

THE POPULATION BIOLOGY OF OAK GALL WASPS (HYMENOPTERA: CYNIPIDAE)

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Key Words cyclical parthenogenesis, host alternation, food web, parasitoid, population dynamics

■ **Abstract** Oak gall wasps (Hymenoptera: Cynipidae, Cynipini) are characterized by possession of complex cyclically parthenogenetic life cycles and the ability to induce a wide diversity of highly complex species- and generation-specific galls on oaks and other Fagaceae. The galls support species-rich, closed communities of inquilines and parasitoids that have become a model system in community ecology. We review recent advances in the ecology of oak cynipids, with particular emphasis on life cycle characteristics and the dynamics of the interactions between host plants, gall wasps, and natural enemies. We assess the importance of gall traits in structuring oak cynipid communities and summarize the evidence for bottom-up and top-down effects across trophic levels. We identify major unanswered questions and suggest approaches for the future.

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INTRODUCTION

Oak gall wasps (Hymenoptera: Cynipidae) have fascinated and intrigued generations of biologists because of three principal biological attributes, each of which leads to its own set of questions. (*a*) Each species induces a highly characteristic and often highly complex gall structure, and the group as a whole induces an incredible diversity of galls on their host plants. How are these galls induced, and what are they for? (*b*) They have complex cyclically parthenogenetic (hetero-*gonic*) life cycles, which in some cases also involve host alternation (*heteroecy*). How are these life cycles controlled? Have any species become secondarily obligately parthenogenetic, as in other cyclically parthenogenetic taxa? (*c*) Oak cynipid galls support complex and characteristic communities composed of the gall wasp, inquiline, and hymenopteran parasitoids. What structures these communities, and how do their members interact? We build on excellent existing reviews of oak cynipid biology (8, 122), considering recent advances in the study of all three sets of questions given above. First, we briefly consider the adaptive significance of

insect galls, looking beyond the oak cynipids into other insect groups. The main body of the review is then divided into two sections. (a) We update what is known of the basic biology of oak cynipids, highlighting recent advances in taxonomy, gall-induction, host plant associations, biogeography, and life cycles. (b) We consider the factors that structure the communities associated with cynipid galls and the processes that influence their dynamics.

THE ADAPTIVE SIGNIFICANCE OF GALLS

Debate continues over the adaptive significance of gall induction as a life history trait (6, 12, 95, 129, 139, 143) both over the selective forces acting on gall phenotypes and over which elements of gall phenotypes have been shaped by selection. Available evidence suggests that gall induction is a wholly parasitic relationship (27, 37, 56, 64), and current hypotheses center on the adaptive value of the gall to the gall inducer. Three general mutually compatible hypotheses for the adaptive significance of insect galls have been proposed (95): (a) The nutrition hypothesis, which states that gall inducers regulate the nutritive value of the plant tissues on which they feed to their own benefit; (b) the microenvironment hypothesis, which states that gall occupation protects the gall inducer from external fluctuations in microclimate; and (c) the enemy hypothesis, which states that gall structures have been selected to reduce mortality imposed on the gall inducer by natural enemies. Of these three, only the enemy hypothesis can account for diversity in gall structure (95, 129), an issue of particular relevance given the enormous diversity of oak cynipid galls. We consider the significance of these hypotheses for cynipid galls throughout this review.

CYNIPID RELATIONSHIPS

Gall wasps are members of the Cynipoidea, a major lineage of predominantly parasitoid wasps within the Hymenoptera (104, 105). The groups closest to cynipids (Figitidae, Eucoilidae, Charipidae, and Anacharitidae) are all parasitoids that attack insect larvae, which suggests that gall induction in cynipids has evolved from an ancestral parasitoid life history (105). All gall wasps are obligate parasites of plants and either induce their own galls in plant tissues or develop asinquilines within the galls induced by other gall wasps. The first gall wasps probably induced galls on herbs (105) and subsequently diverged into six recognized tribes (with species richnesses given in 104, 105). The "Aylacini" (ca. 180 species) are a basal paraphyletic group, most of which gall herbaceous plants, that gave rise to two main monophyletic lineages. One lineage consists of four tribes whose members gall woody plants (the woody rosid gallers) (105): the Diplolepidini (rose gall wasps, ca. 63 species), the Pediaapidini (galling *Acer*, 2 species), the Eschatocerini (galling *Acacia* and *Prosopis*, 3 species), and the Cynipini (oak gall wasps, ca.

900–1000 species). A second lineage, distinct from the woody rosid gallers, gave rise to the tribe Synergini (ca. 173 species), whose members are inquiline inhabitants of the galls of other gall wasps. Although able to induce the development of nutritive plant tissues within other cynipid galls, they cannot induce their own galls *de novo*.

GALL INDUCTION

Mechanisms of cynipine gall induction remain little known (47, 49, 111), and understanding the molecular tools used by cynipids to manipulate plant development is the Holy Grail of current cynipid research.

Cynipid gall development can be divided into three phases: initiation, growth, and maturation (60, 122). Initiation begins with oviposition by the female gall wasp. She determines the host plant, gall location on the host, and (by the number of eggs she lays) the number of larvae developing in the resulting gall. As far as is known, gall induction results from secretions derived from the egg and larva and not from any maternal secretion. It is widely agreed that cynipids need meristematic or otherwise omnipotent cells to initiate gall growth (60, 110, 111, 122), although specific requirements in terms of degree of host tissue differentiation tolerated and nutritional state required are unknown. This lack of knowledge becomes an issue when we later discuss ways in which host plants may affect gall wasp–population dynamics. Plant cells neighboring the egg lyse to produce a small chamber. After hatching, the larva enters this chamber and controls all subsequent tissue differentiation. Each larva develops in its own chamber (Figure 1*a*), and galls induced by a specific gall wasp species are usually either single chambered (unilocular) or many chambered (multilocular) (Figure 1*b*).

The next phase, gall growth, takes place while the gall wasp larva remains very small. The larval chamber forms and enlarges, a network of vascular bundles develops that joins those supplying the host organ, and layers of outer parenchyma develop around the larval chamber (Figure 1*a*; 60, 122). In virtually all cynipid galls, the larval chamber is lined with nutritive cells and bounded externally by a layer of vacuolate parenchyma and a thin shell of sclerenchyma (Figure 1*a*). The nutritive tissue is characteristic of cynipid galls, and to date only galls induced by the chloropid fly *Lipara lucens* are known to possess similarly specialized gall tissue (47, 122, 137). Nutritive tissue consists of large thin-walled cells whose chromosome structure, protein content, and physiology is similar to seed tissue (47–49, 111). These cells represent the gall wasp's sole source of food throughout development (122). The larval chambers are morphologically similar in all cynipid galls, and generation- and species-specific gall structures result from variation in the development of the outer parenchyma and epidermis (60, 122). The complexity of these outer tissues varies enormously across gall wasp tribes, among species, and between the generations of cyclically parthenogenetic species (122, 129; Figure 1*b*).

During the growth phase, the gall acts as a major sink for mineral nutrients and photoassimilates (carbon fixed during photosynthesis) (14, 15, 85). The outer gall tissues also synthesize tannins and phenolics (48), which were originally thought to be a deterrent against free-feeding insect larvae (3, 4, 112). However, these compounds are now known to be feeding stimulants for some insect species (119), and an additional function as a fungicide has been proposed (135, 150). Manipulation of plant metabolites is achieved through several routes. Galls on leaves elevate photosynthetic rates on the affected leaf and intercept the resulting photoassimilate (14, 37, 38). Galls on leaves and other tissues also concentrate nutrients and photoassimilate through mobilization of these resources from neighboring regions of the plant (14, 85). Some cynipids that gall ephemeral plant structures (such as catkins) prolong the life span of these structures on the host, extending the period available for development (29).

The maturation phase is characterized by decreased rates of cell division, and the gall ceases to be a major sink for host plant resources. The gall wasp larva now grazes the nutritive cells lining the larval chamber, and the action of feeding triggers the conversion of neighboring vacuolate parenchyma into further nutritive cells (122). Feeding continues until the sclerenchymatous shell of the larval chamber is reached. The larval intestine is closed between the midgut and the hindgut for most of the larval life and only opens for defecation immediately prior to pupation, thus avoiding fouling of the larval chamber (121). In many oak galls, the tissues surrounding the larval chamber become lignified, and in some cases regional tissue death results in internal airspaces (14, 15, 122, 129). Lignification makes the tissue unusable for other herbivores, and in some species the onset of lignification determines when the galled organ (e.g., catkins, leaves or acorns) is shed from the host. The timing of lignification is under larval control and may have important consequences, particularly in deciduous galls that overwinter. Many galls fall slightly before leaf fall in the autumn, ensuring a covering of leaves and a suitable microclimate in which to pupate or enter diapause.

HOST PLANT RELATIONSHIPS IN THE CYNIPINI

The Taxonomic and Geographic Distributions of Host Plants

The majority of Cynipini gall oaks (genus *Quercus*) in the subfamily Fagoidea of the family Fagaceae. Small numbers of cynipids gall hosts in the other subfamily of the Fagaceae, the Castanoidea, including chestnuts (*Castanea*), chinquapins (*Castanopsis*, *Chrysolepis*), and tanbark oaks (*Lithocarpus*) (24, 55, 56, 146). A genus of cynipids, *Paraulax*, is also known from southern beech, *Nothofagus*, in Argentina and Chile, although the tribal affinity of these cynipids is unknown.

The genus *Quercus* is divided into two subgenera—the strictly Asian subgenus *Cyclobalanopsis* and the more widespread subgenus *Quercus* (80). Little is known about the cynipids associated with *Cyclobalanopsis* oaks. The subgenus *Quercus* is

divided into four sections (65). Nearctic oaks belong to three sections—*Quercus sensu stricto* (white oaks), *Lobatae* (red oaks), and *Protobalanus* (golden cup oaks), whereas Palearctic oaks include members of the section *Q. sensu stricto* and an endemic Eurasian taxon, the section *Cerris*. Cynipids gall hosts in all sections within the subgenus *Quercus* (Table 1), and with the exception of the host-alternating species described below, each cynipid species is generally associated only with a closely related group of oak species (5, 24, 69, 77).

Oak distributions and patterns of species richness have probably played a major role in the distribution and species richness of oak cynipids, and we therefore describe them briefly. The subgenus *Quercus* contains approximately 500 species worldwide (80), distributed throughout the temperate regions of the Northern Hemisphere and extending southwards as far as Indonesia and Ecuador. Oaks are more species rich in the Nearctic (ca. 300 species) than in the Palearctic (ca. 175 species) (65, 80), and the greatest richness is found in Mexico (ca. 135–200 species) (65). The Western Palearctic has a low diversity of oaks, with approximately 40 species, and large areas of northern Europe are dominated by just two species—*Quercus robur* and *Quercus petraea* (128, 131). The Eastern Palearctic contains ca. 130 species, and oaks are a major component of climax forests in highland areas from the eastern Himalayas to the Philippines. The southernmost record of an oak cynipid in Asia is from *Quercus spicata* in Java (31).

Host-Alternating Cynipids

Host alternation (heteroecy) in cynipids is known only from the Cynipini, and within this tribe it is known only for Western Palearctic species in *Andricus* and *Callirhytis* (12, 41, 79). In both cases, the alternation is between hosts in the sections *Cerris* and *Quercus*. In all host-alternating *Andricus* species, the asexual generation females oviposit on the section *Cerris* host, and the sexual generation females oviposit on the section *Quercus* host, whereas in *Callirhytis* the situation

TABLE 1 The distribution, host associations, and species richness of genera in the tribe Cynipini^a

Genus name	Global range	Species richness ^b	<i>Quercus</i> sections ^c	Non- <i>Quercus</i> hosts
Holarctic				
<i>Andricus</i>	Holarctic ?Oriental	>300	C, L, P, Q	<i>Lithocarpus</i>
<i>Callirhytis</i>	Holarctic	150	C, L, P, Q	none
<i>Dryocosmus</i>	Holarctic	25	C	<i>Castanopsis</i> , <i>Castanea</i>
<i>Neuroterus</i>	Holarctic	100	C, P, Q	none
<i>Paraulax</i> ^d	Chile and Japan	1		<i>Nothophagus</i>
Nearctic				
<i>Acraspis</i>	Nearctic	>30	L	none
<i>Amphibolips</i>	Nearctic	30	L, Q	none

TABLE 1 (Continued)

Genus name	Global range	Species richness ^b	<i>Quercus</i> sections ^c	Non- <i>Quercus</i> hosts
<i>Antron</i>	Nearctic	40	P, Q	none
<i>Atrusca</i>	Nearctic	40	Q	none
<i>Bassettia</i>	United States	9	L, Q	none
<i>Belonocnema</i>	United States	2	L	none
<i>Besbicus</i>	United States	8	L, Q	none
<i>Disholcaspis</i>	Nearctic	40	L, P, Q	none
<i>Dros</i>	Nearctic	11	Q	none
<i>Erythes</i>	Nearctic	2	L	none
<i>Eumayria</i>	United States	5	L	none
<i>Eumayriella</i>	United States	2	L	none
<i>Euxystotheras</i>	United States	1	L	none
<i>Heteroecus</i>	United States	15	P	none
<i>Holocynips</i>	United States	4	L, P, Q	none
<i>Liodora</i>	United States	3	Q	none
<i>Loxaulus</i>	Nearctic	14	L, P, Q	none
<i>Odontocynips</i>	United States	1	Q	none
<i>Paracraspis</i>	United States	3	P	none
<i>Philonix</i>	United States	8	Q	none
<i>Phylloter</i> (= <i>Xystoter</i>)	Nearctic	6	L, Q	none
<i>Sphaeroter</i>	United States	8	L, Q	none
<i>Trichoter</i>	United States	8	L, P, Q	none
<i>Xanthoter</i>	United States	12	L, Q	none
<i>Zopheroter</i>	United States	6	L, Q	none
Palaeartic				none
<i>Aphelonyx</i>	Palaeartic	4	C	none
<i>Belizinella</i>	E. Palaeartic	2	C	none
<i>Biorhiza</i>	Palaeartic	2	Q	none
<i>Chilaspis</i>	W. Palaeartic	3	C	none
<i>Cynips</i>	Palaeartic	25	?C, Q	none
<i>Neoneuroter</i>	E. Palaeartic	5	C	none
<i>Parandricus</i>	China	1	?Q	none
<i>Plagiotrochus</i> (= <i>Fioriella</i>)	W. Palaeartic and Himalayas	14	C	none
<i>Repentinia</i>	Central Europe and Azerbaijan	1	C	none
<i>Trichagalma</i>	Japan and China	2	C	none
<i>Trigonaspis</i>	Palaeartic	<10	Q	none
<i>Ussuraspis</i>	Mongolia	1	C	none

^aBased on Weld (145) with additional data from several sources (17, 59, 61, 63, 65–68, 70, 71, 73, 78, 80, 97a).

