

INQUILINE EFFECTS ON A MULTILOCLAR GALL COMMUNITY

LÁSZLÓ, Z.¹ and TÓTHMÉRÉSZ, B.²

¹*Ecological Institute, University of Debrecen, H-4010 Debrecen, P. O. Box 71, Hungary*
E-mail: feherlofia@puma.unideb.hu

²*Ecological Institute, University of Debrecen*
H-4010 Debrecen, P. O. Box 71, Hungary. E-mail: tothmerb@delfin.klte.hu

The influence of inquiline on the gall of *Diplolepis rosae* (Hymenoptera: Cynipidae) and its community was investigated. It is expectable that inquilines should cause major changes in the gall-community. Evidences for inquiline effect on multilocular galls are provided and the result suggests that the outcome shows similarity with unilocular ones. Gall size, number of emerged individuals and diversity increased significantly for inquilined galls. Inquiline-free galls showed highly significant positive correlation between gall size and number of emerged individuals. The presence of inquiline entirely annihilated the correlation between gall size and number of emerged individuals. This radical change implied within relationships of gall size and specimen number indicates that inquilines play an important role in shaping the community structure of *D. rosae* gall.

Key words: Cynipidae, *Diplolepis rosae*, species diversity, gall size, number of emerged specimens, *Periclistus brandtii*, polythalamous gall.

INTRODUCTION

Plant-herbivore interactions are strongly influenced by species on higher trophic levels (PRICE *et al.* 1980, WEIS & ABRAHAMSON 1985). Higher trophic level species may cause changes in interactions between lower trophic level ones (PRICE *et al.* 1980). Relationships between different trophic levels can be easily studied in gall communities which provide simple models of multilevel trophic systems (SANVER & HAWKINS 2000, STONE & SCHÖNRÖGGE 2003, HAYWARD & STONE 2005). Cynipid gall formation is an interaction between the insect and the host-plant where the cynipid gall wasp influences the plant development to form new structures that protects and feeds developing larvae (ASKEW 1984, STONE *et al.* 2002). Characters of the internal tissues are similar across all cynipid galls, with an outer cortical parenchyma and an inner-gall, housing one (unilocular, respectively monothalamous) or many (multilocular, respectively polythalamous) larval chambers.

In case of various galling systems the published studies focused on the effects of parasitoids on gall community (SCHRÖDER 1967, SHORTHOUSE 1973, JONES 1983, WEIS 1983, WEIS *et al.* 1983, STILLE 1984, CLANCY *et al.* 1986, WIEBES-

RIJKS & SHORTHOUSE 1992). Whereas studies on effects of inquiline (cynipid wasp species which lost their ability to initiate galls, but whose larvae are developing in gall tissues and various insects feeding on gall tissues) species were rarely reported. Inquiline effect was studied mainly for unilocular cynipid galls on oak and rose and dipteran galls on goldenrod, regarding the percentage of parasitized galls, emergence date, gall enlargement, wall thickness and layer modification (SCHÖNRÖGGE *et al.* 1995, 1996a, b, ABRAHAMSON & WEIS 1997, SCHÖNRÖGGE *et al.* 2000, LEBLANC & LACROIX 2001, SHORTHOUSE *et al.* 2005).

A large percentage of cynipid galls are host to numerous inquilines and parasitoids (SHORTHOUSE 1998, SANVER & HAWKINS 2000, STONE *et al.* 2002, HAYWARD & STONE 2005). Galls induced by *Diplolepis rosae* (Hymenoptera: Cynipidae) on rose shrubs are inhabited by a single inquiline and several parasitoid species (BLAIR 1945, ASKEW 1960, SCHRÖDER 1967, NORDLANDER 1973, STILLE 1984). The inquiline *Periclistus brandtii* (Hymenoptera: Cynipidae) is unique considering the multilocular structure of its host galls (*D. rosae* & *Diplolepis mayri*). While the rest of *Periclistus* species inhabit unilocular galls (SHORTHOUSE 1998). According to GEORGE MELIKA (personal communication) *Periclistus caninae* was also reared out from multilocular *D. rosae* and *D. mayri*. All *Periclistus* species have their life cycles obligatorily associated with galls induced by *Diplolepis* species (SHORTHOUSE 1998).

