Factors affecting parasitism in the oak-galler Neuroterus quercusbaccarum (Hymenoptera: Cynipidae)

Olivier Plantard and Michael E. Hochberg

We investigate the influence of seven extraneous variables on individual characteristics of galls in parasitized oak-galleter Neuroterus quercusbaccarum (53×15 cm). The community consists of three species of parasitoid and one species of inquilene (which is lethal to the gall). Our analysis shows that there is considerable spatial heterogeneity in parasitism from site to site and from tree to tree within sites. With regard to the placement of galls on tree organs, galls on cankers are less parasitized than those on twigs. Gall size does not explain this difference because the external diameter of canker galls is significantly different from those on twigs. We hypothesize that the precarious anchorage of canker galls prevents their exploitation by parasitoid species with long developmental times. Moreover, there is a distinct sequence of parasitism, reflected by a partitioning in the sizes of galls attacked by each parasitoid species. However, the growth dynamics of the galls themselves show that just external diameter is not the only size parameter affecting the niches of the different parasitoids. Even though Neochrysis spp is one of the earliest acting parasitoids, it attacks galls with thicker walls relative to external diameter than occurring in unparasitized galls from which the gall emerges. A delay between gall growth and feeding activity of the gallmaker would influence host-growth of galls thickening, with major consequences for the accessibility of the host larvae to the parasitoids.

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Explaning species diversity is one of the central pursuits of ecology. One parameter of diversity, species richness, has recently been the subject of a series of studies by Hawkins (1994 and references therein). He investigated how sets of ecological and geographic variables contributed to explaining local and regional richness of insect parasitoid assemblages associated with herbivorous insect hosts. The ecological variable that he analysed indicates as the most pervasive correlate of species richness was host refuges from parasitism. Both data based on structural refuges provided by plant tissues (Hawkins and Lawton 1987), and more general representations of refuges regardless of their origin (Hochberg and Hawkins 1992, 1993), are in accord with species richness patterns of parasitoid assemblages attacking herbivorous hosts. One of the central theoretical results of these studies is that parasitoid richness should be dictated by two rules (Hochberg and Hawkins 1993); see also Brown 1981): given a large regional pool of parasitoid species, local richness is promoted when, (1) refuges from parasitism for each parasitoid species must be sufficient (but not too large), refuges are determined by a blend of sufficiently low attack rates and/or high levels of host to host variabili-

Accepted 14 July 1997  
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ISSN 0300-1299  
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OKOS 61 (1998) 289
ity in susceptibility to parasitism (e.g., Gerts and Mills 1990; and 5. There must be sufficient refuges from direct competition between parasitoids; this includes spatial, temporal, or biological differences in niche exploitation by the members of an assemblage (see discussion by Cornell and Lawton 1992).

Hawkins’ work was significant in the importance of the first of these axioms, whereas there has been for less attention given to how the second of these may promote coexistence (but see Price 1972, Verwey 1974, Wes 1982, Selling and Koss 1990). Parasitoid assemblages associated with gallmakers have often acted as biological models of insect communities (Askew 1961a, 1965, 1975, Hawkins and Goodson 1984, Askew and Shaw 1986, Wiberg-Riiks and Shorter 1992, Schouten et al. 1995, 1996), and the mechanism by which host refuges from parasitism serve to structure these communities is relatively well explored (Askew 1961a, Jones 1983, Weis and Arcehelamon 1985, Price and Clausen 1986, Rumschlag-Koelri 1990). What is less well understood is how variation among parasitoid species may reflect specialization, which create niches, so avoid direct competition with other species in the assemblage. In a previous study (Plantard et al. 1996), we investigated niche partitioning in the parasitoid assemblages of Squarea cicerarum. The objective of the present study is to determine whether or not spatial and biological parameters linked to gall parasitism (and refuges of the gallers from parasitism) may or may not vary significantly among parasitoids in the assemblage associated with the actual galls of this species.

Material and methods

Life cycle of the gallmaker

Squarea cicerarum (L.) is a cosmopolitan species that occurs in significant Europe (e.g., Askew 1962, Buhle 1965, Ambrus 1974, Bjornel 1978, Hals 1989, Branco 1992). Like most other gallmakers associated with oaks, this species is bi- vuline and reproduces by cyclical parthenogenesis (alternation of one sexual and one asexual generation per year). The female of the asexual generation lays her eggs in oak buds in March, April, giving rise to the spherical, unilocular galls of the sexual generation that appear on leaves and catkins. Adults of this sexual generation emerge from the galls in May (Plantard et al. 1990) and lay their eggs in oak leaves producing Nuttallian-shaped galls on the underside of the leaves. This aspect converts the sexual generation only.

