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Plant Galls

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P L A N T   G A L L S

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Plant galls, or cedidia, are defined as

> . . . pathologically developed cells, tissues, or organs of plants that have risen mostly by hypertrophy and hyperplasy under the influence of parasitic organisms like bacteria, fungi, nematoda, mites, or insects.[1]

The plant gall is unique in providing not only food, but shelter as well for its host. While the host benefits, damage to the plant results. Among other things sap flow is disturbed, premature decay results, non-essential parts are developed at the cost of essential parts, and many other injuries occur. A few examples of the benefits of plant galls may be cited. Nitrogen fixing by _Bacterium radicicola_ on Leguminosae in root nodule galls and the cross-pollination of fig flowers by gall-forming insects are two such examples.

One theory presented is that by developing a gall around a parasite, the plant is actually defending itself. The result is that the parasite is localized and is prevented from invading other parts of the plant.

There are two basic types of plant galls, One, the organoid type galls, does not show growth abnormalities at the place where it has been attacked by the parasitic host. For example, a root parasite may cause flower deformities. These abnormalities are usually manifested in external parts of the plant. The tissues involved are normal tissues. This type of gall includes elongated or abnormally stunted internodes, bunched leaves, chloranthy of petals, etc. Parasitic fungi, mites, aphids, and occasionally Diptera and Hymenoptera are the parasitic gall makers involved in organoid galls. All classes of plants are involved.

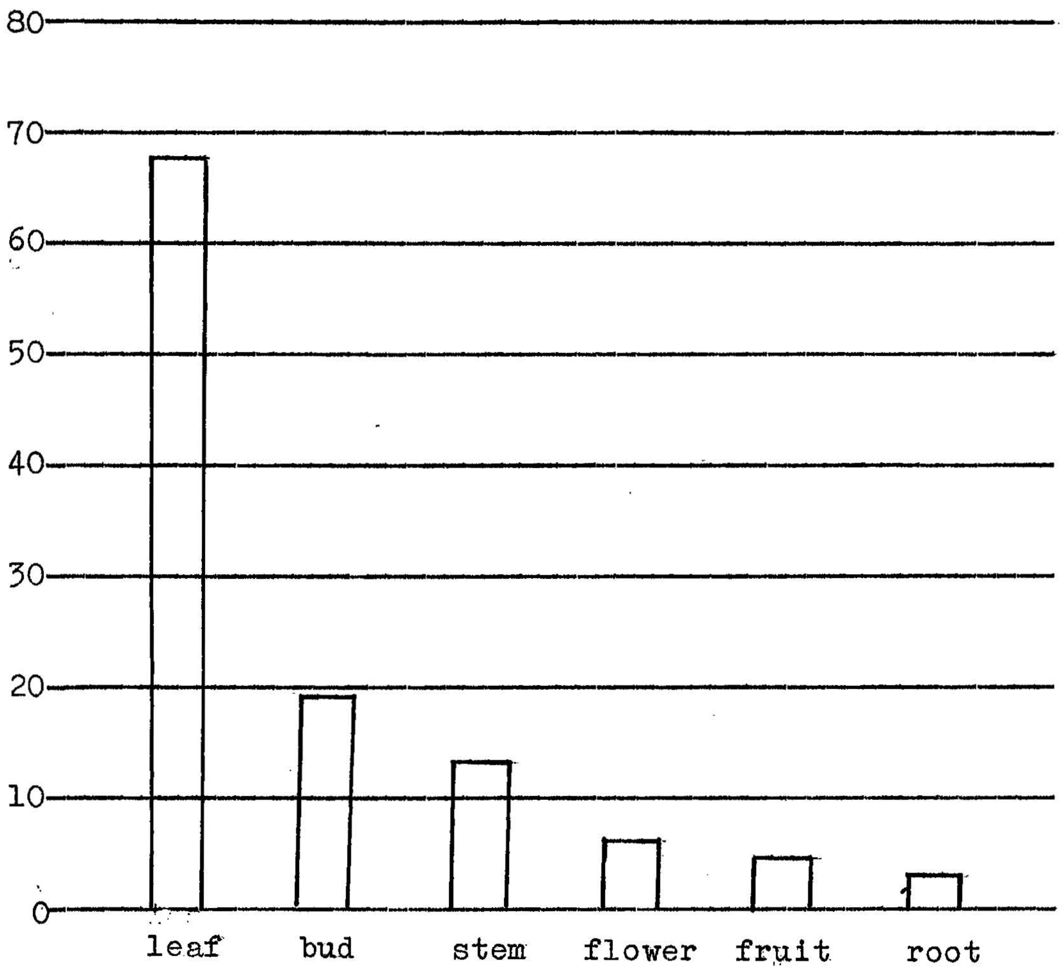
The galls primarily dealt with in this paper are of the histioid type of gall. These differ fundamentally in their anatomy and histology from the normal organ on which they develop.

