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Studies on the Feeding Habits of the Brown Planthopper, *Nilaparvata lugens* (STÅL) (Hemiptera : Delphacidae) IV. Probing Stimulant

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The brown planthopper was observed to make only infrequent attempts to probe the aerial space or distilled water behind a parafilm membrane. Most of the stylet sheaths produced in these regions were very short and did not branch. Sucrose and aspartic acid showed little influence on the probing response despite their action as sucking stimulants. Salicylic acid was found to stimulate the stylet probing, and its optimum effect was recorded when 0.001 to 0.004 M salicylic acid was present together with 2% sucrose. In such media, the planthopper deposited a large number of branched and well extended stylet sheaths similar to those produced in rice plant tissues, indicating an enhanced stylet probing response. Other aromatic monocarboxylic acids occurring in rice plants had no effect. Salicylic acid suppressed the sucking response at the efficient concentrations as the probing stimulant. The saps obtained from rice plants and four kinds of non-host plants stimulated stylet probing of the brown planthopper.

INTRODUCTION

The feeding process of the brown planthopper, *Nilaparvata lugens*, whose sucking sites are restricted to the vascular elements of the host plants (SŌGAWA, 1970a, b), consists of two distinct behavioral phases; namely, probing which is performed in non-digestible parenchymal tissues, and sucking which takes place after penetration into digestible vascular elements. It is considered that they are independent from and incompatible with each other, being under the control of particular sets of stimuli occurring in either parenchymal tissues or vascular elements.

Recently an important role of dietary carbohydrates and amino acids is being realized as sucking stimulatory factors for various hemipterous insects (FEIR and BECK, 1963; AUCLAIR, 1965; MITTLER, 1967a,b,c; ARN and CLEERE, 1971; HARREWIJN and NOORDING, 1971; KLINGAUF and NÖCKER-WENZEL, 1972; SŌGAWA, 1972). Several kinds of botanically restricted substances have also been reported to have a significant influence to the preferential behaviors of the insects through gustation, duration and frequency of the stylet penetration, and the rate of sap intake (WENSLER, 1962; SMITH, 1966; DAHLMAN and HIBBS, 1967; MOON, 1967; WENSLER, 1968; KLINGAUF, 1971; NAULT and STYER, 1972; SCHOONHOVEN and DERKSEN-KOPPERS, 1973); and some of them have been referred to as arrestants or phagostimulants.

So far little attention has been paid to the specific chemical stimulants involved in the probing reactions. This report deals with the probing response of the brown planthopper in various liquid media, and evidence is presented that salicylic acid serves as a probing stimulant for this species. A preliminary discussion concerned with the possible role of salicylic acid in the sucking site location within the host plant tissues, is presented in the latter part of this report.

MATERIALS AND METHODS

Insects. Macropterous female adults were taken from a stock colony of brown planthoppers, which had been maintained on rice seedlings in the laboratory for several years.

Probing media. Tested chemicals were dissolved either in distilled water or in sucrose solution (2 or 20%) at known concentrations and offered to insects. Distilled water was used as a test medium as well as a control. Penetration of the stylet into the aerial space behind a stretched parafilm was also observed. Plant saps from rice (*Oryza sativa*), chikenpanic grass (*Echinochloa Crus-galli* var. *hispidula*), umbrella sedge (*Cyperus microiria*), cabbage (*Brassica oleracea* var. *capitata*), and sweet potato (*Ipomoea Batatas*) were tested. With the exception of rice, the plants are not hosts of the brown planthopper. The plant saps were obtained by pressing the fresh aerial parts of each plant species; the exudate was immediately boiled for a few minutes to inactivate enzymes and for deproteinization, and then filtrated. The filtrate was directly used as the probing medium.

Bioassay for the probing response. For each test, ten insects were confined in a plastic cup (80 ml), whose open end was closed with a sheet of stretched parafilm. The cup was then inverted on a watch glass containing the test medium, so as to enclose the medium between the parafilm membrane and watch glass (Fig. 1). The insects were allowed to probe the medium through the parafilm membrane for a 24 hr period at 25—28°C under fluorescent lamps. At the end of this period, the stylet sheaths deposited on the parafilm membrane were stained with basic fuchsin and observed microscopically. As measures of the effects of each chemical or plant sap on insect probing, the length and branching of the stylet sheaths were recorded. Because the data contained a wide range of values and the frequency distribution was not normal, the numerial values of stylet sheat length (Xmm) were subjected to the transformation ($\sqrt{100X}$) to stabilize the variance before the *t*-test was applied.