^bAll species richnesses are best estimates from available data. For reasons described in the text, richness in all genera is likely to change with further research.

^cSections of the subgenus *Quercus*: C, *Cerris*; L, *Lobatae*; P, *Protobalanus*; Q, *Quercus*.

^dThe tribal affinity of the genus *Paraulax* remains uncertain.

is reversed. Cynipids with heteroecious life cycles have distributions restricted to areas where both host taxa occur together, a requirement that has had significant effects on geographical patterns in cynipid species richness in the Western Palaearctic (considered below). Heteroecy is generally extremely rare in insect taxa (73), although in aphids it has evolved many times (138). Phylogenetic analysis of host use in *Andricus* suggests that it has only evolved once in this genus from a life cycle with both generations on section *Quercus* hosts (22; J.M. Cook, A. Rokas & G.N. Stone, unpublished data).

PATTERNS IN CYNIPID SPECIES RICHNESS

Global Patterns

There are ca. 1000 known species of oak gall wasp in 41 genera worldwide (Table 1), predominantly in the Northern Hemisphere (105). Geographic variation in cynipid diversity generally tracks patterns in oak species richness (24). The greatest richness of oak gall wasps is found in the Nearctic (and particularly in Mexico), where there are an estimated 700 species in 29 genera (Table 1; 146–148). Oak gall wasps are thought to have undergone major radiations in Central America (57, 58, 100) alongside their oak hosts (65). Rose gall wasps and the Eschatocerini show similar patterns (92), which suggests that the woody rosid galls as a group may have originated in the Americas (92, 104, 105). The palaeartic fauna is less species rich. For example, California alone contains more oak cynipid species (150) than the whole Western Palaearctic (ca. 140 species in 11 genera) (Table 1; 69, 77, 146), and three times as many as are known from the Eastern Palaearctic and Asia (ca. 50 species) (59). However, both regional and global estimates of oak cynipid species richness can only be regarded as approximate for two reasons. First, the sexual and asexual generations of many cynipid life cycles have yet to be linked (particularly in the Nearctic), with the result that many species are probably currently classified as two. As life cycles are resolved, species richness will fall. Second, the cynipine faunas of large areas of high-potential species richness remain little known—particularly Central America and highland oak forests in China and Southeast Asia. As these are sampled more intensively, species richness is expected to rise.

Variations in Cynipid Species Richness among Oak Taxa

Studies on cynipid faunas associated with American oaks show that hosts with greater geographic ranges support richer cynipid communities (23, 24). There is also some evidence of variation among oak taxa at the section level; among Californian oaks, section *Quercus* oaks support a greater cynipid richness than section *Protobalanus* oaks, which in turn support more than section *Lobatae* oaks (23). Studies of cynipid faunas in oak hybrid zones have shown that gall wasps are highly sensitive to levels of introgression between host species (19, 72), but the underlying cause of such variation remains unknown. Finally, there is evidence

that cynipid richness is higher for oak species with higher levels of tannins, perhaps because high-tannin hosts support cynipid diversity through reduction in the mortality inflicted by fungi (135, 150).

Invading Oak Cynipids

There are at least three independent examples of enhancement in regional cynipid species richness that have resulted from human activity. Two cases represent introductions of individual species that are significant because they affect economically important hosts. Introduced European cork oak, *Quercus suber*, in California has been colonized by a European cynipid, *Plagiotrochus suberi* (16), and chestnut (*Castanea*) in Japan and North America has been colonized by *Dryocosmus kuriphilus*, a native of China and Korea (70, 74, 86). The most significant example of cynipid range expansion is associated with human dispersal of *Quercus cerris* in Europe. This section *Cerris* oak is native to Italy, the Balkans, and Asia Minor and is the host for one or both generations of a wide diversity of cynipids (69, 128). The natural distributions of all European section *Cerris* oaks correspond closely to glacial refugia for oaks during the Pleistocene ice ages, and following the retreat of the ice sheets, only oaks in the section *Quercus* (particularly *Q. robur* and *Q. petraea*) escaped the refugia and recolonized northern Europe (128). As a result, no cynipids dependent on *Q. cerris* (or any other section *Cerris* oak) for one or both generations in their life cycle occur naturally in northern Europe.

Over the past 400 years *Q. cerris* has been planted widely north and west of its native range (131), creating a mosaic of *Q. cerris* patches within the natural distribution of section *Quercus* oaks. At least nine cynipids have subsequently invaded northwestern Europe, including five host-alternating *Andricus* species (*Andricus ambiguus*, *Andricus gemmea*, *Andricus kollari*, *Andricus lignicola*, and *Andricus quercuscalicis*), three species currently thought to be wholly dependent on *Q. cerris* (*Andricus grossulariae*, *Aphelonyx cerricola*, and *Neuroterus saliens*), and two whose dependence on *Q. cerris* has yet to be demonstrated (*Andricus aries* and *Andricus lucidus*) (41, 113, 130, 131, 151). *A. ambiguus*, *A. aries*, *A. lignicola*, *A. lucidus*, *A. quercuscalicis*, and *A. cerricola* all reached Britain between 1950 and 2000, 2000 km from the nearest natural *Q. cerris* stands, apparently without direct human assistance. *A. kollari* has spread naturally across most of northern Europe but was also deliberately introduced into Britain from the eastern Mediterranean in the first half of the nineteenth century (12, 128). Range-expanding cynipids have proved to be valuable model systems for studies on the recruitment of communities of natural enemies, discussed in detail below.

CYNIPID LIFE CYCLES

Oak cynipids and their Pediaspidini sister group are rare examples of cyclical parthenogenesis (or heterogony) in higher animals (12, 41, 52, 97a). Heterogony involves alternation between sexually and asexually reproducing generations, and

outside the oak cynipids it is known only from six other taxa—monogonont rotifers, digenean trematodes, cladoceran crustaceans, and three insect lineages: the cecidomyiids (Diptera), adelgids and aphids (Homoptera); and one species of beetle (Coleoptera) (52, 73). In most cyclically parthenogenetic animals, including aphids and cladoceran waterfleas, reproduction is predominantly asexual, with a single sexual generation each year triggered by a change in environmental conditions (52, 73; but for an exception see 132). Cyclical parthenogenesis in oak cynipids is unusual in that the two reproductive modes are strictly alternating, and there is just a single generation of each per year. Although there are exceptions, oak cynipids also commonly complete a sexual-asexual cycle in a single year and are effectively bivoltine (12). Bivoltine life cycles have evolved several times in the Aylacini [e.g., *Aulacidea pilosellae*, *Xesrophanes potentillae* (41)]. It is not yet clear whether the two-generation life cycles of Cynipini and Pediaspidini are derived from such a bivoltine Aylacine ancestor. Oak cynipid life cycles represent the most complex end of a spectrum in gall wasps, and we now place them in the context of gall wasp life cycles as a whole.

Life Cycles of Herb and Rose Gall Wasps

The life cycles of many rose and herb gall wasps consist of a single sexually reproducing generation each year. In common with most other Hymenoptera, sexual reproduction in these gall wasps is by facultative (or generative) arrhenotoky (21, 134): Unfertilized eggs develop into haploid males and fertilized eggs develop into diploid females (haplodiploidy). Secondary loss of males is widespread in rose and herb gall wasps (41, 91), and in these cases females produce homozygous diploid daughters by parthenogenesis from unfertilized eggs (126, 127). Recent works suggest that the probable cause of parthenogenesis in these gall wasps is infection by the endosymbiotic bacterium *Wolbachia* (90, 91). In a range of Hymenoptera, *Wolbachia* infection causes gamete duplication following meiosis, such that all offspring are homozygous and diploid (21, 90) and therefore all female. Although the causal relationship between obligate parthenogenesis and *Wolbachia* infection has yet to be demonstrated in these gall wasps, in all cases that have been examined *Wolbachia* infection is correlated with loss of males (90, 91).

Alternation of Generations in Oak and Sycamore Gall Wasps

The complex alternation of generations in the Cynipini and Pediaspidini has been revealed only by detailed rearing experiments [particularly by Roger Folliot (41)] involving the tracking of the offspring of individual females for several generations. The life cycle structure shown for *Neuroterus quercusbaccarum* in Figure 2a has been demonstrated for several European members of the genera *Andricus*, *Cynips*, and *Neuroterus* and represents the most highly derived state in the Cynipini (12, 41). The life cycle involves two different types of asexually reproducing females—androphores and gynephores (Figure 2a). Androphores produce haploid eggs by meiosis that give rise only to sons, whereas gynephores produce diploid

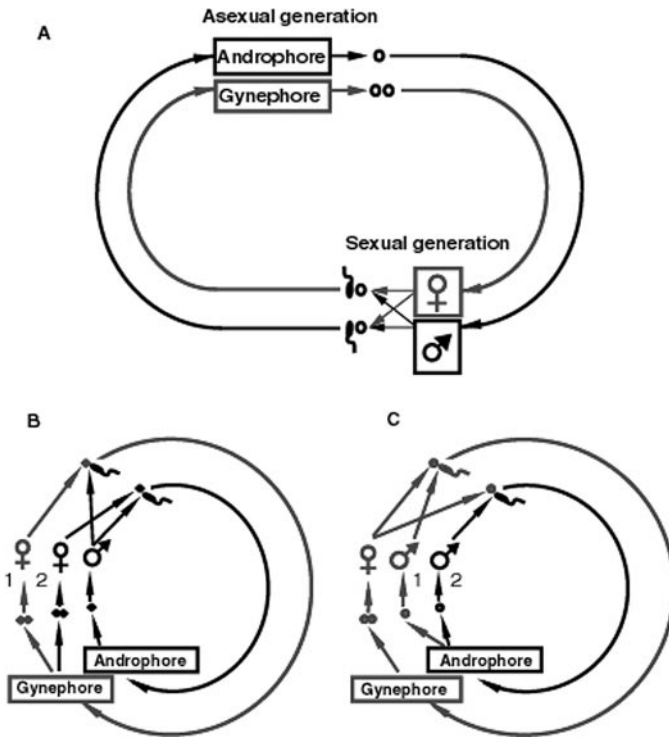


Figure 2 (A) Diagrammatic representation of the life cycle of *Neuroterus quercus-baccarum*, after Folliot (41) and Askew (12). (B, C) Mechanisms for the maintenance of the cynipid life cycle based on (B) two different types of sexual generation female and (C) two different types of male, after Folliot (41).

eggs that give rise only to sexual females (41). Unlike females in arrhenotokous life cycles, the sexual generation females cannot produce sons from unfertilized eggs and must mate to produce the next generation of asexual females. The sexual females can also be divided into two types: one that produces only androphores, whereas the other produces only gynephores. The sycamore gall wasp *Pediaspis aceris* and several oak gall wasps (the best studied is *Biorhiza pallida*) deviate from this life cycle, and its generality should not be assumed.

1. *B. pallida* and some *Andricus* species show departures from the androphore/gynephore dichotomy and produce both males and females from unfertilized eggs (deuterotoky) (134). In most cases, the departure from producing offspring of a single sex is slight, but some asexual females of *B. pallida* (termed gynandrophores) produce males and females in a ratio close to 1:1 (13, 41).
2. In contrast to the life cycle shown in Figure 2a, the sexual generation females of *P. aceris* and *B. pallida* produce small numbers of viable offspring without

mating. These offspring are not haploid males (as they would be in typical hymenopteran arrhenotoky) but diploid asexual females (41).

3. Finally, a proportion of the sexual generation females of *B. pallida* and *Andricus quercusradicis* mated to a single male gives rise to both androphores and gynephores (41).

