Acta Œcologica, 1996, **17** (1), 1-15

Resource partitioning in the parasitoid assemblage of the oak galler *Neuroterus quercusbaccarum* L. (Hymenoptera: Cynipidae)

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Abstract

We investigate the roles of several factors in determining patterns of parasitism on the oak galler species *Neuroterus quercusbaccarum* (L.). We employ exclosures around growing galls to identify the windows of vulnerability of the galler host to two primary parasitoids and one inquiline parasite. There are phenological and temporal patterns in the incidence of parasitism among the three parasite species, with the inquiline *Synergus sp.* tending to attack small galls early, followed by *Mesopolobus tibialis* which attacks medium-sized galls, and by *Torymus auratus*, which attacks the largest galls. Despite the importance of gall size in structuring the parasitoid complex, gall size does not act as an absolute refuge from parasitism. Finally, both *M. tibialis* and *T. auratus* have significant effects on gall growth in reducing the final gall size. This result is in agreement with the idiobiontic life style of these species, since gall growth stops with the death of the gall maker.

Keywords: Parasitoid, Cynipidae, gall, gall size, resource partitioning, competition, window of vulnerability, refuge.

Résumé

Nous étudions le rôle de différents facteurs déterminant le parasitisme chez l'insecte galligène associé au chêne, *Neuroterus quercusbaccarum* (L.). Nous installons des bonnettes autour de galles en période de croissance afin d'identifier les fenêtres de vulnérabilité du galligène à deux parasitoïdes primaires et un parasite inquilin. On trouve des patrons phénologiques et temporels du parasitisme différents suivant les trois espèces parasites, *Synergus sp.* ayant tendance à attaquer assez tôt les petites galles, suivie par *Mesopolobus tibialis* qui attaque les galles de taille moyenne et par *Torymus auratus* qui attaque les plus grandes. Malgré l'importance de la taille des galles sur la structuration du cortège parasitaire, la taille des galles ne constitue pas un refuge absolu contre le parasitisme. Enfin, aussi bien *M. tibialis* que *T. auratus* ont un effet significatif sur la croissance des galles, en réduisant leur taille finale. Ce résultat est en accord avec la biologie idiobiontique de ces espèces, la croissance des galles cessant avec la mort du galligène.

Acta Œcologica 1146–609 X/96/01/$ 4.00/

INTRODUCTION

Explaining the local coexistence of parasitoid species is an important initial step towards explaining their richness and diversity (e.g. MAY & HASSELL, 1981; HOGARTH & DIAMOND, 1984; KAKEHASHI *et al.*, 1984; HASSELL & MAY, 1986; HOCHBERG & HAWKINS, 1992, 1993, 1994; BRIGGS *et al.*, 1993; BRIGGS, 1993; HASSELL *et al.*, 1994). Recently, HOCHBERG & HAWKINS (1992, 1993, 1994) identified key processes and parameters explaining variation in the species richness of parasitoid assemblages. They predicted that highly polyphagous parasitoids should account for rich assemblages when the host has sufficient, but not too pronounced, refuges to parasitism. On the other hand, rich monophagous assemblages require, in addition to sufficient host refuges, some form of niche partitioning of the host.

Cynipid galls constitute model systems for investigating the roles of host refuges and niche partitioning in the coexistence of parasitoid species. Their parasitoids are relatively monophagous, highly interactive (sometimes involving tens of insect species; ASKEW, 1961*a*), and occur within an immobile plant structure. Despite the fact that galls, and in particular oak galls, have received increased attention in recent years (SITCH *et al.*, 1988; GILBERT *et al.*, 1994; SCHÖNROGGE *et al.*, 1994, 1995), relatively few direct investigations of parasitoid coexistence have been conducted (ASKEW, 1961*a*, 1961*b*, 1965; WASHBURN & CORNELL, 1979, 1981).

The present study is aimed at discriminating some of the mechanisms governing the species richness of parasitoid assemblages associated with cynipine gall wasps. We conduct a series of exclosure experiments on the sexual generation of the oak galler *Neuroterus quercusbaccarum* (L.) to see how different factors affect the incidence of parasitism by members of its parasitoid assemblage. We have two main objectives. First, we seek how parasites may influence the growth of the gall structure as possible protection against subsequent parasitoid attack. Second, we evaluate to what extent different species of primary parasitoid may exhibit niche divergence as an indicator of competition over evolutionary time.

NATURAL HISTORY

Like most oak-dwelling cynipids, *N. quercusbaccarum* is bivoltine and reproduces by cyclical parthenogenesis (alternation of one sexual and one asexual generation per year). The sexual generation occurs in the spring. Its spherical galls are produced by a single larva, and grow on the leaves and the catkins of various species of oak. Both sexes emerge in May and the females oviposit in the lower side of oak leaves, producing the gall of the asexual generation. Its unichambered, lenticular-shaped galls grow during the summer, falling from the tree in the beginning of autumn. Only females emerge from these galls in March, ovipositing in oak buds, which will produce the gall of the sexual generation. Our investigation only concerns the galls of the sexual generation and their inhabitants.

