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Transmission of stridulatory signals of the burrower bugs, *Scaptocoris castanea* and *Scaptocoris carvalhoi* (Heteroptera: Cydnidae) through the soil and soybean

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Abstract. Males and females of the burrower bug species *Scaptocoris castanea* Perty and *Scaptocoris carvalhoi* Becker emit stridulatory signals when on the roots of soybean. The substrate-borne components of the signal can be recorded on the plant but not on the surrounding soil surface. The stridulatory apparatus is composed of the tergal plectrum (lima) and the stridulitrum (stridulatory vein) on the underside of the hind wings. The male plectrum has one ridge and the female lima has 13 ridges. Stridulitra of different species differ in the length and in the number of teeth. Rubbing of plectrum (lima) ridges over the stridulitrum in one or both directions produces pulse trains. The velocity of signals that are recorded less than 0.5 cm from the bug is below 0.013 mm s^{-1} on the soil and below 0.066 mm s^{-1} on the leaf surface. Broadband spectra have a dominant frequency of less than 1 kHz and subdominant peaks extending up to 7 kHz. The dominant frequency of the stridulatory signal transmitted through a plant decreases together with the proportion of its higher frequency spectral components. Signals are attenuated for 3–9 dB cm^{-1} when transmitted through the soil or soybean leaf and for approximately 1 dB cm^{-1} when transmitted through soybean stem.

Key words. *Scaptocoris carvalhoi*, *Scaptocoris castanea,* soil, soil insects, soybean, vibratory songs.

Introduction

Substrate-borne communication is prevalent in insects (Cocroft, 2001; Cocroft & Rodriguez, 2005). All Heteroptera species investigated so far emit low-frequency narrow-band signals by body vibration (Čokl & Virant-Doberlet, 2003) and/or broadband signals produced by stridulation (Drašlar & Gogala, 1976; Schaefer, 1980; Schaefer & Pupedis, 1981; Gogala, 2006). Subsequent to the pioneering work of Michelsen *et al.* (1982), it has been generally accepted that broadband signals are better suited for communication through plants than those of narrow-band characteristics. Nevertheless, efficient long-distance communication through plants has been demonstrated for Pentatominae whose narrow-band and low-frequency songs (Čokl & Virant-Doberlet, 2003; Moraes *et al.*, 2005; Virant-Doberlet *et al.*, 2006) are well tuned to the resonant spectra of their host plants (Panizzi, 1997; Čokl *et al.*, 2005). Data on vibratory signal transmission through different substrates are scarce (Magal *et al.*, 2000; Elias *et al.*, 2004; Čokl *et al.*, 2004; Henry & Martinez, 2004; Casas & Magal, 2005; Čokl *et al.*, 2006) and their transmission through the soil and/or roots does not appear to have been investigated. There appears to be no experimental evidence confirming the high efficiency of broadband signal transmission through plants. Thus,

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transmission of vibratory signals through plants and soil by sympatric species of the burrower bug subfamily Cephalocteinae, *Scaptocoris castanea* and *Scaptocoris carvalhoi*, which spend most of their life underground feeding on roots of soybean and other host plants (Lis *et al.*, 2000) is investigated in the present study. By comparing the morphology of the stridulatory apparatus, the study aims to analyse differences both between species and sexes. The transmission of broadband signals through plants and soil was studied under natural conditions. In addition, two artificial (model) situations are designed to determine the efficiency of their transmission through a green plant.

Materials and methods

Insects and plants

Vibratory signals were recorded in the Laboratory of Entomology of Embrapa Soja in Londrina, Paraná State, Brazil, under laboratory conditions (22–26 °C ambient temperature, 65–75% relative humidity, between 09.00 and 16.00 h (i.e. 2.5 h after the start of the photophase). Insects were brought from the field to the laboratory together with host plants surrounded with soil and were placed in pots (20 × 14 × 16 cm), where they stayed until used in experiments. Each individual was tested only once.

Vibratory signals were recorded from different points on a soybean plant occupied by burrowing bugs and from the surface of the soil surrounding the plant's roots.

To study the efficiency of stridulatory signal transmission through plant leaves and stem, two experiments were designed. In the first, a soybean leaf (length: 10–14 cm, width: 6–8 cm) was placed on soil in a plastic box (11 × 11 × 3 cm). Signals were recorded at different distances from the bug singing, either on or in the soil or on the leaf surface. The distance between the bug and the edges of the box was more than 10 cm in all cases and the soil layer was more than 2.5 cm thick. In a second experiment, the efficiency of broadband signal transmission through a soybean stem was studied. A daily fresh 72-cm long soybean stem with a leaf (10 × 6 cm) at its distal end was placed with both ends on foam (20 × 20 × 5 cm) so that the middle of the stem (65 cm) remained in the air. A singing bug was placed on the leaf and the emitted signals were recorded from the stem at different distances from the source.

Recording and analysis of vibratory emissions

Substrate vibrations were recorded by a laser vibrometer (PDV 100, Polytec, Germany) and were stored directly on a computer for later analyses by Cool Edit/Pro, Vers. 2 (Syntrillium Software Corp., Phoenix, Arizona) and Sound Forge 6.0 (Sonic Foundry Inc., Madison, Wisconsin) software. To optimize the amount of light scattered back from the object under investigation small areas (approximately 1 mm^2) on the soil or plant surfaces were painted with white correction fluid.

Morphology of the stridulatory apparatus

The characterization of the stridulatory apparatus of *S. castanea* and *S. carvalhoi* was carried out at Núcleo de Microscopia Electrônica Applicada e Pesquisa Agropecuária, Escola Superior de Agricultura Luiz de Queiroz (ESALQ/USP), at Piracicaba City, São Paulo Sate, Brazil. For both species, the abdomen and posterior wings were separated and cleaned in detergent solution. After drying, the samples were fixed on metal stubs and submitted to Sputtering Balzers Union Medical SCD 010 (Balzers AG, Liechtenstein). The material was analysed under a scanning electron microscope.

Mean length (μm), number of teeth and distance between teeth (μm) of the stridulitrum were recorded from wings of males and females of *S. castanea* and *S. carvalhoi*. Preliminary analyses showed an increase of the distance between the teeth along the stridulitrum. To demonstrate this difference, the stridulitrum was divided into the anterior, middle and posterior thirds, and the intertooth distance measured. Furthermore, the mean number of ridges located in the middle third of the plectrum (lima) was compared between both sexes and species.

