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Interactions between oak tannins and parasite community structure: Unexpected benefits of tannins to cynipid gall-wasps

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Abstract. Plant species vary tremendously in the number of phytophagous species they support. May (1979) and Price (1980) proposed that some of this variation may be due to variation in biochemical defenses. We find that variation between oak species in leaf tannin levels is *positively* correlated with 1) variation in the numbers of species of leaf-galling cynipid wasps those trees host; and 2) the density of individual galls per oak leaf. We hypothesize that leaf and gall tannins serve a protective function for cynipids, decreasing the amount of cynipid larval mortality due to fungal infestation. This defensive function would explain the observed positive relationships between oak tannin levels and cynipid diversity as well as cynipid abundance.

Key words: Oak – Cynipid gall-wasps – Species number – Tannin

May (1979) and Price (1980), as well as others, have proposed that much of the tremendous variation among plant species in the numbers of phytophages that utilize them may be due to variation among plant species in biochemical defenses.

Many studies of phytophages and plant chemical defenses have measured the efficacy of specific purported defenses against specific phytophages (Jones 1962, 1972; Ehrlich and Raven 1964; Feeny 1968; Gilbert 1971, 1975; Sen Gupta and Miles 1975; Roeske et al. 1976; Fox and Macauley 1977; Bernays 1978; Reese 1978; Schoonhoven and Meerman 1978; Morrow and Fox 1980; Edmunds and Alstad 1978; Carroll and Hoffman 1980; Bernays and Woodhead 1982). The effects of these plant chemicals on the herbivores studied has ranged from lethality through neutrality to beneficiality. Extrapolating the results of these studies to predictions about the effects of plant chemicals on the phytophage community as a whole is very difficult.

Clearly plant chemicals can influence phytophage community structure. Faunal similarities of some plants have been reported to mirror their chemical similarities (Berenbaum 1981, 1983; Rowell-Rahier 1984). Plant chemistry also influences the degree of phytophage specialization (Hendrix 1980; Price 1980; Berenbaum 1981; Rowell-Rahier 1984). The question still remains as to how these effects translate into effects on phytophage species-richness.

Karban and Ricklefs (1984) find no effect of variation in purported chemical defenses in the species richness of lepidopteran larvae on deciduous trees in southern Ontario. On the other hand Rowell-Rahier (1984) finds that the chemical defenses of *Salix* species do influence the species richness of their weevil, sawfly, and caterpillar herbivores. Those willows with proanthocyanidins but no phenolglycosides have more herbivore species than those with phenolglycosides but no proanthocyanidins. Other authors (Hendrix 1980; Price 1980, pp 34–36) have also attributed observed differences in species richness to unquantified differences in chemical defenses.

The relationship between plant allelochemics and phytophage diversity may be very complex with variation among phytophage taxa in the degree and even the direction of response phytophage species-richness to plant allelochemicals. The patterns will probably depend on the degree of a phytophage taxon's adaptation to the host allelochemicals. Adding to the complexity, plant biochemical defenses can vary in quantity as well as in kind.

In this paper we examine the effects of quantitative variation in a single class of allelochemicals (tannin) among a set of taxonomically related host plants (oaks) on the diversity of a group of highly adapted phytophages (cynipid wasps).

The questions

This study was designed to answer the following two questions concerning the influence of oak lead-tannin levels on the community structure of leaf-galling cynipid wasps using oak species. 1) Is the leaf-tannin level of an oak species related to the number of species of leaf-galling cynipid parasites that use that tree? If so, is the correlation positive or negative? 2) Does an oak species' leaf tannin level affect the density of individual cynipid galls utilizing it?

The system

The *Quercus*/cynipid wasp system is an excellent one for studying the effects of allelochemics on the diversity and ecology of plant parasites. *Quercus* diversity is considerable, with approximately 50 species of oaks in the United States. Oaks possess a class of allelochemic phenolic compounds known as tannins. Also, oaks invest heavily in leaf tannins: as much as 35% of the weight of leaves may be phenolics (Belserene 1980). Tannins act broadly as protein precipi-

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tants, and therefore may serve as "dosage dependent defenses" or "quantitative defenses" in the terminology of Feeny (1975, 1976) and Rhoades and Cates (1976) (but see Zucker, 1983, for a contrary opinion). Tannin content is known to vary among *Quercus* species. These between-species differences in biochemical defenses may be correlated with faunal differences. Unfortunately, this variation has not yet been systematically and quantitatively surveyed (Parker 1977).