MATERIALS AND METHODS

Manipulative field experiments

Determination of the oviposition sequence of parasitoids and associations between parasitoid identity and gall size have been investigated in numerous gall marker/parasitoid systems. Five different methods have been used, based on different types of data: (1) emergence sequences of parasitoids (JONES, 1983; SHORTHOUSE, 1973; SHORTHOUSE *et al.*, 1990); (2) gall sizes from which parasitoids are reared (WASHBURN & CORNELL, 1981; REDFERN & CAMERON, 1994); (3) field observations of parasitoids during the growth period of the galls (JONES, 1983; SHORTHOUSE, 1973); (4) cage experiments with parasitoids enclosed with galls of different sizes (WEIS *et al.*, 1985; CRAIG *et al.*, 1990); (5) exclosure experiments with galls protected from parasitoid attack, except during windows of accessibility (WASHBURN & CORNELL, 1979, 1981; WEIS & ABRAHAMSON, 1985; STILING & ROSSI, 1994). We employed the last method, because it permits one to distinguish the effects of gall size and time.

To determine the role of gall size on parasitism, we conducted a manipulative experiment on galls at the Arboretum de Chèvreloup (10 km Southwest of Paris, France) in the spring of 1993 (day 0 = 16.04.1993). We followed the growth of 367 individual galls on 14 branches distributed over 11 trees of an isolated grove (ca 250 m^2). We used "branch" as the spatial scale for replication in this study, because branches are easily isolated and manipulated. (We shall consider the role of larger spatial levels (*i.e.*, tree and site) on the community in a subsequent study). Galls were located beginning at bud-break by inspecting young leaves and catkins. The location of each gall (leaf, catkin, bud or twig) on the branch was noted for the subsequent survey. Gall diameter was measured to within 0.1 mm with the aid of a calliper. Eight to 10 measurements were made on each gall between its detection and its collection at the end of the experiment, allowing the determination of an individual growth curve for each gall (fig. 1).

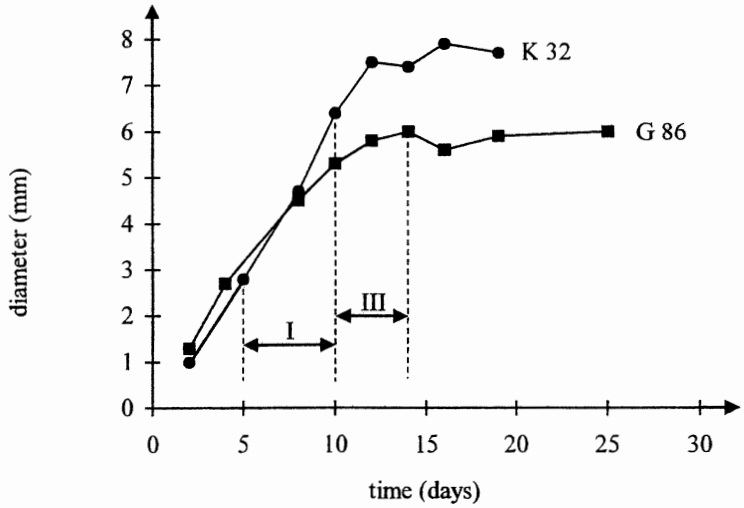

FIG. 1. – Example of two individual growth curves. K 32 was not parasitised during exposure period I, whereas G 86 was parasitised by *M. tibialis* during exposure period III.

Three different treatments were conducted (fig. 2):

Treatment 1: The galls of branches A and B were protected from parasitoids for their full development period by a sleeve (50 cm long and 25 cm diameter, placed around an iron wire, fixed

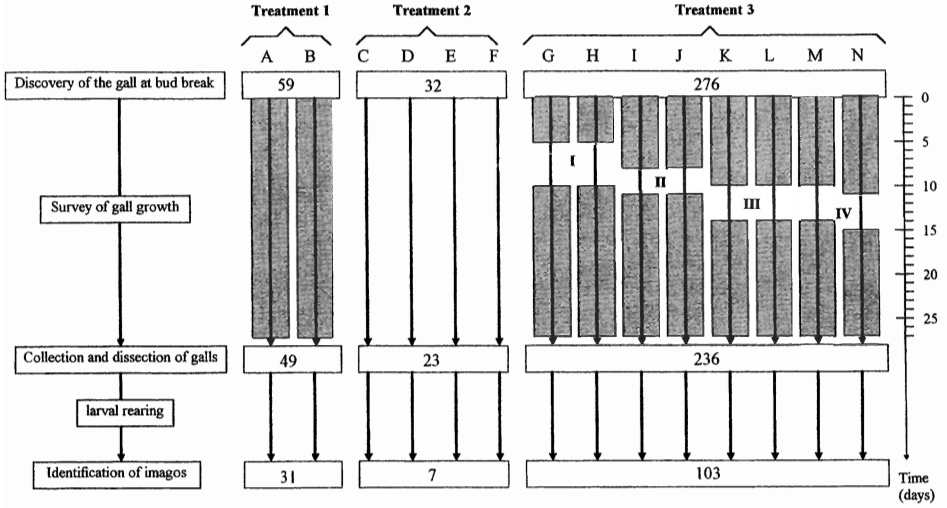

FIG. 2. – Schema of the experimental protocol. Letters A to N indicate the branch number. Numbers of the upper line: galls measured at the beginning of the survey. Numbers of the middle line: galls collected and reared. Numbers of the lower line: galls with identified contents. Shaded area around arrows indicates exclosure period. Numbers I to IV correspond to the four exposure periods.