Bioassay for the sucking response. Liquid intake was measured by incorporating $^{32}P\text{-}H_3PO_4$ into the probing media. The insects, which sucked the labelled media,

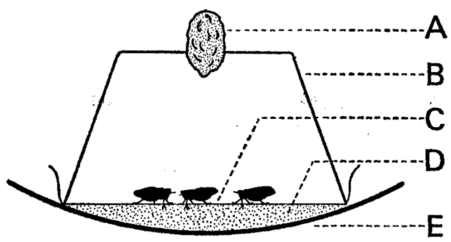

Fig. 1. Apparatus to assay the probing responses of the female adults of the brown planthopper for various artificial media. A, cotton plug; B, plastic cup; C, stretched parafilm; D, probing medium; E, watch glass.

were digested in concentrated nitric acid by heating under an infra red lamp, and their radioactivity was measured with an Aloka SC-IC automatic 2π thin window gas flow G–M counter.

RESULTS

Probing response for aerial space, distilled water, and sucking stimulatory chemicals

In a preliminary experiment, the probing response for the aerial space behind a parafilm membrane, distilled water, sucrose solution and aspartic acid solution were observed. Almost all of the stylet sheaths produced in the aerial space and distilled water were short and rod-like, having a length of about 0.045 mm and 0.06 mm, respectively (Fig. 3A). As shown in Fig. 2, the frequency distribution of sheath lengths was asymmetrical, and the maximum frequency appeared at 0.05 mm. Similar stylet sheaths were deposited in aqueous solutions of sucrose and aspartic acid of various concentrations (Table 1, Fig. 3B). In these media, branched sheaths were rather exceptionally formed, and the insects attempted only superficial probings in most cases, although slightly deeper penetration was seen to occur for the sucrose solutions.

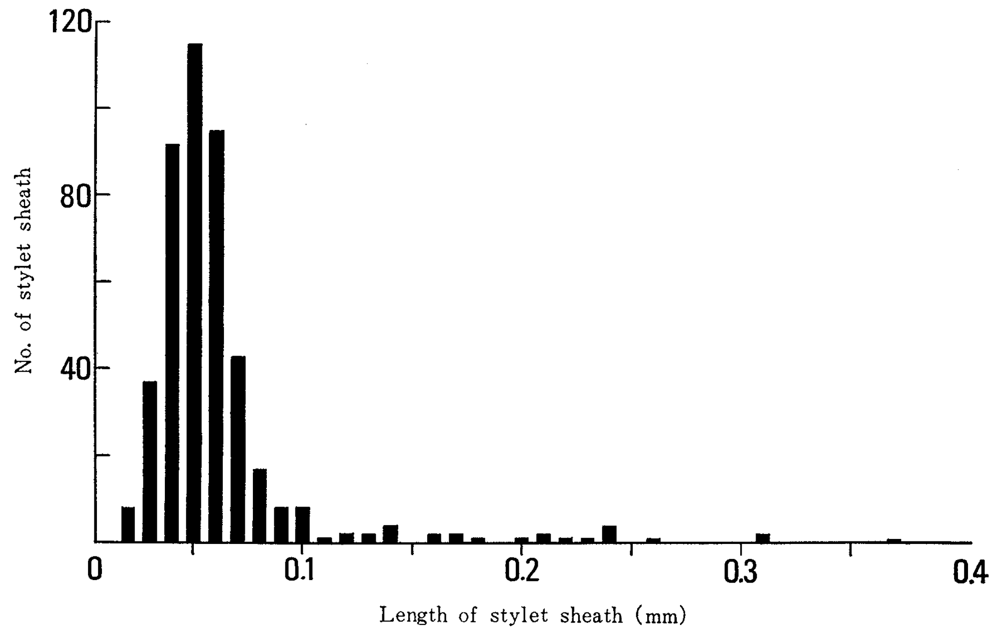

Fig. 2. Frequency distribution of the length of 450 stylet sheaths deposited in distilled water.

