Bull. ent. Res. (1968) **59**, 393–408
With Plates XVII–XVIII
Published 1969

Studies on the biology of the sugar-cane pest *Saccharosydne saccharivora* (Westw.) (Hom., Delphacidae)

J. R. METCALFE *
Sugar Manufacturers' Association Ltd, Mandeville, Jamaica

Introduction

Saccharosydne saccharivora (Westw.), commonly known as the West Indian cane fly, is found on sugar-cane throughout the West Indies and neighbouring parts of North, South and Central America, and in Jamaica has been a major pest of sugar-cane for more than two centuries. It may pass almost unnoticed for years, but at irregular intervals, shorter in Jamaica than elsewhere, epidemic populations develop and may retard the growth of the crop, on occasion posing a serious threat to the sugar industry. There are many references to its outbreaks and natural enemies, yet its original host-plants are almost unknown and surprisingly little has been written of its life-history and habits. The accounts by Ballou (1905) and Wolcott (1921, 1933) lack developmental details, while that of Guagliumi (1953) contains, as will be shown, serious inaccuracies. Ashby's (1954) unpublished report is the most useful account to date but, being based on investigations lasting less than two months, is necessarily limited in scope.

This paper presents an account of laboratory studies and field observations in Jamaica and British Honduras between 1961 and 1967 on the host-plants, life-history and habits of *S. saccharivora*.

Host-plants

Sugar-cane, introduced to the West Indies in the late 15th century, has been available to *S. saccharivora* as a possible host-plant for little more than 450 years. Nevertheless Guagliumi (1953) regarded sugar-cane as the only true host-plant, and other grasses previously recorded as host-plants (Table I) to be populated by casual movements of adults out of sugar-cane fields and to be incapable of supporting breeding populations. Casual observations in Jamaica between 1961 and 1965 had also suggested that *S. saccharivora* was largely dependent on sugar-cane. Many grasses adjoining cane fields were inhabited by adults of *S. saccharivora*, but all developmental stages were found only on *Sorghum sudanense*; occasionally eggs were recorded on *Panicum maximum*, *Brachiaria mutica* and *Paspalum plicatulum*, particularly when growing as cane-field weeds.

In April 1966 came a unique opportunity to search in British Honduras for the original host-plants. An outbreak of *Saccharosydne saccharivora* (believed to be the first in that country for nearly forty years) had developed on a new sugar estate at Tower Hill and could have originated only from the natural flora of nearby river banks, swamps, grassland, scrub and secondary forest. No trace of *S. saccharivora* was found in the forest where grasses were rare. Attention was then focused on an area, comprising recently cleared forest and an adjoining swamp, over which adult *S. saccharivora* had been blown by the prevailing winds. Adults were found on numerous plant species, Gramineae (grasses and reeds), Juncaceae, Cyperaceae and Typhaceae, on which they

* Now at Commonwealth Institute of Entomology, 56 Queen's Gate, London, S.W.7.

TABLE I. *Plants other than sugar-cane on which* S. saccharivora *has been recorded*

Plant species	Country	Stages of *S. saccharivora* recorded	Authority
Gramineae			
*Andropogon bicornis**	Jamaica	All	Author
	Puerto Rico	All	L. F. Martorell (1953 *in litt.*)
? *bicornis**	Br. Honduras	All	Author
*glomeratus**	Br. Honduras	All	Author
	Jamaica	All	Author
Brachiaria mutica	Jamaica	Eggs	Author
Dactyloctenium aegyptium	U.S.A. (Fla)	?	Ingram *et al.* (1939)
Digitaria sanguinalis	U.S.A. (Fla)	?	Ingram *et al.* (1939)
Panicum fasciculatum	Br. Honduras	Eggs	Author
maximum	Jamaica	Eggs	Author
molle (= *barbinode*)	Puerto Rico	?	Wadley (1937)
Paspalum distichum	Grenada	?	Westwood (1833)
*plicatulum**	Jamaica	Eggs	Author
urvillei	U.S.A. (Fla)	?	Ingram *et al.* (1939)
*Sorghum sudanense**	Jamaica	All	Author
Gen. et spp. indet.	Br. Honduras	Adults	Author
	Cuba	Adults	Osborn (1926 *a*, *b*)
	Jamaica	Adults	Author
	Puerto Rico	All	Smyth (1919)
		?	Osborn (1929)
	U.S.A. (Ga)	? all	Spooner (1920)
		?	Ingram *et al.* (1939)
Juncaceae			
Gen. et spp. indet.	Br. Honduras	Adults	Author
Cyperaceae			
Gen. et spp. indet.	Br. Honduras	Adults	Author
Typhaceae			
Gen. et spp. indet.	Br. Honduras	Adults	Author

*Determined by Mr. G. Proctor, Institute of Jamaica.

could be regarded as casual immigrants, and one egg-slit was seen on a common cane-field weed, *Panicum fasciculatum*. However, immature stages were numerous on *Andropogon glomeratus*. This stool-forming grass growing to 1½–3 ft tall proved to be an early coloniser of waste places, *e.g.*, roadsides, chalk-pits, etc., and was almost always inhabited by *S. saccharivora* even at 2 500 ft in the Maya Mountains. At this locality all stages of *S. saccharivora* were found also on another *Andropogon* sp., probably *A. bicornis*. *S. rostrifrons* (D. L. Crawford) was encountered at several localities on *Paspalum virgatum*, a grass found often in association with *Andropogon*, but generally favouring a damper habitat.

Subsequently, both *S. saccharivora* and *S. rostrifrons* at all stages of development were taken on the same two species of *Andropogon* and on *P. virgatum*, respectively, in Jamaica. *A. glomeratus* was common on lightly grazed rough pasture and roadsides in the limestone hills while *A. bicornis* was prevalent in over-grazed pasture and open ditches on heavy soil in wet lowland areas. At every locality, some remote from sugar-cane cultivations, including one at 4 000 ft in the Blue Mountains, *S. saccharivora* was common.

It is ironical that, after this search for the original host-plants, perusal of an old Research Department file revealed a letter, dated 1953, from L. F. Martorell stating that he had frequently found *S. saccharivora* breeding on *A. bicornis* on high ground in Puerto Rico.