to the branch) to prevent the contact of galls with the sleeves (and thus to reduce the risk of fungal development, and to eliminate parasite attack from outside the sleeve). This treatment permits the estimation of gall growth independent of parasitism.

Treatment 2: The galls of branches C to F were exposed to parasitoids for the full duration of their development. These galls served as controls to estimate the effect of sleeves on parasitism.

Treatment 3: The galls of branches G to N were exposed for short periods (3 to 5 days). Four different exposure periods (denoted I to IV in fig. 2) were used to create different "windows of accessibility" for the parasitoids, with 2, 2, 3 and 1 branches, respectively. The different branches of the same window constitute replicates used to measure between-branch differences in parasitism. The diameter of each exposed gall was estimated as the arithmetic mean of the gall size measurements during the exposure period.

At the end of the experiment, each gall was dissected and its contents placed in a gelatine capsule (L.G.A., number 4) and reared at 27°C (RH 90-95%). Identifications at least to genus were made on larval gallers attacked by ectoparasitoids, using the key of ASKEW (1985). Adult insects emerging in the capsules were identified based on ASKEW (1961*a*), GRAHAM (1969), and EADY & QUINLAN (1963).

Three species other than the gall maker were found:

Synergus sp.: Synergus gallaepomiformis (Boyer de Fonscolombe, 1832) and *S. nervosus* (Hartig, 1840). Because identification to species was not possible for all individuals, we employ the global denomination *Synergus sp.* When inquilines were present in a given gall, the galler always perished as a consequence.

Mesopolobus tibialis (Westwood, 1833) and *Torymus auratus* (Geoffroy in Fourcroy, 1785) were observed only feeding on the gall maker. The window of accessibility was created too early in the development of *Synergus sp.* for *M. tibialis* or *T. auratus* to act as secondary parasitoids (*i.e.*, feeding on *Synergus sp.*). Subsequent sampling of galls revealed that parasitoids of *Synergus sp.* occur later in

the season (*i.e.*, in June; unpublished data). We employ the term "parasitoid" for *M. tibialis+T. auratus,* whereas we use the term "parasite" for *Synergus sp.+M. tibialis+T. auratus.*

Statistical analysis

As we are interested in the effect of various parameters of a given gall (diameter, exposure period, and branch) on the identity of the species emerging from it, and as the response variable is qualitative (one of the four different values, corresponding to the four species observed), we conducted three different analyses with a binary response variable opposing (1) the gall maker *versus* parasites, (2) *Synergus sp. versus* parasitoids, and (3) *M. tibialis versus T. auratus.* For each analysis, we first test the role of exposure period and branch. Because there were branch replicates on the same tree for only three trees (namely branches $A+N$, $D+E$, and $L+M$-the latter being the only one of the three with the same treatment), we were not able to investigate the variation in parasitism among trees. Since there were several branches exposed during each period, the variable "branch" was considered as nested in the variable "exposure period". We then compared size of galls parasitised by each species (or group of species) by means of t-tests. ANOVA, nested ANOVA and ANCOVA analysis were conducted using GLIM 3.77 (Royal Statistical Society of London, 1985). We verified that there was no overdispersion in the data using appropriate statistical tests (CRAWLEY, 1993).

RESULTS

Influence of parasitism on gall growth

Gall development follows three phases (ROHFRITSCH, 1992): (1) initiation, (2) growth, and (3) maturation (during which gall growth stops). Our survey starts at the beginning of phase 2 and the galls were collected at the end of phase 3 (nymphosis of the gall marker) (figs. 1 and 2). As we could not follow gall growth before bud-burst, we were not able to determine the initial stage of gall growth and hence could not fit a growth curve to the data. To evaluate the effect of parasitism on gall growth, we used the relationship between the maximal growth rate of the gall (*i.e.* the largest change in diameter between any two measurements), $Gmax$, and the maximal gall size, $Smax$. This relationship is linear for the gall maker ($Smax = 2.646 + 4.246\,Gmax$, $r^2 = 0.530$, $F_{1,22} = 24.76$, $p < 0.01$; fig. 3). Therefore, the maximal growth rate of a gall is a reasonable predictor of its final size. If the parasites do not affect gall growth, then the relationship between $Smax$ and $Gmax$ should not differ between unparasitised and parasitised galls. To avoid cases where $Gmax$ could be influenced by early parasitism, only galls for which $Gmax$ occurred before the window of accessibility, and with first measurements of gall diameter less than or equal to 2 mm, were used in the analysis.

