INSECT SECRETIONS IN PLANTS[1]

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Insects deposit secretions in or on plants when ovipositing or feeding, the effects of which may be injurious or trivial. The criterion of pertinence that will be applied in this review is the probability that a secretion, not merely any mechanical injury that accompanies it, will significantly influence the physiology of the surviving tissues. Previous reviews and texts that cover parts of this topic are those of Carter (27), Kloft (57), and Nuorteva (103) on phytotoxaemias; Allen (2), Newcomb (97), Bloch (14), Maresquelle (76), Mani (75), and Godan (42) on cecidogenesis; and Carter (27), Sylvester (138), and Bradley (19) on virus transmission by insects.

THE SALIVA OF SUCKING INSECTS

Taxonomic Considerations

The order Hemiptera will be considered here to include as suborders both Homoptera and Heteroptera. All the Homoptera appear to be phytophagous. Of the higher taxa in the Heteroptera, only the *Geocorisae* contain plant-sucking insects, and one group of these—the Pentatomorpha—shows greater similarities in physiology of feeding to the Homoptera than they do to the other *Geocorisae*. Figure 1 indicates some of these relationships.

The term plant bug will be used here to indicate all the Homoptera and phytophagous species of the Heteroptera and, where necessary, reference will be made to either the Homoptera and Pentatomorpha on the one hand (the sheath-producing bugs) or the Cimicomorpha on the other.

Stylet Activity

Mechanics.—The functional mouth of the Hemiptera is at the tip of the long flexible stylet bundle, and can reach tissues relatively far from the body of the insect. The stylet bundle is composed of the paired mandibles and maxillae which dovetail by means of ridges and grooves. Each of the two inner members, the maxillae, have two deep grooves that are opposed to form a double canal system (Fig. 2A). Saliva is pumped down the one, and fluids are sucked up the other.

The direction taken by the stylet bundle is at least partially controlled. The stylets of some species seem mostly to follow an intercellular course through plant tissues, probably aided by salivary enzymes that dissolve or soften the pectate layers of the mid-lamellae (70). During this process, the

[1] The survey of literature pertaining to this review was concluded in January 1968.

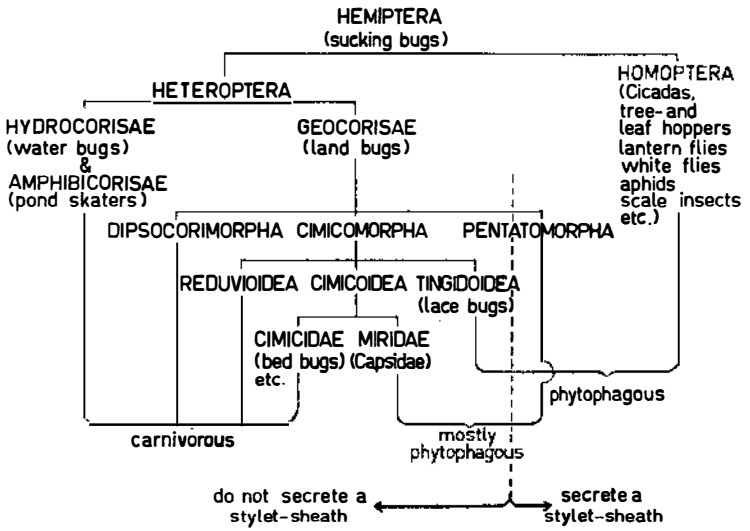

FIG. 1. The feeding habits of Hemiptera in relation to their taxonomy.

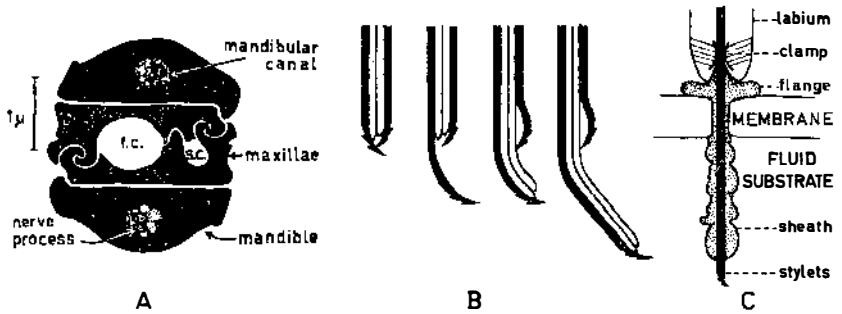

FIG. 2. The stylets and stylet sheath of phytophagous Hemiptera. A. Semidiagrammatic cross-section of the stylet bundle of an aphid. f.c. = food-canal; s.c. = salivary canal; each nerve process contains two axoplasmic filaments [After Parrish (111)]. B. Diagram showing sequence of movements of the tips of the stylets in a solid substrate resulting in direction of the bundle to one side and thence straight on. Note that the barbs on the tips of the mandibles (black) serve as anchors when located at the sides of the maxillae (white) [After Miles, (82)]. C. Formation of the stylet-sheath [Based on diagrams from Nault & Gyrisco (96)].

insect no doubt merely forces its stylets deeper into the plant, letting them follow the path of least resistance, but, at some stage, the stylets may be actively forced into a cell and its contents ingested. Also the insects, having made an initial penetration, can partially withdraw their stylets and push them forward again on a new path branching to one side or the other of the old. The resultant branching seems always to be more or less in the same plane (82, 95). Weber (143) first described the principles on which the stylet bundle works, but his account of how a plant bug is able to control the direction taken by its stylets was incorrect. Weber thought that the maxillae were attached to each other at the tips and that unequal pressure on them caused them to bow to one side. Subsequent investigations (27, 48, 82) of the maxillae have not supported this interpretation, and it has been shown (82) that the capacity for controlled movement of the stylet bundle resides in the curvature of the tips of the mandibles. When one mandible is thrust into a substrate alone, it takes a curved path, and the rest of the bundle follows perforce (Fig. 2B); whereas progress of the bundle in a straight line is achieved when forward movement of either mandible is accompanied by the maxillae—the latter normally move together and their combined strength is sufficient to overcome the tendency of a mandible to curve.

The branching of the path of the stylets of any individual plant bug may not always lie in the same plane throughout feeding, for the ridge and groove on which a mandible moves may have a slight twist. This writer has observed pentatomids that, when continuously directing the stylet bundle to the one side in an agar block, produced a stylet path that was helical. The direction and degree of rotation of the stylet path may be fortuitous, however, and differ between individuals of the same species (27).

The foregoing account is consistent with observations made on all plant bugs, including the phytophagous members of the Cimicomorpha; although those members of the Cimicomorpha that suck mammalian blood have stylets with a different structure and mechanical function (67). A generalization that may be made on present evidence is that species in those families of Heteroptera in which phytophagous members are found possess flexible mandibles that are curved at the tips, whereas insects in the wholly carnivorous families seem to have relatively straight and stout mandibles (90).

