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Oak Galls: A Strange Biology Indeed!

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Two different oak galls. Top photo by John Hayden; bottom photo by Nicky Staunton.

Anyone who takes the time to look closely at several branches of oak will soon find one or another peculiar anomaly among the leaves and twigs. One can easily find structures resembling Ping-Pong balls, hard knots, fluffy tufts, horns—either single or clustered, or irregular thickenings, to mention just a few possibilities. These abnormal growths are galls, structures caused by the presence of small insect larvae living inside the tissue of the plant. Galls can be found on a wide variety of plants. They are common, for example, on the stems of goldenrods, and the leaves of maples, but oaks are host to a bewildering diversity of these little parasites. As many as 400 species of gall-forming flies, wasps, and mites have been documented to occur on white oak alone; and some 700 species of gall-forming wasps have been recorded for North America. Many, but certainly not all, parasitize oaks. Some oak gall-formers are restricted to white oak (*Quercus alba*), the 2011 VNPS Wildflower of the Year, others may occur on other species within the white oak group, and still others parasitize the red / black oak group.

In many cases, galls begin to form early in the season as new stems and leaves emerge from winter buds. What seems significant about this time frame is that host tissues are already in a state of growth; many plant cells are dividing and their daughter cells are enlarging as part of normal development. Concurrently, gall insects hatch from eggs that were deposited by adult female wasps or flies, either in late winter within the dormant bud itself, or in the newly emerging stems and leaves. Somehow, the presence of the insect alters the normal course of plant development so that, within a limited radius in the vicinity of the insect, more than the usual number of plant cells are formed and these extra cells become arranged in patterns unlike that of uninfected tissue. Insect larvae responsible for the gall can usually be found near its center. The gall provides the larva with food and protection. Usually, gall-forming parasites are described as having only a minimal negative impact on their host trees, especially if the infestation is not dense.

The spotted oak apple gall, found on leaves of white and post oaks, provides one example of gall structure. These galls are spherical and roughly the size of a Ping-Pong ball. The gall is thin-walled and its surface green with darker spots. Most of the volume of the sphere is composed of threadlike cells that radiate from a denser central mass containing the gall insect. These "oak apples" fall from the tree in autumn, and mature wasps (*Atrusca quercuscentricola*; synonym *Cynips centricola*) emerge before winter weather arrives. After mating, female wasps deposit eggs in the winter buds.

Details of how gall insects control growth of plant cells that form galls are not well understood. Secretions from the insect alter the plant's normal control of cell division and cell maturation. The secreted substances are sometimes described as "acids" or "enzymes," but such simplistic explanations are silent on what these alleged control substances do. In theory, one can imagine that insect secretions could alter gall-forming plant cells at genetic, biochemical, or physiological levels; i.e., various genes in the host plant may be turned on or off, synthesis of various plant molecules (e.g., hormones) may be enhanced or inhibited, or the cellular receptors for plant hormones may be rendered more or less sensitive. Almost certainly, control of gall growth is a complicated process, and, with equal certainty, one is tempted to assert that the details must vary depending on the taxonomy of the parasite (fly, wasp, or mite), taxonomy of the host (species of oak), location of the gall (stem, twig, or leaf), and morphology of the gall itself. In some cases, bacterial

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• Variety in galls is huge

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symbionts or viral parasites of the gall-forming insects have been reputed to play a role in gall formation. Regulation of gall development should be a fertile area for research.

Many oaks, of course, are deciduous; it follows that insects forming leaf galls in deciduous oaks necessarily complete their life cycles within a single year, as described above for the oak apple gall. On the other hand, stems and twigs are perennial, and galls that form on these organs can harbor insects with longer life cycles, up to three years in some cases. In another life cycle variation, some insects start their life on leaves, emerging from leaf galls as larval instars that then infect twigs of the same plant where they form yet another gall (stem gall) before completing their development. The wasp that makes oak fig galls inhabits twigs and roots in alternate life-cycle stages.

