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Damage to Sugar Cane by Fulgoroidea and Related Insects in Relation to the Metabolic State of the Host Plant

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1. Economic Status of Fulgoroidea on Sugar Cane

More than 150 species of Fulgoroidea have been found on sugar cane (Box, 1953). Twelve families of Fulgoroidea are represented, as follows: Cixiidae (14 species), Delphacidae (53), Meenoplidae (1), Derbidae (45), Dictyopharidae (9), Achilidae (1), Tropiduchidae (3), Issidae (2), Nogodinidae (4), Flatidae (4), Ricaniidae (4) and Lophopidae (12). Of these, Achilidae and Issidae are only casually associated with sugar cane; Cixiidae breed below ground, and in the nymphal stages feed on roots of many plants, including sugar cane (Sein, 1929); the nymphs of Derbidae feed on fungi growing in cane trash or among the stools (Fennah, 1965); and Flatidae normally occur on woody shrubs around cane fields (Wolcott, 1948). There are, in fact, relatively few Fulgoroid species that infest sugar cane at all stages of their life history. The status of those in Papua and New Guinea has been discussed by Szent-Ivany and Ardley (1961); in the Pacific area, by Pemberton (1963); in Mauritius, by Williams (1957); and in the West Indies, by Wolcott (1921).

Most of the species that are major pests belong to the Delphacidae. They include *Perkinsiella* spp. and *Saccharosydne saccharivora* (Westwood). Several others, such as *Eumetopina flavipes* Muir (Uichanco, 1928) (Figs. 23–27), *Eoeurysa flavocapitata* Muir (Mirza and Qadri, 1964), *Dicranotropis muiri* Kirkaldy (Williams, 1957), and *Sogatodes cubanus* (Crawford) (Wolcott, 1948), appear less frequently, or more locally, in large numbers. Of the remainder, the most notorious is a Lophopid, *Pyrilla perpusilla* (Walker) (Misra, 1917). The history of *Perkinsiella saccharicida* Kirkaldy after its introduction into Hawaii, and of its ultimate control by its insect enemies, is well documented (Swezey, 1936). It is now of comparatively little direct economic importance anywhere, but in Queensland and Madagascar it is a vector of Fiji disease (Mungomery and Bell, 1933; Frappa, 1954). This disease is transmitted in the Philippine Islands by *P. vastatrix* Breddin (Ocfemia, 1934), and in Fiji by *P. vitiensis* Kirkaldy (Ayub *et al.*, 1967).

The Fulgoroid pests of sugar cane differ from one another in details of life history and in the circumstances in which they develop large populations. Apart from details of biology and methods of control, the questions of most immediate concern are whether a species in one area is likely to become serious in any other into which it might inadvertently be introduced, and whether the changes that accompany modern trends in sugar cane agronomy are likely to increase the risk of damage by species already present. The relationship between Fulgoroidea and their local biological environments is too complex to permit meaningful generalization, but the weather conditions associated with outbreaks of various species show similar features as does the type of damage sustained by the host plant.

2. Biology of Major Pest Species

Perkinsiella spp. (Delphacidae)

Twenty-two species are recognised in *Perkinsiella*, but not all have been recorded on sugar cane.

P. vastatrix (Breddin) (Figs. 1–3) was the first member of the genus to be cited as a pest of sugar cane (Breddin, 1896). It occurs in Malaysia, Indonesia, Philippine Is., Formosa and Japan (Metcalf, 1943). The following summary of its life history in the Philippines is from Urbino (1927).

The interval between emergence of the adult female and first oviposition varies from 2 to 25 days. Pairing takes place on a leaf and lasts for about one hour. Oviposition may occur at any time of day on the inner surface of the leaf-sheaths, but is restricted to the cooler part of the morning or evening on the midrib of exposed leaves. The female uses the apex of the ovipositor to feel for a suitable oviposition site, and then gradually inserts the serrated valves to cut a slit for the eggs. One to four eggs, per slit, are laid at an angle of 30–55° with the epidermis. The number of eggs laid in a leaf may reach 1,800, but is usually much less. The egg is elongate, slightly curved, 1.1×0.2 mm, and is a little narrower towards the anterior end, which bears a shallowly domed cap. The incubation period of eggs laid in the open averages 14 days, and in shade, 17 days. The nymphs do not disperse before feeding, which takes place on the 'more succulent' (younger mature) leaves and the softer leaf sheaths. There are five nymphal stages, each lasting 3 or 4 days, and the total nymphal period occupies just over 19 days, there being little or no difference between the sexes. The total life cycle is about 47 days, but varies from 32 to 66 days, being shortest in September and October and longest in January and February. In the Philippines the insect breeds on sugar cane almost exclusively. In Java it has been reported on sorghum (Breddin, 1896, following Krueger), and in Malaysia, on corn (Corbet and Gater, 1926).

There are five generations a year in the open field, where the insect is able to breed from July until April, and six in shaded areas, where breeding occurs through-out the year. The insects appear in the fields in September, and conditions in this and in the month following are considered most favourable for population increase. The insects are abundant in November, and may remain so until January. Harvest begins in February or March, and the population dwindles from the middle of March, becoming negligible in the fields from April to the end of July.