Sensory control.—Zweigelt (149) observed the seemingly purposive way in which the stylets probed from side to side within plants, and he imagined that the stylets must be guided by taste organs at their tips. Davidson (28) and Weber (143), on the other hand, found what seemed to be a gustatory organ on the roof of the pharynx of plant bugs (the epipharyngeal organ), and suggested that the insect sampled the medium through which its stylets were travelling by drawing up samples of liquids into contact with the sense organ in the buccal cavity. This interpretation received apparent confirmation with the discovery that the larger plant bugs discharge small quantities of a watery oral secretion onto surfaces and suck the liquid back

while dabbing the labium (and enclosed stylets) back and forth (83). Nevertheless, Bradley (18) was able to show that treatment of the tips of the mandibular stylets with local anaesthetics or strong acids brought about behaviour in aphids similar to the effect of amputating their stylets. He concluded that there must be sense organs at the tips, and that loss of sensation in these was not distinguished by the aphid from loss of the stylets themselves. Müller (94) suggested that movement of the stylets of aphids may be monitored by their sensitivity to pressure, and Nault & Gyrisco (96) considered that any dendrites present in the stylets would subserve a tactile sense. Forbes (38) and Parrish (111) have demonstrated a pair of dendrites in the canal that runs through each mandible (Fig. 2A). The question remains whether these dendrites subserve a sense of taste or touch: a sense of taste would seem inadequately served by two nerve processes alone, although it is possible that the mandibular dendrites subserve a preliminary sense that is augmented by periodic sampling of fluids sucked into the buccal cavity.

Observations on the ingestion by sap-sucking aphids of radiotracers from labelled food plants have apparently demonstrated that the insects penetrate all the way to the pholem without ingesting (59, 78). These results lend support to the concept that plant bugs can taste substrates at the stylet tips, yet they are at variance with the convincing evidence of McLean & Kinsey (72) that aphids frequently sample the substrate by sucking up liquids during penetration to the vascular bundles. Explanations of this apparent discrepancy are possible. In the first place, as Hennig (48) has implied, the sampling may involve no more than the ejection and sucking back of minute quantities of saliva and hence the ingestion of amounts of radioactivity too small to be measured. A second possibility is that fluids drawn up the food canal of the stylets into contact with the epipharyngeal organ are not necessarily ingested, but may be discharged again (see below under Regurgitation). Whatever the means by which aphids monitor penetration of plant tissue by their stylets, Ehrhardt's observations (32) show that penetration of tissue does not necessarily mean its acceptability as food, for an aphid may insert its stylets all the way to the phloem of an unacceptable plant and even ingest measurable quantities of sap before terminating its attempt to feed.

The Stylet Sheath

Occurrence.—Prillieaux (115) in 1878 described the solid lining to the path taken by the stylets of the woolly aphid, *Eriosoma lanigerum* Hausm., when it fed on an apple twig, but he did not recognize this stylet track as originating from the insect and thought he had observed the reaction of the plant to the penetration of the insect's stylets. Büsgen (25), a few years later, observed that aphids and coccids left a similar stylet track when they fed on previously boiled leaves, and he recognised it as a sheath secreted round the stylets by the insects themselves. Despite the seeming finality of this

demonstration, later reinforced by observations that various plant bugs could be seen to start the secretion of the sheath before they inserted their stylets into a plant (147, 149), many biologists continued to ascribe production of the sheath entirely, or in part, to plant cells (125, 127) until it was found that an identical structure was produced by Hemiptera when they fed in wholly artificial media (13).

Although Smith (127) referred to a stylet sheath associated with the feeding of several Homoptera and also of mirids, a true stylet sheath seems to be lacking in the feeding punctures of the latter (55). Sweet (137) was unable to find a sheath associated with the feeding of the Miridae and Tingidae, whereas he observed that a sheath was produced by even the carnivorous members of the Pentatomidae and Lygaeidae. It seems, therefore, that the stylet sheath is a characteristic not of the phytophagous bugs per se, but of the Homoptera and the Pentatomorpha, whether phytophagous or not. Reported exceptions all seem open to doubt (122), although the sheath of some coccids and aleyrodids may be tenuous and easily overlooked (110, 114). Statements that starved Homoptera, or those making momentary probes into substrates, may do so without an accompanying sheath (29, 138) have also been questioned (96, 122). Among the seed-feeding Pentatomorpha, however, the sheath may not accompany the stylets all the way into the food material (83, 87, 118), although the same insects probably secrete a complete sheath when they feed on stems or leaves (83, 87).

Formation.—Before species of Homoptera or Pentatomorpha begin to insert their stylets into a substrate, the labium (rostrum), in which the stylets are housed when the insect is not feeding, is first applied to the substrate, and sheath material is discharged as a viscous fluid that begins to gel as soon as it leaves the stylets. The material sticks to the surface of the plant and, at the same time, surrounds the tip of the stylet bundle and fills the space between it and the labium up to the level of the labial clamp (83, 95) (Fig. 2C). This material gels rapidly and forms a characteristic structure that has been variously called a plug (138), a collar (83), and a flange (96). The first term would seem inappropriate for an object with a hole through its centre, and the second has not won as wide an acceptance as the third. Saxena (118) has suggested that the flange may serve to secure the tips of the stylets on the surface of the substrate as they are forced into it. A sheath-forming bug may attempt to pierce inert or impenetrable surfaces, and at such times an unusually large flange may be built up, providing a source of sheath material uncontaminated by substances from plants (85). Once the stylets have begun to penetrate a substrate, the sheath is continued as a tenuous lining to a passage through hard structures and otherwise as a tube of variable proportions, according to the nature of the medium that is penetrated (33, 86, 96).

Storey (134) and Day et al. (30) described how some Homoptera build a stylet sheath, and their account would seem to apply to the Pentatomorpha

also (90). As the stylets progress through a substrate, typically by a series of forward and backward movements (82), a drop of the sheath material is secreted during or just after a backward movement and, on the next advance, a hole is punched through the already gelling substance. McLean & Kinsey (72) have described how an aphid may secrete sheath material while the stylets are retracted into the previously secreted sheath, and then secrete another nongelling secretion, thereby expanding the newly secreted sheath material into a bulge that protrudes from the end of the existing sheath. Presumably the stylets are then thrust forward almost to the tip of this bulge, for the next ejection of sheath material breaks through to form another bulge, and in this way a sheath can be built while remaining closed at its tip. Although Sukhov (135) thought that it always remained so, sooner or later the stylets emerge from the sheath (29, 48, 56, 72) and backflow of liquid indicates that the medium is then sampled (72). McLean & Kinsey (73) have shown how sap-sucking aphids penetrate plant tissue by periods of stylet movement and sheath formation, alternating with brief periods of suction, until the phloem is reached or the stylets are withdrawn. Conclusive evidence that the sheath is open at times is provided by their observations (72) that particles from the substrate may clog the food canal, and that the activity of the stylets or the discharge of further sheath material then serves to unblock the canal.

