Appl. Ent. Zool. **10** (3): 162—171 (1975)

Substrate Vibrations: Mating Signal of Three Species of Planthoppers which Attack the Rice Plant (Homoptera: Delphacidae)

Toshihide ICHIKAWA, Masayuki SAKUMA and Shoziro ISHII

Pesticide Research Institute, College of Agriculture, Kyoto University, Kyoto 606, *Japan*

(Received March 25, 1975)

Female abdominal vibration (FAV) was observed in three species of planthoppers, *Nilaparvata lugens* STÅL, *Laodelphax striatellus* (FALLÉN) and *Sogatella furcifera* (HORVÁTH), prior to copulation. Males of the three species which were placed on rice plants responded to the substrate vibrations caused by FAV of the same species, and were attracted to the vibrating females even from a distance of about 80 cm—the maximum distance examined. It was observed that males of each species did not show any behavioral response to the substrate vibrations caused by FAV of the other two species. No other sense stimuli, such as visual, acoustic and chemical ones, were concerned for perception of females even from a distance of a few cm. The substrate vibrations caused by FAV were electrically detected and recorded on sound tape. Playback elicited the same response in males as was observed for the intact substrate vibrations. Pulse repetition frequencies of the substrate vibrations were ca. 20/sec. for *N. lugens*, ca. 13/sec. for *L. striatellus* and ca. 9/sec. for *S. furcifera* at 25°±1°C. Wave train pattern of each pulse was also different among the three species. These differences in substrate vibrations caused by FAV are believed to be the principal factor for species discrimination in mating behavior.

INTRODUCTION

Three species of planthoppers, the brown planthopper, *Nilaparvata lugens* STÅL, the smaller brown planthopper, *Laodelphax striatellus* (FALLÉN), and the white backed planthopper, *Sogatella furcifera* (HORVÁTH), are serious insect pests of the rice plant not only in Japan but also in other Asian countries.

Mating behavior of several species of planthoppers including those mentioned above has been studied by several investigators who have demonstrated that females vibrate their abdomens prior to copulation. In *Calligypona lugubrina* (STRÜBING, 1958) and *Sogata orizicola* (MCMILLIAN, 1963), males move toward vibrating females of the same species along the stems of host plants. In *L. striatellus* (OYAMA, 1972) and *N. lugens* (TAKEDA, 1974), copulated females do not vibrate their abdomens even when males of respective species are located in close proximity. STRÜBING (1962) detected a very faint sound emitted during female abdominal vibration (FAV) of *C. lugubrina*. These observations suggest that FAV in planthoppers seems to be an important sense stimulus which induces excitation and orientation of males to females of the same species for the purpose of copulation. ICHIKAWA and ISHII (1974) studied the mating behavior of *N. lugens*, and demonstrated that the substrate vibration caused by FAV was the mating signal for males. The present experiments were undertaken to eluci-

date the role of FAV on mating behavior in the three species of planthoppers which attack rice plants, and to discern the mechanism of interspecific discrimination in the response of males to FAV of the respective species.

MATERIALS AND METHODS

Newly emerged adults of three species of planthopper, *N. lugens*, *L. striatellus* and *S. furcifera*, were collected from colonies fed on rice seedlings under laboratory conditions (25°±1°C; 14 hrs illumination per day) and separated according to sex. Insects which were unmated, sexually mature adults of more than three days after the last ecdysis were used in all experiments.

Response of males placed on a thin paper disk to FAV. A young rice plant was projected through a hole (ca. 4 mm in diameter) made in the center of a thin paper disk (8 cm in diameter). The paper disk was set on a plastic solid plate which had been positioned on a tripod. One female was placed on the stem of the plant and one or two males were released onto the paper disk. The disk was covered with a transparent plastic cup (Fig. 1). Response of the male to FAV was observed through the plastic cup under two conditions, (1) when the paper was detached a few millimeters from the stem of the plant, and (2) when the paper was directly in contact with the stem.