The plants on which *S. saccharivora* has been recorded (Table I) may be classed as follows: (i) those on which adults are casual immigrants, (ii) those on which eggs are occasionally laid, and (iii) those on which eggs are freely laid and on which nymphal development proceeds. Only the last can possibly be regarded as original host-plants, and *A. bicornis* and *A. glomeratus* are undoubtedly two, if not the two, most important species. Herbarium specimens at the Royal Botanic Gardens, Kew had been collected from Mexico and Cuba south to Peru, and from the U.S.A. (California to Massachusetts)

south to Nicaragua and Hispaniola, respectively, well beyond the present distribution of *S. saccharivora* (Commonwealth Institute of Entomology, 1956; Metcalfe, 1968). *Sorghum sudanense* originated from the Old World and cannot therefore be an original host-plant, while the remaining species may be classed as either (i) or (ii), or unknown for want of fuller data. Thus *Saccharosydne saccharivora* falls in line with the other New World species of *Saccharosydne* which breed almost exclusively on indigenous grasses (Guagliumi, 1953; Muir, 1926*a*; Osborn, 1926*a*).

The change in status of *S. saccharivora* with the adoption of sugar-cane as a host-plant is typical of the origin of sugar-cane pests (Pemberton & Williams, 1969), and seems to have occurred to a greater or less extent in all parts of its range. In Puerto Rico (Van Dine, 1913) and in Venezuela (Guagliumi, 1953), the presence of *S. saccharivora* as a pest was believed to be the result of introductions from the 'British West Indies' and from the Lesser Antilles or Trinidad, respectively. This seems improbable. The present-day distribution of *S. saccharivora* is compact and is far exceeded by that of the two *Andropogon* species, so that the presence of *S. saccharivora* in these two countries is more likely to have been overlooked than to be the result of comparatively recent introductions.

Description of developmental stages

The egg

The egg has been described briefly by Ashby (1954) and Guagliumi (1953), but further details are given below (Fig. 1; Plate XVII, fig. 1). Measuring 0·7 × 0·2 mm,

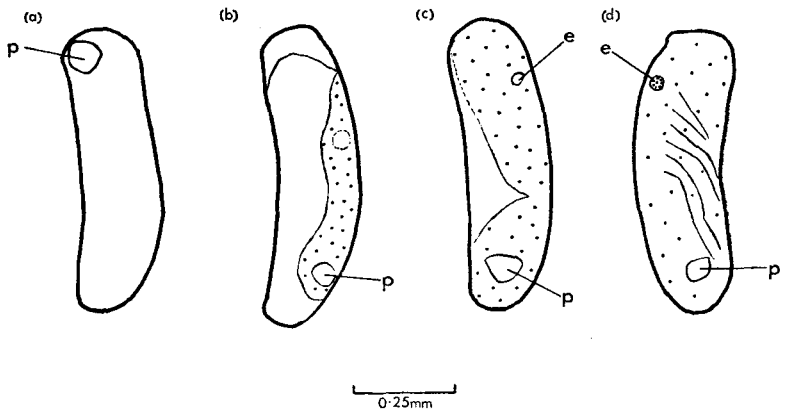

Fig. 1.—*S. saccharivora*, development of egg. (a) 2nd day, pigment spot lying anteriorly; (b) 7th day, pigment spot lying posteriorly, shrinkage of egg contents; (c) 11th day; (d) 17th day, legs distinct. (p = pigment spot; e = eye-spot.)

the egg is cylindrical, slightly curved, with rounded ends, blunter in front than behind. The chorion is transparent and smooth. The newly laid egg is hyaline, but on the second day a pigment spot appears in the yolk, pale yellow at first, but gradually intensifying to a bright orange. Initially the pigment spot lies near the anterior pole, then hard against it, but between the sixth and seventh days moves to the posterior pole as part of the embryo abdomen. This last movement occurs rapidly, the half-way stage being rarely seen. Meanwhile the yolk becomes cloudy, gradually shrinking from the anterior pole, and the embryo may be distinguished as a granular area on the convex side of the egg. Next, red eye-spots appear near the anterior pole, and the embryo

completely fills the egg, causing some distortion of the chorion. One to two days prior to eclosion, the ommatidia, the division between the thorax and abdomen, and the legs are all clearly visible. The overall colour is then pale yellow, with the orange abdominal spot and the red eye-spots in distinct contrast.

The nymph

The most distinctive feature of the nymph is the white wax secreted from glands on the head and abdomen (Plate XVII, fig. 3). This forms a short rod in front of the

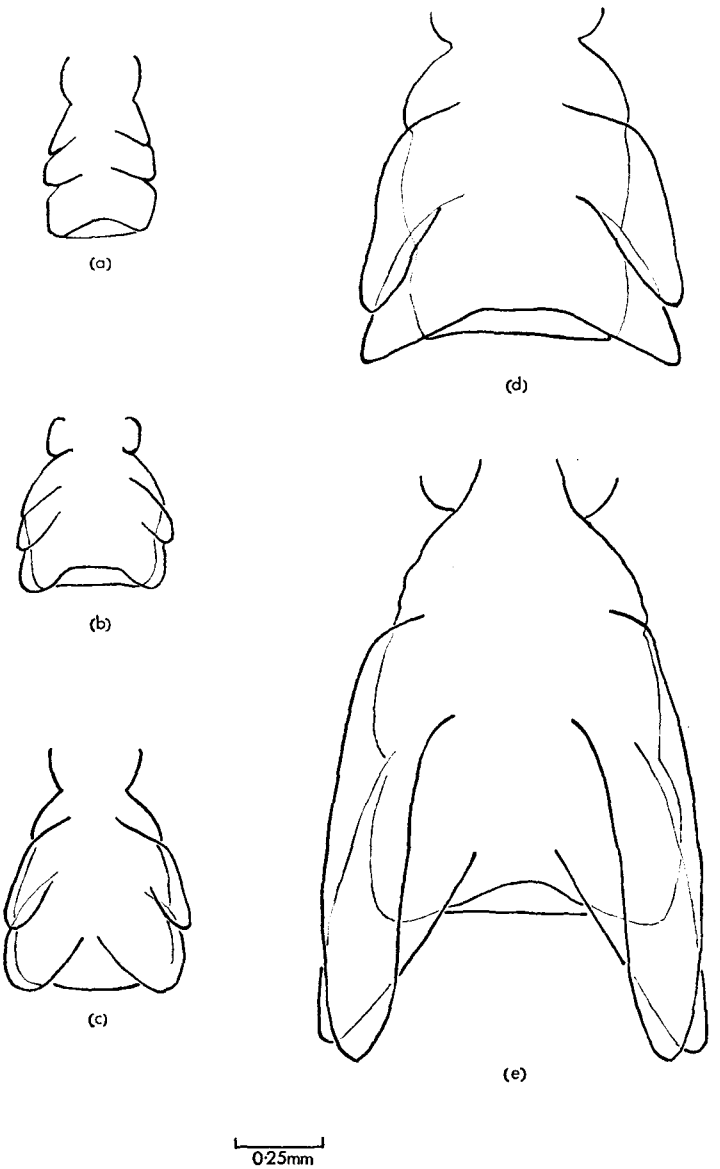

Fig. 2.—*S. saccharivora*, thorax (dorsal view) showing development of wing buds; (a)–(e) instars 1–5, respectively.

head, a long tapering tail often longer than the whole body, and numerous fine filaments extending laterally from the abdomen.