Inquiline larvae cause the gall to be hypertrophied and increasing number of inquilines causes increased growth of host gall tissues and wall thickness (ASKEW 1961, LEBLANC & LACROIX 2001, STONE *et al.* 2002). *P. brandtii* larvae subdivide a single host larval chamber into many inquiline chambers and this fact leads to the prediction that inquiline presence will modify the gall size and the number of emerging specimens (NORDLANDER 1973, SHORTHOUSE 1980, WIEBES-RIJKS & SHORTHOUSE 1992, SHORTHOUSE & BROOKS 1998). Inquilines, particularly if they are many in a single chamber, sometimes kill the larva of the gall inducer. Adults of inquilines emerge from galls soon after gall inducers and oviposit in freshly initiated galls (SHORTHOUSE 1980, SHORTHOUSE & WIEBES-RIJKS 1992). Multilocular galls of *D. rosae*, inhabited by *P. brandtii*, were studied by STILLE (1984). Relationships between species inhabiting galls of *D. rosae* were studied by several authors (SCHRÖDER 1967, NORDLANDER 1973).

The presence of inquiline should influence gall characteristics other than size too, such as the number of emerged individuals, species richness and other measures of diversity of the gall-inhabiting community. The majority of the theories and quantitative relationships for gall communities on rose shrubs were derived from studies based on unilocular galls (SHORTHOUSE 1980, SHORTHOUSE 1998, LEBLANC & LACROIX 2001). On the contrary, the present study is focused on

community of multilocular galls. This is an ecologically significant difference, since the relationship between gall size and emerging individuals may disappear, when inquiline inhabited galls have more chambers per inducer chamber.

We tested the influence of inquiline on gall diameter, number of emerged individuals and diversity of the gall-inhabiting community. Moreover, the influence of the inquiline on the gall diameter – number of emerged individuals relationship was also studied.

MATERIAL AND METHODS

There were two sampling sites located in Romania, Eastern Europe. The first one was in Mureş county (46°31'N, 24°34'E) and the second one in Cluj county (46°48'N, 23°37'E). Samples were taken in 2001 and 2002. Each situated on a dry pasture. The two sampling sites were used as replication of the study. Although the ecological features of the sites were similar, there were significant differences in the studied parameters of the galls, according to sites. Therefore, we used sites as a covariate.

Galls were collected during March and April. After sampling, galls were introduced individually in plastic cups, with cellophane cover, which enabled airing, and were kept on room temperature. Emerged individuals were stored in 70% ethanol. After emergence three orthogonal diameters were measured for each gall; the mean of these measurements was used as the diameter of a gall during analysis. Inquilined galls collected in 2002 were dissected. Inquiline-free and inquilined chambers, and the number of inquiline cells per inquilined chamber were counted.

A total number of 172 galls were collected altogether. Those which hatched no individuals or which were infected by fungi were left out from all analyses. Statistical analyses were carried out on 145 galls, from which 107 were inquiline-free and 38 were inquilined.

Normality of data sets was analysed using Kolmogorov-Smirnov test, and the normality of distribution was also confirmed visually by normal probability plots. Homogeneity of variances was analysed with Levene test (MILLIKEN & JOHNSON 1984). One-way ANOVA was used to test the difference of the means between sampling sites (SOKAL & ROHLF 1995). Differences between gall diameter, number of emerged individuals and diversity for inquiline-free and inquilined gall were analysed with MANCOVA. The covariate was formed by sampling sites. Type III sums of squares were used (SHAW & MITCHELL-OLDS 1993). Data which showed significant differences from normal distribution were log-transformed.

There was no departure from normality for the Shannon diversity by Kolmogorov-Smirnov test. Log-transformed gall diameter and number of emerged individuals showed no departure from normality. Comparison of the homogeneity of variances by Levene test revealed no significant differences.

Linear regression was used to describe the relationships between gall diameter and number of emerged individuals for inquiline-free and inquilined galls from different sampling sites. Statistical analyses were carried out with R program package for statistical computing (R Development Core Team 2005).

RESULTS

The galls were inhabited by ten species of parasitoids and the inquiline *P. brandtii*. Two parasitoids (*Caenacis inflexa* and *Eurytoma rosae*) attack the inquiline, while the others usually attack larvae of *D. rosae*. The most dominant parasitoid species were *Orthopelma mediator*, *Torymus bedeguaris* and *Glyphomerus stigma* (Table 1).

Within inquilled galls, an average of five host chambers were inhabited by inquilines per a gall, i.e. less than 20% of host chambers were infected. Each inquilled host chamber was divided in average on five inquiline chambers (Table 2). The inquiline showed aggregated distribution between attacked host galls (Fig. 1a). The rate of inquilled chambers decreased significantly with increasing gall size ($N = 24$, $r = -0.59$, $P < 0.01$) (Fig. 1b), while gall diameter and the number of emerged inquiline specimens were independent of it ($N = 36$, $r = 0.08$, $P = \text{N.S.}$) (Fig. 1c).

