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Changes of electric patterns related to feeding in a mesophyll feeding leafhopper *Zyginidia scutellaris*

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Abstract

Zyginidia scutellaris H.-S. (Cicadellidae, Typhlocybinae) is a leafhopper feeding on corn leaves. As most Typhlocybinae, it feeds from parenchymal cells, producing typical white spots on infested leaves. *Z. scutellaris* feeding activities exhibit different waveforms that are tentatively associated with penetration, salivation and active pumping. During ingestion, patterns are composed of a succession of spikes, probably reflecting alimentary and/or salivary pump activity. Labium twisting movements are correlated with specific transition patterns. Alimentation sequences can last some hours. This suggests that feeding occurs also from fluids flowing into the damaged plant tissue area. As mesophyll-feeding seems to be simpler than sap-feeding, this model may help to further elucidate waveforms recorded with this method on other insects.

Introduction

Xylem- and phloem-feeding insects are of great economical importance due to their ability to transmit various phytopathogens like viruses or mycoplasmalike organisms. Investigations on the different mechanisms of penetration, salivation and target tissue localisation can give some guidelines to protect plants against these insects and the transmitted diseases as transmission occurs during feeding or even during a single probing. Therefore actographic techniques seem to be promising insofar they can monitor precisely the different phases of the alimentation and give informations about the type of plant tissues exploited by the insects.

The first actograph proposed by McLean & Kinsey (1964, 1965) gave promising results and was successfully employed to monitor feeding activities of haematophagous insects (Kashin & Wakeley, 1965; Smith & Friend, 1970; Sweatman *et al.*, 1976) and phytophagous insects (Crane, 1970; Chang, 1978; Chang *et al.*, 1978; Kawabe & McLean, 1978, 1980). The principle of the method is simple: a voltage source is connected to the feeding substrate and the insect, attached to a flexible electrode, closes the circuit during stylets penetration. Some controversy still exists on the nature of the voltage source: some researchers use a simple DC voltage to monitor resistance variations and electromotive forces (Schaefers, 1966; Shanks & Chase, 1976; Tjallingii, 1978), others use an AC voltage source arguing that constant current may harm the cell membranes (McLean & Weigt, 1968; McLean, 1977).

Many studies were attempted to correlate the electrical waveforms recorded to the feeding activities. These correlations were carried out by histological techniques to demonstrate stylet location (McLean & Kinsey, 1967; Crane, 1970; Nault & Styer, 1972; Chang, 1978; Kawabe & McLean, 1980; Kimmins & Tjallingii, 1985), observation of stylets movements during feeding behind a Parafilm (R) membrane (McLean & Kinsey, 1964, 1965; Crane, 1970; Friend & Smith, 1971; Tjallingii, 1978; Kawabe & McLean, 1978, 1980), or chemical analysis of frass (Kawabe & McLean, 1980) and radioactive labelling of saliva or ingested fluids (Tjallingii, 1978).

These authors agree to recognize mainly two

phases in the feeding process: salivation during initial penetration and salivary sheath formation which is characterized by a succession of large spikes, and ingestion with smoother oscillations. This last phase is sometimes preceded by the occurrence of patterns (X and Y) that McLean and Kinsey (1967) claimed to take place before ingestion from conducting vessels.

Zyginidia scutellaris can occasionally be found in corn fields in France. This insect is considered as a mesophyll-feeder, as it produces typical whitish stippling on the leaves (Waloff, 1980). Also it is not proved that mesophyll-feeders do not feed at all in vascular bundles, they exhibit strong differences with sap-feeders in their anatomy (stylets length, no filter chamber in the midgut) as well in their behaviour (stylet sheath restricted to epidermal cells, dark-colored fecal material). The feeding process of a mesophyll-feeder is well described by Pollard (1968) in *Eupteryx melissae* on sage: after an initial penetration with formation of a short salivary sheath, the maxillary stylets are subsequently penetrating mesophyll cells and emptying their content.

The study of a mesophyll feeder like *Z. scutellaris* is of particular interest in that it is the first time that electric penetration graphs (EPG) are presented for this particular group of insects and it may provide a useful comparison to feeding activities recorded in sap-feeders. EPG records are first analysed in order to classify the different waveforms observed, and then tentatively interpreted in terms of salivation-ingestion sequences on the basis of behavioural observations and duration of the insertion of the stylets at the same site.

Materials and methods

Adult females were obtained from a colony maintained on corn (*Zea mays*, var. Limagrain LG11, France) in a greenhouse. Periodically new adults captured in the vicinity were introduced in the cages to maintain genetic variation as much as possible. They were tested on freshly cut young corn leaves (var. LG11) or wheat leaves (var. Top).

