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THE AETIOLOGY OF SOME THRIPS GALLS FOUND ON LEAVES OF MALAYSIAN SCHEFFLERA SPECIES

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Introductory

The galls that are caused by thrips have not yet received the attention they deserve. This is perfectly comprehensible, because the few thrips-galls found in Europe have a very simple structure. The leaves are partly rolled inwards and poorly developed, and in case of heavy infection there is a general wilting of the whole plant, so that it looks diseased, (Grevillius, 1910). The infection takes place when the tissues are as yet little differentiated. They remain in this stage, and the infected organs show the symptom of hypoplasia.

The number of thrips-galls in the tropics of the old world is very large, particularly so in the Indo-Malay region, which has been best examined for galls. About one tenth of all zoocecidia are caused by these insects (Docters van Leeuwen–Reijnvaan, 1926). Some galls have a very simple structure, but others show a distinct tissue differentiation and also hyperplasia. Similar highly developed thrips-galls have also been found in Australia.

The subject of the present study are the galls caused by thrips on species of *Schefflera*. They have been chosen because there are particularities in their aetiology which have not been observed in the development of any other gall. The galls are common, and it is relatively easy to experiment with the insects.

The representatives of the genus *Schefflera* are erect or climbing shrubs; several grow epiphytically. The most common species is *Schefflera elliptica* and on this species too the thrips-galls are very common. The plant ascends, with its rather flaccid shoots high into the crown of the host-plant, the ends of the shoots often hanging down. As the growth goes on throughout the greater part of the year, the various stages in the development of the gall are often found close together. The plants are easily reproduced by cuttings, so that all the year round material can be at the student's disposal.

The galls

There are two kinds of thrips-galls on *Schefflera:*

1) Involute leaves. The two halves of the leaflet are incurved and meet along the main-nerve. The long, narrow gall-chamber formed in this way contains thrips in all stages of development.

I found this gall in Java on *Schefflera scandens* (Bl.) Vig. and in Sumatra and Java on unclassified species of *Schefflera*. These involute leaves, so commonly caused by thrips on other plants species too, will not be discussed here.

2) Horn galls. According to the species of *Schefflera* on which the galls develop, the upper and, rarely, the undersurface of the leaflets show either long, tubular or shorter and more irregularly formed galls.

Schefflera divaricata (Bl.) Koord. The galls are short and horn-like; they are 4–6 mm long and 1 to 1½ mm across. The position of the gall relative to the surface of the leaflets is often oblique. The opening is at the base. This gall was once collected at an altitude of 1600 m above sea-level near Tjinjiruan above Bandung, West Java.

Schefflera elliptica (Bl.) Harms. The gall is attached to the upper-surface of the leaflets and has a narrow, round aperture at the under-side. These galls are tubular with a sharp or rounded top; they are often inclined towards the leaf-blade, and sometimes they are more or less spirally twisted. Sometimes they are thin and long, sometimes shorter and thicker, often with irregular, small knobs on the outer surface. The surface. is smooth, green, often covered with brown and particularly red stripes. (See the coloured pictures of these galls in Docters van Leeuwen–Reijnvaan, 1926, pl. III, fig. 6–9). The wall is fairly succulent and encloses a long, narrow gall-chamber, which extends almost from the opening to the top. The galls are from 10 to 30 mm long and from 2 to 4 mm across, see fig. 1.

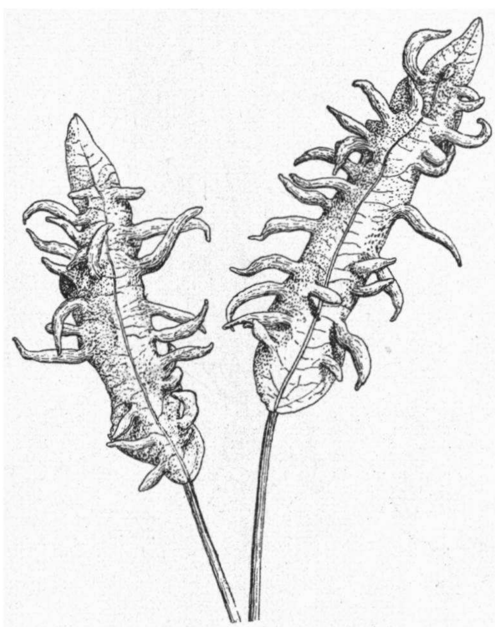

Fig. 1. Two leaflets of *Schefflera elliptica* with many mature thrips-galls, x 3/4.

