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Abundance and life history of two gall-inducing homopterans on *Nectandra salicina* (Lauraceae) in Monteverde, Costa Rica

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Abstract: This paper presents information on the abundance and life-history characteristics of two gall-inducing homopterans and a parasitic wasp that occur on *Nectandra salicina* (Lauraceae). The more common gall replaced the fruit and contained *Trioza* sp. (*magnoliae* group) (Homoptera: Triozidae). the stem gall contained a Coccoidea sp. (Homoptera). *N. salicina* were heavily infested with the psyllid gall. the mean ratio of galled to normal fruit was 6.2: 1. Galls had one to three chambers, with 2.0 ± 0.1 individuals per chamber and 3.0 ± 0.2 psyllids per gall. *Trioza* sp. had four instars and at the time of collection 71% of the psyllids were 3rd or 4th instar. The galls increased in size as the number and size of the psyllids, and the number of chambers increased. Eighteen percent of the 3rd and 4th instar psyllids were parasitized by *Metaphycus electra* Noyes and Hanson (Hymenoptera: Encyrtidae). Thirty-three percent of galls containing 3rd or 4th instar psyllids had one or more parasitoid, and within these attacked galls 69% of the psyllids were parasitized. The likelihood of a gall being attacked by *M. electra* had less to do with the size of the gall than with the frequency distribution of the various gall sizes. Similar to the *Trioza* sp. galls, the size of the Coccoidea galls increased as the mother matured and the number of offspring increased.

Key words: insect gall, *Trioza* sp., *Metaphycus electra*, tritrophic interactions, plant-reproductive fitness

There are approximately 13,000 described species of gall-forming insects, with representatives in seven orders (Dreger-Jauffret and Shorthouse 1992). Gall formers account for only 2% of all insect species, but because of the diverse and unusual architecture of their dwellings, these insects have fascinated naturalists since antiquity (Weis *et al.* 1988). Insects that induce plant galls are often monophagous and site specific (i.e., leaf, petiole, fruit or stem). Feeding is the usual stimulus for gall formation, but in a few cases the female insect provides the stimulus during oviposition.

Several hypotheses regarding the benefits of the galling habit have been advanced, but protection against natural enemies, nutritional enhancement and an improved microenvironment continue to be the most widely accepted hypotheses (Price *et al.* 1987). More recently, Fernandes and Price (1991) suggested that the galling habit was an adaptation to low soil fertility. However, Blanche and Westoby (1995) found that in Australia the incidence of galling had more to do with *Eucalyptus* attributes (e.g. secondary chemistry, leaf longevity, drought tolerance and sprouting capacity) than with soil fertility.

Here we describe the demographics and gall characteristics of two homopteran cecidogens and a gall parasitoid that occur on *Nectandra salicina* in Monteverde, Costa Rica. This is the first report of a *Metaphycus* wasp attacking a gall-inducing psyllid and the first record of a Coccoidea gall on Lauraceae. Our findings are discussed in relation to the current views on the benefits of the galling habit and on its prevalence in the tropics. Additionally, the impact that these particular galling organisms may have at Monteverde, Costa Rica, is considered.

MATERIAL AND METHODS

The study site was at Monteverde, Costa Rica and comprised 15 km^2 of lower montane wet and rain forests in the Cordillera de Tilaran (10°18'N, 84°48'W). The hábitat consists of undisturbed forests, pastures and woodlots. Nearly 85% of the yearly precipitation occurs during a distinct wet season (mid-May to late December). Temperature is relatively constant throughout the year (19.8-22.5°C T_{max}, 12.8-16.2°C T_{min}) and daylength changes by less than one hour (Wheelwright 1985).