A preliminary study was conducted on *Z. scutellaris* males and females allowed to feed *ad libitum* on cut corn leaves to study initial penetration sites. Feeding sites were located afterwards by staining salivary sheath with lactophenol-fuchsin (Waters, 1977).

The recording apparatus was built with common IC circuits (Fig. 1). A function generator (XR 2206, Exar, USA) delivered a sinusoid voltage of 500 mV root-mean-square (rms) under a 2 kHz frequency. To cope with the very high impedance of the signal passing through the insect, a biFET operational amplifier (TL 081, Texas Instruments, France) was mounted in an inverting configuration with a variable gain, usually ten (input impedance: 10 MOhms). As the signal delivered by the amplifier was modulated in amplitude, a true rms converter (AD 536, Analog Devices, USA; time constant: 2.5 ms) was used to convert AC symetrical amplitudes into DC variations that could be observed either on an oscilloscope or permanently recorded on paper (Graphispot, Sefram Paris, France). During experiments it was useful to hear the signal by converting DC variations into frequencies in the range of 10 Hz – 20 kHz with a voltage-frequency converter chip (9400, Teledyne Semiconductor, USA) driving a 0.2 W loudspeaker. Permanent records of the signals were made on common magnetic tapes before true rms conversion as the 2kHz frequency falls into the middle of the response spectrum of audio tapes.

Z. scutellaris females (2.8 – 3.2 mm long) were immobilized between two streched Parafilm (R) membranes (Caudwell *et al.*, 1977). A thin tungsten wire (diameter 11 μm) was then carefully attached to the thorax or the head with a drop of silver paint (n° 200, Demetron, Hanau, RDA). The other side of the wire was connected to a shielded cable with silver paint. Such animals were placed in a small Faraday cage enclosing an excised leave placed in a slightly saline solution. A hole in the top cover of the cage allowed a direct examination of the insects under the dissecting microscope. Feeding activities of males could not succesfully be recorded due to their small size (2.0 – 2.5 mm) and their mobility.

Recordings were mainly analysed by visual examination of paper recordings in order to identify waveforms and compute sequences duration. Some selected records were submitted to Fourier analysis (FFT) after digitization (12 bits resolution, sampling frequency: 500 Hz) in order to check if alimentation sequences could be separated in the frequency domain.

