%) de la infección, en comparación a otras interacciones parasíticas donde la castración resultante es total.

Palabras claves: Insectos calcidoideos, herbivoría, castración de plantas.

INTRODUCTION

Studies on herbivory in the matorral shrub formation of central Chile have been focused mainly on chewing insects (Montenegro *et al.* 1980). Only a few studies described

plant-gall maker interactions. Aljaro *et al.* (1984) found that the shoot gall-maker *Rachiptera limbata* (Diptera, Tephritidae) alters the branching pattern of the matorral shrub *Baccharis linearis* (Compositae). Two gall-making insects were described by

Philippi (1873) as affecting reproductive structures of the euphorbiaceous matorral shrub, *Colliguaja odorifera*; since then, information about the insect species has been scant and mainly taxonomic (e.g. Kieffer 1903, Porter 1926, 1928. Ebel 1928). In this study nomenclature follows De Santis (1979). Two chalcidoid (Hymenoptera) insect species are associated with *C. odorifera* galls. *Torymus laetus* (Torymidae), the larger sized species, was thought to be a consumer parasitoid on the smaller species, *Exurus colliguayae* (Eulophidae). The assertion of a parasitoid relationship between these two insects is still accepted, probably because feeding-habit descriptions made for other *Torymus* species have been expanded and are, in general, hard to assess (Suarez & Calvo 1989a, 1989b). Most *Torymus* species are parasites of other hymenopteran and dipteran species, and a few are phytophagous (Grissell 1976). Some *Exurus* species are plant parasites and others are parasitoids (Burks 1979). The trophic status for *T. laetus* and *E. colliguayae* has not been clearly addressed. On the other hand, although Philippi (1873) recognized that the attacked organs were inflorescences, no other plant organs were ever surveyed to determine alternative oviposition sites. The aims of this study are: 1) to describe the galls made by chalcidoid insects, *Exurus colliguayae* and *Torymus laetus* on the shrub *Colliguaja odorifera*, relating gall morphology to the organs attacked and to the season of insect attack (emphasis will be given to description of reproductive structures and their galls) and 2) to describe the distribution and abundance of gall makers.

MATERIALS AND METHODS

Study site. Observations, collection of galls and manipulation of inflorescences were carried out at Los Dominicos (33°27'S, 70°42'W), 20 km east of Santiago, in central Chile. The vegetation corresponds to the semi-arid foothill matorral of the Andes Mountains, 800 m elevation, with evergreen and summer deciduous shrubs as

part of the shrubby strata. Annual and perennial species compose the herbaceous strata.

Shrubs surveyed. Although *C. salicifolia* is present at the site, only shrubs of the more abundant species (*C. odorifera*) were tagged. No shrubs of *C. integerrima* are present at this site. Fifty shrubs were surveyed in November 1987, 25 of these were tagged and revisited in 1988. Comparisons made between these two dates correspond to statistically related samples (Siegel & Castellan 1988).

Description of reproductive structures and galls. The common type described by Navas (1973) and variations of the host plant reproductive structures, as well as gall types, were described. The relationship between gall structure and plant morphology was established.

Distribution and abundance of galls. Evaluation of the relative abundance of galls and host plant reproductive structures as well as gall density (estimation of intensity), prevalence and persistence of galls in tagged shrubs was carried out from November 1987 to December 1988. Two areas of 0.25 m² were haphazardly sampled on the canopy of each tagged shrub (organs tend to develop only at the canopy surface), in November 1987, September and December 1988. Only one area was sampled where shrubs were too small. Within those areas all reproductive structures (attacked by gall inducing insects or not) and gall types were counted. Distribution of galls within and between shrubs was evaluated by the variance/mean ratio of gall density per canopy area, as an index of aggregation. When this index is significantly higher than one, it indicates contagious distribution, near zero indicates uniform distribution and values close or equal to one indicate random distribution. Insect emergence was surveyed examining gall contents in 56 galls of *C. odorifera* and of *C. salicifolia*, collected in January 1988.