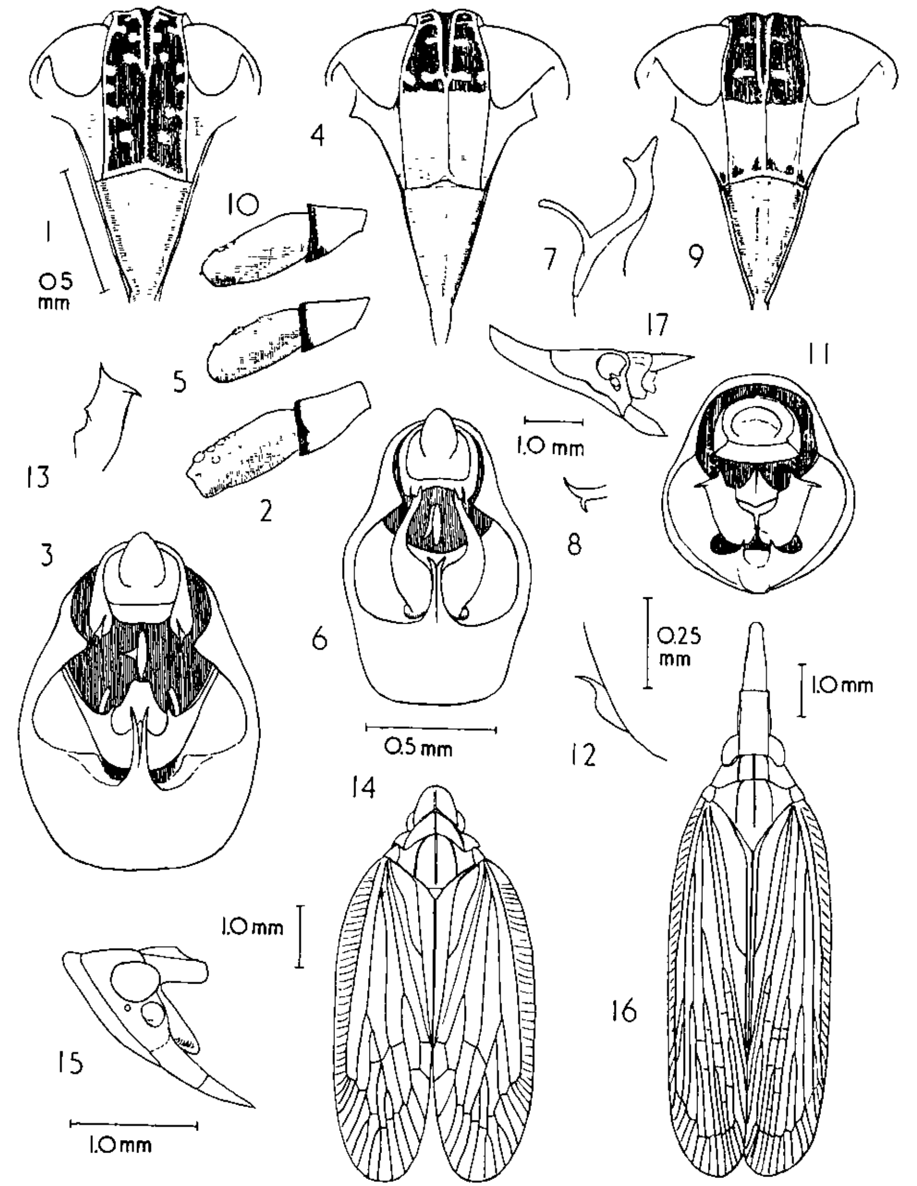
The decline in population, culminating in its virtual disappearance between February and April, was attributed to the seasonal prevalence of higher temperatures and lack of rain affecting both the insects themselves, and, by suppressing succulent growth, availability of food and of sites suitable for oviposition. The heavy rainfall and the relatively lower temperature of July and August were considered to affect the host plant in a manner favourable to the insect. *Perkinsiella* was scarce at the time of year when relative humidity was highest. The effect of climatic changes was more evident in the shade than in the open, and this was tentatively ascribed to an increased susceptibility of the host plant to damage as a result of suboptimal light intensity.

Of cane varieties observed, Uba, H.109, Toledo, Morado, DI–52, CAC. 87, P.B. 68 and P.B. 94 were found to be the least damaged; most heavily infested were Pampanga Purple Striped and Badila.

Perkinsiella saccharicida Kirkaldy (Figs. 9–13) originally occurred in Java, Formosa, southern China, the Malay States and Australia (Queensland and New South Wales), but has been accidentally introduced into the Hawaiian Islands, Mauritius, Réunion, Madagascar, South Africa (Metcalf, 1943; Williams, 1957) and more recently, Ecuador and Peru.

The life history, which has been most closely studied in Hawaii (Perkins, 1903) and Mauritius (Williams, 1957), is very similar to that of *P. vastatrix*.

The adults leave the leaf funnels and other day-time places of shelter at dusk, and pairing takes place at night. Oviposition takes place usually at night, occasionally by day. The female may live for 1–2 months, and lay up to 300 eggs. The eggs are usually laid in the midrib of the leaf, low down on the upper (inner) surface, but they may be placed in the leaf sheath, leaf blade, shoot, or internode. The egg is 1.0 × 0.35 mm, elongate-cylindrical, and slightly curved. From 1 to 12 eggs may be laid in a single incision at an angle to the surface, and the upper ends, which have a dome-like cap, sometimes project slightly above the leaf surface, and are covered with a white, wax-like secretion. The incubation period in warm weather is about 14 days, but in cooler weather may be 35–40 days. After hatching, the young tend to congregate near the bases of the leaves, including those of the crown. Each of the five nymphal stages lasts 4–9 days (Van Dine, 1904). The total length of the life cycle is 48 days at an average temperature of 77° F, and 56 days at about 72° F. The adults feed along with the nymphs, but are more active, especially at night. Adults may disperse by short flights from one plant to another, or by sustained flight. In Hawaii, occasional flights of adults downwind occurred in such numbers as to form migratory swarms. At certain periods, some adults are



Figs. 1–3. *Perkinsiella vastatrix* (Breddin). (1) Frons and clypeus, (2) Antenna, (3) Male genitalia, posterior view.

Figs. 4–8. *Perkinsiella vitiensis* Kirkaldy. (4) Frons and clypeus, (5) Antenna, (6) Male genitalia, posterior view, (7) Distal portion of right genital style, (8) Latero-apical process of anal segment of male.

Figs. 9–13. *Perkinsiella saccharicida* Kirkaldy. (9) Frons and clypeus, (10) Antenna, (11) Male genitalia, posterior view, (12) Medioventral process of pygofer, lateral view (Australian specimen), (13) Right genital style, posterior view (Hawaiian specimen).

Figs. 14–15. *Numicia viridis* Muir. (14) Head, thorax, and tegmina, (15) Head in profile.

Figs. 16–17. *Pyrilla perpusilla* (Walker). (16) Head, thorax, and tegmina, (17) Head in profile.

brachypterous and flightless. In Hawaii, only females of this form have been observed, but in Mauritius both sexes may be brachypterous.

This species, like *P. vastatrix*, normally breeds only on sugar cane. In Hawaii, it has been found on 'Hilo grass' and *Paspalum conjugatum* (Pemberton, 1919). Both very young and fully mature cane were liable to attack in Hawaii, and the worst outbreaks occurred during the colder months of the year. The damage to the leaves comprises laceration of tissue by the ovipositor, with subsequent reddening and drying, and desiccation of leaves as a result of the primary and secondary effects of feeding. Sooty mould frequently develops on the film of liquid excreta that spreads over the leaves when the insects are numerous.

In Hawaii, the distribution of infestation in a sugar cane field shortly after the immigration of adults from outside was at first uniform, but later was often very uneven (Perkins, 1903). Van Dine (1911) listed several environmental factors that might have contributed to the leafhopper outbreak of 1903 in Hawaii. Among these were the incidence of cool, rainy weather, impoverished and poorly drained soil, lack of water in dry weather following the rainy season, long duration of the prevailing winds, and damage to sugar cane by other agents such as the cane borer *Rhabdoscelus obscurus* (Boisd.).