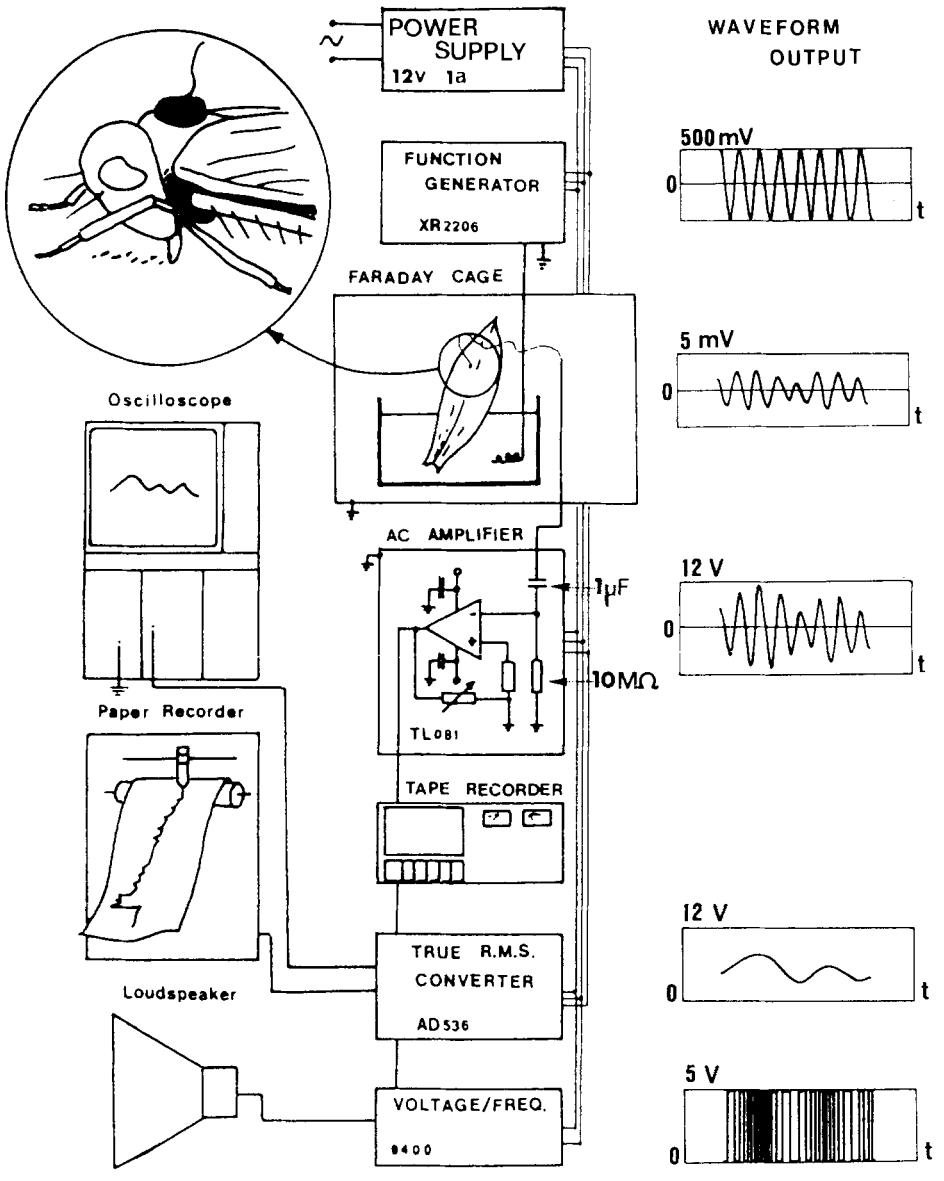


Fig. 1. General diagram of the experimental setup. See text for explanations.

Results

Labial imprints location. The lactophenol-fuchsin technique allows a precise location of the initial penetration point of the stylets. *Z. scutellaris* male and female preferably select surface grooves in the leaves. Stomatal guard cells, junctions between two or three cells and stomatal aperture represents respectively 58%, 21% and 17% of the observed sites of perforation (408 feeding sites noted). This strongly suggests that exploratory dipping on the surface of the leaves involves tactile stimuli and that a groove in the surface is necessary for the insertion of mandibular stylets.

Behavioural observations. High magnification examination of the insect feeding during recordings give little information on the correlation with observed EPG patterns. However, we can point out following: (a) exploratory dipping with the apex of

the labium and saliva excretion and reingestion occur before penetration. This behaviour can be observed even on a glass substrate; –(b) stylets are inserted perpendicular to the leaf surface. The leafhopper presses its labium against the substrate, and bends its body down, leaving only the hind legs on the leaf, i.e. lifting fore- and middle legs; –(c) before they choose a site to stay for a long time, females often insert only briefly their stylets in the leaf on many contiguous places: we will call probing these short sequences; –(d) penetration can last many hours at the same site without any stylet retraction (6 h max.): these long sequences are named here alimentation. If females are not disturbed, subsequent stylet penetration often occur near the first puncture; –(e) during alimentation sequences, leafhoppers may move their labium up and down (leaving contact with substrate but the stylets) and even rotate it around the stylets for 90°. We can also observe general body movements such as head up and down bending with the labium remaining in position, or droplet excreta.

Main characteristics of the recordings. Examination of the records reveals following patterns: –(1) When the insect rests on a connected leaf, a small voltage can be observed, reflecting current flowing through tarsi (Fig. 2a,b). –(2) Typical exploratory dipping of the surface with the apex of the labium and subsequent surface saliva excretion-reingestion produce small deviation patterns (Fig. 2b, arrows). –(3) Penetration of the stylets always produces very high amplitude spikes (pattern (A): Figs 2c to 2e): this may correspond to the formation of the salivary sheath. –(4) Probing sequences are characterized by high amplitude spikes without a clear occurrence of other patterns (Fig. 2c, 2d): total duration of probing: 4 to 230 s. Retraction of the stylets is immediately followed by a drop of the voltage. Prolonged probing can occur with small periods of restricted amplitude (R) during 20–30 s (Fig. 2e). –(5) Alimentation sequences always begin with pattern (A) which is followed by more quiet periods and smoother spikes (s) (Fig. 3). (A) patterns characterize initial penetration and sometimes occur during alimentation (Fig. 3c) or just before stylets retraction. This initial (A) phase can last 14 s to 60 s. –(6) Ingestion presumably mainly occurs during subsequent (B) phase, which is commonly composed of a succession of small spikes (s) (Figs. 3 and 4). Periods of reduced amplitude patterns (R) are scarce (Fig. 3b). Just after initial phase (A), (s) spikes occur at a frequency of 0.5 Hz but then become progressively more spaced (0.20–0.02 Hz) (Fig. 4a to 4d). –(7) Transition patterns (T: Fig. 5) separate subsequent ingestion phases defined by a progressive slowing of the occurrence of (s) patterns. Two kinds of transitions