The variable "species" has a global effect on the regression of $Gmax$ on $Smax$, indicating the need to test for different slopes among species (table I). *M. tibialis* and *T. auratus* each have a significant effect on gall growth, diminishing

TABLE I. – *Analysis of Covariance of maximal gall size among species with maximal growth rate as covariate.*

Source	SS	d.f.	MS	F	Significance
Adjusted means (among species)	22.17	3	7.39	7.189	0.0003
Error (deviations from a common slope)	69.89	68	1.03		
Total	129.13	72	1.79		

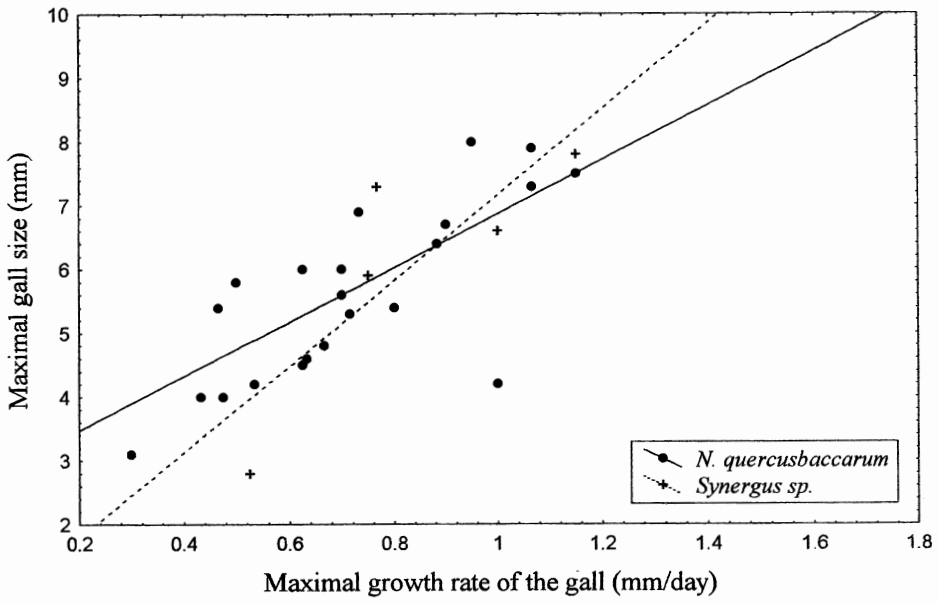

FIG. 3. – Regression of the maximal growth rate of the gall *versus* maximal gall size for unparasitised galls (*N. quercusbaccarum*) and galls parasitised by *Synergus sp.*

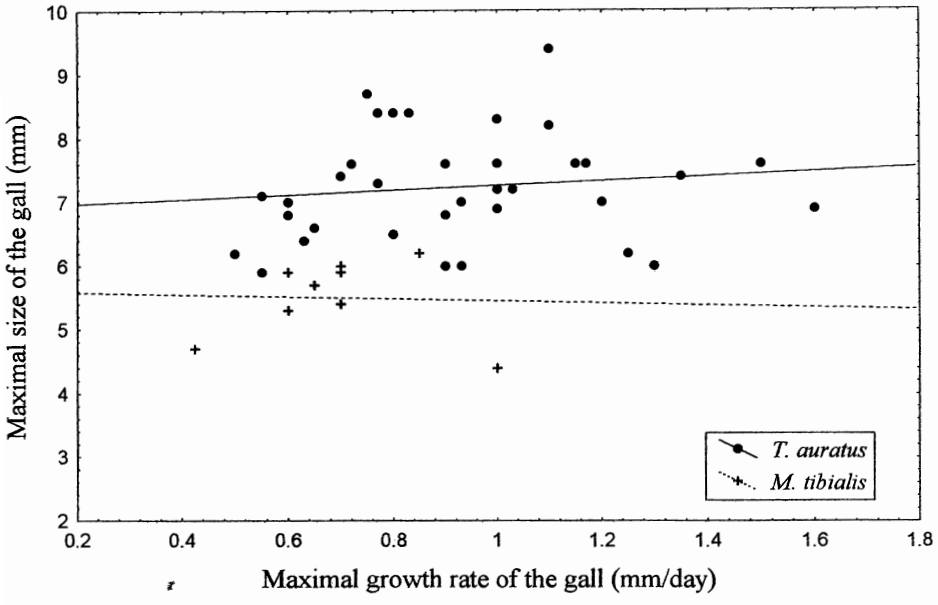

FIG. 4. – Regression of the maximal growth rate of the gall *versus* maximal gall size for galls parasitised by *T. auratus* and by *M. tibialis*.

the final size attained by the galls they attack (t-test on the parameter estimates from the ANCOVA: $t = 2.64$ and 4.92 respectively, d.f. $= 65$, for both $p < 0.01$, fig. 4). *Synergus sp.*, on the other hand, has no effect on final gall size ($t = 0.930$ d.f. $= 65$, $p > 0.05$, fig. 3), but this result should be taken with caution because of the small sample size ($n = 5$).

