Feeding Habits of Leafhoppers

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Studies on feeding habits of green leafhoppers were initiated by Smith et al.[11] who carried out a comparative study with some leafhoppers of the genus *Empoasca*. Then, Putman[10] carried out a similar study on leafhoppers attacking fruit trees. Day et al.[1] compared differences in the insertion of stylets into a same host plant with a reference to virus transmission. Damage of crop plants caused by leafhoppers are closely related to their feeding habits, needless to cite the above studies, and its relation to virus transmission is also of importance. From this point of view, a whole picture of the author's research on the feeding habits of leafhoppers attacking crop plants in Japan will be summarized in the present paper.

Location of stylet insertion to host plants

1) Location of insertion at plant surface

The leaf of rice plants has a big midrib and a number of smaller veins running longitudinally. Along both sides of veins, stomatal cells are located with motor cells between them. At what location of such leaf surface structure is the stylet inserted? Examinations with *Nephotettix cincticeps* Uhler indicated that the insertion takes place most frequently at around stomata, followed by motor cells, and the direct insertion on veins is very rare, because veins are covered by a hard tissue of dumbbell-shaped cells to protect vascular bundles.

Although the insertion is made more frequently at the vicinity of stomata, the stomata is not necessarily discriminated from other cells and the insertion is made almost at random. Other kinds of leafhoppers also show a same tendency, but *Erythroneura limbata* Matsumura insert the stylets into stomata and intercellular space. It is interesting that this behavior is compared to that of aphids.[12]

It is a convenient method to detect the point of insertion by examining feeding marks. Leafhoppers excrete the salivary material at the time of stylet insertion to the portion not only surrounding the stylet but also between labium and plant surface. Taking advantage of the fact that the salivary material is well stained with basic dye, in contrast to plant tissues, the feeding marks are easily detected by the staining method. It can be identified under the microscope that the feeding mark varys in size almost proportionally to the size of insect and its shape differs with different kinds of insect. The size of feeding marks of some leafhoppers is shown in Table 1.

2) Location of stylet insertion in plant tissues

There are two methods, direct and indirect, to examine the point of insertion in plant tissues. In the direct method, insects are killed by an electric shock method just when their stylets are inserted, and then the cross section of the tissue is examined. This method requires a skill and is difficult to deal large number of insetcs. With *N. cincticeps*, the third instar larva is relatively suitable to be used for this test, but larva older than fourth instar and adult are difficult to be handled. On the other hand, in the indirect method the stylet sheath and the trace of stylet passage

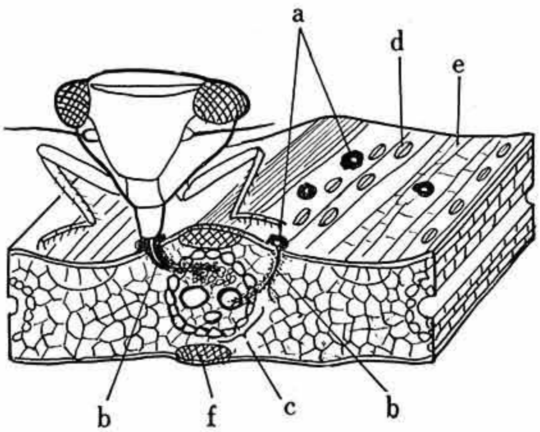

Fig. 1. Shematic illustration showing the stylet insertion to rice leaf by *Nephotettix cincticeps*

a: Feeding mark b: salivary sheath
c: Vascular bundle d: stomatal cell
e: Moter cell f: Dambbell-shaped cell

which are produced by the stylet insertion are examined with continuous sections of the tissue. The advantage is that it is easy to handle a large number of feeding marks. Examination of stylet insertion by *N. cincticeps* to rice plant revealed that 70.3% reached to vascular bundle and the balance reached to other parenchymatous tissues. With rice leaves, application of xylol which makes leaves transparent is also useful to know approximately the destination of inserted stylets. The destination differs with kind of leafhoppers, as described below.