In common with other Delphacids (Williams, 1957), obvious morphological changes allowing recognition of each instar occur in the nymph during development. These include increasing size, differentiating wing buds, increasing spinosity of the metathoracic tibia and tarsus, increasing sensorisation of the antennae and changes in pigmentation. From a practical point of view the first three are the most useful. The number of instars has been reported as four (Guagliumi, 1953) and five (Ashby, 1954): in the present study five instars were recognised.

Wing buds.—The differentiation of the forewing buds relative to those of the hind wing and to the thorax is characteristic of each instar (Fig. 2). Wing buds are absent from the first-, just apparent in the second-, and distinct in the third-instar nymph. In instar 4 the tips of the forewing buds are short of those of the hind wing, and in instar 5 they overlap. Guagliumi (1953) confused instars 4 and 5: in his Lamina V, the wing buds of A and B, both representing a ' ninfa del cuarto instar ', are characteristic of those of instars 4 and 5, respectively.

Size.—Body length is unreliable for separation of the instars for, unlike a sclerotised unit such as the femur, changes in size may occur during each instar. For this reason the length of the right metathoracic femur, from the tip of the knee to the rounded part of the joint with the trochanter, was selected as the standard.

TABLE II. *Length of the metathoracic femur of the nymph of* S. saccharivora

Source	Instar	Length (mm) Mean and S.E.	Length (mm) Range	Growth increment
Masemure	1	0·17±0·002	0·16–0·18	—
	2	0·23±0·002	0·21–0·24	× 1·34
	3	0·32±0·002	0·30–0·34	× 1·40
	4	0·42±0·003	0·38–0·45	× 1·32
	5	0·56±0·005	0·51–0·61	× 1·35
Mixed origin	1	0·18±0·001	0·16–0·19	—
	2	0·23±0·001	0·22–0·24	× 1·33
	3	0·33±0·003	0·30–0·35	× 1·41
	4	0·43±0·003	0·42–0·46	× 1·30
	5	0·60±0·006	0·56–0·64	× 1·40

Means each based on measurements of 20 individuals.

TABLE III. *Length of the metathoracic leg of the nymph of* S. saccharivora; *from Ashby (1954)*

Instar	Mean length (mm)	Growth increment
1	0·6	—
2	0·8	× 1·33
3	1·1	× 1·37
4	1·5	× 1·36
5	2·0	× 1·33

Femurs were measured on nymphs from Masemure (Frome) and from the Research Department (mixed origin) which had been provisionally sorted into their respective instars by size and by the development of the wing buds, there being twenty of each instar from each locality. The measurements, made with a micrometer eyepiece to the nearest unit (=0·016 mm) confirmed the existence of five instars, there being no overlap between the maximum of one instar with the minimum of the one following (Table II). The ratio, femur length of instar n + 1 / femur length of instar n, was a constant (the growth increment), thus conforming with Dyar's Law (Wigglesworth, 1965).

From tibial measurements Ashby (1954) concluded that five instars existed, and comparison of Tables II–III shows how closely the growth increment derived from his

TABLE IV. *Body length of the nymph of* S. saccharivora

Authority	Instar	Mean length (mm)	Growth increment
Guagliumi (1953)	1	0·9	—
	2	1·3	× 1·44
	3	1·9	× 1·46
	4	2·8	× 1·47
	[5]	3·5	× 1·25
Ashby (1954)	1	0·8	—
	2	1·2	× 1·50
	3	1·8	× 1·50
	4	2·2	× 1·22
	5	4·0	× 1·81

data agrees with that found in the present study. Both he and Guagliumi (1953) measured body length, and their data correspond for instars 1–4 (Table IV). Guagliumi did not appreciate that the greater length of his instar 4 just before ecdysis was due to another instar (Table III). The growth increment for body length is generally slightly higher but more erratic than that for the femur.

Structure of the metathoracic tibia and tarsus (Fig. 3).—This was described briefly by Ashby (1954), but his illustrations were inaccurate in respect of scale, shape of the spur and number of spines. Guagliumi's (1953) descriptions were accurate only for instars 1–3.

Instar 1: Tibia with four spines distally on the ventral side; one, larger than the others, is destined to become the tibial spur of later instars. Tarsus two-segmented, the first bearing four, occasionally (2 specimens out of 20) three, spines ventrally, and the second none.

Instar 2: Tibia with four spines and mobile spur, the latter spineless. First tarsal segment with five spines.

Instar 3: Tibia with five, sometimes (4 specimens out of 17) six, spines distally; spur with 0–4, usually (13 specimens out of 17) 1–3, spines along edge. First tarsal segment with six, occasionally (1 specimen out of 17) five, spines.

Instar 4: Spur with distinctly serrate edge comprising 7–13, usually (18 specimens out of 20) 9–11, spines. Tibia with seven, occasionally (2 specimens out of 20) six, spines distally. First tarsal segment with seven, occasionally (1 specimen out of 20) six, spines, second with one spine in the centre, ventrally.

Instar 5: Number of spur spines 13–21, usually (16 specimens out of 20) 15–19, but tibial spines six or seven. Tarsus with three segments, first with 7–8 spines, second with three, occasionally (2 specimens out of 19) four, third with none.

Guagliumi (1953) described the fourth instar with a three-segmented tarsus, again showing his complete confusion of instars 4 and 5.

The adult

The adult (Plate XVII, fig. 4) has been adequately described by Anon (1833), Crawford (1914), Fennah (1945), Guagliumi (1953, 1962), Kirkaldy (1907), Muir (1926*a*), Van Duzee (1907), Westwood (1833) and Wolcott (1921). The genitalia were featured by Fennah (1945), Guagliumi (1953), Muir (1926*b*) and Osborn (1935).

The sexes are easily distinguished by the external genitalia. Useful additional characters are size (males smaller than females) and the presence or absence of a puff of white wax posteriorly (present only in females).

Duration of the developmental stages

Most of the following data on the duration of the life-cycle were obtained in a glasshouse at Mandeville, altitude 2 200 ft. The glasshouse, approximately 46 × 25 ft, had full-length flanged sides that opened nearly horizontally, thus allowing good ventilation by day, and conditions inside were not dissimilar to those on sugar estates, most

of which are at or near sea level. Shade temperatures, recorded by standard climatological maximum and minimum thermometers, showed a daily range of 10–30°F, about 10°F more than on the estates. Excessive heating in the summer months (June–August) was prevented by white-washing the roof and end walls; light intensity was thereby reduced but did not apparently affect cane growth.

