Support for the microenvironment hypothesis for adaptive value of gall induction in the California gall wasp, *Andricus quercuscalifornicus*

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Abstract

Three major hypotheses have been advanced for the adaptive nature of plant galls: nutrition, enemy-avoidance, and microenvironment. Of these, the microenvironment hypothesis has been frequently invoked, but rarely tested directly. We tested this hypothesis in a population of *Andricus quercuscalifornicus* (Bassett) (Hymenoptera: Cynipidae) wasps inducing galls on *Quercus lobata* Née (Fagaceae) trees in Northern California, USA. Relative humidity and temperature data gathered from both immature and mature galls in the field indicated that *A. quercuscalifornicus* larvae modify their microenvironments significantly by raising and stabilizing relative humidity levels inside galls to near saturation. In addition, excised larvae maintained under experimental conditions survived significantly longer under levels of high relative humidity. These data support the hypothesis that through gall induction, *A. quercuscalifornicus* manipulates its environment adaptively.

Introduction

Many species of animals modify their immediate surroundings by creating domiciles providing shelter from natural enemies and serving as environmental buffers against unfavourable temperature and humidity levels. Among birds, sociable weavers (*Philetairus socius* Latham) of the Kalahari Desert build communal nests serving as insulation chambers from the daytime heat and the nighttime chill (White et al., 1975). The distinctive incubation mounds constructed by crocodilians and chelonians are characterized by levels of internal humidity approaching saturation, protecting against desiccation of the eggs (Seymour & Ackerman, 1980). Likewise, a diverse array of arthropods modulate their microenvironments through building or inducing protective shelters, e.g., termites (Turner, 2000), honey bees (Winston, 1987), leaf miners (Connor & Taverner, 1997), and a variety of gall-formers, for instance, mites (Oldfield, 2005), aphids (Wool, 2004), thrips (Crespi et al., 2004), flies (Yukawa & Rohfritsch, 2005), and wasps (Askew, 1961).

The induction of galls, with the exception of mutualistic agaonid fig wasps (Kjellberg et al., 2005) and some yucca moths (Pellmyr et al., 2008), is widely regarded as a parasitic relationship in which the galling organism benefits at the expense of the host plant (Mani, 1964; Dreger-Jauffret & Shorthouse, 1992; Stone et al., 2002). Three major arguments for the adaptive value of gall induction have been advanced: the nutrition-, natural-enemy-, and microenvironment hypotheses (Price et al., 1987; Stone & Schönrogge, 2003). None of these hypotheses is exclusive of the others.

The nutrition hypothesis holds that galls enhance nutritive qualities of the host plant as a result of larval feeding activities on plant tissues or fluids. For example, some gall midges (Diptera: Cecidomyiidae) specialize on fungi associated with gall tissue (Uechi & Yukawa, 2006). In aphids (Hemiptera: Aphididae), the rates of energy conversion from plant sap to animal biomass are significantly higher for galling species than for free-living aphids (Llewellyn, 1982). Hence, nutrients essential to larval development, e.g., nitrogenous compounds, may be concentrated in galls (Shannon & Brewer, 1980; Abrahamson & McCrea, 1986; Koyama et al., 2004), especially in the nutritive tissues surrounding the larval chamber (Bronner, 1992; Csóka et al., 2005).

The natural-enemy hypothesis asserts that galls act principally to protect their inducers from attacks by predators,

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parasitoids, and pathogens. Little direct support for this hypothesis has been provided (Stone & Schönrogge, 2003; but see Price & Pschorn-Walcher, 1988), as abundant evidence suggests gall inducers are in fact attacked by more parasitoid species than are free-feeding forms (Hawkins & Lawton, 1987; Price et al., 1987). However, gall inducers may benefit from lower rates of disease than either leaf miners or external feeders (Cornell, 1989; Connor & Taverner, 1997). Greater gall size might appear to enhance protection from predators and parasitoids (Askew, 1961; Stone & Schönrogge, 2003), but in at least some instances in which gall size varies within species, larger galls suffer increased rates of avian predation (Abrahamson & Weis, 1997). Nevertheless, the enemy hypothesis may ultimately prove the most powerful in explaining the great diversity in shape, texture, and composition of arthropod-induced galls (Cornell, 1983; Stone & Schönrogge, 2003).