Table 1. Size of feeding marks of some leafhoppers (adult) living in paddy field (Number examined: 40)

Species		Size
Tettigella viridis	♀	210×177±26μ
	♂	184×164±24
Nephotettix cincticeps	♀	73× 61±13
	♂	63× 53±13
Inazuma dorsalis	♀	52× 49± 7
	♂	47× 43± 6
Macrosteles horvathi	♀	40× 36± 5
	♂	38× 34± 5

3) Comparison of feeding habits based on the location of stylet insertion

Adults of 10 species of leafhoppers which attack crops were caged together with *Sorghum bicolar* (graminous) or *Trifolium repens* (leguminous). After 2 days of feeding in the cages, the location of stylet insertion was determined by examining salivary sheath and trace of stylet passage on continuous sections of plant tissue. Results are given in Tables 2 and 3. Interesting is that no difference in the basic feeding habits occurred in spite of such a difference in host plants as graminous vs leguminous plant. From these results, the feeding habits of leafhoppers can be classified as follows:

- Vascular bundle feeder
  - more insertion to phloem
  - more insertion to xylem
- Mesophyll feeder

Table 2. Frequency distribution of stylet insertion in different leaf tissues of sorgo

Species	No. salivary sheath examined	Vascular bundle: parenchymatous tissue %	No. salivary sheath examined	Phloem: Xylem %
Tettigalla viridis	477	57.8 : 42.2	309	31.2 : 68.8
Nephotettix cincticeps	211	79.0 : 21.0	46	43.4 : 56.6
Psammotettix striatus	365	79.3 : 20.7	88	77.2 : 22.8
Deltocephalus sp.	166	74.3 : 25.7	56	56.6 : 43.4
Thammnotettix tobai	531	78.5 : 21.5	152	69.6 : 30.4
Macrosteles horvathi	857	75.3 : 24.7	197	60.0 : 40.0
Balclutha viridis	96	68.3 : 31.7	—	—
Stragania diminuta	100	23.3 : 76.7	—	—
Empoasca sakaii	174	26.1 : 73.9	—	—
Erythroneura limbata	613	1.9 : 98.1	—	—

Table 3. Frequency distribution of stylet insertion in different leaf petiole tissues of *Trifolium repens*

Species	No. salivary sheath examined	Vascular bundle : parenchymatous tissue %	No. salivary sheath examined	Phloem : Xylem %
Tettigella viridis	263	71. 6 : 28. 4	207	31. 6 : 68. 4
Nephotettix cincticeps	249	65. 0 : 35. 0	210	38. 8 : 61. 3
Psammotettix striatus	160	53. 6 : 46. 4	96	81. 1 : 18. 9
Thammnotettix tobai	94	57. 6 : 42. 4	60	88. 9 : 11. 1
Macrosteles horvathi	354	67. 0 : 33. 0	265	88. 4 : 11. 6
Balclutha viridis	104	58. 0 : 42. 0	69	94. 5 : 5. 5
Stragania diminuta	128	49. 3 : 50. 7	72	69. 1 : 30. 9
Empoasca sakaii	132	55. 6 : 44. 4	95	91. 1 : 8. 9
Erythroneura limbata	371	16. 4 : 83. 6	70	98. 6 : 1. 4

Vascular bundle feeders are *Tettigella viridis* L., *Nephotettix cincticeps* Uhler, *Psommotettix striatus* L., *Deltocephalus sp.*, *Thammnotettix tobai* Matsumura, *Macrosteles horvathi* Wagner, *Balclutha viridis* Matsumura, and *Stragania diminuta* Matsumura. Of them, *Tettigella viridis* feeds more phloem, *Nephotettix cincticeps* feeds phloem and xylem equally, and the others feed more phloem. Some of the last ones seem to be phloem feeders.