As there are approximately 580 species of cynipids parasitizing the United States oaks (Cornell and Washburn 1979 after Weld 1957, 1959, 1960), phytophage species richness is great enough for statistically meaningful comparisons of diversity. Furthermore, the cynipids comprise at least 93% of all gall makers on *Quercus* species (Cornell and Washburn 1979 after Felt 1940). This concordance between the taxon of cynipids and the guild of gall makers facilitates ecological interpretation.

Host range size has been the most generally successful predictor of phytophage species diversity. Thus it is advantageous that the relationship between the geographical range of an oak species and the diversity of its cynipid fauna has already been investigated by Cornell and Washburn (1979) and Cornell (1985).

Methods

Oak and wasp species

The data for the occurrence of leaf-galling cynipid species on different species of oak trees were extracted from species lists published by Weld (1957, 1959, 1960). For the California oaks revisions in cynipid occurrences by Cornell (1985) and others are included (Doutt 1959; Lyon 1959, 1963, 1969; Burnett 1974). Gall species can be counted two ways: 1) including only those species that are properly described with latin binomials or 2) as well all the distinct gall morphologies described and photographed by Weld. Method 1) will be hereafter referred to as "described species", and method 2) will be designated "all forms". Both methods have advantages and disadvantages. Using only described species may underestimate the number of cynipid species parasitizing an oak. Cynipids are often heterogonic, having alternate generations with distinct forms. Counting "all forms" is likely to overestimate the fauna by including non-cynipid galls and heterogonic forms of cynipids already included. Unknown heterogony is certainly possible even in described cynipids, but it is less likely. Cornell and Washburn (1979) and Cornell (1985) use all the gall forms found. We have done our analyses using both indices. Since the results differ little, we will in general limit our discussion to described species.

Cornell (1985) includes one species of oak (*Q. dunnii*) which we have not used because it has not been sufficiently sampled. We have added two species of oaks that Cornell did not consider (*Q. englemanii* and *Lithocarpus densiflora*). *Lithocarpus densiflora* is an oak closely related to *Quercus*.

The area of oak ranges was derived from planimetry of range maps in Little (1971, 1976). For the most part our ranges agree with those used by Cornell and Washburn (1979), and Cornell (1985). We believe, however, that ranges based on Little's maps supersede those used by Cornell and Washburn because their original sources, as well as others, were considered in Little's compilations.

Gall wasp densities

Estimating cynipid gall densities on a individual tree is difficult since cynipid densities vary considerably from leaf to leaf, branch to branch, tree to tree, region to region and year to year (Washburn and Cornell 1981). Herbarium collections contain samples collected over a long period of time from a large number of locations and thus average out local fluctuations. Because collectors tend to take undamaged specimens. Herbarium specimens are probably biased, underestimating cynipid gall densities in the field.

However, it is important to realize that herbarium collections were made in complete ignorance of the average leaf tannin levels of oak species. Thus the ranking of gall densities should be unaffected by historical collection bias, even though absolute densities may be suspect. For this reason we have chosen to only use nonparametric rank statistics when analyzing our gall density data.

Data was collected using herbarium specimens of the following collections: The California Academy of Science, the Dudley Herbarium of Stanford University, the Rancho Santa Ana Herbarium, and the San Diego Museum of Natural History.

Each herbarium specimen was visually scanned and the kinds and numbers of cynipid galls found on its exposed surface recorded. Gall types were identified from descriptions in Weld (1959). The area of exposed leaf surface was estimated for each specimen by placing a clear plastic sheet with a grid of squares over the sample and counting each square that was more than half filled by leaf. Each square was 3 cm on edge. This grid underestimates the leaf area for samples with small leaves widely spread apart. For these samples a grid with squares 1.5 cm on edge was used. In the majority of samples, two grids gave the consistent results, for those that had large leaves or overlapping. Overall, 240,000 cm^2 of exposed leaf area in 703 samples were surveyed. All tree species used were represented by at least 27 samples and a surveyed leaf area of 9300 cm^2 (av no. of samples = 60, s.D. = 28; Av leaf area = 20,000 cm^2, S.D. = 10,400 cm^2).

