Structure and Growth of Mite-induced Galls of *Hoberia sexstylosa* Col.

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THE FIRST ACCOUNT of mite-induced galls of *Hoheria populnea* A. Cunn was published by Lamb (1952). Attention was devoted chiefly to a description of the gall mite *Eriophyes hoheriae,* and no details of the anatomical structure of the gall were given (Lamb, 1952). Galls of *Hoheria sexstylosa* Col. caused by the same mite were reported eight years later (Lamb, 1960).

The present study is concerned only with *Hoheria sexstylosa,* an evergreen tree widely cultivated in gardens in Christchurch, Canterbury, and often seen to bear galls of varying size and age.

Young galls are greyish-green in colour, shaped like a top, and attached to the smaller branches by a prominent stalk. In older specimens the gall-stalk is generally obscured as the continued growth of the gall encompasses the twig which bears it (Fig. 1). Galls arise also on leaves but this is of less common occurrence.

The salient characteristic of all galls of *Hoheria sexstylosa* is the uneven, creased surface, tufted with grey epidermal hairs, below which the mites live in numerous small cavities.

As the result of insect attacks, dead greyish brown galls are common, but many galls grow vigorously for several years and are readily distinguished by their greener hue from moribund specimens. This perennial habit of proliferation which produces galls up to 4 cm in diameter is often associated with the loss of leaves on the infested branches and a consequent disfigurement of the tree.

Nevertheless trees vary greatly in their propensity to gall formation and it has been observed that two trees may grow close together for several years with branches interlaced, and only one of the trees bears evidence of galls. The basis of this variation in susceptibility is at the moment unknown.

The chief aims of the present investigation were to find which of the plant organs of *Hoheria sexstylosa* are transformed into galls, to examine the structure of the gall, and to account for the perennial mode of growth.

METHODS AND MATERIALS

Galls, flower buds, and leaves were fixed at various times throughout the year in formo-acetic-alcohol. Selected specimens from five different trees were embedded in paraffin, and serial sections 10 μ in thickness were cut and stained in safranin and fast green (Johansen, 1940).

Numerous freehand sections of living galls were also made.

Three unsuccessful attempts were made to induce galls on immature leaves and stem tips of seedlings of *Hoheria sexstylosa.* Twenty-four seedlings about 9 inches high were raised in pots in the glasshouse and used for these experiments.

In winter (July) small slices of living galls containing moving mites and eggs were inserted into three tender, freshly opened leaf buds in each of 10 plants.

A second experiment involved a crude gall extract. Thirty grams of fresh galls were macerated in 200 ml of 30% glycerol (Parr, 1940) in a domestic blender at room temperature. A fluid containing the mites was obtained by expressing the macerated preparation through silk. The fluid was smeared on 30 freshly cut soft stem tips on each of five seedlings. Thirty stem tips of five other plants were smeared with 30% glycerol only.

With the remaining four plants a tap water extract of macerated galls containing moving mites was smeared on freshly cut stem tips in a similar manner except that glycerol was omitted.

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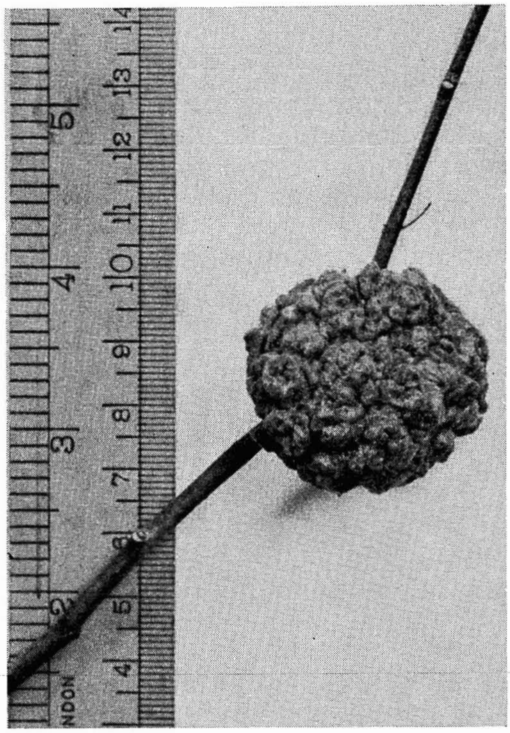

FIG. 1. A large actively growing mite gall.

