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INJURIES TO PLANTS CAUSED BY INSECT TOXINS¹

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Toxaemias of plants caused by insects may be defined as those induced by the secretion of substances by the insect which are toxic to the plant cell, which do not increase in the plant tissue and which cause injuries distinct from those arising from traumatic injury incident to the insect's feeding. With the exception of the gall formers which include insect species in several orders, all the insects referred to in this review are sucking insects and belong to the Homoptera and Hemiptera.

To classify the phytotoxaemias of insect origin is merely to list them in an ascending order of complexity, but this may serve a useful purpose even if it only emphasizes the extreme diversity of type encountered, with no more relationship between contiguous items than might be found in the items of a chemical catalogue arranged alphabetically.

The simplest type is that represented by the various forms of leaf-spotting where the spot is localized at the insect's feeding point. Many of these spots are undoubtedly due to the withdrawal of cell contents and it is difficult to determine to what extent this withdrawal and traumatic injury contribute to the symptoms. There is, however, a close intergrading between such spots and those spots where the visible injury spreads from the point of feeding to produce a round or irregular margined spot, frequently of considerable size, which is clearly due to a diffusion process. The association of spotting with specific insects is one of the significant data leading to the conclusion that injury to the host plant is due to the introduction into the plant of specific secretions by the insect.

Injuries characterized principally by tissue derangements are perhaps the most commonly encountered phytotoxaemias, and the

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insect species responsible are found in several families of the Homoptera and Hemiptera. In this group are found the leaf curlings due to aphis feeding and the injury by mirids (capsids), including the complex of injuries associated with the several species of the genus *Helopeltis*, wherein the local injury is followed by more or less systemic injuries at points well removed from the original point of entry of the toxic element. Perhaps, strictly speaking, galls should also be included in this category although these are so diverse and are produced by so many unrelated groups of insects that they could, quite properly, be considered in a category of their own. Even such a category, however, would require many subdivisions if classification per se was an objective of this review.

Notable among the more complex types is that exemplified by froghopper blight of sugar cane in which a distinct local lesion is followed by pronounced systemic effects. Finally are to be considered those cases where no local lesions occur but where the effect is systemic as in psyllid yellows of potato and tomato and mealybug wilt of pineapple.

LEAF SPOTTING

Spotting of leaves by leafhoppers is specific for the five species of *Empoasca* studied in comparison with *Empoasca fabae* (Harris) by Smith and Poos (221). All these five species, *E. bifurcata* DeL., *E. erigeron* DeL., *E. filamenta* DeL., *E. abrupta* DeL. and *E. maligna* Walsh, are primarily mesophyll feeders and the result of their feeding is a definite stippling on the upper surface of the leaves which is characteristic for each species; whitish spots are produced on the upper surface of the leaves that are fed on from the lower epidermis. The cell walls of the spongy mesophyll and the palisade layers are torn, and the cells emptied of their contents and in some cases even large portions of the cell wall disappear.

It is difficult to understand how these changes could be accomplished without the introduction of some digestive secretion but the authors conclude that the injury is largely mechanical. Smith (223) in studying the feeding of the leafhoppers Eupteryx auratus Liv. and Zygina pallidifrons Edwards, found intact cells devoid of contents and concluded that the white spots, typical of jassid feeding, are due to the destruction of chlorophyll by the diffusion of the salivary secretion through the cell wall.

Horne and Maxwell Lefroy (112) using Eupteryx atropunctata Goeze, Chlorita viridula Fall (? C. solani Koll.), described the destruction of chlorophyll and assimilatory tissue in the white spotted area. DeLong (55) illustrates a comparison between E. fabae and E. abrupta. The latter species produced a speckled white appearance over the entire leaf as a result of chlorophyll losses.

When differences between nymphal and adult feeding of the same species are found, it is evident that injury cannot be ascribed to mechanical causes. The work of Fenton (73) and of Carpenter (27) on Eutettix strobi Fitch is an interesting case in point. Fenton showed that the characteristic crimson spots caused by E. strobi on pigweed (Chenopodium album L.) are produced by the nymphs, but not by the adults, and that these spots appear not less than 24 hours after feeding has commenced. Carpenter, continuing the study of the same insect, showed that these spots varied in size. When a single nymph made a number of spots on a single leaf they were small, not bigger than the size of a pin point, but when a nymph remained feeding in one place a single, much larger spot was produced. This spotting is evidently preliminary to a curling and stunting of the leaves with subsequent death. The ability to spot the leaves increases with the age of the nymphs, and the observation of Fenton with respect to the inability of the adults to produce these spots was confirmed by Carpenter.

In Hawaii *Empoasca solani* DeL. produces the typical stippling effect on the leaves of *Amaranthus* species, but on castor bean and some other hosts the effects are typical of *E. fabae* feeding and hopperburn, as will be discussed later in this paper.²

The aphid *Toxoptera graminum* Rond., produces pale yellow spots with reddish centers on oats and other graminaceous plants and according to Wadley (247) this is due to injections of an enzyme-like substance.

The preliminary symptom of *Helopeltis* damage to tea leaves and to cacao fruit is a round reddish-purple spot.³ The fact that local spotting may appear as a precursor of more serious damage to plant tissue does not necessarily mean that the secretions responsible for the local lesion are those causing the later damage, and the

² Author's observations. ⁸ Material illustrating this was demonstrated to the writer by Iz. de Haan at the Proefstation, West Java, Buitenzorg.

spotting by E. strobi and Helopeltis are mentioned here on that account. A single sucking insect species may produce more than one secretion with entirely different effects, or may produce two entirely separate types of lesions.

The rhododendron lacebug, Leptobyrsa rhododendri Horvath, is also a case in point. The insect is a mesophyll feeder and the chief damage is caused by emptying the palisade cells of their contents, but two types of lesion are produced. The first and more common type is a whitish or pale yellowish spot which does not increase in size and which is caused by active and repeated probing of the stylets within the palisade layers of the leaf. The second type of lesion is a dark brown spot which spreads outward from the point of insertion of the stylets as long as the insect is feeding, but the spread is very slight after the stylets are withdrawn.

Lesion 2 is of less frequent occurrence than lesion 1 and is produced by a non-probing feeding method which enables saliva to spread to intact cells without mixture with cell contents. Browning of the leaf tissue can be accomplished by scratching with a needle, but it occurs with much greater speed when produced by bugs, so it is almost certainly the result of the action of the saliva. The absence of this browning in lesion 1 is probably due to the fact that saliva is mixed with the contents of the ruptured cells, and is sucked out of the leaf before it has an opportunity to spread. Vascular bundles are only accidentally pierced and never become plugged as the result of salivary action, neither are stylet sheaths easily demonstrable.

According to Slocock (215) the discoloration in general is caused by a toxin which the insect injects. Johnson (125) accepts this explanation only in the case of lesion 2, and even then makes the qualification that the browning of the cells may be due rather to the effect of the oxidases in the leaf than to an injected extracellular oxidase.

The distinction between a direct toxic secretion and one in which the toxicity results from disturbance of the normal enzymatic functions of the plant cells is perhaps a fine one, but important nevertheless in suggesting that toxicoses may arise not only as the result of injection of actually toxic material, but also as a result of the injection of material which may catalyse abnormal reactions which may have toxic effects. With respect to white fly (Aleyrodidae) feeding, Baker (7) states that this does not injure the mesophyll cells in which the setal secretion is laid down. These cells become enlarged, oedematous and devoid of chloroplasts. The reaction of this secretion appears to vary with different species of white fly and different host plants.

The spotting of leaves by the Coccidae is frequently encountered. Diaspis bromeliae (Kern.) on pineapple, produces a circular, chlorotic area which extends beyond the margins of the scale if feeding is prolonged. On rare occasions the circular, chlorotic spot is two or three times the diameter of the insect and obviously indicates a diffusion from the point of entry. A Diaspis species, probably bromeliae, producing chlorotic spots approximately one centimeter in diameter was observed by the writer in Fiji (43).

The spotting of pineapple leaves by *Pseudococcus brevipes* (Ckll.) has been described by the writer (33). The chlorotic spots, usually with irregular margins, and the result of long feeding by the insect and often by a number of individuals feeding in one place, appear to be similar to the general type of spotting already described in which the chloroplasts are degenerated. Cell walls are thickened in the chlorotic area, the thickening being more pronounced in the center of the area and reduced at its periphery. Within the area of pronounced cell wall thickening the cells are full of a homogeneous non-granular substance which takes a slightly less dense stain than the thickened cell wall.

The green spotting which this same species of insect makes, is in an entirely different category. In its most typical form it is bizonate with a deep green central zone and a lighter green outer zone, the outer zone being, however, deeper green than the surrounding non-spotted area of the leaf. This type of spot, which is undoubtedly a strictly localized secretion effect, is probably due to a complex of secretions, one of which diffuses further than the other. There is no evidence of thickening of cell walls, emptying of cell contents or dissolution of chloroplasts; on the contrary, the typical condition is a hyperplasia with enlargement and increase in the number of chloroplasts. This can be seen most clearly in a green spot which is being formed at or near the junction of the white and green tissue at the base of the leaf. There the chloroplasts are

⁴ Incorrectly stated as "vein thickening" in the original paper (12), p. 247.

clearly formed within the green spotted area, while the normal white tissue surrounding it contains no visible chloroplasts. A green spot retains its identity as long as the leaf is alive and in its later stages becomes a raised, welt-like area, due to the shrinking of the otherwise normal tissue around it.

In Hawaii there is a clear association between the symbiont flora of the mealybug and its ability to produce green spots. The green spotting strain contains within its mycetome a large rod-shaped symbiont which is absent from the non-green spotting strain. A short coccus rod, found in the non-green spotting strain, may be the rod-shaped symbiont in a polymorphic form and the finding, very rarely, of what appeared to be intermediate forms is a datum in support of this hypothesis. Whether the coccus rod in the nongreen spotting form and the large rod of the green spotting form are phases of the same organism is not proved by any means, but the association of these two forms with their respective mealybug strains has been clearly demonstrated (35, 37). The findings by Ito (116) that the non-green spotting mealybug is an obligate parthenogenetic, and the green spotting mealybug an obligate bisexual form, increases both the interest and the complexity of these relationships. In other parts of the world green spotting, sometimes typical and sometimes not, has been found by the writer (43) with sufficient frequency to indicate that more than one strain of P. brevipes or even very closely allied species of mealybugs may be responsible. Whether the spotting is all of the same type would require comparative studies difficult to make in view of the wide area over which the insect is found, and the necessity for study of fresh material.

TOXIC EFFECTS OF FEEDING BY MIRIDAE (CAPSIDAE)

The injury caused by some species of mirids is specific. That by *Plesiocoris rugicollis* Fall. and *Orthotylus marginalis* Reut. was described by Fryer (84). The areas around the insect punctures are seriously injured, the leaves become covered with red or brown spots, the shoots are stunted, particularly at the terminal shoot, and there is an excessive production of lateral twigs. Attacked fruit is deformed, with rough discolored areas; it cracks at the original puncture points and later develops corky tissue. Such fruit usually drops prematurely.

Petherbridge and Husain (186) found that P. rugicollis was the only mirid which caused any serious injury to apple trees, four other species being responsible for only negligible damage. This was confirmed by Smith (222) who investigated the nature of the injury and came to the conclusion that neither mechanical injury nor transmission of bacteria could account for the damage, but that the insect injected a violently toxic secretion. Smith conducted experiments on the toxic effect of excised salivary glands and found a definite correlation between the effects produced by these glands on potato tissue and tissues of apple buds and the injury caused by the living insect. Injection of glandular material from insects normally living on apple, but not damaging it, produced no noticeable effects. It is unfortunate that this study, which appears to represent the earliest attempts at an experimental approach to the question of toxicity of insect secretions, has not been developed more fully by workers in general. Petherbridge and Husain (186) also found by comparing the stylets of the species of mirids studied that similarity between these would militate against any theory of specific mechanical damage. In the case of P. rugicollis early injury occurs in the mesophyll and dead mesophyll may be present under healthy epidermis and the damage therein may spread for some time after the feeding has taken place. The same authors also presented what seems to be a fundamental premise, that these salivary injections of a single insect species may cause different reactions in different species of plants, varietal susceptibility being exhibited by some plant species, and immunity by others. An interesting corollary to this, namely, that insects feeding on a specific plant species, or even on a-specific nutritional state of such a plant species, may develop secretions which are specifically toxic to that same plant species only, will be discussed later in this paper. Knight (133) suggested that the type of wound made by apple red bugs (Lygidea medax Reut. and Heterochordylus malinus Réut.) in their feeding was characteristic for the species and therefore probably due to the effect of some insect's secretion.

Smith (224) believes that the saliva of the Miridae is the most toxic to plants of any sucking insects. He accounts for the infrequency of virus transmittal by this group with the hypothesis that the saliva is so toxic and causes such profound chemical changes in the plant that viruses cannot be successfully introduced, since they require to be introduced into living cells.

Roberts (207) discussing the tobacco mirid (Engytatus volucer Kirk.) in Rhodesia describes one of the few instances where macerated tissues of the insect cause symptoms comparable to those obtained by the insect's feeding, in this particular case, a rolling and puckering of the leaf surface due to contraction. This is brought about by the action of the insect's saliva which spreads into the neighboring cells from the seat of the original puncture. Injuries are most severe on plants growing in poor soils or under conditions that reduce the vigor of the root system.

The injuries caused to cotton by mirids present additional evidence that their feeding is toxic to the plant. Although specific mirids vary in the injury they cause to cotton, they do, in general, produce the same type of injury even though in varying degrees. Psallus seriatus Reut., the cotton fleahopper, is the most important mirid pest of cotton with Lygus pratensis L., the tarnished plant bug, coming next in importance. Damage to cotton is expressed by a shedding of the squares, a decrease in the length of and an increase in the number of internodes, and swellings which may occur at intervals over the entire plant. Ewing (63) and Painter (181) agree that the swellings on the plant, which develop to the typical split lesion of the damaged cotton plant, are local in their extent and do not affect the tissues for more than 5 mm. from the point of puncture. The apparent systemic effect observed on cotton is due, according to Painter, to the frequency of these local lesions, which may be so great as to cause swellings over the entire plant. Painter (181) obtained typical split lesions by injections of macerated cotton fleahoppers and in a test with a number of commercial enzymes obtained somewhat comparable results by the injection of diastase. Painter also observed the apparent fixation of the normal red pigment on the cotton leaf at the point where the insect had fed. At these points the red pigment was insoluble to the action of Carnoy's solution, whereas it was dissolved out of a normal leaf. A comparable effect was obtained with diastase after soaking a leaf in a diastase solution. Failure to obtain this same result with crushed leafhopper suspensions was ascribed to the dilution of the maceration. It might well be pointed out here that successful results following injection of macerated whole insects indicate an extremely stable toxic element, for any other type would probably be inactivated by the admixture of miscellaneous compounds from the numerous organs of the insect's body. Negative evidence following such injections is not by any means conclusive, for it is probable that the more specific a secretion is, the more unstable it will be.

King and Cook (132) experimenting with the feeding of 10 different species of insects on cotton concluded that the feeding of all the species resulting in the same type of internal injury and in lesions that split open, seemed to be a matter of degree of injury rather than a specific injury of another kind. It is interesting to note that the species which caused the greatest percentage of external or split lesions (Poeciloscytus basalis Reut.) is one seldom found on cotton, which illustrates how a new disease may arise as the result of a change of host plant preference on the part of a toxicogenic insect. In view of the fact that some authors have attributed damage of this nature to the stylet sheath left by the feeding of many sucking insects, the datum in this paper on this point is of interest, since only three of the species used, namely two jassids and one membracid, produce a well-defined sheath. No sheath material was found about the punctures made by mirids and the rupturing of cells was minor. These authors concluded that the damage was due to a toxic injected material rather than to a transmittable disease, because of the fact that the injury caused was similar for all of the species. The relatively minor role of P. seriatus compared with L. pratensis in producing the split lesions in this test requires some explanation in view of the findings of other authors. Ewing and McGarr (64) conducting cage experiments in Louisiana with jassids, found no appreciable injury caused by them, whereas three mirids tested, P. seriatus, L. pratensis and Adelphocoris rapidus Say, produced typical injury. McGarr (157). confirming the role of the Miridae in causing the typical injury on cotton, found that six other mirids, not normally feeding on cotton, produced the same type of damage when caged thereon.