This gall is very common, and has been collected in many places in Sumatra, Java, Celebes, the Salajar Islands and Sumba. In Java it has been found from Bogor (Buitenzorg) in West Java to Djember in East Java. It is likely that it occurs wherever this common plant is present. The host-plant is found in Java from the plain up to the lower mountain regions.

Schefflera lucescens (Bl.) Vig. var. *grandifolia* (K. et V.). Bakhf. and var. *rigida* (Bl.) Bakhf. The galls which develop on this plant are also horn-like but the shape is different from that described for the gall on *Schefflera elliptica*. The horns are more irregular, often somewhat wider than high, and they sometimes give the impression of a vesicle. The surface of the galls is not smooth but scabrous, and the galls are often twisted and inclined obliquely towards the leaf-blade. Now the galls are green, and then again the colour is red or purple. The galls are from 2 to 10 mm high and from 2 to 5 mm thick; sometimes they are attached to the underside of the leaf with the opening at the upperside. In case of heavy infection the leaflets develop irregularly with deep incisions and contortions. Apart from these true galls one occasionally finds near the leaf-edge and particularly on the petioles long or short, curved, gibbose excrescences, which prove to be solid and are therefore no true galls. These excrescences may be up to 20 mm long and from 3 to 5 mm across. I collected these galls on the two varieties of *Schefflera lucescens* in various places in West Java. See figure 2.

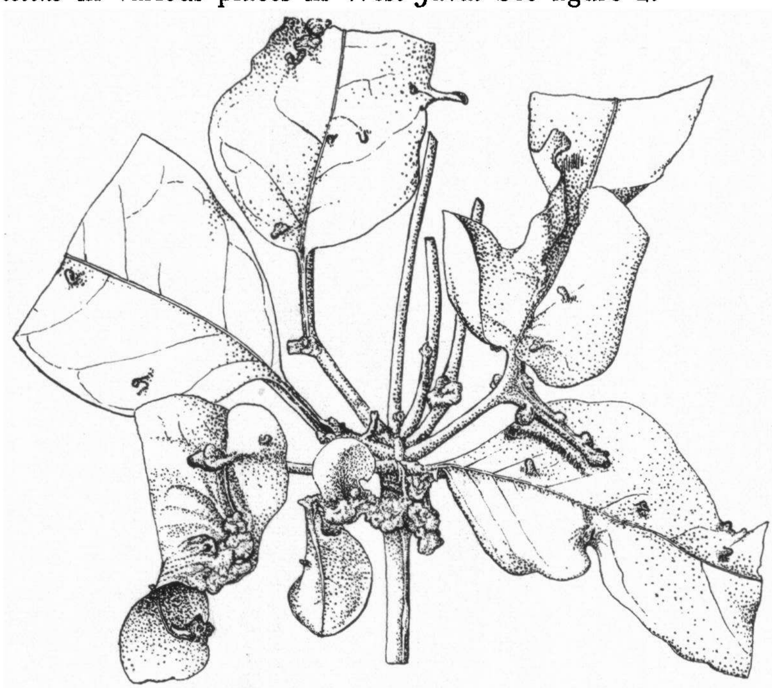

Fig. 2. A leaf of *Schefflera lucescens* var. *rigida* with many thrips-galls and solid outgrowths, x 3/4.

Schefflera polybotrya (Miq.) Vig. The galls on this plant look like those on *Schefflera elliptica*, but they are always green and the top is sharply pointed. Their position with regard to the leaf-blade is oblique; often they are pressed against it. The galls are from 5 to 30 mm long and from 1½ to 2 mm across. The gall-chamber is very narrow and ends where the top contracts. As far as I know this gall was collected only on Mount Gedé in West Java. See fig. 3.

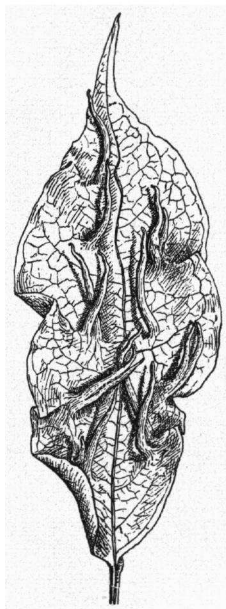

Fig. 3. A leaflet of *Schefflera polybotrya* with full-grown hrips- galls, × 3/4.