Terminology and statistical analysis

Pulses are defined as unitary homogeneous parcels of waves of finite duration, and pulse trains as temporally distinct groups of pulses (Broughton, 1963). Syllables comprise groups of two pulse trains emitted by movement of the stridulatory apparatus in both directions. For single pulses and their groups, the duration (the time between the signal's onset and end), repetition time (the interval between onsets of two consecutive units) and pause (defined as the time interval between the end of the preceding and onset of the next unit) were analysed. Spectra were described from 3-s long recordings or from single pulse trains by defining the dominant and subdominant frequency peaks. Intensity of signals was expressed in velocity units determined for the peak amplitude of a pulse. Two-tailed Student's *t*-test and analysis of variance (ANOVA) were used for statistical data processing. Mean ± SD values were calculated between different individuals only in cases when the difference between individuals, determined by ANOVA test, was not significantly different. Tukey's test with 5% significance was used to compare the mean values of length and number of teeth of the stridulitrum whenever a two-way ANOVA indicated significant differences between them.

Results

Time and spectral characteristics of signals

For technical reasons, it was not possible to record vibrations directly from the roots of plants occupied by undersoil living *S. castanea* and *S. carvalho*. To compare characteristics of male and female signals of both species, recordings were made at the surface of a soybean leaf at a distance of less than 0.5 cm from the singing bug.

Sequences of pulse trains were recorded from soil and soybean in males and females of both species (Fig. 1). The velocity of signals recorded on the leaf surface ranged between 18 and 66×10^{-6} m s^{-1} (distance < 0.5 cm). Trains of pulses were repeated continuously up to 30 s or were grouped into sequences of irregular duration and repetition time. Within the same sequence, pulse trains of equal pulse amplitude appeared together with pulse train couples (syllables) in which pulses of the first pulse train had a higher amplitude, and those of the next one a lower amplitude, indicating that signals were produced either by movement of the stridulatory apparatus in one or the other direction, or in both directions.

Time and frequency characteristics of male and female *S. castanea* pulse trains are shown in Table 1. Duration of the first pulse train of a syllable varied individually in the male and female sequence between 30 and 80 ms. Differences between male and female emissions were expressed significantly ($P < 0.001$) in syllable repetition time, in the repetition time of the first and second pulse train, and in the interval between them, in the number of pulses per pulse train and in their repetition rate. The first and the second pulse train of a syllable differed significantly ($P < 0.0001$) in their duration, in the interpulse interval time and, in females, in the number of pulses per pulse train.

Spectra of male and female signals were broad, with the dominant frequency varying individually below 1 kHz and subdominant peaks not exceeding 7 kHz (Fig. 2). Subdominant peaks below 100 Hz belonged to the external noise, and those above 4 kHz appeared only occasionally. Spectral differences could be observed between pulse trains of a syllable (Fig. 3). Dominant frequencies of the first pulse trains were distributed below 900 Hz and those of the second between 600 and 1800 Hz. In 71% ($n = 70$) of syllables, the dominant frequency of the second pulse train exceeded the dominant frequency of the first one, with the differences ranging from a few to 1140 Hz. In 29% ($n = 70$), the dominant frequency of the first pulse train exceeded the value of the second for less than 500 Hz.