A cage was required that would hold a single individual of *S. saccharivora* on a sugar-cane leaf *in situ*, yet still allow the normal processes of both leaf and insect.

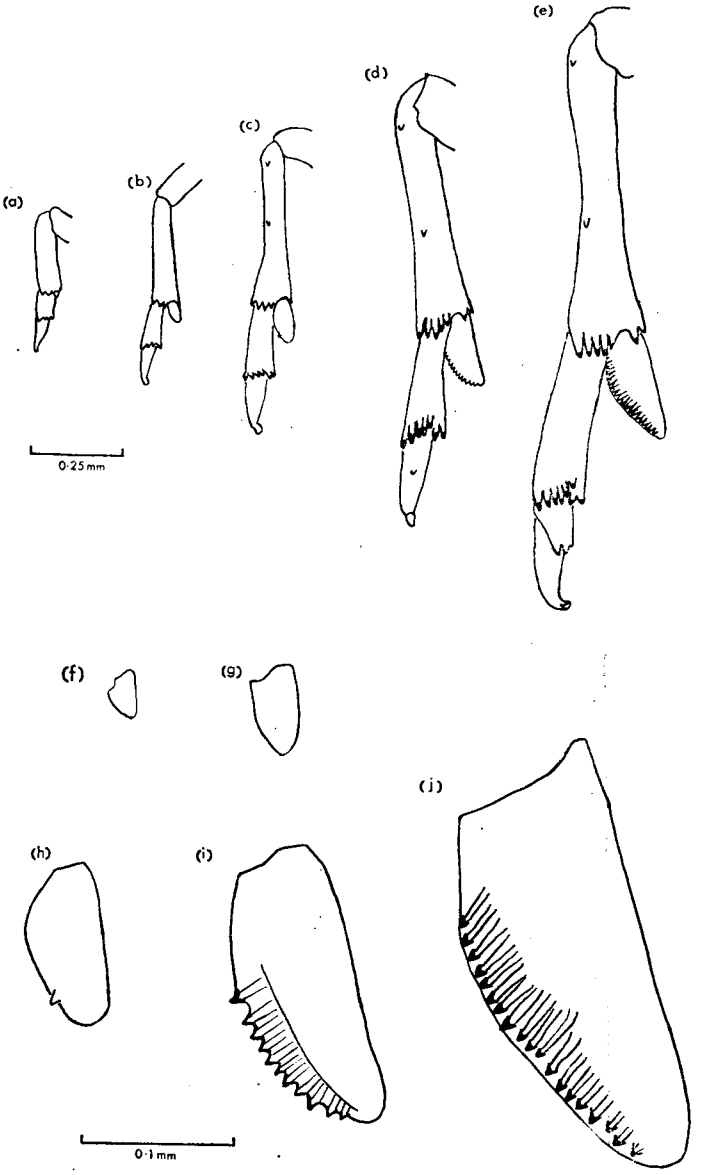

Fig. 3.—*S. saccharivora*. (a)–(e) right metathoracic tibia and tarsus (ventral view) of instars 1–5, respectively; (f)–(j) spur of right metathoracic tibia of instars 1–5, respectively.

The type designed (Plate XVII, fig. 5) consisted essentially of two rectangles of $\frac{1}{16}$-in. perspex ($4\frac{1}{2}$ × 3 in.) with a foam-rubber border; one was fitted with a bung for introducing the insect and the other with plastic mesh to allow circulation of air. The two rectangles, one on each side of the leaf and about one-third of the way up, were clamped together, mesh side downwards, by means of thick rubber bands. The elasticity of the foam rubber generally allowed a close fit around the leaf midrib; any small gaps through which the insect might pass were blocked with cotton wool. The cage was supported at an angle by an adjustable string hooked to wires between the glasshouse girders, and only rarely caused the midrib to break.

This type of cage proved very satisfactory. There was slight chlorosis immediately under the foam rubber, especially if the bands were too tight, and occasionally young leaves exposed to direct sunlight were scorched, but without obvious signs to the contrary it was assumed that both the leaf and the insect confined on it otherwise continued to function normally. Escape of early-instar nymphs through the mesh was prevented by a card held in position by the rubber bands. All stages could be readily examined with a hand lens. Accumulations of honeydew on the mesh were sometimes a problem, but could be removed with a damp cloth. Maximum temperatures inside the cages (measured with a standard climatological thermometer) were 2–5°C higher than those of the glasshouse, and the upper perspex sometimes became hot to the touch, especially if exposed to direct sunlight, unless the rubber bands, which were black and absorbed heat, were kept to the border of the rectangles (see Plate XVII, fig. 5).

The egg

Field and preliminary experimental records had indicated the incubation period of eggs to be about 17 days (range 14–19 days). More precise data were obtained from 27 batches of eggs (each of 1–3 egg-slits) laid on young sugar-cane plants, where each batch represented an individual female's production of eggs for one day. Hatchlings were removed daily, the days on which they appeared being recorded. Seventeen batches gave uninterrupted records from which the mean duration of the egg stage was estimated.

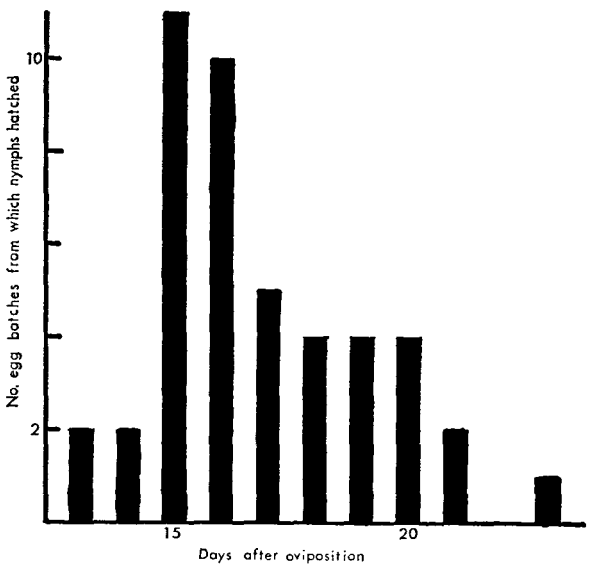

Fig. 4.—Incubation period of eggs of *S. saccharivora*.

The incubation period ranged from 13 to 23 days, with peak hatching after 15–16 days (Fig. 4) and a mean of 16·8 ± 0·3 days. Hatching within any one batch of eggs extended over 1–7 days (mean 3·3 days), the first eggs hatching in 13–20 days, the last in 15–23 days. Average maximum and minimum temperatures in the glasshouse during the experimental period were 90 and 65°F, respectively, and, as all eggs were laid within four days, what little daily variation in temperature there was could not have significantly affected their rate of development.