Response and orientation of males placed on a rice plant to FAV. Three young rice plants cultured individually in three pots were arranged in a row as described in a previous paper (Ichikawa and Ishii, 1974). One female was placed on either of the outer rice plants, and one or three males were placed on the lower part of the stem of the rice plant set in the center. Response of the males to FAV was observed both when the tip of the leaf blades of two adjacent plants were not in contact and slightly separated, and when in immediate contact.

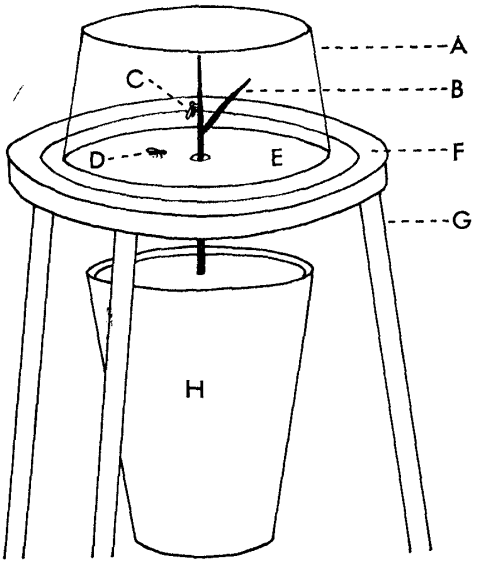

Fig. 1. An apparatus for examining the response of a male to FAV. A, transparent plastic cup; B, rice plant; C, virgin female; D, male; E, thin paper disk; F, plastic solid plate; G, tripod; H, pot.

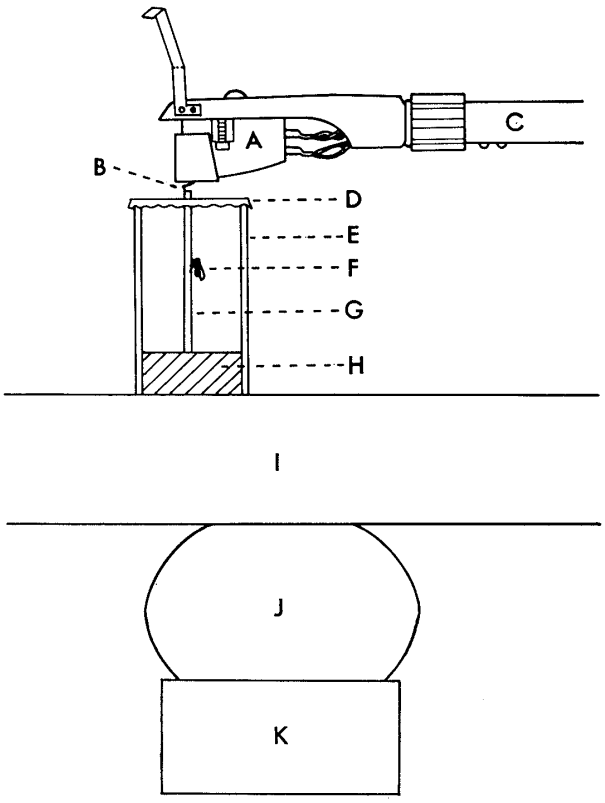

Fig. 2. An apparatus for the detection of vibrations of a rice plant caused by FAV. A, cartridge; B, stylus; C, tone arm; D, parafilm membrane; E, plastic cylinder; F, virgin female; G, stem of rice plant; H, polyurethan mat; I, wood plate; J, rubber ball; K, plastic cylinder.

Response of males to FAV of different species. The following experiments were conducted to evaluate the response of males of the three species to FAV of each species. Experimental methods used were the same as those mentioned above.

1. Two males of 2 different species were placed together on a paper disk and their response to FAV of each of the two species was observed. Thus, three combinations between two species were tested (See Fig. 1).