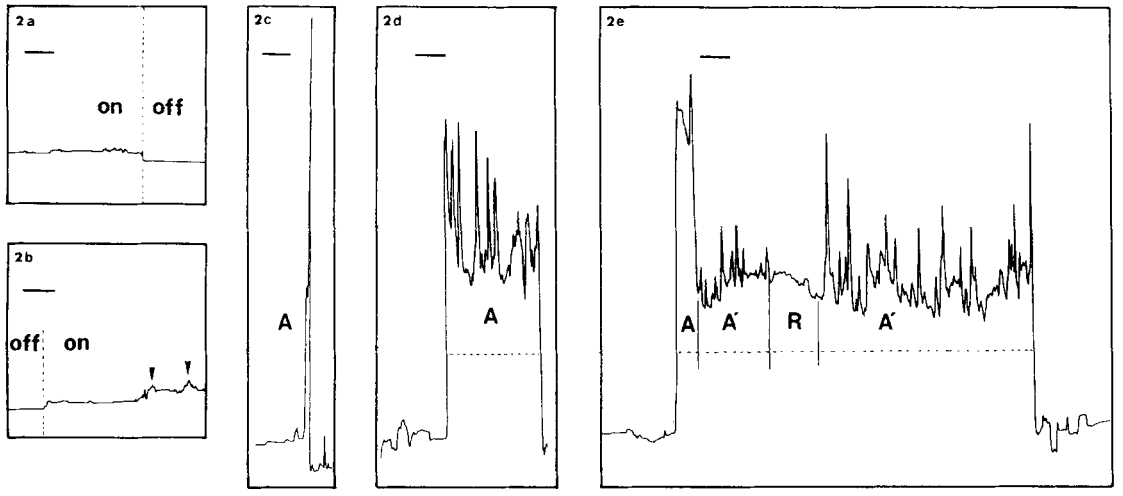


Fig. 2. (a,b): Ambulatory movements or rest on a leave produces a small voltage. Arrows in (2b) indicate labial dipping. – (2c–e): probing behavior. Probing is mainly characterized by the occurrence of high amplitude (A and A') patterns without installation of (s) waveforms. Probing can last from a few s (c,d) to several minutes (e) during which an intercalary period of reduced amplitude (R pattern) can be observed. Horizontal bar: 20 s in all figures.