Whatever the mode of formation of the sheath, it has a typically beaded appearance when it is secreted into a liquid or a soft homogenous medium. When it passes through plant tissues, however, the sheath tends to fill intercellular spaces and take on a more irregular appearance (27, 33). It may also fill whole plant cells and in this way block vascular tissue (46, 51, 128, 133). When an insect ingests from a phloem cell, however, the tips of the maxillae alone enter the cell, and no sheath material is secreted until the stylets are withdrawn (48, 56, 57, 73).

Composition.—Sheath material is mainly protein (85, 125). It gels under water (85, 98) as well as in reagents that are used to dissolve proteins by the disruption of hydrogen bonds. In the latter instance, gelling is due mainly to the formation of disulphide bonds from the sulphydryl groups present in the precursors (85–87), and in this sense the sheath may be said to be keratinized. It probably contains about 10 per cent phospholipid (85, 87), and it readily becomes radioactive after the insect has ingested ^{32}P as inorganic phosphate (57).

It is tempting to ascribe to the phospholipid the ability of the sheath to adhere to a waxy surface such as the cuticle of a leaf, with the fatty acid residues partially dissolved in the waxy film, and the amino base hydrogen bonded to the main mass of sheath protein. The capacity of the sheath material to adhere to waxy surfaces is limited, however, and when an aphid withdraws its stylets it may pull up the external flange, unless this is anchored by continuation as a sheath within the plant (96, 138).

The identification of chitin and calcium pectate in sheath material (125)

is almost certainly in error (84). When ^{14}C is injected into plant bugs as glucose, some of it finds its way into the sheath, but the carbohydrate content is small (88). Persistent reports (108, 147, 149), that the stylet sheath contains tannins, however, although not always corroborated (125), may have a basis in fact. Sheath material seems always to be secreted along with a polyphenoloxidase and a substrate for it, probably the *o*-diphenolic amino acid, dihydroxyphenylalanine (DOPA) (86, 89). Attempts to link the diphenol-polyphenoloxidase system with the rapid gelling of sheath material have been unsuccessful (87), although the yellow to brown colouration that is sometimes reported, whether of sheath material that has been discharged within (108) or outside the plant (85), is probably due to quinone tanning brought about by the diphenol-polyphenoloxidase system.

Function.—The secretion of a stylet sheath during feeding by apparently all members of a numerous, widespread, and morphologically-varied order such as the Homoptera, and by members of a phylogenetically distinct group—the Pentatomorpha—that feed in the same manner, is a powerful indication, to this writer at least, that the sheath confers some benefit on its elaborators. What such a benefit may be, however, is still a matter of dispute. Mittler (91) discussed the various suggestions that; (*a*) it provides support for the stylets; (*b*) it functions as a tube in which the stylets are bathed in lubricant; (*c*) it acts as a filter that prevents bacteria from entering the plant or that prevents plant viruses from infecting the insect: (*d*) it contains enzymes that break down cell walls or digest food materials; (*e*) it prevents air from reaching the plant tissues and facilitating the development of wound substances; and (*f*) prevents sap from escaping around the stylets to the exterior. Consideration of these possibilities must take into account that the plant bugs of the Cimicomorpha secrete no sheath; and that some, at least, of the seed feeders of the Pentatomorpha secrete only a short sheath through the seed coat and then insert their stylets further into the seed without an accompanying sheath.

Mechanical support may be an important factor in initiating a puncture at a hard surface (118), but mirids and seed feeders demonstrate that the stylets do not need support thereafter, and that they do not need a special structure for the retention of lubricants. The suggestion that sheath material is a vehicle for enzymes was made in ignorance of the existence of another nongelling watery saliva (see below). The idea that the sheath might prevent viruses from entering the insect [Sukhov (135)] was due to the mistaken belief that the stylet sheath is always closed at its tip. On the other hand, the statement of Büsgen (25) that the sheath excludes bacteria from the plant is probably true, for the insects fill the end of the sheath with saliva on withdrawal (59, 96). Büsgen's suggestion need not be considered teleological, since successful parasites are those that cause minimal damage to their hosts. Nevertheless, mirids produce no sheath, and not all of them cause long-term damage to the plants on which they feed (55, 126).

Comparison of the feeding of the insects that produce a complete stylet

sheath with the feeding of those that produce an abbreviated sheath, or none at all, should provide a key to the function of the sheath. Mittler (91) concluded that the sheath served to prevent the escape of plant liquids that might otherwise well up around the insect's stylets. In stating this, he was concerned principally with the sap feeders, which connect to a source of liquid under an appreciable pressure. The concept of the sheath as a device that prevents loss of liquids can, however, be applied to any insect that feeds cell by cell below the epidermis, for loss of nutrients into intercellular spaces would result in inefficient feeding. An alternative to the mode of feeding of the insects that produce a complete sheath is the breakdown and partial homogenization of a large pocket of cells, the contents of which are then flushed out with an excess of watery salivary secretion. This method is employed by the seed feeders (87, 119), and by those mirids that are notorious for the damage they do (43, 55, 126). It remains to account for the inconspicuous lesions produced by some mirids and tingids. Possibly they feed on individual cells immediately below the epidermis, for such circumstances would provide a minimal opportunity for the escape of cell contents in the absence of a stylet sheath.

The Watery Saliva

Occurrence and composition.—Storey (134) was unable to detect any secretion other than sheath material, and, although Day, Irzykiewcz & McKinnon (30) claimed evidence for another secretion, they did not reveal it. Day & Irzykiewicz (29) later collected a watery nongelling secretion from the mouthparts of a pentatomid, conclusive evidence that such a secretion existed. Braun & Maramorosch (21), whose method for collecting saliva was used by Day & Irzykiewicz, probably witnessed the secretion by the same insect of both a watery saliva (that they collected into a pipette) and the sheath material (that gelled into a thread on exposure to air), although they did not interpret their observations in this way.

The first unequivocal demonstration of both sheath material and a watery nongelling saliva secreted by the same plant bug was made by Miles (83) on a lygaeid, and recognition that aphids likewise secrete a watery saliva independently of the stylet sheath soon followed (86). It seems safe to ascribe to the watery secretion many of the soluble substances, including enzymes and metabolites, that can be shown to occur in the saliva.

A polyphenoloxidase appears to be an invariable component of the saliva of all the phytophagous bugs, as well as of some of the carnivorous bugs (85). Pectin polygalacturonase (66, 70), and perhaps cellulase (1) are associated with intercellular penetration by the stylets. Otherwise, only a few enzymes that hydrolyze sugars have been found in the saliva of bugs that suck phloem or xylem sap (100, 102), whereas esterases, proteinases,

amylases, other enzymes that hydrolyze carbohydrates (35, 142), as well as phosphatases and phosphorylases (57), have been found in the saliva of mesophyll and seed feeders. An increase in the amount of proteinase in the saliva may be stimulated by increased protein in the diet (104).