Probing response for plant saps

The planthoppers deposited apparently longer and more branched stylet sheaths in the rice plant sap, and even in the non-host plant saps tested here than in distilled water (Table 2). It was noticed, however, that branched sheaths were only infrequently produced in the non-host plant saps as compared to the rice plant sap.

Probing response for salicylic acid and related chemicals

In a series of experiments, the effects of 0.005 M aqueous solution of several kinds of aromatic monocarboxylic acids, which were known to be present in rice plants

Table 1. The Probing Responses of the Female Adults of the Brown Planthopper for Sucrose, Aspartic Acid, Distilled Water and Aerial Space

Compound (M)	Average length of sheath		Stimulated probe (≥0.12 mm) (%)	% Sheath with indicated number of branch			
	Numerical value (mm)	Transformed value (±S. E.)		1	2	3	≥4
Sucrose							
1.2	0.075	2.68±0.07[a]	6	99.5	0.5	0.0	0.0
1.0	0.081	2.79±0.07[a]	12	98.3	1.4	0.0	0.3
0.8	0.097	2.96±0.13[a]	20	99.6	0.2	0.2	0.0
0.6	0.089	2.91±0.08[a]	18	98.5	1.5	0.0	0.0
0.4	0.096	3.05±0.11[a]	22	97.3	1.6	1.1	0.0
0.2	0.080	2.70±0.11[a]	18	97.0	1.5	1.5	0.0
Aspartic acid							
0.4	0.052	2.36±0.06[a]	4	98.6	0.0	1.4	0.0
0.2	0.063	2.46±0.07[a]	6	98.3	1.7	0.0	0.0
0.1	0.067	2.50±0.09[a]	12	100.0	0.0	0.0	0.0
0.05	0.056	2.27±0.08[a]	4	100.0	0.0	0.0	0.0
Distilled water	0.061	2.39±0.01	5	98.7	0.7	0.6	0.0
Aerial space	0.045	2.09±0.05	2	100.0	0.0	0.0	0.0

[a] Means in the same block with the same superscript letter are not significantly different at the 5% level in *t*-test.

Table 2. The Probing Responses of the Female Adults of the Brown Planthopper for the Saps of Host and Non-Host Plants

Plant sap	Average length of sheath		Stimulated probe (≥0.12 mm) (%)	% Sheath with indicated number of branch			
	Numerical value(mm)	Transformed value (±S. E.)		1	2	3	≥4
Rice	0.171	3.99±0.11[ab]	70	33.3	25.0	11.7	30.0
Chicken-panic grass	0.143	3.65±0.11[a]	28	73.9	15.3	5.9	4.9
Umbrella sedge	0.211	4.45±0.14[bc]	45	57.6	26.8	10.8	4.8
Cabbage	0.241	4.82±0.13[c]	46	89.8	8.6	1.6	0.0
Sweet potato	0.198	4.34±0.14[bc]	39	78.6	12.4	6.2	2.8

[a~c] Means with the same superscript letter are not significantly different at the 5% level in *t*-test.

(Kuwatsuka and Oshima, 1961; Ishii et al., 1962), were tested (Table 3). Among the compounds tested, salicylic acid was noticed by an evidence that it definitely, though to a lesser extent, activated the probing. The mean length of sheaths produced in salicylic acid was 0.08—0.09 mm, while less than 0.07 mm in the other chemicals. The effect of salicylic acid was therefore further tested at various concentrations ranging from 0.0005 to 0.008 M either in the presence or absence of sucrose (Table 4). Through these experiments, it was evident that salicylic acid could promote stylet probing at concentrations greater than 0.001 M, and its effect was remarkably potentiated in the presence of sucrose. The optimum effect was exerted when 0.001 to 0.004 M salicylic acid coexisted together with 2% sucrose in the probing media. In such media, sometimes nearly 50% of sheaths were branched, and a considerable number of them had more than three branches (Fig. 3C). Even single tubular ones

Table 3. The Probing Responses of the Female Adults of the Brown Planthopper for Aromatic Monocarboxylic Acid Occurring in the Rice Plants

Compound[a]	Average length of sheath		Stimulated probe (≥0.12 mm) (%)	% Sheath with indicated number of branch			
	Numerical value (mm)	Transformed value (±S. E.)		1	2	3	≥4
Salicylic acid	0.085	2.84±0.06[b]	19	92.6	5.3	1.1	1.0
Benzoic acid	0.068	2.53±0.06[c]	9	99.4	0.6	0.0	0.0
Ferulic acid	0.055	2.32±0.03[d]	0	99.4	0.6	0.0	0.0
p-Hydroxybenzoic acid	0.055	2.28±0.05[d]	1	98.3	1.7	0.0	0.0
p-Coumalic acid	0.054	2.26±0.04[d]	2	99.7	0.3	0.0	0.0
Vanillic acid	0.043	2.03±0.04[e]	1	99.8	0.0	0.2	0.0

[a] 0.005M in distilled water.

