

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

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We investigate the influence of seven explanatory variables based on individual characteristics of galls on parasitism in the oak-galler, *Neuroterus quercusbaccarum* (sexual generation). The community consists of three species of parasitoid and one species of inquiline (which is lethal to the galler). 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 catkins are less parasitised than those on leaves. Gall size does not explain this difference because the external diameter of catkin galls is not significantly different from those on leaves. We hypothesise that the precocious abscission of catkin 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 parasite 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 parasites. Even though *Synergus* spp. is one of the earliest acting parasites, it attacks galls with thicker walls relative to external diameter than occurring in unparasitised galls from which the galler emerges. A delay between gall growth and feeding activity of the gallmaker would induce non-linear growth of gallwall thickness, with major consequences for the accessibility of the host larva to the parasitoid.

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Explaining 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 his analysis 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 species 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 variabil-

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ity in susceptibility to parasitism (e.g., Getz and Mills 1996); and (2) 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 has shown the importance of the first of these mechanisms, whereas there has been far less attention given to how the second of these may promote coexistence (but see Price 1972, Force 1974, Weis 1982, Stiling and Rossi 1994). Parasitoid assemblages associated with gallmakers have often served as biological models of insect communities (Askew 1961a, 1965, 1975, Hawkins and Goeden 1984, Askew and Shaw 1986, Wiebes-Rijks and Shorthouse 1992, Schönrogge 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 Abrahamson 1985, Price and Clancy 1986, Romstock-Völkl 1990). What is less well understood is how variation among parasitoid species may reflect specialisations which create niches to avoid direct competition with other species in the assemblage. In a previous study (Plantard et al. 1996), we investigated niche partitioning in the parasitoid assemblage of *Neuroterus quercus-baccarum*. 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 parasites in the assemblage associated with the sexual galls of this species.

Material and methods

Life cycle of the gallmaker

Neuroterus quercusbaccarum (L.) is a common cynipid species throughout Europe (e.g. Askew 1962, Buhr 1965, Ambrus 1974, Ejlersen 1978, Hails 1989, Braune 1992). Like most other gallmakers associated with oaks, this species is bivoltine and reproduces by cyclical parthenogenesis (alternation of one sexual and one asexual generation per year). The females of the asexual generation lay their 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. 1996) and lay their eggs in oak leaves producing lenticular-shaped galls on the underside of the leaves. This report concerns the sexual generation only.

Composition of the parasitoid assemblage

Six species of parasitoids and inquilines emerged from the 667 galls collected during the study, four of which accounted for 99.4% of global parasitism. The four principal species are:

Synergus spp. (Cynipidae). These inquiline species of the Synergini tribe do not induce gall formation, but rather parasitise already established gall tissue induced by species of the Cynipini tribe. Despite being phytophagous, their presence in the gall leads invariably to the death of the gallmaker (Plantard et al. 1996).

Aulogymnus arsames (Walker) (Eulophidae). This early larval, ectoparasitic koinobiont, is the only univoltine species of the parasitoid assemblage (Askew 1960, Askew and Shaw 1986).

Mesopolobus tibialis (Westwood) (Pteromalidae). A late larval–nymphal ectoparasitoid (Askew 1961b, Plantard unpubl.).

Torymus auratus (Fourcroy) (Torymidae). A late larval–nymphal ectoparasitoid (Askew 1965, Plantard unpubl.).

Two other species (*Eurytoma brunniventris* Ratzeburg and *Mesopolobus fasciventris* Westwood) were only found in two galls and one gall, respectively, and were not used in the analyses presented below.

Explanatory variables measured for each gall

Seven explanatory variables were measured for each of the 667 galls collected. Three reflected spatial and temporal parameters associated with galls (1 to 4) and four were related to the gall's individual characteristics (5 to 9).

1) Site. Four different sites in Brittany, France were sampled: one at Guipry (47°49'N, 01°51'W), and three others (ca 1 km from one another) at Le Rheu (48°0'7N; 01°50'W). 30 km separate the site at Guipry from those at Le Rheu. The oaks (*Quercus robur* and *Q. petraeae*) 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 roughly 10-d intervals. For 32 trees with low gall abundances, 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 19–20 May 1994 (sample 2) to check if galls were collected at their maximal size (i.e. the galls did not grow between the two dates).