Influence of exposure period, sleeve, and gall size on parasitism

Global parasitism

Global parasitism is defined as parasitism due to the three parasite species. In the nested design, only exposure period showed a significant relationship with global parasitism (table IIa). Despite the increase in gall size through time (mean size of the galls of the different exposure periods ($\pm$ SE): period I $= 4.66 \pm 1.26$ mm, $n = 24$; period II $= 5.42 \pm 1.33$ mm, $n = 30$; period III $= 5.60 \pm 1.08$ mm, $n = 43$; period IV $= 5.78 \pm 1.71$ mm, $n = 7$), there is no significant effect of exposure period or branch on gall size (table IIIa). We then combined the data from all the branches and exposure periods to compare the size of the unparasitised *versus* parasitised galls. Parasitised galls were significantly bigger than unparasitised ones (mean size of the unparasitised galls $= 4.13 \pm 1.20$ mm, $n = 16$; mean size of the parasitised galls $= 5.56 \pm 1.07$ mm, $n = 88$; $t = 4.468$, df $= 102$, $p < 0.001$), indicating that, during exposure periods, large galls are more vulnerable to parasitism (fig. 5).

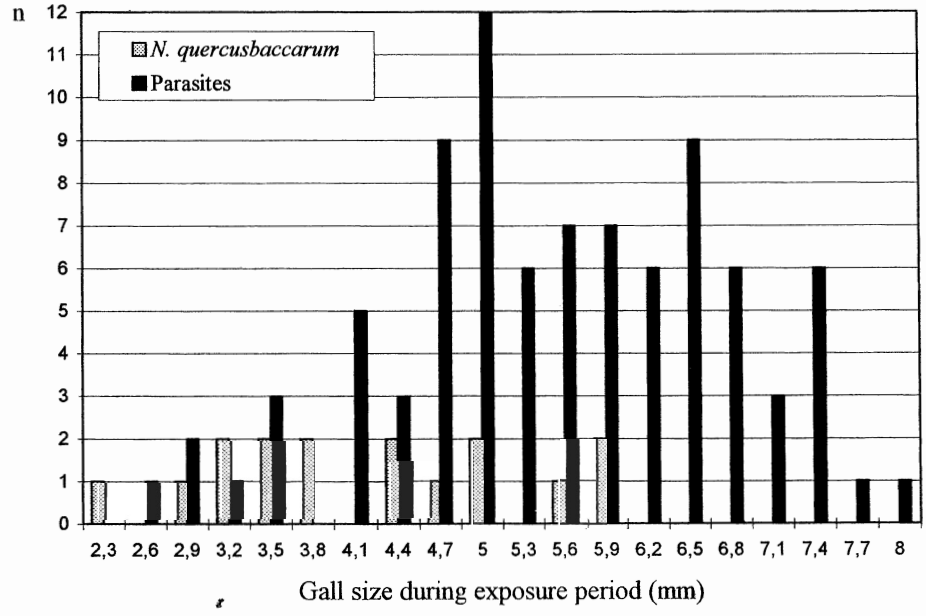

FIG. 5. – Distribution of gall sizes during the exposure period for galls escaping parasitism (*N. quercusbaccarum*) and galls parasitised by *Synergus sp.*, *M. tibialis* or *T. auratus*.

TABLE II. – *Occurrence of the different species as a function of exposure period and branch*

a) Parasitised *versus* unparasitised galls

Exposure Period	I		II		III			IV
Branch	G	H	I	J	K	L	M	N
Parasitised	4	11	16	7	29	1	13	7
Unparasitised	5	4	2	5	0	0	0	0

χ^2 (effect of exposure period) = 24.945; $p = 0.001$

χ^2 (effect of branch nested in exposure period) = 5.73, $p = 0.2203$

b) Galls parasitised by *Synergus sp. versus* galls parasitised by *M. tibialis* and *T. auratus.*

Exposure Period	I		II		III			IV
Branch	G	H	I	J	K	L	M	N
Synergus sp.	3	1	0	0	1	0	0	1
Ectoparasitoids	1	10	16	7	28	2	12	6

χ^2 (effect of exposure period) = 11.169; $p = 0.0109$

χ^2 (effect of branch nested in exposure period) = 6.997, $p = 0.1361$

c) Galls parasitised by *M. tibialis versus* galls parasitised by *T. auratus.*

Exposure Period	I		II		III			IV
Branch	G	H	I	J	K	L	M	N
M. tibialis	0	3	8	0	8	2	6	0
T. auratus	1	7	8	7	20	0	6	6

χ^2 (effect of exposure period) = 5.49; $p = 0.393$

χ^2 (effect of branch nested in exposure period) = 13.894; $p = 0.0076$

Parasitism by Synergus sp. *versus parasitoids*

As with global parasitism, only exposure period affected relative parasitism rates of the inquilines and parasitoids (table IIb). There is no significant effect of exposure period or branch on gall size (table IIIb). Galls attacked by *Synergus sp.* where significantly smaller than galls attacked by all other parasitoid species (mean size of galls attacked by *Synergus sp.*= 3.59 ± 0.98 mm, $n = 6$; mean size of galls attacked by *M. tibialis* and *T. auratus*= 5.71 ± 0.98 mm, $n = 82$; $t = 4.650$, df = 86, $p < 0.001$) (fig. 6).

