**RESEARCH**

# Probing Behavior of *Empoasca vitis* (Homoptera: Cicadellidae) on Resistant and Susceptible Cultivars of Tea Plants

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**ABSTRACT.** Feeding activities of the tea green leafhopper, *Empoasca vitis* (Gothe) (Homoptera: Cicadellidae), on resistant and susceptible cultivars of tea plants (Camellia sinensis L.) were recorded and analyzed using the direct current electrical penetration graph (EPG) system. Six distinct EPG waveforms characterizing the feeding behavior of the tea green leafhopper, categorized as waveforms A, C, E, S, F, and R, were obtained during the investigation. Duration of passive ingestion, possibly of phloem (E), was the longest among all the probing waveforms on susceptible cultivars, whereas durations of the salivation (S) waveform and stylet work waveform (F) became longer on resistant cultivars. The durations of waveforms S and F on the resistant cultivar *Jiandecha* were slightly longer than those on the less resistant cultivar *Yunguidaye*, and both were significantly longer than those on the susceptible cultivars *Hangzhoudaye* and *Zhushan-1*. Waveform E was shorter on the resistant cultivar *Jiandecha* than on the less resistant cultivars *Yunguidaye* and was significantly shorter than on the susceptible cultivars (*Hangzhoudaye* and *Zhushan-1*). It is suggested that E, S, and F are the important waveforms related to leafhopper feeding behavior and tea plant resistance. Based on the results, the resistance levels of tea cultivars against the tea leafhopper can be evaluated quickly by direct current EPG.

**Key Words**: DC-EPG, tea green leafhopper, feeding behavior, tea plant, waveform

Tea is a major crop in the southern China, and top-grade teas are mostly processed from the young shoots of the tea plants (Han and Chen 2002). The tea green leafhopper *Empoasca vitis* (Gothe), one of the most serious tea plant (*Camellia sinensis* L.) pests, occurs throughout the Chinese tea growing areas. The leafhoppers pierce into and suck the sap from tender tea shoots, lay eggs into the tender stems, resulting in significant losses in tea yield and deterioration in quality. Over the past 30 years, the main control measures for the leafhopper have been spraying insecticides, which of course have obvious drawbacks like insecticide residues, resistance, and killing of natural enemies. However, some tea cultivars and individual clones show obvious resistance to the leafhoppers (Hong et al. 1997, Zeng et al. 2001, Hu et al. 2003), which might lead to a better alternative to the insecticides. Identification of a highly resistant plant species or cultivar is a complex and time-consuming process, and therefore, quicker and more reliable techniques are needed.

The electrical penetration graph (EPG) technique, originally developed to study feeding behavior of aphids by McLean and Kinsey (1964) using an alternating current (AC) circuit, was later modified by Tjallingii (1978) using a direct current (DC) circuit. EPG techniques were also used to investigate the stylet penetration activities of other Hemipteran insects (Backus 1994), such as leafhoppers (Crane 1970, Triplehorn et al. 1984, Rapusas and Heinrichs 1990, Lett et al. 2001). The initial recording of EPGs on leafhoppers revealed that feeding patterns and waveform types were similar to those recorded from the aphids; therefore, some of the EPG terminologies and definitions for aphids also apply to certain leafhopper species (Lett et al. 2001). Leafhoppers are divided into two groups based on their feeding patterns (during EPG), i.e., A sheath-feeding group that mainly ingests from vascular cells, and a cell-rupture-feeding group that ingests from either vascular or nonvascular tissues (Wayadande 1994, Backus et al. 2005). The cell-rupture feeders are in the large leafhopper subfamily

Typhlocybinae, which include the genus *Empoasca*, whereas the Cicadellidae and Delphacidae are considered to be vascular feeders (Wayadande 1994, Backus et al. 2005). Vascular-feeding leafhoppers may target xylem, phloem, and nonsieve elements as their preferred ingestion sites, although individual species usually do not exhibit all three types (Heinrichs and Heinrichs 1990, Wayadande and Nault 1993). Cell-rupture feeders may target mesophyll tissues (in which case, the plant damage is firmed stippling) or phloem tissues (Backus et al. 2005). *E. vitis* damage to tea is hopperburn (Jin et al. 2012). The objectives of this study were to apply these principles to *E. vitis* EPG by 1) physically characterizing tea green leafhopper feeding waveforms, 2) considering all previous EPG studies of leafhoppers' feeding, especially *Empoasca* spp., to suggest biological meanings of waveforms, such as ingestion, laceration or salivation, and 3) quantitatively comparing EPG recordings from *E. vitis* feeding on resistant and susceptible tea cultivars. Our results will provide important background information for further studies on host plant resistance to tea green leafhopper feeding, as well as co-evolution between the tea green leafhopper and its host plants.