2. Three males of different species were placed together on the stem of a centrally positioned rice plant, and one female of each species was placed on the rice plant set at the right side. Response of these males to FAV of each species was observed when the leaf blades of the two rice plants were in contact. (See ICHIKAWA and ISHII, 1974)

Analyses of the substrate vibration caused by FAV. In order to detect vibrations of the rice plant caused by FAV, a cartridge (M–2100/5, Micro Sound Co. Ltd.) was attached on the stem of the rice plant on which one female had been placed (Fig. 2). Vibrations detected by the cartridge were amplified by an amplifier (PMA–350z, Nippon Columbia Co. Ltd.) and recorded (tape deck A–3300–2T, TEAC Co. Ltd.) on a sound tape (SLH–1100–BL, Sony Corp.). The experiments were conducted at a temperature of 25°±1°C. The recordings were fed on an oscilloscope (Model 181 A, Hewlett Packard), and oscillograms were analyzed.

Vibrations recorded on the sound tape were reproduced from a sound speaker

(Toa electric Co. Ltd.) and transmitted through a piece of thin paper on which one male of the same species had been placed. Male response to the vibrations was observed.

RESULTS

FAV and mating behavior

Virgin females of the three species of planthoppers began intermittent vibrations of their abdomens within one week following the last ecdysis, and was continued through almost their entire lives. Mated females, however, did not demonstrate this behavior. As seen in Fig. 3, females usually insert their stylets into the stem of the rice plant and vibrate their abdomens finely in a dorso-ventral direction without contacting the stem directly with their abdomens.

To observe the mating behavior of *N. lugens*, a pair of sexually matured planthoppers of both sexes were confined in a glass tube (2 cm in diameter and 17 cm in height) containing a rice seedling. Roots of the seedling were fixed with a piece of moistened polyurethane mat. A female was placed on the stem of the seedling.