The genetic mechanism underlying cynipid heterogony remains completely unknown. Explanatory hypotheses fall into two types: those involving the genesis of two types of sexual female by gynephores (Figure 2*b*) and those involving the genesis of two types of male by androphores (Figure 2*c*; 41). For two genotypes of sexual female to be generated by a single gynephore, the cytology of egg production must include a process generating genetic diversity in the daughters. In an asexual female, this could only be achieved by automixis from a heterozygous mother (134). Recent population genetic work on *B. pallida* and *Andricus curvator* shows, however, that in these species the offspring of a single gynephore are genetically identical and are produced not by automixis but by clonal apomixis (13, 13*a*), arguing against this proposal. The second hypothesis (Figure 2*c*) assumes that all sexual generation females potentially produce either gynephores or androphores and that the type of asexual offspring a female actually generates depends on which of two possible male types mate with her (41). This hypothesis predicts that matings between a range of virgin females and the same male should all give rise to the same type of asexual female—a conclusion supported by experiments involving *A. kollari* (41).

The original mechanism proposed to explain these data envisaged a locus for which gynephores and sexual females were obligately homozygous, but for which androphores were obligately heterozygous (41). This proposal was based on the view that gynephores reproduce by a form of automictic gamete duplication that can give rise only to homozygous offspring (41). In contrast, androphores must produce haploid sons by meiosis, and if heterozygous they would inevitably give rise to the two types of male required in Figure 2*c*. Although an elegant explanation, available evidence suggests that sexual females are not produced by automixis. In *B. pallida* and *A. curvator*, daughters of a single gynephore are always genetically identical but can be heterozygous (13). This is incompatible with gamete duplication and instead implies clonal apomixis (13, 134). Folliot's data remain the most detailed experimental analysis of oak cynipid life cycles, and revealing the underlying mechanism remains one of the most interesting and least studied aspects of cynipid biology.

The Duration of Cynipid Life Cycles

In most oak gall wasps the sexual generation gall (the gall containing the sexual generation) develops in the spring or early summer, whereas the asexual generation gall develops through the summer and autumn of the same year. Asexual generation females emerge from their galls in autumn and lay eggs that remain dormant until the following spring or overwinter in the gall. There are many deviations from this

general pattern, and most cynipid species show considerable plasticity in response to environmental fluctuation (112, 117). Many cynipids have life cycles in which the asexual generation obligately or facultatively requires more than one year to develop (e.g., *B. pallida*) (12), whereas in others the sexual and asexual generations each take a year [e.g., *Andricus albopunctatus* (41)]. In *A. albopunctatus* and similar species the galls of both generations are often found together, representing two cohorts a year out of phase. Unless the life cycle is occasionally completed in a single year, these cohorts are effectively discrete sets of genotypes. In *A. kollari* the life cycle is annual in the south of its range (Asia Minor and southern Europe) (41, 128) but takes two years in northern Scotland (117). Within Britain, there is a gradual south-to-north increase in the proportion of individuals taking two years to develop (117). As for *A. albopunctatus*, in the north of its distribution, sexual and asexual generation galls of *A. kollari* present in the same year belong to cohorts a year out of phase.

EVIDENCE FOR LOSS OF SEX FROM CYNIPID LIFE CYCLES

Many oak cynipids are known only from a single generation (69, 77), and in the majority of cases the known generation is asexual. This raises the question of whether some or many oak cynipids have lost the sexual generation from their life cycle and have become obligately parthenogenetic. Secondary loss of sex has occurred in five of the six taxa of cyclically parthenogenetic animals, repeatedly in some groups (52, 61, 73, 123), and is thus perhaps to be expected in oak cynipids. To date, ability to bypass the sexual generation has been demonstrated experimentally for only three oak cynipids. *Plagiotrochus suberi* is a European oak cynipid that is cyclically parthenogenetic in Europe but obligately parthenogenetic as an invader in North America (16). *Andricus targionii* is a wholly parthenogenetic species from eastern Asia, and it is the only purely parthenogenetic species at least partly in sympatry with its probable cyclically parthenogenetic ancestors (1). *Andricus quadrilineatus* is a European species that may represent an intermediate step in the loss of the sexual generation (41), with asexual females that produce both sexual and asexual offspring. The impact of *Wolbachia* in the life cycles of rose and herb cynipids raises the question of whether this symbiont could play a role in loss of sex in oak gall wasps. Although some oak cynipids are infected with *Wolbachia*, in contrast to rose and herb cynipids, the infected populations still produce males (102). The phenotypic impact of *Wolbachia* in oak cynipids remains unknown.

Demonstration that oak cynipids can sustain purely asexual life cycles raises the question of how many of the species known only from parthenogenetic generations are genuinely obligately parthenogenetic. Until recently, rearing experiments have been the only technique available to resolve this issue (e.g., 41, 62, 97). This approach is extremely time-consuming, labor intensive, and difficult to apply to whole communities. Two alternatives, based respectively on population genetic

analysis and DNA sequencing, provide alternatives applicable to large numbers of species.

First, analysis of gene frequencies in population data can detect signals of sexual reproduction in apparently purely parthenogenetic taxa. Wholly parthenogenetic populations lack genetic recombination among alleles and also inherit their chromosomes as entire sets (134). These processes are predicted to lead, respectively, to departures from Hardy-Weinberg and linkage equilibrium (13, 123, 133). Taxa that show no significant departure from these genetic equilibria are thus unlikely to be purely parthenogenetic and more likely to possess a cryptic sexual generation. Analyses of allozyme data for all seven putatively asexual European *Andricus* species studied to date have revealed cryptic sexual generations in this way, confirmed in one case by collection of the sexual generation female (13, 97, 128).

Second, DNA sequencing can be used to match previously unpaired sexual and asexual generations sharing identical sequence (J.M. Cook, A. Rokas & G.N. Stone, unpublished data). Sequencing has also revealed that samples of sexual generation adults thought on the basis of morphology to represent a single taxon in fact contain the previously unidentified sexual generations of several species (J.M. Cook, A. Rokas & G.N. Stone, unpublished data). It is clear that cynipids whose asexual generations may be clearly distinguishable as galls or insects may have sexual generations for which both galls and insects are currently indistinguishable. The consensus from these results is that although cynipids capable of purely asexual reproduction do exist, life cycles in this group should be assumed cyclically parthenogenetic until proven otherwise.

OAK GALL COMMUNITIES

One reason that oak cynipid communities have become one of the model systems in community ecology is that they are well defined and closed, although not necessarily simple (10). Although some inhabitants are opportunists, most are obligately associated with cynipid galls either as inquilines or as parasitoids. Oak cynipid galls support a taxonomically diverse but well-structured community with the oak tree as primary producer, the gall wasp(s) and inquilines as grazers, and parasitoid, predators, and fungi as natural enemies.

The Composition of Cynipid Gall Communities

In addition to the gall-inducing cynipid, these communities generally contain the following components.

INQUILINES Inquilines in oak cynipid galls belong to two groups. The cynipid inquilines (tribe Synergini) feed only on gall tissue. Although unable to induce their own gall, they have some ability to modify the plant tissue that immediately surrounds them (20, 103, 104). Cynipid inquilines either induce their larval

chambers in peripheral gall tissue (nonlethal inquilines) or develop within the gall inducer's own larval chamber, smothering it in the process (lethal inquilines) (12). The second inquiline group includes a range of moths whose larvae feed predominantly on gall tissue (3, 4, 35, 113). The larvae of these moths often kill the gall inducer, perhaps to prevent the lignification of gall tissues associated with gall maturation.

PARASITIDS The true parasitoids all depend on an insect host as their main or only food source, and most of those found in cynipid communities are found only in cynipid communities. *Eupelmus urozonus* and *Macroneura vesicularis* are exceptions and attack a range of endophytic hosts from a number of orders. A few [*Sycophila biguttata*, *Sycophila flavicollis*, *Torymus auratus* (= *nitens*), *Mesopolobus sericeus*, *Aulogygnus skianeuros*] have been reported to occasionally attack cynipid galls on plants other than oak (usually *Rosa*), whereas the majority find hosts in the galls of a more or less extensive range of oak cynipid species. Few parasitoids are restricted to just one type of oak gall. Most of the parasitoids in oak cynipid galls are idiobionts as solitary ectoparasitoids, whereas endoparasitoids, such as *S. biguttata*, and gregarious species, such as *Baryscapus berhidanus*, are rare (10, 113).

PREDATORS In addition to the inquiline Lepidoptera discussed above, other Lepidoptera may cause high mortality in leaf galls by consumption of the host leaf and/or gall tissue. An example is the virtual extinction of three *Neuroterus* species at a site in Denmark due to consumption of their leaf galls during an outbreak of a defoliating caterpillar (33). A range of vertebrate predators are known to extract cynipid larvae from their galls. Woodpeckers and rodents can open even large and heavily lignified galls, whereas smaller insectivorous birds can cause significant mortality in smaller thin-walled galls (29, 117). Vertebrate predation has yet to be studied in detail in many oak cynipid galls, and it is possible that it has a more important role in the population dynamics of cynipids and the evolution of gall traits (6).

FUNGI Fungi may be important sources of mortality in cynipid galls (135, 150). Plant tissues are commonly occupied by a range of fungi (termed endophytic) whose hyphae grow through plant tissues without symptoms in the host. The endophytic fungus *Discula quercina* (Coelomycetes) has been shown to cause almost 100% gall wasp mortality in artificial infection experiments (150). It has been proposed that cynipids and other endophytic insects minimize contact with such potential causes of mortality by occupying plant regions that maintain low levels of endophyte infestation ("low-endophyte space") (150). Suppression of fungal infestation has also been proposed as a selective advantage for high-tannin levels in oak galls (135). Fungi may have a benign role in other insect galls (142).

The Significance of Gall Structure for Cynipid Gall Communities

Cynipidae are probably unmatched in the structural sophistication and diversity of their galls. Although enormously varied in form, position on the tree, and season of growth, each generation of each species has highly characteristic gall traits. Several authors have suggested that this diversity may be best explained by the enemy hypothesis, i.e., that diversity has evolved in response to selection for exclusion of natural enemies (enemy-free space) (95, 96, 129). There is good reason to believe that gall traits should be sensitive to selection imposed by natural enemies. Natural enemies can inflict high mortality in cynipid galls (12, 88, 114, 115, 130), and gall tissues mediate all interactions between the cynipids and their natural enemies. In all groups studied to date, gall traits are determined largely by the gall inducer (28, 81, 129), and gall traits that confer protection against attack by natural enemies should spread through natural selection. Much of the current interest in insect gall research is centered on the role of gall traits in mediating tritrophic interactions between the plant, the gall inducer, and its natural enemies (6, 88, 94, 143).

Circumstantial support for the enemy hypothesis in oak cynipids is provided by the fact that a number of traits of potential defensive value have evolved repeatedly in independently evolving lineages (129). Examples include spines, sticky coatings of resin, internal airspaces, and larval chambers that roll freely within a hollow gall (Figure 1*b*). However, the fact that many parasitoids and inquiline attack a wide structural diversity of host galls suggests that no gall structure provides an absolute refuge in the present. Although parasitoids may not be wholly excluded, it remains possible that specific gall traits reduce the mortality inflicted by specific community members. We summarize evidence for the impact of a range of gall morphological traits on parasitoid communities. We then comment on factors other than gall morphology that might affect parasitoid communities and discuss the overall effect these factors have in the gall wasp–parasitoid/inquiline system.

Nectar Secretion

Nectar secretion has the clearest demonstrated significance of any oak cynipid gall trait for protection against natural enemies. Oak cynipids in the genera *Andricus* (2), *Disholcaspis* (40, 120, 140), and *Dryocosmus* (129) induce galls that secrete nectar and recruit ants. Four independent studies have demonstrated that ants significantly reduce parasitoid and inquiline attack on these galls (2, 40, 120, 140).

Gall Toughness

Tougher galls are thought to be harder to attack than softer galls because of the physical difficulty of drilling into tougher galls with an ovipositor and because of the risk of predation associated with prolonged oviposition (107). Two parasitoids of some of the toughest galls, *Ormyrus nitidulus* and *Torymus auratus* (= *nitens*), have particularly high concentrations of manganese in the valvae of the ovipositor

(99). This is associated with increased toughness of chitin and may be an adaptive response to gall hardness. Tough outer gall structures may also be important in excluding lepidopteran larvae (4).

Gall Wall Thickness

Studies of intraspecific variation in gall structure in a range of systems show that parasitoids are restricted to attacking larvae within reach of their ovipositor and that larvae in thicker-walled galls on average suffer a lower rate of parasitoid attack (6, 26, 54). In oak cynipid galls, parasitoid species such as *Torymus flavipes* (= *auratus*) have different ovipositor lengths in their two annual generations, which correlate with the gall wall thickness of their respective host galls (9). That parasitoid species can act as a selection agent for gall size has been demonstrated particularly well for the gall-inducing Tephritid fly *Eurosta solidaginis*. Here gall size is a reliable indicator of host quality, and parasitoid species select gall sizes according to the host size they require for successful development (6). This effect of wall thickness may explain why cynipid larvae do not start to grow until the gall wall is fully developed (see above): If parasitoids halt host growth on oviposition, such a strategy would exclude larger short-oviposited parasitoid species through resource limitation (144).