## Materials and Methods

**Insects and Plant Materials.** Third instar nymphs of the tea green leafhopper collected from tea gardens of the Tea Research Institute of Chinese Academy of Agricultural Sciences were used in the EPG study. Four tea cultivars (1-yr-old seedlings in pots) with different resistance levels to the leafhopper were chosen for the feeding tests. Cultivars *Zhushan-1* and *Hangzhoudaye* were considered to be susceptible, whereas cultivars *Yunguidaye* and *Jiandecha* were medium resistant and resistant, respectively, according to Hong et al. (1997). In addition, Hu et al. (2003) reported that fecundity of the tea green leafhopper was lower on resistant varieties.

**EPG Recording.** Feeding behaviors of the tea green leafhopper were electronically monitored using a DC-EPG system (Wageningen

University, The Netherlands) with a $10^9$ $\Omega$ input resistance (Tjallingii 1988) and a gain of 50–100 ×. The output signals from the EPG were recorded with a PC computer using a DI-710 analogue-to-digital (A–D) board and a WINDAQ software (both from Dataq Instruments, Akron, OH), which converted the signals of the eight channels into digital data. The data were acquired at 100-Hz sample frequencies, stored on a hard drive and simultaneously displayed on a screen at intervals of 10 s. The electrical signals produced by the probing activities of the leafhoppers were analyzed using the STYLET 3.8 acquisition software (Tjallingii and Hogen 1993). The DC substrate voltage was initially set at 30 mV and then adjusted to fit the +5 V to −5 V range. Experiments were carried out at 21–32°C, 80–83% relative humidity, and 3,200–3,600 lux.

Live leafhoppers were placed on ice for 10−20 s. A gold wire (2−3 cm, Ø 20 µm) was then fixed on the dorsum of each leafhopper with water-based silver paint. After wiring, the leafhoppers were starved for 2 h, and then each connected to an amplifier before being placed on the backside of the first tea leaf. The probing behavior was recorded simultaneously on four seedlings with only one insect on each plant for 5 h, and at least 10 replicates per cultivar were obtained. Thus, a total of 40 insects were recorded per cultivar.

**Waveform Identification and Terminology.** Different EPG waveforms were identified and separated based on their unique characteristics and differences in duration, voltage level, relative amplitude, and electrical origin according to Janssen et al. (1989). Waveform terminology used herein matches that used by Miao and Han (2007). A more recent paper (Jin et al. 2012) introduced new waveform names for their study correlating *E. vitis* DC EPG waveforms during feeding on susceptible tea leaves and in viscous and liquid artificial diets. Both studies identified and characterized the same waveforms but in usefully complementary ways. The present article's waveform A is the same as waveform E1 from Jin et al. (2012). Likewise, the present E matches their E2, C matches their E3, F matches their E4, R matches their E5, and S matches their E6.

**Waveform Characterization and Statistical Analysis.** The fast Fourier transform (FFT) of waveforms were calculated and illustrated using the STYLET 3.8 acquisition software (Tjallingii and Hogen 1993). Numbers and durations of six waveforms during 5 h stylet probing of the tea green leafhopper on four tea plant cultivars were counted manually using the method of Backus et al. (2007). The means of EPG variables were compared by one-way analysis of variance followed by the Tukey's multiple range test in PROC-GLM (SAS 8.1, SAS Institute 1997) at $\alpha = 0.05$.