Chi-squared and Spearman rank order correlation statistical tests followed the nonparametric methods of Siegel & Castellan (1988).

RESULTS AND DISCUSSION

Description of unattacked flowers, floral and vegetative galls. Reproductive structures of *Colliguaja* species develop from three different buds. The apical bud develops into a male inflorescence (ament) and the two sub-apical buds into female flowers. Petals and sepals are absent and the female floral structure consists of a three-capsular ovary with three feathery stigmas. The number of autochorously dispersed seeds per fruit is three. New floral buds are pre-formed at the end of spring time (Montenegro *et al.* 1989) and during the next spring season, they can develop (or abort), as shown in figure 1. Developed aments can have two female flowers (ovaries) at their bases (developed from each sub-apical bud), only one or no ovaries at all (Fig. 1). The mean number of each of these structures per canopy area sampled in shrubs of *C. odorifera* in 1987 and 1988 is shown in Table 1. Galls are only induced on floral or vegetative buds (Fig. 1). Gall morphology of these two bud types, at maturity, is highly differentiated. Oviposition on floral buds usually occurs within the apical meristem, which might otherwise develop into the ament axis. The ament developed by the attacked floral bud has a swollen axis, with a central larval chamber. When the apical bud is attacked, sub-apical buds do not develop into ovaries, and no fruits are produced. However, the swollen aments do produce pollen (of unknown quantity and quality).

Exurus colliguayae usually oviposits on floral buds. The mean amount of this type of gall per area of shrub sampled in 1987 and 1988 ranged from 0 to 27.5 (see mean and variance in Table 1). When infected, vegetative buds do not develop into branches, producing a swollen apex containing the larval chamber; and only two small leaves are formed at the base (Fig. 1). Usually, there is only one larva per chamber. *Torymus laetus* usually oviposits within vegetative buds. The mean amount of this type of gall per sampled shrub area ranged from 0 to 15.5 (see mean and variance in Table 1).

The frequency of flower and vegetative gall types for the two gall forming species is shown in Table 2. When larvae of both insect species occurred in the same gall, they were found in different larval chambers. The phenomenon of co-occurrence had a very low frequency (2.3%, of 173 galls surveyed) and those galls are not included in Table 2. Larvae of both insect species, observed in different sampling months, corresponded to different developmental stages, and always, small to large sized larvae were seen in separate chambers. These observations suggest that *T. laetus* is not a parasitoid on *E. colliguayae* (non *vice versa*) as had been previously sustained (Philippi 1873, Kieffer 1903, Ebel 1928). Both insects are parasites of the plant, one insect not being a parasitoid on the other, even though parasitoidism is a common feature in the family Torymidae (Grissell 1976) and in other chalcidoids (De Santis & Fernandes 1989). These gall makers partition host-plant organs ($X^2 = 61.8$, $df = 1$, $P < 0.001$). *Exurus colliguayae* preferentially attacks floral buds and *T. laetus* oviposits more frequently in vegetative buds. Insects also differ in time of adult emergence. By January 1988, adults of *T. laetus* had emerged from 56% of galls, while *E. colliguayae* had emerged from only 10% of floral bud galls. This pattern was consistent for galls of both *C. odorifera* and *C. salicifolia* (Table 3).

Prevalence, persistence and intensity of insect attack. Prevalence of attack of both types of gall makers in fifty shrubs surveyed in 1987 was as high as 76%. Persistence of attack, as evaluated in 1988 by resampling 23 of 25 tagged shrubs (two of them were cut down by intruders) was as high as 100%. So, all shrubs attacked by some type of gall-making insect in 1987, also had new galls in 1988.