The sugar cane varieties then grown in Hawaii, all noble canes, on occasion suffered severe damage in a large outbreak of *Perkinsiella*, but some fared consistently better than others. Rose Bamboo was one of the most susceptible, and Yellow Caledonia, the least. In Mauritius, where the insect is seldom very abundant, M. 134/32 was on occasion heavily infested whereas B. 3337, of the same age and growing in an adjoining field, was virtually free (Williams, 1957).

Perkinsiella vitiensis Kirkaldy (Figs. 4–8) has been recorded in Fiji, Samoa and Niuë (Metcalf, 1943). The life history is very similar to that of *P. saccharicida* (Veitch, 1923). Direct damage due to oviposition and feeding is recorded as being 'considerable' in Fiji, but the insect is held in check by its local natural enemies.

Saccharosydne spp. (Delphacidae)

There are seven species of *Saccharosydne*. One, *S. procerus* Matsumura, occurs in Japan, Manchuria and China; *S. saccharivora* (Westwood), the only species that breeds on sugar cane, ranges from U.S.A. (Louisiana) to Trinidad and Venezuela; *S. rostrifrons* (Crawford) has been found in Cuba and St. Lucia, West Indies; the remainder occur in South America (Metcalf, 1943).

The following account of the biology of *S. saccharivora* (Figs. 33–35) is based on Wolcott (1921) and Guagliumi (1953). The eggs, 0.6×0.15 mm, are usually inserted in batches of 4–12 on the underside of the midrib, or less frequently along a vascular strand of the leaf-blade. The egg-slits are covered with a mass of white threads from glands on the valvifers of the female. Some 200 eggs may be

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laid by a single female over a period of 3 weeks. The incubation period in Venezuela varies from 5 to 20 days, being usually about 7 days, and in the Greater Antilles 15 days has been recorded.

The nymphs are yellow in the first stage, and later become greenish, until in the final instar they are almost uniformly pale green. They do not normally disperse after hatching, but remain feeding on the leaf in which the eggs were laid. White flocculent threads are secreted from glands situated on the head and the abdomen, and ultimately form white rods extending before and behind the insect. The nymphs pass through five stages in about 36 days (range: 25 to 64 days), remaining quiescent for a day before the final moult.

The adults often stay with the nymphs, but may disperse to other leaves, including those of the central whorl. Pairing takes place in the evening or at night, and there is a preoviposition period of usually about 4 but sometimes as long as 20 days. The male lives for about 8 days.

S. saccharivora appears to live and breed only on sugar cane, but has occasionally been observed on other grasses, including Rice Grass *(Sorghum vulgare)* in Jamaica, *Paspalum distichum* in Grenada and *Digitaria sanguinalis*, *Dactyloctenium aegyptium* and *Paspalum urvillei* in Florida.

Sugar cane is subject to attack at all stages of growth, and damage may be severe. Red rot develops in the oviposition slits and infested leaves may wilt and dry out. On tall mature cane, damage becomes evident only when the insects are very numerous, though little discoloration of the leaf occurs. Sooty mould usually develops on the film of liquid excreta that covers the leaf surface where the insects have fed (Ballou, 1912). Gowdey (1927, 1928) reported that outbreaks of *Saccharosydne* in Jamaica tended to become most serious between December and March, when the incidence of entomogenous fungi is light, a view in agreement with the earlier observations of Ritchie (1917). In this island, the annual development of the pest in recent years has been found to be synchronous over relatively extensive areas, apparently as a result of the combined effect of a Strepsipteran parasite, *Stenocranophilus quadratus* Pierce, and three species of entomogenous fungi. Their swift reduction of the nymphal and adult population restricts the oviposition period of each generation to a period of 3–6 weeks (Metcalfe, 1964). In Venezuela (Guagliumi, 1953), outbreaks are confined to small areas and occur in the dry season (February to May). They terminate at the onset of the rains, but may recur on a minor scale in October and November.

Gowdey (1928) stated that in Jamaica attack was especially serious on the varieties White Transparent and B.H. 10(12), whereas Badila, Uba and Ba. 11569 growing near them were at most only slightly attacked and their growth was not retarded. In an outbreak in Florida, Co. 281 sustained only slight injury, whereas in some fields of Co. 290 leaf damage was serious. Examination of varieties under test in the field indicated a preference on the part of *Saccharosydne* for broad-leafed varieties (Ingram *et al.*, 1939).

Dicranotropis muiri Kirkaldy (Delphacidae) (Figs. 28–32)

The distribution of *D. muiri* originally included Formosa, southern China, Luzon (Philippine Is.), Java and Borneo, and it has been accidentally introduced into Mauritius, Réunion and Madagascar (Williams, 1957). The life history has been described in Mauritius (Williams, 1957), and is generally similar to that of *Perkinsiella saccharicida*. *D. muiri* lays only 1 egg in each slit cut by the ovipositor, the egg stage lasts for 11–15 days, the total life cycle is a few days shorter than that of *P. saccharicida*, and the adults generally shelter on the lower surface of the exposed leaf blade, in contrast to those of *P. saccharicida* which typically hide in the leaf funnels.

Eoeurysa flavocapitata Muir (Delphacidae) (Figs. 18–22)

E. flavocapitata, the only species of the genus, has been recorded in East Pakistan, Malaysia and China (Metcalf, 1943; Qadri, 1963). The eggs are elongate-cylindrical and slightly curved, and are deposited in the tissues bordering the midrib of the leaf. The nymphs live concealed within the leaf funnels. Damage to cane first appears as a drying of the leaves; later, red streaks develop in the injured tissue and the leaf surface becomes blackened with sooty mould (Mirza and Qadri, 1964).

Numicia viridis Muir (Tropiduchidae) (Figs. 14, 15)

Numicia is a closely-knit genus with some 32 species distributed through tropical and southern Africa. With the exception of *N. viridis*, none is known as a pest of economic crops, and the history of this species as a pest is limited to a recent outbreak on irrigated sugar cane (variety N.Co. 310) in northern Swaziland (Dick, 1963) where population densities up to 500 insects/stool were recorded. *N. viridis* occurs in Swaziland, Natal, Zululand and Pongola (Metcalf, 1954; Dick, 1963).

The eggs, 10–20 in a row, are laid in the side of the midrib on the lower surface towards the apex of the leaf. Each egg is placed in a separate incision, and bears an operculum which protrudes above the surface and becomes detached at hatching. The nymphs are green and bear long glassy spicules secreted from abdominal glands at the posterior end of the body. The incubation period of the egg is 4 weeks in August, and the life cycle requires almost 6 months in the colder half of the year: there is evidence of the occurrence of two generations during the warmer period. The adults leap when disturbed and can make short flights. In July and August they tend to be sluggish, and at this time have been observed to be heavily parasitized by larvae of an Epipyropid moth. These live below the wings and appear to feed mainly on secretions from their host.