The number of free amino acids that occur in the saliva of different species has been reported as being between 4 and 15 (57, 120). The appearance in the watery saliva or salivary glands of amino acids labelled with radioisotopes after their injection into the haemolymph (88), and of some nonmetabolites such as D-valine and D-tryptophan (87, 103), whether injected or ingested, makes it seem likely, however, that any free amino acid that occurs in the haemolymph will occur in the watery saliva also, even if in very low concentration. Glucose and glycerol are similarly transferred unchanged to the watery saliva (88). Injected cysteine rapidly disappears from the haemolymph, but when this amino acid has been labelled with ^{35}S, some of the radioactivity subsequently appears in a water-soluble, nonamino compound in both haemolymph and the lumen of the salivary glands (90). Direct evidence of the transfer of 3-indoleacetic acid (IAA) from haemolymph to saliva has been obtained (87), as well as indirect evidence of the transfer from food to saliva of IAA and gibberellic acid (103). Inorganic ^{32}P is also transferred from diet to the watery saliva, for some of it diffuses into plant tissue well beyond the sheath (57, 68).

The watery saliva is probably ejected during feeding only at times when ingestion is not possible (83). Salivation ceases when the stylets penetrate a phloem vessel, although it occurs during penetration into and withdrawal from plant tissues (56, 57, 72). Saliva is probably ejected continually by parenchyma feeders (5, 57).

Dilution.—The watery saliva collected directly from the mouthparts may prove exceedingly dilute, probably due to the activity of the accessory gland (44, 88). The discharge of saliva that contains compounds present in the haemolymph can be interpreted as indicating an excretory function for the salivary glands (4, 88, 119), especially when, as in the grape phylloxera, *Viteus vitifolii* Shimer, no alternative excretory organs exist or, as in some mirids (43), drops of saliva are voided and not reingested. Thus, the very dilute secretion, probably derived from the accessory gland, that may be collected directly from the stylets (87) probably has a diuretic significance and is not necessarily representative of the watery saliva ejected within plants. The latter often contains active concentrations of enzymes that originate in the principal salivary glands (35, 70, 87).

The pH of the two types of salivary secretion differs markedly. The sheath material, once it has gelled, is slightly acid (87), but the watery saliva is distinctly alkaline (43, 134), with a pH above 8 (86, 87) and probably near 9 (4, 29). This reaction is particularly suitable for the functioning of the salivary polyphenoloxidase.

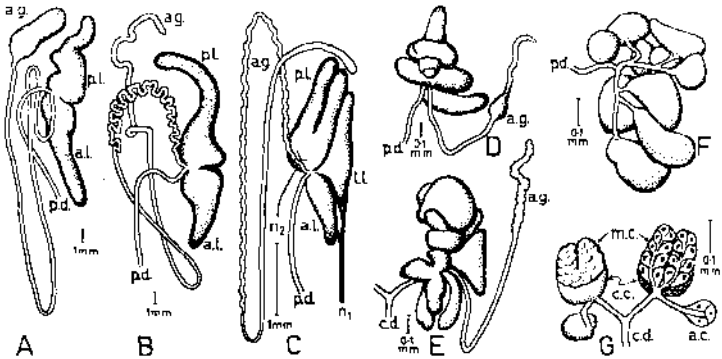

FIG. 3. Salivary glands of phytophagous Hemiptera. Cimicomorpha: A, a tingid (9). Pentatomorpha: B, a pentatomid (9); C, a lygaeid (87). Homoptera: D, a cercopoid (100); E, a jassoid (100); F, a fulguroid; G, an aphid, showing right gland in section, [after Weber (143)]. a.c. = accessory cells; a.g. = accessory gland; a.l. = anterior lobe; c.c. = cover cells; c.d. = common salivary duct; l.l. = lateral lobe; m.c. = main cells; n_1 = nerve to posterior lobe and accessory gland; n_2 = nerve to anterior and lateral lobes; p.d. = principal duct; p.l. = posterior lobe.

THE SALIVARY GLANDS

Identification of function.—In the Pentatomorpha, three functional parts of the salivary glands can be distinguished (Fig. 3). The hydrolytic enzymes of the watery saliva are provided by the posterior lobe; the sheath precursors are elaborated in the other lobe(s) of the principal gland; the accessory gland secretes a polyphenoloxidase, and can also produce a very dilute solution—probably an ultrafiltrate of the haemolymph (44, 87, 88).

Although the three types of secretion produced within the gland can be identified with discharged secretions, the ways in which they are combined during natural feeding processes are by no means clear. The secretion of sheath material while the stylets are penetrating plant tissue will always be accompanied by the free amino acids present in the original solution of sheath precursor, and these include a substrate for the polyphenoloxidase from the accessory gland (85, 88). This enzyme is also secreted with the sheath material, but it would seem most unlikely that the accessory gland also discharges large quantities of water while the sheath is being formed. It is not known whether the hydrolytic enzymes from the posterior lobe are also ejected at this time.

Saliva collected from the tip of the rostrum probably represents the dilute watery saliva that is dabbed onto surfaces by the large bugs and is then sucked back again, presumably into contact with an internal gustatory organ during a sampling process (83). It may also correspond with the secre-

tion that serves to flush out the feeding excavations made by mirids and the seed feeders (43, 87, 118). The involvement of the nongelling secretions of the posterior lobe in these circumstances is again uncertain. Possibilities that are consistent with observations on live bugs and with the nerve supply to the salivary glands (23, 83) are that either (*a*) all parts of the salivary apparatus discharge simultaneously, or (*b*) only the posterior lobe and accessory gland discharge, and (*c*) in the latter event, the secretions can be augmented by a flush of water via the accessory gland—perhaps under hormonal control.

The salivary glands of the Homoptera may be complex in form or deceptively simple (86). The glands are normally provided with a tubular accessory gland, but nothing seems to be known of its function. It is not strictly comparable with the accessory gland of the Heteroptera, since, although the Homoptera also secrete a salivary polyphenoloxidase, it originates from cells in the principal gland and not, as in the Heteroptera, from the accessory gland (87).

Watery saliva and sheath material are miscible if kept away from air (87). When aphids expand the beads of the stylet sheath by discharging watery saliva into a newly secreted droplet of sheath material (72), the two secretions not only mix to some extent, but the jelly-like mixture may also be sucked back. Moericke & Mittler (92) have described such a material ingested by two species of aphids during the initial phase of their probing through an inert membrane into solutions of sucrose.

Use of salivary glands in experiments.—Where the salivary glands of bugs are used in experiments in place of the actual salivary secretions, such preparations may have the following unnatural features: (*a*) The pH may be significantly different from normal; it will be affected by the contents of the ruptured cells and by the ungelled sheath precursors, both of which are acidic (87, 89), while the true watery saliva is alkaline. (*b*) The salivary secretions may be at unusual concentrations since the accessory gland will not be providing water or ultrafiltrate from the haemolymph. (*c*) The natural diphenol-polyphenoloxidase system of the saliva will be absent or almost nonfunctional since it normally comes into play only as the secretions are mixed immediately prior to their discharge, and it is effective only at the alkaline pH of the watery saliva (89).