In all the above experiments plastic bags were kept over the treated plants for a week.

After two years no galls had appeared on any of the plants. It remains to repeat these experiments at other seasons of the year.

OBSERVATIONS

The opening of flower buds of *Hoheria sexstylosa* in late summer marks the recrudescence of gall formation. Some infested buds show traces of stunted petals and stamens, but often only the calyx and pedicel remain unchanged, and a mass of convoluted greyish-green tissue takes possession of the interior region. It is the persistence of the pedicel and calyx which gives to young galls their top-shaped appearance (Fig. 2).

A small percentage of unfolding young leaves may develop galls at this time. The distortion may be considerable and the leaf blade may be almost lacking. In other cases leaf development may not be greatly impeded and the galls may be relatively insignificant.

On some trees hardly one in a thousand flower buds escapes attack, so that by autumn the plant is festooned with the new growth of galls and it is difficult to find one seed head on the whole tree.

Sections through living galls show them to consist chiefly of a solid mass of green parenchyma interspersed by clear mucilaginous cells. Within the parenchymatous cells crystals of the druse type are not infrequently encountered. The cavities beneath the surface in which mites can be seen moving are lined by a definite grey meristematic layer. The exterior of the gall is bounded by a well-marked and active periderm.

In older galls the core of the gall is white, being made up of abundant vascular tissues and non-chlorophyllous parenchyma. This massive development of vascular tissues is readily demonstrated by allowing a gall to decompose for a week in tap water. Disintegration of the soft tissues reveals a compact mass of xylem radi-

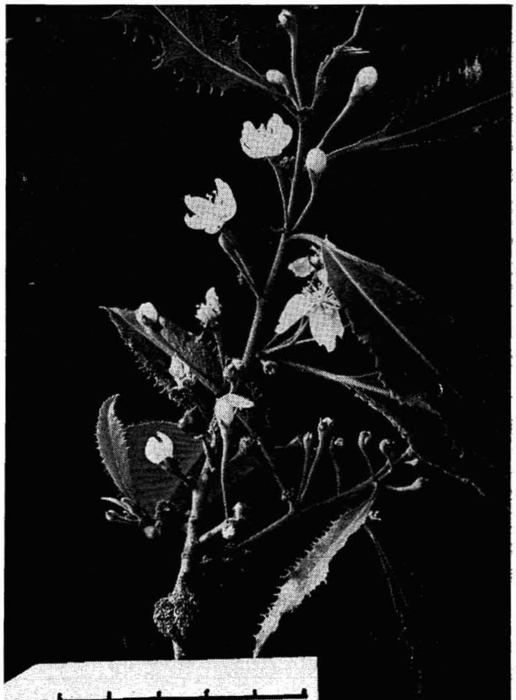

FIG. 2. Flowering twig of *Hoheria sexstylosa* Col., showing some flower buds recently transformed into galls, and one older gall at base.

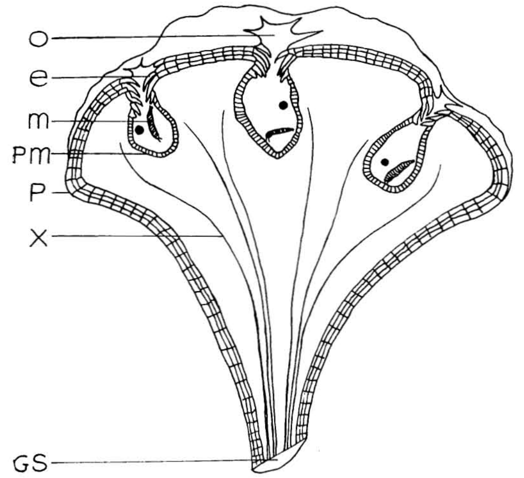

FIG. 3. Diagram of a cut gall (not to scale). *m*, mite; *e*, epidermal hair; *x*, xylem strand; *pm*, pouch meristem; *o*, orifice of mite cavity; *p*, periderm.

ating from the embedded pedicel, and giving the appearance of the spiky "coat" of a chestnut fruit.

The mite-containing cavities are undoubtedly the most remarkable feature of the galls. The mouths of the cavities are irregularly creased (Fig. 3) and surrounded by stout epidermal hairs which are also found in clumps on other regions of the gall surface. The lining of each mite cavity is in fact a sac-like growth centre—a kind of pouch meristem analogous to the shoot growing point of higher plants (Figs. 3 and 4).