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N. viridis has been found on *Stenotaphrum secundatum* and *Sorghum* sp. probably *verticilliflorum*, in addition to sugar cane. Its feeding causes a general loss of turgor, leading to buckling and drooping of the leaves, followed by the development of a blotchy yellow discoloration and necrosis of the tip and edges of the leaf. When cane is heavily attacked, the central whorl becomes soft and flabby. Juice from cane showing severe symptoms of attack has a lower sucrose content and higher glucose ratio than normal.

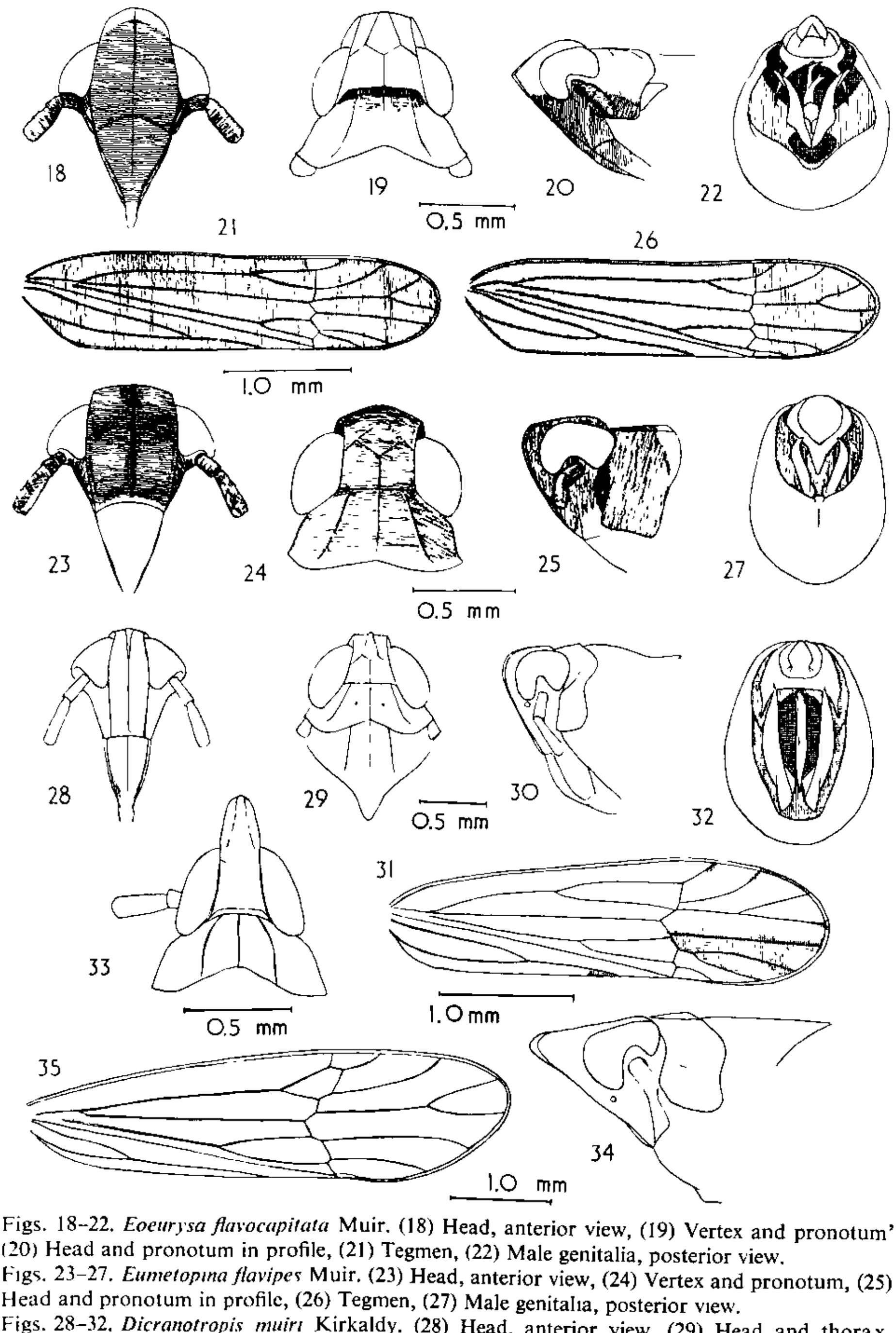
Pyrilla perpusilla Walker (Lophopidae) (Figs. 16, 17)

P. perpusilla occurs in India and Ceylon, and in Bihar, Orissa and Rajasthan is ranked as a major pest, whereas in Andhra Pradesh, Bengal and Assam it is of only minor importance. It has been the subject of an extensive literature (Butani. 1964).

The life history, based largely on Butani (1964), is as follows. After an interval varying between 6 hours (Misra, 1917) and 11 days (Qadri and Aziz, 1950) from the time of emergence, the female mates, the process occupying 1–2 hours, and after a further interval varying from a few hours (Misra, 1917) to 3 days (Qadri and Aziz, 1950), begins to lay eggs. The eggs are pallid, ovoid, 1.0×0.5 mm, and are deposited almost contiguously on the leaf in two to four irregular rows covered with a white thread-like secretion from the anal glands. Each batch contains 30 to 50 eggs. The eggs hatch in 6 to 18 days, and after 3–4 hours the nymphs begin to disperse. Feeding is most frequent on the lower leaf surface or near the midrib, but may become general. As feeding proceeds, two bundles of white filaments are developed by secretions from glands situated at the posterior end of the body. The fluid excreta form a film on the leaf surface which is eaten by ants or becomes overgrown with sooty mould. There are five nymphal stages, and their total duration varies from 5 to 20 weeks, though 8 is perhaps usual. The adults are able to move about freely 4–5 hours after emerging. They are not strong fliers, and when disturbed often sidle away, though they are capable leapers. The complete life cycle occupies 50–55 days at New Delhi under a temperature range of 25.5–27.8°C and a humidity range of 65–70%. The life cycle is shorter (40–42 days) in August and September, and in winter is greatly prolonged (Gupta, 1953).

P. perpusilla breeds on sugar cane, great millet *(Andropogon sorghum)*, wheat and maize, but develops large populations only on sugar cane. It occurs on other grasses, including Kans *(Saccharum spontaneum)*, and on some Dicotyledonous plants. It is chiefly on the latter that the sparse over-wintering population is found between February and March, when sugar cane is not available.