These estimates agree with those of Ashby (1954) who gave at least 11, 13 and 17 days for the incubation period. On the other hand, Guagliumi (1953) recorded an average of 7 days at similar temperatures, with a very wide range from 5 to 20 days. Field records in British Honduras and Jamaica never suggested the incubation period to be less than 13 days, so it is hard to credit that in Venezuela it should be so much shorter.

The nymph

The durations of each of the instars 2–5 were determined from nymphs caged individually during the first instar on young cane plants; the instar reached and the presence or absence of exuviae were recorded daily. Except in series II, the nymphs were caged on the third leaf (the spindle leaf = no. 1).

Three series were run. The rates of development of males and females were compared, in series I on a mixture of plant and ratoon cane, in series II on plant cane on leaves of different ages, no. 2 and no. 4, and in series III, on host-plants of contrasting vigour, plant cane fertilised with sulphate of ammonia, and ratoon cane unfertilised. The complete history of the successive instars of an individual was often lost due to overlooking an ecdysis, escapes, natural mortality or accidents; only complete histories were used in analysis of the data. The nutrient status (nitrogen, phosphorus (P_2O_5) and potash (K_2O) per cent dry matter) of series III plants was determined from leaf samples (leaf no. 3) taken after most nymphs had completed their development. Glasshouse temperatures were similar in each series, average maxima being 93, 90 and 91°F, and average minima 71, 70 and 67°F, in series I, II and III, respectively.

The results are presented in Tables V-VII. The durations of instars 2–5 were the same for males and females except in series I where males developed significantly

TABLE V. *Development time (days) of males and females of* S. saccharivora *through instars 2–5 on a mixture of plant and ratoon cane (series I)*

	Males			Females		
Instar	No. individuals	Mean and S.E.	Range	No. individuals	Mean and S.E.	Range
2	12	4·0±0·2	3–5	8	4·0±0	4
3	12	4·1±0·1	4–5	9	4·3±0·3	3–6
4	13	4·2±0·2	3–5	9	4·8±0·2	4–6
5	13	5·5±0·3	3–7	9	6·0±0·2	5–7
2–5	13	17·6±0·4	14–20	8	19·2±0·5	17–21

faster ($P = < 0·05$), and were not affected by age of leaf. The latter result was contrary to expectation, but as the sugar-cane plant may produce several new leaves each week, any differences between leaf no.'s 2 and 4 would have disappeared quickly. On the other hand, there was a marked contrast between the fertilised plant cane and the unfertilised ratoon (series III), the former being green and thriving, the latter yellow and stunted. The contrast was even more apparent from leaf analysis, N being 1·77 and 0·89% dry matter and K_2O 1·69 and 1·38% dry matter in fertilised and unfertilised cane, respectively. The durations of instars 2–5 (females only) differed correspondingly ($P = < 0·001$), each being longer and totalling on average 11·5 days more on the unfertilised cane. Establishing first-instar nymphs on the unfertilised cane

TABLE VI. *Development time (days) of males and females of* S. saccharivora *through instars 2–5 on young and old leaves of young plant cane (series II)*

		Males		Females	
Leaf	Instar	Mean and S.E.	Range	Mean and S.E.	Range
No. 2		(6 individuals)		(7 individuals)	
	2	4·5±0·2	3– 5	4·0±0·2	3– 5
	3	4·0±0	4	4·0±0	4
	4	4·2±0·2	4– 5	4·3±0·2	4– 5
	5	6·0±0	6	5·9±0·1	5– 6
	2–5	18·7±0·2	18–19	18·1±0·3	17–19
No. 4		(10 individuals)		(10 individuals)	
	2	3·9±0·1	3– 4	3·9±0·1	3– 4
	3	3·8±0·1	3– 4	4·0±0	4
	4	3·8±0·1	3– 4	4·0±0	4
	5	5·6±0·2	5– 6	6·1±0·1	6– 7
	2–5	17·1±0·2	16–18	18·0±0·1	17–19

TABLE VII. *Development time (days) of females of* S. saccharivora *through instars 2–5 on cane plants of contrasting vigour (series III)*

	Instar	Mean and S.E.	Range
Fertilised plant cane		(8 individuals)	
	2	5·1±0·1	5– 6
	3	4·8±0·2	4– 6
	4	5·1±0·3	4– 7
	5	7·5±0·4	6–10
	2–5	22·5±0·9	10–28
Unfertilised ratoon cane		(6 individuals)	
	2	7·3±0·6	6–10
	3	6·5±0·6	5– 9
	4	7·7±0·3	7– 9
	5	12·5±1·6	9–18
	2–5	34·0±1·5	28–37

proved very difficult, only 7, all females, out of 102 nymphs (6·9%), being successfully reared to maturity; on fertilised cane 20 out of 78 (25·6%) reached maturity, with an equal proportion of males and females. Nymphs on unfertilised cane produced much more honeydew per day than those on fertilised cane, suggesting a lack of nutrients in the former that was only partly compensated by greater uptake of sap. Adequate nitrogen is essential for the growth of insects (Wigglesworth, 1965), so that the low nitrogen content of unfertilised cane could be the factor limiting the rate of nymphal development. The slower development of males and females in series III compared with series I–II would be consistent with this view as the nitrogen content at 1·77% was 0·2–0·4% lower than normal for such plants.

The full duration of first-instar nymphs could not be determined from the above experiments. Accordingly, 30 egg-slits were enclosed in cages, and as soon as the nymphs from each slit emerged, all except one were removed. Each of the remaining individuals was examined daily until the first ecdysis. Nineteen were successfully reared to second instar, the average duration being 6·7 ± 0·3 days (range 6–10 days). Average maximum and minimum temperatures in the glasshouse were 90 and 66°F, respectively.

Guagliumi (1953) found instars 1, 2 and 3 to last 6, 7½ and 7 days, respectively, the times of the latter two being more typical of unfertilised host-plants. His instar 4 is not comparable with the true instars 4 and 5.

The adult

Data from fecundity experiments (Metcalfe, unpublished) showed that males lived for about one week and females for up to four weeks (occasionally longer), and confirmed impressions gained in the field. The ratio of males to females in pre-oviposition experiments (Metcalfe, unpublished) was approximately equal, 39:37.

The complete life-cycle therefore takes 6½–7 weeks and theoretically allows seven generations per annum. Indications were that development in the open was a little slower in the cooler conditions of the Mandeville hills than on the sugar estates below. However, such an effect would be slight compared with that of the nutrient status of the host-plant, which in turn is dependent on many climatic and edaphic factors.