The cat-facing of peaches appears to be a case of a specific injury arising from the feeding of *L. pratensis* (200), but whether or not the result of mechanical injury does not appear to have been determined; it would seem to depend on the criteria established for toxic feeding. If sucking insects of approximately the same size and with the same general method of feeding produce specific pathological effects on the plant tissue, it would seem to be a safe

deduction that the specific nature of the injury is not due to mechanical differences in the puncturing process but rather a reaction to a specific secretion. The development of a technique for the micro-chemical determination of insect secretion in a standard medium would go far towards settling this particular question, which is a fundamental one in the subject.

A potato wilt is associated with L. pratensis. Leach and Decker (142) have shown that two weeks' feeding by tarnished plant bugs on the stems of potato plants will produce a characteristic wilt. When the bugs are removed after two weeks' feeding, a marked chlorosis appears in the terminal leaves three weeks later. Ten days after this the stems wilt in a typical fashion. The importance of this finding lies in the fact that systemic toxic effects of insect feeding are relatively rare and have not been previously recorded from the Miridae. In this case there is evidence of the diffusion of the toxic principle since the insects were allowed to feed only on the stems. Leach advises, however, that the disease as known in the field was suspected of being a virus: the symptoms described above resulted from greenhouse experiments and are ascribed to an aggravated form of tarnished plant bug injury.

Leaf crinkle of the vine caused by Lygus spinolae Mey. has been recorded from Europe (86).

So-called froghopper damage, not caused by froghoppers but by unnamed species of jassids and a mirid, is reported by Ripley (204) as causing malformations on young wattle trees. The bugs feed on the leaves where the injected saliva produces dead spots, resulting in the withering and shedding of the leaves. When the terminal leaf bud is attacked, a witch's broom or cluster of leaders is produced instead of a single shoot; this finally causes a crook in the timber, as the dominating leader does not exactly follow the line of the original trunk. Serious injury only occurs when trees more or less weakened by drought or injury to the roots are attacked by large numbers of the insects. Fertilized trees suffer less, owing to their increased canopy and vigor, although occasionally the witch's broom is more luxurious in its growth (205).

At least seven species of the mosquito bug (Miridae) genus *Helopeltis* have been recorded as injurious to a considerable number of economic crop plants in India, Java, Ceylon and the tropical African countries of Nigeria (145), Tanganyika (105),

⁵ Personal communication.

Nyasaland (144), French Equatorial Africa (170) and the Belgian Congo (231). The insects have been known for many years primarily as pests of tea but cacao, cinchona, cotton, mango, avocado, nim (*Melia azedarach* L.), kapok, black pepper, cinnamon, camphor and rubber have all been recorded as being attacked.

The typical lesion caused by these insects is a circular red spot at the point of feeding which, on leaves, ultimately causes necrosis and withering. This symptom appears to be typical of all the species of insects concerned. Within recent years, however, it has been shown that the widely distributed stem canker of tea; stem canker, leaf spot, anthracnose and "blackarm" of cotton; stem canker, angular spot, fruit scab and fruit rot of mango and black scab of avocado are caused by the feeding of this insect, although previously they had been attributed to fungi. In one case, that of nim, the symptom resulting from the insect's feeding is described as wilt.

The feeding of this insect has been studied by Cohen-Stuart (46), who in 1922 showed that the proboscis of the insect penetrates to the vascular bundle and that the penetration is associated with a large area of killed and collapsed tissue. The exact puncture is visible only in preparations made immediately after the attack. De Jong (52) confirmed these findings and noted that the greater the concentration of the carbohydrates in the leaves the smaller was the discolored area. Smee (216) working with tea, found that a small brown patch only resulted unless feeding was continued for a long time, in which case the leaves became dry and brittle within three days. Leach (143) showed that the primary lesions could be recognized on mangoes before the feeding of the insect had stopped, indicating an extremely active feeding process. On mango stems, cankers followed when the insect's stylus ended in the pericycle parenchyma. On fruits, scab lesions resulted when the stylus penetrated to the middle skin, and when penetration to the inner skin was achieved, rot lesions occurred. The development of symptoms following Helopeltis feeding is much more rapid than that of fungus or bacterial infection and this datum appears to be the principal support for the numerous suggestions in literature that the secretions are toxic. This rapidity of feeding is, of course, associated with extremely extensive damage by a small population of Helopeltis. Smee (216) has estimated that four to six Helopeltis can destroy one pound of green leaves during their developmental cycle and that one bug can destroy two shoots of three leaves and a bud each per day, and in Java the writer has seen young tea shoots completely covered with red, discolored feeding areas resulting from the feeding of one nymph for one day. According to Smee and Leach (217) the damage varies with the developmental stage of the bug, this vastly increasing as the insect approaches maturity until one individual eventually has the capacity to kill a single shoot in one night.

Environmental factors favoring outbreaks have been referred to by several authors. Roepke (208) reported that the insect can, on occasion, stand long droughts although it is generally recognized that during dry seasons, populations of Helopeltis become very low. Smee (216) found a measure of correlation between outbreaks and seasons of many rainy days, particularly in November and February. De Jong (50) accounted for the relative freedom from Helopeltis damage in eastern Sumatra by pointing out that a strong mountain wind with very low humidity was probably a limiting factor and that there the insect only developed in the protection of fairly dense shade. Later, however (53), he reported that Helopeltis increases in the shade where the ground is already rich in organic matter and shelter against wind plays no part, but decreases if the shade trees enrich a poor soil and shelter the tea against The same author has the interesting suggestion that increase of Helopeltis during the wet season may be due to changes in the plants, which favor the reproduction of the insect. The concept of the interrelationships between plant status and Helopeltis nutrition has been a dominant one in Helopeltis studies, and a thoroughly documented inclusive study of the subject would be of great fundamental value.

Leefmans (146, 147) has found a relationship between altitude, species and damage. Under 4300 feet *H. antonii* Sign. injures both tea and cinchona. Above that altitude a darker variety of antonii is found which prefers cinchona but does no serious damage to it. Cinchona grown near tea below the 4300 line, however, provides a dangerous neighbor for tea, in view of the capacity of the insect to reproduce on cinchona. The system of alternate pruning (17, 87, 241, 242) and the Pegat system of interspersed green manure crops (88) are interesting practical applications of data on the response of the insect to environmental conditions. When tea plantations are pruned in alternate strips of approximately 10 feet width, the development of the insects in the pruned areas is very

much reduced, and these pruned areas also constitute a barrier through which *Helopeltis* will not move freely from foci of infestation.

According to van Hooff (242) the alternate pruning method interferes with the negative phototropic habits of *Helopeltis*. Bernard (13) pointed out that freedom from rust is essential if alternate pruning is carried out but agrees that the method is successful if the insects are confined to certain foci of infestation and not generally distributed throughout the plantation. According to de Jong (53), however, the factors influencing infestation by the insects run parallel to those affecting infestation by the fungus, so that practices used to control the red rust will make the plant less susceptible to attack by *Helopeltis*.

The Pegat system of control consists of planting green manure plants between the tea rows. Feuilletau de Bruyn (79) suggests that the isolation of *Helopeltis* infestations in this manner results in degeneration of insects through inbreeding, but this explanation seems unlikely unless the isolation is absolute, a condition which could hardly be expected. Hart (107) considers that the green manure crops may produce substances unfavorable to the development and reproduction of *Helopeltis*, or may strengthen the tea by a manurial effect. The green manure plants used in this method of control, however, must not be *Helopeltis* hosts. For that reason lamtoro (*Leucaena glauca* Benth.) is superior to *Tephrosia* for this purpose. *Albizzia* as a green manure crop should not be used on account of its association with large populations of *Helopeltis* (61).

The factors affecting the susceptibility of the tea plant to *Helopeltis* damage have received considerable attention. There is general agreement that soil conditions affect susceptibility to an extreme degree. According to Smee (216) a soil condition unsuitable to the plants increases the latter's susceptibility. Light (150) concurs that serious defoliation only occurs in plants in poor condition. Smee and Leach (217) described water-logged hollows, slopes with underlying water pans and sites surrounded by bush, as primary susceptibility factors. Anstead and Ballard (6) also stressed the factors of drainage and malnutrition of the plant when the original topsoil had been lost. Contributions of Andrews and his associates to the question of soil factors and susceptibility to *Helopeltis* are of great interest. According to Andrews (1) mosquito blight was

less on soils with a high ratio of available potash to available phosphoric acid. Carpenter and Andrews (28) showed that the vigor of the plant depended on soil conditions, and that a vigorous plant suffers little from Helopeltis attack. Andrews (2) confirmed his previous conclusions with regard to the factor of the potash-phosphoric acid ratio, and in addition demonstrated that by direct injection of tea bushes with potash, the increased potash quickly freed the bush from any infestation by Helopeltis. That this was due to the production of an unfavorable food supply was indicated when new arrivals to the treated bushes abandoned their attempts at feeding and migrated to untreated bushes in the vicinity. Potash applied to the soil gave very irregular results, since some soils evidently rendered the potash unavailable. Andrews (3) showed that the ratio of potassium to phosphoric acid in the leaf produces increased resistance to attack by Helopeltis, and that the addition of potash to the soil had actually increased that ratio.

No results were obtained with any other elements, although it would be of great interest to learn the relationships of the minor elements to susceptibility in view of the importance that is now ascribed to minor elements in work done since Andrews' publications. Andrews recognized that local soil conditions materially affected the response to treatments, so that the failure to achieve similar results in southern India and other places with entirely different soil conditions is not surprising. The important thing, that the nutritional status of the plant definitely affected the insect's ability to feed on the plant, seems to ha e been well-established, and it is quite conceivable that in other locations a similar nutritional relationship might be established, even though different elements may be involved. Andrews himself in 1923 (4) pointed out the influence exerted by soil drainage and aeration on susceptibility. Continuous water-logged conditions and increased soil acidity led to greater liability to serious attacks. Tea trees of different species might well produce a different soil aeration due to the development of their root systems.

In a study of three districts Andrews found "That there is a correlation between the ratio of available potash to available phosphoric acid, between the percentage availability of the phosphoric acid, between the value of the ratio of available potash to available phosphoric acid for a given percentage availability of phosphoric acid, and between the soil acidity of the soils of the three districts,

and the varying degree in which the gardens situated in the three districts suffer from attack. No relation can be traced between the total quantities of potash and phosphoric acid present in the soil and the incidence of the pest."

It was concluded that the chemical composition of the leaf was controlled by some factor which could not be shown by the usual methods of soil analysis, and that the transient effect of potash application was in some way due to the operation of this factor. If a constant supply of soluble potash was provided, serious infestations of *Helopeltis* are thrown off and immunity maintained for the rest of the season.

The factor of nutrition has been shown to be of significance in what is termed the suitability of the host plant for the insect. De Jong (51) showed that female Helopeltis feeding on sugar-rich leaves lay fewer eggs than when feeding on leaves of low sugar content. The same author also described an interesting interrelationship between the mealybug Pseudococcus lilacinus Ckll., the sugar content of the plant, and Helopeltis. The high sugar content leaves increase P. lilacinus colonies, which in turn increase the activity of the ants and decrease the activity of *Helopeltis*. On the other hand, low sugar content leaves are unfavorable for P. lilacinus colonies, with the result that ant activity is very much decreased and Helopeltis populations usually high. When this relationship was first understood, workers generally considered that it was due to the interference by the ants with the activity of Helopeltis (240). At pres nt, however, it seems to be recognized that an increased activity of ants is usually an indication that Helopeltis activity will be low and vice versa, but the actual relationship appears to be more than mere mechanical interference by the ants with Helopeltis. On cacao, for instance, Helopeltis confines its attack to maturing pods (48) but according to Kalshoven.6 cannot survive on pods with a high sugar content. De Jong (53) found that susceptibility on the part of the tea plant rises as the proportion of carbohydrate falls, or as the relative quantity of albumens increases.

With respect to resistance either to *Helopeltis* itself or to the toxic secretion of the insect, there are little data available. Carpenter and Andrews (28) considered that the variety of tea was insignificant in this respect, but Anstead and Ballard (6) state that

⁶ Oral communication, 1938.

in southern India, China varieties and their hybrids are more susceptible to attack than other varieties. Roepke (208) considers the existence of a resistant variety doubtful but suggested that selection of a particular type might be profitable.

TISSUE DERANGEMENTS BY THE APHIDIDAE

Aphids are notable for the tissue derangements resulting from their feeding (257). Zweigelt (255) concluded that the salivary secretions must be able to convert starch into sugar by an enzyme similar to diastase. Rawitscher (199) studying five species of aphids as to their method of penetration into plant cells, found that only a few sieve-tubes were pierced, and concluded that injury must be due, therefore, to the toxic effect of the saliva. Smith (223) showed that Myzus persicae (Sulz.), M. circumflexum (Buckt.) and Macrosiphum solanifolii (Ashm.), normally penetrated the leaf intercellularly into the vascular bundles, but M. solanifolii sometimes showed an intracellular stylet tract.

The writer has observed that M. persicae and Aphis gossypii Glover produced no visible curling or lesions on Commelina nudiflora Linnaeus, but M. solanifolii curls the leaves badly with yellow areas left along the veins. Tate (232) studied a long series of aphid species, none of which induced true gall formation. Where leaves became curled, rolled and otherwise distorted as a result of heavy aphid infestation, areas of pseudo-vascular tissue were found when sections of the leaf were examined. Tate considers that the extent of development of this pseudo-vascular tissue probably depends on severity of infestation, the duration of the feeding, and the reaction of the plant to the stimulus of insect secretion.

Capitophorus fragariae Theo. causes crinkling, splitting, stunting, and discoloration of leaves of strawberry. According to Briton-Jones and Staniland (25) the number of aphis present at the time of planting is a factor in the amount of damage. Later work associating this particular species of aphis with strawberry virus disease indicates the desirability of repeating the work of these workers and that of Ball, Mann and Staniland (12) so that the injury caused by the insect exclusive of the virus can be ascertained.

INSECT GALLS

Historically the galls are the oldest known toxic effects of insects on plants, and since early conceptions as to their arising by spontaneous generation there has been a long series of hypotheses regarding their origin. The taxonomy of galls has also proved a fertile field for study and hypothesis. No attempt will be made to review the exhaustive literature of this field of study, but rather to indicate the more recent attempts to determine the mechanism of gall formation, as well as to discuss in somewhat more detail, typical cases of plant diseases caused by specific insects, where the type of damage falls into the category of insect galls.

Gall producers are found in a large number of insect orders as well as among the mites. The latter are probably the principal gall formers and the majority belong to the genus *Eriophyes*. The number of insect gall formers is very large. From the Dutch East Indies (58) 1536 separate and distinct galls are listed. From Central and South America a single paper (113) lists 1341 galls in 98 plant families with only 229 of the insect species known. Wells (249) lists 17 distinct galls from a single species of plant (*Celtis occidentalis* L.). A single insect family may contain gall formers of several types, *i.e.*, bud galls, flat circular galls on leaf lamina, galls folding or rolling the leaf, and stem galls (26).