Mitotic divisions are found most often within a zone about three cell layers from the cavity. The histological methods used in this investigation were selected to provide a general anatomical picture of the gall and a cytological analysis of mitotic rates was not intended.

What clearly emerges is the fact that perennial growth of the mite-induced galls of *Hoheria sexstylosa* is dependent on the regular activity of the "pouch meristems."

Only at the orifice of the cavities are the epidermal hairs differentiated (Fig. 4), no doubt giving shelter to the colonies of mites below. To the interior of the gall and close to the middle region of the "pouch meristem," xylem elements are seen to differentiate and lead backwards in an anastomosing system with vascular traces from other mite cavities to unite in the central stalk (Fig. 3). A coherent and efficient conducting system is thus constructed and the gall is able to flourish to the detriment of the rest of the twig (Fig. 5).

To the superficial glance the appearance of *Hoheria sexstylosa* galls, whether borne on leaves or on flower stalks, is of an irregular spherical or conical shape, furrowed by indefinite crevices. But the underlying histogenetic processes of periderm formation, cavity growth, and vascularization are remarkably regular. No essentially different cellular components, except the mites, distinguish the galls from the normal shoot tissues, but the growth pattern is unique.

DISCUSSION

So little is known of the biology of *Eriophyes hoheriae* that it is premature to consider in what manner the gall mites may influence growth of galls in *Hoheria sexstylosa.* Whether the mites provide a stimulus in the mechanical act of feeding, or by the liberation of growth substances or enzymes, remains to be investigated.

The preliminary attempts to induce gall formation (described in the section on Methods and Materials) proved ineffective, possibly because the winter season was an unfavourable time. However, other workers have reported promising results from experiments in which galls were artificially induced by extracts from various insects (Bloch, 1954; Boysen-Jensen, 1948; Braun, 1959).

Although the onset of galls in young leaves has been noted at the same time as the galling of flower buds in summer, observation of several trees over a number of years has failed to disclose galling of leaves in spring when there is a mass unfolding of leaf buds. The lack of success in the attempted transmission of mite infection to young leaves in the glasshouse in July, though not very cogent evidence, tends to support the view that new galls arise predominantly in late summer.

The production of galls on leaves would appear to be less favourable to the maintenance of the mite population than the induction of galls on flower buds, which give rise to longer lived galls. Badly galled leaves frequently absciss in