The Number of Larval Chambers per Gall

There is growing evidence that multilocularity (many larval chambers in a single gall) (Figure 1b) may represent a strategy associated with protecting larvae from parasitoid attack through induction of a larger gall (6, 56, 129). Though larvae in peripheral chambers remain vulnerable, those deeper within the structure are protected by a thicker shield of gall tissue and other larval chambers (54). A similar effect has been observed for inquiline larvae that develop as multiple larvae within a host gall. The inquiline larvae induce increased thickness of host gall tissues, and the more larvae there are, the thicker the gall wall (8, 20, 60, 122, 144).

Additional Morphological Traits

Further morphological characters that might affect parasitoid attack have been suggested, although their effectiveness has not yet been tested (Figure 1b). (a) Coatings of sticky resins have evolved repeatedly in oak cynipid galls (129). These may prolong parasitoid oviposition and therefore increase their risk of predation to the gall inducer's benefit (107). (b) Many galls change color during development, normally from green to red. The extent to which the cynipid larva controls pigment synthesis remains unknown, but there is evidence that parasitoid females recognize color and use it in assessment of host quality (7, 30). (c) Coatings of hairs and spines of a range of lengths and densities have also evolved repeatedly in oak cynipid galls. Dense coatings of fine hairs or spines might influence parasitoid attack, whereas more open arrays of stout spines are probably more effective deterrents for vertebrate predators. (d) Many oak galls contain airspaces between

the larval chamber and outer gall tissues, another trait that has evolved repeatedly (129). An airspace means that the ovipositor of an attacking parasitoid is unsupported for part of its length, which reduces the force that a parasitoid can exert with the tip of its ovipositor without buckling (98). Having traversed such an airspace, an ovipositor has to penetrate the thin layer of sclerenchyma surrounding the larval chamber—often the toughest tissue in the gall. Only parasitoid species that possess a particularly toughened ovipositor are likely to be able to penetrate the sclerenchyma in such galls.

Impacts of Nonmorphological Traits of Cynipid Galls on Parasitoid Communities

Host plant taxon, gall location on the host plant, and the time required for gall development are all thought to affect parasitoid species richness (88, 89, 112–114, 124). For example, the sexual generation galls of *Neuroterus quercusbaccarum* can develop either on leaves or on catkins, and after a period of growth they fall from the tree to mature on the ground. Parasitoid attack rates and species richness were lower in galls developing on catkins than in galls developing on leaves (88). However, in this case, the galls in different locations also have different phenologies (galls on catkins are shed earlier), so the effects of gall location and time taken to develop cannot be separated.

Variation in Community Structure within and among Cynipid Species

Although most parasitoids and inquilines associated with oak galls are common to several or many host cynipids, there is variation in the species richness and diversity of communities both within and among host species. What generates such variation?

As discussed above for *Neuroterus quercusbaccarum*, variation in gall location for a single generation may have significant consequences for the associated communities (88, 89). Work on *Andricus quercuscalicis* illustrates two further aspects of community variation found within species.

SPATIAL AND TEMPORAL VARIATION IN THE COMMUNITY ASSOCIATED WITH A SINGLE GENERATION *A. quercuscalicis* is an invader in Western Europe (described above) and has established populations along a 2000-km invasion route from the Balkans to Britain and Ireland (113, 114, 131). This demographic history allows examination of the development of the communities of parasitoids recruiting to this novel host in its invaded range and of spatial patterns along the invasion route. The most detailed data have been collected for the “knopper” galls of the asexual generation (112–115). In Britain, the asexual generation galls remained virtually free of parasitoid attack from the invader’s arrival in the late 1950s until the early 1980s. New species slowly recruited to the community, and levels of parasitism remained low for the next 10 years. Between 1990 and 1995, colonization of the

asexual generation galls by inquiline *Synergus* species provided additional hosts for parasitoids and triggered a sharp increase in the abundance of some parasitoid species (114, 115).

A. quercuscalicis populations closest to the native range have been established for the longest time, and sampling along the invasion route provides snapshots in the development of the community associated with this host. Initially there was a decline in asexual generation community species richness along the invasion route (113, 115), with parasitoid communities in the invaded range forming a subset of those recorded from the native range (113). Over time, within limits imposed by the size of the local pool of parasitoid species, the community richness in native and invaded ranges has converged (Figure 3). The same general pattern is true for the sexual generation galls (116, 130). The convergence of the parasitoid faunas in the invaded and native ranges, despite differing environmental conditions and resident cynipid faunas, suggests a strong link between gall attributes and parasitoid community composition, species richness, and abundance.

DIFFERENCES AMONG HOST GENERATIONS The galls induced by the two generations of *A. quercuscalicis* differ in several respects. The sexual generation gall is thin walled, 1–2 mm long, and develops very rapidly on the catkins of

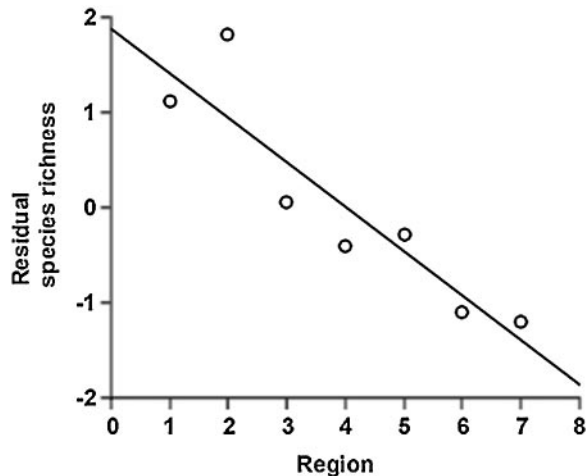


Figure 3 The geographic gradient in parasitoid species richness associated with the asexual generation galls of the invading gall wasp *Andricus quercuscalicis*. The values shown are residuals having controlled for variation in sample size. The seven regions along the x-axis are in order of increasing distance from the native range: 1, Native range; 2, Italy; 3, Germany; 4, France and Benelux; 5, Britain (region with high-inquiline abundance); 6, Britain [region with low-inquiline abundance (see 116)]; and 7, Ireland. The line is fitted by hand to show the general trend.

Quercus cerris. In contrast, the asexual generation gall has a thick woody wall, reaches a diameter of up to 20 mm, and develops over several months on the acorns of *Q. robur*. These differences have two major consequences for the associated communities: (a) The asexual generation galls develop through a clear sequence of structural stages, and the parasitoids attacking this generation form a successional series associated with increasing host size from small species with short ovipositors to larger species with long ovipositors (113). In contrast, the rapid development of the sexual generation galls prevents such temporal structuring of parasitoid attack. (b) The asexual generation galls are attacked by several inquiline *Synergus* species, but the far smaller sexual generation galls never harbor inquilines, perhaps because they develop too rapidly to allow development of secondary inquiline larval chambers.

Despite the major differences in host gall properties, in its native range the two generations of *A. quercuscalicis* support equally rich communities: 12 species in the sexual generation (all parasitoids) and 13 in the asexual generation (10 parasitoids, 3 inquilines) (113, 130). A difference is that in the asexual generation only 4 of the 10 parasitoids feed predominantly on the gall wasp larva (the rest attacking inquilines), whereas in the sexual generation all of the parasitoids attack the gall wasp or other parasitoids (113, 130). Only a single parasitoid is common to the communities of both generations, and this occupies a different role in each. In the sexual generation gall, the parasitoid *Cecidostiba adana* attacks the gall wasp larva. In the asexual generation this parasitoid attacks only inquilines in the outer wall of the gall, probably because at the time *C. adana* attacks, the gall wasp larva is beyond the reach of its short ovipositor. A final difference between the two communities is that across the range of *A. quercuscalicis* the mortality inflicted by parasitoid attack is far higher in the sexual generation (20–45%) than in the asexual generation (5–15%) (45, 46, 113, 130). Although the reasons for this difference are probably complex, it is tempting to suggest that the thin-walled sexual generation galls are more vulnerable to attack by a rich assemblage of small, short-oviposited parasitoids than the asexual generation galls. The differences in size and phenology between the galls induced by the two generations of *A. quercuscalicis* are shared with other *Andricus* species and the members of other cynipid genera (69, 146–148). Although detailed studies have been made of both generations of few species (see also 8, 11), differences across host generations are probably a common feature of oak cynipid communities.

The basis of variation in the communities associated with sympatric gall wasp species remains little understood. A major difficulty in comparative analyses is variation in sampling effort among host species and generations, many of which are rare or cryptic. Existing data for European oak cynipids support the general conclusion that hosts occupying structurally similar galls that develop on the same part of the same host plant at the same time will share community members (8, 11, 118). The impact of the shared parasitoids may vary substantially across alternative hosts, and a major goal of current work on cynipid communities is the analysis of such impacts using quantified food webs (109). The significance of

interspecific variation in gall structure and location for parasitoid attack remains unknown and awaits detailed study of parasitoid behavior.

TRITROPHIC INTERACTIONS IN OAK CYNIPID GALLS

A long-standing question in studies of the interactions among plants, herbivores, and their natural enemies is how does the system persist, which trophic level drives the population dynamics of the system? Are the main effects imposed from higher trophic levels downwards (top-down) or from lower trophic levels upwards (bottom-up) (50, 51, 66)? Evaluation of whether top-down or bottom-up effects regulate cynipid population dynamics requires assessment of many parameters (random effects, scale-dependent effects, auto- and cross-correlations), and to our knowledge no data set exists that would meet the requirements for such an analysis. However, beyond the question of population regulation, assessment of whether specific factors influence population fluctuations in a density-dependent manner is possible and requires fewer parameters to be assessed and quantified (50). An additional consideration in cynipid population dynamics is that a number of species show evidence of population cycling over time scales ranging from 2 to 7 years (27, 43, 70, 118, 122). Are such cycles real? If so, what maintains them and generates the diversity in their periods? Here we discuss the cynipid–natural enemy and cynipid–host plant interactions in turn.

INTERACTIONS BETWEEN CYNIPIDS AND NATURAL ENEMIES

Natural enemies commonly cause high mortality in gall wasp populations (88, 89, 117, 124, 130, 141). However, few of the many studies on parasitoid attack in cynipid galls have reported significant top-down effects [or influences *sensu* Hassell et al. (50) because none of the studies were designed to assess population regulation]. A number of studies specifically designed to establish the magnitude of top-down interactions have also failed to find significant effects (45, 46).

The only continuous time series of reasonable length available on gall wasp population densities and parasitoid attack is for *Dryocosmus kuriphilus*, the chestnut gall wasp. This species became a pest of chestnut (*Castanea*) in Japan following accidental introduction from China. Native parasitoids failed to regulate *D. kuriphilus* populations, and a parasitoid that is a natural enemy of this host in its native range (*Torymus sinensis*) was deliberately introduced to Japan (83). *T. sinensis* inflicted density-dependent mortality on *D. kuriphilus*, and within a few years had reduced Japanese population densities of the pest considerably. This example suggests a strong top-down effect in the dynamics of *D. kuriphilus* (70, 74). This example may be a special case in that a normally generalist parasitoid, *T. sinensis*,

acted as an effectively monophagous species on a superabundant host. It raises the question of whether the same parasitoid would act in a similarly density-dependent manner when in a community of multiple hosts (53).

Another case of top-down effects has been reported from North America, where populations of the oak cynipid *Xanthoteras politum* were apparently driven to extinction by two lethal inquiline species, *Periclistus* sp. and *Synergus* sp. (141). This is a top-down effect in a loose sense only because unlike a parasitoid-host relationship, there is no trophic link between the gall inducer and the inquiline. *X. politum* is an early colonist and transitional species, inducing galls on regrowth shoots in areas that have recently been burnt. This species displays a metapopulation dynamic in which frequent long-distance dispersal allows it to escape high mortality inflicted by the inquilines in individual patches. Further examples that suggest top-down effects have been reported from other cynipid and noncynipid gall systems (32, 106).

However, two extremely detailed studies have failed to find uniformly top-down or bottom-up effects. One study of survivorship in the asexual generation galls of *Cynips divisa* in Britain is particularly important because it considered both the interactions between individual gall inducers mediated by the host plant (discussed under competition below) and the consequences of attack by parasitoids and lethal inquilines (43). Over seven years of sampling, percentage survival of the asexual generation leaf galls of *C. divisa* ranged between 0 and 50%, but path analysis failed to identify any dominant top-down or bottom-up effects (43).

A second study (45, 46) examined the population dynamics of an invading gall wasp in Britain, *A. quercuscalicis*. In particular, the study looked for evidence of spatial-density dependence in parasitoid attack on the galls of the sexual generation with a view to understanding patterns of patch exploitation by the parasitoid species. The sexual generation galls of *A. quercuscalicis* develop on catkins, a resource patchily distributed within the canopy of the host tree (20a). Parasitoid attack rates of these galls were analyzed in relation to host densities across a hierarchical series of spatial scales, from catkins within twigs (terminal 2 years' growth of a shoot), through twigs within branches, to trees within sites, and found no overall pattern in mortality (45, 46). Significant density dependence was found in only 20% of cases, and relationships within and among spatial scales ranged from positive-density dependence through density independence to negative-density dependence (45, 46). Seventy percent of the significant cases of density dependence were negative, a result taken to indicate that local parasitoid populations may be limited in their exploitation of high host densities by egg limitation (46). In order to assess whether the absence of consistent patterns was due to the recent arrival of *A. quercuscalicis* in Britain, patterns of mortality in the same generation were also studied in Austria and Hungary, in the species' native range. Although the parasitoid community in the native range was far more species rich, the magnitude and sign of spatial-density dependence was as variable as in Britain (46, 130; G.N. Stone & K. Schönrogge, unpublished data), which suggests that such variation is a general feature of this system. It has been pointed out that density-independent

variation in parasitoid attack rate (as characterized for the sexual generation of *A. quercuscalicis*) is sufficient to let otherwise unstable model populations of hosts and parasitoids persist and that it is not necessary for regulation to occur at all places or at all times to allow persistence (46, 49a, and references therein). In discussing the issue of density dependence, it is also important to appreciate that two forms of density dependence (temporal and spatial) can affect populations and that the relationship between them is not simple. In particular, environmental stochasticity or variability in resource supply in bottom-up-controlled species can obscure temporal-density dependence, whereas within-generation spatial-density dependence remains detectable (49a). In galling systems in general (and cynipid galls and their parasitoids in particular), plant-galler interactions might well introduce additional heterogeneity that is unaccounted for in studies only of the distributions and attack rates of the species involved and which could obscure both temporal- and spatial-density-dependent relationships.