A gall may be defined as hypertrophy or hyperplasia of plant cells related to certain parasitic animals (249) and there have been numerous hypotheses, summarized up to 1914 by Magnus (158), as to the nature of the injury. Malpighi (161), the earliest writer on gall formation, postulated the introduction of a substance into the plant tissue which caused gall development, and the generally held point of view, even now, is that chemical secretions of the larvae are primarily responsible for proliferations, although Rahn (198) suggests that radiation from the larvae may have some effect. Wells (249) found that galls were not similar to wound wood, and suggests that all the evidence arising out of experimental studies so far point to a chemical interpretation, but that a definite support to this point of view has not yet been demonstrated. Form characters of the gall tissues are ascribable to the specific physiological phenomena of the insect and Wells' study, dealing as it did with a long series of different galls arising from the same plant tissue, is significant in this respect.

The specificity of the gall-forming secretion is illustrated by the example of a gall which was transformed into another gall under the influence of another gall-forming insect (59). Dieuzeide (57) found evidence of the toxic effect of the gall on young elms caused

by aphids. Küster (139) found that the aphid Tetraneura ulmi L. produces typically structured galls on the white portions of the variegated Ulmus leaves but they are smaller than those that are produced on normal green leaves. According to Balch (8) Chermes, cause of gout disease of balsam fir, produces one type of injury on stems and another type on twigs. Twigs swell and bud development may be suppressed. The degree of swelling bears no relationship to the number of larvae, but rather to the vigor of the plant. On the stems slight swellings only occur at the crevices of the lenticels. Zweigelt (256) in connection with the aphid galls, showed that the type is determined by the reaction of plant cells to irritants irrespective of the number of parasites.

Following Küster's classification (138), Wells (249) found that the acarinas and lepidopterous galls on *Celtis* were kataplasias, or those forms of heteroplasias whose cells and tissues did not vary widely from the normal. The hemipterous and dipterous galls were prosoplasias, or those forms of heteroplasias whose cells, and particularly whose tissue forms, differ fundamentally from those of the normal parts. According to Cook (47) all insect galls arise from the meristematic cells and are kataplasias first, many becoming prosoplasias with fibrous and sclerenchymatous tissues prominent. Cell activity ceases when the gall larvae reach maturity, and in this respect insect galls differ from fungous, slime mould and bacterial galls.

Mite galls are not a protective device or a storehouse of nutrition, but a reaction product on the part of the plant to counteract the injury by means of antibodies (130). Noble (177) studying the citrus gall wasp, showed that excess wood is laid down by the cambium except near the larvae. There, green cellulose-walled nutritive cells, rich in fluid, developed from the cambium, and from these cells the larvae derived their nutriments. Nierenstein (176) concluded that the tannin in the galls caused by Pontania proxima Lep. on Salix caprea L. inactivates the diastase and invertase of the larvae but that tannase produced by the larva protects its enzymes from destruction by tannin. The enzymes in galls acting in a centrifugal direction from the larval cavity have been described by Kostoff and Kendall (135). Although all the starch may be hydrolized directly by the insect secretions, the question of the role of the unicellular organisms, which are abundant between the insects and the plant tissue, in this respect, is yet to be settled. A decrease of

the pH value in the galls in a centrifugal direction from the larvae has also been shown.

The effect of mechanical and chemical stimuli on the living tissues during gall formation appears to be similar to that in plant and animal tumors, graft unions, bacterial nodules and certain calluses. Polyploid cells or irregular mitoses near the larval tissues would seem to indicate the presence of active foreign substances. The presence of irritating substances on gall insects have been described so that it is rather unlikely that the actual wound, due to oviposition, is responsible for the initiation of proliferation. Egg excretions have also been determined and according to Kostoff and Kendall (135) the egg excretions, the irritating substances produced by bacteria and other unicellular organisms next to the eggs, and the wound hormones when the oviposition is accompanied by an injury to the plant tissues, are the substances which give the first impulse for cell proliferation, but wound hormones, in the opinion of these authors, are of great significance.

Cell division in gall development can be attributed partly to the disintegration products of the cells injured: mechanically, by wounding in oviposition and by chewing of the larvae; chemically, by action of the egg or larval secretions and the toxic substances produced by the unicellular organisms. According to these same authors proliferation ceases when the protective substances produced by the plant become strong enough to eliminate the stimulus for cell division. They conclude that cynipid galls are a reaction product of the plant tissue dependent on plant specificity; the quantity of sap entering the organ or tissue where the gall originates; the specificity of the insect determining the specificity of the foreign substances; mechanical injuries and their disintegration products; the presence of unicellular organisms and the activity of their products, qualitative and quantitative.

Felt (71) summarizes certain points of view with respect to the relation of insects and plants in gall production. Galls produced by mechanical injury are few. In some others the injury is central and is due to the levies of gall producers upon the vitality of the seeds and adjacent parts of the young fruit, as for example, the bud galls associated with *Eriophyes avellanae* Jaru. This mite produces the typical big bud as a gall, but then becomes so numerous in the gall as to kill the tissues. According to this author, the stimu-

lant to gall formation by most mite and hemipterous gall insects, a very large proportion of the diptera, and probably all the cynipids comes from the salivary gland. Stimulation is a cardinal principle in gall production and the production of plant galls is dependent on stimulation of plant cells in a meristematic or plastic condition. There is a close analogy between the insect gall and the development of adventitious buds. Since the development of adventitious buds is, however, closely related to the production of plant hormones, the possible relationship between gall hosts and hormones is of The indeterminate galls are greatly modified in size and shape by the degree of infestation. The determinate galls have relatively little in common with the normal tissues from which they are developed and usually are characterized by rather definite sizes and shapes. There are degrees of development in insect galls which are produced by closely related species, for example, Phylloxera and Caryomyia, upon the same host and even upon similar structures such as the leaf blade of identical hosts.

There has been some success obtained by workers in producing tumors, or gall-like formations on plants by the introduction of certain chemicals. Annand (5) produced tumors in kale by the injection of simple laboratory chemicals. Kostoff and Kendall (136) produced tumors by means of various chemicals similar in structure to naturally occurring tumors. Kendall (131) produced growths analogous to galls by the injection of chemicals and foreign biological material. Levine (149), working with carcinogenic agents of animals on plants, concluded that the injury of injection tends to initiate cell proliferation and that the cambium or the meristem responds to the agents. Martin (113) produced stem galls on sugar cane by the introduction of the macerated bodies of a leafhopper and concluded that auxines were in some way concerned.

Lutz and Brown (155) suggest that galls attributed to insects may be really due to bacteria and fungi, the insects being merely vectors, but the weight of evidence is definitely against this view.

Galls on economic plants are few in number compared with the number of galls described, and some are useful articles of commerce (251). Some gall-engendering insects produce serious diseases of economic plants as for example, the woolly aphis of apple, *Phylloxera* of the vine, a considerable number of diseases attributed to gall mites, some to psyllids, with scattered examples in other insect orders.

The woolly apple aghis Eriosoma lanigerum (Hausm.) was first described in 1802. The insect is remarkable for its variable life history in different geographical areas. In the eastern United States the American elm (Ulmus americana L.) is a primary host and apples and related trees the secondary hosts. In the western United States, and in other parts of the world where the American elm does not exist, the insect has adapted itself to a single host plant. In either case, the insects are primarily bark feeders, feeding either on the bark under the top 2 or 3 inches of soil or, rarely, on the true roots. Leaf galls are also produced by both species. The warty galls of woolly apple aphis are produced by stimulation of the cambium layer, the dissolving of the middle lamella, which in the sclerenchyma results in the formation of separated sclerenchyma masses and the formation of gall tissue in the medullary rays (226). The damage tends to be accumulative in that young warty galls are very suitable places for young aphis to establish. The relationship between this insect and perennial cankers (Gloeosporium perennans Z. & Ch.) as shown by Childs (45) is also significant from the standpoint of the economic role of the insect, although not related to primary gall formation by the insect.

The difficulty of artificial control measures has led to a considerable study of resistance and immunity of apple stocks and this problem, as well as the general one of woolly aphis have been admirably summarized by Greenslade (95). Immunity, not to the aphis, but to gall formation, exists in the variety Northern Spy and breeding for immunity has been carried on with the object of combining the resistance of Northern Spy with the more suitable horticultural characteristics of other varieties. This has resulted in a large number of seedlings immune to gall formation, but nursery tests of these naturally require a considerable period of time. Jancke (118) records tests of 103 varieties of edible apples and 79 wild apples and hybrids which indicate that immunity or a very considerable degree of resistance to the aphis is found in hybrids. Resistance and susceptibility have been defined by Underhill and Cox (237). Resistant varieties are those on which the aphids established temporary infestations but did not reproduce and did not stimulate the formation of galls. The term "susceptible" refers to varieties on which the aphids established permanent infestations and stimulated the formation of galls. Resistance and susceptibility appear to vary with geographical location and this has been attributed to differences in soil type. It is possible, however, that vegetatively reproduced plants grown in widely diverse environments might react to the environment as a whole, and that this reaction might condition the frequency of vegetative mutations which might vary in susceptibility.

Since resistance must be to the toxic secretion of the insect it is probable that physiological considerations will be the determining factors rather than such mechanical factors as thickness of cell walls in the epidermis. The acidity of the cell sap of resistant varieties is higher than that of susceptible varieties (169) but it is perhaps likely that the pH of specific tissues would be more significant. Indications that the factor of resistance is correlated with the chemical constitution of the bark have been found by Roach and Massee (206) and by Greenslade, Massee and Roach (96).

Phylloxera of the vine presents many aspects similar to those seen in the woolly aphis problem. The insect's life history varies with location and much of the literature is concerned with these differences (233, 234). Damage is due to the formation of galls on the small feeding roots which results in the decline and final death of the vine. Leaf galls are not found universally and in some locations many years have elapsed before the leaf forms have appeared (22, 83, 244). Gescher (89) suggested, that for the maintenance of a colony of Phylloxera, it is eventually essential for the forms that are the result of sexual reproduction on the aerial parts of the vine to be regenerated by migration to the roots.

The question of biological races of *Phylloxera* raised by Börner (20, 21) was followed by considerable controversy (162, 175, 233, 234, 235, 243). Whether the two biotypes can be clearly differentiated morphologically, whether they have arisen by separation from mixed stocks imported from America, or whether they represent mutations as a result of their new environment are not questions particularly germane to this review. What is of significance is the evidence that biotypes do exist which react differently on different varieties of vine.

Stellwaag (227) showed that *Phylloxera* perishes on the roots of immune vines owing to a reaction of the cells around the puncture; galls develop on the leaves of vines with susceptible roots but *Phylloxera* perishes on the leaves of other vines. Variations in susceptibility of a given variety of vine is due to different types of *Phylloxera*, not to changes in immunity. Printz (197) shows that

Phylloxera bred on European or Asiatic vines for 20 to 30 years loses the ability to form galls on American vines and recovers it only after a long period of development on their roots.

Vodinskaya (246) was able to artificially infest the different varieties of American vines and hybrids with the leaf form if the infestation was made during the period of leaf formation. If infestation occurred when all the leaves were already developed, the number and quality of the galls varied on different varieties of vines. No preference was shown for roots of different varieties when exposed to attack.

Faes, Staehelin and Bovey (70) stated that observations on *Phylloxera* from 1924 to 1931 showed that the leaf gall form is always more or less abundant in a year following one with a hot dry summer and autumn. Borg (19) records leaf galls of *Phylloxera* occurring on European vines which were growing among a number of American varieties. The American varieties were covered with leaf galls but on the European vines they were very few in number. Whitehead (250) reporting on *Phylloxera* on pecans in Oklahoma states that twigs, petioles and leaves are heavily infested with galls 3–5 days after the aphids appear.

Relationship between the age of the vine and its susceptibility was discussed by Makarov-Koshukhov (160). If recently planted vine slips are infested, 75 per cent are killed in the year of attack, and all in the following year irrespective of variety, type of soil, or character of the locality. If attacked in the second year a few may survive, whereas a considerable number of those attacked in the third year are resistant, and stocks 5-6 years old are not affected.

Relation of soil type to *Phylloxera* infestation has been reported on by Nougaret and Lapham (178). Correlation between damage and shallow rooted vines caused by poor drainage, compact and impervious subsoils and hardpan has been shown. On the contrary, vines growing in deep friable soils having porous subsoils are less susceptible to damage. Whether this is due to the effects of the physical character of the soil on the life of the insect, or whether the vines grown in the more suitable soils are better able to resist the injury, is not known.

As is the case with woolly apple aphis, chemical controls of *Phylloxera* have proved difficult although Grandori (91) reported satisfactory results with the use of paradichlorobenzene as a soil

fumigant. The insect can persist in the soil for long periods of time, however, as shown by Makarov-Kozhukhov (159). In this case *Phylloxera* was still found in the soil 12 and 16 years after the vineyard had been uprooted and the soil treated with large quantities of carbon bisulphide. Based on the work of Müller (172, 173, 174), the same author calls attention to the possibility of using internal treatment of vines against *Phylloxera*. Jancke (117), also following Müller, found that nicotine was absorbed by the grape vine shoots and found in the leaf-tissue, but did not penetrate the tissue of *Phylloxera* leaf-galls in 7 days. Doses tolerated by the plants were also tolerated by the insects. The general method of attack on the problem of control, however, is by the use of resistant stocks, the stocks of resistant American vines being used generally for this purpose.

A report on testing of *Phylloxera*-resistant grape stocks by Husmann (114) indicates some of the complications that arise when resistant non-commercial stocks are hybridized with desirable commercial varieties. Hybrids reverted either too far toward the vinifera with the *Phylloxera*-resistant qualities lacking, or too much toward the resistant, thus impairing the quality of the fruit. It is clear, however, that the severity of the *Phylloxera* problem can be very materially reduced by the use of resistant stocks suitable for a particular territory. Resistance to the leaf form of *Phylloxera* in Germany, according to Börner and Schilder (23) appears to be confined to crossings that contain "cinerea" "berlandieri" or "rupestris" varieties in addition to "riparia."

Mite induced diseases of plants are numerous and the following are cited as examples. In that caused by blister mites of apples and pear (Eriophyes pyri Pagens.), the typical blisters first appear as pale greenish spots on the leaves, which later turn brown and fall off. Injury to fruit is generally outgrown (245). Killing of fruit buds in winter, weakened flowers and resultant misshapen fruit, due to a species of blister mite, morphologically indistinguishable from E. pyri, but differing from it in biology and the damage it causes, has been described by Borden (18). Heriot (110) believes that E. pyri causes blisters on pear by first inciting enlargement of the loose mesophyll cells which expel intercellular air, thus closing the stomata and raising the epidermis from the underlying tissue. Wilson (253) states that E. pyri oviposits in parenchyma and the

young larvae extend the cavity in all directions, resulting in a mass of blisters over the whole leaf.

Crinose or felt mites, so called from the thick felt of pubescent brown hairs which grow on the lower side of the leaf, have been noted by Wilson (253) on grape vines caused by E. vitis Land. The upper surface of the leaf is distorted. A similar condition on English walnut caused by E. tristriatus var. erineus Nal. differs in the color of the pubescence, which is white and the galls are more distinctly outlined. A crinose gall, Eriophyes sp., on litchi is serious in Hawaii. A thick felt of reddish brown hair appears on the lower surface of the leaf. The upper surface is arched rather than swollen, with a corresponding depression on the lower crinose surface.

Blister mite on cotton ($E.\ gossypii$ Banks) is a major pest in some places. According to Fife (80) injury is seen in crumpled leaves, distorted growth and lack of fruiting branches. The development of types of sea island cotton immune to $E.\ gossypii$ was reported on as long ago as 1919 (104). F_2 generations segregated in immune and non-immune, while in the F_3 generation, the immune bred true and non-immune segregated further into immune and non-immune.