Parasitism by M. tibialis *versus* T. auratus

In contrast to the other comparisons, there is a branch effect between *Mesopolobus* and *Torymus*, whereas there is no exposure-period effect (table IIc). Again, there is no significant effect of exposure period or branch on gall size (table IIIc). Among all the galls attacked by these two parasitoid species, those

TABLE III. – *Analysis of Variance of gall size during the windows of accessibility when comparing*:

a) Parasitised *versus* unparasitised galls

Source	SS	d.f.	MS	*F*	Significance
Exposure Period	15.73	3	5.243	2.056	0.2488
Branch within Exposure period	10.2	4	2.55	1.703	0.1556
Total	143.7	96	1.497		

b) Galls parasitised by *Synergus sp. versus* galls parasitised by *M. tibialis* and *T. auratus.*

Source	SS	d.f.	MS	*F*	Significance
Exposure Period	8.097	3	2.699	1.057	0.4599
Branch within Exposure period	10.21	4	2.5525	1.919	0.1153
Total	106.39	80	1.329875		

c) Galls parasitised by *M. tibialis versus* galls parasitised by *T. auratus.*

Source	SS	d.f.	MS	*F*	Significance
Exposure Period	3.589	3	1.196	3.446	0.1316
Branch within Exposure period	1.388	4	0.347	0.287	0.8862
Total	89.883	74	1.215		

attacked by *M. tibialis* are significantly smaller than those by *T. auratus* (mean size by *M. tibialis* = 4.69 ± 0.67 mm, $n = 27$; mean size by *T. auratus* = 6.21 ± 0.88 mm, $n = 55$; $t = 7.917$, df = 80, $p < 0.001$) (fig. 6).

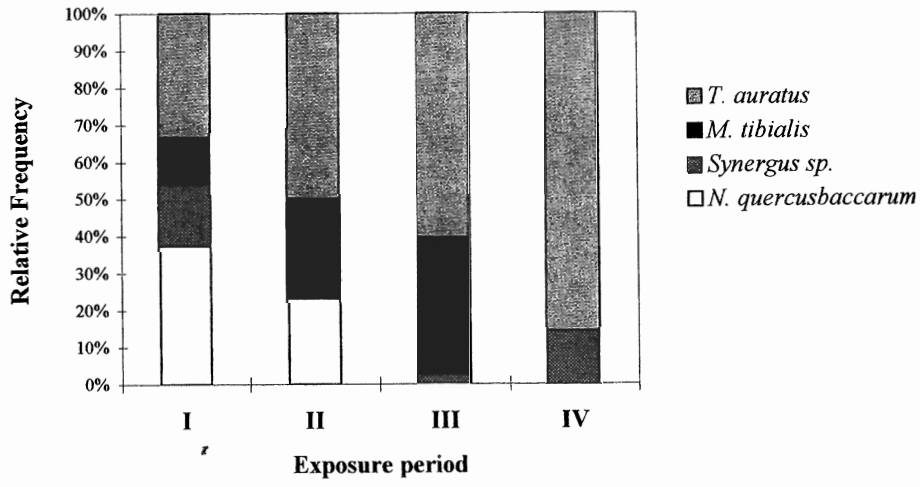

FIG. 6. – Relative frequencies of the different species for the four different exposure periods.

Parasitism rates

Despite the very short windows of accessibility (3 to 5 days) of treatment 3, global parasitism was high (84.6%, $n = 104$). Only eight galls unprotected by sleeves (treatment 2) had identifiable contents (the remaining galls were not collected at the end of their development due to early necrosis on the leaves or due to loss on the ground): seven were parasitised by *Synergus sp.* and one by *T. auratus*. The high frequency of *Synergus sp.* in unsleeved galls and in other field collections (unpublished data) indicates that the lower observed frequency of galls with *Synergus sp.* in galls of treatment 3 (5.8%, $n = 104$) is probably an artefact of the exclosure design; the galls attacked by *Synergus sp.* are relatively small in size (*see* below), and *Synergus sp.* would have probably attacked smaller galls if available in the exposure period (fig. 5). In fact, the exclosure experiments were biased towards the sampling of *M. tibialis* and *T. auratus* (respectively 25.9% and 52.9%, $n = 104$), and away from the sampling of hyperparasitoids, which tended to be present after the exposure treatments (unpublished data).