Tannin assays

The assay we have developed to quantify tannin levels is a modification of the "hemanalysis" assay (Bate-Smith 1973a, 1973b, 1977; Swain 1979). The major mode of biological action of tannins is thought to be their ability to precipitate proteins. (Feeny 1968, 1969, 1970; Goldstein and Swain 1965). Our assay quantifies this functional activity of the tannins in a leaf powder sample by measuring the sample's ability to precipitate hemoglobin. Thus our assay does not strictly measure tannins but rather astringency, or protein precipitating ability.

Most of the leaves collected for tannin assays came from tree species that were sampled at a single geographic site. Collections were made of fully mature leaves. The Pacific Coast oaks were collected in late April. The Atlantic Coast oak leaf samples were collected at the end of June and the beginning of July. Leaf astringency will change slowly if the leaf is left undried and exposed to air at ambient temperatures. However, frozen samples are remarkably stable. Samples have been stored for 5 years without significant change in astringency. In the field, samples were frozen over dry ice, usually within an hour of collection.

Dried ground leaf powder is shaken with a known amount of hemoglobin for a standard time. Afterwards both leaf powder and precipitated hemoglobin are removed by centrifugation. The hemoglobin remaining in solution is determined spectrophotometrically. The amount precipitated is the difference between the initial quantity of hemoglobin and that remaining in solution. The assay was calibrated using commercially prepared tannic acid (Sigma Chemical Co.). A relative measure of astringency for a sample can be derived by dividing the amount of tannic acid required to precipitate the same amount of hemoglobin as the sample by the weight of the leaf sample. This relative astringency is reported as the tannic acid equivalent (T.A.E.) of the sample. Because relative astringency is a common measure of a real biological activity, we feel that for ecological comparisons hemanalysis is superior to the identification of individual tannin moieties, or the estimation of general chemical classes (e.g. proanthocyanidins, hydrolysable tannins, total phenolics).

Our procedures have been altered from those developed by Bate-Smith in several ways. Solutions of lyophilized hemoglobin (purchased from Sigma) have been substituted for fresh osmotically shocked blood. We buffered the system (0.01 M citrate buffer pH 4.8) since the assay is pH sensitive and variation in the size of the leaf powder sample is enough to change the pH significantly. We find that the reaction is not complete after 5 minutes; under our conditions, precipitation increases more or less linearly for 10–12 h before it reaches a plateau. Consequently, the incubation period in our assay has been extended to twelve hours at a constant temperature of 19° C. We suspect that the long period over which hemoglobin continues to be precipitated is due to the slow equilibration of tannins bound to other substances either naturally in the leaf or during the preparation process.

We utilize the direct precipitation of hemoglobin with finely milled leaf powders, ground to pass no 120 mesh screen (as reported by Bate-Smith 1977). Leaf moisture is variable. To avoid making comparisons which are based largely on moisture content and less on tannin content, we freeze-dry our leaves prior to grinding. With these modifications our assay yields a coefficient of variation of about 5–10% among duplicate samples.

The tannin levels of oak leaves are known to undergo phenological changes, however, there is no general pattern to these changes. Feeny (1970) indicates that tannins in *Quercus robur* increase throughout the season, while Belserene (1980) found the astringency of *Q. wislizenii* to decrease. The work of Schultz and Baldwin (1982) indicates that, although there is between-tree variation, the astringency levels of *Q. rubra* are constant throughout June and decrease somewhat at the end of July. A broad survey of the tannin phenology of a number of oaks would be of great interest but was not possible in this study. We will show, in a comparison between the Pacific and the Atlantic coasts, that neither the altitudes nor the slopes of the regressions of cynipid diversity on leaf astringency differ significantly between the regions. We interpret this to mean that the differences between collection dates in the two regions has not substantially influenced our results.

The specific identities of all specimens were verified by either Dr. J. Tucker of U.C.D. or Dr. W. Hardin of U.N.C. Any specimens that were suspected, by these authorities, of having a hybrid character have been eliminated from the data set. For a few tree species this resulted in an unfortunate reduction in sample size.