The arrival of four host-alternating *Andricus* species (*A. ambiguus*, *A. kollari*, *A. lignicola*, and *A. quercuscalicis*) in Britain represents a convenient, large-scale natural experiment in which the impact of a group of new hosts on each other and on the native cynipid community can be assessed (109). The four species have spread through Britain to different degrees, creating zones containing 4, 3, 2, or 1 invaders in a south-to-north gradient. Both generations of all four invaders and native cynipids were sampled over several years. Both generations of all four invaders were attacked by native parasitoids and (in the asexual generation galls only) inquilines, many of which were shared among the communities of invading and native cynipid species. If shared parasitoid species act in a density-dependent manner, one would expect them to mediate indirect interactions among the hosts (apparent competition) (53, 109). Quantified webs were used to summarize indirect interactions between gall wasp species through all shared parasitoids (75, 108, 109), but no strong interactions were identified. However, the invaders had significant effects on local parasitoid populations (109, 117). Several parasitoid species showed significant host shifts from native to invading cynipids. One consequence of such a shift was that where the size of the invading host allowed only male offspring of a given parasitoid species to develop, the sex ratio of its local population became male biased (118).

One of the invaders, *A. kollari*, provides an example of bottom-up impacts on parasitoid and inquiline populations associated with life cycle variation. In Scotland *A. kollari* has a two-year life cycle, with two cohorts running a year out of phase with each other. The population densities of each generation also vary over a two-year life cycle, with one cohort far more abundant than the other. This has a dramatic impact on the dynamics of parasitoids and inquilines attacking *A. kollari*. Parasitoids and inquiline populations appear limited by resource availability (*A. kollari*) in the low-abundance years. A potential solution for parasitoids and inquilines is the adoption of a similar two-year life cycle, but there is no evidence for this to date. This example illustrates the value to the gall inducer of disrupting the coupling of host–natural enemy dynamics and may explain in part

why a high proportion of the asexual generation larvae of a wide range of cynipids show diapause for periods ranging from 1 to 8 years (29, 45, 76, 112).

In summary, clear evidence for top-down and bottom-up effects between cynipid gall wasps and their parasitoids and inquilines have only been found in somewhat extreme and/or artificial situations (biocontrol using an introduced parasitoid species and populations where the host shows an extreme type of phenology for that species). The majority of studies, whether explicit single-host studies (43) or whole-community studies summarizing interactions between hosts over all natural enemies (109), have been inconclusive.

INTERACTIONS BETWEEN CYNIPIDS AND HOST PLANTS

Gall inducers generally require specific host tissues at specific developmental stages, and there is abundant evidence that cynipid oviposition and subsequent gall development can be sensitive to host attributes including genotype, age, size, phenology, and nutritional status (12, 33, 34, 87, 125). Timing and site of oviposition are crucial to successful gall development in many other gall inducers (143, 149). However, because little is known about the mechanism of cynipid gall induction (47), it is currently difficult or impossible to quantify variation in potentially crucial host plant characteristics. Although studies to date assess secondary effects, i.e., galls induced, and correlate those with plant traits, density-dependent effects involving egg mortality (and so gall induction) may go unnoticed (see also the discussion on resistance below).

Existing studies provide at least suggestive evidence that bottom-up effects are important in cynipid–host plant interactions. In contrast, although there is no doubt that cynipids can harm or even kill their hosts (27, 37, 56, 64), no studies to date show significant top-down effects of gall wasps on the population dynamics of oaks.

The one available time series data set for an oak–cynipid interaction is for the asexual generation of *A. quercuscalicis* in Britain. The asexual generation galls develop on the acorn galls of *Q. robur*, and gall densities, acorn crops, and weather data were recorded for 25 years on 30 individually marked trees (27). Analysis of the acorn crop time series suggested a two-year cycle between high- (mast) and low- (trough) yield years, thought to be due to resource limitations (27). Until 1993, the proportion of acorns galled showed a significant negative-density-dependent relationship with the number of acorns per shoot. This indicates satiation of *A. quercuscalicis* in mast years where galling rates are low and resource limitation in trough years when galling rates were high. This relationship is similar to the bottom-up effect on parasitoid population dynamics imposed by biannual fluctuation in the abundance of *A. kollari*, as discussed above (117). However, in 1993 a mast year coincided with high-galling rates, and the significant relationship was lost (27) (data between 1993 and 2000 show the same negative-density dependence, M.J. Crawley personal communication). Crawley & Long (27) suggested

that disruption of an otherwise uniform biannual cycle in acorn yields might prevent seed predators in general (and *A. quercuscalicis* in particular) from evolving a two-year life cycle, therefore escaping resource limitation during trough years. That this is a risk for oak hosts is supported by the high-phenotypic plasticity in cynipid life cycles (112, 117).

The asexual generation of *A. quercuscalicis* in Britain, where it is a recent arrival, experiences a low rate of parasitoid-induced mortality in contrast to the higher mortality inflicted by natural enemies in its native range (113–115). One might then argue that the bottom-up effect of the oak masting cycle on *A. quercuscalicis* population dynamics is an artifact resulting from its status as an invader. There has been no comparable study of oak-cynipid interactions in the native range of *A. quercuscalicis* with which the results in Britain can be compared. An interesting feature of the *A. quercuscalicis* system is that the high mortality inflicted by parasitoids on the sexual generation galls has had no apparent effect on the dynamics of the asexual generation (27, 45).

Two other plant traits important for bottom-up effects in an increasing number of galler–host plant interactions are plant vigor and plant resistance. Though the importance of these effects has largely been established in noncynipid systems, they are of obvious importance to oak gall wasps. These phenomena are discussed in turn.

Plant Vigor and Host Resistance

The plant vigor hypothesis is based on the suggestion that vigorously growing plant organs reflect high-resource quality for herbivores, and traits that allow ovipositing females to identify such sites should be favored by selection (25). Detectable variation in resource quality could lead to competition for good sites, potentially resulting in density-dependent mortalities. The plant vigor hypothesis makes two predictions: (a) ovipositing females should choose vigorously growing plant organs, and (b) immature stages developing on vigorously growing plant organs should perform better (25).

Of all groups of insect herbivores, these predictions have been tested most extensively on gall inducers, including chloropid flies (137), cecidomyiid midges (36), adelgid bugs (18), tenthrinid sawflies (42, 101), and most recently in cynipids (37, 87). With the exception of the chloropid *L. lucens*, which prefers thin shoots of the reed *Phragmites australis* to more vigorous but possibly better defended shoots (137), all other tests of one or both predictions supported the plant vigor hypothesis. It has been noted that gall inducers could generate similar correlations between resource quality and gall inducer growth by enhancing the quality of gall tissue—a proposal termed the resource regulation hypothesis (84, 93). Although this may apply to larval growth rates, observed preferences of females for high-quality sites are only compatible with the plant vigor hypothesis.

Although there is a general agreement that plant vigor does affect gall densities on plant organs, the most recent studies suggest that plant vigor is only one of a

range of plant traits to affect gall densities. Although predictions of the plant vigor hypothesis are upheld, plant vigor indicators such as shoot length explain only small amounts of the variance in gall densities and show significant interactions with factors such as host plant genotype (42, 84). Work on a range of cynipid systems has shown intrapopulation variation in plant susceptibility to galling (12, 33, 34), but the basis of such variation is unknown. Although gall inducers have considerable if not total control over the physiology of gall tissues once induction is under way, a small but increasing body of work suggests that plants may mount defensive responses that prevent gall initiation.

Resistance to gall induction is best studied in the Hessian fly, *Mayetiola destructor*, which induces galls in wheat and related crops. Host and gall inducer in this system have the only known gene-for-gene correspondence between host plant and herbivore virulence known for any insect-plant relationship (136, 152). Fernandes (39) describes a plant-resistance response to cecidomyiid eggs that involves localized necrosis of surrounding cells and death of the cecidomyiid larva. The symptoms are similar to a plant defense against viral or microbial attack termed the hypersensitive response (HR) (44), but the molecular basis of the response to cecidomyiids is unknown. Such localized cell death around cecidomyiid eggs has been described in *Bauhinia brevipetala* against the gall midge *Contarinia* sp. where it caused >95% mortality in the gall inducer (39). A similar response to cecidomyiids is known on willow, where the response is induced systemically and also involves the local increase in concentrations of phenolic compounds (similar to HR) (O. Ollerstam & S. Larsson personal communication). Possibly related is a response in Norway spruce galled by the adelgid homopteran *Adelges abietis*. Under drought conditions, susceptible clones of Norway spruce produce an as yet unidentified phenolic compound (18) that reduces success rates of gall induction by stem mothers of the adelgid. Although resistance reactions to cynipids galls are currently unknown, avoidance of plant defenses is probably an important component of cynipid gall induction.

COMPETITION AND FACILITATION IN CYNIPID POPULATIONS

Cynipids are potentially exposed to two types of competition: apparent competition mediated by shared natural enemies (53) and direct competition for limiting resources. As described above, the only study to examine apparent competition in cynipids to date (109) found no evidence for significant effects. Nevertheless, where parasitoid attack is density dependent (see *D. kuriphilus* and *T. sinensis* above), apparent competition could still occur.

Limitation in the availability of oviposition sites, or of resources in a particular host organ, has the potential to generate more direct inter- and intraspecific competition in gall inducers (43, 149). An important distinction needs to be made here between interactions among cynipids in different galls and among cynipids within the same multilocular gall. There is evidence for competition between individual

galls, but within individual galls the interaction among the cynipid larvae is more likely to be one of facilitation. We discuss these situations in turn.

Several studies suggest that where many individual cynipid galls exploit resources channeled through the same host organ, there can be intra- and interspecific competition. The most informative study is on the leaf galls of the asexual generation of *C. divisa* (43). The galls develop along the lateral veins on the underside of oak leaves in summer and autumn, and this study examined the impact on three traits (gall size, female fecundity, and survivorship) of gall density on individual leaves and of gall order along an individual vein. Survivorship decreased significantly with increasing gall density, and survivorship, fecundity, and gall size decreased with distance of a gall from the leaf midrib on multiply galled veins. These patterns are consistent with intraspecific competition for limiting resources. An additional tritrophic effect in this system was that smaller galls were more likely to suffer parasitoid and inquiline attack (43).

Many cynipids in all the gall-inducing tribes induce multilocular galls (containing many larval chambers), and the abundance of this trait in many other gall-inducing insects suggests that individuals developing in the same structure need not compete (6). Oak cynipid galls containing a larger number of larvae are themselves larger and heavier, which suggests that the effect on plant investment in gall tissue of multiple larvae is additive (6, 55, 82) rather than competitive. There may, however, be potential for competition between the offspring of different mothers (foundresses) developing within the same multilocular gall. It has usually been assumed that the larvae within a single multilocular gall are the offspring of a single female, but population genetic evidence suggests that this is not always the case (13, 13a). A proportion of the multilocular galls of *B. pallida* and four *Andricus* species (*A. coriarius*, *A. lucidus*, *A. pantelli*, and *A. seckendorffi*) contain the offspring of more than one female (multiple founding). In all cases, the distribution of offspring attributable to different mothers was highly skewed, with one female inferred to be the mother of most of the emergents from a single gall. This pattern suggests two alternative explanatory scenarios. First, females may lay eggs in the same bud in equal numbers, but the eggs of one female come to dominate gall induction, and their development smothers those of subsequent foundresses (as for lethal inquilines). This might well happen if one batch of eggs was laid long enough before the second to initiate gall induction. An alternative noncompetitive hypothesis is that the females contributing smaller numbers of emergents actually laid smaller numbers of eggs. Distinction between these two requires an ability to assess how many eggs are laid in the same oviposition site by each foundress.

A second issue arising from the demonstration of multiple founding is what causes more than one female to use the same site. All species surveyed only gall a small proportion of host buds (13). Are eggs only laid in this small proportion, or are eggs laid in a much larger distribution of buds but fail to induce galls? There is good evidence that oak cynipids have specific oviposition preferences (12, 33). If cynipid requirements for oviposition sites do depend crucially on the state of individual targets, and host organs vary in suitability in an individual host, then (as for the plant vigor hypothesis) female traits allowing recognition of

high-quality sites should have been favored by selection. In this case, multiple founding could result from competition for limited suitable oviposition sites. If this is true, experimental manipulation of the relative density of suitable sites and ovipositing females should result in predictable changes in levels of multiple founding. Again, lack of knowledge of the precise requirements of cynipids makes the design of such experiments extremely difficult.

