Leaf gall

Leaf galls can be abundant and noticeable, but are usually not physically damaging.

Most gall-makers on oaks are native and naturally occur in the landscape, and are not regulatory/quarantine pests.

One species of wasp (*Neuroterus quercusbaccurum*) develops in tiny disc-like spangle galls, which are abundant on the undersides of oak leaves in the autumn. The galls drop to the forest floor, where the grubs develop over winter under the cover of fallen oak leaves. In the spring an all-female generation emerges. These are 'agamic', meaning that they are able to reproduce without mating. They lay their eggs in oak buds, producing currant galls on the catkins and leaves. The sexual generation of male and female wasps emerge from the currant galls in June, mate, and then lay their eggs on the undersides of the leaves. Spangle galls develop, and so the cycle continues.

There are actually hundreds of species of oak gall wasps - or cynipids as they are known - and they cause a fantastic variety of galls on oaks. A single oak tree may support many thousands of galls. Each cynipid species creates its own unique and outlandish structure: some resemble cotton wool or marbles, pineapples or tiny UFOs! Their life histories and interactions with other species are no less fascinating than the structures themselves.

As there are so many cynipids, and they have been relatively well studied, it is worth paying them some closer attention. The process begins when the female wasp lays her egg in some part of the tree using a special egg-laying device called an ovipositor. Depending on the species of wasp and the stage in its life-cycle, the egg may be laid in any number of parts of the tree, for example the leaf bud, catkin or even the roots. Either the eggs or the larvae themselves then exude special chemicals (with some non-cynipids, the adult does this herself while laying the eggs), which begin to have strange effects on the tree, deforming and stimulating cell growth to create the perfect microhabitat for the wasp grub. A chamber (or multiple chambers) develops for the larva or larvae to grow in. Remarkably, the larva is able to stimulate the plant to direct more nutrients, such as proteins and sugars, to the cells immediately surrounding the moist chamber. The grub thus has a ready supply of food to speed it towards maturity. The outer layer of the gall has particularly high concentrations of tannins for reasons we'll explore below. Through most of its development the mid- and hindgut of the larva are sealed so that it doesn't foul its chamber. They only open just before the adult wasp emerges. This a general picture of how some galls develop.

Let's look at some specific examples of a full cynipid life cycle. Many of the gall wasps have two distinct generations, each one galling a different part of the tree. It would be easy to

assume that these very different galls were instigated by two separate species, and it is thanks to the dedicated work of patient naturalists, rearing gall wasps through successive generations, that we know more about their complex life histories.

The plot thickens
The development and the lives of the gall inducers are intriguing enough, but the story doesn't end there. There is often a whole community – a mini ecosystem – that develops within and around the gall. This is where some other fascinating players enter the stage. Many galls will host lodgers, which zoologists refer to as 'inquilines'. The term can be applied to many different members of the animal kingdom and comes from the Latin inquilinus, which means 'lodger' or 'tenant'.

The inquiline wasps are closely related to the true gall wasps, but unlike their cousins they cannot create galls. So they do the sensible thing and occupy an existing gall, rent-free! Some inquilines dwell fairly benignly in the tissues of the gall, only modifying their immediate surroundings, and with each occupant minding its own business. Others however, grow in the same chamber as the original occupant, outgrowing and smothering their reluctant 'landlord'.

Under siege
Again, each kind of gall varies and some of them may have numerous original occupants, and many inquilines. However, before long, both the cynipid larvae and inquilines will need to watch out. Enter the parasitoid wasps. These may sound like something out of a science fiction film and frankly that's just what they're like! Parasitoids are different to true parasites in that whereas a parasite feeds from its host, usually without killing it, a parasitoid will occupy a host, eventually leading to the victim's death. In the case of the parasitoid wasps, they lay their eggs within the larvae of gall inducers or inquilines. As the invader's egg hatches, the larva develops inside the host grub, devouring it from within.

Holding the fort
Naturally, the besieged occupants of the gall have had to evolve to resist such intrusions. In the later stages of the life of a gall, it will often develop a hard exterior, through a process known as lignification (lignin is the chemical compound that gives rigidity to wood). This makes it much harder for parasitoid wasps to penetrate the gall with their ovipositors.
The diverse structures of the galls themselves are largely a result of the need to ward off invaders. Many galls, not only those caused by cynipids, have very complex exteriors making it much more difficult for parasitoids to land and effectively penetrate all the way in towards the grub. Some galls even have a sticky surface. This slows down the invader's efforts, and the more time it spends in the open air, trying to lay its egg, the more vulnerable it is to passing predators such as birds, which is great news for the cynipid. The parasitoids have therefore adapted by laying their eggs in the earlier stages of gall formation, when their prey's defences are not fully developed.

In some galls, the chamber is deep enough within the structure that it is just out of reach of the parasitoid. Others have an air space between the outer tissues and the larval chamber. This frustrates the efforts of the invading wasp, as its ovipositor can only penetrate the grub if it has structural support from the surrounding gall tissue. Where these hollows are present, the ovipositor bends and the eggs remain unlaid. One-nil to the cynipid!

Some gall wasps invest in numbers to ensure at least some of their offspring avoid being parasitised. Galls such as the oak apple have numerous chambers within them. While some of the larvae on the periphery may be found and parasitised by an invading wasp, it can't

attack all of them, especially those right in the centre. The invader leaves contented and many of the gall wasps still hatch.

It's not just the parasitoids that cynipids have to be aware of. Fungi are ever-present in the forest, and if they invade and decompose the gall, the cynipid larvae will not survive. This is where the tannins come in. Oaks, like many other plants, produce high levels of tannins. These chemicals protect the tree against decay, and also against browsing herbivores, since tannins inhibit the absorption of proteins by animals. In galls, however, the concentrations of tannins can be many times higher than they are in the surrounding plant tissue, which helps to prevent fungal attack, and in some cases wards off parasitoids and herbivores. Interestingly, this concentrated source of tannin has even been used by humans. The oak marble gall (*Andricus kollari*) was originally introduced to Britain because it yields a black dye, although it was found that the tannin content of galls grown here is actually too low for this purpose.

Further up the food chain

Even the most aggressive parasitoid is vulnerable, as there are bigger, hungrier mouths about. While effective against smaller foes, the tough lignin exterior of some mature galls is not enough to deter a great spotted woodpecker (*Dendrocopus major*), which will peck the gall open to extract the soft and juicy prize within. Other gall predators include rodents such as wood mice (*Apodemus sylvaticus*) and birds including great tits (*Parus major*). When the tiny, frisbee-like discs of spangle galls drop from oak leaves onto the forest floor in the autumn, wood pigeons (*Columba palumbus*) can be seen feasting among the leaf litter, and one pigeon may eat dozens of galls in a single feeding session.

Unsolved mysteries

Although some specialists have spent a lot of time studying galls, there is still a huge amount we don't know about these strange growths and their causes. Perhaps they have been overlooked as they are so challenging to understand, or easy to pass by. Much about their chemistry remains to be discovered and many of the life cycles of the organisms that cause them are completely unknown. Nevertheless it is clear that galls make a huge contribution to the diversity of life in the forest.

Gall wasp

The female wasp of the bisexual generation is about 1.8–2.4 mm in length; largely brown in colour with clear wings and hairy legs. The male is also winged and slightly shorter than the female.

The agamic generation consists of only female wasps which measure approximately 2.5 mm in length. The pointed head is black, with pale brown eyes and long clear wings are present with dark brown veins and hairs.