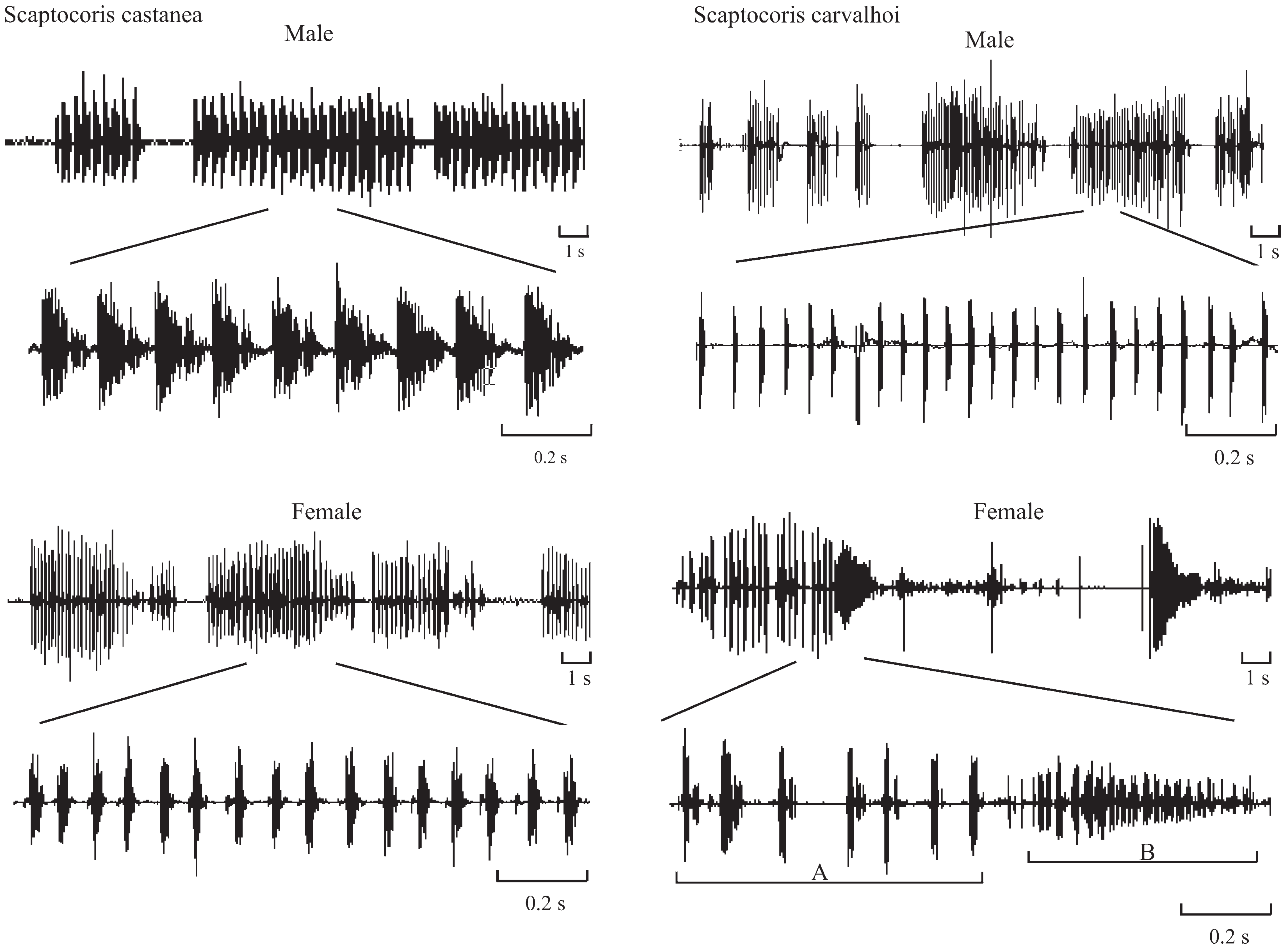

Fig. 1. Vibratory emissions of *Scaptocoris castanea* (left) and *Scaptocoris carvalhoi* (right) males and females. The two types of female *S. carvalhoi* pulse train groups are marked A and B. Time scales are marked below oscillograms.

Table 1. Time (ms) and frequency (Hz) characteristics of male and female *Scaptocoris castanea* vibratory songs.

	Scaptocoris castanea male		*Scaptocoris castanea* female	
	First pulse train	Second pulse train	First pulse train	Second pulse train
Pulse train duration	65 ± 11 (100/5)	19 ± 3 (100/5)	68 ± 9 (80/4)	19 ± 4 (100/5)
Pulse train repetition time	129 ± 17 (120/6)	38.3 ± 4.4 (30) 32–87	186 ± 35 (140/7)	57.0 ± 11.4 (30) 23–83
Pulse train pair pause		16.1 ± 3.4 (30) 11–39		10.2 ± 3.7 (30) 5–14
Pulses/pulse train	4.1 ± 0.4 (30)	4.1 ± 1.2 (30)	25.3 ± 7.2 (30)	14.4 ± 4.2 (30)
Pulse pause	7.1 ± 0.7 (30)	3.8 ± 1.0 (30)	1.9 ± 0.3 (30)	1.1 ± 0.3 (30)
Dominant frequency (Hz)	344 ± 25 (28/7) Min. = 169 ± 30 (14/3) Max. = 741 ± 112 (15/2)	399 ± 54 (38/7)	Min. = 265 ± 34 (10/2) Max. = 763 ± 30 (8/2)	
Subdominant frequency peaks > 1 kHz	1215 ± 138 (70) 1722 ± 137 (50) 2453 ± 296 (48) 3499 ± 246 (43)		1340 ± 262 (32) 1529 ± 286 (81) 2481 ± 253 (44) 3448 ± 278 (21)	

Values are expressed as means ± SD (*n*) or (*n* of total).

Compared with *S. castanea*, vibratory emissions of *S. carvalhoi* showed similar characteristics. In males, a significant difference ($P < 0.001$) between the first and second pulse train existed only in the number of pulses per pulse train. Female single or paired pulse trains were grouped into sequences of two types (Fig. 1, Table 2). In the first, pulse trains had similar amplitude and, in the second, the pulse train amplitude decreased from the beginning to the end of the sequence. Significant differences ($P < 0.01$) between pulse trains of both sequences were expressed in the duration and repetition time of syllables; in the interval between the onset of the first and the second pulse train; in the number of pulses per pulse train; and in the repetition rate of first pulse train pulses. No significant difference could be measured in the pause between the first and the second pulse train ($P = 0.6521$).

High individual variation of the dominant frequency was observed in male and female emissions (Fig. 2). In several cases, the dominant frequency peak in *S. carvalhoi* signals was observed in a frequency range above 1 kHz. Male and female signal spectra contained several subdominant peaks that did not exceed 6 kHz.

Stridulatory apparatus of S. castanea and S. carvalhoi

Spectra of vibratory signals of *S. castanea* and *S. carvalhoi* species showed characteristics typical of stridulatory emissions in other representatives of the group (Gogala, 2006). In both species, the stridulatory apparatus was composed of the stridulatory vein on the hind wing, the stridulitrum and of the stridulatory plectrum (the lima in females) on the tergal plate (Fig. 4). Mean length and number of teeth of the stridulitrum differed significantly between species ($P < 0.001$ for length and the teeth number) and sexes ($P = 0.042$ for length and $P < 0.001$ for teeth number) (Table 3). The stridulitrum was significantly ($P = 0.039$) longer in males than females in *S. castanea*, but not in *S. carvalhoi* ($P = 0.999$). The mean number of teeth of the stridulitrum did not show significant differences between the sexes for *S. castanea* ($P = 0.057$). However, for *S. carvalhoi,* the mean tooth number was significantly higher in males ($P > 0.05$). *Scaptocoris castanea* showed a significantly ($P < 0.001$) higher mean length of the stridulitrum over those of *S. carvalhoi*. Additionally, the mean number of teeth was significantly lower for *S. castanea* than *S. carvalhoi* individuals ($P < 0.001$).

The teeth were distributed irregularly through this structure in both species (Fig. 4A,B). For *S. castanea*, the distance between the teeth increased from the anterior to the posterior third of the stridulitrum, being significantly different among the thirds of males and females ($P < 0.001$; Table 4). On the other hand, for *S. carvalhoi*, the mean distance between the teeth increased only for the posterior third of the stridulitrum. For this species, the mean distance between teeth of the middle third of the stridulitrum was significantly different between the sexes ($P < 0.001$).

The ridges of the dorsal stridulatory plectrum (lima), which were located transversally on both lateral sides of the tergal plate were different in males and females of both bug species (Fig. 4C,D). In females, the mean number of ridges was 13.2 ± 1.0 ($n = 4$) and 13.0 ± 1.4 ($n = 4$) for *S. castanea* and *S. carvalhoi*, respectively. Only one simple ridge was found in males of both species.