Regurgitation

It has been generally accepted that regurgitation by plant bugs does not occur. Valves that would prevent regurgitation have been described (77, 78), and ingested dyes that are not passed through the walls of the alimentary tract do not seem to find their way, via the mouthparts, back into food materials (83). Nevertheless, were there a complete nonreturn of liquids taken into the food canal, either the mandibular dendrites (38, 111) would

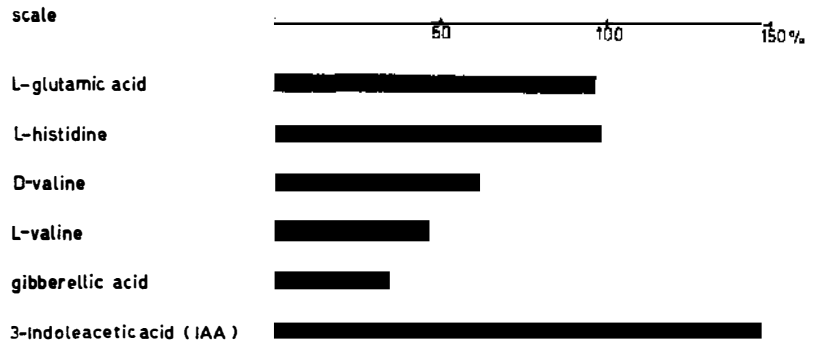

FIG. 4. Influence of substances fed artificially to *Calligypona pellucida* (F.) (Fulguroidea) on the growth of oats on which they fed subsequently; scale values are percentages of the effects on growth of oats caused by insects from the field [From Nuorteva (103)].

have to monitor the taste of liquids before ingestion, or the insect would have to swallow unacceptable liquids once they got as far as the sense organs in the pharynx. The writer has occasionally observed the expulsion of very small volumes of liquid that were initially taken into the food canal both of Heteroptera and of aphids. The possibility should be entertained that at least the column of liquid filling the food canal up to the sucking pump can be rejected by plant bugs.

PLANT RESPONSES TO THE SALIVA

Several layers of intact cells around the stylet sheath may show an increased permeability, loss of starch, degeneration of chloroplasts, and enlarged nuclei (8, 57, 131, 149). Loss of starch has been attributed to salivary amylase (147, 149), but the possibility that other stimuli may increase the plant's own amylolytic activity should be borne in mind (123). Kloft (57) made a careful study of the effects of the injection into plant cells of free amino acids such as those found in the saliva. He described streaming of the cytoplasm, increased cell permeability and respiration rate, and decreased photosynthesis. These effects could account for the toxic reactions of plants to the feeding of some plant bugs (26, 27, 64), although it remains to be seen whether free amino acids are released in sufficient quantities to cause the systemic effects attributed to feeding by the insects (2, 27, 68, 112, 126, 145, 146). Some dietary amino acids have been shown by Nuorteva (103) to reduce the overall growth of monocotyledons (Fig. 4). Some of the reported effects of salivary toxins are, however, almost identical to effects produced by viruses (27), and conditions at first ascribed solely to the toxic secretions of insects have, on more thorough investigation, proved to involve viruses that are transmissible by the insects (27, 103). The simple hypothesis

that, in these instances, the symptoms of viral infection of the plant are slight or latent until aggravated by the normal feeding of the insects has been rejected by both Carter (27) and Nuorteva (103). There is, however, still no direct evidence in favour of their hypothesis that feeding on the virus-infected plants gives rise to the elaboration of potent nonviral toxins in the salivary glands of the insects.

Simple blockage of the vascular tissues with sheath material could be expected to cause the accumulation of photosynthates and auxins above blocked phloem vessels, giving rise to localized intumescences or pigmentation (36, 51, 128). Blockage of the xylem would lead to wilting (128), and Kloft (57) reported that a drop in transpiration accompanies the feeding of plant bugs. Nevertheless, Kloft has also shown that physiological effects of the feeding of sap-sucking aphids on plants are associated with the piercing and withdrawal by the stylets, and there is a partial recovery of normal function in the intervening period. This phenomenon is presumably related to the fact that phloem-sucking bugs secrete saliva only while the stylets are in motion, and cease salivation when a phloem vessel is tapped (57, 72). Kloft believes that the effects of the feeding of sucking bugs on plant physiology are due mostly to the amino acids secreted into plant tissues during piercing and withdrawal. Any effects during withdrawal would presumably be due to the emission of secretions from the end of the stylet sheath, for the sheath appears to be impermeable (56), and the plant would receive no mechanical stimulus from movement of the stylets while they remained completely enclosed within their sheath.

The amino acids in the saliva of sucking bugs can be shown to reduce the overall growth in the plants on which they feed (Fig. 4). However, when a localized increase in the growth of plant tissues follows applications of particular amino acids, whether externally (3) or by injection via the insects' stylets (89), the effect is probably related to a localized increase in concentration of growth hormones in the plant. A similar phenomenon is observed when the saliva of plant bugs or the localized application of IAA increases or prolongs photosynthesis in isolated patches or green islands of leaves (27, 42). Further instances of increased or prolonged growth of plant cells under the influence of sucking insects will be considered in the section on Cecidogenic Insects.

Virus Transmission

Types of transmission.—The persistent, vector-latent, or circulatory viruses are ingested and transferred to the salivary glands of the insect, eventually to be discharged in its saliva. The nonpersistent, vector-direct, or stylet-borne viruses, however, are somehow carried as contaminants of the feeding apparatus (19, 27, 54, 138). The persistent viruses are mostly, but not exclusively, carried by the Cicadellidae (Homoptera); these viruses are acquired almost without exception from the plant's vascular tissues and,

after a latent period of from a few hours to a few days following ingestion of the virus, are discharged in the insect's saliva and can reinfect plants. The nonpersistent viruses, on the other hand, are acquired most readily when an insect inserts its stylets into epidermal cells and no further (19, 138), and transmission has no latent period; indeed, the ability of the insect to infect healthy plants falls off rapidly with time after acquisition of the virus.

Sylvester (138) recognized a third class of insect-borne viruses which he termed semi-persistent. These have no latent period, but are acquired when the insect penetrates deeper than the epidermis, and are probably held more tenaciously by the stylets than nonpersistent viruses, for they are not lost or inactivated as readily.

Nonpersistent viruses.—The transmission of the nonpersistent viruses is not a simple "flying-pin" phenomenon. The immediate
affects its ability to acquire and to transmit the virus; once acquired, the virus can be transmitted serially to a (small) number of plants; and there are puzzling specificities in the virus-vector relationship (19, 29, 138). The nonpersistent viruses are not necessarily carried at or near the tip of the stylet bundle, as was at one time thought (19), but they must be contaminants either adhering to the outer surfaces of the stylet bundle, or drawn by capillarity into the canals and spaces between the stylets (27, 138). Bradley (19) considered that the virus particles could be drawn into the very small spaces that must occur between the maxillae and the mandibles. Sylvester (138) suggested that the viruses may be mixed with sheath material as it is secreted within the epidermis, and carried from plant to plant with the flange of sheath material that sometimes adheres to the stylets when they are withdrawn after a shallow probe.