The seasonal population of *Pyrilla* appears as a succession of three to five generations of which the first two are clearly distinguishable. Oviposition on sugar cane begins in April, the population building up to a broad peak between July and



Figs. 18–22. *Eoeurysa flavocapitata* Muir. (18) Head, anterior view, (19) Vertex and pronotum' (20) Head and pronotum in profile, (21) Tegmen, (22) Male genitalia, posterior view.
Figs. 23–27. *Eumetopina flavipes* Muir. (23) Head, anterior view, (24) Vertex and pronotum, (25) Head and pronotum in profile, (26) Tegmen, (27) Male genitalia, posterior view.
Figs. 28–32. *Dicranotropis muiri* Kirkaldy. (28) Head, anterior view, (29) Head and thorax, dorsal view, (30) Head and pronotum in profile, (31) Tegmen, (32) Male genitalia, posterior view.
Figs. 33–35. *Saccharosydne saccharivora* (Westwood). (33) Head and pronotum, dorsal view, (34) Head and pronotum in profile, (35) Tegmen.

October, and declining to a very low level by the end of December. It is generally agreed that populations are profoundly influenced by climatic conditions. Adults disappear from the crop by early January if the minimum temperature falls below about 9.4°C. The weather during the period between April and June appears to be of special importance. If dry and hot, or if stormy and changeable, the development of the population is depressed: if, however, it remains relatively mild, and July and August are humid and with low maximum temperatures, conditions are favourable for multiplication. Spells of dry weather during the monsoon months also appear to be associated with outbreaks. Singh and Kalra (1951) reported that dense and luxurious growth of cane provides an environment that favours the development of attack.

Sen (1941) noted that sugar cane was more generally infested with *Pyrilla* and *Aleurolobus* in north Bihar than in south Bihar, and attributed the difference in part to there being less waterlogging in south Bihar.

3. Influence of Environment on the Susceptibility of Sugar Cane to Injury from Feeding by Fulgoroidea and Cercopoidea

Variable Extent of Damage Caused by a Feeding Puncture

The amount of damage to the host plant depends upon the number of insects present and the volume of tissue irreversibly injured by their feeding and oviposition. The damage begins with an incision, made with the ovipositor or the mouthparts, and is aggravated by desiccation and fungal invasion of the bordering cells. Oviposition damage is primarily mechanical, and is usually inflicted on the midrib, leaf sheath, or rind of the stalk. Feeding damage is both mechanical, due to insertion of the stylets and withdrawal of cell solutes, and biochemical, from injection of saliva; it usually occurs on the leaf blade or the leaf sheath, and less often on the funnel leaves. The volume of necrotic tissue originated by a single feeding puncture varies from a negligible spot to an extensive streak that may reach the apex of the leaf. Apart from the secondary effects of desiccation due to blockage of vascular tissue, the factors that determine the extent of damage include the quantity of cell solutes imbibed by the insect during the feeding period and the metabolic status of the leaf at the time of attack.

Saliva of the Pest Species and Feeding Damage

There is little direct evidence as to the effect of normal saliva of any Fulgoroid species on the tissues of the host plant, but such as there is indicates that it does not contain intrinsically toxic substances that are capable of causing serious damage in all circumstances. Laurema and Nuorteva (1961) examined the saliva of one Cixiid and four Delphacid species and found, as in other Homoptera, that it contained no pectin polygalacturonase, an enzyme that can disrupt plant tissues by breaking down the pectin in the cell walls. Virtanen *et al.* (1961) investigated the salivary glands of three sample populations of *Javesella pellucida* (F.) (Delphacidae) for the presence of 3–indoleacetic acid and of amino-acids, substances that in all but very low concentrations derange cell metabolism. One sample consisted of specimens that had been fed for 24 hours on an artificial diet of sucrose, l-histidine, l-glutamic acid and d-valine in aqueous solution, and the others were collected in or outside an area of oats that showed damage. No 3-indoleacetic acid was detected, and the amount of free amino acids found was negligible, showing that these substances were not transferred to the salivary glands. No proteases or amylases were found in the salivary gland secretion of this species (Nuorteva, 1958). Yet it is well attested in literature that the degree of damage that may result from feeding by Delphacid Fulgoroidea and other Homopterous pests is widely variable. For example, after the termination of an outbreak of *Saccharosydne saccharivora* on sugar cane in Barbados, Maxwell Lefroy (1901) noted little feeding injury to the cane. On the other hand, feeding by this species may lead to drying out of the leaves (Guagliumi, 1953). Similarly, Withycombe (1926) noted no 'blighting' on leaves of caged sugar cane plants on to which he transferred sugar cane froghoppers, *Aeneolamia varia* (F.) (Cercopoidea), whereas Williams (1921) was able to produce 'blighting' by similar means.

Distribution and severity of feeding injury in relation to metabolic status of leaf cells

Fennah (1939) observed points on the leaf at which *Aeneolamia* was feeding and measured the rate of development of the 'blight' streaks. However, the streaks that developed were only moderately long, and appeared only on certain varieties. The response to feeding most commonly found was the development of a hair-thin red streak less than 3 cm long. Leaf tissue did not necessarily become necrotic above and below the feeding puncture. In this lack of reaction all the mature leaves, except the oldest, of the same and neighbouring stools of a single variety, typically behaved alike. Conversely, where streaks of necrotic tissue developed on the leaves of one stool, they usually did so on those of adjacent stools of the same variety. On individual stems, the leaves of the central whorl were usually the least affected, the younger mature leaves had less extensive blight marks than the older mature leaves, and the basal two-thirds of the leaf less than the apical third. The apparent contradiction in such reactions to feeding can be explained by assuming that the effect of the saliva can be localized, to a variable extent, by the 'buffering capacity' of the solutes in the tissues penetrated by the stylets, *Olfactory Responses to Sugar Cane in Respect of Variety and Metabolic Condition*

Aeneolamia varia, which in its natural habitat feeds rather generally on grasses, moves towards the odour of a leaf extract devoid of sugar and to that of a 3% solution of sucrose, and responds strongly to a combination of the two (Fennah, 1939), a behaviour suggesting that it would be attracted to sugar cane of high sucrose content. No similar data are available regarding any Fulgoroid species. It seems justifiable to assume that species are not strongly attracted to sugar cane when they cannot breed on it and are not restricted to it in the adult stage: the Derbidae, for example, alight on the leaves merely because of their proximity to the fungus-infested trash in which they breed. In Hawaii, *Perkinsiella* was distributed uniformly between newly infested fields where growth was uniform, but was more abundant in sheltered spots where growth of cane was lush (Perkins, 1903), or where field drainage was poor (Van Dine, 1911).