4) Position. *N. quercusbaccarum* (sexual generation) is one of the few European oak-gallers to be found on different tree organs (leaf or catkin), thus providing the opportunity to investigate variation in parasitism rates

Table 1. Life stage of the gall in the different samples (n = number of observations).

Stage of the gallmaker	Healthy gallmaker		Gallmaker parasitised by	
	Sample 1	Sample 2	<i>M. tibialis</i>	<i>T. auratus</i>
Larva	0	0	2	10
Pupa	14	2	1	39
Melanised pupa	19	0	0	1
Imago	19	0	1	0
(Emergence hole)	194	58	0	0
Unidentified	0	0	36	47
Total	246	60	40	98

according to gall position. We distinguish three different positions, based on the possibility that different parasitoid species are specialised 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 calliper 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 gallmaker, this parameter was used to estimate the larval stage of the host. If galls were attacked by the inquiline *Synergus* spp., the larval chamber is modified by the presence of the inquilines (proliferation of plant cells around each inquiline larva, forming new larval chambers that will progressively fill the original gallmaker's larval chamber). Since we were only interested in knowing the characteristics of the gall at the time of parasitoid attack, only galls with very young larvae of *Synergus* spp. (i.e. before modification of the inner gall) were taken into account.

7) Gallwall 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 gallmaker larva.

Species identification

Identifications were made based on larvae and adults reared in gelatine capsules following the protocol of Plantard et al. (1996). Note that *A. arsames* 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 (ANODEV) employing the following binary response variables (with binomial errors and a logit link

function): (1) the presence of the gallmaker versus the presence of all parasite species; (2) *Synergus* spp. and *A. arsames* versus *M. tibialis* and *T. auratus* (i.e. early-versus late-attacking parasites); (3) *Synergus* spp. versus *A. arsames* (i.e., differences between the two early-attacking parasites); and (4) *M. tibialis* versus *T. auratus* (i.e., differences between the two late-attacking parasitoids). 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 thus gall position being nested in tree, itself nested in site). Statistical significance was assessed by comparing change in deviance to χ^2 values (Crawley 1993).

Since gall-size variables change during gall growth, we can not associate gall-size characteristics of unparasitised galls to variation in risk of parasitism. Thus, we did not include them with other variables in the ANODEV, but rather analysed them separately by ANOVA with contrasts to compare characteristics of galls inhabited by the different species. Interactions between the different gall-size variables were analysed 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 (ANODEV 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 (94.8%, $n = 306$; Table 1), and as parasitoids mainly attack the gallmaker in its larval stage, we consider that all parasitised galls are represented in the samples. Moreover, since date and 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 maximal 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. quercusbaccarum*. Only significant ($p < 0.05$) changes in deviance (χ^2) are indicated (n = number of observations).

(n)	unparasitised/ parasitised		<i>Synergus</i> spp. + <i>A. arsames</i> / <i>M. tibialis</i> + <i>T. auratus</i> (284)		<i>Synergus</i> spp./ <i>A. arsames</i> (145)		<i>M. tibialis</i> / <i>T. auratus</i> (138)	
	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.
Explanatory variables								
Site	24.5	3	19.72	3	–	–	24.3	3
Site \times Tree	154.4	48	102.96	37	62.37	25	46.4	29
Site \times Tree \times Position	61.7	16	34.7	14	–	–	–	–

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 parasitised on catkins than on leaves (28.4% versus 61.5%, respectively; see Fig. 1). This difference is further elaborated by the effect of the position variable when opposing early- versus late-acting parasitoids. In particular, *A. arsames* and *Synergus* spp. are, respectively, 4.5 and 5 times less abundant in catkin galls than in leaf galls (1.4% versus 6.3% and 5.8% versus 29.2%, respectively; see Fig. 1).