Intensity of attack, estimated by gall density per sampled canopy area, is summarized in Table 1. Intra- and inter-shrub spatial distribution of intensity was estimated by the index of aggregation variance/mean ratio). Within shrubs, for floral galls the average index of aggregation is

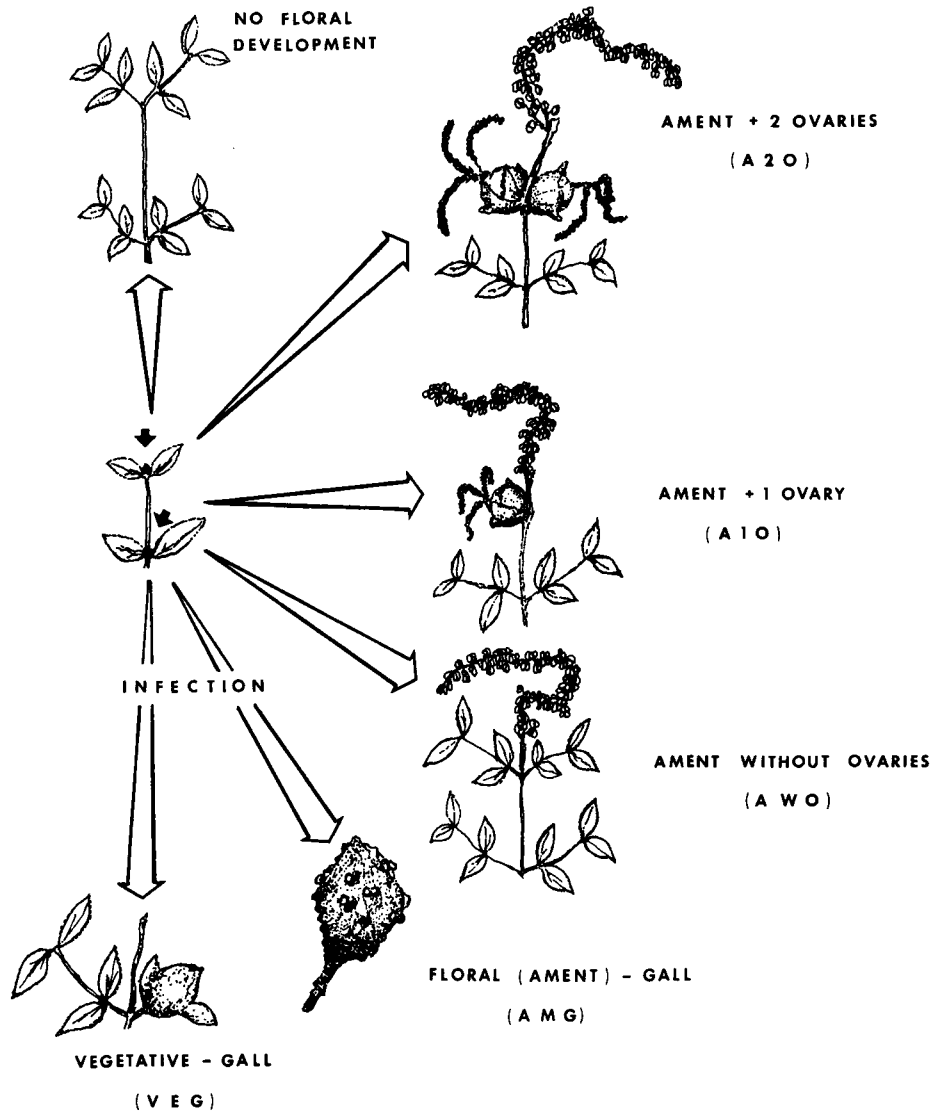


Fig. 1: Possible development of vegetative and reproductive buds from a previous year's stem. Blackened arrows show infected buds which develop galls (apical portions of stems have one apical and two sub-apical buds). Abbreviations: A20: Aments with two ovaries, A10: Aments with one ovary, AWO: Aments without ovaries, AMG: Ament type of gall, VEG: Vegetative type of gall.