Habits

The following account, based on field and glasshouse observations, of the habits of *S. saccharivora* complements those of Ashby (1954), Ballou (1912), Guagliumi (1953, 1962) and Wolcott (1921, 1933).

General

The nymphs hatch through a slit formed near the anterior pole of the egg, and scramble through the wax threads overlying the egg on to the leaf surface. Some are trapped in the wax, particularly under glasshouse conditions where it is not eroded by wind and rain. After hatching the nymphs aggregate on the underside of the lamina, avoiding the midrib and the lamina edges, the more nymphs on a leaf the larger the groups. They are always orientated head-up, the body parallel to the long axis of the leaf, so that those groups on opposite sides of the point of curvature of the leaf face each other. As they grow, the individuals move further apart, their numbers often apparently swollen by the exuviae sticking to the leaf. They move little, and throughout their development may remain on the leaf on which they hatched. However, if death of the leaf intervenes, as may happen in young sugar-cane plants, they move to younger leaves. When disturbed, young nymphs sidle to the other side of the leaf, but old nymphs jump away. They are most easily disturbed in bright midday conditions, and are usually much quieter in the early morning and evening, or when it is windy.

After the final ecdysis the adults may remain on the same leaf, but more often move to younger leaves, the cane 'funnels' formed by the unfurling leaves being preferred. They are particularly active at this stage which might be described as a dispersal phase, during which they readily take to flight and may be carried miles by the wind. Mating occurs on the leaf at any time of the day, but most frequently in the morning. (According to Guagliumi (1953) it occurs only in the evening and at night.) A female may mate more than once, but whether this is obligatory for maximum fertility is not known. Pairs are often seen with the male to one side and a little behind the female; males are more active than females, and more easily disturbed.

Feeding

Nymphs and adults feed on the leaf sap, and the excretory products are in the form of honeydew. Feeding may be on the underside of expanded leaves or on either side of funnel leaves and, judging from the formation of honeydew droplets, is more or less continuous except on the day preceding ecdysis. During feeding, both nymphs and adults are less likely to be disturbed.

The source of the sap taken up by the stylets was determined from sections of leaves on which many nymphs had been feeding. Lengths of leaf were preserved in formalin-acetic-alcohol and de-silicified with hydrofluoric acid, as described by Metcalfe (1960). Transverse sections were cut with a sledge microtome from pieces of lamina held between pith and, on mounting in glycerine, stylet sheaths, the mucilaginous secretion around the stylets that is left in the leaf after feeding, were clearly visible. Definition was improved by staining with methylene blue in glycerine or cotton blue in lactophenol.

Plate XVIII shows the stylet sheaths, each with its characteristic hilt at the leaf surface, penetrating the leaf tissues. Entry is through the cuticle, not through the stomata, and probes are directed, sometimes after one or two trials, towards a vascular bundle. Repeated branching of the sheaths in the large bundle sheath cells suggests

that the latter are an important source of food, as for adults of *Aeneolamia varia saccharina* (Dist.) (Fewkes, 1969), but the phloem is also tapped. No stylets reach the xylem. Phloem sap would be very nutritious, but the food value of bundle sheath cells is unknown.

The effects on the plant are not immediately evident. Significant amounts of sap must be taken up particularly when populations of *S. saccharivora* are large; necrosis of the cortex is slight but some blockage of bundle sheath cells and phloem elements occurs (Plate XVIII, fig. 4). Wilting of heavily infested two- or three-week-old ratoon shoots was seen by the author and has been recorded previously (Hall, 1882*a*; Westwood, 1833), but it is hard to distinguish the effects of drought and of feeding. Puncture points become yellow and then red, but discoloration is so slight as often to pass unnoticed (Ashby, 1954; Guagliumi, 1953); the distinctive phytotoxaemias of other Hemipterous sugar-cane pests such as *Sipha flava* (Forbes) (Metcalfe, 1965) or *Aeneolamia* spp. (Fewkes, 1969) never occur. The saliva, therefore, is presumably non-toxic, and stylet penetration causes only local disruption of tissues, followed by slight secondary infection.

Honeydew is excreted in large quantities and forms a sticky layer on the lower foliage and on the ground. Fifth-instar nymphs and females each produce enough honeydew to block parts of the mesh of experiment cages, but young nymphs do not produce as much. The honeydew becomes infected with a black fungus, *Capnodium* sp., which forms a light-proof layer, thick enough to form a definite crust, on the upper surface of the leaves. This gives cane fields that are heavily infested with *S. saccharivora* a characteristic black appearance, sometimes mistaken for factory soot, and earned the names "sooty mould", "black blast" or "black blight" (Ballou, 1914; Box, 1950). Affected leaves presumably photosynthesise and transpire less, and the senescence of older leaves may be hastened. The brown colour of senescent leaves could, if *S. saccharivora* were present, be mistaken for, but is not, a direct effect of feeding.

Oviposition

Oviposition is invariably on the leaf of the host-plant. In sugar-cane, eggs are inserted in rows of about seven into the midrib (Plate XVII, fig. 1) or, less often, into the thick basal portion of the lamina, with the anterior pole just protruding beyond or flush with the epidermis. Insertion may be from either surface, and eggs inserted into the midrib from below tend to be at right angles to the surface, while those from above and in the lamina lie obliquely. In *Andropogon*, oviposition is in the midrib or leaf sheath, and eggs can be accommodated only if placed obliquely. Within a few days of insertion into sugar-cane, the cortex and parenchyma surrounding the eggs become necrotic, and characteristic red patches are visible through the upper epidermis of the midrib; with heavy infestations the patches may become continuous (Plate XVII, fig. 2). According to Ingram *et al.* (1951) oviposition causes the leaves to wither, but in the author's experience withering is restricted to leaves of stalks suffering from within-stool competition; heavy oviposition in such stalks may hasten the onset of withering and death.

At the start of oviposition the female adopts a head-up position, the body is raised and the saw-like ovipositor swung out ready to cut into the leaf. After penetration (Plate XVII, fig. 4), a vertical sawing motion extends the cut downwards to form a slit between two vascular bundles, and the eggs, usually 5–8, are deposited in a row, each hard against the next. After the ovipositor has been withdrawn, the slit is covered with fluffy wax removed from the valvifers by the hind legs, the whole process taking 15–20 min. Up to three slits are made each day for two to four weeks, the female remaining in much the same position unless disturbed. Slits may be side by side, separated by only one or two vascular bundles, or in line between the same two bundles. In the event of the latter, the eggs of successive slits may be distinguished by a slight difference in the angle of insertion and/or by a gap between two adjacent eggs.