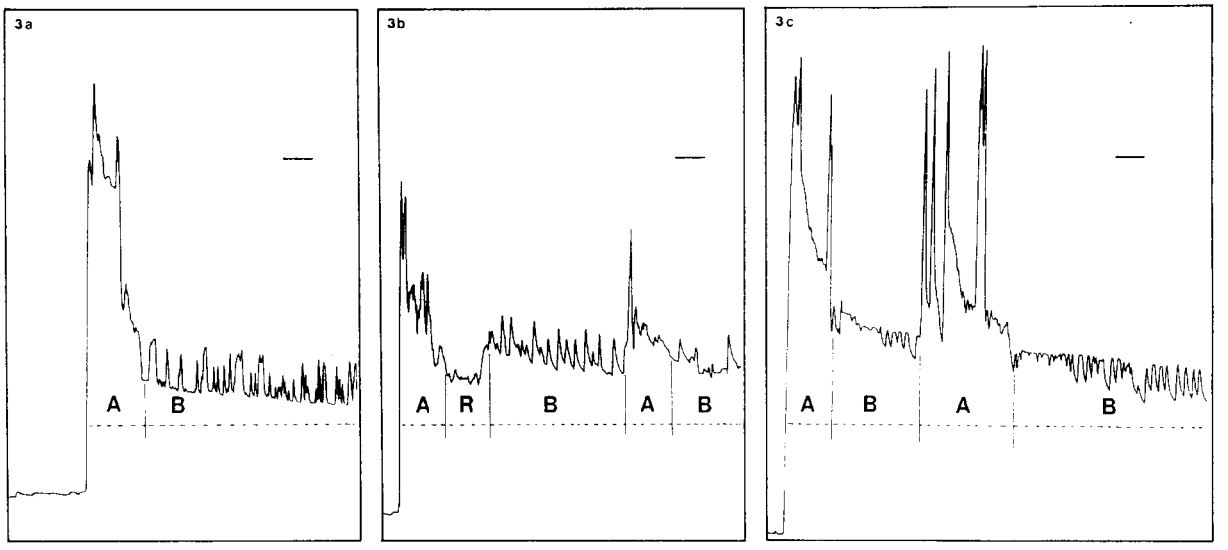
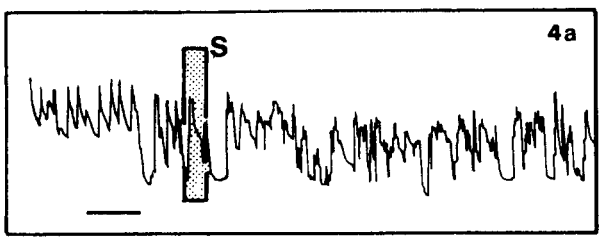
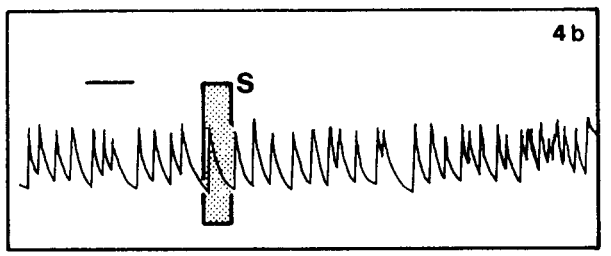
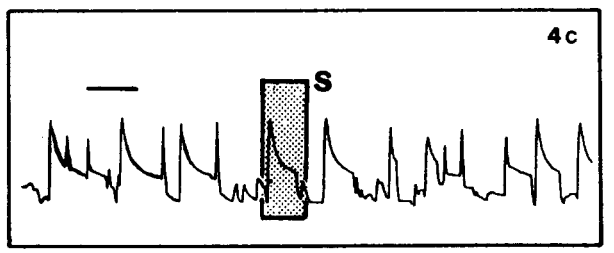


Fig. 3. Initial patterns (A) recorded on suitable host. Initial salivation patterns mainly characterized by the occurrence of very high amplitude spikes. On a suitable substrate, they are often directly followed by (s) patterns and sometimes are repeated once (b,c). On some records appears an intercalary period of reduced amplitude (R).







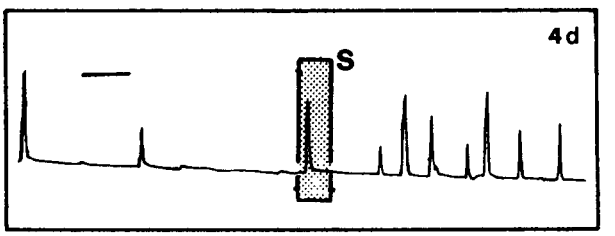


Fig. 4. Alimentation sequences (B) and (s) waves. The most stable pattern occurring during sustained alimentation. Composed of successive spikes which frequency and DC-level progressively decrease during alimentation (a to d). Spikes (s) probably reflect salivary and alimentary pump activity.

occur, T1 with no apparent labium movements and only (s) patterns of greater amplitude and frequency (Fig. 5a) and T2 during which twisting of the labium can be observed (Fig. 5b to 5d: arrows). T2 patterns include an intercalary (R) period of variable duration (Fig. 5b to 5d).

Duration of feeding sequences. When we only examine the duration of the stylets insertion (Fig. 6a), plotting an histogram of these intervals shows two major modes: short sequences of 1–30 s and longer sequences with a sharp maximum between 3–7 min. and a long tail towards longer durations (up to 6 hours): these two modes correspond with probing and alimentation. The