The insects' salivary secretions could limit the effectiveness of an aphid as a vector by: (*a*) the stylet sheath scouring the virus from the stylets during long penetrations [Bradley (19)]; or (*b*) the watery saliva inactivating viruses [Day & Irzykiewicz (29)]; or (*c*) the saliva affecting the plant cells in such a way that they become less susceptible to infection [Sylvester (138)].

Suggestions that the viruses are carried in the column of liquid entirely within either food canal or salivary canal, or that they are carried in the flange of sheath material pulled up after superficial probes, would seem to provide for a "single-shot" type of transmission. At a subsequent attempt to feed, the food canal would be sucked clear or flushed out with ingested watery saliva (83), the contents of the salivary canal would be replaced, and any flange of gelled sheath material that remained on the tips of the stylets would be unlikely either to remain attached or to be in a sufficiently plastic condition to allow the transfer of virus particles from it to plant cells, for more than one subsequent probe. On the other hand, should the viruses be held in crevices, whether externally or between the maxillary and mandibular stylets, several possibilities could account for specificities in the virus-vector

relationship. (*a*) Virus particles held by capillarity or adhesion could be flushed out by saliva with varying degrees of ease, depending on the structure of the stylets and the nature of the physical relationship between virus and stylets [Van der Want in (138)]. (*b*) The salivary diphenol-polyphenoloxidase system could act as a nonspecific disinfectant, by producing quinones that would attack the viral particles. Differences in the susceptibility of the viruses to such chemical inactivation, and differences in the potency of the saliva of different species, would seem almost inevitable and would provide for variations in virus-vector relationships. (*c*) Sylvester's suggestion that the insects' saliva could render cells more or less susceptible to infection would apply if toxic compounds are produced by an interaction of the salivary oxidase system with the plant's own mechanism of resistance to parasites (45); see below under Counters to Plant Resistance.

ORAL SECRETIONS OF OTHER INSECTS

Secretions from Thysanoptera have been shown by Kloft & Ehrhardt (58) to penetrate plant tissues when the insects feed. This secretion (presumably salivary) is no doubt involved in the toxic reactions of plants to the feeding of some species of thrips, as well as in the transmission of viruses and the formation of galls by such insects (27, 75, 117), but little or nothing is known of its composition.

There are well-authenticated records of the transmission of viruses by a long-horned grasshopper (Tettigoniidae), a short-horned grasshopper (Acrididae), as well as by an earwig (*Forficula auricularia* L.) (27). *Melanoplus differentialis* (Thos.) (Acrididae) transmits viruses in the buccal fluid, a brown, amylolytic liquid that is said to be a mixture of saliva and regurgitated matter from the crop (27). Markham & Smith (77) also recorded the transmission of viruses by various chrysomelid beetles, and concluded that all instances of virus transmission by chewing insects are due to regurgitation since, in the beetles at least, salivary glands are lacking.

OVIPOSITIONAL SECRETIONS

The sawflies (Hymenoptera: Tenthredinoidea) deposit their eggs with a secretion that initiates growth of a gall. A larval secretion later stimulates completion of the gall, but if the larva is removed, the gall can be brought to maturity by the repeated introduction into it of the fluid from the ovipositional gland of the female. The secretion is said to contain nucleic acids, protein, and carbohydrate, and its cecidogenic activity is thermolabile [Hovanitz (50)].

The wood wasps (Hymenoptera: Siricidae) belong to the same sub order (Symphyta) as the sawflies, but do not produce galls. The egg is laid in the wood along with fungal "arthrospores" that subsequently send hyphae into the wood ahead of the larvae (24). The fungus reduces the water content of the wood and produces an environment to which the larvae are closely

adapted, and the larvae feed apparently exclusively on the hyphae [Morgan & Boros (93)]. *Sirex noctilio* F. produces at least two kinds of maternal secretion that accompany the egg and arthrospores: a complex of protein and acid mucopolysaccharide (sulphuric ester type) from the paired mucus glands, and a secretion from the unpaired oil gland that contains at least five acidic lipids along with other lipids. The mucoid is viscous and lubricious when secreted, but it rapidly becomes brittle on exposure to air unless it is mixed with the oily secretion, when the resultant emulsion is resistant to desiccation. Both secretions initiate vigorous growth of the hyphae [Boros (16)].

The gall wasps (Hymenoptera: Cynipoidea) belong to a different suborder (Apocrita) from the siricids and tenthredinids, yet the ovipositional secretions of *Cynips folii* (L.) bear a striking similarity to those of *Sirex noctilio*. The single ovipositional gland of *Cynips* produces secretory globules of two kinds: one is a complex of protein and acid mucopolysaccharide (sulphuric ester and hyaluronic acid types), and the other is similar but associated with phospholipid. These secretions neither initiate the gall nor provide nutrition for fungi, however, and are said to protect the egg from the noxious effects of the surrounding plant tissue (62).

CECIDOGENIC INSECTS

Types of gall.—Perhaps all plant bugs are incipiently cecidogenic, for cells close to the feeding punctures of many sucking insects become hypertrophied to a varying degree (55, 89). When a species is sedentary, such effects may be magnified, and the woolly aphid, *Eriosoma lanigerum* Hausm., thus causes a swelling to form on young apple twigs immediately beneath the colony of insects. Even some mirids that feed on cacao plants and cause gross necrotic lesions where they feed nevertheless cause stimulation of growth of tissues at the periphery of the lesion and, if the tissues are young enough when attacked, the lesion may eventually become entirely occluded (27). This phenomenon is comparable with the galls caused by sucking insects and by thrips that feed continually at the same point on the plant, causing more or less depressed growth at the actual point of penetration but increased growth further away, so that the insects themselves become partially or completely occluded (75, 110).

Simple intumescences occur within the tunnels of some leaf miners of the Lepidoptera and Diptera. La Rue (65) showed that this was probably due to contact with the insects' faeces. Stem miners that remain in the same part of the stem may similarly stimulate the growth of the tissues surrounding them (probably by means of oral secretions), and, although the plant's cells are constantly eaten away, their increased rate of growth becomes evident as an external swelling (10). Larvae of the cecidogenic Cynipoidea and Chalcidoidea in the Hymenoptera, and of the cecidogenic Diptera and

Coleoptera, whether they burrow into plant tissues on hatching or whether the egg is thrust into the plant during oviposition, similarly stimulate the cells surrounding them, and the galls thus formed may reach a considerable degree of morphological complexity (75). The sawflies of the Tenthredinoidea, alone among cecidogenic insects, initiate a gall with an ovipositional secretion, but the gall aborts unless the larva hatches and stimulates further growth (50, 71).