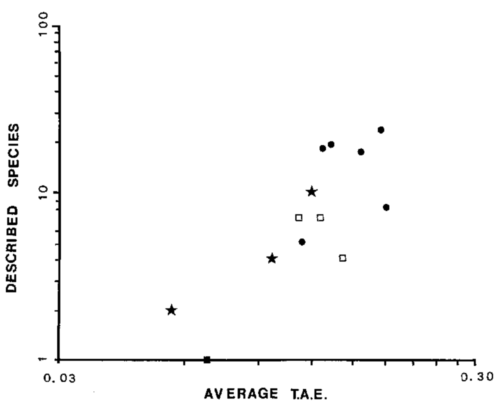

Fig. 1. The described leaf-galling cynipids of the Pacific region plotted against the average T.A.E. (tannic acid equivalents) of the host oak. Circles are white oaks; open squares are black oaks; stars are intermediate oaks. The filled square is *Lithocarpus densiflora*

Results

Cynipid diversity and host-oak leaf tannins

We first studied the relationship between the number of cynipid species utilizing a species of oak and that oak's characteristic tannin level in a survey of Pacific Coast oaks. We find a highly significant positive correlation between the log of mean leaf tannin level and the log of the number of leaf galling cynipid species ($r = 0.80$, d.f. $= 11$ and $P < 0.005$).

Despite the significance of the regression the interpretation of these results is far from clear. Inspection of Fig. 1 reveals a great deal of taxonomic clustering. That is, although the white oaks have both high levels of tannins and high numbers of cynipid species, the black oaks have low tannin levels and low numbers of species. The intermediate oaks have intermediate levels of both. This raises the specter of spurious correlation. Perhaps the differences in numbers of cynipid species are due to some other difference between the subgenera which has not been studied. This relationship between oak subgenera and number of cynipid species has also been noted by Cornell (1985). He attributes it loosely to "taxonomic isolation".

We resolved this problem by surveying the leaf-tannin/cynipid relationship in the oaks of the Atlantic seaboard. In these eastern oaks, no relationship exists between subgenera and number of leaf-galling cynipid species. Of the 28 species of oaks that Weld (1959) considered adequately sample for cynipids, fourteen are white oaks and fourteen are black oaks. Seven species of each subgenus have above the median number of cynipid species and seven species of each subgenus have below the median number of cynipids.

The leaf-tannin/cynipid species number relationship for the oaks of the east coast is very similar to that on the west coast. The correlation of the log-log transformed data is highly significant ($r = 0.72$, d.f. $= 16$ and $P < 0.001$).

The slopes and elevations of the double logarithmic regression for the east and west coast oaks were compared with F-tests (Zar 1984 pp 292–298). No significant differ-

Table 1. Characteristics of Pacific region oaks. The column headed "All Forms" includes gall types from which adult wasps have not yet been reared and described. The column headed T.A.E. lists relative acerbities, measured by hemananalysis and reported as tannic acid equivalents (T.A.E.). The number of trees sampled indicates the sample size used in estimating the average T.A.E. The standard error is the error of the estimate of average T.A.E.

Pacific region oaks

Taxon	Species	Number of described cynipids	"All forms"	Range $mi^2 \times 100$	T.A.E.	No. of trees sampled	Standard error
Leucobalanus (white oaks)	*douglasii*	23	29	216	0.177	2	0.013
	dumosaa	17	25	167	0.158	31	0.004
	durata	8	15	25	0.182	5	0.016
	engelmanii	5	9	100	0.114	7	0.016
	garryana	18	22	213	0.128	1	–
	lobata	19	26	336	0.134	4	0.005
Erythrobalanus (black oak)	*agrifolia*	7	10	310	0.112	8	0.015
	kelloggii	4	4	319	0.142	10	0.005
	wislizenii	7	10	270	0.126	8	0.013
Protobalanus (intermediate oaks)	*chrysolepis*	10	30	266	0.120	3	0.008
	tomentella	2	4	5	0.056	7	0.004
	vaccinifolia	4	7	86	0.097	4	0.003
Lithocarpus (tan oak)	*densiflora*	1	1	86	0.068	4	0.008

Table 2. Characteristics of Atlantic region oaks. Explanation of column headings as in Table 1