### Results

**Waveform Characteristics Identified During Probing of the Tea Green Leafhopper.** Based on the descriptions by Hunter and Backus (1989), Janssen et al. (1989), Tjallingii and Hogen (1993), Lett et al. (2001), and Jin et al. (2012), six distinct waveforms from EPG recordings of the tea green leafhoppers on tea plants were identified. Typical probes by a third instar of the tea green leafhopper on the tea plant consist of waveforms A, C, E, S, and F (Miao and Han 2007) in the order of their appearances during the recordings (Fig. 1A and B), waveform R also appeared occasionally in some probes (Fig. 1C). Stylet penetration always started with waveform A, its amplitude (from minimum peak voltage to maximum peak voltage) was highly variable because voltage lever moved rapidly either up or down (Figs. 1A and 3, 1a). Nevertheless, the median of waveform A (voltage) was significantly lower than the medians of waveforms C and S. After a nonprobing phase (waveform NP), waveform A started with a short phase (being about 1–30 s) with one or two peaks of high positive amplitude (0.5–1.5 V). The FFT of waveform A generally showed a spectral band of low frequencies between 0 and 10 Hz, with the most predominant frequencies between 0.05 and 0.2 Hz (Table 1 and Fig. 3).

Waveform C always appeared after a waveform A period (Fig. 1A), the duration was between 5 and 60 s. The amplitude of waveform C ranged from 1 to 3 V and was always positive and significantly
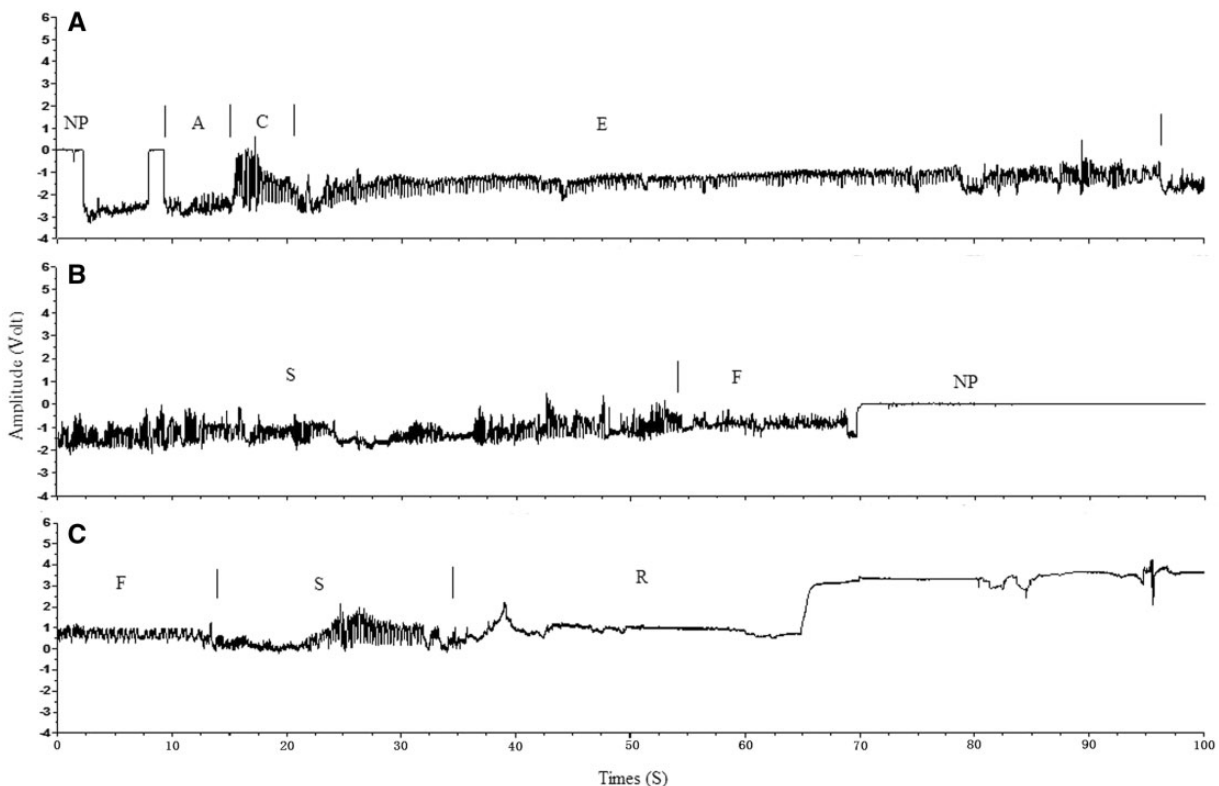


**Fig. 1.** Waveforms NP, A, C, E, S, and F recorded during a typical probe by a third instar of the tea green leafhopper on a tea plant (A + B). Waveform R appeared in a probe occasionally (C).