Sampling and Analyses - During February and March of 1991, we examined 25 *N. salicina* trees for galling organisms. The number and type of gall, and number of fruits per plant were determined with the help of a pair of binoculars. When the galls were below 2 m, subsamples were collected. up to five galls per tertiary branch (two forks after the main trunk). In the laboratory, the maximum length and width (mm) of the psyllid and coccid galls were determined using a pair of calipers (N=137 and N=25, respectively). Galls were then dissected and number of chambers per gall, number of individuals per chamber, stage of nymphal development and the number of psyllids parasitized were recorded. Parasitism could only be determined for 3rd and 4th instar psyllids. To determine the age structure of the population, the number of shed exoskeletons within a gall were counted, and then the head width and body length of all size categories (N=10 for each size class) were measured with an ocular micrometer.

After checking for normality and homogeneity of variance, differences among size classes were determined with Analysis of Variance (ANOVA). Correlation analyses were performed to determine whether there were associations between 1) gall area and number of individuals, 2) gall area and number of chambers and 3) gall area and mean size class. Because gall area could be influenced by the number and size of the psyllids, a new variable was created by multiplying the number of individuals by the mean size class of individuals within the gall. Regression analyses were used to determine whether gall parameters (number of chambers, number of psyllids and gall area) influenced parasitoid success. In these analyses we assumed that parasitoids had no effect on the gall parameters. Kolmogorov-Smirnov two-sample test was used to determine whether the frequency distributions of gall sizes and parasitoid attack were different.

Coccid gall mothers were measured, and the number of offspring were counted. Correlation analyses were used to determine whether the size of the mother and the number of offspring were related to gall area. All measures of central tendency are expressed as means (+ SEM). Specimens of the psyllid and parasitoid were reared to the adult stage and voucher specimens were deposited in the Museo de Insetos at the University of Costa Rica. Specimens were sent to the Natural History Museum in London, UK, where the identification of *Trioza* sp. was made by David Hollis and the identification of *Metaphycus electra* was made by John Noyes.

RESULTS

1. Abundance of Galls on N. salicina: Only mature fruit-bearing *N. salicina* (N=6) were found to harbor galling organisms. The fruit gall contained an undescribed species in the genus *Trioza* (Homoptera: Triozidae) (Fig. 1A), and the stem gall contained a Coccoidea sp. (Fig. 1B). All six of the mature *N. salicina* had *Trioza* sp. (*magnoliae* group) galls, and two of them also had the coccid galls. On the two trees with coccid galls, one had a high incidence of stem galls and a low incidence of fruit galls (243 versus 32), whereas the other tree had a high incidence of fruit galls and a low incidence of stem galls (726 versus 2). *N. salicina* were heavily infested by *Trioza* sp. as indicated by the number of galled to normal fruit (1084 versus 174). Although there was considerable variability among trees, the mean ratio of galled to normal fruit was 6.2: 1 (range 1: 1 to 12.4: 1). on three trees very few normal fruit were present.

Fig. 1. A) Normal and *Trioza* sp. (*magnoliae* group) galled fruit and B) Coccoidea stem gall on *Nectandra salicina* (Lauraceae), Monteverde, Costa Rica.

2a. Trioza sp. Gall Characteristics: The galled fruit was rose colored and measured 11.7 ± 0.3 mm x 6.6 ± 0.2 mm (L x W), with a mean area of 80.4 ± 3.5 mm^2. Eighty-two percent of the galls still contained residents. Ten galls were artifically opened and within 24 hours winged adults emerged from the 4th instar psyllids.

2b. Nymphal Characteristics: Sixty percent of the *Trioza* sp. galls had one chamber, 32% had two chambers and 8% had three chambers. The mean number of psyllids per gall was 3.0 ± 0.2 (range 1-10), and the mean number of individuals per chamber was 2.0 ± 0.1 (range 0-8). Psyllids could be divided into four distinct size classes (=instars) based on differences among head widths and body lengths (Fig. 2. F=612, P=0.0005, df=3,39). Seventy-one percent of the individuals were either 3rd or 4th instars. The number of psyllids, the number of chambers, the size of the psyllids and the size x the number of psyllids were all significantly correlated with gall size (Fig. 3).