Transmission of stridulatory signals from roots to the plant and soil

When *S. castanea* and *S. carvalhoi* were placed on the soil, they started to dig into it with specially adapted legs emitting continuously stridulatory signals. Signals were

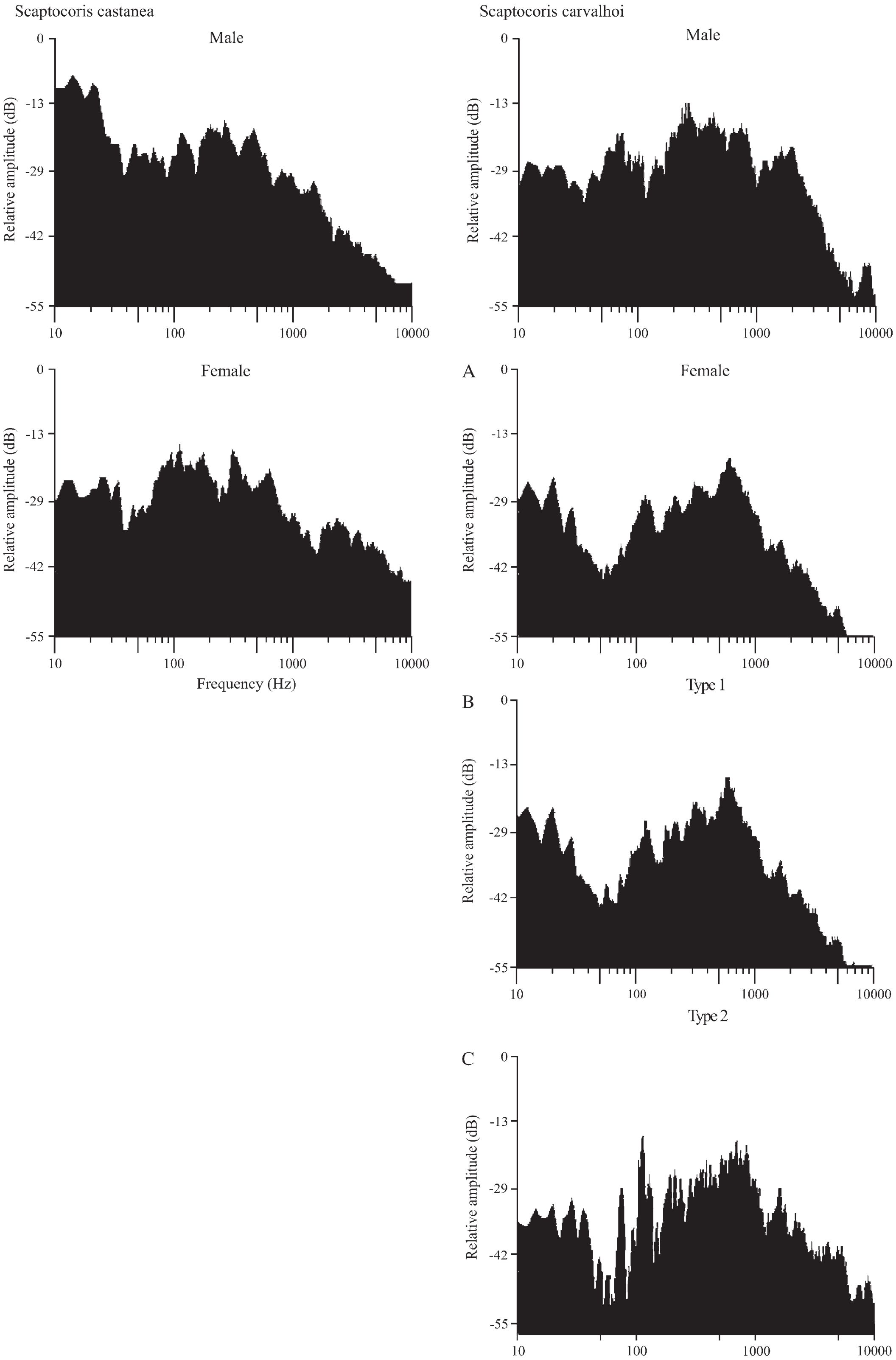

Fig. 2. Spectra of *Scaptocoris castanea* (left) and *Scaptocoris carvalhoi* (right) male and female signals.

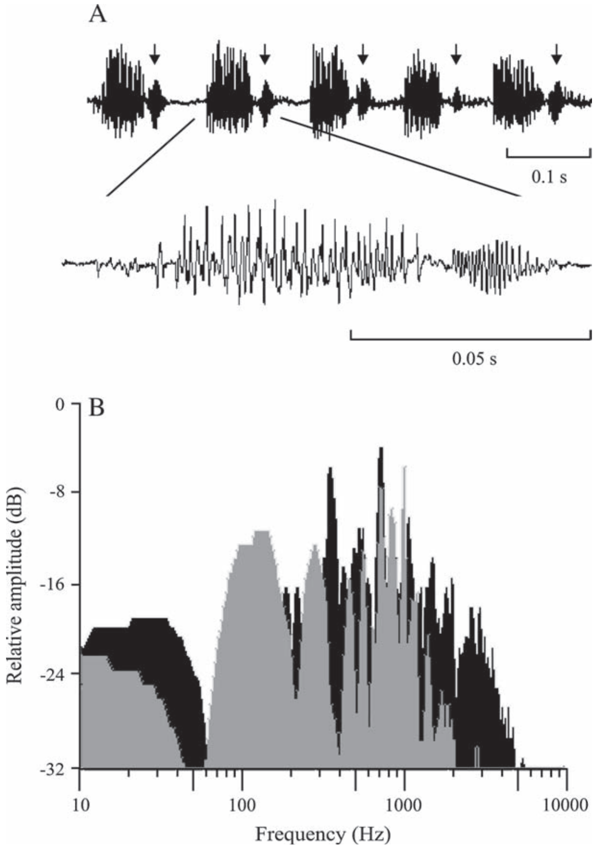

Fig. 3. (A) Pulse trains grouped into syllables (pulse trains elicited by backward movement of the stridulatory apparatus are marked with arrows). (B) Spectra of foreward (black) and backward (grey) movement of the stridulatory apparatus.