Whatever the final appearance of a gall, development starts with a general stimulation of the growth of young plant cells. The nuclei enlarge and the nucleic acid content of the cells increases; chloroplasts degenerate and starch is converted to sugar; cell-permeability is increased and the cells enlarge (8, 42, 97, 131). The rate of division of meristematic cells is increased and young parenchymatous cells may become meristematic, and are then said to dedifferentiate. Further stimulation of growth leads to the appearance of vascular tissue that joins up with the plant's main vascular supply but, as with the rest of the tissues of the gall, has a polarity related to the insect rather than to the rest of the plant (10, 42, 49). At this relatively undifferentiated stage the gall is termed a kataplasma; if it goes on to develop sclerenchymatous layers, specialized epidermal structures, or other complex formations, it is termed a prosoplasma (27, 74, 75).

At the centre of the gall, the insect may suck or chew the surrounding cells rich in anabolites, or it may abrade and imbibe liquids that ooze from a jelly-like layer of nutritive cells, possibly disintegrating under the influence of hydrolytic enzymes produced by the organism (61).

The cecidogenic stimulus.—However exotic its final structure, the gall is composed of cells that are essentially replicas or simple modifications of normal cells, albeit in abnormal relationship to each other and to the rest of the plant (49, 76). The growth and differentiation of the healthy plant is primarily under the control of a small number of chemical substances with nonspecific activity (45, 107). The central problem of cecidogenesis is: Does the gall-former produce its own specific chemical organizers of the plant tissue, or does it duplicate the nonspecific hormonal controls of the plant but with a polarity and timing related to the cecidogenic organism? Some writers have believed with Bloch (14, 131) that "the evidence points towards some sort of chemical influence associated with the salivary secretions which must be rather specific for each gall making insect." Others (17, 49, 74) have adopted the viewpoint of Boysen-Jensen that the chemical stimulus is nonspecific and hence only animals are capable of stimulating the production of complex galls, because only they can control application of the stimulus so that it is given in definite places and at particular concentrations.

Recent work (12, 45, 60) has shown that IAA plays an integral part in RNA and protein synthesis in plants, and has given further point to the many attempts that have been made to simulate natural cecidogenesis by applying IAA to plant tissues. Amorphous calluses are easily produced in

this manner, but only when IAA has been applied in the right way and in an appropriate situation have successful imitations of cecidogenic processes been obtained (8, 42, 71, 74, 105, 123, 129). More spectacular results have sometimes been achieved with synthetic auxins (74), probably because they are not subject to control by the natural inhibitors of IAA activity (52, 107).

Attempts to find IAA in cecidogenic insects have not always been successful, but neither have attempts to demonstrate that the gall insects themselves or that parts of them are cecidogenic (97). Possibly the living insects produce IAA externally (89) and are thus not themselves extractable sources of the compound. Nevertheless, the salivary glands of coccids (110) and the ovipositional gland of a tenthredinid (50) have been shown to be cecidogenic, auxins have been extracted from aphids (2, 79, 105), and IAA has been recognized in their saliva (121). It is possible that the IAA extractable from insects is ingested and not elaborated by them (80, 102), but the salivary glands are competent to produce IAA from tryptophan at the pH of the watery saliva (89). The presence of IAA in excrement, whether of arthropods or mammals, probably explains the cecidogenic properties of faeces (65).

In published work on the possible involvement of the growth-substances of plants in cecidogenesis, the gibberellins and cytokinins have received scant attention compared with IAA. Nuorteva (103) has recorded that a synthetic diet high in gibberellic acid caused an increase in the phytotoxicity of the oral secretions of a plant bug (Fig. 4), but, leaving aside the possibility of direct transfer from diet to saliva, it is not as easy to conceive, on the basis of present knowledge, how gibberellins and cytokinins would fit into the biochemistry of insect saliva, whereas IAA is readily derivable from compounds that are known to be present.

Other substances that have been proposed as the cecidogenic agents of insects are the B vitamins (39), and certain free amino acids (3). Anders (3) induced nodules on the roots of grape seedlings by growing them in solutions of amino acids (especially tryptophan, histidine, and glutamic acid, either singly or in combination) that he claimed were present in the saliva of the grape phylloxera. He attacked the hypothesis that IAA is responsible for cecidogenesis by these insects on the grounds that the compound could not be detected in sufficiently high concentration in the saliva.

Anders' analysis of amino acids in the saliva of phylloxera has not been substantiated, however (120), and nodules have been produced on the roots of vines merely by growing them in potassium phosphate buffer (89). His criticism of the role of IAA in cecidogenesis ignores the possibility of its production in the saliva after ejection by the insects (Fig. 5), and his calculations of the concentration at which IAA would be effective as a cecidogenic stimulus are based on the quantities that are effective when applied to the plant externally, although these are of dubious relevance, and IAA is subject to rapid exogenous destruction by plants (144, 148).

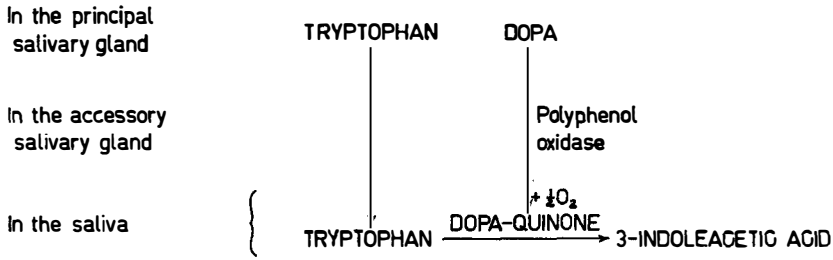

FIG. 5. Reactions thought to lead to the production of 3-indoleacetic acid in the saliva of a plant bug (89) DOPA = 3,4-dihydroxyphenylalanine.

The similarity between the effects of IAA on plant cells (7, 34, 45, 60, 81) and the observed events that take place in galls (8, 42, 129, 131), the presence in the saliva of plant bugs of the chemical conditions that would favour the production of IAA (89), the known presence of IAA in cecidogenic insects or their immediate environment, and the instances in which the cecidogenic influence of insects can be replaced by the careful application of IAA, are powerful indications of its implication in natural cecidogenesis. Nevertheless, the metabolic pathways by which it is produced in different insect-plant relationships could well vary, and the presence of anabolites could conceivably modify the primary cecidogenic stimulus (69, 71, 76, 107, 132). The possibility that a cecidogenic organism increases the activity of the plant's own IAA by inhibiting its IAA oxidase must also be entertained (22, 113, 131).

COUNTERS TO PLANT RESISTANCE

A number of mechanisms may be involved in resistance of some varieties of plant to attack by insects (109, 130): morphological factors such as the texture of the plant surface; nutritional factors such as the nonavailability of nutrients in the sap of some varieties of plant that are resistant to sucking insects (6); the production by plants of toxins (11, 41, 108, 139) or of hormonelike compounds that affect the development of the insect (106).