Under the microenvironment hypothesis, galls shield the inducer from unfavourable abiotic factors, such as excess ultraviolet radiation and the major problem of desiccation (Strong et al., 1984), and they aid attachment to the host plant. Although this hypothesis has been invoked frequently (Felt, 1940; Price et al., 1987; Fay et al., 1993; Williams et al., 2002), direct experimental evidence supporting it is scarce or lacking (Danks, 2002). Here, we tested the microenvironment hypothesis for gall induction under field and laboratory conditions, using the California gall wasp, *Andricus quercuscalifornicus* (Bassett) (Hymenoptera: Cynipidae), on valley oak, *Quercus lobata* Née (Fagaceae), as a model. We predicted galls would moderate ambient relative humidity and temperature levels, thus enhancing conditions favouring larval survival. We focussed especially on environmental modifications effected by larvae of *A. quercuscalifornicus* in immature galls in the growth phase, because these are succulent and would be expected to demonstrate stronger microclimatic buffering against ambient conditions.

Materials and methods

Study organisms

Cynipid wasps induce galls varying considerably in size and morphological complexity, even among closely related species (Cornell, 1983; Stone & Schönrogge, 2003). Cynipids are the most specialized gall-inducing insects: few if any plant galls surpass their great structural and histological complexity (Kinsey, 1920; Abrahamson & Weis, 1997; Ronquist & Liljeblad, 2001). Over 80% of cynipid taxa parasitize oaks (*Quercus* spp.) (Cornell, 1983). *Andricus quercuscalifornicus*, a common species on various white oaks in California, often induces massive galls, measuring up to 12 × 8 cm at their maximum dimensions

(Russo, 2006). Their abundance, great size, and ready access make these galls a study system ideal for testing the microenvironment hypothesis.

As in other gall-inducing insects, the life history of *A. quercuscalifornicus* is tightly coupled with the phenology of its host plants. *Quercus lobata*, a deciduous species broadly distributed throughout California's Sacramento Valley, occurs in Mediterranean-climatic regimes, characterized by winter precipitation and summer drought. However, the riparian habitat to which this species is restricted is conducive to a long growing season. In the Sacramento Valley, the primary leaf flush begins in March and leaves persist until November or December. In some years, a secondary leaf flush commences in July. Females oviposit on the stems and branches of *Q. lobata* in late fall (Russo, 2006). Larval hatching and gall initiation occur the following spring, with galls reaching their maximum size within about 2 months (Russo, 2006), between March and May. Galls may be monothalamous (containing a single larva) or polythalamous (containing multiple larvae) (Weld, 1957; Swiecki & Bernhardt, 2006). Gall initiation and continued growth require active stimulation by the wasp larvae and occur only in undifferentiated meristematic cells of stems of the host plant (Swiecki & Bernhardt, 2006). In its initial stages and during growth, the gall tissue is spongy, moist, and bright green. Fully differentiated cynipid galls comprise the larval chamber, the inside surface of which is lined with nutritive tissue supplied by a dense network of vascular tissues. The larval chamber is surrounded by a dense layer of lignified sclerenchyma. This in turn is enveloped by a relatively thick layer of spongy parenchyma, all of which is enclosed by epidermal tissue (Rey, 1992; Stone et al., 2002; Sliva & Shorthouse, 2006). Larval feeding, development, and pupation occur in the gall and fully formed adults emerge in the fall. As far as is known, *A. quercuscalifornicus* is entirely parthenogenetic (Russo, 2006). This does not, however, rule out the possibility of a sexual generation, as recent evidence suggests widespread cryptic cyclical parthenogenesis in apparently asexual cynipid lineages (Abe, 2006; Stone et al., 2008). Upon completion of larval development, galls dry out and become lignified (Swiecki & Bernhardt, 2006), and, over the course of the winter rainy season, darken from a pale brown to a sooty black, possibly from fungal attack of the gall epidermal layer. Although adults typically emerge within a year, galls often remain attached to trees for 2 years or more, and can host a number of inquiline species. Apparently, some eggs laid in late fall diapause until the following summer, after which hatching larvae initiate a second set of galls, followed by growth and maturation during July–September (DG Miller, CT Ivey & JD Shedd, unpubl.). Regardless of their season of origin, galls pro-