Erythroneura limbata Matsumura belongs to the mesophyll feeder, and *Empoasca sakaii* Dworakowska has a duality of mesophyll feeder and vascular bundle feeder (in this case phloem feeder).

How does the leafhopper insert the stylets so as to reach the intended location? Fife[2] suggested that the high pH of phloem may have an important bearing on the insertion to the phloem. However, based on more detailed experiments, Day et al.[1] suggested that although there is no definite direction of insertion, the stylets get the location by trial and error. Recently, Forbes et al.[3] found the existence of nerve tissue running longitudinally in stylets, mandibular and maxillar stylets, with it top contacting the outisde. Behavior of stylet insertion needs to be reexamined from such viewpoint.

4) Comparison of feeding habits among different growth stages of insects

Feeding habits of *N. cincticeps* was examined at each instar and adult stage using Sorgo as a host plant. As given in Table 4, almost no difference in feeding habits was observed between larval and adult stage, except male adult showed a tendency to feed more on phloem.

Table 4. Frequency distribution of stylet insertion to different leaf tissues of sorgo by *Nephotettix cincticeps*

Developmental stage of insect	No. salivary sheath examined	Vascular bundle : parenchymatous tissue %	No. salivary sheath examined	Phloem : Xylem %
Larva I Instar	333	70. 9 : 29. 1	15	47. 1 : 52. 9
II	596	66. 7 : 33. 3	98	33. 3 : 66. 6
III	497	60. 8 : 39. 2	101	41. 1 : 58. 9
IV	468	63. 8 : 36. 2	71	40. 7 : 57. 3
V	300	54. 6 : 45. 4	57	43. 6 : 56. 4
Mean		63. 4 : 36. 6		41. 2 : 58. 8
Adult ♀	211	79. 0 : 21. 1	46	43. 4 : 56. 6
♂	204	65. 6 : 34. 4	48	53. 7 : 46. 3
Mean		72. 3 : 27. 7		48. 6 : 51. 5

Stylet insertion behavior

Usually a leafhopper insert stylets to host plant several ten times a day. Frequency of stylet insertion of *N. cincticeps* to matured leaves of rice averages about 40 times a day at a room temperature. Considering the life duration of adult, the total frequency during an adult period comes to be as high as 12,485 ±4,343 times.

1) Diurnal changes of insertion behavior

Insertion behavior of leafhoppers shows apparent diurnal fluctuations. Result of observation with *N. cincticeps* on rice leaves is given in Fig. 2. During a daytime, the insects do not move, keeping their stylets being inserted into leaves, but in the evening, especially during a period between 5 to 9 p.m., the insects behave vigorously, repeating the insertion successively. After 10 p.m. they rest again. In early morning 5 to 6 a.m., the frequency of insertion is slightly high. Such diurnal pattern was recognized with *Hishimonus sellatus* Uhler too[4], which gave more apparent bimodal crepuscular type.

2) Insertion frequency as related to temperature and host plants

The insertion frequency increases with an increase of temperature up to 30°C, but it

Table 5. Frequency of stylet insertion to rice leaf by female adult of *Nephotettix cincticeps*

No. insect examined	Average frequency/day	Total frequency of stylet insertion during an adult period	Period of adult stage (days)
8	43.7±9.2	12,485±4,343	29.0