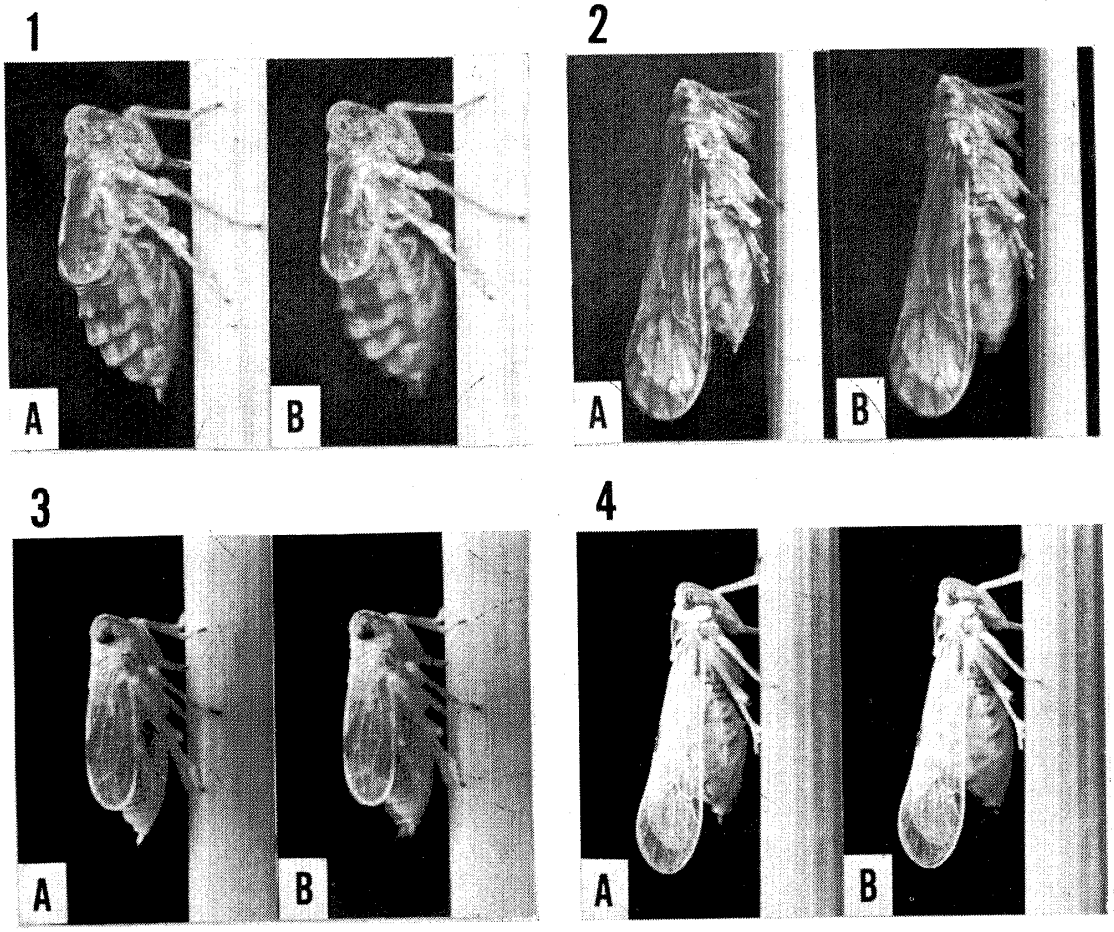

Fig. 3. FAV of the three species of planthoppers. 1, brachypterous female of *N. lugens*; 2, macropterous female of *N. lugens*; 3, brachypterous female of *L. striatellus*; 4, macropterous female of *S. furcifera*. A, not vibrating. B, vibrating. All photographs were taken at 1 sec. exposure.

When a male was released on the rice seedling or the polyurethane mat, it moved toward the female immediately after the initiation of FAV; movement on the mat or seedling stopped just after the cessation of FAV. Further movement was not observed unless FAV was resumed. Thus, the male approached the female while FAV was being performed and then copulated. On the contrary, when the male clung to the inner wall of the glass tube, it did not show any response to FAV even from a distance of about 1 cm from the female.

Observation of mating behavior was also conducted with *L. striatellus* and *S. furcifera* using the same method and similar results were obtained.

These observations of mating behavior suggest that males responded to the substrate vibration caused by FAV, and olfactory, visual and auditory senses do not participate in the mechanism(s) by which males perceive receptive females of respective species.

Male response to FAV on a thin paper disk

Fig. 4 shows examples of traces of male movement on paper disks. A large circle indicates the disk. A young rice plant on which one female had been placed is indicated as a solid circle in a small hole shown as a small circle in the center of the disk. Males of the three species did not show any response to FAV of the same species when the disk was not in contact with the stem of the rice plant and separated by only a few millimeters. On the contrary, the same males immediately responded to FAV of the same species and ran about the disk when the paper was in contact with the stem of the plant. Five males of each species were used for the present experiment, and all showed the same behavior described above.