Composition of the parasitoid assemblage

Six species of parasitoids and inundaties emerged from the 607 galls collected during this study, four of which accounted for 99.4% of global parasitism. The four principal species are

*Synopis spp.*, *Cyperidae*. These two species of the Syrphidae tribe do not induce gall formation, but rather parasitize already established galls induced by species of the Cyperidae tribe. Despite being Phytophagous, their presence in the galls is leady invariably to the death of the gallmaker (Plantard et al. 1996).

*Acrobasis arnaútes* (Walker) *Eulophidae*. This larval, eutrophic orichotrid, is the only univoltine species of the parasitoid assemblage (Askew 1960, Askew and Shaw 1986).

*Metopius tribulus* (Westwood) *Proromatidae*. A tetralarval *mephitid* was parasitoid (Askew 1960, Plantard unpubl.).

*Furtho arium* (Fourcroy) *Trichopteridae*. A late larval *mephitid* was parasitoid (Askew 1969, Plantard unpubl.).

Two other species (*Ceratoma brenviserrata* *Kutschke* and *Metopius pocinieros* *Westwood*) were only found in two galls and one gall, respectively, and were not used in the analysis presented below.

Explanatory variables measured for each gall

Seven explanatory variables were measured for each of the 607 galls collected. Three reflected spatial and temporal parameters associated with galls (1-4) and four were related to the gall’s individual characteristics (5-7).

1. Site. Four different sites in Britain, France were sampled: one at Guîpres (48°49'N, 01°51’W), and three others (each 1 km from one another) at Le Rheu (48°17’N, 01°39’W). 30 galls per site at Guîpres from those at Le Rheu. The oak (Quercus rotundifolia) galls sampled at all sites were either part of hedges around fields or occurring along roadsides.

2. Tree. Eighty-five trees were each sampled twice at about 10-12 intervals. For 52 trees with low gall abundance, galls were only sampled on a single occasion. In statistical analyses, the variable tree is a nested variable within site.

3. Date. Galls were collected in two sampling periods, 11-19 May 1994 (sample 1) and then again 19-29 May 1994 (sample 2). To check if galls were collected at their maximal abundance, the galls did not grow between the two dates.

4. Position. *N. cicerarum* (sexual generation) is one of the few European oak-gallers to be found on different tree species (e.g., Quercus or Betula), thus providing the opportunity to investigate variation in parasitism rates.
Table 1. Life stage of the gall maker in the different samples (n = number of observations).

<table>
<thead>
<tr>
<th>Sample 1</th>
<th>Sample 2</th>
<th>M. thalii</th>
<th>T. avenae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larva</td>
<td>0</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>Prep</td>
<td>14</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>Malformed pupa</td>
<td>19</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Imag</td>
<td>19</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>(Emergence hole)</td>
<td>194</td>
<td>38</td>
<td>0</td>
</tr>
<tr>
<td>Unidentified</td>
<td>0</td>
<td>0</td>
<td>41</td>
</tr>
<tr>
<td>Total</td>
<td>346</td>
<td>60</td>
<td>98</td>
</tr>
</tbody>
</table>

according to gall position. We distinguish three different positions, based on the possibility that different parasitoid species were specialized to exploit one or more of each: (1) galls on leaves collected on the tree, (2) galls on catkins collected on the tree, (3) galls on catkins collected from the ground.

5)External diameter. The largest diameter was measured with a digital caliper to the nearest 0.01 mm.

6)Larval chamber diameter. After dissection under a binocular microscope, the diameter of the larval chamber was measured with a micrometer (to the nearest 0.01 mm). Since larval chamber growth follows the consumption of the nutritive layers by the gall maker, this parameter was used to estimate the larval stage of the host.

7)Gall wall thickness. Estimated as: (External diameter – Larval chamber diameter)/2. This variable represents the minimum thickness that the parasitoid's ovipositor must penetrate to reach the gall maker larva.