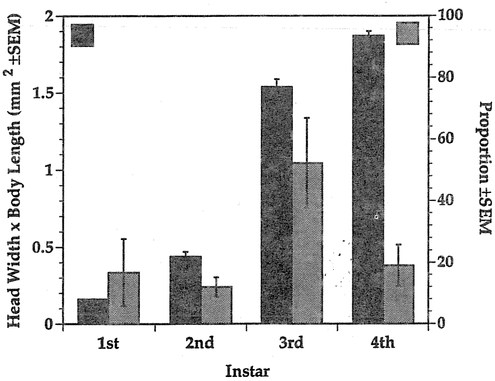

Fig. 2. Head width x Body length (mm^2) and proportion of 1st-4th instar nymphs of *Trioza* sp. (*magnoliae* group) (Homoptera: Triozidae) on *Nectandra salicina* (Lauraceae), Monteverde, Costa Rica.

2c. Nymphal Parasitism: Eighteen percent of the 3rd and 4th instar psyllids were parasitized by *M. electra*. Thirty-three percent of all galls containing 3rd and 4th instar psyllids had one or more parasites, and within these attacked galls 69% of the psyllids were parasitized. Number of chambers and number of psyllids per gall did not influence the number of parasitoids (P=0.42 and P=0.09, respectively), and although gall area was a significant factor (F=6.6, P=0.01, df=1,96) it accounted for only 6% of the variability in parasitoid numbers. The frequency distribution of attacked galls was similar to the frequency distribution of gall sizes in our collection (Fig. 4. n_1=99 and n_2=33, P>0.05 Kolmogorov-Smirnov two-sample test). Parasitoid emergence apparently was not always synchronized with gall splitting. On three occasions, when galls were cut open, adult parasitoids had already emerged. The wasps were dead in two cases, but in one gall four live wasps were found.