When opposing 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. arsames* to *Synergus* spp. (Table 2). Note in particular that *A. arsames* is almost absent at one site (Guipry) (Fig. 2).

Analysis of gall-size parameters

Gall size and parasitism rates by the different parasitoid species

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

Because there were no differences in the three gall-size parameters between galls on leaves versus galls on catkins (on the trees), these galls are lumped in the subsequent analyses. Galls on catkins 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).

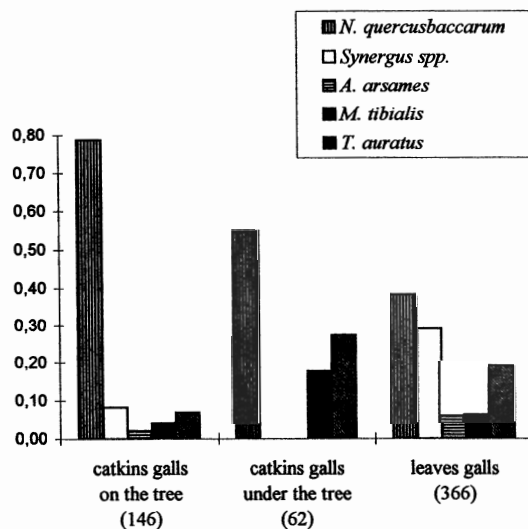


Fig. 1. Variation in frequency of the different species inhabiting galls as a function of gall position, combining samples from the different trees and sites (sample size).

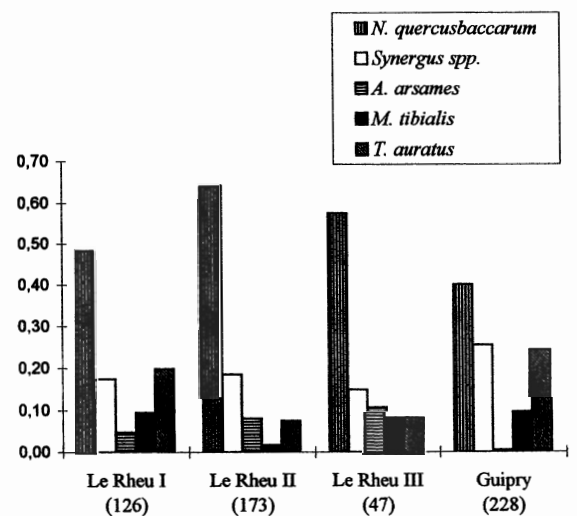
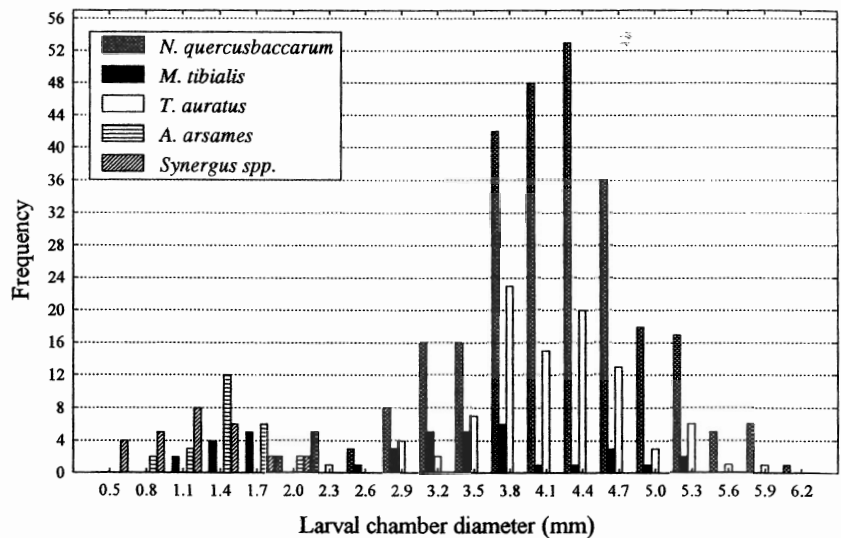


Fig. 2. Variation in frequency of the different species inhabiting galls across sites, combining samples from the different positions and trees (sample size).