CONCLUSIONS AND FUTURE DIRECTIONS

Major aspects of the biology of oak cynipids remain dominated by unanswered questions. The cynipid life cycle remains an enigma, and the generality of demonstrated life cycle structures cannot be assumed. We do not know the mechanisms underlying gall induction nor the specificity of cynipid requirements for host tissues. This lack of knowledge makes quantitative analysis of the cynipid–host plant interaction difficult. We also have little idea of the extent to which shared parasitoids mediate interactions between gall inducers or exert selection on gall traits.

Novel approaches are, however, allowing advances in many other areas. Indirect genetic techniques offer the potential for rapid resolution of cynipid life cycles, and early signs are that obligately parthenogenetic species are rare. The same tools have revealed mechanisms of inheritance in cynipid life cycles and hitherto unexpected contributions of multiple foundresses within individual galls. Analysis of differential patterns of gene and protein expression show similarities between cynipid galls and plant seeds, suggesting signaling and developmental pathways for further research. Quantified webs allow assessment of the interactions within and among communities, and the generation of time series data sets allows detailed analysis of temporal dynamics. Much can be learned by application of these same techniques in a wider diversity of oak cynipid systems.

The two key questions in cynipid community biology remain: (a) How are galls induced, and (b) why are they so diverse? Painstaking dissection of the molecular messages exchanged between gall wasp and host is necessary to provide the answer to the first question. The issue of diversity can perhaps be more easily addressed. Generation of quantitative webs for a range of oak cynipids in the same community can be used to assess the mortality imposed on each by a common pool of natural enemies. Combined with a phylogeny for the cynipid species in question, such data would allow analysis of the correlations between gall traits and mortality inflicted and testing of whether parasitoids are currently exerting selection on gall traits. We may know the “why” before we know the “how.”

ACKNOWLEDGMENTS

We would like to thank all those who have helped with comments and ideas throughout the work leading to this review. We dedicate it to Dick Askew and Roger Folliot for the contributions they have made to oak gall wasp biology. We

thank Dr. Gyuri Csóka for use of his photographs in Figure 1. We thank Rich Bailey, Gordon Brown, James Cook, Mick Crawley, Lisa Harper, Jack Schultz, Conrad Lichtenstein, Gil McVean, George Bableves Melika, Jose-Luis Nieves-Aldrey, Olivier Plantard, Antonis Rokas, Fredrik Ronquist, and Csaba Thuróczy for their many thoughts and discussions on the subjects covered in this review. Most of all, we thank all those who have supported us in the field, particularly Gyuri, Ániko, Ági, Bence “the bandit” Csóka, and the Hungarian heroes of forestry. This work was supported by a NERC grant (GR12847) to G.N. Stone and K. Schönrogge, and by two NERC grants, Gst/03/2035 to G.N. Stone and NER/B/S/2000/00658 to K. Schönrogge.

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LITERATURE CITED

1. Abe Y. 1986. Taxonomic status of the *Andricus mukaigawae* complex and its speciation with geographical parthenogenesis (Hymenoptera, Cynipidae). *Appl. Entomol. Zool.* 21:436–47
2. Abe Y. 1992. The advantage of attending ants and gall aggregation for the gallwasp *Andricus symbioticus* (Hymenoptera, Cynipidae). *Oecologia* 89:166–67
3. Abe Y. 1995. Relationships between the gallwasp *Trichagalma serratae* (Ashmead) (Hymenoptera, Cynipidae) and 2 moth species *Andrioplecta pulverula* (Meyrick) (Lepidoptera, Tortricidae) and *Characoma ruficirra* (Hampson) (Lepidoptera, Noctuidae). *Appl. Entomol. Zool.* 30:83–89
4. Abe Y. 1997. Well-developed gall tissues protecting the gall wasp, *Andricus mukaigawae* (Mukaigawa) (Hymenoptera: Cynipidae) against the gall-inhabiting moth, *Oedematopoda* sp. (Lepidoptera: Stathmopodidae). *Appl. Entomol. Zool.* 32:135–41
5. Abrahamson WG, Melika G, Scrafford R, Csóka Gy. 1998. Gall-inducing insects provide insights into plant systematic relationships. *Am. J. Bot.* 85:1159–65
6. Abrahamson WG, Weis AE. 1997. Evolutionary ecology across three trophic levels: goldenrods, gallmakers and natural enemies. *Princeton Monographs in Population Biology* No. 29. Princeton, NJ: Princeton Univ. Press. 456 pp.
7. Askew RR. 1961. A study of the biology of the species of the genus *Mesopolobus* Westwood (Hymenoptera: Pteromalidae) associated with cynipid galls on oak. *Trans. R. Entomol. Soc. London* 113:155–68
8. Askew RR. 1961. On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain. *Trans. Soc. Br. Entomol.* 14:237–68
9. Askew RR. 1965. The biology of the British species of the genus *Torymus* Dalman (Hymenoptera: Torymidae) associated with galls of Cynipidae (Hymenoptera) on oak, with special reference to alternation of forms. *Trans. R. Entomol. Soc. London* 9:217–32
10. Askew RR. 1975. The organisation of chalcid-dominated communities centred upon endophytic hosts. In *Evolutionary Strategies of Parasitic Insects and Mites*, ed. PW Price, pp. 130–53. New York/London: Plenum. 346 pp.
11. Askew RR. 1980. The diversity of insect communities in leaf-mines and plant galls. *J. Anim. Ecol.* 49:817–29
12. Askew RR. 1984. The biology of gallwasps. In *The Biology of Galling Insects*,

- ed. TN Ananthakrishnan, pp. 223–71. New Delhi: Oxford & IBH Publ. 324 pp.
13. Atkinson R. 2000. *The genetic analysis of natural history, reproductive strategy and population structure in European oak gallwasps (Hymenoptera: Cynipidae)*. PhD thesis. Univ. Oxford. 286 pp.
 - 13a. Atkinson RJ, McVean GAT, Stone GN. 2002. Use of population genetic data to infer oviposition behaviour: species-specific patterns in four oak gallwasps (Hymenoptera: Cynipidae). *Proc. R. Soc. London Ser. B*. In press
 14. Bagatto G, Paquette LC, Shorthouse JD. 1996. Influence of galls of *Phanacis taraxaci* on carbon partitioning within common dandelion, *Taraxacum officinale*. *Entomol. Exp. Appl.* 79:111–17
 15. Bagatto G, Shorthouse JD. 1994. Mineral nutrition of galls induced by *Diptolepis spinosa* (Hymenoptera: Cynipidae) on wild and domestic roses in central Canada. In *Plant Galls: Organisms, Interactions, Populations*, ed. MAJ Williams, pp. 405–28. Oxford: Clarendon. 488 pp.
 16. Bailey SF, Stange LA. 1966. The twig wasp of Cork Oak—its biology and control. *J. Econ. Entomol.* 59:663–68
 17. Bellido D, Ros-Farre P, Kovalev O, Pujade-Villar J. 2000. Presence of *Plagiotrochus* Mayr, 1881 in the Himalayan area, with redescription of *Plagiotrochus semicarpifoliae* (Cameron, 1902) comb. n. (Hymenoptera: Cynipidae). *Insect Syst. Evol.* 31:241–45
 18. Bjorkman C. 2000. Interactive effects of host resistance and drought stress on the performance of a gall-making aphid living on Norway spruce. *Oecologia* 123:223–31
 19. Boecklen WJ, Spellenberg R. 1990. Structure of herbivore communities in 2 oak (*Quercus* spp.) hybrid zones. *Oecologia* 85:92–100
 20. Brooks SE, Shorthouse JD. 1998. Developmental morphology of stem galls of *Diptolepis nodulosa* (Hymenoptera: Cynipidae) and those modified by the inquiline *Periclistus pirata* (Hymenoptera: Cynipidae) on *Rosa blanda* (Rosaceae). *Can. J. Bot.* 76:365–81
 - 20a. Collins M, Crawley MJ, McGavin GC. 1983. Survivorship of the sexual and agamic generation of *Andricus quercuscalicis* on *Quercus cerris* and *Q. robur*. *Ecol. Entomol.* 8:133–38
 21. Cook JM, Butcher RDJ. 1999. The transmission and effects of *Wolbachia* bacteria in parasitoids. *Res. Popul. Ecol.* 41:15–28
 22. Cook JM, Stone GN, Rowe JA. 1998. Patterns in the evolution of gall structure and life cycles in oak gallwasps (Hymenoptera: Cynipidae). See Ref. 110, pp. 261–79
 23. Cornell HV. 1985. Local and regional richness of cynipine gallwasps on California oaks. *Ecology* 66:1247–60
 24. Cornell HV, Washburn JO. 1979. Evolution of the richness area correlation for cynipid gallwasps on oak trees. A comparison of two geographic areas. *Evolution* 33:257–74
 25. Craig TP, Itami JK, Price PW. 1989. A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. *Ecology* 70:1691–99
 26. Craig TP, Itami JK, Price PW. 1990. The window of vulnerability of a shoot-galling sawfly to attack by a parasitoid. *Ecology* 71:1471–82
 27. Crawley MJ, Long CR. 1995. Alternate bearing, predator satiation and seedling recruitment in *Quercus robur*. *J. Ecol.* 83:683–96
 28. Crespi B, Worobey M. 1998. Comparative analysis of gall morphology in Australian gall thrips: the evolution of extended phenotypes. *Evolution* 52:1686–96
 29. Csóka Gy. 1997. *Plant Galls*. Budapest: Agroinform. 160 pp.
 30. Czczuga B. 1977. Carotenoids in leaves and their galls. *Marcellia* 40:177–80

31. Docters van Leuwen-Reijnvaan J, Docters van Leuwen WM. 1926. *The Zooecidia of the Netherlands East Indies*. Jakarta: Drukkerij de Unie. 230 pp.
32. Eber S, Brandl R. 1994. Ecological and genetic spatial patterns of *Urophora cardui* (Diptera: Tephritidae) as evidence for population structure and biogeographical processes. *J. Anim. Ecol.* 63:187–99
33. Ejlersen A. 1978. The spatial distribution of spangle galls (*Neuroterus* spp.) on oak (Hymenoptera: Cynipidae). *Entomol. Med.* 46:19–25
34. Eliason EA, Potter DA. 2000. Budburst phenology, plant vigor, and host genotype effects on the leaf-galling generation of *Callirhytis cornigera* (Hymenoptera: Cynipidae) on pin oak. *Environ. Entomol.* 29:1199–207
35. Eliason EA, Potter DA. 2000. Dogwood borer (Lepidoptera: Sesiidae) infestation of horned oak galls. *J. Econ. Entomol.* 93:757–62
36. Faria ML, Fernandes GW. 2001. Vigour of a dioecious shrub and attack by a galling herbivore. *Ecol. Entomol.* 26:37–45
37. Fay PA, Hartnett DC. 1991. Constraints on growth and allocation patterns of *Silphium integrifolium* (Asteraceae) caused by a cynipid gall wasp. *Oecologia* 88:243–50
38. Fay PA, Hartnett DC, Knapp AK. 1993. Increased photosynthesis and water potentials in *Silphium integrifolium* galled by cynipid wasps. *Oecologia* 93:114–20
39. Fernandes GW. 1998. Hypersensitivity as a phenotypic basis of plant induced resistance against a galling insect (Diptera: Cecidomyiidae). *Environ. Entomol.* 27:260–67
40. Fernandes GW, Fagundes M, Woodman RL, Price PW. 1999. Ant effects on three-trophic level interactions: plant, galls, and parasitoids. *Ecol. Entomol.* 24:411–15
41. Folliot R. 1964. Contribution a l'étude de la biologie des cynipides gallicoles (Hymenoptera: Cynipoidea). *Ann. Sci. Nat. Zool. Paris.* (Ser. 12) 6:407–564
42. Fritz RS, Crabb BA, Hochwender CG. 2000. Preference and performance of a gall-inducing sawfly: a test of the plant vigor hypothesis. *Oikos* 89:555–63
43. Gilbert FS, Astbury C, Beddingfield J, Ennis B, Lawson S, Sitch TA. 1994. The ecology of the pea galls of *Cynips divisa*. See Ref. 15, pp. 369–90
44. Greenberg JT, Guo AL, Klessig DF, Ausubel FM. 1994. Programmed cell-death in plants—a pathogen-triggered response activated coordinately with multiple defense functions. *Cell* 77:551–63
45. Hails RS, Crawley MJ. 1991. The population dynamics of an alien insect, *Andricus quercuscalicis* (Hymenoptera; Cynipidae). *J. Anim. Ecol.* 60:545–62
46. Hails RS, Crawley MJ. 1992. Spatial density dependence in populations of a cynipid gallformer *Andricus quercuscalicis*. *J. Anim. Ecol.* 61:567–83
47. Harper LJ, Schönrogge K, Lichtenstein CP. 2001. Mechanisms and effects during cynipid gall formation: a review. In *The Oak Gallwasps of the Western Palaearctic*, ed. GN Stone, Gy Csóka. London: Ray Soc. In press
48. Hartley SE. 1998. The chemical composition of plant galls: are levels of nutrients and secondary compounds controlled by the gall-former? *Oecologia* 113:492–501
49. Hartley SE, Lawton JH. 1992. Host plant manipulation by gall insects—a test of the nutrition hypothesis. *J. Anim. Ecol.* 61:113–19
- 49a. Hassell MP. 2000. Host-parasitoid population dynamics. *J. Anim. Ecol.* 69:543–66
50. Hassell MP, Crawley MJ, Godfray HCJ, Lawton JH. 1998. Top-down versus bottom-up and the Ruritanian bean bug. *Proc. Natl. Acad. Sci. USA* 95:10661–64
51. Hawkins BA. 1992. Parasitoid-host food webs and donor control. *Oikos* 65:159–62
52. Hebert PDN. 1987. Genotypic characteristics of cyclic parthenogens and their obligately asexual derivatives. In *The Evolution of Sex and Its Consequences*, ed. SC