transmitted through the soil with high attenuation and could be recorded only at distances below 6 cm from the source. The velocity of soil transmitted signals varied in ten tested *S. castanea* bugs between 1.5 ± 0.5 and 12.8 ± 1.7 × 10^{-6} m s^{-1} ($n = 20$) at a distance of less than 0.5 cm and decreased in the same male for 5.5 dB at the 0.5 cm (11 dB cm^{-1}) and for 15–19 dB at the 3.5 cm (4–5 dB cm^{-1}) greater distance. The spectra of male and female signals recorded on the soil less than 1 cm from the bug (Fig. 5) were characterized by a broad peak whose dominant frequency varied individually between 157 ± 20 Hz ($n = 4$) and 770 ± 55 Hz ($n = 5$). Differences between corresponding male and female signal mean dominant frequency values around 270, 415 Hz, 540 Hz and 765 Hz were not significant ($P = 0.7802$, 0.8089, 0.1090 and 0.5385, respectively). The highest subdominant peak was 1643 ± 35 Hz ($n = 3$) in female and 3324 ± 282 Hz ($n = 3$) in male emissions. Spectral peaks below 100 Hz were due to external noise.

Stridulatory signals could also be recorded from plants whose roots were occupied by bugs, but not from the soil surrounding it. The velocity of signals recorded on plants at different distances above the soil (6, 22, 28, and 33 cm) ranged between 4.5 ± 1.4 ($n = 20$) and 5.5 ± 2.9 × 10^{-6} m s^{-1} ($n = 20$) ($P = 0.3849$) and was 8–13 dB lower when measured at distances of 2, 39 and 44 cm above the ground. The spectra of plant recorded signals were different from those recorded on the soil (Fig. 5). The dominant frequency of plant recorded signals decreased from 500 ± 22 Hz ($n = 20$) to 296 ± 10 Hz ($n = 14$) with an increasing distance of 2 to 28 cm above the soil (Fig. 5). With increasing distance, the proportion of higher frequency components decreased. Spectral peaks extended up to 2–3 kHz at distances below 25 cm and up to 1 kHz in plant recordings at longer distances. Spectral peaks of plant recorded external noise were below 250 Hz.

Spectral and intensity variations with distance during transmission through plants

Spectral and intensity variations with distance were analysed for *S. castanea* signals transmitted through the soybean leaf and stem. The velocity of male and female signals emitted by bugs on a soybean leaf varied at a distance of less than 0.5 cm between 18 ± 3 ($n = 10$) and 66 ± 13 × 10^{-6} m s^{-1} ($n = 10$) in nine bugs stridulating on three different leaves. During transmission through a leaf, the velocity decreased for 12–27 dB at a distance of 3–4 cm from the source and, at distances of 6–7 cm, velocity dropped with a rate of up to 8 dB cm^{-1} to values between 0.3 ± 0.1 ($n = 10$) and 5.2 ± 1.9 × 10^{-6} m s^{-1} ($n = 10$).

To determine the efficiency of transmission of broadband stridulatory signals through a soybean plant, they were recorded on the stem at different distances from a male singing on a leaf of a leaf/stem model (see Materials and methods). The velocity of signals measured on the leaf immediately below the singing bug (distance < 0.5 cm) (19.7 ± 3.8 × 10^{-6} m s^{-1}, $n = 20$) was not significantly different ($P = 0.5652$) from that measured on the stem 1 cm from the source (20.7 ± 5.9 × 10^{-6} m s^{-1}, $n = 20$). The intensity of signals decreased with distance (Fig. 6). Most distally on the stem (72 cm from the source), the velocity decreased for 31 dB to 0.6 ± 0.3 × 10^{-6} m s^{-1} ($n = 20$). Intensity decrease with distance was not linear: during transmission through the proximal part of the stem, the velocity decreased for 24 dB (1.2 ± 0.5 × 10^{-6} m s^{-1}, $n = 20$) at a distance of 20 cm and steady velocity decrease was interrupted at distances of 7, 24 and 40 cm from the source where the velocity increased above the values of neighbouring measuring points (Fig. 6).

The spectra of signals recorded on the leaf close to a singing male had dominant peaks either at 188 ± 11 Hz ($n = 31$) or 299 ± 44 Hz ($n = 19$). The spectra of stem recorded signals differed by higher dominant frequency and a lower proportion of higher frequency spectral components (Fig. 6). The narrow spectral peak between 500 and 700 Hz was accompanied at most measuring points by a broader peak between 200 and 300 Hz. At different distances, one or another peak became dominant.

Table 2. Time (ms) and frequency (Hz) characteristics of male and female *Scaptocoris carvalhoi* vibratory songs.

	Scaptocoris carvalhoi male		*Scaptocoris carvalhoi* female	
	First pulse train	Second pulse train	First pulse train	Second pulse train
Pulse train duration	18 ± 7 (74)	17 ± 5 (21)	23 ± 5 (148/2)[a] 15 ± 4 (74)[b]	16 ± 5 (122/3)[a] 7 ± 2 (57)[b]
Pulse train repetition time	64 ± 11 (74)	45 ± 9 (30)	90 ± 22 (148/2)[a] 30 ± 5 (74)[b]	25 ± 5 (30)[a] 19 ± 3 (30)[b]
Pulse train pair pause		27 ± 8 (30)		5 ± 2 (30)[a] 5 ± 2 (30)[b]
Pulses/pulse train	11 ± 4 (30)	6 ± 2 (30)	11 ± 3 (30)[a] 6 ± 2 (30)[b]	8 ± 3 (30)[a] 6 ± 1 (30)[b]
Pulse pause	1 ± 1 (20)	2 ± 1 (20)	2 ± 0 (178/20)[a] 3 ± 0 (136/20)[b]	1 ± 0 (224/20)[a] 1 ± 0 (159/20)[b]
Dominant frequency	616 ± 45 Hz (10) Min. = 313 ± 45 Hz (2) Max. = 2215 ± 350 Hz (3)		488 ± 35 Hz (30)[a] Min. = 294 ± 54 Hz (3)[a] Max. = 908 ± 23 Hz (11)[a] 575 ± 43 Hz (14)[b] Min. = 363 ± 42 Hz (5)[b] Max. = 1526 ± 36 Hz (4)[b]	

Values are expressed as means ± SD (*n*) or (*n* of total).

[a]Female pulse train group type 1.