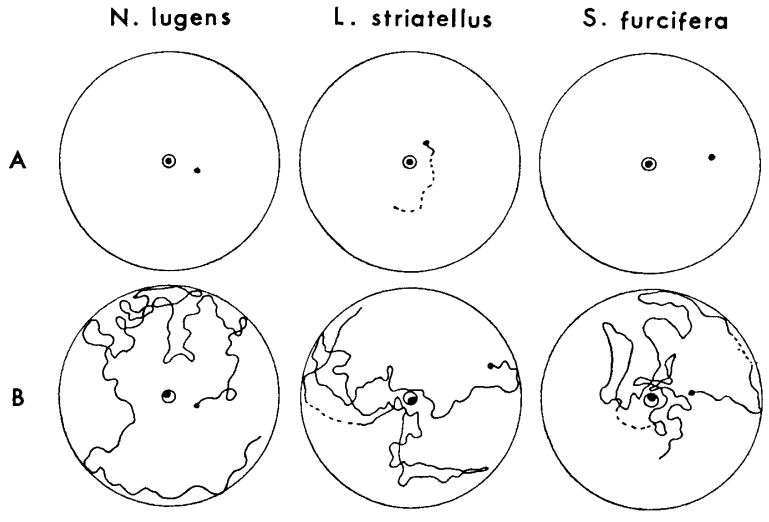

Fig. 4. Response of a male to FAV of the same species. Each large circle indicates a thin paper disk. A small circle and a small black circle in the center of each large circle indicate a small hole and the stem of rice plant, respectively. The stem was not in contact (A) and in contact (B) with the disk. Male movement accompanied with FAV was traced with solid lines, and that without FAV with dotted lines. Refer to Fig. 1.

The result of these experiments indicated that the males of the three species responded to the substrate vibrations which were caused by FAV and transmitted from the rice plants to the paper disks.

Attraction of males by FAV on rice plants

In the former experiments, males placed on the paper disks responded immediately to FAV of the same species, and ran about the disks. Most males, however, could not approach the females placed on stems of rice plants even from a distance of less than 8 cm. Therefore, the present experiments were undertaken to learn whether or not the males could respond and orient to FAV of the same species on the rice plants. The experimental method was the same as previously described (Ichikawa and Ishii, 1974).

Results of the experiments with the three species of planthoppers are shown in Table 1. The males did not show any response if a leaf blade of the rice plant on which a male had been placed was not in contact with a leaf blade of the adjacent rice plant where a female of the same species was vibrating her abdomen. On the contrary, in the case where two leaf blades of two adjacent rice plants were in contact, most males immediately responded to FAV, moved upward and across the contacted leaves, then down the stem to the female and displayed copulatory behavior. Some of the males moved upward and chose an opposite leaf blade at first, but returned midway and moved toward the female as mentioned above.

When a black cardboard screen was set between the center rice plant and outer ones to obstruct visual senses between both sexes, the male responded to FAV in the same manner.

The males of three species could respond to FAV and orient from a distance of 60 to 80 cm. The movement of the males on rice plants continued almost during FAV, and it stopped when FAV ceased. Two examples of *N. lugens* are shown in Fig. 5 and demonstrate synchronization between the duration of FAV and that of male movement.

Interspecific relation in the response of males to FAV

The following results were obtained in the three species of planthoppers by applying the same methods mentioned in the former two series of experiments. When

Table 1. Excitation and Attraction of Males by FAV of the Same Species on Rice Plants[a]

Female		Number of males[b] and direction of movement		
Species	Relative placement on rice plant	Left	Right	Stationary
N. lugens	Left	9	0	1
	Right	0	10	0
L. striatellus	Left	9	0	1
	Right	0	8	2
S. furcifera	Left	7	0	1
	Right	0	8	0

[a] Experimental method was the same as shown in the previous paper (Ichikawa and Ishii 1974). See text.

[b] The males were tested for each species, and each was placed on the rice plant set in the center.

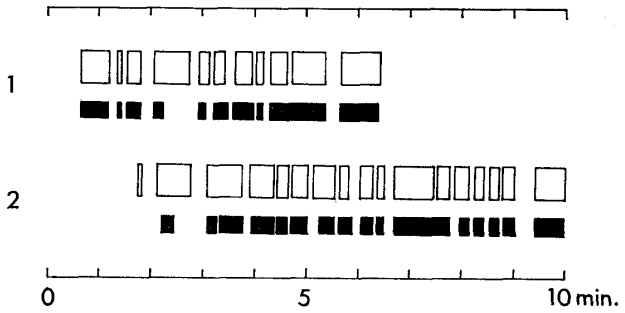

Fig. 5. Duration of FAV (hollow rectangles) and that of the male movement (solid rectangles) on rice plants observed in *N. lugens*. 1, brachypterous female and macropterous male; 2, macropterous female and macropterous male.