DISCUSSION

Influence of parasitism on gall growth

The hypothesis that parasite attack can affect gall growth has been made by different authors (ASKEW, 1961*a*, 1975; DUFFET, 1968; WASHBURN & CORNELL, 1981; WIEBES-RIJKS, 1982), but has never been directly tested for the process of cecidogenesis due to Cynipids (ROHFRITSCH, 1992) (but *see* SHORTHOUSE, 1973, for the particular case of *Periclistus pirata* on *Diplolepis polita*), although it has been investigated for other gall maker/parasitoid systems (PRICE & CLANCY, 1986; WEIS & ABRAHAMSON, 1985). Changing gall sizes or growth patterns have both methodological and biological implications. Methodologically, if some species stop gall growth and others do not, the determination of the sequence of parasitism based on the final size of galls could lead to erroneous conclusions. Biologically, if a species attacks galls early, it could be important that it does not reduce gall growth if the thickness of the gall wall constitutes a protective refuge from later-arriving, competitively superior parasitoid species.

In killing the gall-former, both *T. auratus* and *M. tibialis* have significant effects on gall growth and final gall size. This is in accord with the hypothesis that idiobionts (*i.e. T. auratus* and *M. tibialis*) should alter gall growth (ASKEW, 1961*a*), in contrast to koinobiont species which should not (e.g. *Torymus (Syntomaspis) cyanea* in ASKEW, 1975; WIEBES-RIJKS, 1982).

Cynipid inquilines have complex effects on gall growth and gall structure (WIEBES-RIJKS, 1974, 1982; SHORTHOUSE, 1980). In contrast to parasitoids, in our study, *Synergus sp.* appears to have no effect on gall growth, despite the death of the gall maker. From an evolutionary perspective, and considering recent advances in cynipid phylogeny (RONQUIST, 1994), our results suggest that the monophyletic clade formed by the cynipid inquilines should have lost only their ability to induce gall formation, but not the capacities to alter gall growth and gall maturation. However, without a better understanding of the process of cecidogenesis, this evolutionary scenario should be interpreted with due caution.

Influence of exposure period, sleeve and gall size on parasitism

Using exclosure experiments allowing the direct measure of both the effects of time and gall size on parasitism, we have shown the potential for resource partitioning, along a niche axis of gall size, among parasitoids of the cynipid oak galler *N. quercusbaccarum.* Despite their presence in all the exposure periods (except *Synergus sp.* absent from period II) (fig. 6), the three parasite species attack the gall at different, but somewhat overlapping, sizes, leading to the following sequence of parasitism (fig. 7):

1. *Synergus sp.*: The window of vulnerability of *N. quercusbaccarum* is closed to galls of intermediate size (maximum size attacked = 4.9 mm).

2. *Mesopolobus tibialis*: Its window of accessibility to the galler is bounded by large galls (maximum size attacked = 5.9 mm) and small galls (minimum size attacked = 3.1 mm).

3. *Torymus auratus*: There is no upper limit in gall size limiting access to this species, but they were not found to attack the smallest galls (minimum size attacked = 4.2 mm).

Although *T. auratus* and *M. tibialis* appear to attack different gall-size distributions, their parasitism rates do not differ in time (*i.e.,* the lack of effect of exposure period when comparing *T. auratus* to *M. tibialis*); rather, parasitism between the two differs in space (*i.e.,* the "branch effect"). Such spatial heterogeneity in attack distributions theoretically contributes to monophagous parasitoid coexistence as long as the distributions are sufficiently independent from one another (MAY & HASSELL, 1981; KAKEHASHI *et al.,* 1984).

Parasitism rate

The very high level of parasitism observed in the galls of treatment 3 (84.6%, $n = 104$) is striking, given the short exposure period. As possible support of this finding, BRAUNE (1992) found the parasitism rate of the sexual generation of *Neuroterus quercusbaccarum* in Germany to be 90% (89 and 91% on samples of respectively 4 852 and 1 180 galls). Although the sample size of our control is too small to be confident, parasitism rate would have probably approached 100% for galls exposed during the whole of the one month period of their development, as opposed to the 3 to 5 days employed in the experiment. For instance, the few gallers that survived the early exposure period escaped parasitism by *T. auratus* because of their small gall size (fig. 5), but after subsequent growth, nothing would have protected them from later-emerging individuals of this same parasitoid species (100% of parasitism for gall size classes greater than or equal to 6.05 mm ($n = 32$), fig. 6). Given such high parasitism and the lack of an absolute refuge due to gall size, how do local populations of *N. quercusbaccarum* persist?

One possibility is that there is substantial between-tree variability in bud-burst, such that the galls on the most precocious trees partially escape parasitism due to a temporal refuge. A second possibility is a large-scale spatial refuge, such that *N. quercusbaccarum* persists regionally due to the periodic colonisation of sites where it has previously gone extinct. At present, we do not have sufficient information to test these hypotheses, but rather only the observation that gall density in the study grove was at least three orders of magnitude smaller in spring 1994 as compared to spring 1993 (suggesting the near local extinction of