[b]Female pulse train group type 2.

Discussion

The burrower bug species, *S. castanea* and *S. carvalhoi*, are root-feeders and spend most of their life in the soil. They feed on rice, cotton, black beans, sugarcane, maize, peanuts and soybean (Lis *et al.*, 2000). Recently Johnson & Gregory (2006) summarized data on interactions between host plants and root-feeding insects, demonstrating that host plant location and selection is by chemical signals. Little is known about mating behaviour and related communication in burrower bugs. The present technology does not enable the investigation of undisturbed behaviour together with simultaneous recording of vibratory emissions *in situ*. In the present study, stridulatory signals are recorded for hours from a plant whose roots are occupied by members of both species. The number, sex, or species of the stridulating bugs cannot be determined from group recordings and the behavioural context of signalling remains unknown. The low species and sex specificity of pure stridulatory signals indicates that vibratory emissions may play a role in disturbance (defensive), aggregation or some other behavioural context (Gogala, 1984). Cydnid courtship, acceptance and rivalry songs show higher specificity and are produced by low-frequency body vibration and/or by stridulation in most cases (Gogala, 2006). The absence of low-frequency components of the emitted signals and the uniformity of songs of group living *Scaptocoris* species indicates that calling and courtship may be mediated by signals of other modalities.

The lack of low-frequency signals can be explained by the specific environment of the species. Males and females do not dig tunnels and are in direct contact with surrounding soil particles, which mechanically prevent free vibration of the abdomen. On the other hand, the stridulation as described for Cydnidae (Gogala, 2006) is not prevented by surrounding soil: rubbing of both stridulatory apparatus counterparts is produced by active movement of the tergal plate covered and protected by the hind wings.

The morphology of the stridulatory apparatus of *S. castanea* and *S. carvalhoi* shows that the stridulitra are different between species and sexes, and that the stridulatory plectra (lima) are different only between the sexes. Compared with *S. carvalhoi*, the stridulitrum of *S. castanea* is longer with greater distance between the teeth. On the other hand, the stridulatory plectrum (lima) in the females of both species shows approximately 13 ridges in the middle third of this structure, whereas the males present only one ridge. A similar situation is described in *Thyreocoris scarabeoides* (L.) in the cydnid subfamily Thyreocorinae (Drašlar & Gogala, 1976).

The results suggest that sexual dimorphism observed in the stridulatory apparatus may render different sounds produced by males and females but it appears that the stridulitrum determines the signal specificity of both species. However, further studies using different *Scaptocoris* species will be necessary to characterize and associate the stridulatory structures with the emitted sounds.

The intensity of signals could not be measured on the root surface. The velocity between 18 and 66 × 10^{-6} m s^{-1} is measured for signals emitted and recorded on the soybean leaf at distances below 0.5 cm. Stridulatory signals emitted on roots are transmitted through the whole plant with significantly different spectral properties than signals recorded in or on the soil: the dominant frequency decreases to characteristic peaks of plant resonant spectra and higher frequency components are extensively damped, confirming the low-pass filtering properties of green plants (Čokl *et al.*, 2005).