Posibles desarrollos de yemas vegetativas y reproductivas de un tallo del año anterior. Las flechas negras muestran yemas infectadas que se desarrollan en agallas (las porciones apicales de los tallos tienen una yema apical y dos subapicales). Abreviaturas: A20: Amentos con dos ovarios, A10: Amentos con un ovario, AWO: Amentos sin ovarios, AMG: Agallas tipo amento, VEG: Agallas tipo vegetativas.

not significantly different from one ($t = 0.94$, $df = 44$, $P > 0.20$) therefore the distribution in intensity of attack is random. For vegetative galls, within shrubs, the index of aggregation (1.7) was significantly higher than one ($t = 3.28$,

$df = 44$, $P < 0.01$), indicating a contagious distribution.

The index of aggregation between the 50 shrubs was significantly higher than one (11.7 for floral galls, 5.5 for vegetative galls, t values = 52.9 and 22.3, $df = 49$,

TABLE 1

Mean number and variance of inflorescence and gall types, per area of canopy sampled (0.25 m²), for shrubs of *Colliguaja odorifera* visited in November 1987 (n = 50) and 1988 (n = 23). Number of samples per shrub = 2.

Abbreviations as in Figure 1.

Número promedio y varianza de tipos de inflorescencias y agallas, por área de dosel muestreada (0.25 m²), para arbustos de *Colliguaja odorifera* visitados en noviembre de 1987 (n = 50) y 1988 (n = 23). Número de muestras por arbusto = 2. Abreviaturas como en Figura 1.

Inflorescences and gall types	1987		1988	
	Mean	Variance	Mean	Variance
A20	1.8	9.2	3.4	22.8
A10	3.2	18.6	10.3	117.5
AWO	1.7	19.0	40.7	1,347.7
AMG	1.6	18.7	3.7	29.0
VEG	2.8	15.5	1.0	10.5

TABLE 2

Frequency of gall-inducing insect species related to each gall type found in *Colliguaja odorifera* (N = 169).

Frecuencia de especies de insectos inductores de agallas relacionadas con cada tipo de agalla encontrada en *Colliguaja odorifera* (N = 169).

Insect species	Gall type	
	As percentage of all galls sampled Floral	Vegetative
<i>Torymus laetus</i>	10.1%	18.3%
<i>Exurus colliguayae</i>	66.9%	4.7%

TABLE 3

Contents of vegetative and floral galls in two species of *Colliguaja*, in samples collected during January 1988.

Contenidos de agallas vegetativas y florales en dos especies de *Colliguaja* en muestras colectadas durante enero de 1988.

	<i>C. odorifera</i>		<i>C. salicifolia</i>	
	Vegetative	Floral	Vegetative	Floral
Only larvae	2	12	4	20
Only pupae	0	0	0	3
Larvae and pupae	0	0	0	1
Only adults	0	0	1	0
Empty chambers (adults emerged)	4	2	5	2
Totals	6	14	10	26

respectively, $P < 0.01$), i.e.) a contagious distribution of galls, where some shrubs were much more heavily attacked than others. Moreover, for the ament-type gall, the maximum within shrub index of aggregation (6.3) was lesser than the between shrub index of aggregation (11.7).

Intensity of attack in 1987 (adding both types of galls) was positively correlated with intensity of attack in 1988 ($r_s = 0.630$, $n = 23$, Spearman rank correlation test, $P < 0.001$). This suggests that insects emerging from galls tend to stay in the same shrub or/and that shrubs are differentially susceptible to insect attack, and that such susceptibility would not change in different years. Shrub susceptibility to insect attack seems to be similar for both insect species, as indicated by a significant positive correlation between the abundance of both type of galls ($r_s = 0.606$, $n = 50$, Spearman rank correlation test, $P < 0.0005$). Other explanations for the maintenance of the hierarchy in intensity of attack through time shown in different shrubs have less statistical support. For example, the intensity of insect attack affecting floral buds and the abundance of fruits, although showing a positive relationship, it is not statistically significant ($r_s = 0.171$, $n = 50$, Spearman rank correlation test, $P > 0.10$). Such intensity, on the other hand, does not correlate with the abundance of uninfected reproductive structures ($r_s = -0.202$, $n = 23$, Spearman rank correlation test, $P > 0.10$). A positive correlation between intensity of attack and host brood size has been found in some parasitically castrated invertebrates (Blower & Roughgarden 1988).