In sugar-cane, the leaves on which the eggs are laid depends on the age of the plant, but the youngest are preferred. On young shoots eggs may be laid on any leaves except the oldest, and on any part of the midrib except the tip. Females in the leaf funnels may oviposit on the surface presented to them, *i.e.*, the upper, but oviposition is rarely on this surface after the leaf has unfurled unless it becomes twisted through 180°. In older plants oviposition occurs first in the unfurled portion (the apical half, excluding the tip) of the youngest leaves, but often continues in the same zone after the whole leaf has unfurled; in heavy infestations oviposition may extend further down the midrib and also take place in the basal part of the lamina of fully developed leaves.

The preference for young leaves as an oviposition site is very marked in the field. Egg-slits may be abundant on young shoots, but rare on mature cane immediately adjacent. In fields of mature cane the preferred sites are side shoots (gourmandisers) on canes with dead or suppressed growing points, and on the late shoots springing from the base of the stool. The latter sometimes wither before the incubation period of the eggs is complete, and the eggs perish. Among canes of subequal height, the less robust are preferred. This preference is undoubtedly due to an attractive feature of the leaves. Its expression in stands of different height and at different heights within a stand shows that it is not a response to light or microclimate. The most plausible explanation is that cutting the egg-slits is easiest in the preferred leaves. An alternative, that the preferred leaves are more nutritious, does not seem tenable as their total nitrogen content, a likely limiting factor, is different (Burr *et al.*, 1957; Farqhar & Lee, 1963; Van Dillewijn, 1952).

Migration

Pre-harvest burning of a sugar-cane field destroys almost the entire population of *S. saccharivora*, but even without burning a harvested field becomes temporarily uninhabitable. Adults may escape to a suitable environment, but eggs become desiccated in the dead trash and nymphs die for want of food. Only a small proportion survives on the few remaining suckers.

Initial infestation of young plant or ratoon cane is by migration of adults from sugar-cane or from wild grasses. Dramatic immigration from other cane fields is a feature of epidemics (Ashby, 1954; Bennett, 1959; Hall, 1882 *a*,*b*; Murray, 1912), and Ashby recorded an increase from 10 to 24 adults/shoot in three days, and populations of over 30 adults/shoot (approximately 2 million/acre) in four-week cane. During the present studies, immigration on to young cane was seen frequently at all times of year. It seems likely therefore that immigration is not solely due to habitat destruction during the harvest period (generally late December to July), as was thought possible by Ashby (1954), but also to the passive dispersal, common to many insect species (Johnson, 1960; Southwood, 1962), of young adults and their preference for young shoots as an oviposition site. Adults often apparently disappear from half-grown or mature cane before oviposition (Metcalfe, unpublished; Ashby, 1954), and where mature cane and young shoots adjoin an outbreak zone, the former remains free of adults while the shoots become densely populated with males and ovipositing females. Outbreaks tend to spread downwind, and strong localised, thermal upcurrents, which often occur over cane fields during the harvest period, may also aid in dispersal. On one occasion adults were seen falling from the sky during a lull in the breeze.

Summary

An account is given of laboratory studies and field observations in Jamaica and British Honduras on the host-plants, life-history and habits of *Saccharosydne saccharivora* (Westw.), a major pest of sugar-cane. The original host-plants of *S. saccharivora* are shown to be two species of grasses, *Andropogon glomeratus* and *A. bicornis*. The immature stages of *S. saccharivora* are described and illustrated; the five nymphal instars may most easily be distinguished by their increasing size, the differentiation of the wing buds and the increasing spinosity of the metathoracic tibia and tarsus. Daily records of

individuals of *S. saccharivora* show the duration of the different stages on fertilised plant cane at *c.* 80°F to be as follows: egg, 15–19 days; instar 1, 6–7 days; instars 2, 3 and 4, each 4–5 days; instar 5, 6–7 days; adult male, about one week; adult female, up to four weeks. The complete life-cycle took $6\frac{1}{2}$–7 weeks, but was slower on unfertilised ratoon cane. In describing the habits of *S. saccharivora*, particular attention is given to feeding (feeding probes reach the bundle sheath cells and phloem of the lamina), oviposition (young leaves are the preferred oviposition site) and migration (immigration of adults on to young cane occurred at all times of year).

Acknowledgements

To Mr. R. F. Innes (lately Director), Mr. T. Chinloy (Director) and to my other colleagues at the Research Department of the Sugar Manufacturers' Association (of Jamaica) Ltd. I owe a debt of gratitude for their encouragement, interest and co-operation at all times. The work would never have been completed but for the patience, perseverance and willingness of my technical assistants Mr. K. M. Baker and Mr. L. V. Williams.

Apart from sugar estates in Jamaica and British Honduras, many organisations including the Jamaica Institute, the British Museum (Natural History), the Joddrell Laboratory, Royal Botanic Gardens, Kew and the University College of North Wales provided technical services or facilities. The photographs on Plate XVIII were processed by Mr. T. Harwood of the Joddrell Laboratory.

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(*Received 29 July 1969*)