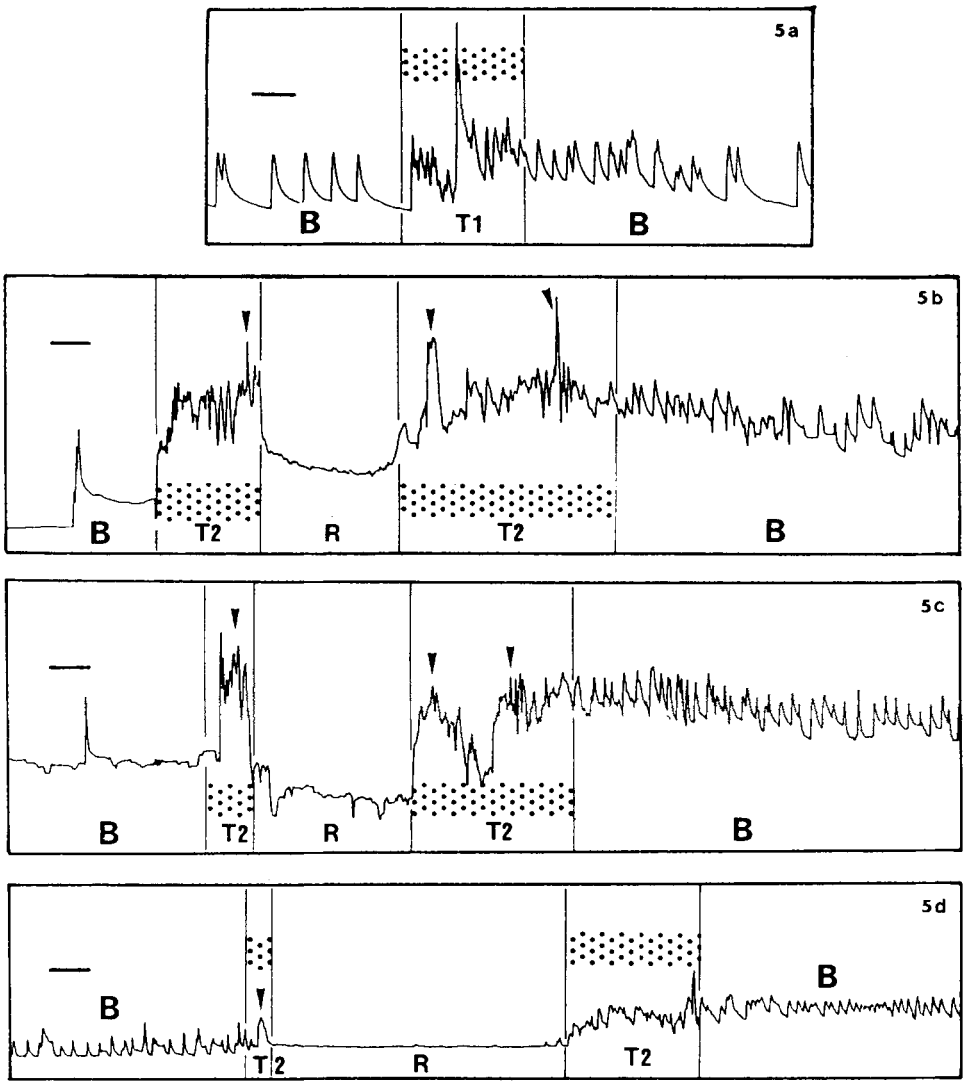


Fig. 5. Transition patterns occurring between ingestion periods. T1 (a) characterized by higher salivation-like spikes (A'), separating two ingestion sequences and followed by an acceleration of the (s) waves. – T2 (b to d) complex waveforms correlated with labium movements (arrows) and a variable intercalary (R) period, and also followed by an acceleration of (s) patterns.

corresponding histogram of the time intervals spent without stylet insertion presents a similar distribution but with three maxima at 5–10 s, 46 s–2 min. and 15–30 min.

Analysis of the same records by the occurrence of the patterns defined as above, shows that even sequences of the same duration can be further differenciated by the occurrence of different patterns, i.e. probing (only (A) pattern), probing-salivation ((A) and (s) patterns) and alimentation ((A), (s) and (T) patterns) (Fig. 6b).

Fourier analysis of the recordings. Spectral analysis of time series can give a better representation of the frequency components describing the recordings. Selected records were submitted to Fourier analysis (FFT) in order to check if (A) and (B) sequences could be clearly separated on this basis. Unexpectedly, (A) and (B) patterns differ only slightly in their main spectral energy, situated between 60 and 75 Hz with a clear spike around 50 Hz. Although 50 Hz is mainly due to line noise pickup, the use of a digital notch filter centered at 50 Hz does not re-