[b~e] Means with the same superscript letter are not significantly different at the 5% level in *t*-test.

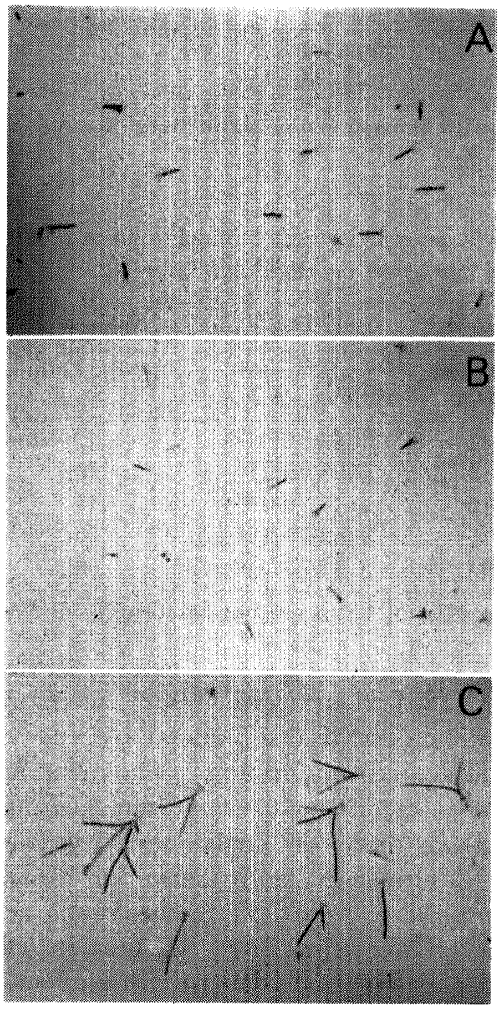

Fig. 3. The stylet sheaths (×27) produced in distilled water (A), 1% sodium aspartate aqueous solution (B), and 2% sucrose solution containing 0.004 M salicylic acid (C).

Table 4. THE PROBING RESPONSES OF THE FEMALE ADULTS OF THE BROWN PLANTHOPPER FOR SALICYLIC ACID

Concentration of salicylic acid (M)	Average length of sheath		Stimulated probe (≥0.12 mm) (%)	% Sheath with indicated number of branch			
	Numerical value (mm)	Transformed value (±S. E.)		1	2	3	≥4
(without sucrose)							
0.008	0.099	3.05±0.05[ab]	28	88.7	8.0	2.0	1.3
0.004	0.096	2.99±0.06[ab]	23	94.1	5.1	0.7	0.1
0.002	0.106	3.14±0.06[a]	34	81.3	13.3	3.9	1.6
0.001	0.090	2.87±0.06[b]	24	96.7	2.9	0.4	0.0
0.0005	0.074	2.63±0.06[c]	13	95.0	3.8	0.6	0.6
0	0.061	2.38±0.05[d]	7	99.6	0.0	0.4	0.0
(with 2% sucrose)							
0.008	0.114	3.27±0.08[b]	34	73.2	17.6	6.2	2.0
0.004	0.176	4.07±0.11[a]	67	47.4	24.5	16.9	11.2
0.002	0.170	3.98±0.10[a]	71	83.4	9.8	3.5	3.3
0.001	0.146	3.79±0.10[a]	71	84.5	8.7	4.2	2.6
0.0005	0.106	3.19±0.08[b]	37	87.0	8.7	4.3	0.0
0	0.084	2.74±0.09[c]	24	91.3	3.9	4.8	0.0
(with 20% sucrose)							
0.008	0.139	3.60±0.09[a]	53	86.8	10.7	2.5	0.0
0.004	0.144	3.70±0.09[a]	60	80.0	13.5	3.7	2.8
0.002	0.142	3.63±0.09[a]	53	83.5	10.5	3.6	2.4
0.001	0.095	3.00±0.06[b]	23	78.9	14.0	3.9	3.2
0.0005	0.077	2.70±0.05[c]	14	93.4	5.3	1.3	0.0
0	0.078	2.72±0.06[c]	12	97.8	1.5	0.0	0.7

[a~d] Means in the same block with the same superscript letter are not significantly different at the 5% level in *t*-test.

were as long as 0.16 to 0.18 mm in average length. Occasionally they were longer than 0.3 mm. The stylet sheaths formed in the above media were generally the same as those in the rice plant sap.