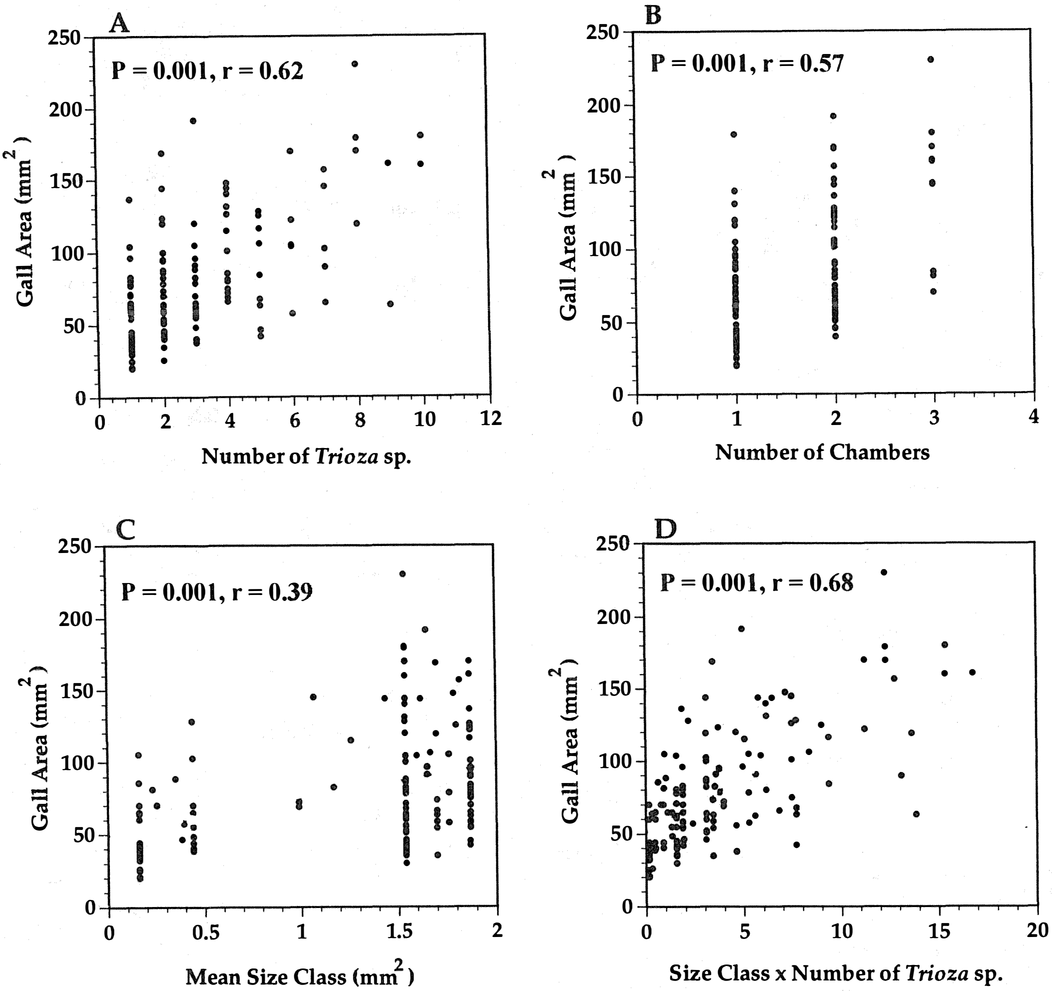

Fig. 3. Relationship between *Trioza* sp. (*magnoliae* group) gall area (mm^2) and A) number of individuals, B) number of chambers, C) mean size class (mm^2) of psyllids and D) size class x number of *Trioza* sp. individuals found on *Nectandra salicina* (Lauraceae), Monteverde, Costa Rica.

3a. Coccoidea Gall Characteristics: Stem galls were abundant on only one *N. salicina* tree, in which 275 galls (32 of which were psyllid galls) and 9 normal fruit were found. The gall began as a slight swelling on the stem and enlarged to an average size of 75.1 ± 29.5 mm^2, when it resembled an acorn (Fig. 1B). The mature gall consisted of a dorsal waxy black plug (2.6 ± 0.7 mm long) that was connected to a wax-lined cavity. The waxy substance was secreted by the colonizing insect. when gently touched with forceps, the gall mother exuded a clear substance that solidified rapidly. Mites were feeding and ovipositing on the black plug, which was covered with a fungus. In some cases when the gall was vacant, ants in the genus *Camponotus* sp. (*senex* group) (T. Schultz, pers. comm.) had moved into the gall and were rearing their brood.

3b. Nymphal Characteristics: Initially, gall mothers were small (0.5 ± 0.05 mm^2), ovoid and white, with few distinct features. Reproduction began when the insect reached approximately 10.5 mm^2. Gall dimensions were significantly correlated with the number of offspring and the size of the mother (Fig. 5).

No parasitoids were found in these galls, but approximately 30% were vacant and the size of these galls (56.8 ± 4.2 mm^2) would suggest that something (*i.e.*, death or parasitism/predation) happened to the gall mothers before they began to deposit their offspring.

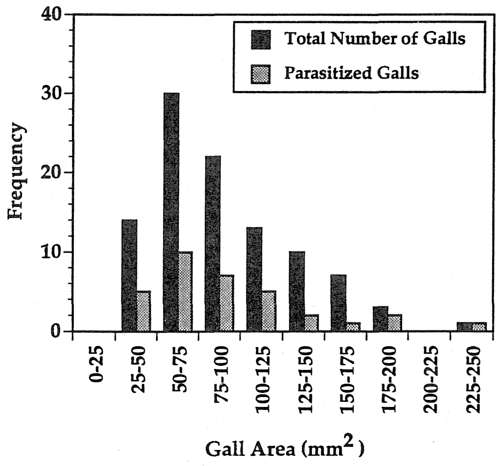

Fig. 4. Frequency distribution of *Trioza* sp. (*magnoliae* group) galls within a particular size category and the frequency distribution of galls that contained *Metaphycus electra* parasitoids on *Nectandra salicina* (Lauraceae), Monteverde, Costa Rica.