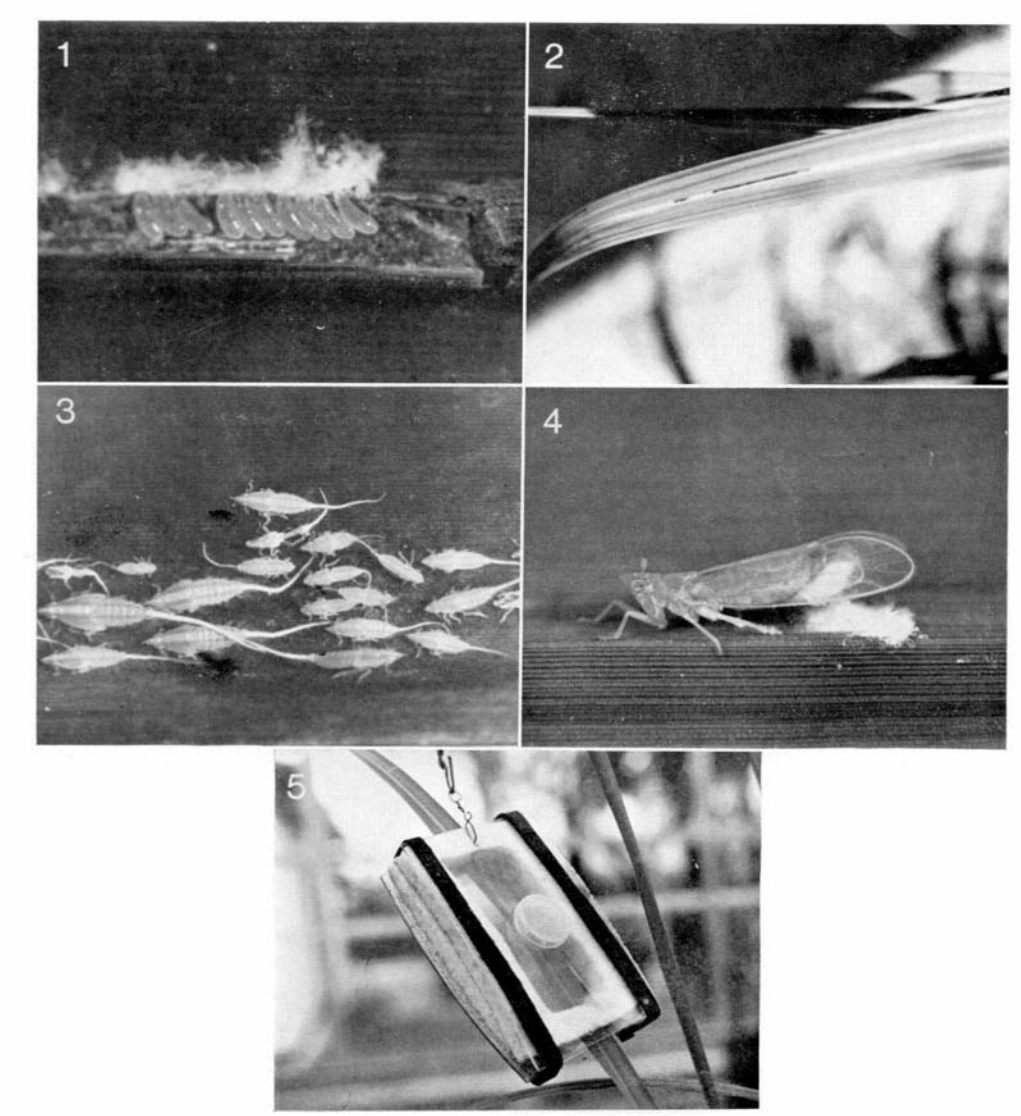

FIG. 1–4. *S. saccharivora.* 1, part of a sugar-cane leaf with the midrib opened to show eggs *in situ*, ×10; 2, necrosis of midrib of sugar-cane leaf due to oviposition damage; 3, nymphs of instars 1–5 on sugar-cane, ×4½; 4, female ovipositing, ×7. FIG. 5. Observation cage for individual *S. saccharivora.*

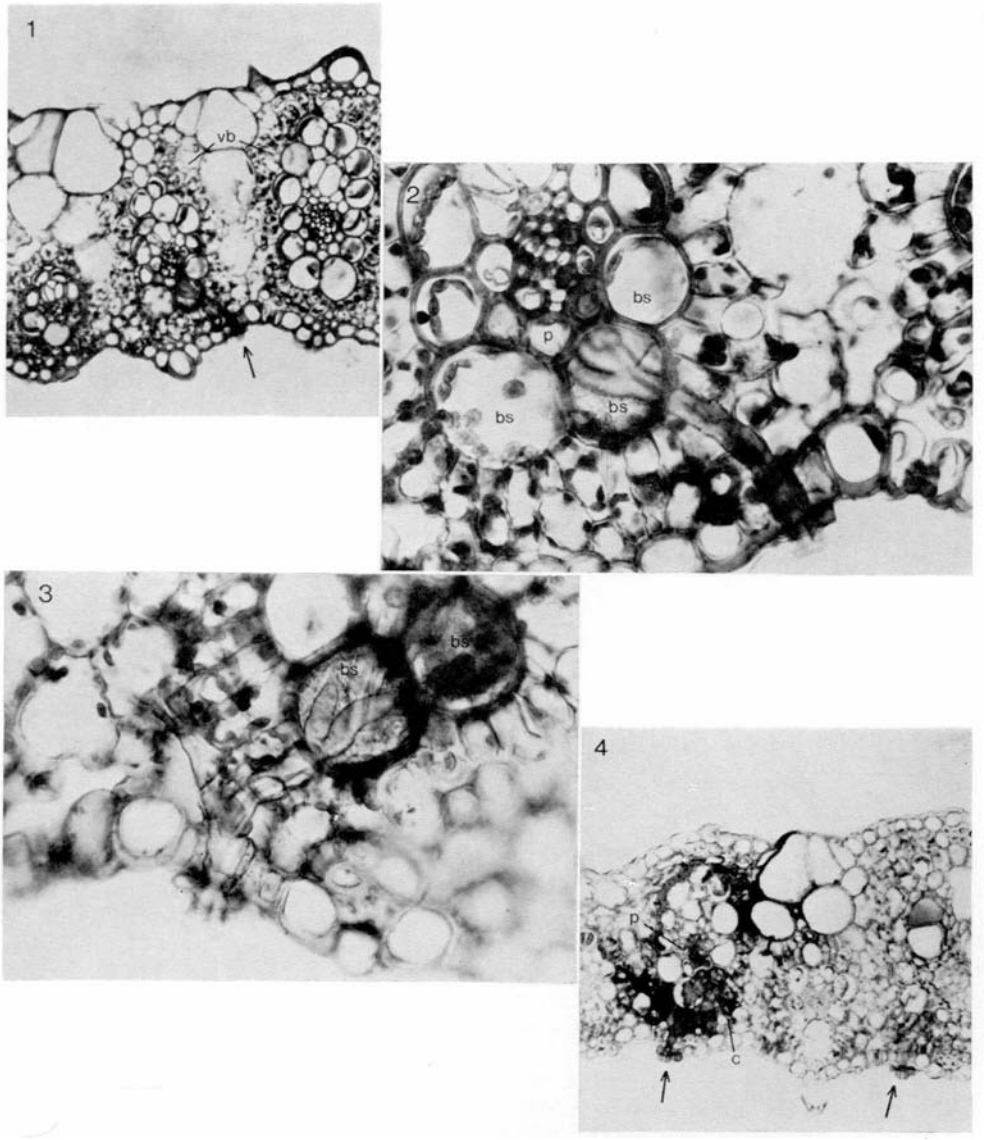

FIG. 1–4. Feeding probes of nymphs of *S. saccharivora* in sugar-cane leaves. 1, probe (shown by arrow) leading directly to a vascular bundle (vb), ×160; 2, the same probe branching in a bundle sheath cell (bs) and penetrating the phloem (p) which is occluded, ×640; 3, probe branching repeatedly in bundle sheath cells (bs), ×640; 4, probes (shown by arrows) accompanied by necrosis of the phloem (p) and cortex (c), ×160.