In similar experiments, several chemicals related to salicylic acid were tested at a concentration of 0.005 M in combination with 2% sucrose solution in order to evaluate their effects on the probing response. In dinitrosalicylic acid, significantly longer sheaths were deposited than in the salicylic acid medium, where the sheaths shorter than 0.1 mm length were scarcely recognized (Table 5). The longest one was 0.43 mm. The other compounds tested were all apparently less effective than salicylic acid.

Effect of salicylic acid on sucking response

In an attempt to evaluate the effect of salicylic acid on liquid intake, it was offered to the insects incorporating ^{32}P–H_3PO_4 in 20% sucrose solution. Sucrose acted as a sucking stimulant for the brown planthopper, and its maximal intake was obtained at 0.6 M(about 20%). In the presence of salicylic acid above 0.001 M, the intake of sucrose solution decreased proportionally with increase of salicylic acid concentration, and the insect sucking was almost completely inhibited at 0.008 M (Table 6).

Table 5. THE PROBING RESPONSES OF THE FEMALE ADULTS OF THE BROWN PLANTHOPPER FOR SEVERAL COMPOUNDS RELATED TO SALICYLIC ACID

Compound[a]	Average length of sheath		Stimulated probe ($\geq$0.12 mm) (%)	% Sheath with indicated number of branch			
	Numerical value (mm)	Transformed value ($\pm$S. E.)		1	2	3	$\geq$4
Dinitrosalicylic acid	0.238	4.76 ± 0.10^{e}	94	77.8	15.7	4.5	2.0
Salicylic acid	0.163	3.91 ± 0.09^{c}	71	66.0	20.2	9.2	4.6
Protocatechuic acid	0.122	3.40 ± 0.08^{d}	50	90.4	6.4	2.4	0.8
p-Hydroxybenzoic acid	0.113	3.24 ± 0.09^{d}	35	87.2	6.5	4.8	1.5
p-Chlorobenzoic acid	0.107	3.17 ± 0.07^{d}	38	87.9	7.2	4.1	0.8
Gallic acid	0.106	3.15 ± 0.08^{d}	30	93.8	3.5	1.9	0.8
Control (2% sucrose)	0.083	2.69 ± 0.06^{e}	11	93.7	4.9	1.4	0.0

[a] 0.005M in 2% sucrose solution.
[b~e] Means with the same superscript letter are not significantly different at the 5% level in *t*-test.

Table 6. EFFECT OF SALICYLIC ACID ON THE SUCKING RESPONSES OF THE FEMALE ADULTS OF THE BROWN PLANTHOPPER[a]

Concentration of salicylic acid (M)	Mortality (%)	Total No. of sheath formed	Radioactivity ingested (ratio)	Radioactivity ingested / No. of sheath (ratio)
0.008	100	178	0.01	0.07
0.004	65	229	0.15	0.08
0.002	30	182	0.25	0.14
0.001	5	64	0.64	0.79
0.0005	0	38	0.95	1.86
0 (20% sucrose)	10	68	1.00	1.00

[a] Data are an average of two replications, each containing ten insects.

DISCUSSION

As reported in the previous paper (SŌGAWA, 1970a), the brown planthopper deposits stylet sheaths having a coherent tubular structure in the course of probing within the rice plant tissues. The insects usually insert the stylets repeatedly to various direction through the same point of entry, and branched sheaths are consequently formed. The stylet insertion is considered to be regulated by certain chemical factors rather than physical factors, because the brown planthopper produces sheaths similar to those deposited in the live plant tissues when allowed to probe the rice plant sap through a parafilm membrane, whereas they probed only sparingly into aerial space or distilled water.

