

HYPOTHESES ON THE ADAPTIVE NATURE OF GALLS

PETER W. PRICE, GWENDOLYN L. WARING,
AND GERALDO WILSON FERNANDES

Department of Biological Sciences, Box 5640, Northern Arizona University,
Flagstaff, Arizona 86001.

Abstract.—Hypotheses on the adaptive nature of galls are reviewed. The Non-adaptive, Plant Protection, Mutual Benefit, Nutrition, Microenvironment, and Enemy Hypotheses are evaluated and the last three are supported. Questions in need of study are suggested for each of the viable hypotheses.

The adaptive significance of insect galls has been discussed in the literature many times, but little emphasis has been placed on testing hypotheses. To foster such activity we review the ideas generated in the literature and suggest studies needed to evaluate the hypotheses.

Bequaert (1924) regarded gall characters as having no selective value—*The Nonadaptive Hypothesis*. He noted that nectaries on galls performed no important function. However, Washburn (1984) showed that nectaries on galls attract ants that suppress parasitism on the galler from 48% in their absence to 25% in their presence. Other adaptive features, discussed later, include increased nutritional quality of the gall and reduced chemical defenses. There seems to be no support for this hypothesis and it will not be considered further.

Mani (1964) has argued that galls are a form of plant defense by which the plant encapsulates a herbivore—*The Plant Protection Hypothesis*. However, galls reduce growth and reproduction of plants (e.g. Craig et al., 1986). Also, if galling capability is a plant defensive trait we should see galling strongly linked to plant phylogenies, as are chemical defenses such as mustard oils, cardiac glycosides and alkaloids. In fact analysis of lists in Felt (1940) clearly indicate that phylogenetic links are much stronger with the galling taxa than with the plant taxa. The first line of plant defense against a galler seems to be resistance to gall formation (e.g. Whitham, 1980). Therefore, we do not regard this as a viable hypothesis.

Cockerell (1890) suggested that galls act as protection for the plant and abundant food for the galler—*The Mutual Benefit Hypothesis*. However, gallers reduce plant reproduction (except fig wasps), and must be regarded as parasites (Weis and Kapelinski, 1984). No increased fitness in galled plants has ever been demonstrated (except the figs), so the hypothesis must be rejected.

Many authors have noted higher concentrations of potentially nutritive compounds in galls, such as nitrogen, protein, phosphate, and lipids (e.g. Shannon and Brewer, 1980), as well as reduced defensive chemicals (e.g. Meyer, 1957)—*The Nutrition Hypothesis*. In our own studies on *Euura lasiolepis* Smith, total protein is higher, and total phenols are much lower in gall tissue than in equivalent

tissue in ungalled shoots. A weakness in this hypothesis is that nutritional requirements of gallers are largely unknown. Therefore, two questions that need to be studied are: 1. Do increased "nutrients" in the gall really improve nutritional quality for gallers?; and 2. Do reduced defenses improve survival of gallers? At present there is support for the nutrition hypothesis, but it is correlational in nature, not mechanistic.

Felt (1940) took it for granted that galls provide food and protection for the galler, with emphasis on "shelter from the elements." Which physical factors are of importance is debatable. Plant tissue follows ambient temperatures closely, so insulation is unimportant, as confirmed for gallers by Uhler (1951) and Baust et al. (1979). Hygrothermal stress seems to be a more likely selective force in this *Microenvironment Hypothesis*. On an altitudinal gradient from the San Francisco Peaks down into the Sonoran Desert in Arizona, Wilson Fernandes has documented a significant increase in the number of galling species in the drier environments at lower elevations. Such a pattern is not seen in riparian habitats on the altitudinal gradient, indicating that altitude is less important than dryness of the habitat. Therefore, the microenvironment hypothesis is supported, although again the evidence involves correlation. Answers to the following questions would help in testing this hypothesis: 1. What are the benefits of transitional stages between free leaf feeders and gallers (e.g. leaf folders)? 2. What are the global geographic distributions of galling species richness?

Many authors have noted the protective nature of galls against natural enemies, particularly parasitoids. Larger galls reduce parasitoid attack (e.g. Weis et al., 1985), and diversity of gall types in a community has been accounted for by selection for divergence by parasitoids (e.g. Askew, 1961; Cornell, 1983)—*The Enemy Hypothesis*. One problem with the hypothesis is that gallers without parasitoids seem to show divergence of gall types as well developed as those with parasitoids (e.g. eriophyid mites, *Pemphigus* aphids, and *Adelges* galls without parasitoids, compared to cynipid, cecidomyiid and tenthredinid galls with parasitoids). Another problem is that divergence in gall morphology frequently does not reduce access to parasitoids, as in *Neuroterus* spangle galls on oak leaves (cf. Darlington, 1975). Also, larger *Pontania* galls are more heavily parasitized than smaller galls in the Flagstaff area (Karen M. Clancy, personal communication), so large gall size is not always associated with better protection. Finally, an alternative hypothesis seems to be equally viable: genetic drift results in divergence of gall morphology because there is no stabilizing selection keeping galls of reproductively isolated species the same in morphology. Thus, two questions need to be addressed: 1. Does character displacement occur in gall morphology? 2. Do galling species with parasitoids show more gall divergence than those without parasitoids? Since gall size provides protection against parasitoids in some cases, there is some support for this hypothesis. However, more studies are needed before its validity is adequately tested.

During the evolution of the galling habit two pathways have been followed, one via plant mining and boring (e.g. tephritid and agromyzid flies, and Lepidoptera), and the other via sedentary feeding, and production of differential plant growth (e.g. aphids, psyllids, thrips, mites, and cecidomyiids). The selective advantages involved with galling will be slightly different in each case. Plant miners are already protected from hygrothermal stress, so initiation of swelling in plant tissue during

gall formation would provide improved food supply and protection from enemies. Sedentary surface feeders which cause differential plant growth to form feeding depressions would benefit mainly from a more protected microenvironment, since nutrition and protection from enemies need not change. The further development of feeding depressions into closed galls would be favored by selection for improved microenvironment and nutrition, and reduced enemy attack.

Although the Nutrition, Microenvironment, and Enemy Hypotheses seem to be the most viable of the six discussed, none has been adequately tested and various problems need resolution. However, we hope that this discussion will revive the old debate on the adaptive nature of galls (e.g. Romanes, 1889; Wetterhan, 1889), and stimulate more detailed tests among hypotheses.

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