The blackberry mite (*E. essigi* Hassan) causes the disease known as redberry disease of the Himalaya variety of blackberry (62), (164). According to Essig (62) other varieties are not attacked, even though they may be growing in such close proximity that their stems are interlaced. The disease is characterized by the presence of berries which may be entirely red or partly so. These red berries never ripen. The disease is caused by the mites entering the flowers and feeding near the bases of the immature drupelets (98, 99, 171). The mite also attacks loganberries and raspberries.

Mite disease or "Akarinosis" of the vine is widely distributed in continental Europe. In France it is known as "court noue." Shortening of the internodes with consequent stunting of growth is the typical symptom (85). The same condition has been referred to as "mite crinkle" by Stellwaag (228, 229) who has ascribed it to three species of gall mites, namely, Epitrimerus vitis Nal., Phyllocoptes vitis Nal. and P. viticulus Pant., and who has indicated leaf crinkling as a conspicuous symptom.

⁷ Author's observation.

A witch's broom of lilac caused by *Eriophyes lowi* Nal. has been described by Smolak (225) as resulting from the feeding of the mite on epidermal and subepidermal tissues of the buds.

The "big bud" disease of black currants (E. ribis Nal.) has been studied in connection with "reversion" disease, but it seems clear that the two are separate entities, the latter being a virus disease. Big bud is a disease due to the attack of mites which stimulates the growing point to make irregular development (148). On red currants "big buds" are not produced, but instead a somewhat swollen bud, or a dense growth of buds which do not develop normally (165).

The psylla disease of indigo is a disease caused by *Psylla isitis* Buckt. Curling of leaflets and the knotting of the apical shoot occur only as the result of nymphal feeding. The extent of the curling and knotting varies with variety. "Java" curls into a hard knot; "Sumatrana" into a less compact mass. Recovery follows when the psyllids are removed (97, 166).

Citrus leaves are pitted by the nymphs of Trioza (Spanioza) erythreae Del. G. according to Harris (106). The pits enlarge with the growth of the nymphs. Nymphs of Phytolyma lata Wlk., on the other hand, produce galls on Chlorophora excelsa Benth. & Hook. which enclose the insect, and with heavy infestations of the latter, large multiple galls are formed.

The gall making of a coccid has recently been described by Parr (184). The feeding of the first instar of this scale insect (Matsucoccus sp.) results in a collapse and disintegration of plant tissue around the base of the stylets, and the insect gradually sinks into the depression thus formed. The second instar is completely covered by plant tissue. As the insect grows the plant tissue surrounding it swells and later dies. Extracts of the insect's salivary glands injected into the collenchyma of new growth of uninfested trees has resulted in tissue derangements similar to those produced by the feeding of the insect.

HOPPERBURN

One of the most notable examples of a toxic effect of insect feeding is that associated with *Empoasca fabae* Harris. Establishing the relation of *E. fabae* to hopperburn of potatoes was one of the pioneer contributions of Ball (9) in this field. The symptoms of hopperburn have been adequately described by Ball (9, 10), Parrott

and Olmstead (185) with a significant note by Leach (141). Wrinkling of the leaves is followed by upward rolling and marginal burning, with the marginally burned area increasing in severe cases, causing the death of the leaf and the defoliation of the plant. Leach pointed out that the shortening of the leaf petioles with a crowding of leaflets was the first symptom preceding the typical hopperburn symptoms of curling and marginal burn. The disease was at first confused with physiological tipburn, and for a time considered synonymous with it, but the term "hopperburn" was definitely ascribed to it by Ball and Fenton (11).

Manifestations of E. fabae feeding on other crops have from time to time received specific names, as for example, alfalfa yellows (129), but the term "hopperburn" seems to be generally applicable and should be used (195). On apples (92) discoloration of the leaf margins is followed by curling of the tips and the distal margins of the leaves. On the legumes, yellowing and dwarfing are additional symptoms, the number of flowers is reduced and the root system is weakened. On alfalfa there is a mottling and blotching of leaves, which fuse to form striated discolorations between lateral veins; deep yellow to orange discoloration with bronzing of leaf edges; stunting and shortening of internodes; rosetting and proliferation of new dwarfed shoots (93, 111, 129, 168). On eggplant, Poos and Haenseler (192) showed a very distinct cupping of the vounger leaves with the margins light green or yellowish, with later death; further cuppings were followed by extreme irregularity of the leaves. The symptoms on hollyhock are essentially as on potato. On marigolds, in addition to upward curling and reddening of leaflets, there is a twisting of the petioles and the killing of young shoots (219). Ball (10), Dudley (60), Hartzell (108) and Beyer (14) added to the list of plants affected with symptoms typical of hopperburn by E. fabae. More recently Metcalf (167a) has definitely shown that E. fabae is responsible for a tipburn of peanuts known as "peanut pouts."

Factors affecting susceptibility have been considered by Dudley (60) who pointed out the close relationship between the extent of the disease and the number of hoppers present; that varieties with more tender foliage were more susceptible, and that potato plants grown from tubers from diseased plants were more susceptible than others. This last observation suggests that one effect of the disease is to reduce the vigor of vegetative reproductions from the

affected parent plant, and that this reduced vigor is a factor in susceptibility. Soil types and moisture, sunlight and reduced leaf transpiration had no final effect on the development of symptoms (72). Eyer (66) showed that sunlight was important but the disease can occur in its absence, while according to Beyer (14) hot dry weather increased susceptibility and humid weather with moist soil decreased it, but merely its rate of development, not the ultimate result. Relative freedom from injury depends upon slow and continuous growth with an abundance of leaf surface (75).

On the nature of injury by E. fabae there is apparent agreement in connection with potato hopperburn, but distinct difference of opinion as to the nature of the injury on clover and alfalfa. Ball (9) suggested that marginal burn could not be accounted for by sap withdrawal only and that probably a toxic injection was involved. Fenton and Ressler (76, 77) achieved positive results with injection of macerated adults and nymphs and this was confirmed by Eyer (66, 67). Fenton and Ressler again (78) attained additional positive results with artificial injection, although there is some difference in results as to the relative toxicity of macerated nymphs and adults. Lutman (154) considered that the destruction of veins mechanically and water withdrawal were essentially responsible for the symptoms. Fenton and Ressler (78) conducted a potometer experiment which gave positive hopperburn results, which appear to be conclusive, in that they avoided any wound reaction due to mechanical injury to the leaves which showed symptoms. Fenton and Hartzell (75) obtained negative evidence with mutilation of leaves, injection of poisons, or the tissue of hopperburned leaves, and positive results with macerations of adults. but not with nymphs of E. mali Le B.

Granovsky (92) was able to obtain symptoms similar to hopperburn on apples by leaf inoculations of macerated insects. A low percentage of positive results is also recorded by the use of sap of injured leaves. With the legumes, however, the only attempt to produce the disease by inoculation of macerated insects is that by Johnson (126) and this was negative. Johnson is of the opinion,⁸ however, that the use of entire insects rather than specific tissues, as for example, the salivary glands, left the matter inconclusive.

Authors seem to be agreed on the differences in ability to produce symptoms by different stages of the insect. According to Fenton

⁸ Personal communication.

(72) all nymphal stages produced the disease, but the first and second instars produced no effect unless in large numbers. Adults were not so effective as the older nymphs and then only when in large numbers; the older the nymph, the more injurious it is. According to Dudley (60) one adult or one nymph is sufficient to produce symptoms. Fenton and Hartzell (75) showed that the last three instars were more toxic than either the first and second, or the adults. Symptoms appear on alfalfa 5 or 6 days after leafhoppers have fed, and 10 nymphs of the later instars can severely injure a plant in 2 weeks (93). The ability to produce the disease is common to the species and hereditary in the insect and the injury is in direct proportion to the number of leafhoppers feeding. Recovery is general after the removal of the insect (191, 193, 196).

Monteith (168) considered that the evidence indicated something besides mechanical injury. Accumulation of carbohydrates was first shown by Granovsky (94), who considered that enzymic secretions of the leafhopper caused the disorganization and granulation of plastids and the disorganization of the phloem of affected tissues. Jewett (119) considered that infested plants were more subject to winter injury than normal plants and the more yellow the plants the less the injury sustained. Johnson (126) showed a gradually accumulating injury with the feeding of a single adult for 8, 16 and 24 hours respectively, but failed to get positive results by artificial inoculation of plant juice and from macerated adults and nymphs of E. fabae. He concluded that the results of E. fabae's feeding was not due to a virus or toxin, but was caused by over-accumulation of the carbohydrate products of photosynthesis, for the sheath material, largely of insect origin, found in the insect punctures. definitely interferes with translocation (220). Johnson (127) presents additional evidence of the carbohydrate accumulation by the leaves with a deficiency in the stem, believed due to the clogging of the food-conducting elements and improper translocation. economic losses due to injury to alfalfa are shown to be due not only to loss of weight but to loss of nutritive value in the leaves.

Varietal resistance is a matter of host resistance to ovipositing females. Succulent and rapidly growing leaves are preferred. The slow, but continuously growing varieties with a large leaf surface are relatively little damaged (75). European strains of red clover are more susceptible than the native ones (111). The relatively glabrous English clover is more susceptible than the pubescent Ten-

nessee strain. The Italian clovers are more susceptible than the native hairy strains. Hairy Peruvian alfalfa is practically immune unless the leafhopper concentration is very large (93). Monteith (168) showed great variations in varietal susceptibility and believed that the difference was due to qualities of the plant which made it unfavorable for the feeding and reproduction of the hoppers. The correlation between amount and type of pubescence and varietal resistance is not a direct one, since breeding tests do not show any correlation between pubescence and the numbers of nymphs hatching (120, 194). Searls (211) points out that the more naturally vellow a variety the less the injury, and conversely, the greener the variety the more the injury. Jewett (121) showed that in order to drive a needle through the leaves of resistant strains, greater pressure was required than needed with susceptible strains, indicating that the resistance factor may be, in some way, concerned with the mechanical structure of the leaf: again (123), that the varieties most resistant to E. fabae were most resistant to puncture. The correlation in other varieties was not significant. Johnson and Hollowell (128) showed that the appressed hairy varieties were less susceptible, and that the factor for resistance was evidently hooked up with the gene complex controlling pubescence. forms seem to be less suited for oviposition (193).

It is evident that the feeding process of *E. fabae* differs materially from that of many closely allied members of the same genus, as has been shown by Smith and Poos (212). Apparently no attempt has been made to compare the enzymes of *E. fabae* with those of other species, and as far as the writer is aware no other *Empoasca* species on the mainland United States has been shown to be the cause of leafhopper burn. However, in Hawaii, *E. solani* produces essentially the same type of injury on a number of hosts, particularly castor bean and watermelon and to a lesser extent, on potatoes. Herford (109), studying this same leafhopper in Hawaii, showed that both diastase and invertase were secreted by the insect.

Control of *E. fabae* on potatoes is accomplished by the use of Bordeaux mixture sprays (54, 56, 65, 74, 137, 167, 182, 183, 209); on dahlia by repellent dusts (156); and in the forage crops by timing the cutting schedules (90, 122, 195, 212, 213). Jewett (124) refers to the development of a resistant strain of red clover in Kentucky.

FROGHOPPER BLIGHT

Froghopper blight of sugar cane, caused by the feeding of the cercopid Tomaspis saccharina Dist., has been the subject of intensive study for many years, with the result that the problem has been approached from a good many angles. The disease has been known since 1862 and was definitely associated with the froghopper in 1889 (101, 252). The most extensive study of the subject is that by Williams (252), and an important source of information is to be found in the "Minutes and Proceedings of the Froghopper Investigation Committee" of Trinidad and Tobago. symptom is a pale area surrounding the puncture which is elongated slightly longitudinally. By further elongation this spot becomes a long, narrow pink streak which later becomes brown and discolored. Necrosis follows in the pink area. According to Williams (252), a single froghopper puncture may result in the destruction of half a square inch of leaf tissue. The length and width of internodes of the plant are both reduced and, below the area of maximum shortening of the internodes, adventitious buds develop. Adventitious roots may also be formed as high as three feet above the soil level. Following injury by froghopper the pH of the cell sap gradually falls. In fairly good soil it rarely drops below pH 5.7 but on some heavy soils it may be as low as 5.4. This increase in acidity is most noticeable at the top of the cane where enzyme activity is greatest (254). The root systems of blighted cane are invariably poor and superficial. Under favorable conditions for growth, recovery takes place when the attack of froghopper has passed.

The relation of the insect to froghopper blight was proved by Nowell and Williams (180), who showed that froghoppers could produce a definite form of blight in the absence of fungi or any other insects. Nowell (179) records that severity of blight in many cases does not correspond with the degree of froghopper infestation. Pickles (189, 190) believes that the periodical occurrence of outbreaks following severe dry season is brought about due to the effect of the environment on the green muscardine fungus, Metarrhizium anisopliae (Metch.) Sarok. The same author (190), in discussing the difference in blight incidence, suggests that it may be due to the preference of froghoppers for unhealthy cane, or to different micro-climatic conditions, dependent on plant growth,

small or large canes, thick or sparse canes, etc., and that these characteristics are probably of more significance than any food preference on the part of the froghopper for canes of different types.

Withycombe (254) studied the relationship of the insect to the disease and describes the effects of the insect's saliva upon the plant tissue. The saliva has been shown to penetrate cell walls and lignified xylem vessels. Plasmolysis of the cell contents often occurs. The saliva of the froghopper has a distinctly diastatic action upon starch and in addition, it contains oxidases. In reaction it is slightly acid and does not invert disaccharides. Saliva is pumped into the wound and shortly afterwards there is a distinct bleaching of the chlorophyll, more longitudinally than laterally. In a few cases where the sucking of the froghopper had continued for an hour or more, certain cells showed a slight brown or pink coloration, due probably to oxidation of catechol tannins. The most striking effect, noticeable even after a short feeding, is upon the contents of the border parenchyma cells, for whose contents the saliva appears to be specific. The chlorenchyma around a froghopper puncture allows of slight spreading of the insect's saliva, but in the border parenchyma the saliva passes rapidly in a longitudinal direction. Lateral extension is, however, slow and is usually associated with prolonged salivary action. The effect of the saliva upon the contents of the border parenchyma is believed by Withycombe to be due to the fact that the enzymes of the froghopper's saliva exert their greatest activity at the pH concentration of these cells. The phloem has nearly the same pH, while the chlorenchyma is slightly more alkaline, and the xvlem more acid.

In the case of short periods of feeding, the main apparent effect is upon the plastids of the border parenchyma; with prolonged sucking, both chlorenchyma and vascular tissues become more involved. Prolonged feeding is believed to provide mass effects which are associated with extensive post-mortem changes. After sucking has ceased, paling of the chlorophyll extends in a longitudinal direction from the puncture, usually more often more towards the apex of the leaf than towards the base. Extension is accompanied by the appearance of a red pigment. The injury spreads as a yellow, ill-defined streak for a time and then becomes dead and brown in the center. With less susceptible varieties such as Uba, there may be very little yellowing but a red, finely stippled, streak appears, which later also becomes brown and dead. If feed-

ing is prolonged, blanching of the chlorenchyma and faint local reddening, due to oxidase action, may be seen. After a day or two the cells of the phloem show deposits which give a tannin reaction; these deposits are often associated with red pigment.