MITTLER and DADD (1965) reported marked differences in the probing response of the aphid, *Myzus persicae*, in various media. They considered that shallow probing could result from at least two possible causes, either rapid stylet withdrawal after brief probes into relatively unacceptable diets or prolonged sucking without penetration into acceptable diets. Diets of intermediate preference evoke a production of long sheaths as a result of exploratory response. In this explanation, the probing response is regarded as a subordinate phenomenon to the sucking response, and difference in the length of sheaths is accounted for in relation to acceptability of the media for sucking. The results obtained in the present study do not necessarily support this idea. It has been shown that sucrose and aspartic acid act as phagostimulants for the brown planthopper (Sōgawa, 1972, 1973), but the probing responses were almost constant throughout the concentrations tested. This evidence clearly indicates that probing and sucking are behavioral responses independent from each other, which are governed by different chemical stimuli.

It was evident that brown planthoppers produced stylet sheaths with considerable variation in length depending on the chemical nature of the given media. The short rod-like sheaths (0.02—0.06 mm) were generally considered to be a reflection of rapid interruption of probing after a single thrust of the stylet insertion and a single puff of sheath saliva. Almost all sheaths deposited when the planthopper probed aerial space or distilled water were of this type. On the other hand the type of elongated sheaths that were often found, for example, in the rice plant sap were thought to be formed by sequential motion of the stylets and secretion of sheath saliva, as described by Sōgawa(1971). Nault and Gyrisco(1966) have also mentioned that aphids make two types of stylet probes which are termed the test probe and the phloem-seeking probe. For the present study, probings more than 0.12 mm depth were tentatively regarded as stimulated probing, since deeper probings were seldom made in aerial space and distilled water. A positive correlation (r=0.83) was found between the percentage of stimulated probing and the transformed mean value for the length of sheaths produced in each medium tested, as shown in Fig. 4. The percentage of branched sheaths which increased with an increase in the average length of sheaths, attained a maximum at about 4.0 (0.16 mm), and again tended to decrease (Fig. 5). This indicates that excessively deep penetrations tend to reduce the repeated probings toward different directions through the same point of entry. Such an example can be found in the probing response for the cabbage sap or dinitrosalicylic acid-sucrose solution.

Salicylic acid was discerned to be a probing stimulant of the brown planthopper. Planthoppers tended to produce more densely branched and longer stylet sheaths in media containing salicylic acid above 0.001 M. Formation of such branched and

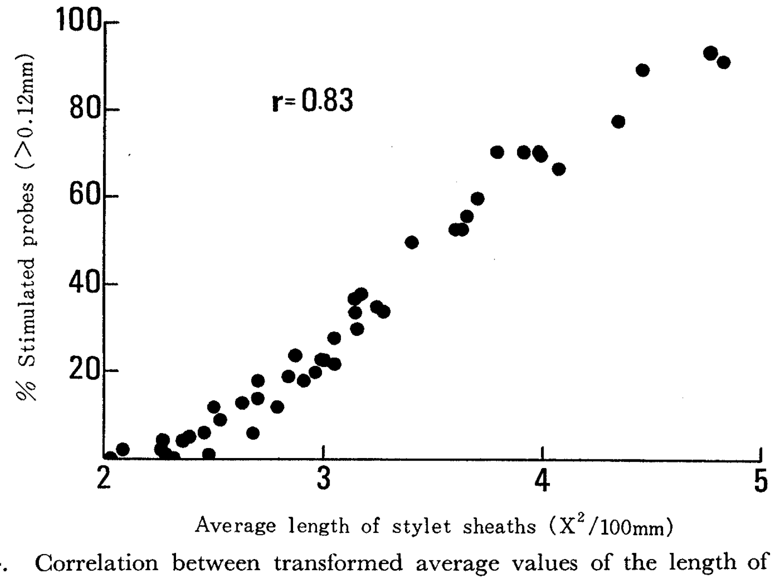

Fig. 4. Correlation between transformed average values of the length of stylet sheaths and percentages of the stimulated probes made in various media.