Atlantic region oaks

Taxon	Species	Number of described cynipids	"All forms"	Range $mi^2 \times 100$	T.A.E.	No. of trees sampled	Standard error
Leucobalanus (white oaks)	*alba*	29	39	9,342	0.166	7	0.009
	bicolor	16	18	3,050	0.123	8	0.005
	macrocarpa	17	20	8,895	0.124	3	0.007
	prinoides	7	8	6,580	0.151	4	0.009
	prinus	13	16	2,952	0.115	8	0.004
	stellata	20	29	7,698	0.237	3	0.006
	virginiana	6	8	3,083	0.050	4	0.009
Erythrobalanus (black oaks)	*ilicifolia*	13	16	1,576	0.123	4	0.004
	incana	3	3	2,942	0.069	3	0.014
	falcata	11	11	5,285	0.088	5	0.017
	laevis	5	5	1,536	0.115	5	0.010
	laurifolia	8	8	2,057	0.071	4	0.009
	marilandica	11	14	7,135	0.162	3	0.021
	nigra	5	5	3,923	0.065	3	0.009
	palustris	8	8	3,337	0.143	4	0.025
	phellos	7	13	3,830	0.083	4	0.010
	rubra	20	23	10,961	0.179	10	0.021
	velutina	18	19	8,134	0.191	4	0.030

ences were found and the data for the two regions can be pooled. The slope for the pooled log-log regression was 1.36 and the intercept equaled 5.09 with $r^2 = 47\%$ and $P < 0.001$ (d.f. = 29). In this larger data, set both the white oaks and the black oaks show clear within-subgenus positive correlations between the number of species and tannin levels. The untransformed correlation between the number of species of leaf-galling cynipids on black oaks and the tree species average T.A.E. is 0.690, significant at the 0.01 level with d.f. = 12. The log-log transformation is also significant, but at the 0.05 level.

For the white oaks the parametric correlation between the number of gall species and leaf-tannin levels falls just short of statistical significance ($0.1 > P > 0.05$), regardless of which transforms are used. However, unlike the case for pooled data, the residuals from the white oak regression show considerable deviation from normality. A non-parametric Spearman rank order correlation is thus more appropriate for the white oaks and reveals a significant positive relationship between species number and leaf-tannins ($P = 0.616$, $P < 0.05$, d.f. = 11).

Cynipid diversity and host-oak geographic range

As discussed in the introduction, host geographic area has often been a significant predictor of the number of phytophagous insects species utilizing the host. Cornell and Washburn (1979) have indicated that cynipid diversity is

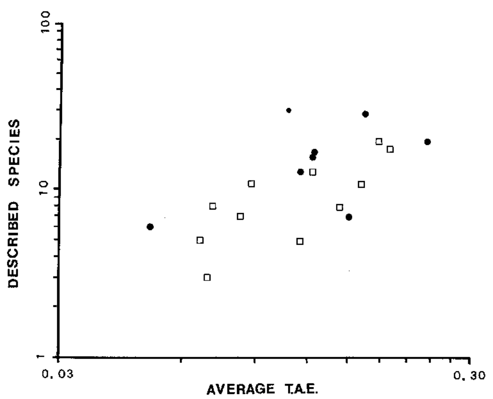

Fig. 2. The described leaf-galling cynipids of the Atlantic region plotted versus the host oak's average T.A.E. Symbols are as in Fig. 1

also positively correlated to the host's range. Their study, however, did not differentiate between leaf galling cynipids and cynipids attacking other parts of the tree. Data in a more recent study (Cornell 1985) show that leaf-galling cynipids in California are not significantly correlated to oak range. We also find that the correlation with host area is positive but not significant. This is true whether cynipids are counted as "described species" or as "all forms", and regardless of whether the data is log-log transformed or untransformed. The effect of host area on the west coast oaks can be explained entirely by its correlation with T.A.E. (log-log transform $r=0.532$, $n=13$, $P>0.05$). Forcing log-area into a multiple regression with log-T.A.E. only increases the r^2 value from 0.636 to 0.647, which is an insignificant improvement.

On the east coast the qualitative relationships between cynipid diversity, area, and leaf-tannin are similar. However, both the correlation of cynipid diversity to oak-range and the correlation of oak-range and leaf-tannins are significant. The stepwise regression of log-described species on log-T.A.E. and log-area enters only log-T.A.E., as does the stepwise regression of log-"all forms".