Nierenstein (99) suggested that a natural defence of plants against parasites was the production of tannins that could precipitate the enzymes of the invader, and that the tenthredinid *Pontiana* counters this resistance mechanism by producing a tannase and other oxidizing enzymes that convert the plant's tannins to insoluble coloured compounds. Similar coloured deposits have been reported in the lesions of mirids (126) and a number of galls (15, 42).

Injuries to plants, whatever their cause, are liable to induce an increase in the content of toxic phenolic compounds in the injured cells, the effective toxins probably being quinones (41, 45, 47). A counter to such a system

would seem a *sine qua non* for sedentary sap-sucking and other insects that are exposed to the prolonged action of the plant's juices. The quinones are produced by the activity of the plant's phenolases, yet fungal pathogens secrete their own polyphenoloxidase (PPO)—possibly with the effect of oxidizing the plant's quinones further to nontoxic polymers (136). The fact that sucking insects also inject PPO into plant tissues is likely to be more than mere coincidence.

Henke (47) suggests that the production of quinones in the plant is controlled by a quinone reductase, and he has shown that the healthy unattacked leaves of vines resistant to the grape phylloxera have either larger titres of phenolic compounds, or lower ones of quinone reductase. Either circumstance is likely to give rise to larger quantities of quinones when the plant tissues are attacked. If the phenol-phenolase content of a plant is above a certain threshold, the quinones produced during attack by fungi may kill the cells that produce them, giving rise to the hypersensitive reaction (136). It is interesting to note that Bramstedt (20) described just such a hypersensitive reaction in the cambium of resistant apple varieties when attacked by the woolly aphid.

Resistance and cecidogenesis—a hypothesis.—The phenol-phenolase system of plants has been related by Tomaszewski & Thimann (140) to the activity of the plant's IAA during growth and development. A diagram of some of the possible interactions of the phenol-phenolase system, growth factors, and the resistance of the plant to attack by fungi and insects is shown in Figure 6.

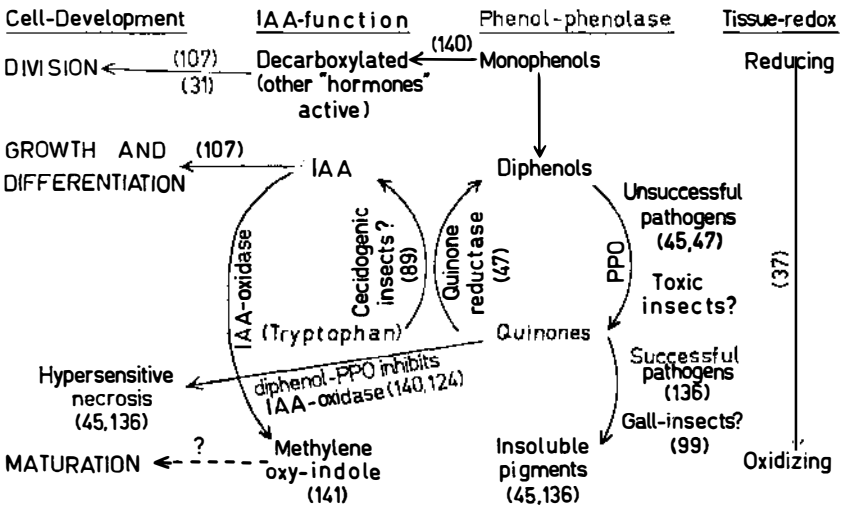

FIG. 6. Some possible relations of the phenol-phenolase system of plants to their development and resistance to pests and diseases (figures refer to the numbered references cited in the text).

Phenols and PPO are ubiquitous in insects, and a PPO has even been found in the salivary glands of larval *Drosophila* (40). The salivary diphenol-PPO system in the sucking bugs possibly originated as a nonspecific detoxification mechanism, forming quinones that would affect many complex compounds (116). Quinones are themselves toxic, but the final product of a diphenol-PPO interaction depends on the relative concentrations of the enzyme and substrate, and the redox potential. If the oxidation proceeds far enough, the quinones will autoxidize to insoluble compounds with less, or no, biological activity (45, 63, 136). For a salivary diphenol-PPO system to be functional, it may be supposed that the diphenol and PPO would have to be separated until ejected to prevent their reacting prematurely, and that the saliva would have to be alkaline for the enzyme to work. Both circumstances are found in the salivary system of the sucking bugs.

It is suggested here that the PPO in the saliva of the sedentary plant bugs, like the PPO of fungal pathogens, interacts with the plant's own phenol-phenolase system (63, 140). When the plant produces quinones that act as resistance factors, an interaction occurs between the PPO of the attacker and the phenolase-quinone content of the plant; if the attacking organism's oxidizing system predominates, the plant's quinones are oxidized and the attack is successful; if the plant's quinones persist, the plant is resistant, even though the cells in which the quinones accumulate may die due to a hypersensitive reaction (45, 47, 136).

The stylet sheath of plant bugs, which probably evolved as a result of the denaturation of salivary proteins by the detoxifying PPO system, must serve to reduce contact and hence interaction between the insect and the plant; and it is further suggested that a secondary effect of this interaction, where it is weak or at the margins of zones of stronger interaction, is the stimulation of auxin activity in the plant's cells. This could be brought about by inhibition of the plant's IAA-oxidase by diphenols or quinones (42, 124) or by the production of more IAA from free tryptophan in the saliva by some process such as that indicated in Figure 5. Any increase in the rate of growth of plant tissues would be likely to be advantageous to insects feeding on them, primarily because of an increased mobilization of anabolites (53, 101), and secondarily, where tissues are stimulated selectively, because of the possibilities afforded for protection or concealment.

It seems likely that the specific types of gall produced by sedentary insects have evolved along with instinctive patterns of feeding behaviour that cause the selective stimulation of surrounding plant cells by IAA, as proposed by Boysen-Jensen (17, 76). There would seem to be neither direct evidence nor need to postulate that cecidogenic insects secrete specific morphogenetic compounds. To Boysen-Jensen's account of cecidogenesis can be added three further points: (*a*) The sucking bugs are well equipped to reach and stimulate selectively various tissues surrounding them by means of the long stylet bundle. (*b*) Selective decrease of growth in some parts of the plant tissues can occur (76), due either to withdrawal of cell contents (80) or

to localized concentrations of salivary diphenol-PPO that inhibit instead of stimulate growth. (*c*) The capacity of plant tissues to grow with a polarity and form related to the cecidogenic insect must necessarily be limited by the genetic character of the plant and the overall polarity and degree of development of the surrounding tissues (36, 49, 74). The final form of a gall can thus be considered as the result of an interaction between the inherent characteristics of the plant tissues on the one hand, and the nonspecific chemical and the specific behavioural characteristics associated with the feeding of the insect on the other.

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