duce the parthenogenetic adults in late fall (Russo, 2006). The bimodal pattern of galling activity suggests that distinct opportunities for gall initiation may be synchronized with optimal periods of growth of the host plant's meristematic tissues.

During October–November 2006, we haphazardly selected trees in a population of *Q. lobata* by Big Chico Creek on the campus of California State University, Chico, CA, USA, and the nearby municipal park, Bidwell Park (39°44.2′N, 121°49.2′W, 65 m a.s.l.). All galls studied were on the lower branches, and could be measured without climbing the trees.

Test of the climatic buffering effect of gall

We measured a total of 27 galls (representing 19 individual trees) in which galling larvae were present ('immature') and 20 galls (from five trees) from which adult *A. quercus-californicus* had emerged at least 10 months prior to measurement ('mature'). All field data were collected under fair weather conditions. Eleven of the immature gall measurements were recorded between 09:00 and 12:00 hours ('morning'), when the contrast in temperature and humidity between inside and outside the gall was presumed to be smaller; all other measurements were recorded between 12:00 and 18:00 hours ('afternoon'). All galls selected were at least 2.5 cm in diameter; maximum gall width was recorded to the nearest 1 mm, with calipers. Using a humidity and temperature meter (with a sensor of 4 mm diameter; Vaisala, Helsinki, Model HMI41SET; hereafter 'probe'), ambient relative humidity and temperature were measured 2 cm from the surface of the gall, out of direct sunlight. We wished to compare nearby ambient conditions with those inside the gall, but to avoid the spurious effect of direct sunlight on temperature measurement. To measure the interior humidity and temperature of the gall, we used a 5-mm-diameter screwdriver to bore a channel through the parenchyma tissue to the midpoint of the gall, just outside the lignified larval chamber(s), immediately after which the probe was inserted into the gall and measurements were recorded.

For both relative humidity and temperature of each gall measured, we calculated the difference between the interior of the gall and ambient conditions ('differential relative humidity and temperature'). We used a mixed model ANOVA (Proc MIXED; SAS Institute, 2001) to test the effect of gall age on differential relative humidity and temperature. The fixed effect for this model was gall age and we included a random effect of individual tree, as multiple galls sampled within a single tree cannot be considered independent replicates, assuming gall phenotype is in part influenced by the unique characteristics of the host tree. Because the experimental design was unbal-

anced, we corrected calculations of degrees of freedom using Satterwaithe's approximation (Littell et al., 1996). We tested the hypothesis that the mean difference between external and internal environments was zero using a Z-test (Zar, 1998). We used a similar model to test the effect of time of day on the difference between internal and external environments, although for this model we used only the data from immature, succulent galls, as these galls would be expected to exhibit the strongest microclimatic buffering effects.