Gall diameter (one-way ANOVA, $df = 1$, $F = 12.88$, $P < 0.001$) and number of emerged individuals (one-way ANOVA, $df = 1$, $F = 8.30$, $P < 0.01$) differed significantly between sampling sites. On the other hand, diversity showed no difference between sites (one-way ANOVA, $df = 1$, $F = 2.03$, $P = \text{N.S.}$).

Table 1. The inquiline *Periclistus brandtii*, parasitoid species and parasitism rates in the inquiline-free and inquilled galls of *Diplolepis rosae*. Notations: * – inquiline-free galls, † – inquilled galls.

Species	site1				site2			
	2001		2002		2001		2002	
	*	†	*	†	*	†	*	†
<i>Periclistus brandtii</i>	–	0.65	–	0.29	–	0.35	–	0.35
<i>Orthopelma mediator</i>	0.07	0.10	0.24	0.32	0.16	0.17	0.26	0.13
<i>Torymus bedeguaris</i>	0.28	0.04	0.07	0.01	0.12	0.15	0.13	0.05
<i>Glyphomerus stigma</i>	0.26	0.01	0.16	0.14	0.23	0.11	0.12	0.14
<i>Pteromalus bedeguaris</i>	0.17	0.04	0.06	0.02	0.01	–	0.08	0.06
<i>Torymus rubi</i>	–	–	0.01	0.01	–	–	0.01	–
<i>Caenacis inflexa</i>	–	0.04	–	0.08	–	0.01	–	0.11
<i>Eurytoma rosae</i>	–	0.03	–	0.01	–	0.03	–	0.02
<i>Eupelmus urozonus</i>	0.03	0.01	–	0.01	–	–	–	–
<i>Eupelmus vesicularis</i>	–	–	–	–	–	–	–	0.01
Eulophidae	–	–	–	–	–	–	0.01	–
Number of species	5	8	5	9	4	6	6	8
Reared individuals	69	365	941	340	270	175	1129	692
Number of galls	6	7	30	9	7	5	64	17

Table 2. The number and the ratio of inquilined chambers per gall, number of inquiline chambers in an inquilined host chamber in the galls with *Periclistus brandtii* in 2002.

	site 1 and 2	site 1	site 2
Number of galls	26	9	17
Number inquilined chambers per gall	5.37±1.65	4.77±1.46	5.73±2.54
% inquilined chambers per gall	16.35±3.87	22.24±5.33	12.82±5.22
Inquiline chambers per inquilined chamber	5.55±0.78	6.71±1.16	4.86±1.02

Sampling sites and the presence of inquilines showed highly significant effects on the tested gall parameters (MANCOVA; sites: Wilks' lambda = 0.81, F = 12.91, P < 0.001; inquilined feature: Wilks' lambda = 0.75, F = 17.84, P < 0.001). After controlling for the differences between sampling sites by a covariance analysis, significant differences were found between inquiline-free and inquilined galls

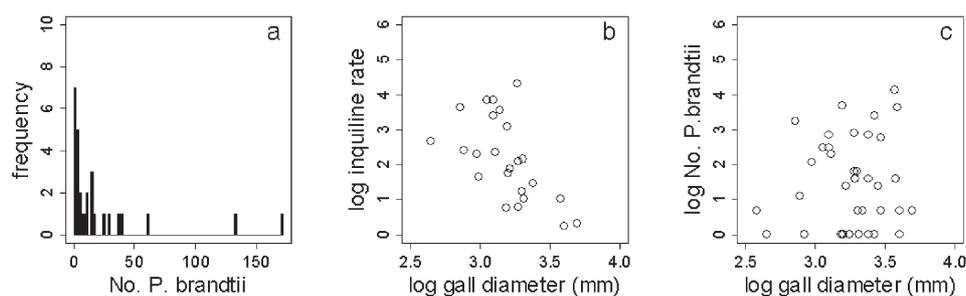


Fig. 1. a) Distribution of emerged *Periclistus brandtii* individuals among attacked galls; b) Scatter plot of the gall diameter and the rate of inquilinism (*P. brandtii*) ($r = -0.59$, $P < 0.01$); c) Scatter plot of the gall diameter and the number of emerged inquiline (*P. brandtii*) specimens ($r = 0.08$, $P = N.S.$)