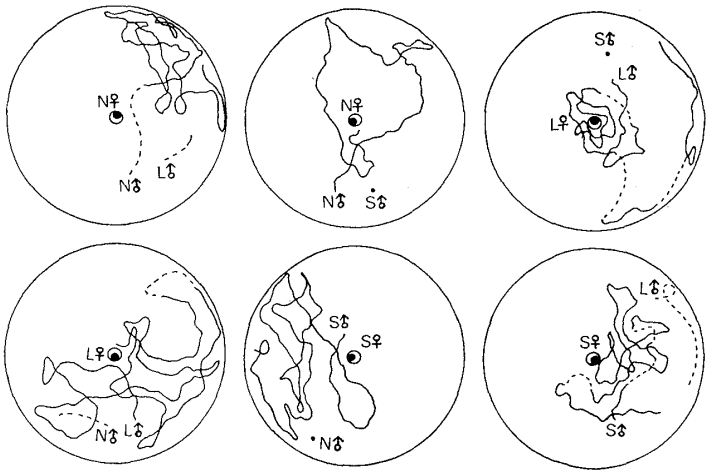

Fig. 6. Species specificity in the response of the males to FAV on a thin paper disk examined by the apparatus shown in Fig. 1 and 4. The rice plant was in contact with the paper disk throughout the experiment. N, *N. lugens*; L, *L. striatellus*; S, *S. furcifera*.

Table 2. SPECIES SPECIFICITY IN THE RESPONSE AND ORIENTATION OF THE MALES TO FAV ON RICE PLANTS[a]

Species	Female: Relative placement on rice plant	Number of males[b] and direction of movement					
		N. lugens		*L. striatellus*		*S. furcifera*	
		Right	Stationary	Right	Stationary	Right	Stationary
N. lugens	Right	5	0	0	5	0	5
L. striatellus	Right	0	5	5	0	0	5
S. furcifera	Right	0	5	0	5	5	0

[a] Experimental method was the same as shown in the previous paper (ICHIKAWA and ISHII 1974). See text.

[b] Males were placed on the rice plant set in the center.

males were placed on the paper disk, FAV of each species elicited a distinct response from males of the same species. However, FAV of a given species did not elicit behavioral response from the males of other two species (Fig. 6). When three males of different species were placed together on the rice plant, they only responded and oriented to FAV of the same species (Table 2).

Analyses of the substrate vibrations caused by FAV

As shown in Fig. 7, males of the three species clearly responded and ran about the paper when a playback of the substrate vibrations caused by FAV of the same species was transmitted to the paper.

These results were the same as those obtained in the response of males to the direct substrate vibrations caused by FAV.

Oscillograms of the substrate vibrations caused by FAV of the three species of planthoppers are shown in Fig. 8. Pulse repetition frequency of the substrate vibrations was almost the same in brachypterous and macropterous forms of each species. The frequency examined was different among the three species, i.e., ca. 20 per sec. in *N. lugens*, ca. 13 per sec. in *L. striatellus* and ca. 9 per sec in *S. furcifera* at 25°±1°C. The wave train in each pulse was also somewhat different among the three species.

Analysis of FAV of the three species by using a video taperecorder (Model SV-512J Shiba Electric Co. Ltd.) showed that one pulse was emitted during one dorso-ventral vibration of their abdomens.