Species identification

Identifications were made based on larvae and adults reared in gelatin capillaries following the protocol of Plaut et al. (1996). Note that A. araneus emerged the spring of the year following collections.

Response variables and statistical analyses

In order to measure the impact of various qualitative variables (site, tree and position) on the identity of the gall inhabitant, we conducted series of analysis of deviance (ANOVA) employing the following binary response variables (with homoscedastic errors and a log link function): (1) the presence of the gall maker versus the presence of all parasite species; (2) Synegrus spp. and A. araneus versus M. thalii and T. avenae (i.e. early versus late-attacking parasites); (3) Synegrus spp. versus A. araneus (i.e., differences between the two early-attacking parasites); and (4) M. thalii versus T. avenae (i.e., differences between the two late-attacking parasites). For each analysis, we fitted the variables by adding them to the null model, beginning with the term at the top of the hierarchy (i.e. site) and adding the other terms in the model through their interactions with higher-level terms (in order to follow the nested design of the sampling, i.e. galls and then gall position being nested in tree, itself nested in site). Statistical significance was assessed by comparing change in deviance to chi² values (Crowley 1993).

Since gall size varies change during gall growth, we can not associate gall-size characteristics of unparasitized galls to variation in risk of parasitism; thus, we did not include them with other variables in the ANOVA, but rather analyzed them separately by ANOVA with contrasts to compare characteristics of galls inhabited by the different species. Interactions between the different gall-size variables were analyzed using ANCOVA, while interactions between gall size and other variables were investigated through separate ANODEV with gall size as the response variable. Analyses were performed using GLIM (ANOVE and ANCOVA) and STATISTICA software (ANOVA by contrasts).

**Results**

**Date of sampling and parasitism**

Because most of the gallmakers were in post-larval stages at the time of collection (94.6% = Table 1), and as parasitoids mainly attack the gallmaker in its larval stage, we consider that all parasitized galls were represented in the samples. Moreover, since data on external diameter were not significantly linked (see interactions between gall-size parameters and other parameters), we can be reasonably sure that galls had reached their maximum size by the time of sampling.
Table 2. Results of the analysis of deviance opposing the different species or group of species inhabiting the galls of *N. quercus-cerrus*. Only significant ($p < 0.05$) changes in deviance ($\chi^2$) are indicated ($n =$ number of observations).

<table>
<thead>
<tr>
<th></th>
<th>Unpartitioned</th>
<th>Syneura spp.</th>
<th><em>A. aruzum</em></th>
<th><em>M. thibali</em></th>
<th>T. aurata</th>
<th>M. thibali</th>
<th>T. aurata</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Explanatory variables</strong></td>
<td>($n=574$)</td>
<td>($n=284$)</td>
<td>($n=145$)</td>
<td>($n=138$)</td>
<td>($n=145$)</td>
<td>($n=138$)</td>
<td>($n=138$)</td>
</tr>
<tr>
<td>Site</td>
<td>$\chi^2$</td>
<td>d.f.</td>
<td>$\chi^2$</td>
<td>d.f.</td>
<td>$\chi^2$</td>
<td>d.f.</td>
<td>$\chi^2$</td>
</tr>
<tr>
<td>$\times$ Tree</td>
<td>24.8</td>
<td>3</td>
<td>19.72</td>
<td>5</td>
<td>3</td>
<td>24.3</td>
<td>5</td>
</tr>
<tr>
<td>$\times$ Tree * Postion</td>
<td>134.4</td>
<td>48</td>
<td>102.96</td>
<td>37</td>
<td>62.37</td>
<td>25</td>
<td>46.4</td>
</tr>
<tr>
<td>$\times$ Tree * Postion</td>
<td>63.7</td>
<td>16</td>
<td>54.7</td>
<td>14</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Nested analysis of parameters other than gall size

When opposing the different species or groups of parasitoid species, the different ANODEVs highlight the roles of gall position and spatial heterogeneity on parasitism (Table 2). In particular, galls are far less parasitized on carkins than on leaves (18.4% versus 61.5%, respectively; see Fig. 1). This difference is further elaborated by the effect of the position variable when opposing *A. aruzum* or late-acting parasitoids. In particular, *A. aruzum* and *Syneura* spp. are, respectively, 4.5 and 5 times less abundant in carkin galls than in leaf galls (1.4% versus 6.3% and 5.8% versus 29.2%, respectively; see Fig. 1).