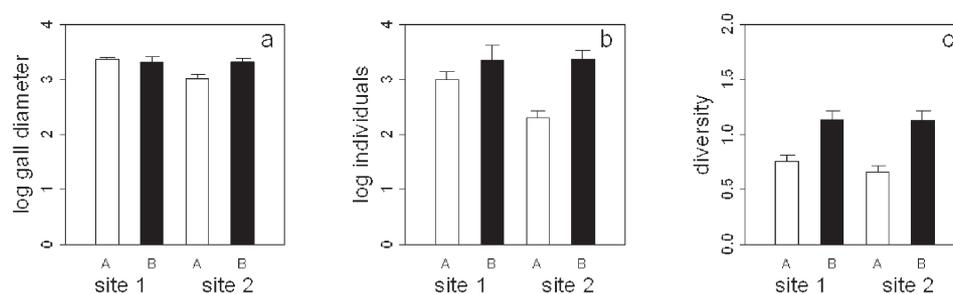


Fig. 2. Averages and SE of the studied parameters for the inquiline-free and inquilined galls for the diameter (a), number of emerged individuals (b), and Shannon diversity (c); A – inquiline-free galls, B – inquilined galls.

Table 3. Summary of MANCOVA for gall diameter, number of individuals and diversity of the inquiline-free and inquilined galls, with the sites as covariate.

Source	Dependent variable	Type III SS	df	MS	F	P
Intercept	Gall diameter	256.19	1	256.19	1711.46	<0.001
	Number of individuals	318.55	1	318.55	307.00	<0.001
	Diversity	20.67	1	20.67	144.03	<0.001
Sites	Gall diameter	4.11	1	4.11	27.48	<0.001
	Number of individuals	34.18	1	34.18	32.95	<0.001
	Diversity	0.37	1	0.37	2.61	N.S.
Inquiline presence/ absence	Gall diameter	0.80	1	0.80	5.37	<0.05
	Number of individuals	18.40	1	18.40	17.73	<0.001
	Diversity	4.98	1	4.98	34.74	<0.001

for each studied parameter of galls (Table 3). Gall diameter, number of emerged individuals and Shannon diversity showed a significant increase for inquilined galls (Table 4, Fig. 2).

Linear regression analysis of gall diameter and number of emerged individuals for the two sampling sites revealed a strong relationship for the inquiline-free galls (Table 5, Fig. 3); the number of emerged individuals is increasing with gall size. However, inquilined galls showed no such relationship (Table 5, Fig. 3). Number of emerged individuals and the size of the gall were independent.

DISCUSSION

For inquilined galls all three characters – gall diameter, number of emerged individuals and species diversity – were significantly higher than for non-inquilined ones. Moreover, the correlation between gall size and number of emerged individuals disappeared due to inquilines.

Table 4. Means and SE of the untransformed data rows of the studied three characters for inquiline-free and inquilined galls. Notations: * – inquiline-free galls, † – inquilined galls.

	site 1		site 2	
	*	†	*	†
Number of galls	36	16	71	22
Gall diameter (mm)	28.8±1.37	29.22±2.3	22.89±1.34	28.78±1.6
No. of emerged individuals	27.94±4.01	44.06±9.91	19.7±3.28	39.31±8.52
Shannon diversity	0.76±0.05	1.12±0.08	0.66±0.04	1.12±0.09

The size of inquilined galls increased significantly (Table 4, Fig. 2) due to the growth of cellular mass of the inquilined chambers. This was already demonstrated for unilocular galls of *Diplolepis* (SHORTHOUSE 1980, SHORTHOUSE 1998). BLAIR (1945) stated that increased gall size in inquilined *D. rosae* is caused by the inward growth of cells of *Periclistus* larvae. Until now, no statistical evidence has been provided for the size increase of inquilined *D. rosae* galls. Increased size of inquilined multilocular galls is not as obvious as in the case of unilocular ones because of the possibility of large number of inquiline-free chambers. In spite of simultaneous presence of inquiline-free and inquilined chambers the inquilined *D. rosae* galls showed a significantly higher size, even if the magnitude of this difference was smaller than in the case of the other two characters (Table 3, Table 4, Fig. 2). This result is also coherent with those published for other inquilined *Diplolepis* galls (SHORTHOUSE 1980, 1998).

The number of emerged individuals was significantly higher in inquilined galls (Table 4, Fig. 2). Inquilines increase insect biomass per gall and serve as an important source of food for other entomophagous species (WIEBES-RIJKS & SHORTHOUSE 1992). In the case of galls of *D. rosae* the presence of inquiline *Periclistus* involves the appearance of parasitoids like *C. inflexa* and *E. rosae*. It seems that they are strictly the parasitoids of the inquiline (BLAIR 1945, CLARIDGE & ASKEW 1960). The significantly higher number of emerged individuals from inquilined *D. rosae* galls is due to a higher number of individuals per inquilined host chambers.