If all vegetative and floral buds are considered as having the same potential for successful development, and insect abundance were only related to available buds, it would be expected that galls on vegetative buds should be six times more abundant than on floral buds, since vegetative buds are six times more abundant than floral ones, on each branch. However, opposed to the expectance, in 1988 galls on floral buds were more abundant than on vegetative buds ($t = 2.06$, d.f. = 44,

$P < 0.025$, data taken from Table 1) but, in 1987, the difference in abundance was not significant ($t = 1.45$, d.f. = 98, $P > 0.05$). Probably, the higher number of individuals per gall chamber in floral gall insects is reverting the expected relative abundance of gall-makers. Also, floral buds are located closer to the canopy shrub surface than vegetative ones, being more exposed to insect infestation.

The effect of parasitic castration by gall-inducing insects on plants is an extreme case of externally-induced organ differentiation of reproductive structures in a gradient which depends on the time of attack. The earlier the attack, with respect to plant development, the stronger the effect caused (Meyer & Meresquelle 1983). The case reported in this study shows an extreme alteration of organ development. The alterations provoked by insect oviposition in the bud stage of stems and flowers affect both reproductive and vegetative structures. In this case the phenomenon is termed partial castration, since not all buds in a single shrub are simultaneously attacked. Even though the male bud inflorescence (ament) is directly attacked (usually by the chalcidoid *Exurus colliguayae*), damage on the reproductive structure formation occurs by inhibition of female flower bud development, probably by nutrient drainage induced by the growing gall (Abrahamson & Weis 1987). Pollen is still produced by the attacked ament, but we do not know its quality and quantity, with respect to unattacked aments. Castration by gall-inducing insects occurs in addition to what might be referred to as natural castration of the shrub. The two sub-apical buds, usually producing two ovaries at the base of the ament, sometimes do not develop the three-capsular female flowers, and sometimes only one is developed. In a separate work (unpublished data) we suggest that the amount of reproductive structures and the ratio between all types described is affected by weather conditions (cold days and rainfall). Besides natural and insect-induced castration, shrubs attacked by *T. laetus* are affected by insect-induced inhibition of vegetative-bud development. This pheno-

menon in which stems do not develop, alters the branching pattern reducing the number of branches and probably also reduces the foliar area. This implies a castration effect to flowers (male and female) of future generation of branches, which, if not infected, would have developed leaves and apical flowers.

The two gall-inducing insects also differ in the time in which adults emerge from their larval chambers. Insects affecting vegetative buds (*T. laetus*) tend to emerge first, in early summer, probably to oviposit in the pre-formed vegetative buds. *Exurus colliguayae*, on the other hand, tends to emerge later in summer.

The impact of gall-inducing chalcidoid insects on the euphorbiaceous shrub will depend on plant factors such as the variation in potential production of reproductive and vegetative structures, the spatial distribution of host plants, and also on population parameters referring to the insects themselves. Weather conditions affecting plant phenology might also affect insect populations.

Prevalence (% of shrubs with galls) in *C. odorifera* was high (76%) compared to other interactions where castration is produced. For instance, in barnacles, no more than 8% of the population is infected by a castrating parasite (isopods), but castration is complete for each affected individual (Blower & Roughgarden 1988). High prevalence contrasts with the distribution of high intensity (number of galls per shrub) which is restricted to some shrubs only. This, finally, implies that the attack is aggregated or contagious. When the same shrubs were observed in two consecutive years, intensity in one year was proportional to intensity in the next one, for each shrub.