Injuries from a froghopper puncture can be summarized thus: direct injury and drain upon the contents of the vascular tissues and injurious effects upon the border parenchyma which extend longitudinally, with removal of carbohydrates stored therein. The injury produced by the saliva is effected by several ferments with diastatic and oxidizing enzymes demonstrated as present. The rate of respiration increases locally with oxidation. Super-normal oxidation is influenced by the action of plant oxidases, in combination with the oxidases of the insect's saliva. Local translocation is hindered and the effect is further intensified when the phloem becomes blocked. Water deficiency prevents recovery of the protoplasts in all affected cells and culminates in a drying-up of the tissues. Assuming continued effect of the enzymes introduced by the froghopper, the metabolic equilibrium of the plant will continue to be upset, unless a sufficiently powerful counter-reaction is forthcoming.

Withycombe also records great differences in the amount of blight obtained with given numbers of froghoppers in experimental cages. The situation is somewhat similar to that encountered in mealybug wilt experiments. The tips of leaves are apparently more susceptible to injury than the bases, also, the older the leaf, after prime, the more susceptible it is to injury.

There is a definite relationship between certain types of soil and blight incidence, the roots of diseased plants are invariably poor. Canes growing in soils more acid than pH 5.5 are severely damaged in bad froghopper years (239). Canes growing on markedly alkaline calcium-satisfied soils appear to be capable of resisting froghopper damage. According to Hardy (100) alkaline, calcareous, black soils support heavy crops of cane that are generally much less prone to froghopper blight than canes grown on other soils, such as the acidic, pale-red soils of the same district, and the acidic fawn-colored soils of the great alluvial plain of the central and northern regions of Trinidad.

Withycombe rejected the soil-reaction theory as did de Verteuil (100), both of whom employed colorimetric methods for determining soil reaction. The work was repeated using the quinhydrone electrode, and a very positive correlation was obtained

between reaction and degree of blight. Both "normal" and "exchange" alkalinity were measured. Canes that were badly blighted, especially in the ration stages were supported on soils having "normal" reaction below pH 5.5 in nearly every case.

The mechanism whereby liming apparently confers resistance to blighting of canes growing in alkaline soils has not yet been explained. The water relations may be one factor, another may be the nutrient relations, such as the potassium relation between plant and soil. Control depends on the correction of acidic, calciumstarved and humus-deficient sugar cane soils. Turner (102) found that the higher the degree of saturation of the soil with combined lime the less the susceptibility to blight. The soils of blight-free areas are all adsorptively saturated or nearly so, as regards lime, and the soils of regularly blighted areas are less than 60 per cent saturated. Turner (236) further confirmed the relationship between the exchangeable calcium of typically blighted and blightfree soils and he concludes that in soils containing more than 7 mg.E. per cent, the effect of the soil deficiency in exchangeable calcium on the reaction of the cane to froghopper attack is mainly indirect, by reason of its influence on the physical condition of the soil. Where the soil content falls appreciably below this value, the data obtained indicate that calcium starvation of the cane may contribute to the damage it sustains. According to Withycombe the most serious froghopper attacks occur upon heavy compacted soils in thoroughly bad physical condition. Water-logged and oxygen deficient soils behave as though in a state of water deficiency. Withycombe's statement, that interference with water absorption by the roots is one of the first effects of the removal of oxygen, should perhaps be amended. Loss of oxygen would result in the death of the feeding roots, which in turn would result in wilting due to interference with water absorption.

Pickles (188) showed that soils may differ materially in their suitability as places for oviposition. This is a new point of view on the relationship between the soil and blighting, which in the past has been ascribed to influence of the soil on the metabolic activity of the cane. Pickles goes on to say "Although there is thus strong support for the theory that the production of froghopper blight is determined by the abundance of froghoppers and not by metabolic activity of the canes, it is admitted that recovery from blight may be affected by the physiological relations of the cane," and thinks

that soil characters are directly responsible for determining the severity of blight, because of the relation between the type of soil and the abundance of froghopper eggs.

According to Follett-Smith (82), the general indications are that the leaf sap of sugar canes growing in good soil is likely to contain a greater amount of hydrophilic colloidal matter than that of canes growing in poor acidic soil; this may account, at least in part, for the greater resistance to drying-out of leaves of canes growing in good soil. Studies on the nutrient status of the soils in good and poor areas was reported on by Follett-Smith (81). All the soils on which cane is susceptible possess low nutrient-supply rates as measured by the electrical conductivity of water extracts. potential plant nutrients appear to be released very slowly. This may account for the slow rate of recovery of injured leaf-tissue of blighted canes. Marked fluctuations in conductivity values would be expected for a fertile soil where micro-organic flora is vigorously active, and information might be gained regarding the significance of the micro-organic flora of a soil by making measurements of the electrical conductivities of extracts of soils that had previously been rendered sterile by treatment with toluene.

It seems clear, as Hardy concludes (101) that an agriculturally imperfect condition of the soil, from whatever cause it may arise, is favorable to the development of froghopper infestation in years when the general climatic conditions are suitable, but no studies appear to have been made on the actual effect of the froghopper in producing the collapsed root system. As will be seen under the discussion of mealybug wilt, collapse of the roots is a primary effect of the mealybug's feeding.

Variety and age of cane are both considered as susceptibility factors. The leaf sap of ratoon canes at the commencement of the wet season apparently is more suitable for inducing oviposition than is the sap of plant crop cane or of pasture grasses. These first ratoon canes are preferred as hosts for the first brood adult froghoppers. Briton-Jones (24) believes that the question of the relative liability of ratoon and plant-cane to blight is a question of condition of growth, rather than the age of the stool from which young growth arises. Plant canes, however, hardly ever suffer to the same extent as ratoons, and the percentage of blight is usually small for the plant-cane crop. The question of source of froghopper infestation with respect to relative toxicity in connection with these

differences, does not appear to have been studied, although Smith (218) reported that no instances have yet been noted of blight caused by first brood froghoppers arising from permanent pastures. The situation apparently is again comparable to that of mealybug wilt, where it has been shown by Carter (32) that the source of the insect materially affects its toxicity to pineapple plants.

According to Urich (238) Uba is a fairly resistant cane. It is deep-rooting, covers the ground well, prevents the growth of grass and is not trashed. Thin type canes are less affected by blight than the thick type canes (230), and the degree of blight affects recovery, the varieties least severely blighted recovering most completely (103).

PSYLLID YELLOWS

This disease of the potato and tomato was first described by Richards (201) in further detail in 1931 (202), and in collaboration with H. L. Blood in 1933 (203). The disease has been recorded in the United States from Utah, Colorado, Idaho, California, New Mexico, Arizona, Wyoming, Kansas, Nebraska and in Canada from Alberta (49, 69, 201, 210).

Psyllid vellows belongs to the small group of complex toxicoses in which the effect of the toxic secretion of the insect is systemic. The systemic effects are probably more highly developed in this disease than in any other of its type since the entire plant is affected. The symptoms include the rolling and cupping, with marginal yellowing of younger leaves, with subsequent necrosis and degeneration. Stem elongation in aerial shoots is hindered and axillary tubers, or small rosettes of leaves malformed in witch's broom fashion, may develop at the internode. Underground, a characteristic response is the formation of numerous small potatoes, many of which are prematurely sprouted. Aerial tuber formation in potato has resulted in confusion of this disease with that of Rhizoctonia, while in the tomato the symptoms produced are similar to those of curly top of beet. There is a single reference to natural transmission of this disease (214) but the record has not been confirmed.

The insect concerned in the production of psyllid yellows, *Paratrioza cockerelli* Sulc., is primarily a feeder on solanaceous plants, but Knowlton (134) lists 40 species of host plants on which the insect can complete its life cycle. In addition, a large number of plants other than Solanaceae can serve as temporary hosts.

The association between the insect and the disease, which was referred to by Richards in his first note on the disease (201), is unique in the fact that only the nymphs are capable of producing the disease, and the use of populations of adults numbering up to 1000 to a single plant has failed to produce psyllid yellows. When nymphs are applied, the time required to produce symptoms, as well as the intensity of these symptoms, is related to the number of nymphs used. Although the first symptoms appear after three days' feeding, a complete symptom picture is not obtained unless the nymphs feed continuously for 36 days. If the feeding period is less than 26 days, the attacked plants recover.

An important datum is that of infectivity of nymphs reared from eggs removed from healthy plants. Richards and Blood (203) found that such nymphs were more intense in their infectivity than nymphs of the same age which fed on diseased plants, which indicated that the insect was inherently toxicogenic. positive evidence of the infectivity of nymphs hatched from eggs from a healthy plant negatives the findings of Binkley (15), who declared that it was necessary for a nymph to be transferred from diseased potato plants in order to produce the disease. This finding of Binkley's which appeared to be confirmed by Ever and Crawford (69) was, no doubt, due to experimental conditions which did not permit the expression of symptoms and one of the latter authors (68) agrees with the original statement of Richards and Blood (203) when he says that "Nymphs need not have fed previously on infected plants in order to produce typical symptom." Eyer and Crawford (69) have shown that most of the feeding by P. cockerelli occurs in the border parenchyma surrounding the vascular The authors found nothing that would indicate that bundles. psyllid yellows symptoms were induced by either mechanical plugging or destruction of the vascular tissues. Daniels (49) reported that the vascular system in the diseased plants was broken down, and that the abnormal quantities of starch present in the pith indicated the disturbance of translocation.

Eyer (68) has made a significant contribution to the physiology of the disease. The injury to the border parenchyma is extended laterally since necrosis of the phloem is found in both midrib and petiole. In the regions of injury the cell proteins are broken down. Nitrate nitrogen content of healthy potato plants is definitely higher than that of diseased plants. The same is true also of the chlorophyll and carotin content, both being decreased in the diseased plant.

Control of this disease is based primarily on the facts previously mentioned, that nymphs only are capable of inducing symptoms, the number required is considerably greater than unity and recovery follows the removal of the insect. It follows logically that reduction of the insect population should reduce the incidence of the disease. List (151, 152) and List and Daniels (153) have shown that lime sulphur sprays and dusts were effective in giving field control, with the sprays showing a definite superiority over the dusts. According to Blood, Richards and Wann (16) the disease has not affected the economic production of tomatoes, since not less than 30 psyllid nymphs, continuously feeding, are necessary for the production of symptoms.

MEALYBUG WILT OF PINEAPPLES

This disease, which is now known to occur in most of the pineapple growing areas of the world (34, 43) was first mentioned by Larsen (140), although at that time the term "wilt" was used in a generic sense, and included some other causes of pineapple failure not strictly wilts. By 1930 mealybug wilt had reached such proportions as to jeopardize the future of the industry in Hawaii, and even now can become a serious factor if control operations are relaxed for even a short time.

It is not surprising that mealybug wilt was ascribed in the past to root pathogens, for when the first symptoms appear on the leaves, the root system is already collapsed and invaded by secondary organisms. When the leaf symptoms were first described (32) it was necessary to distinguish between typical "quick wilt" and plant failure caused by the feeding of large numbers of mealybugs. The latter case was designated as "slow wilt" and ascribed to depletion of the plant's reserves by the destruction of functional leaf area. The withdrawal of sap by large numbers of mealybugs over a period of many months is undoubtedly a major contributing factor. "Quick wilt," which is mealybug wilt per se, is clearly in another category, and is definitely the result of the feeding of a relatively small number of mealybugs for a limited time. Symptoms are characterized by loss of turgidity first of the inner leaves, and finally, in severe cases of the whole plant. Accompanying this are striking color changes from the normal green to shades of pink, red or brown. Roots of affected plants are invariably collapsed, except for newly emerged roots which are apparently normal.

latter observation, which has been confirmed by sand culture experiments⁹ is indicative of the mechanism whereby wilt occurs. It is clear that the primary effect of the mealybug toxin is to kill the existing roots, which results in the appearance of leaf symptoms closely comparable with those ensuing as a result of drought. Proof that the meristematic tissue, either of the growing point or of root primordia, is not killed is found in the sequelae. New roots emerging some time after the infestation has passed are apparently normal, and this is no doubt associated with the recovery and continued growth of the plant. The disease may occur at any stage of the plant's development, but younger growth, whether of the mother plant or vegetative slips and suckers growing from a mature mother plant, is definitely more susceptible.

The time required for symptoms to develop after infestation is very variable. In experimental series a minimum period of 6 weeks has elapsed before the earliest visible leaf symptoms occurred but in many cases typical symptom expression has not become evident for several months. Green spotting is not a symptom of wilt as thought by Illingworth (115), but, as has been discussed earlier in this paper, is a local toxic effect of the feeding of a strain of *P. brevipes*. Whether the green spotting strain is more effective than the non-green spotting strain in the production of wilt is not definitely established.

P. brevipes as a factor in connection with wilt was first mentioned by Illingworth in 1931 (115). The fact that the insect is the primary causal factor was established by the writer (32), and studies in Hawaii since that time have been limited to those by him and his associates.

Entry of mealybugs into pineapple fields is accomplished in several ways. Normally, a considerable percentage of the planting material used is infested to a greater or less degree, and this constitutes a serious danger if ants are established in the field area at planting time. If the field to be planted is free of ants, mealybug colonies on planting material disappear almost entirely (30). Whether this is due to the necessity, on the part of the mealybug, for ant attendance, or to the uninterrupted action of casual predators, or a combination of these factors, cannot readily be determined. Occasional instances of wind-blown infestations have been by Unpublished data.

proved in newly planted fields lying to leeward of heavily infested old pineapple fields.¹⁰

Invasion of mealybugs from wild growth on field margins is the most frequent source of infestation in newly planted fields (30), and *Pheidole megacephala* (Fabr.) is undoubtedly the agent of most importance. Once established under the mulch paper *Pheidole* extends its nests very rapidly with a coincident extension of mealybug infestation on the pineapple plant. *Solenopsis geminata* var. *rufa* Jerdon is second in importance with respect to distribution, but in the only pineapple growing area where it is established, is important because of its habit of nesting, and its persistence in fallow fields, with the consequent assurance of the survival of mealybugs introduced later into the fields on planting material (187).

Incidence of wilt follows closely that of the mealybugs. Without mealybug control, a typical condition is that of scattered wilted plants on the margins of fields, surrounded by plants more or less heavily infested with mealybugs. As additional plants wilt, the mealybugs forsake the wilting plants and move, or are moved by ants, to adjoining healthy ones in the field proper. Within this field area, at points remote from the field margins, isolated pockets of mealybug infestation may be found, which in due course are followed by wilting, first of the original area infested, then by extension out from the periphery of the original spot. At these sources of original infestation within the field, and on the outer margins of fields where infestation occurs to a considerable degree while the plants are young, wilt may occur over considerable areas prior to the maturity of the first crop. As the plants become older, however, susceptibility decreases and populations of the mealybugs build up without the mother plants wilting. By the time the plant crop has come to fruit and the young slips and suckers have developed, mealybug populations have become extensive. The young suckers and slips are extremely susceptible and it is at that time that fields, almost in their entirety, in the past, have "gone out." The occurrence of single plants wilted in scattered incidence throughout a field is somewhat confusing, but has been accounted for on the hypothesis that the plants have grown from planting material removed from mother plants after they had received a toxic dose from mealybugs, but prior to the expression of symp-

¹⁰ Unpublished data.

toms. With the advent of mealybug control the occurrence of this type has been very much reduced. At the same time, edge infestation has been held down to a minimum, and control of the infield areas of infestation is primarily a matter of locating them. Edge infestation, is of course, extremely variable, but in some cases is so constant and uninterrupted that a certain percentage of wilt of very young plants occurs in spite of frequent spraying.

One of the most intriguing aspects of the problem is found in the evidence that the toxicity of a mealybug colony to pineapple plants is conditioned by the host plant from which it is transferred. and the further evidence that the toxicity of mealybugs from the roots of some grasses is intensified in succeeding generations reared on pineapples (32). The relative freedom from wilt during the first crop of pineapples planted in new land, in spite of the presence of large mealybug colonies which come in from nearby wild hosts. is all too frequently followed by serious wilt incidence, either in ratoons arising from the original planting, or in later crop cycles on the same land. From the standpoint of developing resistant varieties the same phenomenon is also significant, since there is some evidence¹¹ that mealybugs transferred from a test variety to that same variety are more toxic than mealybugs transferred from Cayenne to Cayenne. Conclusive evidence of resistance in a variety or hybrid can only be obtained when resistance has been established to mealybugs grown on that variety or hybrid.