When the data for the east and west coasts are combined, T.A.E. was always entered first in stepwise regressions. In the stepwise regressions of "all forms" (or log-"all forms"), T.A.E. or log-T.A.E. are the only variables entered. In the regressions of described species (or log-described species) both the tannin and the area variables are entered. The addition of the independent variable log-area to the regression of log-described species on log-T.A.E. improves the r^2 from 0.469 ($P<0.05$) to 0.578 ($P<0.01$). This is a statistically significant improvement ($P<0.025$).

Cynipid density and oak leaf tannins

Figure 3 shows a semi-logarithmic plot of the average number of galls per cm^2 of leaf area in herbarium specimens versus the species average T.A.E. for 11 Atlantic oak species. The positive relationship between gall density and leaf-tannin level is significant using the nonparametric Spearman rank order correlation test $P=0.800$, $n=11$, $P<0.005$). Interestingly, this is also exactly the rank correlation between density and "all forms", and similar to the rank correlation between density and "described species" (density/"described species" $=0.776$, $n=11$, $P<0.05$).

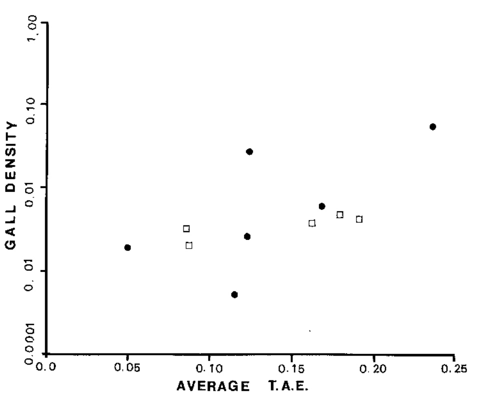

Fig. 3. Gall density on the leaves of eleven east coast oaks plotted versus the average T.A.E. of the oak species. Gall density is in galls per square centimeter of exposed leaf surface. Symbols are as in Fig. 1

Discussion

Do cynipids respond to leaf phenolics in a "qualitative fashion"?

Zucker (1983) has hypothesized that tannins are highly specific and that it is the presence or absence of specific phenolics that will determine if a phytophage can occur on a species of tree. This would mean that the number of species of leaf phytophages using oak species should be correlated with the number of *kinds* of phenolics in their leaves. This is not the case with oaks and cynipids. Li and Hsiao (1974) have published the results of fingerprint chromotography of the phenolics of the leaves of 49 U.S. oaks. They record the occurrence of more than 60 recognizable phenolic residues. Using their data, we found no significant correlation between the number of leaf-galling cynipid species using an oak species and number of different phenolics in the oak's leaves (Taper and Case unpublished work).

Furthermore under Zucker's hypothesis one would expect that oaks with similar sets of phenolics would have similar sets of cynipid species. This also is not the case. For all pairs of oaks we computed two Sørenson (1948) similarity coefficients: one based on Li and Hsiao's phenolic data and the other on cynipids. No correlation, even approaching significance, emerged between these similarity measures.

Plant allelochemics and phytophage diversity

The degree to which plant allelochemicals are detrimental to herbivores depends greatly on the degree that the herbivores have adapted to the host (Berenbaum 1980; Smiley et al. 1985). Cynipids have been parasitizing oaks for an extremely long time; Burnett (1977) estimates that the association is probably older than twenty million years, and Cornell (1983) feels that it is at least thirty million years. It is plausible that in this time cynipids have not only evolved defenses against the oak tannins but have also evolved means by which to utilize tannins for their own benefit. In short, it is reasonable to view tannins as a potential resource for cynipids just as cardiac glycosides may be for monarch butterflies.