**Table 1. The duration, amplitude, and major frequency of six distinct waveforms from EPG recordings of the tea green leafhoppers on tea plants**

| Waveforms | Duration[a] | Amplitude (V)[b] | Major frequency (Hz)[c] |
|---|---|---|---|
| A | 19.3 (1–30) s | 0.9 (0.5–1.5) | 0.3 (0.1–1.0) |
| C | 42.7 (5–60) s | 1.3 (0.9–2.4) | 4.5 (4.0–5.0) |
| E | 26.5 (2–40) min | 0.4 (0.1–0.5) | 3.2 (2.0–4.0) |
| S | 1.8 (0.5–3) min | 1.5 (0.5–2.5) | 0.8 (0.1–3.2) |
| F | 3.6 (2–5) min | 0.7 (0.5–1.0) | 2.9 (2.1–5.2) |
| R | 31.4 (5–60) min | 2.4 (1.5–4.0) | 1.8 (0.1–3.5) |

[a]Data (minimum–maximum) indicate average durations of six waveforms in one probing by tea green leafhoppers in susceptible varieties of the tea plants.

[b]Data (minimum–maximum) indicate the mean values of amplitude of six waveforms.

[c]Data (minimum–maximum) indicate the mean values of major frequency of six waveforms.

higher than other waveforms. Its frequency calculated through FFT ranged from 5 to7 Hz, with harmonic frequencies of 8–15 Hz (Table 1 and Fig. 3).

Waveform E always appeared after a waveform C (Fig. 1, A), lasting for 1 to 40 min. Its frequency was lower than those of waveforms A, C, and S, but its mean duration was significantly longer than those of waveforms A, C, S, and R. The amplitude of waveform E ranged from 0.05 to 0.5 V. The FFT calculation revealed a major frequency around 3–5 Hz with one or several harmonic frequencies (Table 1 and Fig. 3).

Waveform S appeared frequently after waveform E (Fig. 2). Sometimes, it followed after a waveform A period but preceded the waveform C period. Their amplitudes were generally higher than that of waveform E, and its frequency ranged from 0 to 10 Hz, with the most predominant frequency being about 0.04 Hz (Table 1 and Fig. 3).

Waveform F always followed the waveform E or S and might repeat several times end of recording. The amplitude of waveform F was higher than that of waveform E but was significantly lower than that of waveforms C and S. The FFT calculation revealed the major frequency around 3–5 Hz with one or several harmonic frequencies (Table 1 and Fig. 3).

Generally, waveform R appeared irregularly, and the appearance of waveform R was also irregular. Its frequency calculated through FFT ranged from 0 to 10 Hz, with the most predominant frequency being about 0.1–3.5 Hz. (Table 1 and Fig. 3).

A stereotypical sequence of waveforms often occurred in *E. vitis* recordings. In one sequence, a short duration of A would often be followed by a short C, then a long E (Fig. 1A). Other times, long or short duration S would be followed by F (Fig. 1B) or E (Fig. 1C).

**Numbers and Durations of Probing on Different Tea Plant Cultivars.** Duration of a probe in this study is defined as the duration of time from stylet insertion to stylet withdrawal. The mean number of probes per insect during the recording period on the resistant cultivar, *Jiandecha* was slightly higher than that on the medium-resistant cultivar, *Yunguidaye*, and was significantly higher than those on the susceptible cultivars, *Zhushan-1* and *Hangzhoudaye* ($F = 5.52$; df = 3,39; $P = 0.013$) (Table 2). Furthermore, the duration of waveform NP increased significantly ($F = 6.47$; df = 3, 39; $P = 0.009$) with the resistance level of the cultivars with *Hangzhoudaye* being the shortest, followed by *Zhushan-1*, *Yunguidaye*, and *Jiandecha* (Table 2).