Persistence of attack from one year to the next is 100%. In a review of wind-factors affecting insect dispersal, Pasek (1988) showed that wingless and small insects depend on air currents for dispersal, and that distribution patterns frequently reflect windflow patterns. In the case of these two small (< 5 mm) gall-inducing insects, considering that they

are specific on *Colliguaja* species, uncontrolled wind-borne dispersion could result into landing on the wrong shrubs. Within these insect populations it would then be more advantageous to stay in the same shrubs once colonized, rather than attempt random dispersion trials. Aggregated distribution might be an effect of insect size. Alternatively, the shrubs could be genetically variable in degree of susceptibility or resistance to gall formers (McCrea & Abrahamson 1987, Abrahamson *et al.* 1988). Levels of oviposition and gall initiation should then be determined by host-plant characteristic rather than by herbivore dispersal (Anderson *et al.* 1989). Comparison of the susceptibility to attack by these parasites with that of the other two Chilean species of *Colliguaja* must be evaluated, before any population dynamics results can be predicted for any species (Blower & Roughgarden 1987). Since *C. salicifolia* is a hybrid of the other two species (Navas 1973), this comparison might add valuable information to test resistance to herbivores in hybrid species. Also, this plant-insect interaction can be used to clarify speciation trends within the Euphorbiaceae, as has been done by Armbruster & Mziray (1987) for the euphorbiaceous *Dalechampia* species. They compared evolutionary trends between plants and their associated insects finding that recent and ancient species match between the two groups of associated organisms. The interaction can be used in this sense by botanists as well as by entomologists. Other evolutionary questions related to conditions favoring or preventing shrubs to be attacked by gall-inducing insects are open. Studies in the Chilean matorral made by Ginocchio & Montenegro (1989) have shown that buds of shrub species attacked by gall makers are naturally less protected than buds of unattacked shrub species. Comparisons of these kinds of interactions, with similar vegetation associations (e.g., chaparral in California or scrub in Florida) may add valuable information to the understanding of evolutionary trends in closely-related plant-insect interactions.

ACKNOWLEDGMENTS

We are grateful to Warren G. Abrahamson, Wilson Fernandes Simon R. Leather, Odette Rohfritsch and Donald R. Strong for comments on earlier drafts of this manuscript. We also appreciate assistance in the field provided by Sandra Silva and Luz María del Río. This study was developed as a partial requirement of the first author within the Doctor program on Ecology at the Pontificia Universidad Católica de Chile and financed by FONDECYT 747/91 to G. Montenegro.