Plant galls can generally be considered as neoplastic growths. Limited neoplastic galls are caused by viruses, bacteria, fungi, mites, nematodes, and insects. These galls have characteristic size and shape. The limited character of these are generally attributed to the physiological barriers of the parasite. However, the idea has been presented that they may actually be limited due to nutritional and structural barriers of the plant.

Some galls are classified as non-limited neoplastic galls. The plant seems to have no effect upon the growth of these galls. Only the capacity of the gall maker affects the abnormal growth.[1]

Descriptive terms are useful in separating galls and their producers into easily distinguished groups. Only a few of these terms will be mentioned here. Fungi-filled swellings on leaves are known as blister galls. Gall midges are the primary inhabitants of bud galls. Hairy growths on leaf surfaces are called Erineum galls. Flower, root, fruit, and leaf galls

PERCENTAGE FREQUENCY OF GALLS CAUSED BY ALL AGENCIES ON DIFFERENT PARTS OF HIGHER PLANTS FROM THE WORLD [1]



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and thrips of tropical and subtropical regions.[1]

Gall makers are found in almost every order of insect. However, of the 2,000 such insects in the United States and Canada, some 1,500 are gall wasps and gall midges. The gall wasps are particularly abundant on oak trees.[3]

The term kataplasma applies to those galls that lack definite and constant external shape and size. The prosoplasma galls are characterized by definite and constant general form, tissue differentiation, etc. Because the prosoplasma galls are structurally more highly developed, they are believed to have been derived from the kataplasma galls.

The morphological form of an insect gall depends upon the species of insect that inhabits it. This is often more reliable for distinguishing between closely related insect species than the morphological characteristics of the adult insect. A few are confusing, such as Antisporphus pisium which forms three distinct types of galls.[4]

In some galls the only difference in the gall tissue and normal tissue may be the conspicuously large size of the cells. However, many other differences have been reported. Increased water content, enrichment of cytoplasm and an increase in the number of vacuoles are among the most common types of changes. Other cytoplasmic changes include the disintergration of plastids and mitochondria, tendency of agglutination of chondriomes, fusion of plastids and mitochondria end to end and laterally to form reticular masses, arrest of formation of plastids and mitochondria, inhibition of plastid divisions, and others. Nuclear changes indicate that other important physical and chemical changes occur.

The most evident changes in the nucleus of gall tissue are the change in position of the nucleus, depletion of chromatin material, and gigantism of the nucleus. In a nucleus which has enlarged, it contains more than a normal number of nucleoli. The nucleus may also loose its characteristic shape. They may appear in a grape-bunch-like shape, an amoeboid like form, or may become multinucleated in the hypertrophy cells.

Some of the abnormalities in chromosomes which have been repeatedly observed include abnormal chromosome figures, massed chromosomes in a lobed nucleus, hyploid, heteroploid and polypoliod condition, the failure of chromosomes to reach poles, etc. Often in gall tissue cytokinesis is not followed by karyokinesis. As a result the cells have tetraploid, octoploid, or even higher chromosome numbers.

Gall tissue of histioid galls are seldom rich in chlorophyll. Even when the gall causing stimuli is removed, the tissue still fails to develop chlorophyll.

Tissue differentiation varies greatly in various gall types. Arrangement of layers may be comparable, fundamentally different, or even inverted from that of the normal organ. The tissue differentiation is centered around the larval chamber. In those galls of the simplest organization, the tissue is made up of nearly homogenous, undifferentiated parenchyma. The differentiation of an epidermis may even be absent.

Most galls have an epidermal layer. This layer is generally derived from the epidermis of the gall-bearing organ. In the case of the so-called free galls, the epidermis may arise from parenchyma. There are several modifications which are observed in epidermal tissue. Some of these include enlarged cells, thickened cell walls, thicker cuticle, lignified cells, elongated palisade-like cells, and multicellular layers of epidermis.

Stomata are fewer than normal or totally absent. Even if some are present, they are usually non-functional.

Abnormally strongly and densely developed hairs are characteristic of many galls caused by Acarina, Diptera, Hymenoptera, and occasionally aphids.

Mechanical tissue of the gall is derived from gall parenchyma. It exhibits remarkable complexity in development and arrangement.

A continuous band of nutritive tissue is formed around the larval chamber. A second reserve layer is often found outside the sclerenchyma of the gall. The inner layer contains mainly fats and proteids, and the outer layer mainly starch.

Vascular bundles of the gall are normally an extention of the vascular bundles of the gall-bearing organ. These bundles are directed to the larval chamber.