DISCUSSION

Female abdominal vibration (FAV) has been observed in the mating behavior of the following species of Delphacid insects prior to copulation: *Calligypona lugubrina*,

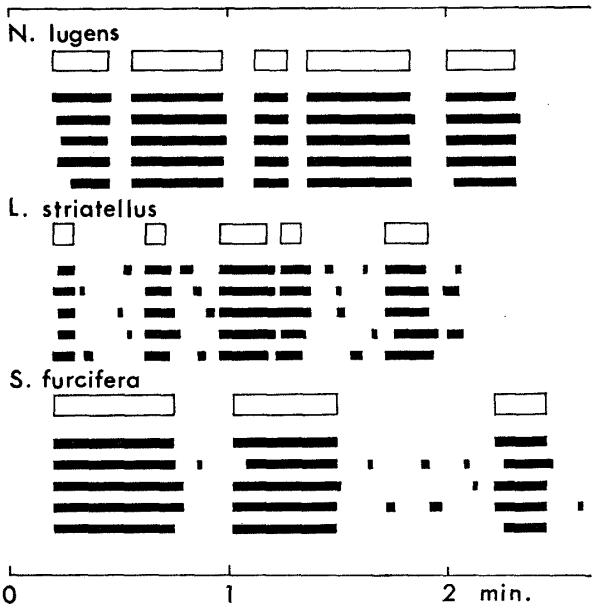

Fig. 7. Response of males on the thin paper disk to playback of vibrations caused by FAV of the same species. Duration of playback is shown as hollow rectangles, and duration of male movement as solid rectangles.

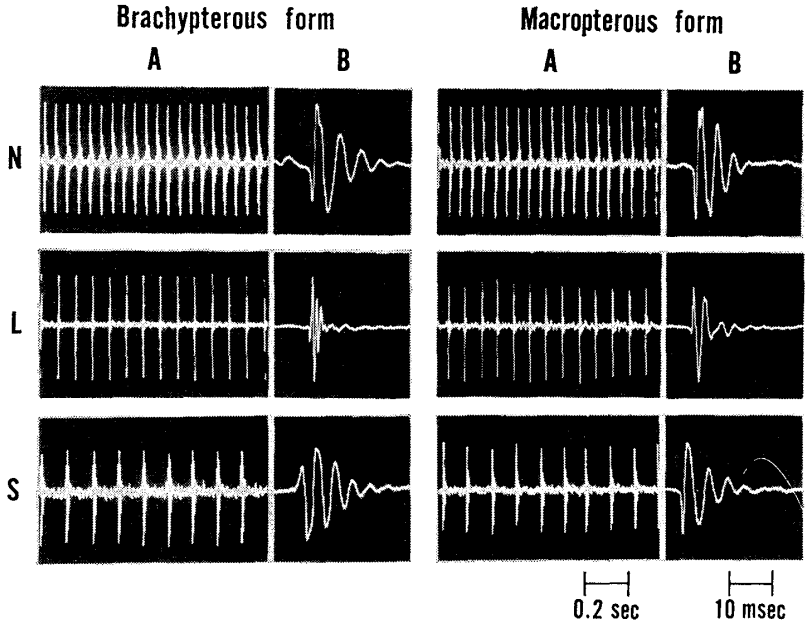

Fig. 8. Pulse repetition frequency (A) and wave train pattern in each pulse (B) in the vibrations of rice plant caused by FAV of the three species of planthoppers. N, *N. lugens*; L. *L. striatellus*; S, *S. furcifera*.

Calligypona adela, *Euidella speciosa* (STRÜBING, 1958, 1962) *Sogata orizicola* (MCMILLIAN, 1963), *Laodelphax striatellus* (OYAMA, 1972) and *Nilaparvata lugens* (TAKEDA, 1974). In the present study, FAV was also observed in *Sogatella furcifera*.

STRÜBING (1958, 1962) recorded very faint sounds emitted from both sexes of *C. lugubrina*, and concluded that acoustic stimuli might be a possible means of communication between both sexes. ICHIKAWA and ISHII (1974) and the present authors have revealed that FAV of *N. lugens*, *L. striatellus* and *S. furcifera* cause species specific substrate vibrations, and which are the mating signal for male perception of receptive females of the same species. On the basis of the behavioral similarity of receptive females belonging to different genera together with results obtained in the present study, it is reasonable to consider that vibrations of the host plants caused by FAV of planthoppers are responsible for excitation and attraction of males of the same species for mating.