Fig. 3. Distribution of larval chamber diameter of galls inhabited by the different species.



ANOVA on larval chamber diameter

Three species groups are distinguished (Fig. 4-1): early-attacking species (*Synergus spp.*, *A. arsames* 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 galler, 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 external diameter

Four groups of species are distinguished, from the smallest galls to the largest (Fig. 4-2): a) *A. arsames* and *M. tibialis I*; b) *Synergus spp.*; c) *M. tibialis II*; d) *N. quercusbaccarum* and *T. auratus*.

ANOVA on gallwall thickness

Thickness of galls inhabited by *Synergus 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 (ANCOVA, $F_{1,458} = 899.3$, $p < 0.0001$). The interaction between gallwall and external diameter being highly significant ($F_{6,453} = 150.6$) 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. quercusbaccarum*, *T. auratus* and *M. tibialis II* share the same regression line (Fig. 5c, e and g; t test between the slope of *N. quercusbaccarum* and those of *M. tibialis II* and *T. auratus*, $t = 1.68$ and 0.89 , respectively, $p > 0.05$ in both cases; t test between the intercept for *N. quercusbaccarum* and those of *M. tibialis II* and *T. auratus*, $t = 0.43$ and 0.70 , respectively, $p > 0.05$).

2) Galls inhabited by *Synergus spp.*, *A. arsames* 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 *Synergus spp.* and *A. arsames* 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. quercusbaccarum* and those of *A. arsames*, *Synergus spp.* and *M. tibialis I* = 6.47, 4.21 and 3.79, respectively, $p < 0.05$ in all cases), but their slopes do not (t test between the slope of *N. quercusbaccarum* and those of *A. arsames*, *Synergus 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 0.963, 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 unparasitised galls only (in order to eliminate the possible effect of parasitism on gall growth) as the response variable and site, tree