As the gall expands, secondary tissue may arise from the cambium of the gall-bearing organ or from the gall meristem. The gall-forming stimulus may also cause cell proliferation among already formed secondary tissue. This new tissue is also secondary type tissue.

Secretory tissue is developed in abnormal quantities, but is fundamentally the same in structure. Anthocyanin is often found in the epidermal and parenchyma tissues. Cork is often found in some galls.

Most galls are periodic in their habits. Some galls are irregular even from year to year. A certain area may be abundant in a particular gall for several years, then become very scarce for a long interval. Others are governed only by favorable conditions. For example, certain galls will be produced as long as there are leaves on trees.

The greater majority of galls are produced at a definite time in the vegetative season. Certain species of galls are characterized by the time at which they appear. The time of active growth on the part of the plant is generally when emergence of adult cecidozoa and oviposition or hatching of young larva occurs. The leaf gall caused by Phylloxera on the North American hickory appears in the spring while the leaves are still young, but on the closely related pecan, the gall arises throughout the summer. This difference is due to the fact that the pecan produces new leaves throughout the summer.

Optimal conditions for gall development have been found to be when the plant is in an active state of growth. The idea that only meristomatic tissue is susceptible to gall makers is erroneous. However, it is only in meristomatic tissue that the action of the saliva of the cecidozoa can be used in the formation of amino acids, which are used in the induction of cell division. The cecidozoa can therefore feed only on an active growing tissue, but this has no direct relation to gall induction. Since the gall maker is dependent upon meristomatic tissue, they are in effect seasonally isolated.

A generalized life cycle of a cecidozoa will be helpful in understanding the role of the plant gall. The life cycle is initiated by the oviposition of the cecidozoa on or within the plant. After a few days the embryonic development of the larva begins. The characteristic bulging begins.as the larva begins to feed.

The nature of the trophic phase is dependent upon the feeding habits of the larva. The cecidozoa produces saliva which is used to either disolve cell walls or liquify cell contents. Active cell proliferation, cell enlargement, differentiation, and growth of the gall follows to give the gall its characteristic form and mean size.

As the gall reaches maturity, proliferation slows and ceases, and hypertrophy of most cells is at a maximum. The flow of sap to the gall stops, the intensity of protein synthesis reaches its zero level, cell walls thicken, and contents disappear or undergo other changes. Shrinkage of tissue, changes in the pH and enzyme composition, and reduction of free permeability of cell walls are other changes that take place. The metabolic products apparently build up to such a proportion that they stimulate the production of hormones which reduce the cecidozoa to a dormant state.

Gall tissue decays faster than normal tissue. However, all galls do not decay immediately and drop off the plant. Many serve as a hardened protective case in which the cecidozoa hybernates or pupates and completes metamorphosis.[1]

The escape of the cecidozoa from a dehiscent gall is accomplished in many ways. One of the most common is for it to simply bore out of the gall through an area covered by a thin membrane. From these galls emerge the adults of the cecidozoa.[5]

A cecidotoxin or gall inducing substance has often been associated with the saliva produced by the gall maker. Marcello Malpighi (1628-1694) was the first to present the idea that insects secrete some type of substance which induces galls.[6]

Beijerinck in 1897 called the gall stimulating substances "growth enzymes." Boysen Jensen suggested that these substances are relatively non-specific. They cause cell enlargement and proliferation, but they have nothing to do with gall organization. He presented the idea that the organization is caused by the larva moving about secreting growth promoting substances in specific places. This theory is satisfactory for the spherical galls which have relatively simple organization. Jensen's theory is inadequate, however, to explain the highly organized galls.[7]

More recent research suggests that the cecidotoxin is either a heterauxin or something similar in nature to such a hormone. Amino acids in suitable combinations have been found to be determining factors in gall formation. The idea has been presented that these amino acids are the breakdown of proteins taken in as food material. These amino acids are then circulated through the haemolymph to reach the saliva and are then injected into the plant.

The plant proteins are converted by the proteolytic enzymes of the saliva in amino acids.by hydrolysis and the whole is absorbed by the cecidozoa. This mixture then can act as food material and as a gall inducing substance.[1]

One of the reasons there is not a definite explanation for cecidotoxins is the difficulties encountered in assaying cecidozoa extracts. This is pointed out by the work done by Leatherdale, who injected extracts of <u>Dasyneura utricae</u> into immaturé leaves of <u>Utrica dioica</u> by means of an ultrafine hypodermic needle. Abnormalities were reported in 12 out of 150 injections of whole insect extracts and in 9 out of 50 injections of larval head extracts. No abnormalities were reported in water treated controls.

The results of this experiment are not surprising. Gall formation probably depends upon the exact amount of the appropriate chemicals placed at the right time in a way that is difficult, if not impossible, to duplicate.