The insect as a toxicogenic species and the fluctuation in its toxiniferous state (40) are demonstrated by the fact that it is not necessary for mealybugs to have fed on wilted plants in order to produce wilt when transferred to pineapples, and by the variability in toxicity of colonies from different hosts, or in the case of pineapples, from various growth states (32). The recognition of this last factor led to the use of mealybugs from the young wilting suckers on plant crop mother plants wherever such were available, in an effort to standardize the source of infection.

Mass action has been considered in numerous experiments to determine the numbers of mealybugs necessary to produce wilt (42, 44). The experiments were conducted in order to determine whether the simultaneous action of a number of mealybugs was responsible for wilt, or whether mealybugs, as individuals, were toxic. There is, undoubtedly, a rough correlation when young

¹¹ Unpublished data.

susceptible plants are infested, between the number of mealybugs, the length of time they feed, and the amount of wilt which follows, although in an experimental series there is extreme variability. In rare cases a single mealybug feeding for one day has produced wilt; on the other hand, 100 mealybugs left on the plant for 10 days have produced only 10 per cent wilt. Since the insects used in these tests were from the same infested area, and were thoroughly randomized prior to separation into aliquots of various insect sizes. it is difficult to account for these differences other than as an expression of plant susceptibility. The statistical aspect of the case has been considered, with rather disappointing results, due to the fact that expectancies for both individually toxic bugs and the effect of bugs acting en masse are so close, that even slight experimental variability is sufficient to render the results extremely difficult to interpret. Watson (248) has recently shown that in the case of the virus transmitting aphis she used, it could be demonstrated statistically that infection was the result of individual insects. rather than the insects acting en masse. The same writer has pointed out, on the basis of the present writer's data (42, 44), that the same conclusion could be arrived at with respect to mealybugs, provided the same statistical formula was used.12 Unfortunately this formula is invalid if plant susceptibility varies, and in the case of pineapples this factor is undoubtedly of predominating importance. The term "mass action" used in these studies is perhaps unfortunate, since mass action by organisms presumably occurs at the same point at the same time. When it is remembered, however, that the primary symptom of mealybug wilt is in the collapse of the roots, not only is the number of mealybugs significant, but also the length of time they feed, with an excellent probability of the effect being accumulative. Indeed the long so-called incubation periods which have been noted may have been associated with the steady collapse of roots over a long period of time. In the spot infestations noted previously, wilt frequently does not occur until ration. If such spots have been infested since planting time. a degree of wilt in ratoon is usual, even though the mealybug population has been kept down by periodic sprayings, and when wilt occurs, no mealybugs, or at most, very few are present. This could quite reasonably be interpreted as an accumulative effect on the root system over a considerable period of time. With final collapse

¹² Written communication.

of the entire root system, the resulting symptoms are similar to those obtained by a single infestation of a pineapple plant with a large number of mealybugs at the same time. The fact that wilt can be, and is being effectively controlled by contact sprays, which materially reduce the mealybug populations but rarely entirely eliminate them, is important evidence that the size of mealybug colonies and the length of time of feeding are significantly related to the production of wilt. Significant also is the converse, that residual populations following spraying will produce wilt if left to develop uninterruptedly.

Recovery of pineapple plants from wilt was recorded in an early paper (32) and since that time it has become evident that the phenomenon is characteristic. When a plant wilts, the mealybug population disperses, although some individuals may remain. plant may remain in a wilted condition for a considerable time, but turgor is finally restored to the central leaves and growth continues. Amount of recovery appears to be governed by the extent to which the plant wilts and its age at wilting; the younger the plant when wilt occurs the greater is the subsequent recovery. Fruits resulting from recovered plants are not usually of commercial size, and vegetative slips, if any, are small. This can be accounted for by the fact that such recovered plants usually fruit shortly after unaffected plants, and their reserves are largely depleted. Plants wilting down severely produce narrow hard leaves as they recover slowly. Such plants frequently do not fruit at the normal season, but hold over until the following year. Vegetative planting material from recovered plants has been grown, and thus far no evidence of wilt symptoms in such progeny has occurred; also, there is no evidence that vegetative parts from wilted plants reproduce the wilt.

A comparison of the characteristics of viruses and toxins was tabulated by the writer in 1935 (39). The relation between the insect's feeding and the production of wilt as described in the previous paragraph, has no counterpart in any virus study thus far reported. The capacity to produce wilt is unquestionably inherent in the insect species, even though the toxiniferous state of the insect is not constant. There is no evidence for multiplication of the toxin in the plant tissue, and recovery and growth of symptom-free tissue is usual.

Factors conditioning susceptibility of the pineapple plant to mealybug wilt are not understood at the present time. From observations made in more primitive agricultural areas than Hawaii, it appears that soil texture and perhaps soil pH are of some importance. The development of wilt in soils rich in organic matter apparently occurs very rarely (43). In Hawaii there is some evidence that a micro-soil complex operates (39, 42).

Control of mealybug wilt has been effected by arrangement of fields (31), and the development and use of contact insecticides (29, 36). Attempts to control P. brevipes by means of introduced parasites and predators have been made over a period of years and several species have become established (37, 41).

LITERATURE CITED

- 1. Andrews, E. A. A note on the relation between the tea mosquito
- (Helopeltis theivora) and the soil. Quart. Jour. Sci. Dep. Ind. Tea Assoc., Calcutta 4: 31-35. 1914.

 A preliminary note on the present state of the mosquito-blight enquiry. Quart. Jour. Sci. Dep. Ind. Tea Assoc., Calcutta 4: 119-129. 1919.
- -. Some notes on attempts to produce immunity from insect attack on tea. Rept. Proc. 4th Ent. Meet., Pusa, Feb. 1921, Calcutta, pp. 56-59.
- Factors affecting the control of the tea mosquito bug (Helopeltis theivora Waterh.). Indian Tea Assoc. 1923. vi + 260
- pp., London.

 5. Annand, P. N. Tumors in kale. Science, N.S., 65: 553-554. 1927.

 6. Anstead, R. D., and Ballard, E. Mosquito blight of tea. Planters' Chron., Coimbatore 17: 443-447; 453-455. 1922.
- 7. BAKER, A. C. Feeding punctures of insects. Jour. Econ. Ent. 15:
- pp. 61-65. 1932.

 9. Ball, E. D. Leaf burn of the potato and its relation to the potato leafhopper. Science 48: 194. 1918.
- The potato leafhopper and its relation to the hopperburn.
- Jour. Econ. Ent: 12: 149-155. 1919.

 ______, AND FENTON, F. A. What per cent. of tipburn is caused by the potato leafhopper? Jour. Econ. Ent. 13: 218-221. 1920.

 ______, MANN, C. E. T., AND STANILAND, L. N. Strawberry investigations at Long Ashton. Jour. Ministry Agr. 34: 497-510; 627-641. 1927.
- 13. Bernard, C. De snoeimethode van Tjiboengoer. De bestrijding van Helopeltis op Tjiboengoer. Meded. Proefst. Thee 81: 32-35. 1922.
- 14. BEYER, A. H. Experiments on the biology and tipburn disease of the BEYER, A. H. Experiments on the biology and tipburn disease of the bean leafhopper with methods of control (Empoasca mali Le Baron). Jour. Econ. Ent. 15: 298-302. 1922.
 BINKLEY, A. M. Transmission studies with the new psyllid-yellows disease of solanaceous plants. Science 70: 615. 1929.
 BLOOD, H. L., RICHARDS, B. L., AND WANN, F. B. Studies of psyllid yellows of tomato. Abs. in Phytopath. 23: 930. 1933.
 BOODE, F. J. C. Van Hooff's Om- De-Andere-Rij-Snoeisysteem tegen Helopeltis. Meded. Proefst. Thee 81: 47-49. 1922.
 BORDEN, A. D. The pear leaf blister mite as a cause of fruit-bud injury. Circ. Calif. Agr. Exp. Sta. No. 324, 8 pp. 1932.

19. Borg, P. Entomological notes. 9 pp. typescript. Malta Dept. Agric., received March 1930.

BÖRNER, C. Neue Aufgaben der Reblausforschung. Zeits. Schädlingsbekämpfung 1: 32–38. 1923.

. Gibt es eine oder zwei Reblausarten amerikanischer Herkunft? Weinbau & Kellerwirtsch. i. pp. 245-249. 1922. Abs. Zeits. Pflanzenkr. & Gallenk. 33: 136-137. 1923. 21.

22. AND SCHILDER, F. A. Ueber das bisherige Auftreten der Blattgallenreblaus in Deutschland. Arb. Biol. Reichsanst. Land- u.

Forstw. 20: 325-346. 1933.

23. · AND Beiträge zur Züchtung reblaus- und mehitaufester Reben. II. Das Verhalten der Blattreblaus zu den Reben des Naumburger Sortiments. Mitt. Biol. Reichsanst. 49:

 CARPENTER, ISETTA PEARL. Study of the life history and spotting habits of Eutettix chenopodii (Homoptera, Cicadellidae). Univ. Kansas Sci. Bul. 18: 457-483. 1928.

CARPENTER, P. H., AND ANDREWS, E. A. Report on tea mosquito blight. Planters' Chron., Bangalore. 14: 634-639. 1919.
 CARTER, WALTER. The use of insecticides on pineapple plants in Hawaii. Jour. Econ. Ent. 24: 1233-1242. 1931.
 Studies of populations of Pseudococcus brevipes (Ckll.) occurring on pineapple plants. Ecology 13: 296-304. 1932.

31.

32.

Dorder plantings as guard rows in pineapple mealybug control. Jour. Econ. Ent. 25: 1-8. 1932.

The pineapple mealybug, Pseudococcus brevipes, and wilt of pineapples. Phytopath. 23: 207-242. 1933.

The spotting of pineapple leaves caused by Pseudococcus brevipes, the pineapple mealybug. Phytopath. 23: 243-259. 1933. 33. 34.

Mealybug wilt and green spot in Jamaica and Central America. Phytopath. 24: 424-426. 1934. The symbionts of Pseudococcus brevipes (Ckll.). Ann. 35.

Ent. Soc. America 28: 60-64. 1935.

Diesel oil emulsions as insecticides. Jour. Econ. Ent. 36. **28**: **2**68–**2**84. 1935.

37. Studies on biological control of Pseudococcus brevipes (Ckll.) in Jamaica and Central America. Jour. Econ. Ent. 28: 1037-1041. 1935.

38. The symbionts of Pseudococcus brevipes in relation to a phytotoxic secretion of the insect. Phytopath. 26: 176-183. 1936.

39. Insects and plant diseases. Proc. Haw. Ent. Soc. 9: 159-170. 1936.

40. The toxicogenic and toxiniferous insect. Science 83:

Importation and laboratory breeding of two chalcid parasites of *Pseudococcus brevipes* (Ckll.). Jour. Econ. Ent. 30: 370-372. 1937. 41.

The toxic dose of mealybug wilt of pineapple. Phytopath. 27: 971-981. 1937. 42.

The geographical distribution of mealybug wilt with 43. notes on some other insect pests of pineapple. (In press.)

- -, AND SCHMIDT, CARL T. Mass action phenomena in mealybug wilt. Ann. Ent. Soc. America 28: 396-403. 1935.

- bug wilt. Ann. Ent. Soc. America 28: 396-403. 1935.

 45. Childs, L. The relation of woolly apple aphis to perennial canker infection with other notes on the disease. Bull. Oregon Agr. Exp. Sta. 243, 31 pp. 1929.

 46. Cohen-Stuart, C. P. Iets over den steek van Helopeltis. Meded. Proefst. Thee 81: 24-25. 1922.

 47. Cook, M. T. The origin and structure of plant galls. Science, N.S. 57: 6-14. 1923.

 48. Cotterell, G. S. Pests of cacao in the Gold Coast. Proc. 1st. W. Afr. Agr. Conf. Ibadan, Nigeria. pp. 98-112. 1927.

 49. Daniels, L. B. The tomato psyllid and the control of psyllid yellows of potatoes. Colo. Agr. Exp. Sta. Bull. 410, 18 pp. 1934.

 50. De Jong, J. K. De invloed van het klimaat op. Helopeltis. I. De invloed van de relatieve vochtigheid op de Helopeltis in theedistricten van Sumatra's Oostkust. Arch. Theecult. Ned.-Ind. 1931. 3: 135-142. 1931. 3: 135-142. 1931.
- -. Helopeltis in cacaotuinen. Bergcultures 8: 658-667. 51. 1934.
- 52. De Voedselopname van Helopeltis. Bergcultures 9: 1935. 292-294.

- 53. ———. Enkele resultaten betreffende de gehouden enquête over Helopeltis en Redrust. Bergcultures 9: 318-327. 1935.
 54. DeLong, D. M. The rôle of Bordeaux mixture as a leafhopper insecticide. Jour. Econ. Ent. 22: 345-353. 1929.
 55. ———. Biological studies on the leafhopper Empoasca fabae as a bean pest. U. S. Dept. Agr. Tech. Bul. 618, pp. 1-60. 1938.
 56. ———, Reid, W. J., and Darley, M. M. The toxicity of copper to the potato leafhopper. Jour. Econ. Ent. 23: 390-394. 1930.
 57. Dieuzeide, R. Contribution à l'étude des néoplasmes végétaux. Le rôle des pucerons en phytopathologie. Actes Soc. Linnéenne Bordeaux 81: 1-241. 1928. Bordeaux 81: 1-241. 1928.
- Bordeaux 81: 1-241. 1928.

 58. Docters van Leeuwen-Reijnvaan, J. (Mrs.), and Docters van Leeuwen, W. M. The Zoocecidia of the Netherlands East Indies.

 's Lands Plantentuin: Buitenzorg 1926. 601 p.

 59. ______, and _______. Über ein von Gynaikothrips devriesii Karny aus einer Gallmücken-Galle gebildetes Thysanoptero-Cecidium. Rec. Trav. Bot. Neèr. 25a: 99-114. 1928.

 60. Dudley, J. E. Control of the potato leafhopper (Empoasca mali Le B.) and prevention of "hopperburn." Jour. Econ. Ent. 13: 408-415. 1920.
- 61. EGIOFFSTEIN, H. A. C. F. E., VON UND ZU. Helopeltis-Bestrijding op de Onderneming Tjikopo-Zuid. Meded. Proefst. voor Thee, Buitenzorg 59: 39-50. 1918.
 62. Essic, E. O. The blackberry mite, the cause of redberry disease of the Himalaya blackberry, and its control. Cal. Agr. Exp. Sta.
- Bull. 399, 10 pp. 1925.
 63. EWING, K. P. Effects on the cotton plant of the feeding of certain Hemiptera of the Family Miridae. Jour. Econ. Ent. 22: 761-765. 1929.
- -, AND McGARR, R. L. The effect of certain Homopterous 64. . insects as compared with three common mirids upon the growth and fruiting of cotton plants. Jour. Econ. Ent. 26: 943-953. 1933.

 65. Eyer, J. R. The influence of leafhopper control on potato fields.

 Jour. Econ. Ent. 14: 69-71. 1921.

 66. Preliminary note on the etiology of potato tipburn.

 Science, N.S. 55: 180-181. 1922.

- 67. · 184. 1922.