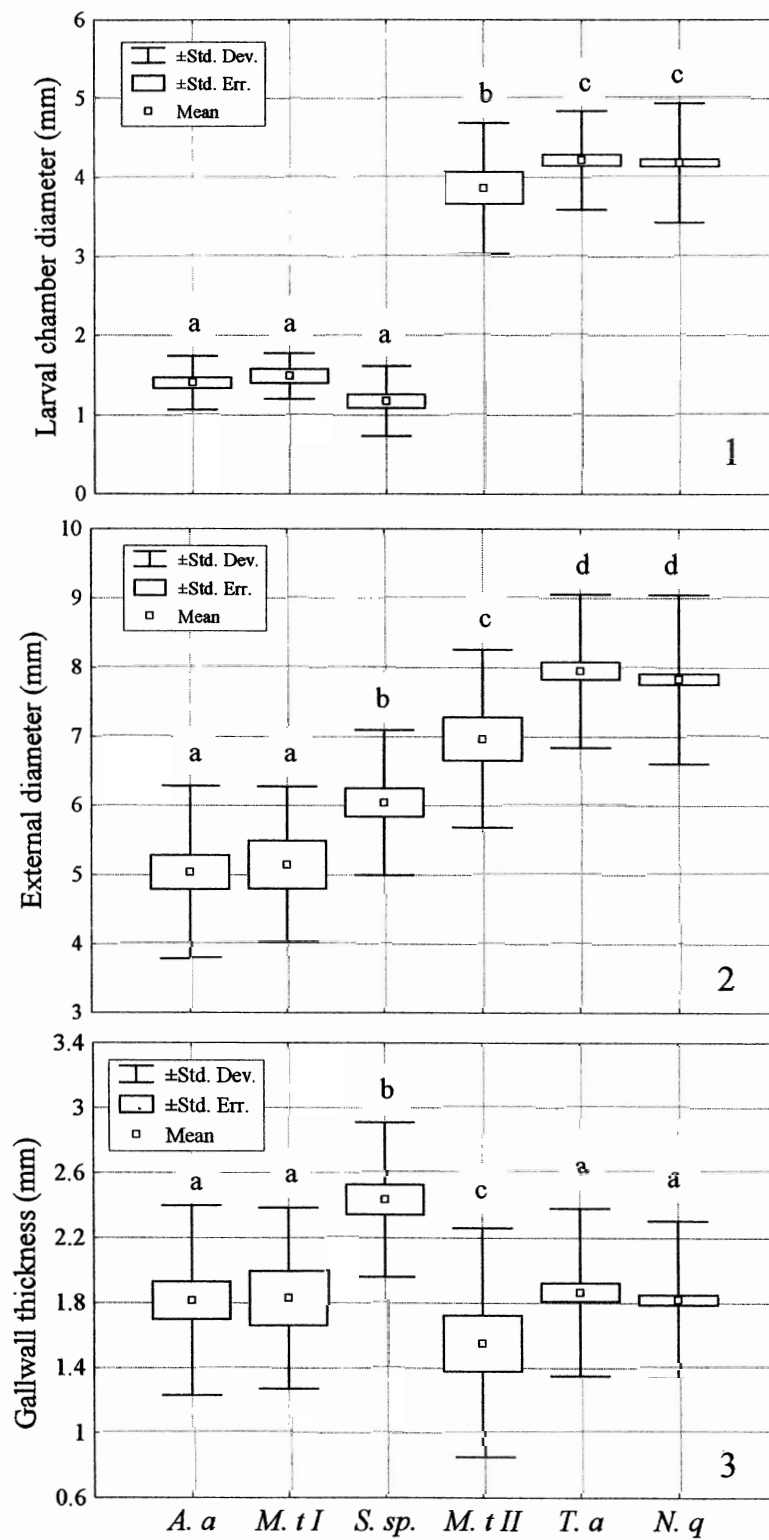


Fig. 4. Mean diameter of larval chamber (1), external diameter (2) and gallwall thickness (3) of galls inhabited by the different species (excluding catkin galls collected under the trees). A. a = *A. arsanus*; M. t I = *M. tibialis* I; S. sp. = *Synergus* spp.; M. t II = *M. tibialis* II; T. a = *T. auratus*; N. q = *N. quercusbaccarum*. Means marked with the same letters do not differ significantly ($p > 0.05$).