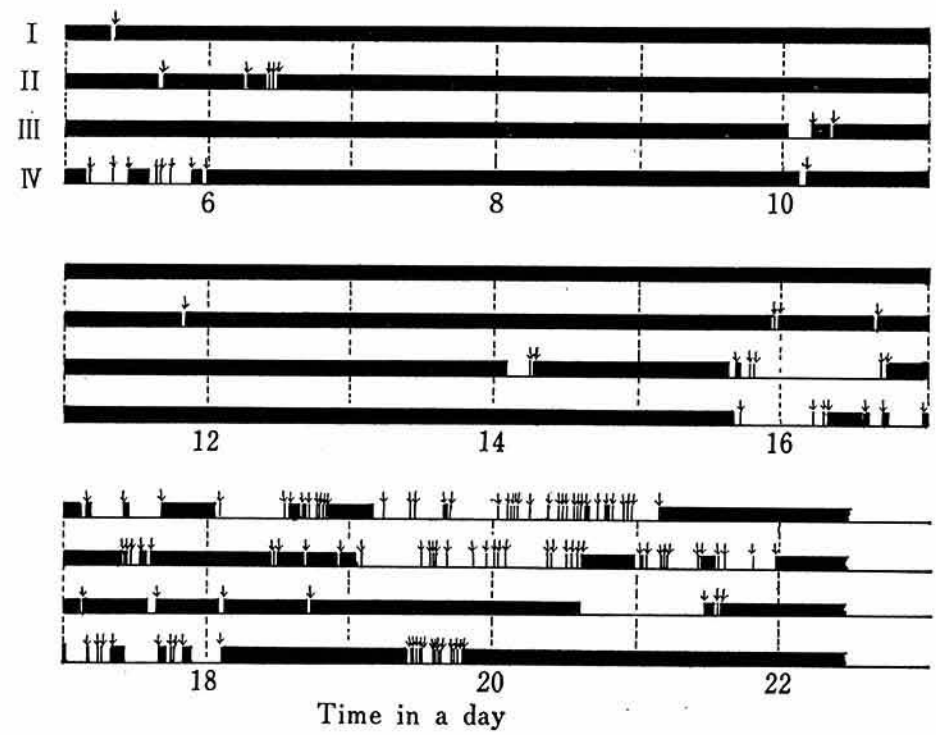

Fig. 2. Diurnal change of feeding behavior of *Nephotettix cincticeps* (observed on 21 August)
Arrow: Begining of stylet insertion, Black band : Duration of insertion
I and II: Female adult, III and IV: Male adult

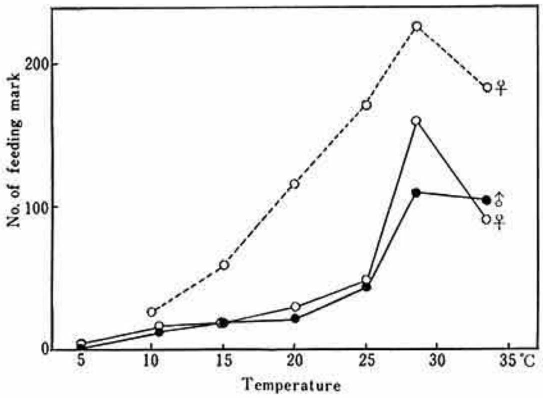

Fig. 3. Relation between frequency of stylet insertion of *Nephotettix cincticeps* adult and temperature (in 48 hr)

Dotted line: Insect sampled from host plant *Alopeculus aequalis* Sobol, var *amurensis* Ohwi in field

Solid line: Insect grown in rearing room with rice plants as host plant

decreases at 35°C (Fig. 3). Male shows a tendency of slightly higher frequency than female. The frequency varys with kinds of host plant too. The insects transferred to rice plant after feeded on *Alopecurus aequalis* Sobol. var. *amurensis* Ohwi growing in April showed a considerably high frequency, as shown in Fig. 3.

The insertion frequency seems to be closely related to the movement activity of insect. It may possibly be used as an indicator of the movement activity. Further research is expected.

It is doubtless that the insertion aims at feeding, but it is not clear why the insertion is made so frequently from one place to another. Experimental data on quantitative relationship between the amount of plant sap sucked and the frequency of stylet insertion are not available. But, based on the result of observations on honeydew which is excreted during the sucking of plant sap, it is assumed that the amount of sucked sap is inversely related to the insertion frequency, because the excretion of honeydew is apparently less during a period of high frequency of stylet insertion.

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