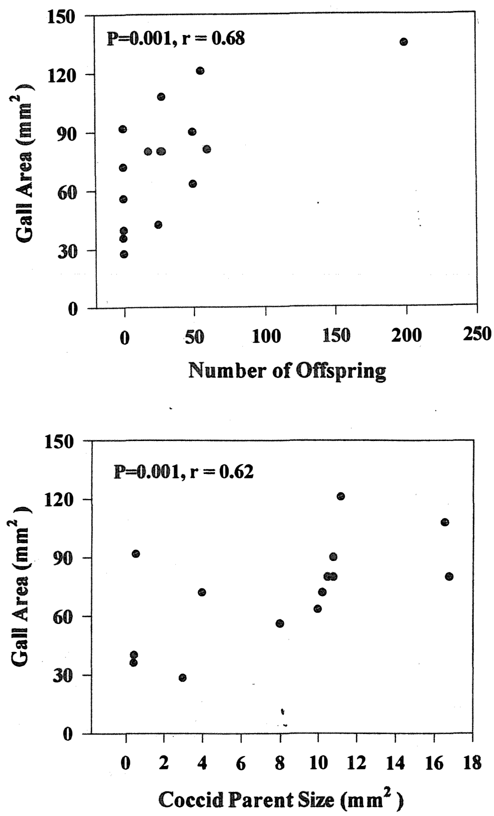

Fig. 5. Relationship between Coccid gall area and A) number of offspring and B) size of the mother (mm^2) found on *Nectandra salicina* (Lauraceae), Monteverde, Costa Rica.

DISCUSSION

Stem and fruit galls account for 20% and 1% of all known galls, but homopterans (*i.e.*, Triozidae and Coccoidea) rarely produce these types of galls (Mani 1964). Previously, pit- and leaf-galling psyllids have been recorded on *Nectandra* sp. and the closely related *Ocotea acutifolia* (see references in Hodkinson 1984), but this is the first reported case of a fruit-galling psyllid on *N. salicina.* As for the coccid cecidogen, only a few species are capable of inducing galls and nearly all of these are associated with *Eucalyptus* on the Australian continent (Beardsley 1984, Rohfritsch and Anthony 1992). Gall-inducing coccids have not been reported from Lauraceae previously, although recently a similar coccid gall was found by oné of us (P. Hanson, unpubl. data) on *Aiouea costaricensis* (Lauraceae).

Both the psyllid and coccid cecidogens appear to be site specific (fruit and stem, respectively) and possibly monophagous, as they were found only on *N. salicina.* Three other closely related lauraceous species were examined for galls, but none were found (Blackmer, unpubl. data). Moreover, over the course of a decade of work on the frugivores of Lauraceae, similar galls have never been observed on closely related species (N.T. Wheelwright, pers. comm.).

Galls that are initiated at flowering are among the most restrictive, because the gall-maker's stimulus is effective for only a brief period of time. Based on phenological studies for *N. salicina*, the peak flowering period would have been from June through August (Wheelwright 1986), so *Trioza* sp. must have initiated their galls around this time. Feeding and maturation would have continued until April or May of the following year, with the galls opening soon thereafter. Some galls split open with increasing relative humidity (Mani 1964). For *Trioza* sp., gall opening would coincide with the beginning of the wet season (mid-May) in Costa Rica. Gall initiation for the coccid cecidogen was not restricted to the flowering period and so we cannot speculate on its life history. Additional studies are warranted for this species with its microcosm of interactions, which encompass two classes of arthropods and at least two orders of insects.

The findings that the psyllid and coccid galls increased in size relative to the number and size of the residents is not surprising. Galls arise mostly by hypertrophy and hyperplasy, which are under the influence of the cecidogen(s). In the cynipid wasp *Diastrophus kindaidii*, and the adelgid *Adelges japonicus*, gall volumes were highly correlated with the total number of insects per gall (Jones 1983, Ozaki 1993).