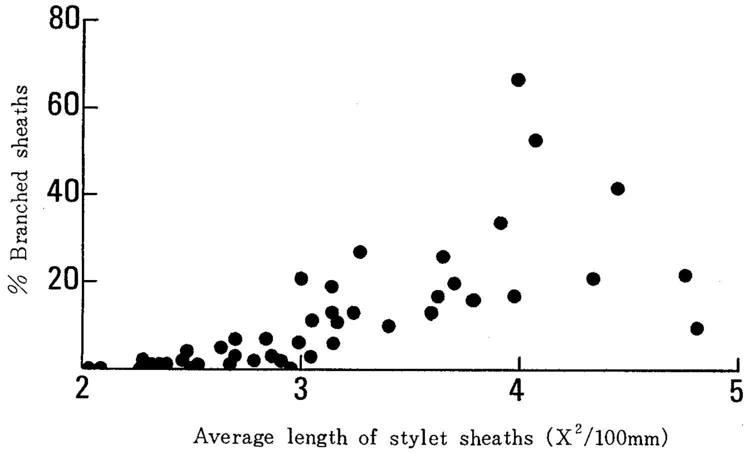

Fig. 5. Correlation between transformed average values of the length of stylet sheaths and percentages of the branched sheaths made in various media.

elongated sheaths indicates that planthoppers are apt to probe repeatedly through the same point of stylet insertion, and at the same time make deeper penetrations. It was also noticed that the probing stimulatory effect of salicylic acid was strikingly accentuated when offered in combination with sucrose. Sucrose has no definite stimulatory effect on the probing responses. The optimal concentration of sucrose as a sucking stimulant was about 0.6 M, but it could potentiate the effect of salicylic acid at concentrations below 0.2 M, at which its stimulatory effect on sucking was not significant. This indicates that sucrose affects both the probing and sucking phases under different modes of action. Ishii et al. (1962) isolated salicylic acid from rice plants. Kitani et al. (1972) also detected it as a major phenolcarboxylic acid of rice plants. It is, therefore, possible that salicylic acid acts as a natural probing stimulant in the rice plant tissues for the brown planthopper.

Although several botanical chemicals including sinigrin (Wensler, 1962; Moon, 1967; Wering, 1968; Nault and Styer, 1972), spartein (Smith, 1966), phlorizin (Klingauf, 1971), and a *n*-paraffin (Klingauf et al., 1971) have been suggested to possess significant effects on the aphid probing behaviors thus far, their mode of action has not been fully analyzed with the exception of sinigrin. Following Moon's finding that sinigrin increases settling behavior of the cabbage aphid but not ingestion (Moon, 1967), Nault and Styer (1972) demonstrated further that sinigrin also stimulated the stylet penetration phase of the phloem seeking probe of the aphids from the evidence that more than five times as many long stylet sheaths were produced in the sinigrin solution as compared to a water control.

Demonstration of a probing stimulant such as salicylic acid is valuable to an understanding of the feeding mechanism of the brown planthopper. Regarding the mechanism whereby homopterous insects are able to localize their sucking tissues in the plants during probing, Fife and Frampton (1936) presented a hypothesis that pH gradient with the plant tissues played a major role for guiding the insect stylets to the objective sites. Later this hypothesis was, however, rejected by Day et al. (1952). Several worker supposed that the sucking site was generally located by means of trial and error (Painter, 1928; Day et al., 1952; Ehrhardt, 1961), but they did not refer to the chemical stimulants concerned to this random probing phase. As reported in the earlier paper (Sōgawa, 1973), the brown planthopper also seemed to localize the sucking tissues by random exploratory probings. In this process, chemical stimuli such as salicylic acid are considered to play an important function in enhancing the random exploratory probings. If such stimulants are absent, insects might fail to localize the sucking sites, because of reluctant probing activity. The probing of the brown planthopper was apparently stimulated not only in the rice plant sap but also in the sap of non-host plants, indicating that the green plants tested here were provided with the necessary stimuli to activate probing response of the brown planthopper in spite of their unsuitability as the host plant. This seems to support Ehrhard's opinion that critical discrimination of host plants by aphids occurs after location of sieve elements and ingestion of sieve sap (Ehrhardt, 1961, 1963). That salicylic acid suppresses the imbibition in the brown planthopper at the concentrations effective onto the probing seems to be desirable property of the probing stimulant, because the probing is always made in the plant tissues outside the sucking objectives.

Recently the innervation in the stylets of various species of sucking insects was demonstrated by means of electron-microscopy (Forbes, 1966; Parrish, 1967; Forbes and Mullick, 1970; Forbes and Raine, 1973). The nerves in the stylets seem to function as chemoreceptors for the probing stimulants.

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