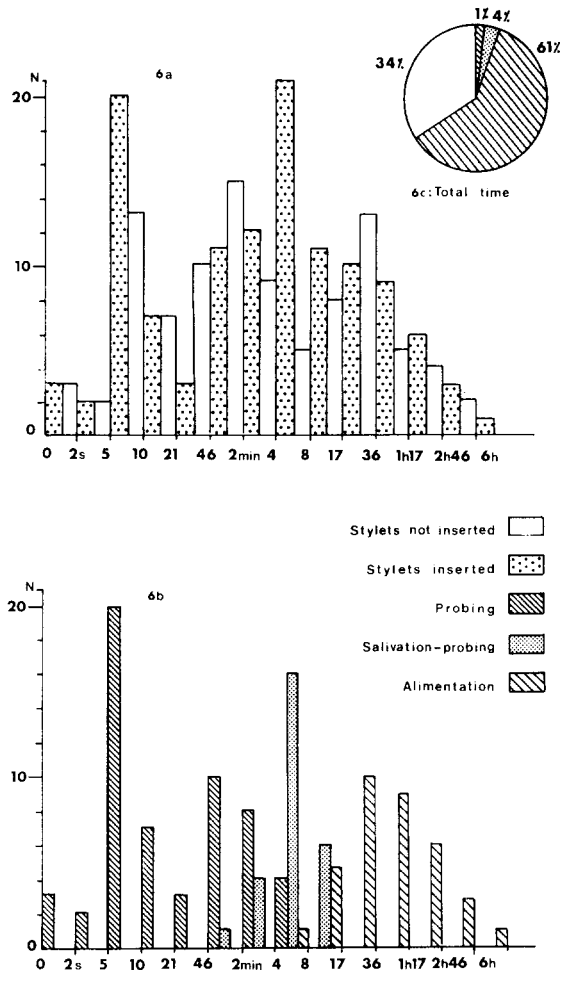


Fig. 6. Duration of the sequences: (a) compares time spent with stylets inserted versus time spent walking or resting on leave. Horizontal axis: logarithmic time scale (Log(s)); vertical axis: no. occurrences observed. – (b) compares no. occurrences of sequences separated by presence of selected waveforms i.e. probing sequences (only A waves), probing-salivation sequences (A and A' waves) and typical alimentation sequences (with A, s and T waves). – Also probing and probing-salivation sequences are numerous, they represent only a small part of total time spent in the different activities (pie chart: Fig. 6c).

move all frequency components: an important spectral component still remains at 48 Hz, which could have a biological origin. However, it seems that spectral components exhibit a tendency to shift towards higher frequency during sustained alimentation. Whether these spectral components represent muscular activity or reflect hidden characteristics of the recordings masqued by lowpass filtering of the experimental setup, remains unanswered.

Corn and wheat comparison. As the analysis of the recordings does not allow clear identification of salivation and ingestion patterns, the only possible comparisons rely upon duration of penetrations and number of probings. On young corn leaves, *Z. scutellaris* females exhibit few probings and maintain alimentation at the same site many hours. (s) patterns occur rapidly and their frequency can decrease from 0.25 Hz to 0.06 Hz. On old corn leaves and wheat leaves, probings are numerous and sustained alimentation is shorter. (s) patterns seem to be more rapid (0.25–0.17 Hz) perhaps indicating difficulties to ingest.

Discussion

Electrical recording of plant sucking insects is an easy and convenient technique that may be applied to a wide range of insects. As can be judged by the great variety of recording devices, the experimental setup is not very critical but comparison between experiences made on different insects is difficult due to the lack of any standardisation in the experimental setups and expression of results. Analysis of the recordings are generally made in terms of salivation and ingestion patterns, with a special attention devoted to specific patterns occurring during ingestion, like X and Y (McLean & Kinsey, 1967) or Sl (Kawabe & McLean, 1980). However despite many strategies were employed to correlate observed waveforms with stylet locations within the tissues (McLean & Kinsey, 1965, 1967; Chang, 1978; Kimmins & Tjallingii, 1986; Kawabe & McLean, 1980; Kawabe *et al.*, 1980; Mentink *et al.*, 1984), no definitive correlation exists between recordings and activities of salivary and alimentary pump, or the different kinds of salivary excretions. Moreover most studies were devoted to the analysis of sap feeders and were related to the identification penetration and ingestion from conducting vessels.

In this work, we attempted to study the electric activities associated with feeding of a mesophyll-feeder, *Z. scutellaris*. A careful examination of the recordings allows to discriminate between different patterns, analogous to initial salivation and subsequent ingestion periods. Ingestion periods seem to be very different from ingestion patterns recorded from sap-feeders, generally described as smooth curves (McLean & Kinsey, 1965, 1967; Nielson &

Don, 1974; Kawabe & McLean, 1980). Mesophyll-feeders like *Z. scutellaris*, introduce their maxillary stylets into cells and suck their content in a sequential fashion (Pollard, 1968). It should be noted that even phloem-feeders like *Perkinsiella saccharicida* Kirkaldy can exhibit similar (s) waveforms when ingesting in the parenchyma (Chang, 1978). Thus the regular and consistent (s) patterns recorded in *Z. scutellaris* females may either represent regular succession of salivation-ingestion sequences and/or cibarial activity. Modifications of the experimental setup are needed to further elucidate this point. But we must point out that the feeding process in *Z. scutellaris* may be more complex than simply penetrating and emptying out parenchymal cells: as alimentation sequences may last some hours and as maxillary stylets are only 300 μm long (Marion-Poll, in litt.) it seems likely that feeding occurs also from fluids flowing into the damaged tissue area.