A significant increase of diversity was found in the case of inquilined galls (Table 4, Fig. 2). While similar differences were not reported for *Diplolepis* species. It is evident that the presence of inquiline species and their parasitoids increases the potential species pool of gall communities. However, it does not automatically involve an increased number of species per single gall. There may be sophisticated competitive and/or predating mechanisms reducing the number of species in a gall. There is no publication reporting results regarding the increased number of species in the presence of cynipid inquilines.

Ample evidence is presented that presence of inquilines in multilocular galls of *D. rosae* annihilated the correlation between gall size and the number of emerged individuals. As shown in Figure 3 inquiline presence causes complete independence of the gall size and number of individuals. The highly significant positive correlation for inquiline-free galls disappeared in inquilined ones (Table 5). Positive correlation between gall size and number of emerged individuals were reported by STILLE (1984) and BJÖRKMAN (2000). However, the disappearance of the correlation between gall size and number of emerged individuals in the presence of inquilines was previously unknown.

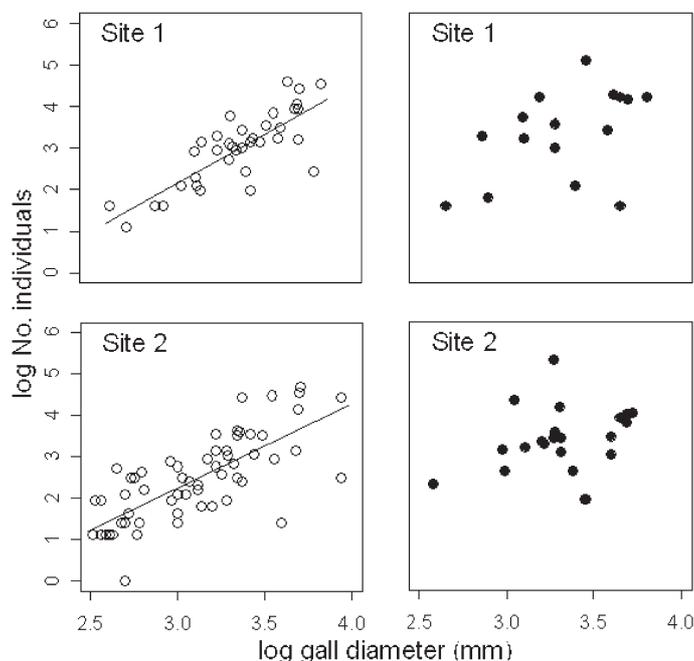


Fig. 3. Scatter plots of the gall diameter and the number of emerged individuals relationships for inquiline-free (○) and inquilined galls (●).

There may be a sophisticated biological background beyond this observation. Parasitoids of the gall inducer do not change the structure of the gall, therefore, the emerged number of individuals in inquiline-free galls reflects the number of chambers in the gall. However, this is not the case for the inquilined galls, because the inquiline species are able to increase the number of chambers in a single gall. On the one hand gall size seems not to be a limiting factor for the inquiline (Fig. 1*b, c*). Moreover, inquiline individuals show strong aggregation (Fig. 1*a*).

Table 5. Correlation between gall diameter and emerged individuals for inquiline-free and inquilined galls.

		site 1	site 2
Inquiline-free	Pearson's r	0.79	0.81
	P	<0.001	<0.001
	Number of galls	36	71
Inquilined	Pearson's r	0.46	0.23
	P	>0.05	>0.05
	Number of galls	16	22

Thus, there are galls with many inquilined chambers, but there are many galls just with a few inquilined chambers, too. The latter galls show no differences in emerged number of specimen from the inquilined-free galls. Therefore, galls equal in size, if they are inquilined, can produce enormous differences in emerged specimen numbers.

Here, the effect of an inquiline species on different parameters of a cynipid induced multilocular gall was revealed. We showed that the presence of inquiline species causes significant changes in case of multilocular galls. Gall size increased significantly, but its magnitude was smaller than in unilocular cases. Number of emerged individuals and diversity was significantly higher. For inquiline-free galls, a highly significant positive correlation was found between gall size and number of emerged individuals. But the presence of inquiline entirely annihilated the correlation between gall size and number of emerged individuals, although this relationship is a basic truism for unilocular galls. Regarding to the complexity of the effect caused by the inquiline multilocular galls are more than just a multiple of unilocular ones. The final conclusion is that in multilocular galls inquiline species changes significantly the parameters that can contribute to the survival of the gall inducer. Thus, the presence of inquiline may affect the relation between host plant and gall inducer.

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