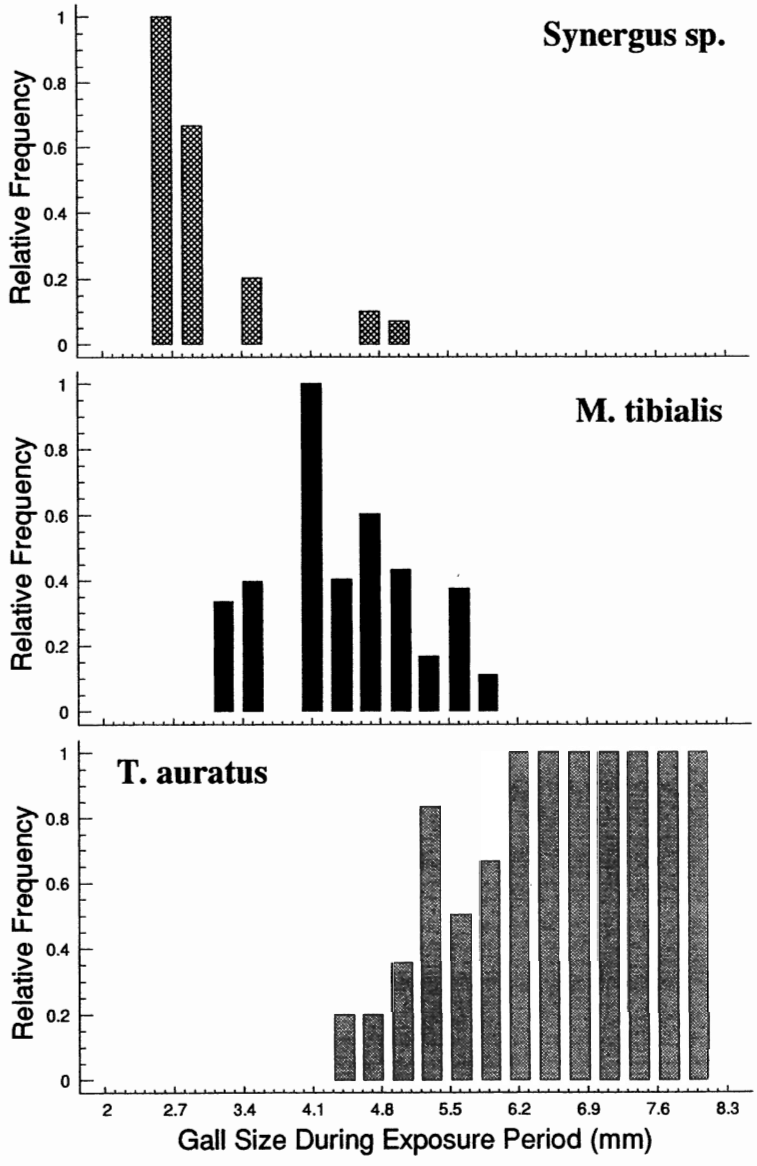

FIG. 7. – Relative frequencies of the different parasitoid species in each gall size class (gall size measured during exposure period).

N. quercusbaccarum), whereas in groves c. 200 km away (located near Rennes, France) gall density was high in 1994 (O. PLANTARD, pers. obs.). Finally, switching behavior of the parasites (CORNELL & PIMENTEL, 1978) could explain the persistence of the different species of the component community. Under this hypothesis, as

N. quercusbaccarum becomes rarer, its polyphagous parasites would "switch" to attack other, more abundant, oak-galler species, reducing the pressure exerted on *N. quercusbaccarum.*

CONCLUSION

The window of vulnerability of *Neuroterus quercusbaccarum* differs for each parasite species. Although an absolute refuge provided by gall size may exist with respect to certain parasitoid species, there appears to be no such refuge when the action of all parasite species are taken into account. Rather, the partial refuge associated with gall size is composed of a physical refuge through gallwall thickness, limiting access to the galler larva if the length of the parasitoid's ovipositor is too short (e.g. the upper limit of the window to *M. tibialis*). It is also composed of a "developmental" refuge of small galls, due to the insufficient food supply provided by young cynipid larva (assuming that parasitoids avoid attacking these galls for this reason). The concept of the "window of vulnerability", first mooted by WASHBURN & CORNELL (1981) and by CORNELL (1983) in the context of insect galls, has since been tested in different gall maker/parasitoid systems with differing conclusions about the existence of such windows (WEIS & ABRAHAMSON, 1985; CLANCY & PRICE, 1986; CRAIG *et al.*, 1990; STILING & ROSSI, 1994). For *N. quercusbaccarum*, the concept appears to hold. Gall size, partitioned in time, is a niche axis along which the different parasite species potentially divide the *N. quercusbaccarum* resource. These findings reinforce the hypothesis that gall size is a major determinant of parasite richness and has an important impact on parasite assemblage structure for these endophytic communities.

ACKNOWLEDGEMENTS

We thank Dr R. R. ASKEW for his useful advice for rearing of oak gall inhabitants. We also thank B. A. HAWKINS, K. SCHÖNROGGE and one anonymous reviewer for their comments on the manuscript, and the Arboretum de Chevreloup, and particularly Mr GENEVÊT for his assistance. This work was partly financed by the French Ministry of the Environment (DRAEI-509352).

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