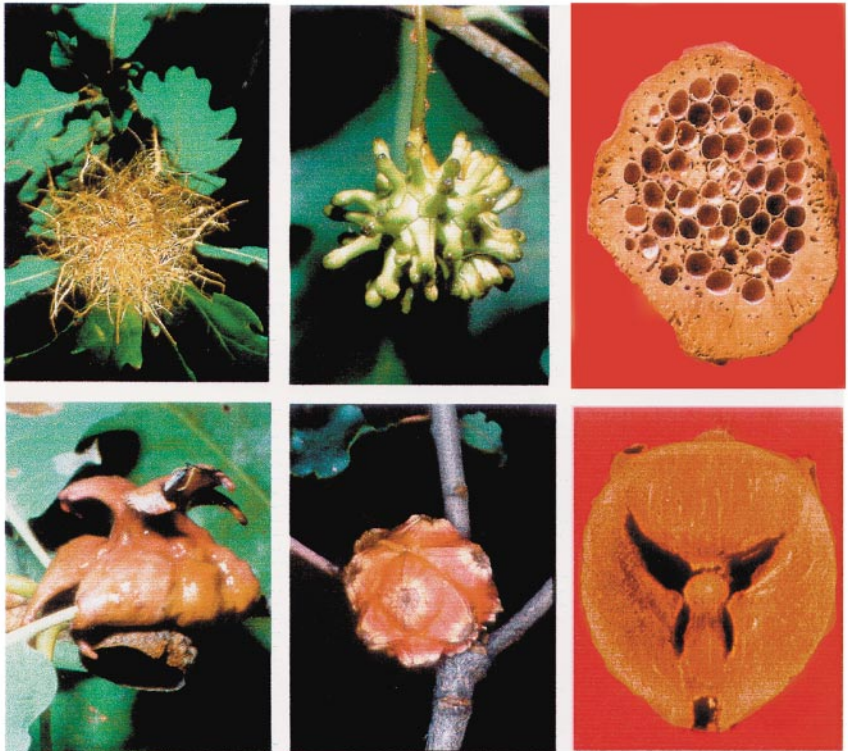
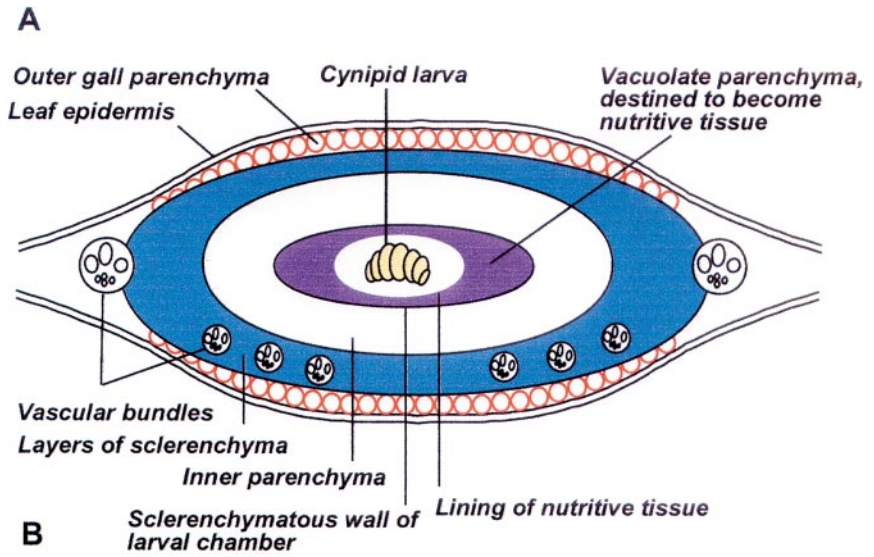
- Stearns, pp. 175–218. Basel: Birkhauser Verlag. 403 pp.
53. Holt RD, Lawton JH. 1993. Apparent competition and enemy free space in insect host parasitoid communities. *Am. Nat.* 142:623–45
 54. Jones D. 1983. The influence of host density and gall shape on the survivorship of *Diastrophus kinkaidii* Gill. (Hymenoptera: Cynipidae). *Can. J. Zool.* 61:2138–42
 55. Kato K, Hijii N. 1993. Optimal clutch size of the chestnut gallwasp, *Dryocosmus kurriphilus* Yasumatsu (Hymenoptera; Cynipidae). *Res. Popul. Ecol.* 35:1–14
 56. Kato K, Hijii N. 1997. Effects of gall formation by *Dryocosmus kurriphilus* Yasumatsu (Hym., Cynipidae) on the growth of chestnut trees. *J. Appl. Entomol. Z. Angew. Entomol.* 121:9–15
 57. Kinsey AC. 1936. The origin of the higher categories in *Cynips*. *Indiana Univ. Publ. Sci. Ser.* 4:1–334
 58. Kinsey AC. 1937. New Mexican gall wasps (Hymenoptera, Cynipidae). *Rev. Entomol.* 7:39–79
 59. Kovalev OV. 1965. Gall wasps (Hymenoptera, Cynipidae) in the south of the Soviet Far East. *Entomol. Obozr.* 44:46–73
 60. LeBlanc DA, Lacroix CR. 2001. Developmental potential of galls induced by *Diplolepis rosaefolii* (Hymenoptera: Cynipidae) on the leaves of *Rosa virginiana* and the influence of *Periclistus* species on the *Diplolepis rosaefolii* galls. *Int. J. Plant Sci.* 162:29–46
 61. Little TJ, Hebert PDN. 1997. Clonal diversity in high arctic ostracodes. *J. Evol. Biol.* 10:233–52
 62. Lund JN, Ott JR, Lyon RJ. 1999. Heterogony in *Belonocnema treatae* Mayr (Hymenoptera: Cynipidae). *Proc. Entomol. Soc. Wash.* 100:755–63
 63. Lyon RJ. 1993. Synonymy of two genera of Cynipid gall wasps and description of a new genus (Hymenoptera: Cynipidae). *Pan-Pac. Entomol.* 69:133–40
 64. Maisuradze L. 1961. Notes on the gall flies (family Cynipidae) which are harmful to oak in the Lenkoran zone. *Ucheniye Zap. Azerb. Univ. Ser. Biol.* 1:21–30
 65. Manos PS, Doyle JJ, Nixon KC. 1999. Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus* (Fagaceae). *Mol. Phylogenet. Evol.* 12:333–49
 66. Matson PA, Hunter MD. 1992. The relative contributions of top-down and bottom-up forces in population and community ecology. *Ecology* 73:723–66
 67. Melika G, Abrahamson WG. 1997. Descriptions of four new species of Cynipid gall wasps of the genus *Neuroterus* Hartig (Hym.: Cynipidae) with redescriptions of some known species from the eastern United States. *Proc. Entomol. Soc. Wash.* 99:560–73
 68. Melika G, Abrahamson WG. 2000. Review of the cynipid gall wasp of the genus *Loxaulus* Mayr (Hymenoptera: Cynipidae) with descriptions of new species. *Proc. Entomol. Soc. Wash.* 102:198–211
 69. Melika G, Csóka Gy, Pujade-Villar J. 2000. Check-list of oak gall wasps of Hungary, with some taxonomic notes (Hymenoptera: Cynipidae, Cynipinae, Cynipini). *Ann. Hist. Nat. Mus. Hung.* 92:265–96
 70. Miyashita K, Ito Y, Nakamura K, Nakamura M, Kondo M. 1965. Population dynamics of the chestnut gallwasp *Dryocosmus kurriphilus* Yasumatsu (Hymenoptera: Cynipidae). III. Five year observation on population fluctuation. *Jpn. J. Appl. Entomol. Zool.* 9:42–52
 71. Monzen K. 1954. Revision of the Japanese gall wasps with a description of new genera, subgenera, species and subspecies (II). Cynipidae (Cynipinae) Hymenoptera. *Ann. Rep. Gakugei Fac. Iwate Univ.* 5:15–21
 72. Moorehead JR, Taper ML, Case TJ. 1993. Utilisation of oak hosts by a monophagous gall wasp—how little host character is sufficient? *Oecologia* 95:385–92

73. Moran NA. 1992. The evolution of aphid life cycles. *Annu. Rev. Entomol.* 37:321–48
74. Moriya S, Inoue K, Otake A, Shiga M, Mabuchi M. 1989. Decline of the chestnut gall-wasp population, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae) after the establishment of *Torymus sinensis* Kamijo (Hymenoptera: Torymidae). *Appl. Entomol. Zool.* 24:231–33
75. Müller CB, Adriaanse ICT, Belshaw R, Godfray HCJ. 1999. The structure of an aphid-parasitoid community. *J. Anim. Ecol.* 68:346–70
76. Niblett M. 1949. Retarded emergences in Cynipidae (Hymenoptera). *Proc. S. London Entomol. Nat. Hist. Soc.* 1948–49:159–60
77. Nieves-Aldrey JL. 1987. Estado actual de conocimiento de la subfamilia Cynipinae (Hym., Parasitica, Cynipidae) en la Península Ibérica. *Eos* 63:179–95
78. Nieves-Aldrey JL. 1990. Sobre las especies europeas del género *Trigonaspis* Hartig, con descripción de una nueva especie de España (Hym., Cynipidae). *Eos* 65:91–108
79. Nieves-Aldrey JL. 1992. Revisión de las especies europeas del género *Callirhytis* (Hymenoptera, Cynipidae). *Graellsia* 48:171–83
80. Nixon KC. 1993. Infrageneric classification of *Quercus* (Fagaceae) and typification of sectional names. *Ann. Sci. For. Suppl. 1 (Paris)* 50:S25–34
81. Nyman T, Widmer A, Roininen H. 2000. Evolution of gall morphology and host-plant relationships in willow-feeding sawflies (Hymenoptera: Tenthredinidae). *Evolution* 54:526–33
82. Otake A. 1982. Weighing of galls as a means of studying the ecology of the chestnut gallwasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera, Cynipidae) and its parasitoids. *Appl. Entomol. Zool.* 17:148–50
83. Otake A, Moriya S, Shiga M. 1984. Colonization of *Torymus sinensis* kamijo (Hymenoptera: Torymidae), a parasitoid of the chestnut gall-wasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae) introduced from China. *Appl. Entomol. Zool.* 19:111–14
84. Ozaki K. 2000. Insect-plant interactions among gall size determinants of adelgids. *Ecol. Entomol.* 25:452–59
85. Paquette LC, Bagatto G, Shorthouse JD. 1993. Distribution of mineral nutrients within the leaves of common dandelion (*Taraxacum officinale*) galled by *Phanacis taraxaci* (Hymenoptera: Cynipidae). *Can. J. Bot.* 71:1026–31
86. Payne JA. 1978. Oriental chestnut gall-wasp: a new nut pest in north America. In *Proc. Am. Chestnut Symp.*, ed. WL Macdonald, FC Cech, J Luchok, C Smith, pp. 86–88. Morgantown, W. Va.: W. Va. Univ. Press. 428 pp.
87. Pires CSS, Price PW. 2000. Patterns of host plant growth and attack and establishment of gall-inducing wasp (Hymenoptera: Cynipidae). *Environ. Entomol.* 29:49–54
88. Plantard O, Hochberg ME. 1998. Factors affecting parasitism in the oak galler *Neuroterus quercusbaccarum* (Hymenoptera: Cynipidae). *Oikos* 81:289–98
89. Plantard O, Rasplus J-Y, Hochberg ME. 1996. Resource partitioning in the parasitoid assemblage of the oak galler *Neuroterus quercusbaccarum* L. (Hymenoptera: Cynipidae). *Acta Oecologica* 17: 1–15
90. Plantard O, Rasplus J-Y, Mondor G, Le Clainche I, Solignac M. 1998. *Wolbachia*-induced thelytoky in the rose gall-wasp *Diplolepis spinosissimae* (Giraud) (Hymenoptera: Cynipidae), and its consequences on the genetic structure of its host. *Proc. R. Soc. London Ser. B* 265: 1075–80
91. Plantard O, Rasplus J-Y, Mondor G, Le Clainche I, Solignac M. 1999. Distribution and phylogeny of *Wolbachia*-inducing thelytoky in Rhoditini 'Aylacini'