As far as we know, the only published recording of an 'unidentified Typhlocybinae' have been reported by Port in Waloff (1980). The recording presents successive salivation and ingestion phases without the spiky pattern that we found in this study. This difference may arise from three different reasons. First, differences in the experimental setup and gain adjustment of the amplification section can alter spikes. Secondly, Typhlocybinae are not always mesophyll feeders: some are reported to feed in the phloem like *Empoasca fabae* Harris or *E. sakaii* Dworakowska (Smith & Poos, 1931; Naito, 1977). Third, we noted that females and males exhibit different feeding behaviours, mainly in the duration of the alimentation at the same site: these differences could explain the disparity with our recordings.

Electrical recordings of *Z. scutellaris* females confirm observations of feeding behaviour and plant symptoms. Females generally remain for a long time at the same place with their stylets in the plant, and move only a small distance from the first probe thus producing white stripes on the leaves. They apparently insert their stylets intercellularly, with a preference towards stomatal guard cells, intercellular junctions and even stomatal aperture, unlike another mesophyll-feeder, *Eupteryx melissae* Curtis (Pollard, 1968). Preliminary comparisons between young and old corn leaves or wheat seems to indicate a difference of palatability between these hosts. It remains to be confirmed if this difference, demonstrated by previous studies in greenhouse by Caruhel (1978), remains true in the field.

It should be stressed that *Z. scutellaris* has a very active labium during feeding. Twisting movements and up and down bending occur frequently during ingestion patterns. These active movements could play a role in the directional control of the stylets within the plant, by labial clamping of the stylets. This mechanism has been observed in *Eupteryx melissae* (Cicadellidae) and other Hemiptera like psyllids (Pollard, 1969). We provide evidence that these labial rotations are correlated with specific patterns in the recordings.

However, despite that EPG can be used to analyse suitability of an host or to correlate patterns with particular stylets locations, the physiological origin of the complex patterns observed is unknown. It is generally assumed that the origin of the signal arise from passive modifications of the impedance of insect-plant junction, considered as an high impedance variable resistance (McLean & Weigt, 1968). It should be stressed that with blood-feeding insects like *Rhodnius prolixus*, alimentary activities can be recorded even without any current or voltage source (Smith, 1979) and may either represent 'impedance changes in association with a voltage source such as electrode junction potential', or 'current due to the activity of the pump muscle'.

We suggest that the use of either a voltage-source/current-to-voltage amplifier or a current-source/voltage follower configuration could help to demonstrate if active processes are superimposed on passive impedance variations. An alternative indirect method is provided by changing the input impedance of the preamplifier as described by Tjallingii (1985a,b): he demonstrated with this method that EPG signal is composed of resistance variations and electromotive forces. These forces may represent plant cell injury potentials as defined by Goldsworthy (1983).

Résumé

Activités électriques liées a l'alimentation dans le mésophylle des feuilles chez un auchenorrhynche, Zyginidia scutellaris

Zyginidia scutellaris (Homoptera, Cicadellidae, Typhlocybinae) s'alimente principalement sur les

graminées, en particulier le maïs. Comme beaucoup de Typhlocybinae, il s'alimente dans le mésophylle des feuilles en vidant le contenu des cellules de l'épiderme, provoquant des stries blanches typiques. L'observation des enregistrements permet de différencier une phase initiale de pénétration caractérisée par une succession de pics de grande amplitude, et des séquences successives de pics de moindre amplitude probablement liés à l'alimentation. Ces tracés permettent également de distinguer des piqûres d'essai (quelques minutes) et des piqûres d'alimentation de longue durée (jusqu'à cinq heures). L'observation simultanée des mouvements des pièces buccales externes comme le labium montre que les tracés peuvent être corrélés aux mouvements des pièces buccales et probablement à l'activité des pompes alimentaires et salivaires. La durée des séquences d'alimentation suggère que l'alimentation consiste non seulement à vider les cellules du mésophylle, mais aussi à aspirer les liquides envahissant la zone de parenchyme détruite. L'origine des signaux enregistrés par cette technique est discutée.

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