Mean durations of waveforms A, C, and R did not differ significantly among the four tea plant cultivars tested (Table 2). In contrast, durations of waveform S on the susceptible cultivars *Hangzhoudaye* and *Zhushan-1* were numerically shorter than those on the medium resistant cultivar, *Yunguidaye*, and were significantly shorter than that on the resistant cultivar, *Jiandecha* ($F = 4.13$; df = 3,39; $P = 0.022$) (Table 2). A similar pattern was also found for waveform F, with the longest duration on *Jiandecha*, and the significantly shorter ($F = 4.62$; df = 3,39; $P = 0.019$) on *Zhushan-1* (Table 1). In contrast to waveforms S and F, the duration of waveform E on the resistant cultivar Hangzhoudaye was significantly shorter ($F = 7.15$; df = 3,39; $P = 0.006$) than those on the two susceptible cultivars, Hangzhoudaye and Zhushan-1, and slighter shorter than that on the medium resistant cultivar, Yunguidaye (Table 2). The percentages of tea green leafhopper showing ingestion (waveforms C + E) recorded during 5 h stylet probing on the susceptible cultivars Hangzhoudaye and Zhushan-1 (22.28% and 14.99%, respectively) were significantly higher than that on the resistant cultivar Jiandecha (5.72%) (Fig. 4).

## Discussion

In this study, *E. vitis* waveforms were characterized by physical description such as relative amplitude and dominant frequencies. Based on a number of waveform recordings, it was shown that despite variations among recordings, the median voltage is a reliable discriminating variable (Lett et al. 2001). The spectral analysis of the waveforms revealed their major frequencies being 0.05 to 0.2 Hz for waveform A, 5–7 Hz for waveform C, 3–5 Hz for waveform E and F, 0.04 Hz for waveform S, and 0.1–3.5 Hz for waveform R, respectively. These quantitative measures might be helpful for future method development of an automatic waveform analyses for a broad application of EPG technology.

**Proposed Biological Meanings of E. vitis Waveforms.** *E. vitis* EPG waveforms began with a waveform NP, followed by a waveform A. The piercing of the stylets through plant tissue and production of viscous and watery saliva were most likely the major activities of the waveform A. In addition, Jin et al. (2012) demonstrated that the stylets perform active laceration-type stylet movements and channel-cutting (Hunter and Backus 1989) during A (their E1), as well as formation of a short salivary sheath (sheath trunk). The active stylet movements and channel-cutting observed during the probing process indicate that the tea green leafhopper, like the potato leafhopper, *Empoasca fabae* (Harris), and *Empoasca kraemeri* (Ross & Mooore) is a cell-rupture feeder (Backus et al. 2005, Jin et al. 2012). Thus, waveform A represents the same behaviors as the Ia waveform (multiple-cell laceration) by *E. fabae* and *E. kraemeri* (Hunter and Backus 1989).

The high amplitude, highly regular appearance, and the frequency (5 Hz) of waveform C strongly suggest that the major component of this waveform is produced by the activity of the cibarial pump (Dugravot et al. 2008). Thus, waveform C was considered to be active ingestion. Similar waveforms have been seen in most sheath-feeding leafhoppers, e.g., waveforms O2 (Trebicki et al. 2012), 2 (Lett et al. 2001) and C (Backus et al. 2005), Active ingestion usually occurs from xylem cells when performed by sheath-feeders. However, in cell-rupture feeders, it can occur following laceration feeding (as in waveform A), to ingest the slurry of cell contents that result from channel cutting. This probably explains why the present C often follows A in *E. vitis* recordings, and thus corresponds to short durations of Ic following Ia by *E. fabae* and *E. kraemeri* (Hunter and Backus 1989). (It should be noted that the older-design AC monitor used by Hunter and Backus [1989] would not have been able to distinguish fine-structure differences separating waveforms C and E [described below] in this study).