- (Hymenoptera: Cynipidae). *Insect Mol. Biol.* 8:185–91
92. Plantard O, Shorthouse JD, Rasplus J-Y. 1998. Molecular phylogeny of the genus *Diplolepis* (Hymenoptera: Cynipidae). In *Proc. 3rd Int. Conf. Biol. Gall-Forming Organisms*, ed. G Csóka, W Mattson, GN Stone, P Price, pp. 247–60. St. Paul, MN: USDA. 329 pp.
 93. Prado P, Vieira EM. 1999. The interplay between plant traits and herbivore attack: a study of a stem galling midge in the neotropics. *Ecol. Entomol.* 24:80–88
 94. Price PW, Bouton CE, Gross P, McPherson BA, Thompson JN, Weis A. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annu. Rev. Ecol. Syst.* 11:41–65
 95. Price PW, Fernandes GW, Waring GL. 1987. Adaptive nature of insect galls. *Environ. Entomol.* 16:15–24
 96. Price PW, Pschorn-Walcher H. 1988. Are galling insects better protected against Parasitoids than exposed feeders?: a test using tenthredinid sawflies. *Ecol. Entomol.* 13:195–205
 97. Pujade-Villar J. 1992. *Andricus kollari* (Hartig) (Insecta: Hymenoptera: Cynipidae) Part II: consideracions sobre el seu cicle biològic. *La Sitja de Llop* 3:12
 - 97a. Pujade-Villar J, Bellido D, Segú G, Melika G. 1999. Current state of knowledge of heterogony in Cynipidae (Hymenoptera, Cynipoidea). *Ses. Entomol.* 11: 85–105
 98. Quicke DLJ, Fitton MG, Tunstead JR, Ingram SN, Gaitens PV. 1994. Ovipositor structure and relationships within the Hymenoptera, with special reference to the Ichneumonoidea. *J. Nat. Hist. Univ. Sheff.* 28:635–82
 99. Quicke DLJ, Wyeth P, Fawke JD, Basi-buyuk HH, Vincent JFV. 1998. Manganese and zinc in the ovipositors and mandibles of hymenopterous insects. *Zool. J. Linn. Soc.* 124:387–96
 100. Ritchie AJ, Shorthouse JD. 1987. A review of the species of *Synergus* from Guatemala, with notes on *Cynips guatemalensis* Cameron (Hymenoptera: Cynipidae). *Proc. Entomol. Soc. Wash.* 89: 230–41
 101. Roininen H, Price PW, Tahvanainen J. 1996. Bottom-up and top-down influences in the trophic system of a willow, a galling sawfly, parasitoids and inquilines. *Oikos* 77:44–50
 102. Rokas A, Atkinson R, Brown G, West SA, Stone GN. 2001. Understanding patterns of genetic diversity in the oak gallwasp *Biorhiza pallida*: demographic history or a *Wolbachia* selective sweep? *Heredity*. In press
 103. Ronquist F. 1994. Evolution of parasitism among closely related species: phylogenetic relationships and the origin of inquilinism in gall wasps (Hymenoptera, Cynipidae). *Evolution* 48:241–66
 104. Ronquist F. 1995. Phylogeny and early evolution of the Cynipoidea (Hymenoptera). *Syst. Entomol.* 20:309–35
 105. Ronquist F. 1999. Phylogeny, classification and evolution of the Cynipoidea. *Zool. Scr.* 28:139–164
 106. Root RB, Cappucino N. 1992. Patterns in population change and the organization of the insect community associated with goldenrod. *Ecol. Mongr.* 62:393–420
 107. Rossi AM, Stiling PD, Strong DR, Johnson DM. 1992. Does gall diameter affect parasitism of *Asphondylia borrichiae* (Diptera: Cecidomyiidae)? *Ecol. Entomol.* 17:149–54
 108. Rott AS, Müller CB, Godfray HCJ. 1998. Indirect population interaction between two aphid species. *Ecol. Lett.* 1:99–103
 109. Schönrogge K, Crawley MJ. 2000. Quantitative webs as a means of assessing the impact of alien insects. *J. Anim. Ecol.* 69:841–68
 110. Schönrogge K, Harper LJ, Brooks SE, Shorthouse JD, Lichtenstein CP. 1998. Reprogramming plant development: two approaches to study the molecular mechanism of gall formation. In *The Biology of*

- Gall-Inducing Arthropods*, ed. G Csóka, W Mattson, GN Stone, P Price, pp. 153–60. St. Paul, MN: USDA. 329 pp.
111. Schönrogge K, Harper LJ, Lichtenstein CP. 2000. The protein content of tissues in cynipid galls (Hymenoptera: Cynipidae): similarities between cynipid galls and seeds. *Plant Cell Environ.* 23:215–22
 112. Schönrogge K, Stone GN, Cockrell B, Crawley MJ. 1994. The communities associated with galls of *Andricus quercuscalicis* (Hym.: Cynipidae), an invading species in Britain: a geographical view. In *Plant Galls*, ed. MAJ Williams, pp. 369–90. Oxford: Clarendon. 488 pp.
 113. Schönrogge K, Stone GN, Crawley MJ. 1995. Spatial and temporal variation in guild structure: parasitoids and inquiline of *Andricus quercuscalicis* (Hymenoptera: Cynipidae) in its native and alien ranges. *Oikos* 72:51–60
 114. Schönrogge K, Stone GN, Crawley MJ. 1996. Abundance patterns and species richness of the parasitoids and inquilines of the alien gall former *Andricus quercuscalicis* Burgsdorf (Hymenoptera: Cynipidae). *Oikos* 77:507–18
 115. Schönrogge K, Stone GN, Crawley MJ. 1996. Alien herbivores and native parasitoids: rapid development of guild structure in an invading gall wasp, *Andricus quercuscalicis* (Hymenoptera: Cynipidae). *Ecol. Entomol.* 21:71–80
 116. Schönrogge K, Walker P, Crawley MJ. 1998. Invaders on the move: parasitism in the galls of four alien gallwasps in Britain (Hymenoptera: Cynipidae). *Proc. R. Soc. London Ser. B* 256:1643–50
 117. Schönrogge K, Walker P, Crawley MJ. 1999. Complex life-cycles in *Andricus kollari* (Hymenoptera, Cynipidae) and their impact on associated parasitoid and inquiline species. *Oikos* 84:293–301
 118. Schönrogge K, Walker P, Crawley MJ. 2000. Parasitoid and inquiline attack in the galls of four alien, cynipid gall wasps: host switches and the effect on parasitoid sex ratios. *Ecol. Entomol.* 25:208–19
 119. Schultz JC, Baldwin IT. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. *Science* 217:149–51
 120. Seibert TF. 1993. A nectar secreting gall wasp and ant mutualism—selection and counter-selection shaping gall wasp phenology, fecundity and persistence. *Ecol. Entomol.* 18:247–53
 121. Shorthouse JD. 1993. Adaptations of gallwasps of the genus *Diplolepis* (Hymenoptera: Cynipidae) and the role of gall anatomy in Cynipid systematics. *Mem. Entomol. Soc. Can.* 165:139–63
 122. Shorthouse JD, Rohfritsch O. 1992. *Biology of Insect-Induced Galls*. New York: Oxford Univ. Press. 285 pp.
 123. Simon JC, Baumann S, Sunnucks P, Hebert PDN, Pierre JS, et al. 1999. Reproductive mode and population genetic structure of the cereal aphid *Sitobion avenae* studied using phenotypic and microsatellite markers. *Mol. Ecol.* 8:531–45
 124. Stille B. 1984. The effect of hostplant and parasitoids on the reproductive success of the parthenogenetic gallwasp *Diplolepis rosae* (Hymenoptera; Cynipidae). *Oecologia* 63:364–69
 125. Stille B. 1985. Host plant specificity and allozyme variation in the parthenogenetic gallwasp *Diplolepis mayri* and its relatedness to *Diplolepis rosae* (Hymenoptera: Cynipidae). *Entomol. Genet.* 10:87–96
 126. Stille B. 1985. Population genetics of the parthenogenetic gallwasp *Diplolepis rosae* (Hymenoptera: Cynipidae). *Genetica* 27:145–51
 127. Stille B, Dävring L. 1980. Meiosis and reproductive strategy in the parthenogenetic gallwasp *Diplolepis rosae* (L.) (Hymenoptera: Cynipidae). *Hereditas* 92: 353–62
 128. Stone GN, Atkinson R, Rokas A, Csóka G, Nieves-Aldrey J-L. 2001. Differential success in northwards range expansion between ecotypes of the marble gallwasp *Andricus kollari*: a tale of two lifecycles. *Mol. Ecol.* 10:761–78

129. Stone GN, Cook JM. 1998. The structure of cynipid oak galls: patterns in the evolution of an extended phenotype. *Proc. R. Soc. London Ser. B* 265:979–88
130. Stone GN, Schönrogge K, Crawley MJ, Fraser S. 1995. Geographic variation in the parasitoid community associated with an invading gallwasp, *Andricus quercuscalicis* (Hymenoptera: Cynipidae). *Oecologia* 104:207–17
131. Stone GN, Sunnucks PJ. 1993. The population genetics of an invasion through a patchy environment: the cynipid gallwasp *Andricus quercuscalicis*. *Mol. Ecol.* 2:251–68
132. Strathdee AT, Bale JS, Block WC, Webb NR, Hodgkinson ID, Coulson SJ. 1996. Extreme adaptive lifecycle in a high arctic aphid, *Acyrtosiphon svalbardicum*. *Ecol. Entomol.* 18:254–58
133. Sunnucks P, DeBarro PJ, Lushai G, Maclean N, Hales D. 1997. Genetic structure of an aphid studied with microsatellites: cyclical parthenogenesis, differentiated lineages and host specialisation. *Mol. Ecol.* 6:1059–73
134. Suomalainen E, Anssi S, Lokki J. 1987. *Cytology and Evolution in Parthenogenesis*. Boca Raton, FL: CRC. 216 pp.
135. Taper ML, Case TJ. 1987. Interactions between oak tannins and parasite structure: unexpected benefits of tannins to gall-wasps. *Oecologia* 71:254–61
136. Thompson JN. 1994. *The Coevolutionary Process*. Chicago: Univ. Chicago Press. 376 pp.
137. Tschamtké T. 1994. Tritrophic interactions in gallmaker communities on *Phragmites australis*: testing ecological hypotheses. In *The Ecology and Evolution of Gall-Forming Insects*, ed. PW Price, WJ Mattson, YN Baranchikov, pp. 73–92. St. Paul, MN: USDA. 222 pp.
138. Von Dohlen CD, Moran NA. 2000. Molecular data support a rapid radiation of aphids in the Cretaceous and multiple origins of host alternation. *Biol. J. Linn. Soc.* 71:689–717
139. Waring GL, Price PW. 1989. Parasitoid pressure and the radiation of a gallforming group (Cecidomyiidae, *Asphondylia* spp.) on creosote bush (*Larrea tridentata*) *Oecologia* 79:293–99
140. Washburn JO. 1984. Mutualism between a cynipid wasp and ants. *Ecology* 65:654–56
141. Washburn JO, Cornell HV. 1981. Parasitoids, patches and phenology—their possible role in the local extinction of a cynipid gallwasp population. *Ecology* 62:1597–607
142. Weis AE. 1982. Use of a symbiotic fungus by the gall maker *Asteromyia carbonifera* to inhibit attack by the parasitoid *Torymus capite*. *Ecology* 63:1602–5
143. Weis AE, Walton R, Crego CL. 1988. Reactive plant tissue sites and the population biology of gall makers. *Annu. Rev. Entomol.* 33:467–86
144. Wiebes-Rijks AA. 1982. Early parasitization of oak-apple galls (*Cynips Quercusfolii* L., Hymenoptera). *Neth. J. Zool.* 32:112–16
145. Weld LH. 1952. *Cynipoidea (Hym.)*. Ann Arbor, MI: Privately printed. 352 pp.
146. Weld LH. 1957. *Cynipid Galls of the Pacific Slope*. Ann Arbor, MI: Privately printed. 64 pp.
147. Weld LH. 1959. *Cynipid Galls of the Eastern United States*. Ann Arbor, MI: Privately printed. 124 pp.
148. Weld LH. 1960. *Cynipid Galls of the Southwest*. Ann Arbor, MI: Privately printed. 35 pp.
149. Whitham TG. 1986. Costs and benefits of territoriality: behavioral and reproductive release by competing aphids. *Ecology* 67:139–47
150. Wilson D, Carroll GC. 1997. Avoidance of high-endophyte space by gall-forming insects. *Ecology* 78:2153–63
151. Wurzell B. 2000. The ram's horn gall of *Andricus aries* spreading around north London. *Cecidology* 15:131–34
152. Zantoko L, Shukle RH. 1997. Genetics of virulence in the Hessian fly to resistance gene H13 in wheat *J. Hered.* 88:120–23



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Figure 1 (See figure on previous page) (a) A diagrammatic cross section of the leaf gall induced by a rose gall wasp *Diplolepis rosaefolii* (Cynipidae: Diplolepidini) on the leaves of *Rosa virginiana* (modified from 62). (b) Structural diversity in galls induced by asexual generation females of six western palaeartic *Andricus* species. Clockwise from top left: *A. caputmedusae* (covered with fine spines), *A. mayri* (covered with large spines and sticky resin), *A. quercusradicis* (a multilocular gall, in cross section), *A. quercustozae* (in cross section, with an internal airspace around the larval chamber), *A. mediterraneae* (brightly colored), and *A. dentimitratus* (= *A. viscosus*) (covered with sticky resins and with an internal airspace around the larval chamber). Photographs by Dr. Gyuri Csóka and G.N. Stone.