It is a given that normal plant structure is altered in the formation of galls. Chemistry, too, can be altered, and in the case of oaks, galls often contain higher than usual concentrations of tannins. In fact, tannin-bearing stem galls from several species of oak have a long history of use in making ink. The recipes vary in detail, but require extracts of gall tannins to be mixed with solutions of ferrous iron (Fe^{2+}) in the presence of a binder substance (usually gum arabic). The resulting ink is initially somewhat pale, but it gradually darkens to an intense purplish black that adheres very well to paper, vellum, or parchment. Unless neutralized, however, the acidity of oak-gall inks can degrade the writing surface. Galls from several European oaks (*Q. robur*, *Q. petraea*) are most prominent in this regard. Tannins from the gall oak (*Q. lusitanica*) of the Iberian Peninsula and Morocco are well known as sources of black dyes, and Native Americans had similar uses for oak galls from various species in North America.

Returning to natural themes, the ecology of oak galls often extends beyond direct interaction between insect and tree. Depending on the gall and its stage of development, some are eaten by wildlife. For example, certain small twig galls found on white oak are eaten by field sparrows and goldfinches in winter. More bizarre, however, are the surprisingly numerous hyperparasites, generally wasps that prey upon different species of gall-forming insects while resident inside their gall. The hyperparasitic female wasp has a long ovipositor with which she inserts her egg directly into the center of the gall; the egg hatches and the hyperparasite consumes the insect that formed the gall. How galling it must be for the gall insect to have its elaborate defenses breached! One is reminded of a famous bit of doggerel by Jonathan Swift, "So, naturalists observe, a flea has smaller fleas that on him prey; and these have smaller still to bite 'em; and so proceed *ad infinitum*."

There is no doubt about it, the web of life is intricate. Next time you enjoy the shade of a spreading oak tree, keep an eye out for oak galls and marvel for a moment about the complexity of the world we inhabit.

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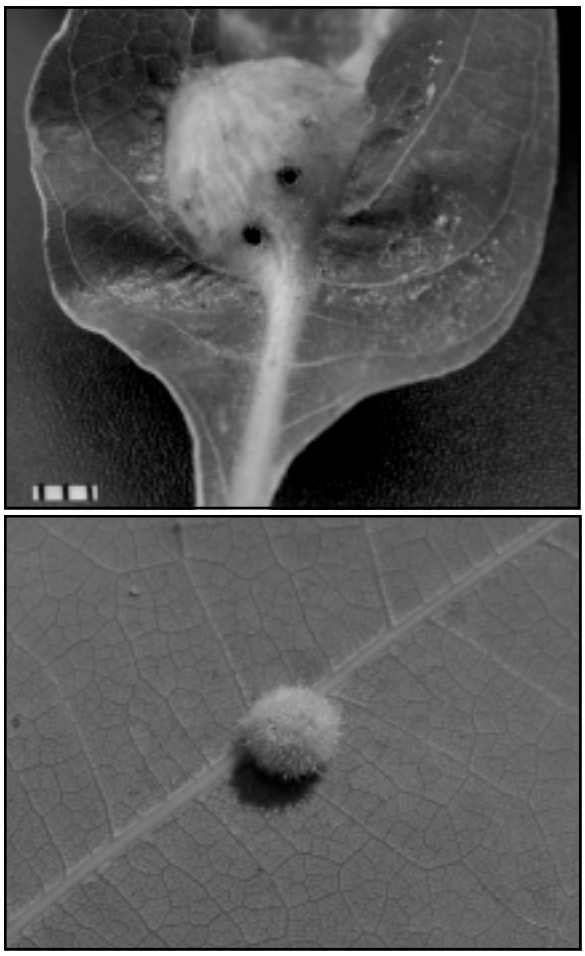
The author claims no special expertise in the biology of plant galls. The overview presented above was distilled from several sources found on the Internet, which will serve as a good starting point for anyone wishing to pursue the subject further. Websites of Agricultural Extension Services of several states in the eastern U.S. were found to be particularly useful. Any errors in the above, however, should be attributed to me. WJH.



*Top photo, Leaf galls on white oak (*Quercus alba*); scale bars equal 1 mm. Below that is a wool sower gall and an oak apple gall, bottom. Top photo John Hayden and bottom two photos Nicky Staunton.*