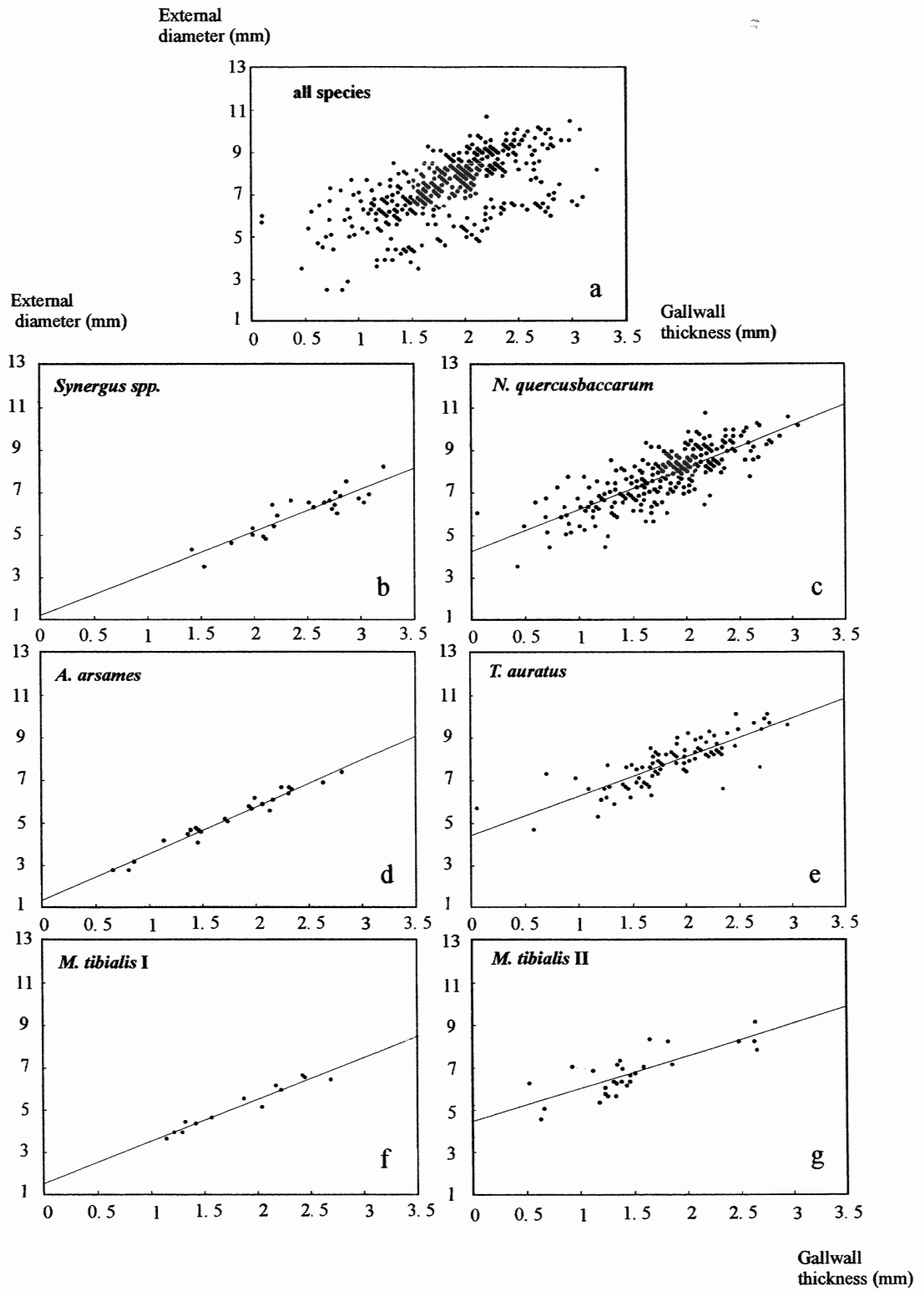


Fig. 5. Regression of external diameter versus gallwall thickness, all species together (a), for galls inhabited by *Synergus* spp. (b), *N. quercusbaccarum* (c), *A. arsames* (d), *T. auratus* (e), *M. tibialis I* (f), *M. tibialis II* (g).

(nested within site), position (nested within tree nested within site) and date as explanatory variables, reveals statistically significant influences only of the tree variable ($F_{35,13} = 2.50$). An ANODEV with position as a response variable (binomial error, logit link) reveals that this variable is largely (44.4% of total deviance) explained by the tree variable and to a lesser extent by the site variable (1.5% of total deviance) (after aggregation of catkin galls on the tree and under the tree, χ^2 [tree, 48 d.f.] = 333.8, $p < 0.001$; χ^2 [site, 3 d.f.] = 11.1, $p < 0.025$).

Discussion

Patterns of variation in parasitism of the gallmaker *N. quercusbaccarum* highlight the importance of gall morphology (Askew 1961a). Not unexpectedly, gallwall thickness is strongly associated with the parasitoid assemblage, presumably by constraining host accessibility to parasites with appropriate ovipositor 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 catkins, 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 catkin galls could constitute a probabilistic refuge for gallmakers, selecting for oviposition in oak buds that produce catkins. It would be interesting to know whether costs other than parasitism are higher for gallers on catkins than those found in leaf galls. One possibility is that galls on catkins tend to fall from the tree before the completion of gall development. This will mean differentially higher mortality for individuals inhabiting galls on catkins as compared to leaves.