There is some evidence that variability in gall size provides protection against natural enemies (Jones 1983, Weis *et al.* 1985). However, for *M. electra*, small unilocular galls were no more susceptible to attack than were large multilocular galls. The chance of encounter seemed to be the most important factor determining whether the psyllids within a gall were parasitized, as indicated by similar frequency distributions for gall size and parasitoid attack. As a whole, 18% of the psyllids were parasitized. however, if percent parasitism within galls attacked is considered, the rate increased nearly four fold (69%). It is interesting that the emergence of some of the parasitoids was not well synchronized with gall opening. This point and the low overall attack rate suggests that this may be a relatively new host for this parasitoid. Although some encyrtid genera are associated with free-living Psylloidea (e.g. *Psyllaephagus*) most species of *Metaphycus* are parasitoids of Coccoidea (Noyes and Hanson 1997).

In the 'microenvironment hypothesis' it has been proposed that the galling habit evolved to reduce hygrothermal stress (Price *et al.* 1987). The apparently reduced number of galls in tropical rainforests has been presented as evidence lending support to this hypothesis (D.H. Janzen pers. comm. to P.W. Price, cited in Price *et al.* 1987). Not including the two homopteran galls described herein, we found approximately 20 galling species, mostly Cecidomyiidae (Diptera), but also Hymenoptera and Homoptera, while traversing a single trail in the Monteverde cloud forest. Although this survey was limited, it suggests that the galling lifestyle, at least in this particular cloud forest reserve, is not as rare as has been suggested.

When galls occur on vegetative structures and infestation levels are low, reduction in plant reproductive fitness is usually minimal. However, when reproductive tissues are directly attacked, the negative impact can be high (Abrahamson and Weis 1987). Based on the high ratio of galled to normal fruit on *N. salicina, Trioza* sp. could have a significant impact on plant reproductive fitness. One of the trees examined has had a large population of psyllid galls for at least 10 consecutive years (N. Wheelwright, pers. comm.). In addition to this possible detrimental effect on the plant, these galls also result in reduced food for four focal bird species in Monteverde: the resplendent quetzal (*Pharomachrus mocinno*), the three-wattled bellbird (*Procnias tricarunculata*), the emerald toucanet (*Aulacorhynchus prasinus*) and the mountain robin (*Turdus plebejus*). These birds rely heavily on these fruits and a low fruit crop could cause a delay in breeding, a switch to alternate foods or migration to other areas (Wheelwright 1991). These birds have never been observed feeding on the galls in the absence of fruit (Wheelwright, pers. comm.). These facts suggest that these small, easily overlooked homopterans could play an important role in shaping Monteverde, Costa Rica. Further studies on these associations could prove "fruitful" by adding to our understanding of the evolution of these host-plant associations and higher-level community interactions.

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RESUMEN

Se estudió la abundancia y ciclo de vida de dos homópteros inductores de agallas y una avispa parasitoide de *Nectandra salicina* (Lauraceae). La agalla más frecuente reemplazó al fruto y contenía *Trioza* sp. (grupo *magnoliae*) (Homoptera: Psylloidea). El segundo tipo de agalla se halló en el tallo leñoso y contenía una escama (Homoptera: Coccoidea). Los árboles de *N. salicina* sufrieron altas infestaciones de la agalla de *Trioza*; el promedio de la proporción de frutos con agallas con respeto a frutos normales fue de 6.2:1. Las agallas presentaron de una a tres cámaras, con 2.0 ± 0.1 individuos por cámara y 3.0 ± 0.2 psílidos por agalla. *Trioza* presentó cuatro estadios ninfales y en el momento de la recolección 71% de los psílidos estaban en el tercero o cuarto estadio ninfal. Las agallas eran más grandes al aumentar los psílidos en número y tamaño, y al aumentar el número de cámaras, un 18 % de los psílidos en el tercer o cuarto estadio ninfal fueron parasitados por *Metaphycus electra* Noyes y Hanson (Hymenoptera: Encyrtidae) y un 33 % de las agallas con psílidos del tercer y cuarto estadio ninfal presentaban uno o mas parasitoides; dentro de estas agallas atacadas, 69% de los psílidos estaban parasitados. La probabilidad de que *M. electra* atacara a una agalla tuvo menos relación con su tamaño que con su distribución de frecuencias morfométricas. Como en las agallas de *Trioza* sp., las agallas de la escama crecieron a medida que la madre maduraba y el número de descendientes aumentaba.