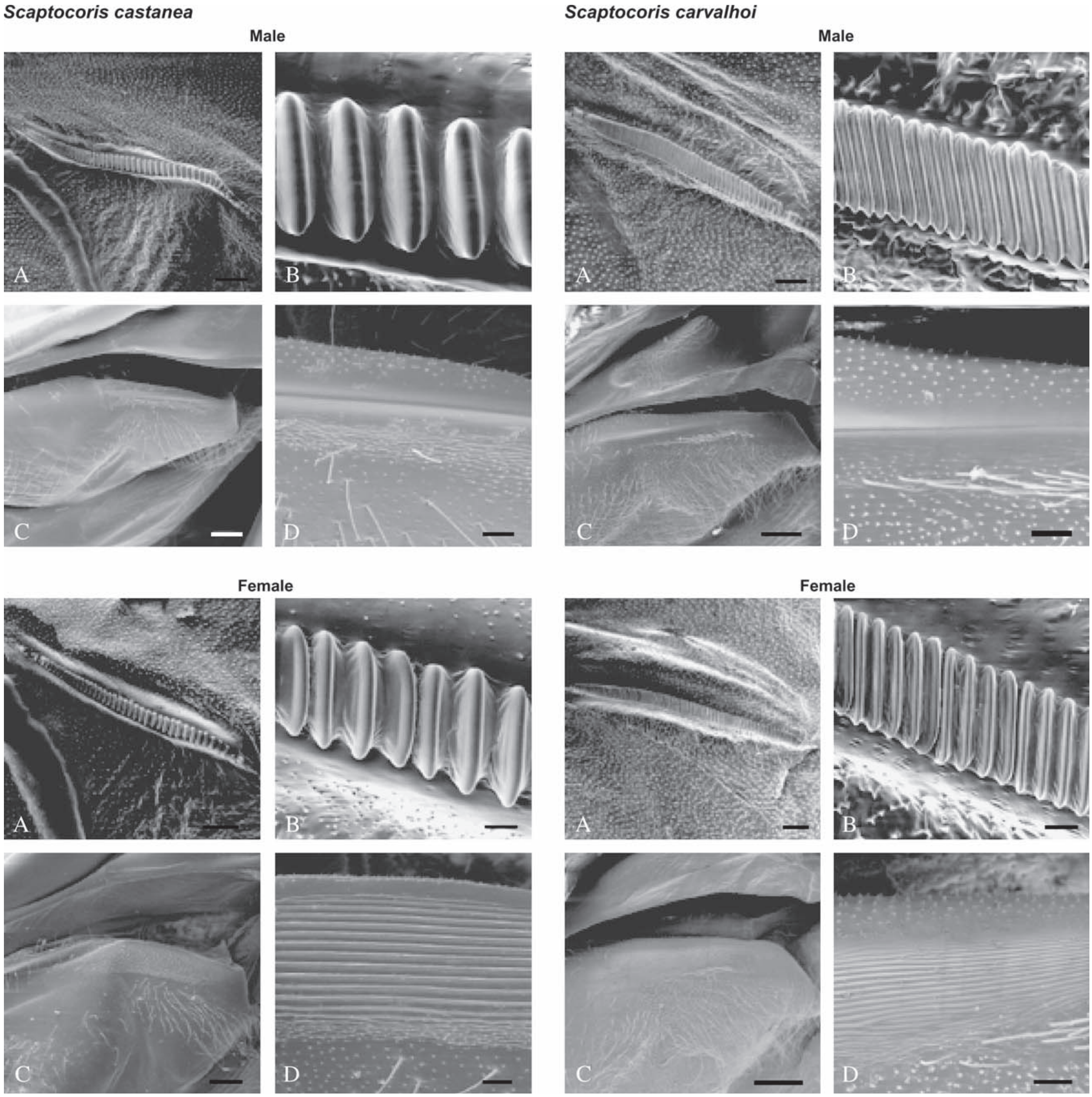

Fig. 4. Male and female stridulatory apparatus of *Scaptocoris castanea* and *Scaptocoris carvalhoi*. (A) Stridulitrum situated on the postcubital vein of the hind wings (scale bar = 100 μm); (B) middle third of the stridulitrum, showing teeth detail (scale bar = 10 μm); (C) stridulatory plectrum situated on both lateral sides of the frontal edge of the tergal plate (scale bar = 100 μm); (D) middle third of stridulatory plectrum (scale bar = 20 μm).

A damping rate of around and below 1 dB cm^{-1} during transmission through the plant stem lies close to the values determined for transmission of vibratory signals through a banana leaf (Barth, 1985). Nevertheless, intensities between 10^{-5} and 10^{-6} m s^{-1} are low and lie at the edge of sensitivity of vibrational receptors described in some cydnid (Devetak *et al.*, 1978) and pentatomid (Čokl *et al.*, 2005) species. Vibratory signals transmitted through the plant above the soil probably play no role in intraspecific communication because bugs of both species cannot climb on the plant.

Vibratory communication through the soil is restricted to short distances. Signals are recorded from the plant and not from the surrounding soil. Recordings from the soil surface reveal that signals are attenuated at a distance above 5 cm for approximately 20 dB. Because the velocity value of the input signal at a distance less than 5 mm from the singing bug lies

Table 3. Mean ± SD of length and number of teeth in stridulitrum of *Scaptocoris castanea* and *Scaptocoris carvalhoi* males and females.

	Stridulitrum		
	Sex	Length (μm)	Number of teeth
Scaptocoris castanea	Female	689.50 ± 69.15^{b}	$45{,}50 \pm 5.68^{a}$
	Male	798.25 ± 48.63^{a}	55.25 ± 4.99^{a}
Scaptocoris carvalhoi	Female	562.25 ± 37.22^{c}	74.25 ± 2.50^{b}
	Male	566.00 ± 35.28^{c}	86.50 ± 5.25^{c}

Means followed by different superscript letters within each column indicate significant differences among thirds by Tukey's test ($P = 0.05$).

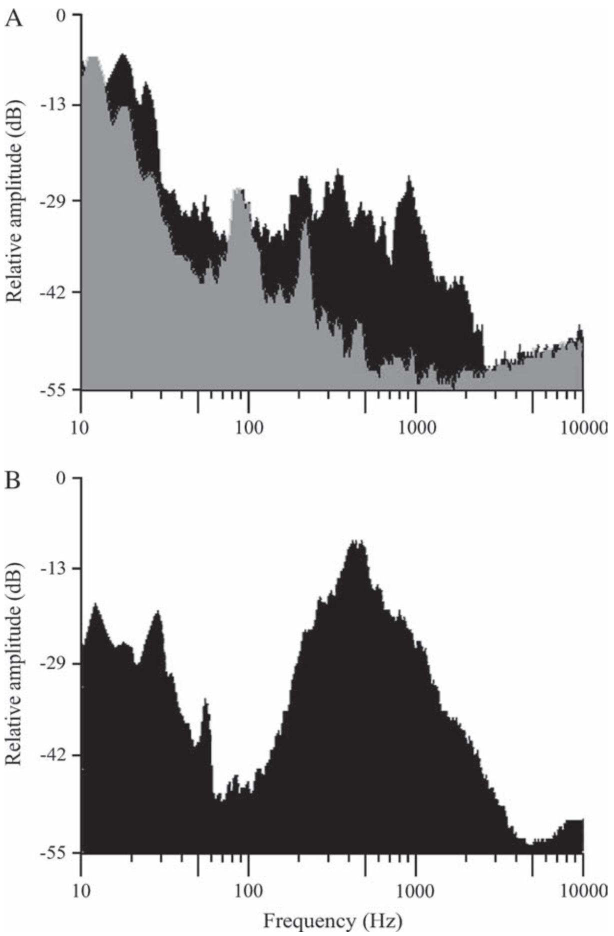

Fig. 5. Spectral properties of vibratory signals emitted by burrower bugs on soybean roots and recorded on a plant: (A) 2 cm (black) and 28 cm (grey) above the soil; (B) spectrogram of male *Scaptocoris castanea* signals recorded on the soil 5 mm from the source.

slightly above sensory threshold level, it is presumed that communication through the soil is possible only at very short distances.

Males and females of both *Scaptocoris* species are found on the roots of the same soybean plant. To allow species isolation, they should carry high species specificity in the time and frequency domain. Although it was not possible to record signals at their place of origin, it is believed that leaf recordings from the vicinity of the singing bug represent reliable characteristics of the input signal. Differences between species and sexes are determined statistically and require experimental confirmation in relevant natural conditions.

Pulse train duration varies within and between individuals and depends on the number of pulses per pulse train and on their repetition rate. Significantly longer first pulse trains of a couple are characteristic for *S. castanea*; duration of the second pulse train varies less and the difference between the species (and sexes) is not significant. Highest specificity in this respect is present in the male *S. castanea* first pulse train, which has just four pulses on average, with significantly lower repetition rate, and in female *S. carvalhoi* whose pulse trains are within the same song grouped into two different ways. Consequently, male and female songs can be differentiated within and between species. Significant species and sex specificity are found also in the repetition rate of syllables. The repetition rate of both pulse trains within a syllable and the interval between both units are time parameters that differentiate significantly only the *S. carvalhoi* female emissions from the remainder because of different pulse train groupings.