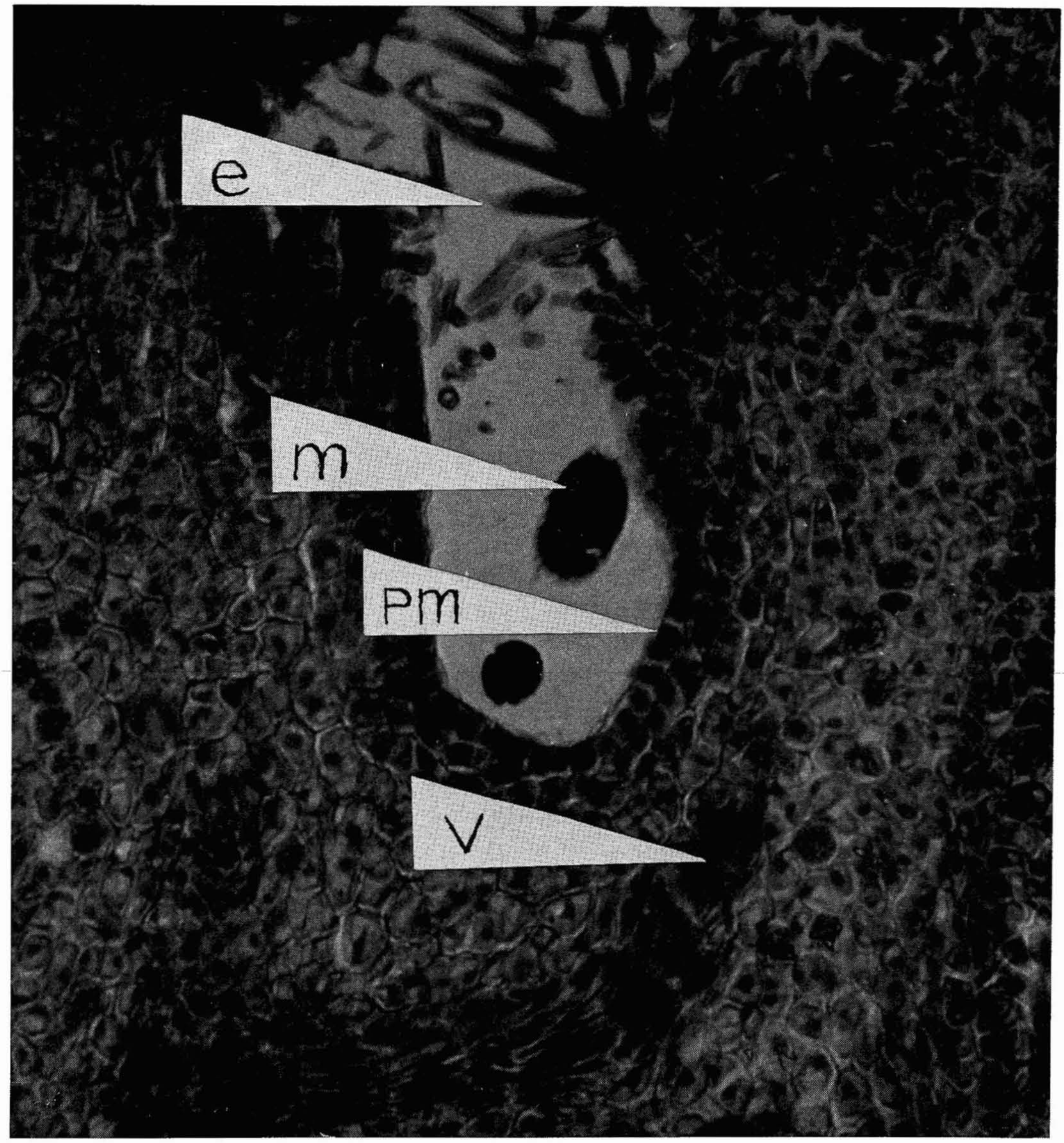

FIG. 4. Longitudinal section through a "pouch meristem," × 250. *m*, section through portion of a mite; *e*, epidermal hair; *v*, vascular strand differentiating; *pm*, inner layer of pouch meristem.

the first three or four weeks, but galls derived from flower buds remain firmly attached by the pedicel, often for several years. It would seem that the tendency to galling of flower buds rather than of leaves represents an evolutionary adaptation favouring the mites.

Furthermore, the mode of enclosure of the mite colonies by the activity of the "pouch meristem" may also be regarded as an evolutionary adaptation shielding the mite colony from the exterior. The majority of eriophyid mites are said to be vagrants on the surface of foliage or in galls of other species of plants (Evans, Sheals, and Macfarlane, 1961).

While one can readily enough draw a parallel between the activity of the "pouch meristem" in *Hoheria* galls and the shoot growing point of angiosperms, it could also be claimed that there

FIG. 5. Defoliation of branch of *Hoheria sexstylosa* Col. caused by galls.

is some analogy with the invaginating growth movements of the developing animal gastrula which is concerned with seclusion and shelter of germinal tissues from the external environment—in the same sense that the embryonic mites are protected from the rigours of the outside world by the invaginated gall-cavity in which they grow.

SUMMARY

The solid perennial galls frequently found on cultivated trees of *Hoheria sexstylosa* Col. are caused by the gall mite *Eriophyes hoheriae* Lamb. Most galls arise from transformed flower buds in late summer, but some galls occur on leaves. Persistence of galls often results in leafless unsightly branches.

Within the galls, colonies of mites and their eggs are enclosed in sac-like cavities with puckered mouths, which are ringed by pointed epidermal hairs.

Each cavity is lined by a zone of meristematic cells which act as a growth region analogous to the shoot growing point of angiosperms.

Vascular traces arise in the vicinity of each "pouch meristem" and differentiate back towards the older vascular strands. In this way is formed an efficient conducting system which radiates from the gall stalk and allows growth of the galls and mites to continue for some years, to the detriment of the rest of the tree.

The cellular make-up of the galls is not essentially different from that of the normal shoot of *Hoheria sexstylosa*, but the pattern of growth is unique and advantageous to the mites and their embryonic young.

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