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. *Synergus* spp., and especially *A. arsames* which emerges from the gall in the spring of the year following parasitism) to attack catkins, because catkins 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 *Synergus* spp. and *A. arsames* in catkin galls already fallen to the ground (no individuals of either

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 catkin bearing the gall they inhabit (see the interpretation of galls as nutrient sinks for the plant, Bagatto et al. 1996). Wiebes-Rijks (1980) reported that "galls" (= aborted acorns) of *Andricus legitimus*, when parasitised by *Synergus clandestinus*, remain on the tree during winter, whereas unparasitised galls fall earlier. The number of *S. clandestinus* larvae are greatly reduced by bird predation. Thus, in both cases (*A. legitimus* and *N. quercusbaccarum*), 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 parasitised by the different species confirm the species sequence suggested by Braune (1992) and determined by experimental manipulation (Plantard et al. 1996). *Synergus* spp. and *A. arsames* attack the gallmaker at a precocious stage. *T. auratus* is found in galls with the same external diameter and larval chamber diameter as unparasitised galls, whereas *M. tibialis* 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. Bronner (1982) made a similar observation for *Liposthenes glechomae*, whose galls, despite exhibiting large variation in wall thickness, all have the same larval chamber diameter. Thus, *M. tibialis*, despite attacking galls when the gallmaker has finished feeding on gall tissue, appears to preferentially attack galls with thinner walls, possibly because of insufficient ovipositor 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 means that, for a given external diameter, galls belonging to the group *Synergus* spp.–*A. arsames*–*M. tibialis* I have thicker walls than those belonging to the group *N. quercusbaccarum*–*T. auratus*–*M. tibialis* II. This is somewhat paradoxical, because *Synergus* spp. and *A. arsames* attack the gall earlier than the two other 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 gallwall can be bell-shaped (Fig. 6) and not linear. Gallwall growth curves are very scarce in the literature. For example, the galls produced by *Eurosta solidago* (Diptera: Tephritidae) on *Solidago canadensis* seem not to exhibit the delay we propose (Weis and Abrahamson 1985). In contrast, Bagatto and Shorthouse (1994), working on *Hemadas nubilipennis*

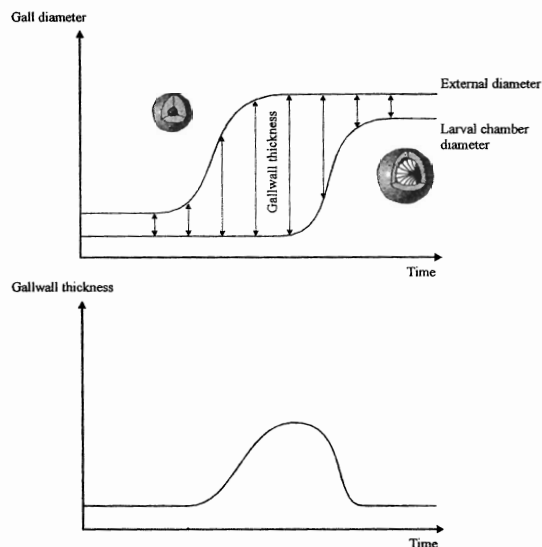


Fig. 6. Illustration of the consequences on the dynamics of gallwall thickness of a delay between growth of external diameter of galls, and the feeding period of the gallmaker larva.

(Ashmead) (Hymenoptera: Pteromalidae) and Bagatto et al. (1996) working on *Phanacis taraxaci* (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 stopped growing. Such a delay, if wide spread among Cynipids, could be an important characteristic for the determination of the "window of vulnerability" to parasitoids (Washburn and Cornell 1981).

This 'delay' hypothesis could also explain why galls inhabited by *Synergus* spp. have significantly larger walls than galls harbouring *A. arsames*, despite the fact that they attack galls with similar larval chamber diameters. These two species attack galls before the gallmaker actively feeds on the nutritive tissue, with *Synergus* spp. attacking later than *A. arsames*. During the interval separating attack by these two species, wall thickness increases, 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 points 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 rare to allow the utilisation of such a niche by a specialised 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-acting species and that of the gallmaker, with *M. tibialis* and *T. auratus* being relatively constant from site to site (Fig. 2). At the community level (i.e. the community constituted by all the parasite 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 Schönrogge et al. (1996).

The site effect found to be significant in most of the ANODEVs could be a result of any number of ecological and genetic variables (e.g. local climate acting on gall phenotype, see Schröder 1967, Sumerford et al. 1990). 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 conjecture is supported by the significant effects of tree-influenced 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 behaviour.

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