Test of the effect of relative humidity on larval survival

To test the consequences of low relative humidity for larval survival, we removed 30 larvae approaching maturity (≥3 mm long) from galls in the late growth phase, using a razor blade and fine brush. Because there were sometimes several larvae in a gall, each gall was carefully cut to obtain the maximum number of larvae. Larvae were randomly assigned to individual 9-cm-diameter plastic Petri plates. Prior to experimental setup, we used a soldering iron to melt a 5-mm-diameter hole in the narrow edge of each Petri plate, through which we could insert the probe to monitor relative humidity and temperature inside the plates. We placed a disk of filter paper (Whatman, Kent, UK) into each plate; also, we randomly assigned half of the plates to receive 250 μl of deionized water. Immediately after placing larvae inside the Petri plates, we sealed them with Parafilm (American National Can, Chicago, IL, USA). Plates were then placed in an incubator at 40 °C, and every 5 min removed from the incubator and placed under a dissecting scope and the larvae were examined. When larval mandibles were no longer moving, larvae were assumed to have died. We chose 40 °C as the test temperature, as ambient temperatures routinely reach this level during the period of gall growth and maturation in the Sacramento Valley. Data for relative humidity, temperature, and survival time did not satisfy assumptions for parametric analyses, and were therefore compared between treatments using a Wilcoxon two-sample normal approximation to a Z-test (Zar, 1998; SAS Institute, 2001).

Results

Relative humidity was about 40% higher inside immature galls than in the immediate external environment, in many cases approaching 100% (Table 1). By contrast, there was only a 3% difference in relative humidity between inside and outside galls from which gall-inducers had emerged. Immature galls had significantly greater differential relative humidity levels (calculated as the difference between outside and inside measurements) than did mature galls ($F_{1,20.8}$ = 19.08, P = 0.0003), and the difference was sig-

Table 1 Arithmetic mean (± SE) relative humidity (%) and temperature (°C) outside and inside galls of *Andricus quercuscalifornicus* occuring on *Quercus lobata* in Butte County, California

Comparison	n	Relative humidity		Temperature	
		Outside	Inside	Outside	Inside
Age of gall					
Immature	27	55.3 ± 3.3	94.6 ± 1.6	19.7 ± 1.0	19.3 ± 0.9
Mature	20	52.0 ± 1.0	55.1 ± 0.9	15.1 ± 0.1	15.5 ± 0.1
Time of day (immature galls only					
Morning	11	66.6 ± 3.8	92.0 ± 0.7	16.0 ± 1.0	14.9 ± 0.9
Afternoon	16	47.5 ± 4.0	96.4 ± 2.6	22.2 ± 1.1	22.4 ± 0.9

nificantly positive only for immature galls (Figure 1A). Also in immature galls, the magnitude of the difference in relative humidity between inside and outside galls more than doubled in the afternoon relative to morning measurements ($F_{1,16.5} = 14.72$, $P = 0.001$; Figure 1A).

Within each age class of gall, differences in temperature between inside galls and ambient conditions were negligible
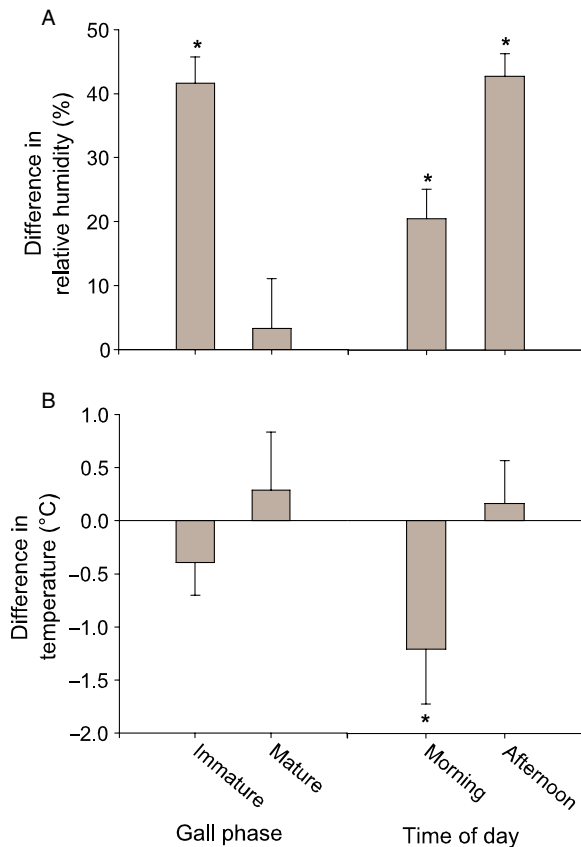