We find positive correlations among leaf-tannin levels, cynipid diversity, and cynipid abundance. An hypothesis explaining these relationships is that tannins may aid in the defense of cynipid larvae either from hyper-parasites, from generalized leaf herbivores, from fungal pathogens or from some combination of these factors. Larew (1982) and also Clive Jones (pers. comm.) have shown that tannins are in low concentrations in the tissue actually being eaten by the larvae but are in much higher concentrations in surrounding gall tissue. Furthermore, they are often in higher concentration in this surrounding tissue than they are in leaf tissue itself (Howes 1953). Evidence supporting the direct role of tannins in cynipid defense is presented elsewhere (Taper et al. 1986; Taper 1987), but it appears that fungal infestation is often the most significant source of mortality to cynipids and that tannins, known antifungal agents (Williams 1963; Feeny 1970; Harborne and Ingham 1978; Cruickshank 1980), have a role in reducing that mortality. Taper et al. (1986) show that cynipid mortality due to fungal attack is lower in the higher tannin regions of *Q. agrifolia.* Taper (1987) has found subsequently that a similar reduction in mortality apparently due to fungus attack can be brought about by the artificial application of tannic acid to leaves with cynipid galls on them. In a similar sequence of research, Faeth (1985, 1986) has reported that leaf-miners on damaged *Q. emoryi* leaves suffer a lower mortality than on undamaged leaves, and that damaged emory oak leaves have higher levels of condensed tannins than undamaged leaves (Faeth 1986). Finally, Faeth and Bultman (1986) show that artificial applications of tannins to oak leaves will also bring about a reduction in mortality to leaf-miners. These authors also believe it is likely that the observed decreases in mortality are due to decreased fungal and bacterial attack.

Of course, we must make the caveat that oaks vary in other aspects of their chemistry as well as tannins. Some other constituent, correlated to tannins, could actually be the causal factor driving our observed relationships. However, the results of manipulative experiments by Taper (1987) and Faeth and Bultman (1986) make this alternative less likely.

The increase in cynipid abundance with the increase in host allelochemics becomes eminently reasonable when considered in light of this hypothesized role of oak tannins in cynipid defense. However, why cynipid species richness should increase with increasing oak leaf tannins is not self-evident.

We entertain two hypotheses regarding this relationship. Both chains of reasoning assume that the primary effect of increased oak leaf tannin levels in the increase in cynipid gall-wasp population sizes, and that these increased population sizes then lead, in turn, to the evolution of increased species-richness. First, it is believed that extinction probabilities are negative functions of population size (MacArthur 1972; Leigh 1981; Goodman 1986). All else being equal, decreased extinction rates will lead to an increased species-richness (MacArthur and Wilson 1967). The observation of Washburn and Cornell (1981) that local populations of cynipid gall-wasps can be subject to extinction lends weight to this hypothesis.

In our second hypothesis, increased species-richness is caused by an increased selection by hyperparasites for cynipid divergence in "escape space". Askew (1980) has indicated that in parasitic communities when the densities of the primary hosts (cynipid species in our case) are low then parasites are generally specific or monophagous. On the other hand, when the densities of primary hosts increase polyphagous parasites enter the community. It is only when parasites are polyphagous that there is selection pressure for divergence in "escape space". Thus, if trees with higher leaf-tannins level have higher densities of cynipids they should also, over evolutionary time, develop hyperparasitic faunas that are richer in polyphagous hyperparasites; the cynipids should then experience an increase in selection for divergence in "escape space". The net result of this argument is that trees with higher tannin levels should have more diverse cynipid faunas.

This second argument is quite hypothetical particularly since knowledge of the ecology of the tannin/fungus/cynipid interaction is still rudimentary. Furthermore the general characteristics of hyperparasitic food webs based on cynipids galling American oak-leaves are virtually unknown. There are only a few studies of these food webs (Washburn and Cornell 1979, 1981) and each of these has focused on a single cynipid primary host so that estimates of polyphagy are currently impossible.

Much further field work will be required to determine if either of these hypotheses is responsible for the observed association between increased oak leaf tannin levels and leaf-galling cynipid species-richness. Yet, this pattern of increased species-richness with increased host allelochemical defenses is not entirely unprecedented in the literature. Wratten et al. (1981) and Edwards et al. (1986) have found that the number of leaf phytophage species utilizing trees in Britain is negatively correlated with palatability to a native herbivore of foliage. The pattern is also found in the work of Berenbaum (1981). Our analysis of her data shows that the number of herbivore species utilizing an Umbellifera species is positively correlated to the number of furanocoumarin compounds produced by the Umbellifera ($r = 0.745$, $n = 12$, $P < 0.01$). Also a Kruskle-Wallis test indicates that the species of Umbellifera with two classes of "defensive" compounds have significantly higher abundances of herbivores than those with one or none ($H = 8.8$, d.f. $= 2$ and $P < 0.025$). This increase in herbivore density is due to a large increase in the density of specialist herbivores.

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