LITERATURE CITED

- ABRAHAMSON WG & AE WEIS (1987) Nutritional ecology of arthropods gall makers. In: Slansky F, Rodriguez JG (eds.) Nutritional ecology of insects, mites and spiders, John Wiley and sons inc., pp. 235-258.
- ABRAHAMSON WG, SS ANDERSON & KD McCREA (1988) Effects of manipulation of plant carbon nutrient balance on tall goldenrod resistance to a gall making herbivore. *Oecologia* (Berlin) 77: 302-306.
- ALJARO ME, D FRIAS & G MONTENEGRO (1984) Life cycle of *Rachiptera limbata* (Diptera, Tephritidae) and its relationships with *Baccharis linearis* (Compositae). *Revista Chilena de Historia Natural* 57: 123-129.
- ANDERSON SS, KD McCREA, WG ABRAHAMSON & LM HARTZEL (1989) Host genotype choice by the gallmaker *Eurosta solidaginis* (Diptera: Tephritidae). *Ecology* 70: 1048-1054.
- ARMBRUSTER WS & WR MZIRAY (1987) Pollination and herbivore ecology of an african *Dalechampia* (Euphorbiaceae): Comparisons with New World species. *Biotropica* 19: 64-73.
- BLOWER SM & J ROUGHGARDEN (1987) Population dynamics and parasitic castration: A mathematical model. *American Naturalist* 129: 730-754.
- BLOWER SM & J ROUGHGARDEN (1988) Parasitic castration: Host species preferences, size selectivity and spatial heterogeneity *Oecologia* (Berlin) 75: 512-515.
- BURKS BD (1979) Family Eulophidae. In: Krombein KV, Hurd PD, Smith DR, Burks DD (eds.) Catalog of Hymenoptera in North of Mexico, Vol. 1, pp. 967-1022, Smithsonian Institut Press, Washington.
- DE SANTIS L (1979) Catálogo de los himenópteros calcidoideos de América al Sur de los Estados Unidos. Publicación especial de la Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, Buenos Aires, 488 p.
- DE SANTIS L & GW FERNANDES (1989) Brazilian parasitoids of gall forming insects: Two new chalcidoid species and host records. *Entomological News* 100: 29-36.
- EBEL GSJ (1928) El *Torymus laetus*. *Revista Chilena de Historia Natural* 32: 167-179.
- GINOCCHIO R & G MONTENEGRO (1989) Organización estructural de yemas vegetativas de especies arbustivas dominantes del matorral. *Medio Ambiente* 10: 51-56.
- GRISSEL EE (1976) A revision of western nearctic species of *Torymus* Dalman (Hymenoptera: Torymidae). Univ. of California Publications in Entomology, Vol. 79, Univ. of California Press, Berkeley, 120 p.
- KIEFFER JJ (1903) Observation sur une galle faussement attribué a un pteromaline. *Revista Chilena de Historia Natural* 7:3.
- McCREA KD & WG ABRAHAMSON (1987) Variation in herbivore infestation: historical vs. genetic factors. *Ecology* 68: 822-827.
- MEYER J & HJ MERESQUELLE (1983) Anatomie des galls. Gebrüder Borntraeger-Stuttgart, Federal Republic of Germany.
- MONTENEGRO G, M JORDAN & ME ALJARO (1980) Interactions between Chilean matorral shrubs and phytophagous insects. *Oecologia* (Berlin) 45: 346-349.
- MONTENEGRO G, G AVILA, ME ALJARO, R OSORIO & R GOMEZ (1989) Chile. In: Orshan G (ed) Plant phenomorphological studies in mediterranean type ecosystems, Kluwer Academic Publishers, The Netherlands, pp. 347-387.
- NAVAS LE (1973) Flora de la cuenca de Santiago, Ediciones Universidad de Chile, Santiago.
- PASEK JE (1988) Influence of wind and windbreaks on local dispersal of insects. *Agriculture Ecosystems and Environment* 22/23: 539-554.
- PHILIPPI RA (1873) Chilenische insekten. *Stettiner Entomologische Zietung* 34: 296-316.
- PORTER CE (1926) Sobre dos insectos chilenos. *Revista Chilena de Historia Natural* 30: 275.
- PORTER CE (1928) Acerca de las agallas del colliguay. *Revista Chilena de Historia Natural* 32: 152-153.
- SIEGEL S & J CASTELLAN (1988) Nonparametric statistics for the behavioral sciences. McGraw-Hill Inc., 2nd ed., N.Y. 399 pp.
- SUAREZ E & R CALVO (1989a) Formación de agallas en los frutos del Güisaro (*Psidium guineense* Swartz) (Myrtaceae) y su relación con los microhimenópteros *Prodecatoma* sp. (Eurytomidae) y *Torymus* sp. (Torymidae). *Brenesia* 31: 43-52.
- SUAREZ E & R CALVO (1989b) Emergencia de avispa *Prodecatoma* sp. (Eurytomidae) y *Torymus* sp. (Torymidae) de agallas del fruto del *Psidium guineense* Swartz (Myrtaceae). *Brenesia* 32: 117-118.