Figure 1 Least-squares mean difference (+ SE) in inside vs. outside (A) relative humidity and (B) temperature of galls of *Andricus quercuscalifornicus* occurring on *Quercus lobata* in Butte County, California, USA. Means comparing morning vs. afternoon measurements involved immature galls only. *Estimate of difference is significantly different from zero at α = 0.05 (Z-test).

(Table 1). The magnitude of this difference was not significantly affected by gall age ($F_{1,16} = 1.15$, $P = 0.3$; Figure 1B). Morning temperature readings inside immature galls were slightly, but significantly cooler than external temperatures (Table 1, Figure 1B). The magnitude of differential temperature in immature galls was only marginally significantly different between morning and afternoon ($F_{1,15} = 4.37$, $P = 0.054$; Figure 1B). Among immature galls, there was no relationship between gall diameter and differential relative humidity (Spearman's rank correlation: $r_s = 0.14$, $P = 0.4$) or temperature ($r_s = -0.24$, $P = 0.2$).

Relative humidity inside Petri plates into which water was added was about 58% higher than under ambient conditions (Wilcoxon, two-sided: $Z = 4.65$, $P<0.0001$; Figure 2A), and on average, nearly identical to the humidity inside immature galls (Table 1). Temperature inside the more humid plates was about 4% higher than in the ambient ones (Wilcoxon, two-sided: $Z = 2.11$, $P = 0.03$; Figure 2B). Larvae in the more humid Petri plates lived nearly twice as long as those in the dry plates (Wilcoxon, two-sided: $Z = 3.14$, $P = 0.002$; Figure 2C).

Discussion

The ameliorating effects of insect-induced environmental modifications have been more often cited than rigorously tested (Fernandes & Price, 1992; Danks, 2002). To the best of our knowledge, this research presents the first data on the magnitude of the buffering effects of gall induction against ambient relative humidity and temperature levels by a galling insect. Our experimental evidence that larval survival rates are a function of microclimatic conditions similar to those experienced within the gall corroborates the hypothesis that gall induction is, indeed, adaptive.

Among immature galls, *A. quercuscalifornicus* modified its microclimate most strikingly by achieving near-saturation levels of relative humidity inside gall tissues. To a much lesser extent, temperatures were ameliorated inside the gall as well. As relative humidity levels are a function of temperature and available moisture, together they may
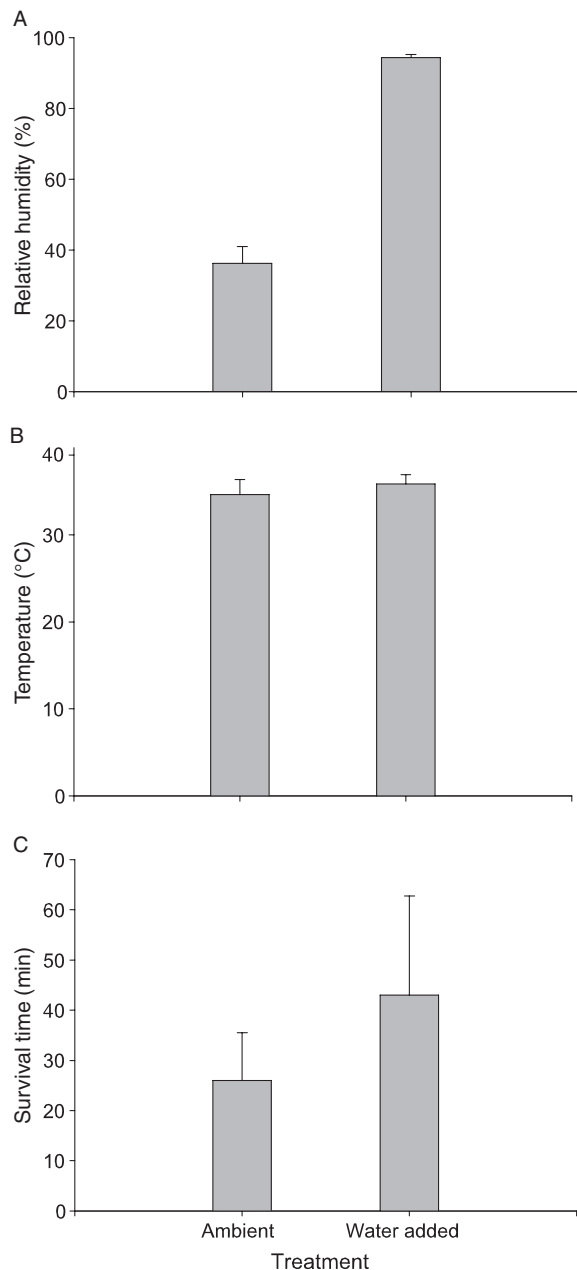
Figure 2 Means (+ SD) of (A) relative humidity (%), (B) temperature (°C), and (C) survival time of *Andricus quercuscalifornicus* larvae (min) inside 9-cm diameter Petri plates into which 250 μl water was added ('water added') or not ('ambient'). See Materials and methods for further details about experimental design; n = 15 per treatment.