The gall-producing insects

The galls are caused by thrips, about 5 mm long and, like most species, coloured black. The insects leave the galls when full-grown; as most galls are inhabited by a few insects only, they are usually found empty. The insects are not very active and therefore they can easily be moved from one place to another. If the new place offers sufficient food, the insects as a rule quietly stay in the new place.

The only species described so far is that which lives in the galls on *Schefflera elliptica*. This insect is very similar to *Gynaikothrips chavicae* Zimm., which causes galls on the leaves of many species of *Piper*. The first insects from the *Schefflera* galls which I sent to the thrips specialist H. H. Karny (1912) in Vienna were indentified by him as *Gynaikothrips chavicae*. Afterwards when he had more material at his disposal he made them into a subspecies *hebtapleuri* (see Karny und Docters van Leeuwen–Reijnvaan, 1913, 109) and at a still later date (see Karny and Docters van Leeuwen–Reijnvaan, 1915) this subspecies became a species *Gynaikothrips heptapleuri* Karny. PRIESNER (1926) who studied the larvae of thrips extensively, states that the larvae of *Gynaikothrips heptapleuri* are distinctly different from those of *G. chavicae*.

The full-grown insects are sometimes found inside the galls, but also fairly often living on the lower surface of very young leaflets of *Schefflera elliptica*. In this case they mostly sit without moving pressed against the main-nerve on the lower surface. However, in order to cause galls it is necessary that the insects move over the leaf surface.

ANATOMY OF THE GALL ON SCHEFFLERA ELLIPTICA (BL.) HARMS

The epidermis of a full-grown leaf consists of two layers of cells. The outer layer consists of small, low cells with a thin cuticle. Underneath lies a layer of larger, more isodiametric cells, which like those of the upper layer lack chloroplasts. Next come three layers of palisade parenchyma cells. The height of the cells of the upper layer is three times their thickness, while that of the second layer is twice their thickness and these cells, moreover, enclose small intercellular spaces. The height of the cells of the third layer is still smaller, about 1½ times their thickness. They are also more rounded. The spongy parenchyma consists of 7 or 8 layers of cells with large intercellular spaces. The dimensions of these cells are larger in the longitudinal direction of the leaf than across, and their corners are rounded. The epidermis of the lower surface consists of a layer of cells that are similar to those of the upper surface; the cuticle is somewhat thicker. The vascular bundles are fairly small; laticiferous tubes are present.

At the time of the infection the small young leaf consists of from 13 to 14 layers of cells, which are not yet distinctly differentiated. The cells are small and closely pressed. The central mesophyll cells are still indistinct. The xylem elements and the cortical fibres are not yet lignified.

The first sign of the infection is a small spot, about 1 mm in diameter, at first transparent, but soon turning red. After a few days it develops into a small knob, which grows out into a tube on the upper side of the leaflet.

The wall of the young gall consists of as many layers as the young leaf, that is 13 or 14. The primordia of vascular bundles are soon visible. When the gall is about 2½ mm high, the differentiation of the cells in the surrounding leaf-tissue has set in; epidermis and spongy parenchyma are distinct, but the spongy parenchyma does not yet contain any clear intercellular spaces.

The cells of the young galls are not rounded, but extended parallel to the axis of the gall. On the outside of the gall the cells are still arranged in regular layers, but towards the interior the structure is more irregular. Near the base of the gall, i.e. near the opening, the tissue grows out towards the interior so that the entrance becomes slightly narrowed. Many wood vessels are now clearly lignified. The vascular bundles anastomose in the top of the gall. The young galls are coloured red. The red pigment, which is dissolved in the epidermis cells, disappears completely, or almost so, during the further development of the gall.

In the full-grown galls too the cells on the outside are arranged in layers. They are long and narrow. The cells situated more towards the interior are larger and reach their greatest dimension perpendicular to the axis. Locally this may lead to the development of small knobs on the interior wall of the gall-chamber. Then the gall-chamber is no longer a regular tube. In such places the vascular bundles join in the growth, less so the xylem, but to a greater extent the phloem and particularly the bast fibres. The latter may be strongly bent; see fig. 4.

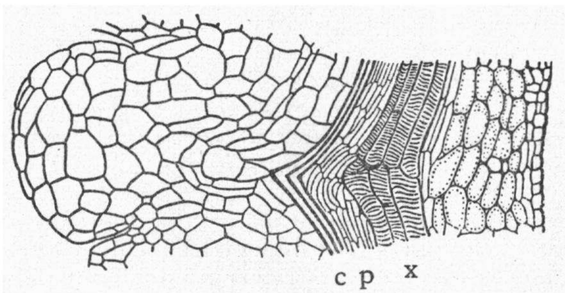

Fig. 4. Part of longitudinal section of the gall on *Schefflera elliptica*, c = cortical fibres; p = phloem and x = xylem.