Waveform E from the tea leafhopper in our study is very similar in appearance and frequency to waveform E2 from aphids and psyllids (Bonani et al. 2010), as well as 5a (Lett et al. 2001) and O5 (Trebicki et al. 2012) from leafhoppers. We recorded a low frequency (0.04 Hz) of waveform S between waveforms E and F. Evidence in the previous papers suggests that the present waveform E from *E. vitis* represents passive ingestion (i.e., using no or minimal cibarial pumping, possibly from phloem sieve elements) combined with watery salivation. This is the same interpretation as waveform E2 from the study by Jin et al. (2012). The present E may resemble long durations of the Ic waveform of *E. fabae* and *E. kraemeri* during the lance-and-ingest tactic of Backus et al. (2005), when it is proposed that the stylets briefly nick a
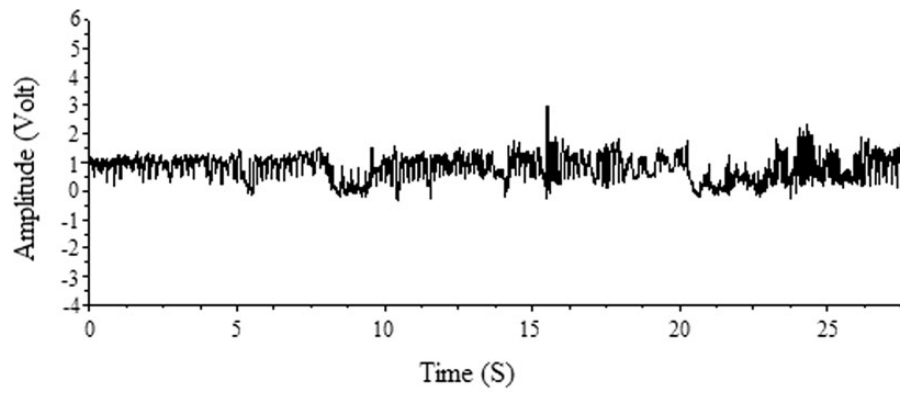
**Fig. 2.** Transition waveforms E–S, which gradually evolves from the relatively low-amplitude and high-frequency waveform E into the high-amplitude and low-frequency waveform S.
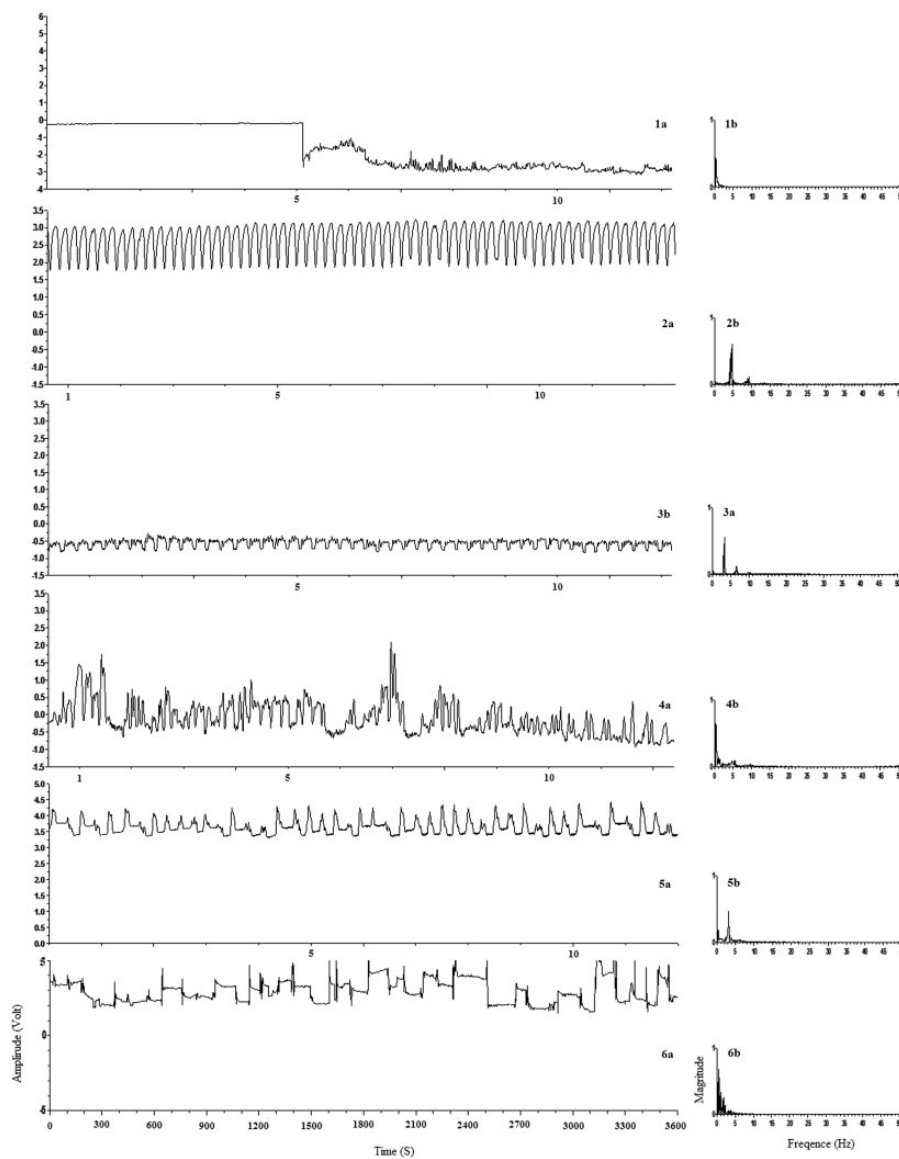