best be regarded as a single microclimatic index, hygrothermal stress (Price et al., 1987). The buffering effects of galls varied significantly with time of day and were most pronounced in the afternoon, when hygrothermal stress

peaks. Hence, galls possess a hygrothermal inertia slowing down rates of change of conditions within galls, but otherwise appear to track ambient temperatures. Modifications of the environment by gall-inducers were most apparent in immature galls, in which larvae were presumably active; the buffering effects measured fell off sharply as galls matured and dried out. Regardless of size, immature galls effectively buffered against desiccation.

Other demonstrated cases of arthropods reducing desiccation stress through modifications in behaviour and physiology include seasonal changes in burrow depth and distance from shore in supralittoral amphipods (Williams, 1995), aggregation during diapause in tropical fungus beetles (Yoder et al., 1992), construction of a cocoon during pupation in the moth *Acrolepiopsis assectella* (Zeller) (Nowbahari & Thibout, 1990), and gall induction in overwintering cynipid wasps on roses (Williams et al., 2002). However, direct measurements of relative humidity and temperature in gall tissues, as well as their consequences for larval survival, have rarely, if ever, been carried out. In an investigation of a non-galling parasitoid wasp, Tagawa (1996) compared survival rates of intact pupae in their cocoons with those of naked pupae under varying levels of relative humidity. Survival rates of naked pupae at 100% relative humidity approached those of intact pupae and were significantly higher than those under lower humidity levels, suggesting the cocoon functions adaptively, at least in part, to reduce desiccation stress.

Our experimental data suggest that *A. quercuscalifornicus* larvae require the buffering effects of galls. Although increasing relative humidity levels in the experimental chambers extended larval survival time significantly, larvae never survived more than 2 h once extracted from galls. The 40 °C temperature in the experimental chamber would not by itself seem to endanger the larvae, because, as indicated above, ambient temperatures routinely reach this level during summer in the Sacramento Valley. Because of the short survival time of both treatment and control larvae, we assume the potentially confounding role of starvation affected both groups equally.