No grass-feeding Fulgoroid is known to be strictly host-specific, but the association between *Saccharosydne saccharivora* and sugar cane, and *Peregrinus maidis* (Ashmead) and maize, in areas where both crops are grown, and the rarity of both species on other grasses (Guagliumi, 1953; Zimmerman, 1948), suggest the existence of attractants typical of the plant genera (or even species) concerned. If response to an attractant should be modified by the amount of sucrose present, differences in attractiveness between leaves of ripe, healthy canes of clones of *S. officinarum* and of hybrids between this and other species would be expected to exist. Differences in attractiveness of leaf odour to *Aeneolamia varia* have been observed in the laboratory in comparisons between B.H.10(12) and Co.213, *Saccharum ciliare*, and Guatemala Grass *(Tripsacum laxum)* (Fennah, 1939). However, the influence of any species- or variety-associated attractants found in vigorous mature leaves cannot yet be assessed, since, as will be shown below, there are overwhelmingly large differences in attractiveness of sugar cane according to its degree of 'thriftiness'.

Nutritional Level of Host Leaf Tissue and Populations of Pest Species

The relative nutritiousness of plant substrates as food for Homoptera is reflected in the fecundity of females that have been reared upon them, and the percentage of survival of nymphs hatching from eggs laid on or in them. The presence of a large nymphal population is clear evidence of the high nutritive value of the substrate during the period of its development. The fecundity of *Saccharosydne saccharivora* is directly correlated with the total nitrogen content of sugar cane leaves (Metcalfe, 1965). A similar relationship between nitrogen supply and female fecundity has been widely recognised in *Pyrilla perpusilla* (Butani, 1964) and other insects (cf. Allen and Selman, 1955). Population density also has been found to be positively related to the nitrogen content of the host plant (cf.

Tanada and Holdaway, 1954; Daniels and Porter, 1956). These observations suffice to establish that in certain circumstances the leaves of some sugar cane plants provide a more nutritive food than others.

Susceptibility of Sugar Cane Varieties to Damage by Fulgoroidea

The tolerance of sugar cane to damage inflicted by a single feeding puncture is the factor principally concerned in the expression of varietal 'resistance' to Homoptera. It sometimes happens that a 'resistant' variety growing near a susceptible variety is almost free from infestation, as well as from feeding injury. Urbino (1927) reported that in the Philippines wild *Saccharum spontaneum* remained uninfested, although a large population of *Perkinsiella vastatrix* was causing great damage to commercial cane nearby. Sometimes one variety of sugar cane, even though quite heavily infested, shows appreciably less leaf damage than another, equally infested, growing near at hand. Such differences in susceptibility to injury between adjacent plots, or even stools, of sugar cane have been reported by observers in different countries with reference to several of the major Homopterous pests, and seem to be of general occurrence.

Misra (1917) recorded that *Pyrilla perpusilla* prefers broad-leafed varieties of cane, and where narrow-leafed varieties preponderate, large populations do not build up; although found in India on Kans *(S. spontaneum)* in March and April, it does not infest this host to any appreciable extent. In the Philippine Islands, Urbino (1927) listed Toledo (a hybrid between a noble and a northern Indian or Chinese cane) and Uba among the varieties least susceptible to damage by *Perkinsiella vastatrix*, and stated that *S. spontaneum indicum* was negligibly affected. In Jamaica, Gowdey (1927, 1928) reported that White Transparent and B.H. 10(12) were seriously retarded as the result of heavy attack by *Saccharosydne*, whereas other varieties, including Uba, Ba.11569 and Badila, were only slightly affected. In Trinidad, Urich (1913) recorded that White Transparent was among the varieties most heavily attacked by froghopper *(Aeneolamia varia)*: Williams (1919, 1921) stated that Uba and Badila were the varieties least liable to damage by this insect, though both might suffer in a bad year, and Taylor and Pickles (1934) noted that Co. 213 was comparatively more resistant than other commercial varieties. These authors concluded that varieties with the most 'wild blood' (*S. sinense* or canes of a low degree of nobilization) were those least susceptible to attack, and Ingram *et al.* (1939) came to a similar conclusion regarding infestation by *Saccharosydne*.

It is evident that *Saccharum spontaneum* is consistently noted as highly 'resistant', and *S. sinense* as generally tolerant to attack but apt to suffer (though relatively less severely than noble canes) in conditions where attack is widespread and heavy. Commercial varieties of sugar cane having a useful degree of resistance include first nobilizations of these two species. Noble canes *(S. officinarum)* are generally rated as susceptible. The only discrepant observations refer to Badila,

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reported as relatively resistant to *Saccharosydne* (Gowdey, 1927) and *Aeneolamia varia* (Williams, 1919), but as very susceptible to *Perkinsiella vastatrix* (Urbino, 1927). There is general agreement that any commercially-grown cane variety may, in certain circumstances, be heavily attacked.

Resistance in commercial sugar cane to leaf injury is evidently not attributable to the presence of specific protective agents, but to a mechanism that can be broken down. An understanding of the factors concerned is clearly of importance for selecting resistant varieties, and for determining measures to lessen the risk of massive attack. Taylor and Pickles (1934), listing the features needed in a froghopper-resistant cane variety, stated that it should not be attractive to the pest, should develop only slight leaf damage when attacked and should recover rapidly from any leaf damage that might occur.

Factors Affecting the Metabolic Status of Sugar Cane

The metabolic status of sugar cane is influenced mostly by the frequency and amount of water reaching the soil, the physical and chemical characteristics of the soil, the variety of cane grown, the age of the crop and the stage in the crop cycle (plant, first ratoon, etc.). The last expresses crudely, with a significance peculiar to each locality, the cumulative effect of beneficial or deleterious factors that have existed, or have arisen, since the time of planting. In some soil-types it may reflect chiefly the effect of progressive soil compaction.

Observations of grossly different degrees of attack by a pest on cane stalks equally affected by all these factors are of value in showing the kind of change that favours attack. In Trinidad, Carmody (1909) reported a dense concentration of sugar cane froghoppers and 'virulent' attack on an area of cane that had been severely damaged by larvae of *Castnia licoides* Boisd., and suggested that changes in the juice composition as a result of attack by *Castnia* had rendered the cane abnormally attractive to the froghopper. He confirmed an observation made by Collens (1909*a*, *b*) that the juice of damaged cane is more acid than that of healthy cane. Withycombe (1926) recorded greater infestation by froghoppers on a stalk that had been seriously damaged by larvae of a stem borer (*Diatraea* sp.) than on three adjacent unbored stalks. He concluded that the damage caused by the borer had interfered with the transport of water, induced water stress in the leaves, and thereby favoured froghopper infestation. Examination of stools heavily infested by *Saccharosydne* in Trinidad showed that the canes had been bored by *Castnia* (Author's unpubl. data). This situation closely parallelled the observation of Carmody.