**Fig. 3.** Representative views and spectral analysis of waveforms NP (1a), A (1a and b), C (2a and b), E (3a and b), S (4a and b), F (5a and b), and R (6a and b) from the same recording.

**Table 2. Number of probes and duration of waveforms (mean ± standard errors of the mean) recorded during 5 h stylet probing of the tea green leafhopper on four tea plant cultivars**

| Tea plant cultivars[a] | No. of probes (*n*) | Waveform duration (min)[b] | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | A | C | E | S | F | R | NP |
| Hangzhoudaye (S) | 15.54 ± 2.92b | 5.71 ± 1.30a | 6.91 ± 2.07a | 59.92 ± 10.71a | 5.45 ± 0.12b | 13.25 ± 2.55ab | 27.87 ± 8.18a | 180.89 ± 11.23b |
| Zhushan-1 (S) | 16.73 ± 3.16b | 5.61 ± 1.42a | 5.51 ± 0.86a | 39.45 ± 11.32ab | 3.33 ± 0.67b | 11.70 ± 8.64b | 23.68 ± 4.35a | 210.72 ± 14.64ab |
| Yunguidaye (MR) | 32.55 ± 7.64ab | 6.23 ± 0.48a | 6.11 ± 1.62a | 28.67 ± 5.18bc | 11.32 ± 4.36ab | 15.98 ± 5.98ab | 16.73 ± 11.33ab | 214.96 ± 15.38ab |
| Jiandecha (R) | 39.24 ± 11.08a | 6.92 ± 2.36a | 5.85 ± 1.42a | 11.31 ± 2.45c | 13.65 ± 1.86a | 24.74 ± 5.67a | 9.88 ± 0.89b | 227.65 ± 10.72a |

[a] S, R, and MR in parentheses indicate susceptible, resistant, and medium resistant varieties of the tea plants, respectively.

[b] Data (mean ± SE) followed by the same letter within a column are not significantly different by one-way analysis of variance followed by the Tukey's multiple range test ($P > 0.05$).
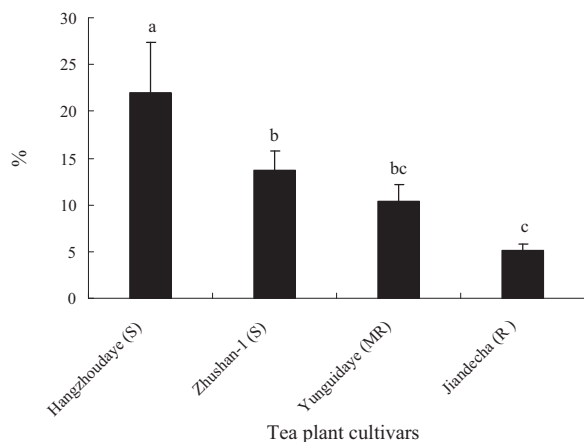


**Fig. 4.** Percentage of the tea green leafhoppers showing sustained ingestion (C + E) recorded during 5 h stylet probing on four tea plant cultivars. Bars with the same letter are not significantly different one-way analysis of variance followed by the Tukey's multiple range test ($P > 0.05$). *S, R, and MR in parentheses indicate susceptible, resistant, and medium resistant varieties of the tea plants, respectively.

sieve element during laceration, subsequently remaining motionless while the insect ingests the phloem sap that leaks out.