When opposed parasitoid species within groups, we found a significant effect of the tree variable, indicating important spatial variation in parasitism. In both analyses there were no significant effects of gall position, while the site variable had a significant effect only when opposing *A. aruzum* or *Syneura* spp. (Table 2). Note in particular that *A. aruzum* is almost absent at one site (Guispy) (Fig. 2).

Analysis of gall-size parameters

Gall size and parasitism parameters by the different parasitoid species

In contrast to the other species, *M. thibali* exhibits a bimodal distribution in larval chamber diameter (Fig. 3). In subsequent analyses, galls parasitized by *M. thibali* are partitioned into small (<2 mm in diameter) and large larval chambers (>2 mm); they are referred to as *M. thibali* I and *M. thibali* II, respectively. Since gall characteristics of *M. thibali* I are always similar to those inhabited by *A. aruzum*, we hypothesize that *M. thibali* I are hyperparasitizing galls already parasitized by *A. aruzum*.

Because there were no differences in the three gall-size parameters between galls on leaves versus galls on carkins (on the trees), these galls are lumped in the subsequent analyses. Galls on carkins collected under the trees were not included, because their significantly smaller size was probably due to premature separation from the tree (inducing desiccation of gall tissue).

![Graph 1](image1.png)

Fig. 1. Variation in frequency of the different species inhabiting galls as a function of gall position, combining samples from the different trees and sites (sample size).

![Graph 2](image2.png)

Fig. 2. Variation in frequency of the different species inhabiting galls across size, combining samples from the different positions and trees sample size.)
ANOVA on larval chamber diameter
Three species groups are distinguished (Fig. 4.1): (a) varnish-attacking species (Synerbus spp., A. atrame and M. tibialis I) are found in galls of significantly smaller larval chamber diameter than those from which the gallmaker emerges. Galls inhabited by *T. auratus* do not differ significantly in their larval chamber diameter from those inhabited by the gall, indicating that attack occurs when gallmakers have stopped feeding on the gall tissue. *M. tibialis II* is found in galls slightly (but significantly) smaller than those inhabited by *T. auratus* or the gallmaker.

ANOVA on exosporal diameter
Four groups of species are distinguished, from the smallest galls to the largest (Fig. 4.2): (a) *A. atrame* and *M. tibialis I*; (b) *Synerbus spp.*; (c) *M. tibialis II*; (d) *N. quercusbaccharum* and *T. auratus*.

ANOVA on gallwall thickness
Thickness of galls inhabited by *Synerbus spp.* are significantly greater, and those by *M. tibialis II* significantly smaller, than the remaining species, which form a single group (Fig. 4.3).

Regression of external diameter against gallwall thickness
Gallwall thickness is a significant covariate of external diameter (ANOVA, $F_{1,112} = 899.3, p < 0.001$). The interaction between gallwall and external diameter being highly significant ($F_{1,111} = 150.6$), suggests differences in the regression lines among the species. The intercepts of the regression lines for the different species differ significantly from one another, but they all have a common slope (Fig. 5). Two groups emerge:

1) **N. quercusbaccharum**, *T. auratus* and *M. tibialis II* share the same regression line (Fig. 5c, e and g, t-test between the slope of *N. quercusbaccharum* and those of *M. tibialis II* and *T. auratus*, $t = 1.68$ and 0.30, respectively, $p > 0.05$ in both cases; t-test between the intercept for *N. quercusbaccharum* and those of *M. tibialis II* and *T. auratus*, $t = 0.43$ and 0.70, respectively, $p > 0.05$.

2) Galls inhabited by *Synerbus spp.*, *A. atrame* and *M. tibialis I* share a regression line with the same slope and same intercept (Fig. 5b, d and f, t-test between the intercept of the regression line of *Synerbus spp.* and *A. atrame* and *M. tibialis I*, $t = 0.29$ and 0.57, respectively, $p > 0.05$). The intercepts of these two regression lines differ ($t$ tests between *N. quercusbaccharum* and those of *A. atrame*, *Synerbus spp.* and *M. tibialis I* = 4.47, 4.21 and 5.79, respectively, $p < 0.05$ in all cases, but their slopes do not ($t$ test between the slopes of *N. quercusbaccharum* and those of *A. atrame*, *Synerbus spp.* and *M. tibialis I*, $t = 0.87$, 0.07 and 0.03, respectively, $p > 0.05$ in all cases).