- Physiology of psyllid yellows of potatoes. Jour. Econ. Ent. 30: 891-898. 1937.
- , AND CRAWFORD, R. F. Observations on the feeding habits of the potato psyllid (*Paratriosa cockerelli* Sulc.) and the pathological history of the "psyllid yellows" which it produces. Jour. Econ. Ent. 26: 846-850. 1933. 69.

70. FAES, H., STAEHELIN, M., AND BOVEY, P. La lutte contre les parasites de la vigne, champignons et insectes, en 1930 et 1931. Ann. Agr. Suisse 33: 1-34. 1932.

71. Felt, E. P. The relations of insects and plants in gall production. Ann. Ent. Soc. America 29: 694-700. 1936.

72. Fenton, F. A. Progress report on the season's work on the produc-

tion of potato tip-burn. Jour. Econ. Ent. 14: 71-83. 1921.

Notes on the biology of the leafhopper Eutettix strobi
Fitch. Proc. Iowa Acad. Sci. 1924. 31: 437-440. 1925.

AND HARTZELL, A. Control of the potato leafhopper. Iowa Agr. Exp. Sta. Circ. 77, 4 pp. 1922. 74.

-. Bionomics and control of the potato *7*5. -, AND -leafhopper Empoasca mali Le Baron. Iowa Agr. Exp. Sta. Res. Bul. 78, pp. 379-440. 1923.

AND RESSLER, I. L. Artificial production of tip-burn.

76. · Jour. Econ. Ent. 14: 510. 1921.

77. , AND -Artificial production of tip-burn. Science 55: 54. 1922.

78. , AND -Artificial production of hopperburn.

AND — Artificial production of hopperburn. Jour. Econ. Ent. 15: 288-295. 1922.
 FEUILLETAU DE BRUYN, W. Helopeltis-bestrijding. Meded. Proefst. Thee 86: 1-14. 1924.
 FIFE, L. C. Damage to sea island cotton by the West Indian blister mite (Eriophyes gossypii Banks) in Puerto Rico. Jour. Agr. Univ. Puerto Rico 21: 169-177. 1937.
 FOLLETT-SMITH, R. R. The nutrient status of the observation plot soils. Min. & Proc. Frog. Invest. Comm., Trinidad & Tobago 13: 145. 151. 1672.

145-151. 1928.

82. A comparison of the hydrophilic celloid content of sap of leaves of sugar canes growing in good and in bad soil. Min. &

Proc. Frog. Invest. Comm., Trinidad & Tobago 13: 158-161. 1928.

83. FROGGATT, W. W. Leaf galls of *Phylloxera* at Howlong. Agr. Gaz. New South Wales 33: 360. 1922.

84. FRYER, J. C. F. Capsid bugs. Jour. Board Agr., London 22: 950-958. 1916.

FULMER, L. Die Kräuselkrankheit (Akarinose) des Weinstockes. Sonderabdruck aus Archiv für Chemie and Mikroskopie, 1913. Heft 6. Mitt. Pflanzenschutz Station in Wein. 32 pp.

86. Milbenkräusel und Wanzenkräusel im steierischen Schilcherweinbaugebiet. Das Weinland, 1930. 7: 251. 1930.

87. GARRETSEN, A. J. Het snoeien om de andere rij ter bestrijding van Helopeltis. Meded. Proefst. Thee 81: 36-39. 1922.
 88. GESCHER, C. Zur Reblauskunde und Reblausbekämpfung. Die kranke

Pflanze 5: 60-62. 1928.

90. GRABER, L. F., AND SPRAGUE, V. G. Alfalfa yellows. Science 78 (2026): Oct. 1933.

91. Grandori, R. Esperimenti di lotta contro la Filossera della vite (Phylloxera vastatrix Plan.) mediante il Para-Italia (Paradichlorobenzolo). Boll. Lab. Zool. Agr. Bachic. Milano. i (1928–1929), pp. 95–110. 1930.

92. Grandovsky, A. A. Studies on leafhopper injury to apple leaves. Phytopath. 16: 413–422. 1926.

Alfalfa "vellow top" and leafhoppers. Jour. Econ. Ent.

93. -Alfalfa "yellow top" and leafhoppers. Jour. Econ. Ent. **21**: 261-266. 1928.

- Differentiation of symptoms and effect of leafhopper feeding on histology of alfalfa leaves. Abs. in Phytopath. 20: 121. 1930.
- 95. Greenslade, R. M. Horticultural aspects of woolly aphis control together with a survey of the literature. Imper. Bur. Fruit Prod.
- Tech. Com. No. 8, 88 pages. 1936.

 ———, Massee, A. M., and Roach, W. A. A progress report of the causes of immunity to the apple woolly aphis (Eriosoma lanigerum Hausm.) Ann. Rep. East Malling Res. Sta. 1933. 21: 96.
- 220-224. 1934.
 97. Grove, A. J., And Ghosh, C. C. The life history of Psylla isitis Buckt. (Psyllopa punctipennis Crawford), the "Psylla" disease of indigo. Mem. Dept. Agr. India, Entom. Ser. 4: 329-357. 1914.
 98. Hanson, A. J. The redberry disease of blackberries. Proc. Wash. St. Hort. Ass'n 26: 199-201. 1930.

- 99. The blackberry mite and its control (Eriophyes essigi Hassan). Bull. Wash. Agr. Exp. Sta. No. 279. 20 pp. 1933.

 100. Hardy, F. The liming problem in Trinidad sugar cane soils. Min. & Proc. Frog. Invest. Comm., Trinidad & Tobago 7: 202-210. 1927.

 101. Investigations into the froghopper blight of sugar cane in Trinidad. Min. & Proc. Frog. Invest. Comm., Trinidad & Tobago 8: 218-235. 1927.
- Tobago 8: 218-235. 1927.

 —, AND URICH, F. W. Progress Report. Biochemical work:
 Soil research. Min. & Proc. Frog. Invest. Comm., Trinidad & Tobago 9: 276-281. 1927. 102.

- 1933.
- 106. Notes on two injurious psyllids and their control. East Afr. Agr. Jour. 1: 498-500. 1936.

 107. Harr, S. J. G. De lamtoro in verband met de *Helopeltis*. Algem.
- Land-bouwweekblad Ned.-Indie 8: 477-478. 1923.
- 108. HARTZELL, A. Further notes on the life history of the potato leaf-hopper (Empoasca mali Le Baron). Jour. Econ. Ent. 14: 62-68.
- HERFORD, G. V. B. Studies on the secretion of diastase and invertase by Empoasca solana DeLong (Rhynchota, Homoptera, Jassidae). Ann. Appl. Biol. 22: 301-306. 1935.
- 110. Herior, A. D. Notes on the blister made by Eriophyes pyri Nal.
- Proc. Ent. Soc. B. C. 31: 41-42. 1935.

 111. HOLLOWELL, E. A., MONTEITH, JR., J., AND FLINT, W. P. Leafhopper injury to clover. Phytopath. 17: 399-404. 1927.

 112. HORNE, A. S., AND MAXWELL-LEFROY, H. Effects produced by sucking ingering and entire tradespide upon active follows.
- ing insects and red spider upon potato foliage. Ann. Appl. Biol. 1: 370-386. 1915.
- 113. HOUARD, C. Les Zoocécidies des plantes de l'Amérique du Sud et de
- 114. Husmann, George C. Testing Phylloxera-resistant grape stocks in the vinifera regions of the United States. U. S. Dept. Agr. Tech. Bul. No. 146, pp. 1-54. 1930.

 115. Illingworth, J. F. Preliminary report on evidences that mealybugs
- are an important factor in pineapple wilt. Jour. Econ. Ent. 24: 877–889. 1931.
- 116. Ito, K. Studies on the life history of the pineapple mealybug Pseudococcus brevipes (Ckll.) Jour. Econ. Ent. 31: 291-298. 1938.

117. JANCKE, O. Beiträge zur innertherapeutischen Schädlingsbekämpfung. I. Mitteilung. Zeits. ang. Ent. 18: 276-318. 1931.

. Über die Blutlausanfälligkeit von Apfelsorten, wilden Malussorten und -bastarden, sowie die Züchtung blutlausfester Edeläpfel und Unterlagen. Phytopath. Zeits. 10: 184-196. 1937. 118.

119. Jewerr, H. H. Leafhopper injury to clover and alfalfa. Kentucky
Agr. Exp. Sta. Bull. 293, pp. 157-172. 1929.

120. — The resistance of certain red clovers and alfalfa to leafhopper injury. Kentucky Agr. Exp. Sta. Bul. 329, pp. 155-172. 1932.

121.

Jour. Econ. Ent. 26: 1135-1137. 1933.

The relation of time of cutting to leafhopper injury to alfalfa. Kentucky Agr. Exp. Sta. Bull. 348, pp. 51-59. 1934. 122.

The resistance of leaves of some pubescent red clovers to puncturing. Jour. Econ. Ent. 28: 697-698. 1935. 123.

A leafhopper pest of clover and alfalfa. Kentucky Agr. 124.

Exp. Sta. Circ. 44, 7 pp. 1936.

125. Johnson, C. G. The biology of Leptobyrsa rhododendri Horvath (Hemiptera, Tingitidae), the Rhododendron lacebug. II. Feeding habits and the histology of the feeding lesions produced in Rhododendron leaves. Ann. Appl. Biol. 24: 342-355. 1937.

126. Johnson, H. W. Nature of injury to forage legumes by the potato leafhopper. Jour. Agr. Res. 49: 379-406. 1934.

Further determinations of the carbohydrate-nitrogen 127. ·

128. of soybeans as related to resistance to injury by the potato leaf-hopper. Jour. Agr. Res. 51: 371-381. 1935.

 Jones, F. R., AND GRANOVSKY, A. A. Yellowing of alfalfa caused by leafhoppers. Abs. in Phytopath. 17: 39. 1927.
 Kendall, J. The structure and development of certain Eriophyid galls. Zeits. Parasitenk. Zeits. Wiss. Biol. Abt. F. 2: 477-501. Ĭ930.

131. -Histological and cytological studies of stems of plants

injected with certain chemicals. (A contribution to the gall problem). Doctorate thesis, Sofia Univ. June 1930.

132. King, W. V., And Соок, W. S. Feeding punctures of mirids and other plant-sucking insects and their effect on cotton. U. S. Dept. Agr. Tech. Bul. 296, 11 pp. 1932.

133. Knight, H. H. An investigation of the scarring of fruit caused by apple redbugs. Cornell Univ. Agr. Exp. Sta. Bul. 396, pp. 187-208. 1918.

134. KNOWLTON, G. F., AND THOMAS, W. L. Host plants of the potato psyllid. Jour. Econ. Ent. 27: 547. 1934.
135. KOSTOFF, D., AND KENDALL, J. Studies on the structure and development of certain cynipid galls. Biol. Bul. of the Marine Biol. Lab., Woods Hole, Mass. 56: 402-458. 1929.

136. -AND . Studies on plant tumors and polyploidy produced by bacteria annd other agents. Archiv. für Mikrobiologie.

LARSEN, L. D. Diseases of the pineapple. Haw'n. Sugar Planters' Assoc. Pathol. and Physiol. Ser. Bull. 10. 1910.

141. LEACH, J. G. Leafhopper injury of potatoes. Abs. in Phytopath. 12: 37. 1922.

, AND DECKER, P. A potato wilt caused by the tarnished plant bug Lygus pratensis L. Phytopath, 28: 13. 1938. 142.

143. Leach, R. Insect injury simulating fungal attack on plants. A stem canker, an angular spot, a fruit scab and a fruit rot of mangoes caused by Helopeltis bergrothi Reut. (Capsidae). Ann. Appl. Biol. 22: 525-537. 1935.

AND SMEE, C. Gnarled stem canker of tea caused by the 144. capsid bug (Helopeltis bergrothi Reut.). Ann. Appl. Biol. 20:

145. Lean, O. B. Observations on the life history of Helopeltis on cotton in Southern Nigeria. Bull. Ent. Res. 16: 319-324. 1926.
146. Leefmans, S. Over Helopeltis in theetuinen. Dept. van Landbouw,

Nijverheid en Handel, Buitenzorg, Med. Proefstation voor Thee, No. 46, 21 pp. 1916.

. Bijdrage tot het Helopeltis-vraagstuk voor de Thee. 147. Meded. v. h. Proefstation voor Thee, Buitenzorg, No. 50. 214 pp. 1916.

148. Lees, A. H. "Reversion" and resistance to "Big Bud" in black currants. Ann. Appl. Biol. 5: 11-27. 1918.
149. Levine, Michael. A preliminary report on plants treated with the carcinogenic agents of animals. Bull. Torrey Bot. Club 61: 103-110. 118. 1934.

150. Light, S. S. Helopeltis in Ceylon. Tea Quart., Jour. Tea Res. Inst. Ceylon 3: 21-26. 1930.
151. List, G. M. Lime-sulfur for tomato psyllid control. Colo. Agr. Exp. Sta. Bull. No. 411, 14 pp. 1934.
152. ———. Psyllid yellows of tomatoes and control of the psyllid.

Paratrioza cockerelli Sulc., by the use of sulphur. Jour. Econ. Ent. **28**: 431–436. 1935.

28: 431-436. 1935.
78. AND DANIELS, L. B. A promising control for psyllid yellows of potatoes. Science 79: 79. 1934.
154. LUTMAN, B. F. An outbreak of hopperburn in Vermont. Phytopath. 13: 237-241. 1923.
155. LUTZ, FRANK E., AND BROWN, F. MARTIN. A new species of bacteria and the gall of an aphid. Amer. Mus. Novitates 305, 4 p. 1928.
156. MCDANIEL, E. I. Control of the potato leafhopper Empoasca fabae on dahlia with flour, talc and infusorial earth. Jour. Econ. Ent. 20: 464, 1936.

29: 464. 1936.

157. McGARR, R. L. Damage to the cotton plant caused by Megalopsallus atriplicis Kngt. and other species of Miridae. Jour. Econ. Ent. 26: 953-956. 1933.

158. Magnus, W. Die Entstehung der Pflanzengallen verursacht durch

torg. S.S.S.R. 3: 776-782. 1931.

MALPIGHI, MARCALLI. Opera omni: de Gallis Londini 2: 17. 1686.

162. MARCHAL, P. La question des races du *Phylloxera* de la vigne. Ann. Epiphyties 16: 232-234 (1930). 1931.

163. MARTIN, J. P. Stem galls of sugar cane induced with an insect extract.
The Haw. Planters' Record 42: 129-134. Second Quarter. 1938.
164. MASSEE, A. M. The gall mites of the Himalaya berry and raspberry.
Ann. Rept. East Malling Res. Sta., 1925 13: 154-156. 1927.

The black currant gall mite on red currants. Ann. Rept. East Malling Res. Sta., 1926 & 1927 14 & 15: 151-152. 1928. 165.

- 166. MAXWELL-LEFROY, H. The psylla disease of indigo in Behar.

 Jour. India 8: 1-25. 1913. Agr.
- 167. Menusan, Jr., H. Leafhopper injury to potato foliage and its relation to tuber yields. Jour. Econ. Ent. 30: 772-777. 1937.
 167a. Metcalf, Z. P. Peanut "pouts." Science 86: 374. 1937.
 168. Monteith, Jr., J. Leafhopper injury of legumes. Abs. in Phytopath. 18: 137-138. 1928.
 169. Monzen, K. The woolly apple aphis (Erisoma lanigera Hausm.) in Joseph With the control of t

- Japan, with special reference to its life-history and the susceptibility of the host plant. Vehr. III. Internat. Ent.-Kongr. Zürich, 1925. 2: 249-275. 1926. REAU, A. P. Un nouvel ennemi du cottonier en Afrique équatoriale
- 170. Moreau, A. P. française Helopeltis bergrothi Reut. Agron. Colon. no. 191. pp. 129-140. 1933.
- 171. Mote, D. C., and Wilcox, J. Redberry mite of the blackberry. Proc. Wash. St. Hort. Ass'n 27: 203-207. 1931.
- 172. MÜLLER, A. Zur inneren Therapie der Pflanzen. Verh. Deut. Ges. Angew. Ent. 4. Mitgliederversamml. Frankfurt a.M. 10. bis 13. pp. 26-33. 1924.
- pp. 20-33. 1924.