OSSIANNILSSON (1949) detected sounds emitted by many species of small Auchenorryncha insects, and he considered that the sound emitted by these insects was transmitted to other individuals mainly by the solid substrate and only in a less degree by the air. Lack of an organ similar to the tympanal organ of cicadas in some of these insects and very low intensity of the sound were the bases of his consideration. Although morphological investigation of auditory organs was not carried out in the present study, there was no experimental evidence that air-borne sound plays a role in the communication between both sexes in the mating behavior of the three species of planthoppers, even when the distance between both sexes is only a few cm. Visual

and chemical stimuli were also not responsible for mating signals in these planthoppers. However, clarification and description of the types of sense stimuli which may play a role in the recognition of an appropriate mating partner just prior to copulation, were not achieved in the present study.

In three species of planthoppers, males of each species showed no behavioral response to substrate vibrations caused by FAV of other species. Such species specificity in male response to substrate vibrations might be due to the differences in the pulse repetition frequency of the vibrations and/or differences in the wave train of each pulse. Considering males in their natural habitat, those of the three species of planthoppers living simultaneously in paddy fields are able to seek out receptive females of the same species without any confusion at mating.

Males of the three species of planthoppers were observed to respond to FAV of the same species positioned not only on the same rice plant, but also from an adjacent rice plant. In the latter case, male response and orientation to FAV was observed when leaf blades of two plants were in contact and maximum effective distance between both sexes was about 80 cm (the longest distance examined thus far). Although the amplitudes of substrate vibrations were not measured, it is believed to be very small because of minute body size, (body length less than 4 mm and body weight less than 4 mg,) and subtle abdominal vibrations. It is speculated that males have specialized receptors which are sensitive to the substrate vibrations. This matter remains a problem for future study.

Studies on signals emitted by males and the role of the signals in the mating behavior of the three species of planthoppers are now in progress, and the results will be presented in subsequent papers.

ACKNOWLEDGEMENTS

The authors wish to acknowledge their indebtedness to Prof. S. UTIDA, and Prof. H. FUKAMI, Kyoto University, who have given their kind advice and suggestions during the present study. Thanks are also due to Miss K. OHTANI for assistance in the biological tests. This work was carried out in part with the aid of special grant from the Ministry of Education, Japan.

REFERENCES

ICHIKAWA, T. and S. ISHII (1974) Mating signal of the brown planthopper, *Nilaparvata lugens* STÅL (Homoptera : Delphacidae) : vibration of the substrate. *Appl. Ent. Zool.* **9**: 196–198.

McMILLIAN, W. W. (1963) Reproductive system and mating behavior of *Sogata orizicola* (Homoptera : Delphacidae). *Ann. ent. Soc. Am.* **56**: 330–334.

OSSIANNILSSON, F. (1949) Insect drummers. *Opuscula Entomol.* Suppl. X: 1–145.

OYAMA, M. (1972) Observation of mating behavior of planthoppers and leafhoppers. *Paper presented at the 32th Ann. Meet. of Entomol. Soc. Japan, Matsuyama, October*, 1972.

STRÜBING, H. (1958) Lautäusserung—der entscheidende Faktor für das Zusammenfinden der Geschlechter bei Kleinzikaden (Homoptera—Auchenorrhyncha). *Zoologisch Beiträge Neue Folge* **4**: 15–21.

STRÜBING, H. (1962) Paarungsverhalten und Lautäusserung von Kleinzikaden, demonstriert an Beispielen aus der Familie der Delphacidae (Homoptera—Auchenorrhyncha). XI. *Intern. Kongr. für Entomol.* Verhandlungen Band III (Symposien), 12–14.

TAKEDA, M. (1974) Mating behavior of the brown planthopper, *Nilaparvata lugens* STÅL. *Jap. J. appl. Ent. Zool.* **18**: 43–51 (In Japanese with English summary).