It is interesting to note that the coefficients of determination ($r^2$) from these 6 regressions range from 0.622 to 0.863, and are much greater than those resulting from the regression of gallwall thickness against larval chamber diameter (ranging from 0.0011 to 0.172). This reflects the variability in gallwall thickness for given levels of larval chamber diameter.

Interactions between gall-size parameters and other parameters
An ANODEV (normal error distribution, identity link; using external diameter of unparasitized galls only in order to eliminate the possible effect of parasitism on gall growth) as the response variable and site, tree

![Image](http://example.com/image.png)

Note: The image contains the distribution of larval chamber diameter of galls inhabited by the different species.
Fig. 4. Mean diameter of larval chamber (1), external diameter (2) and gall wall thickness (3) of galls inhabited by the different species (excluding cinnam galls collected under the trees). A. a = A. arnemey; M. t I = M. thistle I; S. sp = Sygenus spp.; M. t II = M. thistle II; T. a = T. antarctos; N. q = N. guatretaraeocmu. Means marked with the same letters do not differ significantly (p > 0.05).
Fig. 5. Regression of external diameter versus gallwall thickness, all species together (a), for galls inhabited by *Synergus spp.* (b), *N. quercusbaccarum* (c), *A. argus* (d), *T. auratus* (e), *M. thibali* I (f), *M. thibali* II (g).
(nested within site), position (nested within tree nested within site) and date as explanatory variables, reveals statistically significant influences only of the tree variable (F1,24 = 2.50). An ANODEV with position as a response variable (binomial error, logit link) reveals that this variable is largely (44.4% of total deviance) explanatory of the tree variable and to a lesser extent by the site variable (1.5% of total deviance) after aggregation of cactus galls on the tree and within the tree, y2 [tree, 1 df = 133.8, p < 0.001; y2 [tree, 1 df = 11.1, p < 0.025].

Discussion

Patterns of variation in parasitism of the gallmaker N. quercusarum highlight the importance of gall morphology (Askew 1961). Not unexpectedly, gall wall thickness is strongly associated with the parasitoid assemblage, presumably by constraining host accessibility to parasites with appropriate oviposition lengths (e.g. Askew 1965). We have shown how the finer structure of the dynamics of gall morphology mediates this effect and how other variables, such as gall placement on tree organs and abscission from cacti, can have striking differential influences on parasitism.

Influence of the organ bearing the gall on parasitism

The position of a gall has a major effect on patterns of parasitism, which are in accord with the findings of Askew (1961a) and Braune (1992).

Lower parasitism in cactus galls could constitute a probabilistic refuge for gallmakers, selecting for oviposition in oak buds that produce cacti. It would be interesting to know whether costs other than parasitism are higher for galls on oaks than those found in leaf galls. One possibility is that galls on cacti tend to fall from the tree before the completion of gall development. This will mean differentially higher mortality for individuals inhabiting galls on cacti as compared to oaks. We propose the following explanation for the differences in relative frequencies, as a function of position, between the early- versus late-acting parasitoids. It is disadvantageous for species with long larval stages (i.e. Synaptus spp., and especially A. arenae which emerge from gall in the spring of the year following parasitism) to attack cacti, because cacti are nourished by the tree only for a short period of time, and once fallen to the ground are vulnerable to predation and disease. Despite small sample sizes, there are significantly fewer Synaptus spp. and A. arenae in cactus galls already fallen to the ground (no individuals of other species out of 62 galls) than in galls still on the tree. It is possible that these two species, known to modify the internal structure of the gall (see Askew 1960, 1961a), delay the fall of the cactus bearing the gall they inhabit (see the interpretation of galls as nutrient sinks for the plant, Bagatto et al. 1996). Wiebe-Rajks (1980) reported that "galls" (=shredded acorns) of American elm, Ulmus americana, when parasitized by Synaptus clavicornis, remain on the tree during winter, whereas unparasitized galls fall earlier. Thus, cactus larval galls are greatly reduced by bird predation. Thus, in both cases (A. arenae and N. quercusarum), the consequences of parasitism on gall abscission (i.e. preventing in the former case and favouring in the latter case) may lead to greater mortality of gall parasites.