 Die innere Therapie der Pflanzen. Monogr. Ang. Ent. no. 8 (Supplement to Zeits. Ang. Ent., xii), vi+206 pp. 1926.

 Versuche zur inneren Therapie der Pflanzen. Anz. Schädlingsk., iii, nos. 3-4: pp. 29-33; 41-46. 1927. 173.
- 174.
- 175. MÜLLER, K. Reblausimmunität und Brauchbarkeit der Unterlagsreben für deutsche Verhältisse. Mit. deuts. Landw.-Ges., 1928. St. 15, reprint 2 pp. Berlin. 1928. (Abs. Centralbl. Bakt., (2) 75: 317-318. 1928.)
- 176. NIERENSTEIN, M. Galls. Nature (London) 125: 348-349. 1930.
- 177. Noble, N. S. The citrus gall wasp (Eurytoma fellis Girault). Sci.
- Bull. Dep. Agr. New South Wales 53: 1-41. 1936. 178. Nougaret, R. L., and Lapham, M. H. A study of *Phylloxera* infestation in California as related to types of soils. U. S. Dept. Agr.

- Reut., with especial reference to its effect on cotton plant tissues.

 Jour. Agr. Res. 40: 485-516. 1930.

 182. Parks, T. H., and Clayton, E. E. Controlling tipburn or hopperburn
- of potatoes. Cooperative demonstrations establish value of Bordeaux sprays. Monthly. Bull. Ohio Agr. Exp. Sta. 6: 168-171. 1921.
- Bordeaux mixture. Ohio Agr. Exp. Sta. Bull. 368, pp. 243-258. 183.
- 184. PARR, THADDEUS J. Matsucoccus sp., a scale insect injurious to cer-

- PARR, THADDEUS J. Maisucoccus sp., a scale insect injurious to certain pines in the northeast (Hemiptera-Homoptera). (In press.)
 PARROTT, P. J., AND OLMSTEAD, R. D. The work of Empoasca malion potato foliage. Jour. Econ. Ent. 13: 224-226. 1920.
 PETHERBRIDGE, F. R., AND HUSAIN, M. A. A study of the capsid bugs found on apple trees. Ann. Appl. Biol. 4: 179-205. 1918.
 PHILLIPS, J. S. The biology and distribution of ants in Hawaiian pineapple fields. Exp. Sta., Pine. Prod. Coop. Ass'n. Bull. 15. 1934. Pp. 1-57.
- 188. Pickles, A. On the oviposition of Tomaspis saccharina Dist. (Rhynch., Cercop.) an insect pest of the sugar cane in Trinidad. Bull. Ent. Res. 22: 461-468. 1931.

- Entomological contributions to the study of the sugar 189. cane froghopper. Trop. Agr. 10: 222-233. 1933.
- Entomological contributions to the study of the sugar cane froghopper. Trop. Agr. 10: 240-245; 286-295. 1933. 190.
- Poos, F. W. Leafhopper injury to legumes. Jour. Econ. Ent. 22: 146-153. 1929.
- 192. -, AND HAENSELER, C. M. Injury to varieties of eggplant by the potato leafhopper Empoasca fabae (Harris). Jour. Econ. Ent. **24**: 890-892. 1931.
- 193. -, AND JOHNSON, H. W. Injury to alfalfa and red clover by
- the potato leafhopper. Jour. Econ. Ent. 29: 325-331. 1936.

 —, AND SMITH, F. F. A comparison of oviposition and nymphal development of *Empoasca fabae* (Harris) on different host plants. Jour. Econ. Ent. 24: 361-371. 1931.

 AND WESTOVER, H. L. "Alfalfa yellows." Science 79: 194.
- 195. 319. 1934.
- -, AND WHEELER, N. H. On the hereditary ability of certain 196. insects to transmit diseases and to cause disease-like injuries to plants. Jour. Econ. Ent. 27: 58-69. 1934.

 197. Printz, Ya. I. Zur Frage der Virulenzveränderung der Reblaus-Biotypen. Plant. Prot. fasc. 12. pp. 137-142. 1937.
- 198. RAHN, Отто. Invisible radiations of organisms. Protoplasma-Mono-
- 198. RAHN, OTTO. Invisible radiations of organisms. Protoplasma-Monographien. 9: 171. 1936.
 199. RAWITSCHER, F. Wohin stechen die Pflanzenläuse? Zeit. Bot. 26: 145. 1933. (Abstr. in Zeits. Pflanzenk. 43: 699. 1933.)
 200. RICE, P. L. Cat-facing of peaches by the tarnished plant bug Lygus pratensis L. Trans. Peninsula Hort. Soc. 1937, pp. 131-136. 1938.
 201. RICHARDS, B. L. A new and destructive disease of the potato in Utah and the relation to the potato acult.
- and its relation to the potato psylla. Abs. in Phytopath. 18: 140-141. 1928.
- 202. Further studies with psyllid yellows of the potato. Abs.
- in Phytopath. 21: 103. 1931.

 203.

 Agr. Res. 46: 189-216. 1933.

 204. RIPLEY, L. B. "Froghopper" in wattles. Farm. in S. Africa. 1: 423.
- 1927.
- 205. -"Froghopper" in wattles. Farm. in S. Africa. Reprint
- 51, 4 pp. 1929.

 206. Roach, W. A., and Massee, A. M. Preliminary experiments on the physiology of the resistance of certain rootstocks to attack by woolly aphis. 16th-18th Ann. Rep. East Malling Res. Sta., 1928-1930 2: 111-120. 1931.
- ROBERTS, J. I. The tobacco capsid (Engytatus volucer Kirk.) in Rhodesia. Bull. Ent. Res. 21: 169-183. 1930.
 ROEPKE, W. Het Helopeltis-vraagstuk, in het bijzonder met betrekking tot Cacao. Med. Proefsta. Midden-Java, Batavia 21: 40+iii pp. 1916.
- 209. RUGGLES, A. G., AND EYER, J. R. Preliminary notes on the life-history and control of the potato leafhopper *Empoasca mali* LeB. 19th Rep. Minn. St. Ent. 1921-1922, pp. 10-14. 1923.
- SANFORD, G. B. A malady of the potato in Alberta similar to psyllid yellows. Sci. Agr. 15: 46-48. 1934.
- 211. SEARLS, E. M. A preliminary report on the resistance of certain legumes to certain homopterous insects. Jour. Econ. Ent. 25: 46-49. 1932.
- 212. -The effect of alfalfa cutting schedules upon the occurrence of the potato leafhopper (Empoasca fabae Harris) and alfalfa yellows in Wisconsin. Jour. Econ. Ent. 27: 80-88. 1934.

 Further studies on the effect of controlling the potato
- 213. leafhopper (Empoasca fabae Harris) in alfalfa by designed cutting. Jour. Econ. Ent. 28: 831-833, 1935.

- 214. Shapovalov, M. Tuber transmission of psyllid yellows in California.

 Abs. in Phytopath. 19: 1140. 1929.
- 215. SLOCOCK, O. C. A. The lacewing fly. Yearb. Rhododendr. Ass'n. 89-92. 1934.
- 216. SMEE, C. Tea mosquito bug in Nyasaland (Helopeltis bergrothi Reut.) and notes on two potential pests of tea, (1) the tea leaf weevil (Dicasticus mlanjensis Mshl.), (2) the bean flower capsid (Callicratides rama Kirby). Bull. Dept. Agr. Nyasaland, Ent. Ser. **4**: 1–10. 1928.
- 217. , AND LEACH, R. Mosquito bug the cause of stem canker of
- tea. Bull. Dep. Agr. Nyasaland, N.S. 5: 1-7. 1932.

 218. SMITH, E. B. Suggestions for the control of froghoppers on sugar cane estates. Trin. & Tob.: Min. & Proc. Frog. Invest. Comm. 5:
- 118-123. 1926.
 219. SMITH, F. F. Injury to hollyhock and marigold by the potato leafhopper Empoasca fabae (Harris.) Jour. Econ. Ent. 25: 318-321. 1932.
- 220. The nature of the sheath material in the feeding punc-
- 221.
- 222. SMITH, K. M. Investigation of the nature and cause of the damage to plant tissue resulting from the feeding of capsid bugs. Ann. Appl. Biol. 7: 40-55. 1920.
- *223.* --. A comparative study of the feeding methods of certain Hemiptera and of the resulting effects upon the plant tissue, with special reference to the potato plant. Ann. Appl. Biol. 13: 109-139. 1926.
- 224. Recent advances in the study of plant viruses. 1934. 225. Smolak, J. Fytoptosa šeřiku. Sborn. čsl. Akad. Zeměd. 8A: 39-50.
- 1933. 226. STANILAND, L. N. The immunity of apple stocks from attacks of woolly aphis (*Eriosoma lanigerum* Hausmann). Part II. The causes of the relative resistance of the stocks. Bull. Ent. Res. 15: 157-170. 1924.
- STELLWAAG, F. Die Grundlagen für den Anbau reblauswiderstandsfähiger Unterlagsreben zur Immunisierung verseuchter Gebiete.
 Monogr. Ang. Ent. 7: 1-88. Beiheft Zeits. Ang. Ent. 10, 1924.

 Die Milben-oder Kräuselkrankheit der Rebe und ihre Bekämpfung. Flugbl, Biol. Reichsanst. Land- u. Forstw. 102: 1-4.
- 1931.
- 229. Die Milbenkräuselkrankheit des Rebstockes in ihrer Differentialdiagnose gegenüber ähnlichen Schäden im Weinbaugebiet
- terentialdiagnose gegenüber ahnlichen Schaden im Weinbaugebiet der Rheinpfalz. Anz. Schädlingsk. 7: 73-77. 1931.

 230. Steven, R. M., and Potter, J. A. Cane varieties and froghopper blight. Min. & Proc. Frog. Invest. Comm., Trinidad & Tobago 13: 162-164. 1928.

 231. Steyaert, R. L., and Vrydagh, J. Étude sur une maladie grave du cotonnier provoquée par les piqures d'Helopeltis. Mem. Inst. Colon. Belge (Sci. Nat.) 1 fasc. 7, 55 pp. 1933.

 232. Tate, H. D. Method of penetration, formation of stylet sheaths and source of food supply of aphids. Iowa State College Jour. Sci. 11: 185-206. 1937.
- 11: 185-206. 1937.
- 233. Topi, M. Ancora sulla esistenza di diverse specie di filossera della vite e sulla attaccabilita delle viti americane da parte della filossera. Atti R. Acad. Naz. Lincei, Rendiconti, Classe Sci. Fis. Mat. Nat. 33: 1 sem. no. 12: 528-530. 1924.
- Sulle probabili cause del diverso comportamento della fillossera, specialmente gallecola, in rapporto ai vari vitigni americani. Monitore Zool. Ital. 37: 74-84. 1926. 234.

- 235. e sui loro presunti caratteri distintivi. Monitore Zool. Ital. 38: 167-180. 1927.
- 236. TURNER, P. E. The lime status of soil in relation to an insect pest of sugar cane. Jour. Agr. Sci. 19(1). 1929.
 237. UNDERHILL, G. W., AND COX, JAMES A. Studies on the resistance of apple to the woolly apple aphid *Eriosoma lanigerum* (Hausm.). Jour. Econ. Ent. 31: 622-625. 1938.
 238. URICH, F. W. History of sugar cane blight in Trinidad from 1920-1924. Min. & Proc. Frog. Invest. Comm., Trinidad & Tobago 6: 140-152. 1927.
- 149-152. 1927.
- 239. AND HARDY, F. Progress Report: Soil reaction and blight. Min. & Proc. Frog. Invest. Comm., Trinidad & Tobago 8: 213-217. 1927.
- 240. VAN DER GOOT, P. De Zwarte Cacao-Mier (Dolichoderus bituberculatus Mayr) en haar Beteekenis voor de Cacao-Cultuur op Java. Meded. v. h. Proefstation Midden-Java, Salatiga. 25: 1-142. 1917. 241. van Hooff, H. W. S. Snoeien en Helopeltis. Meded. Proefst. Thee.

- 241. VAN Floorf, H. W. S. Snoeien en Helopelus. Meded. Froeist. Thee. 81: 26-31. 1922.
 242. ———. De op Tjiboengoer genomen Maatregelen tegen Helopelus. Meded. Proefst. Thee. 81: 40-44. 1922.
 243. VASIL'EV, I. V. On the race of the Ukrainian Phylloxera. Vestn. Vinodel. Ukrainui. 30: 13-14. 1929.
 244. VEITCH, R. The grape Phylloxera. Queensland Agr. Jour. 39: 79-83. 1022

- 245. Venables, E. P., and Heriot, A. D. The blister mite of apple and pear. Publ. Dep. Agr. Canada No. 577, 3 pp. 1937.
 246. Vodinskaya, K. I. Die Gallenreblaus in Tuapse. Bull. Plant. Prot. (1 Ent.) 4: 97-118. 1932.
 247. Wadley, F. M. Observations on the injury caused by Toxoptera graminum Rond. (Homoptera: Aphididae). Proc. Ent. Soc. Wash. 11. 120, 134, 1020. **31**: 130–134. 1929.
- 248. WATSON (HAMILTON), M. A. Factors affecting the amount of infec-
- tion obtained by aphis transmission of the virus Hy. III. Phil.
 Trans. Royal Soc. London. Ser. B—Biol. Sci. 226: 457-489. 1936.
 249. Wells, Betram W. The comparative morphology of the Zoocecidia of Celtis occidentalis. Ohio Jour. Sci. 16(7). 1916.
- 250. WHITEHEAD, F. E. Preliminary report on the pecan Phylloxerae.
 Rep. Okl. Agr. Exp. Sta., 1930-1932, pp. 265-267. 1933.
 251. WIESNER, JULIUS VON. Die Rohstoffe des Pflanzenreichs. 4th ed.,
- Vol. 1, edited by Paul Krais, Wilhelm v. Brehmer. iv + 1122 pp.
- WILLIAMS, C. B. Froghopper blight of sugar cane in Trinidad. Mem. Dep. Agr. Trin. & Tob. 1: 1-170. 1921.
 WILSON, H. F. Injurious gall mites. 2nd Biennial Crop Pest and Hort. Rep. 1913 and 1914. Oregon Agr. Exp. Sta., pp. 123-126.

- 254. WITHYCOMER, C. L. Studies on the actiology of sugar cane froghopper blight in Trinidad. I. Introduction and general survey. Ann. Appl. Biol. 13: 64-108. 1926.
 255. ZWEIGELT, F. Beiträge zur Kenntnis des Saugphänomens der Blattläuse und der Reaktionen der Pflanzenzellen. Zeits. Pflanzenk. 27(4): 207. 1917. (Abs. Centralbl. Bakteriol., II, xlii, 1915, pp. 265. 2325). 265-335).
- 256. Blattlausgallen, unter besonderer Berücksichtigung der Anatomie und Aetiologie. Centralbl. Bakt. Parasit., u. Infek-
- tionskr., Jena. Ite, Abt. 47 (16-22): 408-535. 1917.

 Blattlausgallen. Histogenetische und biologische Studien 257. an Tetraeura und Schizoneura-gallen. Die Blattlausgallen im Dienste prinzipieller Gallenforschung. Monog. Angew. Ent. no. 11, Zeits. Ang. Ent. xvii, Beiheft, xxi+684 pp. 1931.