The responses of *Saccharosydne* when offered a choice between leaf tissue of its original, bored host plant and of an undamaged plant of the same variety that had been grown elsewhere were observed (Author's unpubl. data). A portion of a stool with leaves infested with a dense nymphal population of *Saccharosydne* was replanted in another area where cane was growing well and was free from borer attack. Two leaves (the fourth open), one on the bored and one on an unbored plant, were bent to lie side by side. The area of the leaves under test, the third quarter from the base, was enclosed in a cage into which adults and nymphs were introduced. Between tests the leaves were moved so as to present a fresh surface. The results are shown below.

Time of exposure (minutes)	No. of tests	No. of insects per test	Percentage of total participating counted on leaf of		Percentage not participating	Significance of difference
			unbored cane	bored cane		
ca. 30	10	33–36	21.8	73.0	5.2	$P < 0.01$

Aeneolamia is attracted towards 'odours' of cane leaf, of weak solutions of sucrose, and of the two combined (Fennah, 1939). Both such attractants are present in normally growing sugar cane, and the aggregations of Homoptera on bored cane noted by Carmody, Withycombe and the author involved discrimination between canes that possessed both these attractants, though not necessarily in equal amounts.

Borer damage to cane results in changes in the sucrose and glucose contents (Skinner, 1930) and in an increased acidity of the juice (Withycombe, 1926). In order to obtain some idea of the difference in their nitrogenous composition, samples of tissue from the leaf areas used in the discrimination tests were analysed and gave the following results:

Source of leaf material	Moisture %	Total nitrogen (% dry wt.)	α-amino N (% total N)
Unbored cane	74.5	1.95	3.4
Bored cane	66.0	1.17	11.6

Measurements were made of the moisture and total nitrogen contents of comparable leaf samples of bored and unbored cane at the site where *Saccharosydne* was abundant, and at another site where it was absent. The differences between bored and unbored cane were broadly similar to those shown in the table, and it was accordingly inferred that the low moisture content and total nitrogen level of

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the leaves of bored cane used in the discrimination tests were primarily a consequence of the heavy damage to the stem caused by *Castnia.*

The high content of α-amino nitrogen can be attributed to drought conditions so created in the leaf. It is possible that changes in the acidity of the juice, as suggested by Carmody, or in α-amino acid content, may provide an attractive odour, or enhance the attractiveness of those already present (cf. Mittler and Dadd, 1964).

In conditions of water stress there is a strong upsurge of α-amino nitrogen in the juice and an increase in sucrose (Wiggins and Williams, 1955). Gough (1911) and Pickles (1939), referring to damage by *Aeneolamia* and *Delassor tristis guppyi*, respectively, stated that damaged canes contain a higher percentage of sucrose than undamaged canes.

Varietal Susceptibility in Relation to Leaf Morphology and Rooting Behaviour

If increases of sucrose and α-amino nitrogen, or accompanying changes, augment the attractiveness of the cane to Fulgoroid pests or to froghoppers, varieties best capable of withstanding conditions of water shortage, 'physiological drought' or deficient root aeration will be least attractive to such pests. Moreover, if it is assumed that juice enriched with sucrose and α-amino acids is more nutritious than normal juice, then cane suffering from the effects of drought or deficient root aeration would be expected to favour the development of a pest population, by increasing fecundity and survival rate.

The author examined the epidermal cells of leaves of a number of sugar cane varieties representing both commercial cane and the progeny of crosses, and found that the pattern of rows of cells on the leaf surface is remarkably constant for each clone, but may vary considerably between clones and less so, though appreciably, between the progeny of a cross. At one extreme, the cells overlying the vascular bundles are narrow and numerous, and only two or three intervascular rows, in which the stomata are situated, lie between them; at the other, the vascular bundles are overlain by fewer rows of cells, and the number of intervascular rows is five, six or even seven. The pattern for each variety was expressed as a number (the 'stomatal index') obtained by counting in a traverse of the upper surface from edge to midrib, the numbers of epidermal cells in fifty consecutive pairs of 'vascular' and intervascular sets of cell-rows, and expressing the result as $\frac{10x}{y}$ where x represents the total number of intervascular rows of epidermal cells in the sample and y the total number of 'vascular' rows (Fennah, 1939). The stomatal indices of a few varieties are given below, together with those of two varieties of noble cane that exemplify the higher values.

Species or variety	Index
Saccharum spontaneum	1.20
S. sinense, (Uba) Hawaiian form	2.45
Kassoer (synthetic)	2.55
Co. 213	2.65
Toledo	4.05
Ba.11569	4.60
P.O.J.2878	4.90
B.H.10 (12)*	5.60
D.625*	6.25

* Noble canes

The order of the varieties, arranged according to index, agrees with their order of resistance to damage by the feeding of Cercopoid and Fulgoroid pests as far as this is known, and also, for a few, of their tolerance of drought or waterlogging. Srinivasan and Batcha (1963) reporting the results of tests of species of *Saccharum* under conditions of artificial waterlogging for a 6-month period, stated that some clones of *S. spontaneum* and *S. robustum* were the most tolerant and *S. sinense* less so, whereas the clones of *S. officinarum* died out completely. One clone of *S. spontaneum* (S.E.S. 220) that grew well under waterlogged conditions had been collected originally from a dry habitat. These writers noted that the incidence of the white fly *Aleurolobus barodensis* Mask. was 'rather severe' under waterlogged conditions. Sen (1941) recorded the incidence of this species and of *Pyrilla* on waterlogged cane in north Bihar. Ojeda (1963) reported that at San Cristobal (Mexico) Co. 213 grows under waterlogged conditions from June to November. *S. spontaneum* and some of its hybrids with *S. officinarum* are able to develop fibrous matrices of roots from the submerged stem nodes, and, if such roots are covered with soil, to send up negatively geotropic roots with much aerenchyma.

Varietal Tolerance of Feeding by Homoptera in Relation to Growth Conditions in the Field

It is known that the fecundity of *Saccharosydne saccharivora* is influenced by the total nitrogen content of the host plant (Metcalfe, 1965). If it is assumed that its saliva, like that of *Javesella* (Nuorteva, 1958) lacks proteases, its food supply would depend on the level of soluble nitrogen in the sap. This may be increased first of all by adverse environmental change, and then even further by the act of feeding. If this relationship holds for all sugar cane Fulgoroidea, it would explain many apparently contradictory observations on occurrence of damage and on resistance of certain varieties. The varieties that remain healthiest under adverse conditions would be those with the lowest soluble nitrogen content, and the most able to seal off tissue damage caused by feeding. Accordingly, they would be the least nutritious to the pest.