Effect of gall-size parameters on parasitism

The distributions of external and larval chamber diameters of galls parasitized by the different species confirm the species sequence suggested by Braune (1992) and determined by experimental manipulation (Plantz et al. 1996). Synaptus spp. and A. arenae attack the gallmaker at a precocious stage. T. auranti is found in galls with the same external diameter and larval chamber diameter as unparasitized galls, whereas M. ribalis inhabits galls of intermediate external diameter size, but having thin walls. We found that galls with the same larval chamber diameter can exhibit substantial variation in wall thickness. Weisser (1982) made a similar observation for Lithocephalus sericeus, whose galls, despite exhibiting large variation in wall thickness, all have the same larval chamber diameter. Thus, M. ribalis, despite attacking galls when the gallmaker has finished feeding on gall tissue, appears to preferentially attack galls with thinner walls, possibly because of insufficient oviposition length for exploiting larger galls. A striking result of this study is the clear separation between two groups of parasitoids in the regression of gallwall thickness on external diameter. The difference in intercepts of the two regressions indicates that, for a given external diameter, galls belonging to the group Synaptus spp.-A. arenae-M. ribalis have thicker walls than those belonging to the group N. quercusarum-T. auranti-M. ribalis II. This is somewhat paradoxical, because Synaptus spp. and A. arenae attack the gall earlier than the other two parasitoid species. If there is a delay between the growth stage of the gall and the growth of the gallmaker larva, then the growth curve of the gall will be bell-shaped (Fig. 6) and not linear. Gallwall growth curves are very scarce in the literature. For example, the galls produced by Eucosma solidaginis (Diptera: Tephritidae) on Solidago canadensis seem not to exhibit the delay we propose (Weiss and Abrahamson 1983). In contrast, Bagatto and Short (1990), working on Homalodisca stubbii
Fig. 6. Illustration of the cyclogenesis of gall forming complex of gallwaxes of a delayed growth of the external surface of the gall, and the necrotic period of the gallmaker leaves.

(Anastirhrista) (Hymenoptera: Phromiidae) and Askaito et al. (1996) working on Phumii Ctenaaster (Ashmead) (Hymenoptera: Cynipidae) observed that galls reach their maximum size during the growth phase, but the gallmaker larvae actively feed on nutritive tissues only once the galls stop growing. Such a delay, if wide spread among Cynipidae, could be an important characteristic for the determination of the "window of vulnerability" to parasitoids (Wahsburn and Cornell 1981).

This "delay" hypothesis could also explain why galls inhabited by S. acarum are much larger than galls hosting other A. aramus, despite the fact that they attack galls with smaller larval chamber diameters. The absence of specific pathogen attack between the two species wall thickness increased, but larval chamber diameter remains virtually unchanged.

The rate of gall growth could explain why there are so few galls with characteristics intermediate to those typically found in the two groups of species (i.e. why are there so few galls between the two clouds in Fig. 5a). If the growth period is very short, galls of intermediate size could be a highly ephemeral resource, too few to allow the utilization of such a niche by a specialized parasite.

Spatial heterogeneity in parasitism

Although all four parasites are present at each of the four sites, there is considerable site-to-site variation in the relative frequencies of the two early-arriving species and that of the gallmaker, with M. obidus and T. amurica being relatively constant (see site to site (Fig. 2)). At the community level (i.e. the community constituted by all the parasitic assemblages associated with oak gall wasps), heterogeneity between sites in the occurrence of other host cynipid gallmakers could contribute to this spatial heterogeneity in composition, as recently demonstrated by Schütz (1996). The site effect found to be significant in most of the ANODEV could be a result of any number of ecological and genetic variables (local climate acting on gall phenotype, see Schütz 1967, Sumner et al. 1999). We currently have insufficient information to discriminate between them.

The tree parameter was significant in all the stepwise multiple regressions, and may be a consequence of variability in plant phenotypes. This conclusion is sup- ported by the significant effects of tree-derived co- variables such as position and external diameter. Heterogeneity in parasitism at the tree level may also be a consequence of differences in species searching be- haviour.

Acknowledgements—We thank the Laboratoire de Zoologie de l'INRA et Le Rheu, for its support in fieldwork, Jaya Jivat Raphe for his assistance during this research, and Bradford Rehms who made helpful suggestions on an earlier draft of the manuscript. This research was supported by the French Ministere de la Recherche (SRETF).

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