The cuticle of the epidermis-cells which form the interior wall of the gall is on the whole well developed, but on the knobs it is thinner. The wall of the gall measures about 20 cells across; on the outside the cells have become more or less collenchymatous. The phloem is situated on the inside, the xylem on the outside of the gall. The xylem consists of smaller and larger groups of wood vessels, alternating with non-lignified elements. The bast fibres on the inside are best developed, less so on the outside, where they are not very much lignified either.

This gall is one of the most highly developed thrips-galls, a typical hyperplasia, therefore according to Küster (1911) a prosoplasmatic gall.

Aetiology

The development of a gall is due either to the influence of an egg or of a growing larva (Hymenoptera, Coleoptera, Lepidoptera and Diptera) or to the influence of a mature insect, as happens in the case of Aphididae, Coccidae and Phytoptidae. The gall arises in the place where the insect, the egg or the larva is in contact with the plant. As soon as the egg, the larva or the adhering insect is killed, the growth of the gall is arrested. The development of the *Schefflera* galls described above takes place in a different way.

The leaves of *Schefflera elleptica* are infected when they are still very young, although already expanded and coloured pale brown. The leaf-tissues are not yet differentiated, see the preceding chapter.

In the open air the following facts can be observed. On the leaves of a shoot where galls are found, a female thrips sits appressed against the main-nerve on the underside of a very young leaflet. The upper surface shows at first transparent spots, which soon turn red, probably a consequence of a wound reaction. Before long small excrescences develop from these red spots, which grow upwards; in the course of a few days these excrescences are from 2 to 3 mm high. The female is still living on the lower surface of the leaflet, but not constantly in the same place. The insect is seen again and again with its head entering some knob.

After about a week's time the gall has developed into a horn, and when this has become from 6 to 8 mm high, eggs can be found and soon afterwards young larvae. The latter grow rapidly, just like the gall; after one week the larva is mature and changes into an imago. The galls mostly contain but a small number of insects. The latter are imagoes and larvae in various stages of development; this shows that the eggs are not all deposited at the same time. When mature the insects soon leave the gall, so that most galls prove to be uninhabited.

These observations in the open air lead to the conclusion that all galls on a leaflet arise under the influence of a single female thrips or, when the leaflet is covered by a larger number of galls, probably of two females.

In March 1925 I undertook several experiments which proved that the above mentioned conclusion was right.

A great many cuttings with roots were planted in pots, one in each, and stripped of their leaves. Each cutting was covered by a wide glass tube. Attention was paid that no thrips were present either on the cutting or in the tube. Some male and some female thrips were then introduced in the tubes, and the results were awaited. The cuttings soon produced young leaflets, and as soon as the latter measured a few mm the females settled on the lower surface.

On March the 15th I introduced a female thrips into a tube. The leaves, however, were slightly too old; red spots arose, but they did not develop any further. In tubes with younger leaves the galls developed in great numbers.

On March the 20th a female was brought into a tube containing a cutting with very young leaves. This female settled immediately on the lower surface of a leaflet, and as early as the 21th of March transparent spots were visible. These spots soon turned red and on the 22nd of March small excrescences of about ½ mm could be found. Next day the young galls measured from 2 to 3 mm. The female insect was seen first here then there penetrating with the front part of the body into the young galls. The galls grew regularly, and on March the 26th some of the galls contained eggs. The female thrips now entered a full-grown gall with her whole body, left it and entered another gall and so on. As soon as the female was taken away the growth of the galls immediately stopped.

A second experiment was made from the 22th March onwards; on

March 26th the galls measured 3 mm. At this moment the female was taken away and the galls did not develop any further.

The two experiments described above and several similar ones lead to the conclusion that all galls on a leaflet arise under the influence of one female thrips; also that the growth of the gall at whatever stage of its development stops when the female is taken away. Only when the galls contain larvae, growth continues without the presence of a female. At that time, however, the galls have practically reached maturity.

A cutting of *Schefflera elliptica* which only bore the petioles of very young leaflets, was covered with a tube containing some thrips. The insects punctured the petioles and took some food; soon after red spots were seen, but no excrescences developed. Further experiments yielded the same result.