The spectra of stridulations for both species differ according to the substrate from which they are recorded. The main

Table 4. Mean ± SD distances between the teeth of the stridulitrum in *Scaptocoris carvalhoi* and *Scaptocoris castanea*.

	Inter-teeth distance (μm)			
	Scaptocoris carvalhoi		*Scaptocoris castanea*	
	Male	Female	Male	Female
Anterior third	4.51 ± 4.14^{b}	5.20 ± 2.35^{a}	8.8 ± 1.45^{a}	11.49 ± 2.28^{a}
Middle third	$3.59 \pm 0.83^{a*}$	5.43 ± 1.58^{a}	13.85 ± 4.18^{b}	14.43 ± 3.06^{b}
Posterior third	9.35 ± 2.25^{c}	9.22 ± 1.94^{b}	22.58 ± 3.15^{c}	19.56 ± 3.22^{c}

Means followed by different superscript letters within each column indicate significant differences among thirds by Tukey's test ($P = 0.05$). *Significant differences between sexes for each third.

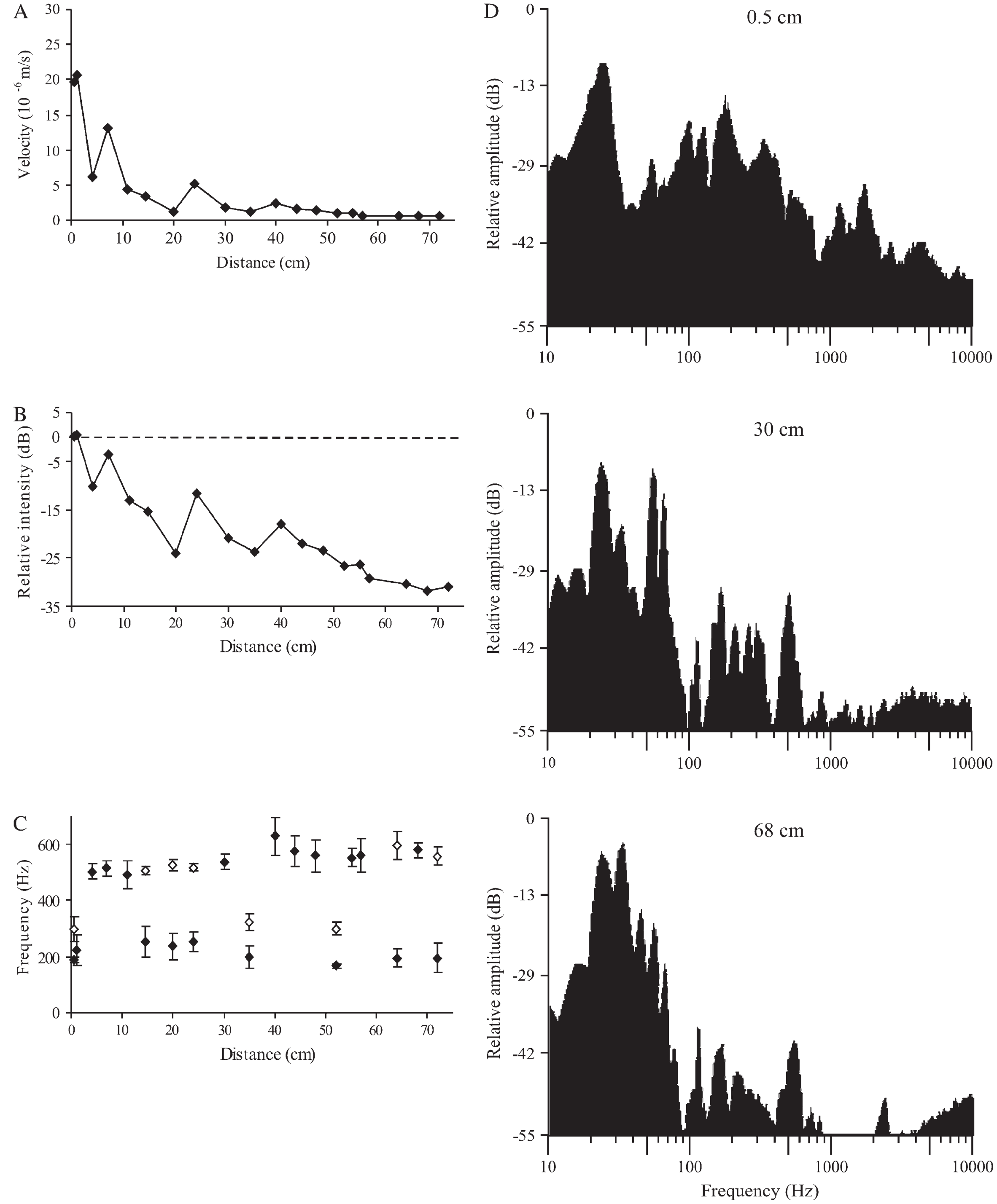

Fig. 6. Male *Scaptocoris castanea* signal velocity (A, B) and dominant frequency (C) variation with distance during transmission through a soybean stem. Velocity values are expressed in absolute (A) and relative (dB reference 19.74×10^{-6} m s^{-1}) units. Spectrograms of a single signal recorded at different distances from the singing male are shown in (D).

emitted energy in both sexes and both species lies below 1 kHz, and broadband spectra extend with highest subdominant peaks up to 8 kHz The dominant frequency of leaf recorded signals of *S. castanea* varies in and between individuals in the range below 1 kHz. The dominant frequency of *S. carvalhoi* is generally higher and can reach 2 kHz in males. The spectra of soil-recorded signals differ significantly with the well-established dominant frequency peak and the low proportion of spectral components above 1.5 kHz. Higher-frequency spectral components decrease during transmission through the soil or plant together with an increase of spectral components below 200 Hz. For plant transmitted signals, this effect can be explained by the resonant properties of green plants (Čokl *et al.*, 2005).

The results obtained in *S. castanea* and *S. carvalhoi* show that broadband stridulatory signals are transmitted through the plant with higher damping than low-frequency narrow band vibratory signals, although their spectra change according to the resonant and low-pass filtering properties of plants. These results confirm the hypothesis that low-frequency and narrow-band vibratory signals produced by body vibrations are well suited for communication through green plants (Čokl *et al.*, 2005).

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