Waveform S resembles secretion of saliva by other leafhopper species, e.g., waveforms A2 and B1 (Backus et al. 2005) and O1 (Trebicki et al. 2012). Thus, S probably results from salivary pump activity, similar to the low frequency salivation phase recorded during waveform E1 of aphids (Tjallingii 1988). That said, S was not recorded from *E. vitis* feeding on artificial diets, although it was seen in tea plant recordings and designated waveform E6 (Jin et al. 2012). Thus, it may be some unique type of salivation that occurs only in plants.

Very few published EPG recordings have shown a waveform similar to the present F (termed E4 in Jin et al. 2012). However, unpublished waveforms from *Empoasca* spp. (E. A. Backus, unpublished data) bear a striking resemblance. In the older AC recordings of *E. fabae* (e.g., Hunter and Backus 1989), F-like waveforms were lumped in with the highly variable-appearing Ib. A later histological study (Njihia 1996) demonstrated that Ib waveforms were correlated with slowly moving stylet puncturing and emptying of large, spongy mesophyll cells. Thus, it is possible that the present F could represent single-cell puncturing, a type of cell-rupture feeding (Backus et al. 2005).

In contrast, EPG waveforms similar to the present R have been recorded from several leafhopper and planthopper species, e.g., the sheath feeders *Nephotettix virescens* (Distant) (Rapusas and Heinrichs 1990), *Nephotettix cincticeps* (Uhler) (Young and Goodman 1990), *Nilaparvata lugens* (Stal) (Kimmins 1989), and *Cicadulina mbila* (Naudé) (Lett et al. 2001). In all of the listed studies, waveform R was

recorded when the insects were resting with their stylets inserted into the leaf tissue and terminating in the mesophyll or air space. In addition, an R-like waveform was commonly observed in *E. fabae* recordings (Hunter and Backus 1989) where, like F, it was lumped in with Ib. Thus, it may represent a type of mesophyll feeding. Finally, waveform R may correspond to labial rotations for the directional control of the stylets as suggested for the leafhoppers *Zyginidia scutellaris* (H. S.) (Marion et al. 1987) and milkweed bugs *Oncopeltus fasciatus* (Dallas) (Pollard 1969). In light of such conflicting possibilities, the general term "stylet work" is suggested for waveform R.

Previous studies with *E. fabae* and *E. kraemeri* demonstrated that three different stereotypical sequences of waveforms, termed stylet penetration tactics, were performed (Backus et al. 2005). It is possible that *E. vitis* also performs tactics, as our work identified typical sequences of waveforms. Thus, the sequence (A – C – long-E) may represent something similar to the lance-and-ingest tactic, whereas (short S – short F) or (short S – short R) might be similar to lacerate-and-flush (renamed a tactic in Backus et al. 2005), and (short S – short C) or (short A – short C) might be similar to lacerate-and-sip. If so, then future quantitative studies might attempt to compare tea plants for the tactics performed on them, as was done for *E. kraemeri* (Serrano et al. 2000). Nonetheless, a more simple comparison was performed herein, as an early attempt.

**Quantitative Comparison of Waveforms on Resistant and Susceptible Tea Plants.** In previous studies, the duration of passive ingestion from the phloem was the longest among all the probing waveforms when insects were feeding on their host plants (Calatayud et al. 1994, Jiang et al. 2001, Gabrysl and Tjallingii 2002, Petr et al. 2004). In this study, the duration of waveform E was significantly longer on susceptible cultivars than that on a resistant cultivar, while the reverse was true for the waveform F. Although waveform R was rare, the duration of waveform R ranged from several minutes to several hours if it occurred.

The durations of salivation are often longer on the resistant plants than those on susceptible hosts (Sauge et al. 1998, 2002). In this study, the durations of waveform S were significantly longer on the resistant cultivars than those on susceptible cultivars.

Waveforms E, S, and F were related to the ingestion behaviors and salivation of the leafhoppers and may provide valuable information on predicting the resistance levels of tea plants to pest insects. The duration of sustained ingestion from the phloem is also an important parameter for analyzing resistance of host plant.

This indicates that DC-EPG technology has a great potential in insect–plant relationship research, and our results will provide a useful basis for future study on tea plant resistance against the tea green leafhopper and their potential coevolution.

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