Another species of *Schefflera, S. lucencens* was also subjected to experiments, because they bore, apart from normal galls, excrescences on the leaf-edges and on the petioles which proved to be solid. The leaves of this species are much larger than those of *Schefflera elliptica.* The leaflets of this very robust species are also infected when still very young. Mostly more than one female thrips was found on the lower surface of the leaflets, and these were often covered with dozens of galls. Cuttings of var. *rigida* were subjected to the following experiments. Female thrips were introduced into a tube containing cuttings, the young leaflets of which had been removed. Only the petioles were left. The thrips sucked the petioles and remained alive; contrary to what had happened in the other species of *Schefflera* we now found that

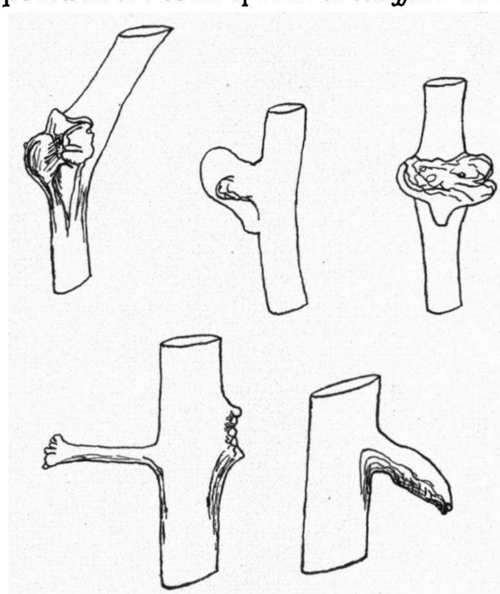

Fig. 5. Solid outgrowths which arose during experiments on the petioles of leaflets of *Schefflera lucescens* var. *rigida,* × 2.

after several days excrescences of various shape developed on the petioles. Sometimes they were clavellate appendages, while at other times they looked like cancerous outgrowths. All these cxcrescences were solid. Some of the excrescences obtained during these experiments are illustrated in fig. 5.

In the description of the gall on *Schefflera lucencens* on page 82 it is stated how by the side of the normal galls on the leaf-edges and on the petioles excrescences of various forms occur. The above-mentioned experiment shows that these excrescences arise under the influence of the sucking thrips. I have not been able to state whether the excrescences arise after one single puncture or whether the insects must puncture the plant several times in the same place.

KÜSTER (1911) calls such excrescences "verirrte Gallen", that is stray galls, although the term gall is stricktly speaking not correct. KÜSTER is of opinion that such stray galls are theoretically of great importance.

CONCLUSIONS

The most important result of the observations and experiments described above is no doubt the realisation that on a *Schefflera* leaflet several galls arise under the influence of a single female thrips. The thrips punctures the very young leaflets on the lower surface in various places, and in these same places the galls are formed. When the latter have reached a certain stage of development the female begins to deposit eggs in them. It was also demonstrated that the growth of the gall stops as soon as the female thrips is taken away.

We are justified in assuming that the sucking thrips introduces substances, probably from the salivary glands, into the young undifferentiated leaf-tissue so that the development of the cells is affected. The nature of only a part of these substances is known. Generally speaking one may say that these galls arise under the influence of chemical substances. In this case the gall is a chemomorphosis. This term has indeed often been used in discussions on the aetiology of other galls. The term in itself, however, implies but little, and does not throw any light on the processes taking place in the development of the infected cells.

During the last few decades of last century and of the beginning of this century many extensive articles have been published on the aetiology of galls. A good review is given in KÜSTER's book (1911). ZWEIGELT (1931) examined the structure and development of some galls caused by plant-lice on *Ulmus;* he extensively discusses the problems turning up during the growth of a gall. BEIJERINCK too has devoted many studies to this subject. WERNER MAGNUS (1914) has written a very clear review. Among other things he points out that FITTING in his examination of the simple postfloral changes of the flowers of some orchids found that several factors play a part in this process; if the galls were really to be looked upon as chemomorphoses, varied influences must be attributed to chemical substances secreted by gall-producing animals or their larvae. If we realize how many factors play a part in the development of a normal cell, it is easy to understand that it must be at this stage impossible to analyze the factors leading to the formation of a gall. I therefore restricted this article to a short description of the problems of gall-forming.

WERNER MAGNUS (1914) ends his discussion with the following words (translated): "Before we can even think of solving the gall problem, many extensive investigations and experiments into the history of their development will be necessary in order to explain some minor details of the aetiology of the galls. We have had enough hypotheses; let us at last see facts".

I fully agree with his words.

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