Other experiments have shown that materials with low molecular weight present in accessory glands of <u>Pontania pacifica</u> on <u>Salix alba</u> possess gall growth stimulants. Chromatographic analysis showed six compounds to make up stimulants. Four of them were uric acids, two unidentifiable adenine derivative, glutamic acid, and possibly uridine as well.[9]

Osborn and McCalla have shown that kinetin has remarkable effects on plant growth.[10] Pelet, Hildebrant, and others have found that auxin and kinetin are required for gall tissue growth in media and that addition of adenine and casein hydrolysate to the medium further stimulated growth.[11] In the assays of the *Pontania* glands, kinin type chemicals were not found. These insects, however, initiate their galls near vascular tissue which has been reported as a source of kinin.[9] The necessity of being near vascular tissue is brought out in experiments of gall development in slash pine needles. The likelihood of development of a gall was directly proportional to the nearness of infection to stem.[12]

By interrupting a sawfly at various stages of its development the following results were obtained. Those interrupted before the laying of the egg but after injection of fluid showed beginning signs of gall development. Those in which eggs had been layed completed the first phase of eight days even when the egg was punctured.

Beyond this point development became dependent upon the larva. The removal of the larve resulted in the stopping of growth in two days.

Glandular sacs of the adult were also placed in forming galls after the larva was removed. The gall continued to mature, needing to be supplemented by more glandular sacs. An oversupply proved fatal to the gall.[3]

Conditions of the plant also have an effect upon gall production. Calcium to Potassium ratios affect the growth of galls. Unlike other plant diseases, galls are supressed when a plant has potassium deficiency.[14]

Insects reproduce other enzymes which have effect upon the plant. One such enzyme produced by the insect converts plant starch into sugar. Many galls produce a large amount of sugar. Honeydew exuded by galls on scrub oaks of the Southwest is collected by honeyants and honeybees.

Tannic acid is another substance produced by galls. Some galls contain large amounts of this chemical. The Aleppo oak gall of Asia Minor is composed of about 65 per cent tannic acid.

The Aleppo gall has been used in medicine since the fifth century B. C. It is a powerful vegetable astringent, a tonic, and an antidote for certain poisons. African Somali women use them for tattoing dye. A fine scarlet dye has been extracted from this gall. In former times the finest inks came from the Aleppo gall. This kind of ink was considered official for many documents throughout the world. Wool, hair, and skins were dyed with Aleppo galls by the ancient Greeks; These galls have been used more recently in dying leather and seal skins.

A small cynipid gall found in Arkansas and Missouri was once harvested because of its high food value. It was processed as feed for domestic animals. These galls were composed of 63.6 per cent carbohydrate and 9.34 per cent protein.[6,15,16]

Galls may indirectly benefit other organisms. The hard shell of a gall left behind by its former inhabitants may provide a protective home for other organisms. These enter through the emergence holes or other splits in the covering. In one study of 500 galls, 44 per cent contained evidence of having been inhabited by other organisms other than those which caused the galls.[17]

Although gall insects seem to live a well-protected life, there are many natural checks which keep them in balance. Weather conditions may play an important role in the life of a fragile gall insect. Unfavorable conditions while the adults are abroad may cause the death of many of these insects. Alternation of generation as found in the gall wasps seems to minimize this danger. The wingless female of the agamous generation appears in the colder months when the winged flies could not survive.

Plants are not always susceptible to gall infection. Therefore, the insect must not only find the proper plant but also find one which is favorable to infection. This is probably the reason that these insects are reduced in numbers. Many insects will only infect a specific species of plant, another check on the balance of nature.[2]

Despite the heavy protection of plant galls, they too are quite susceptible to attack by parasites. In studies made, the idheumonoid wasp, <u>Phaegenes walshiae</u>, was the most common parasite of various gall makers.[18]

There are a certain species of gall producers that are of great economic importance. Fortuantely, the portion of these is relatively small.

The pear blister mite has caused much destruction to the fruit growers. Leaf curling midges of the apples has given eastern New England and central New York State many problems.

Despite the control that has been learned over wheat midges, wheat growers are still faced with the destructive powers of the Hessian fly. The clover midges seriously effects the ability of clover to produce good seed.

Even the home gardener has the gall producing pest. Roses may be infected by rose midges. Violet galls are a pest to the violet growers. Midges are also found to infect chrysanthemums. The gardener also finds his ornamental trees infected. The cone gall may cause injury to his Colorado blue spruce and the box leaf miner and box psyllid affect his other trees.

Although gall wasps are common invaders of oak trees, they cause little damage to the tree. The wasps are seldom found on other plants and are therefore of little economic importance.[2]

Many researchers have attempted to show a close analogy between plant galls and animal cancer or other malignant growths. Both are characterized by irregular mitosis. Plant galls can be traced to some particular stimuli, whereas the

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