REFERENCES

Abrahamson, W.G. & A.E. Weis. 1987. Nutritional ecology of Arthropod gall makers, p. 235-258. *In* F. Slansky Jr. and J.G. Rodriquez (Eds.). Nutritional ecology of Insects, mites, spiders and related invertebrates. John Wiley, New York, N.Y.

Beardsley, J.W. Jr. 1984. Gall-forming Coccoidea, p. 79-106. *In* T.N. Ananthakrishnan (Ed.). Biology of gall insects. Oxford and IBH Publ., New Delhi.

Blanche, K.R. and M. Westoby. 1995. Gall-forming insect diversity is linked to soil fertility via host plant taxon. Ecol. 76:2334-2337.

Dreger-Jauffret, F. and J.D. Shorthouse. 1992. Diversity of gall-inducing insects and their galls, p. 8-33. *In* J.D. Shorthouse and O. Rohfritsch (Eds.). Biology of insect-induced galls. Oxford University, New York, N.Y.

Fernandes,G.W. & P.W. Price. 1991. Comparison of tropical and temperate galling species richness: The roles of environmental harshness and plant nutrient status, p. 91-115. *In* P.W. Price, T.M. Lewinsohn, G.W. Fernandes and W.W. Benson (Eds.). Plant-animal interactions: Evolutionary ecology in tropical and temperate regions. Wiley, New York, N.Y.

Hodkinson, I.D. 1984. The biology and ecology of gall forming Psylloidea (Homoptera), p. 59-77. *In* T.N. Ananthakrishnan (Ed.). Biology of gall insects. Oxford and IBH., New Delhi.

Jones, D. 1983. The influence of host density and gall shape on the survivorship of *Diastrophus kindaidii* Gill. (Hymenoptera: Cynipidae). Can. J. Zool. 61:2138-2142.

Mani, M.S. 1964. Ecology of plant galls. Dr. W. Junk, Publ., The Hague. 434 p.

Noyes, J.S. & P. Hanson. 1997. Encyrtidae (Hymenoptera: Chalcidoidea) of Costa Rica: the genera and species associated with jumping plant-lice (Homoptera: Psylloidea). Bull. nat. Hist. Mus. Lond. (Ent.) 65: 105-164.

Ozaki, K. 1993. Effects of gall volume on survival and fecundity of gall-making aphids *Adelges japonicus* (Homoptera: Adelgidae). Res. Pop. Ecol. 35:273-284.

Price, P.W., G.W. Fernandes & G.L. Waring. 1987. Adaptive nature of insect galls. Environ. Entomol. 16:15-24.

Rohfritsch, O. & M. Anthony. 1992. Strategies of gall induction by two groups of Homopterans, p. 102-117. *In* J.D. Shorthouse and O. Rohfritsch (Eds.). Biology of insect-induced galls. Oxford University, New York, N.Y.

Weis, A.E., W.G. Abrahamson and K.D. McCrea. 1985. Host gall size and oviposition success by the parasitoid *Eurytoma gigantea*. Ecol. Entomol. 10:341-348.

Weis, A.E., R. Walton & C.L. Crego. 1988. Reactive plant tissue sites and population biology of gall makers. Ann. Rev. Entomol. 33:467-486.

Wheelwright, N.T. 1985. Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. Oikos 44:465-477.

Wheelwright, N.T. 1986. A seven-year study of individual variation in fruit production in tropical bird-dispersed tree species in the family Lauraceae, p. 19-35. *In* A. Estrada & T.H. Fleming (Eds.). Frugivores and seed dispersal. W. Junk., Dordrecht, Nederland.

Wheelwright, N.T. 1991. How long do fruit-eating birds stay in the plants where they feed? Biotropica 23:29-40.