In phytophagous insects, galling and leaf-mining may be regarded as parallel feeding strategies. Although leaf-mining species modify their environment comparatively slightly, both guilds are endophagous, and both may gain adaptively from modifying their microenvironments (Cornell, 1989). Connor & Taverner (1997), in their review of the adaptive significance of the leaf-mining habit, found no experimental evidence that leaf-mining reduces the risk of mortality from desiccation in the gracillariid moth *Cameraria hamadryadella* (Clemens), although temperature extremes in occupied mines are moderated. However, relative humidity levels inside mines were not

assessed, perhaps because of the technical difficulties of doing so. The relatively large galls of *A. quercuscalifornicus* facilitated our collection of both temperature and relative humidity data in positions adjacent to where larvae fed, although the tools available to us made it exceedingly difficult to gather data directly from the larval chamber without injuring or killing the larvae. Future research efforts could devise methods to compare conditions inside the larval chamber to those directly adjacent to larvae.

The buffering effects of the galls are most pronounced in immature galls in the growth phase. Toward the end of pupation, mature galls become desiccated and harden, especially tissues of the larval chamber. As indicated above, the microclimate inside the larval (pupal) chamber is unknown. However, as the surrounding pithy tissue constitutes at least 95% of the volume of the entire gall (DG Miller, CT Ivey & JD Shedd, unpubl.), its buffering effect on the larval chamber is likely highly significant.

Support found for the microclimate hypothesis for the adaptive value of galls complements, but does not supplant, the natural-enemy and nutrition hypotheses. Beyond conferring a microclimatic advantage to their occupants, the large galls induced by *A. quercuscalifornicus* and other cynipids may aid in protection from natural enemies, such as parasitoids (Jones, 1983). However, larger galls of some insects are more frequently targeted by avian predators (Abrahamson & Weis, 1997), and the moist microclimate in galls can increase the risk of attack by fungal pathogens (Cornell, 1989; Danks, 2002), in spite of the fungicidal effects of concentrated tannins and phenolic compounds in galls (Stone et al., 2002).

Through its modifications of host plant tissues, *A. quercuscalifornicus* is a keystone species for its ecological community. Hence, larvae act as miniature ecosystem engineers (Jones et al., 1994; Danks, 2002), facilitating living conditions not only for themselves, but for a variety of other species in succession (Wiebes-Rijks & Shorthouse, 1992). For example, while they are occupied by gall-inducers, galls are also shared by parasitic and inquiline cynipids and other wasp and moth larvae. In particular, parasitoids occupying galls benefit by feeding as koinobionts initially before killing the host larvae, so as to preserve favorable conditions for development within the gall (Askew & Shaw, 1986). Even after galls are abandoned by *A. quercuscalifornicus* and have fallen to the forest floor, they may be occupied by opportunistic ants, solitary bees, and beetles.

In our study population, initiation and growth of galls occur in both spring (March–May) and late summer (July–September) (DG Miller, CT Ivey & JD Shedd, unpubl.). The second period of gall induction is noteworthy, as it occurs approximately during the secondary leaf flush, during the long summer drought. Regardless of the season of gall initiation and maturation, the emergence of the adults is timed approximately with leaf fall and acorn maturation in late autumn (November–December). The buffering effects of the summer-developing galls may be more pronounced, as ambient conditions are warmer and drier than in the spring. Low tannin and high nitrogen levels found in newly-emerged oak leaves may favour phytophagy in spring, as witnessed in lepidopteran communities on *Quercus robur* L. (Feeny, 1970). By extension, gall induction in *A. quercuscalifornicus* might otherwise be restricted to the spring growing season, yet late-season galls are abundant in the Sacramento Valley. Perhaps the discrete periods of gall induction reflect a recent loss of a distinct, sexual generation of gall-inducers, as seen in typical cynipids (Kinsey, 1920; Askew, 1961; Csóka et al., 2005). Under this scenario, seasonally alternating generations of parthenogenetic and sexual wasps may have retained the dual period of gall induction, but lost sexual reproduction from one phase of galling activity. Alternatively, multiple galling phases function to disrupt the seasonal tracking of *A. quercuscalifornicus* by its natural enemies (Stone et al., 2002). These hypotheses await investigation through the application of phylogenetic and ecological methods.

Acknowledgments

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