The outbreak of *Aleurolobus* on waterlogged cane noted both by Sen (1941) and by Srinivasan and Batcha (1963) may well have been a manifestation of such a relationship; there are examples from other groups of insects and on other plants (cf. Fennah, 1959).

4. Practical Implications of Varietal and Environmentally Induced Resistance to Attack by Homoptera

The likelihood of breeding varieties of sugar cane both resistant to injury by Homopterous feeding and commercially acceptable depends on the degree of priority assigned to the qualities required. Wherever it may be necessary to select varieties able to withstand drought, or waterlogging, or able to produce new roots to replace those that have died, it seems not unlikely that an appreciable degree of resistance to feeding injury will automatically be embodied in the final selections. However, in cane-growing areas where adverse conditions are of only short duration it may well prove more profitable to protect high yielding but 'susceptible' varieties with insecticides than to use a more tolerant variety with less intrinsic yielding capacity.

The differences in resistance to Homopterous attack noted between noble or highly nobilized cane varieties are comparatively slight, but in any area with a recurrent Homopterous pest problem it may be worth-while to make at least a limited search for resistance among new commercial varieties as they become available. In Jamaica and Trinidad the noble cane variety Badila was noticed as having some resistance to attack by *Saccharosydne* and *Aeneolamia*, respectively, though in the Philippines it showed none against *Perkinsiella*. Another noble cane, Ba.11569, was found in Jamaica to be tolerant of attack by *Saccharosydne*. Probably the best example of the economic importance of a comparatively small superiority in resistance to a Homopterous pest is that afforded by the performance of the variety Yellow Caledonia in Hawaii at the height of the *Perkinsiella* scourge. Whereas estates growing other noble varieties, such as Rose Bamboo, suffered disastrous losses of tonnage, those growing Yellow Caledonia were the least hard hit (Perkins, 1903; Swezey, 1936). In view of its performance under insect attack in Hawaii, it is interesting to note the evaluation of Yellow Caledonia by Earle (1919, 1921) for use under Puerto Rican conditions. Here it was found to be late maturing and to require several weeks of dry weather to ripen. It was recommended as one of the most suitable varieties for growing 'on compact, poorly-drained maritime soils and clay alluviums' and for holding over for a long crop.

In Hawaii, early maturing varieties seemed to be among those most susceptible to injury by *Perkinsiella*, but the late maturing variety Cavengerie also was noted as susceptible (Perkins, 1903).

The reasons for the superiority of Badila over other noble canes in Trinidad have not been ascertained. It was believed that this variety habitually developed a deep root system, but a few observations showed that this was not always so, and investigation was not pursued further (Williams, 1919, 1921). It is possible that useful information might be obtained on such problems by observing varietal characteristics of rooting behaviour, such as degree of uniformity, or frequency, of rootlet production in relation to soil and seasonal weather.

Sugar cane of lush growth has been recorded as being particularly subject to attack by Homoptera. The question arises, therefore, if sugar cane were maintained in the field in conditions appropriate to its age and ideal for the attainment of maximum growth and yield, would it be rendered abnormally susceptible to infestation and injury? Experimental data obtained by the author (unpubl. data) on a similar question with reference to other crops and other Homopterous pests have shown that optimal nutritional status of the host plant is not associated with heavy attack. There is little information on this point regarding sugar cane, but there are a few suggestive observations, such as the failure by Urich (1913) and Withycombe (1926) to produce blighting on sugar cane leaves by bulk introduction of froghoppers *(Aeneolamia)* into stools of vigorously growing cane. In sum, the evidence is sufficiently concordant to suggest, by analogy, that sugar cane maintained at an ideal standard would not be unduly prone to infestation.

Insofar as fertilizer treatments needed to maintain optimal nutrient levels in the plant raise its total nitrogen content, the use of nitrogenous fertilizer must inevitably increase the risk of heavy infestation. But it would seem that for an outbreak of a Homopterous pest to occur two factors must be operative at the same time. Firstly, a potential pest must be under low biological pressure. Secondly, there must be a derangement of normal metabolism in the host plant leading to a retardation of protein synthesis. Such derangement can result from various causes, such as damage to the stalk by rats, stem borers, or hurricanes, or to the roots by nematodes or pathogens, but the most common cause appears to be the onset of adverse soil environmental conditions at certain stages in the growth of the crop (cf. McDonald, 1932). Such conditions include spells of inadequate water supply to the roots, suboptimal root aeration, or untimely vicissitudes such as a brief drought following a period of waterlogging, or excessive fluctuations in water supply in an environment that prevents deep rooting. The stages in the growth of the crop at which serious Homopterous damage has been most frequently recorded are when the plants are 1–3 ft high, and during the 5 months following the period of most rapid growth.

The main contribution that can be made to an integrated control programme is undoubtedly agronomic, and is that of making provision to meet the develop-

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ment of adverse soil conditions during at least two-thirds of the life of the crop. Where means of controlling soil moisture are available, appropriate corrective action becomes possible. There is then need for a sensitive means of detecting the first signs of a metabolic check in the crop.

There is also need for a positive means of rapidly obtaining information about the entomological aspects of sugar cane varietal behaviour under conditions adverse to growth. One possible approach is the provision, on each main soil type, of a small area that, in different sections, can be given different watering régimes, either at fixed levels, or in patterns and amounts calculated to reproduce the worst types of seasonal abnormality likely to be experienced in the area. If cane varieties were exposed to such conditions for one or two seasons it is likely that the incidence of Homopterous pests would be found sufficiently different between treatments to yield valuable information both on the behaviour of the pest and on the tolerance and recovering ability of the varieties under observation.

5. Summary

More than 150 species of Fulgoroidea, representing 12 families, have been recorded on sugar cane. Only a few of them live on the host in all stages of their development, and a summary is given of the life histories of the more important species that do so, i.e., *Perkinsiella vastatrix* (Breddin), *P. saccharicida* Kirkaldy, *P. vitiensis* Kirkaldy, *Saccharosydne saccharivora* (Westwood), *Numicia viridis* Muir and *Pyrilla perpusilla* (Walker).

The nature of the damage to the host plant is discussed and attention is drawn to the wide variability in the amount of damage sustained by leaves from an individual feeding puncture made by the insect. It is suggested that the difference is attributable primarily to differences in the metabolism of the host.

Sugar cane varietal differences are considered in relation to such characteristics as attractiveness to the insect, nutritiousness as food for the insect, and tolerance of feeding injury. It is suggested that the differences in attractiveness or in susceptibility to injury so far observed in the field are likely to have been determined chiefly by the severity of the effects of the environment on the water relations of the crop. The scope available for the development of 'resistant' varieties of sugar cane or of ameliorative agronomic measures is briefly assessed.

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