15. VARIETAL RESISTANCE OF RICE TO THE RICE STEM MAGGOT

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Introduction

The rice stem maggot, *Chlorops oryzae* Matsumura (Diptera; Chloropidae), is one of the serious pests of rice in Japan, and is widely distributed all over the country from Hokkaido to Kyushu. Recent nation-wide outbreaks occurred in 1953 and 1954, causing a large amount of yield losses. The great infestations are usually observed in the northern part of the country and in the mountainous area of the southern part. Among the major pests of rice in Japan, this is the only pest that the rice plant shows the distinct varietal resistance.

Life History and Biology

The number of generations a year varies geographically (Fig. 1). The maggot has two generations in the northern regions, Hokkaido and Tohoku, but three in other regions. Recent studies have proved the existence of the two geographic ecotypes (Iwata, 1963; Hirao, 1970). One of them has two generations and spreads in the north and the other has three generations and spreads in other part of the country. These ecotypes are different in the rate of their larval growth: the larvae of the 2-generation ecotype grow significantly slower than those of the 3-generation one. These two can mate, producing fertile eggs, but are undistinguishable morphologically.

Recently, a transition area was found to exist in the vicinity of the border line of 2- and 3-generation regions and in the area extending to the west from the line (Hayakawa and Kishino, 1962; Ueda *et al.*, 1962; Iwata, 1963). In the transition area, the two ecotypes occur together and occasionally intercross, producing their hybrid progenies. Therefore, the seasonal cycle is much complicated.

The infant larvae hibernate inside the stem of gramineous grasses. The eggs are laid singly on the under surface of leaves, usually near the base of leaf blade. Upon hatching, the infant larvae enter into the stem and reach the vicinity of the growth point. Once the larvae enter into the stem, they never move to other stems. The old larvae move up to the upper part of the stem, and pupate inside the inner part of the leaf sheath. In case of two eggs per stem, only one larva matures.

In the 2-generation region, the first flies emerge in June, and the larvae attack the rice plants throughout the latter half of the growth stage of plants. The larvae injure several developing leaves successively up to the flag-leaf and then the young panicle inside the stem. The larval period is about two months, depending on the growth of the host plants. The pupation occurs after heading. The flies of the next generation emerge from late September to mid October, and oviposit on the winter grasses. In the 3-generation region, the flies appear in May, July, and October. The former two generations attack the rice plants. The first generation occurs in the nursery bed, and the larvae injure about four developing leaves within one month of the larval period. The second generation occurs in the pancile developing stage, and the larvae

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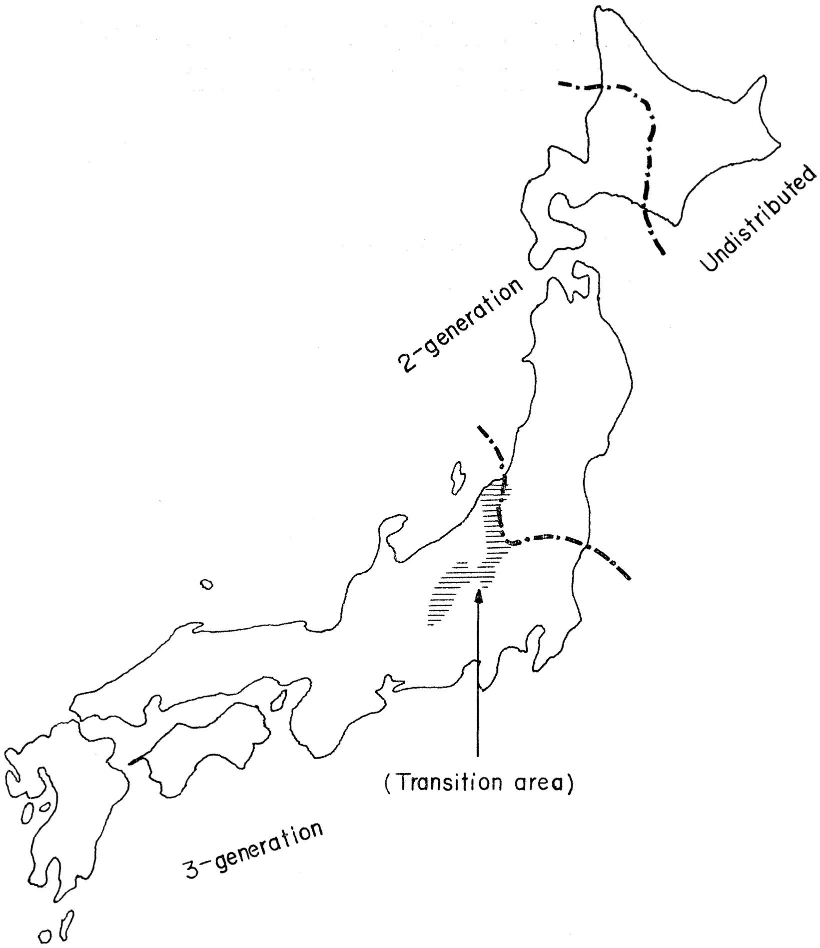


Fig. 1. Generation zone of the rice stem maggot in Japan.

injure about two developing leaves and the young panicle. The third flies emerge from the rice plants, and oviposit on the winter grasses.

The injured panicle is a typical symptom of attack, and causes yield losses. The larvae feed on and injure the immature spikelets, summing up to an average of 40 spikelets per panicle. Consequently, yield losses are mainly due to a marked reductiion in the number of filled spikelets. In addition, the infestation brings forth reduction in the length of the stem and panicle, especially the uppermost internode, and in the weight of the 1,000 filled grains.

Varietal Differences in Infestation

Up to the present time, many data have been presented on the existence of distinct varietal differences in infestation, which is usually measured by the percentage or the number of injured panicles. For example, among 24 varieties tested in the 2-generation region, the number of injured panicles per 50 hills ranged from 2 to 151, and the percentage of injured panicles from 0.3 to 31.4% in 1957 (Fig. 2). The varietal differences in infestation were tested on 23 varieties for several years (Yuasa, 1952;

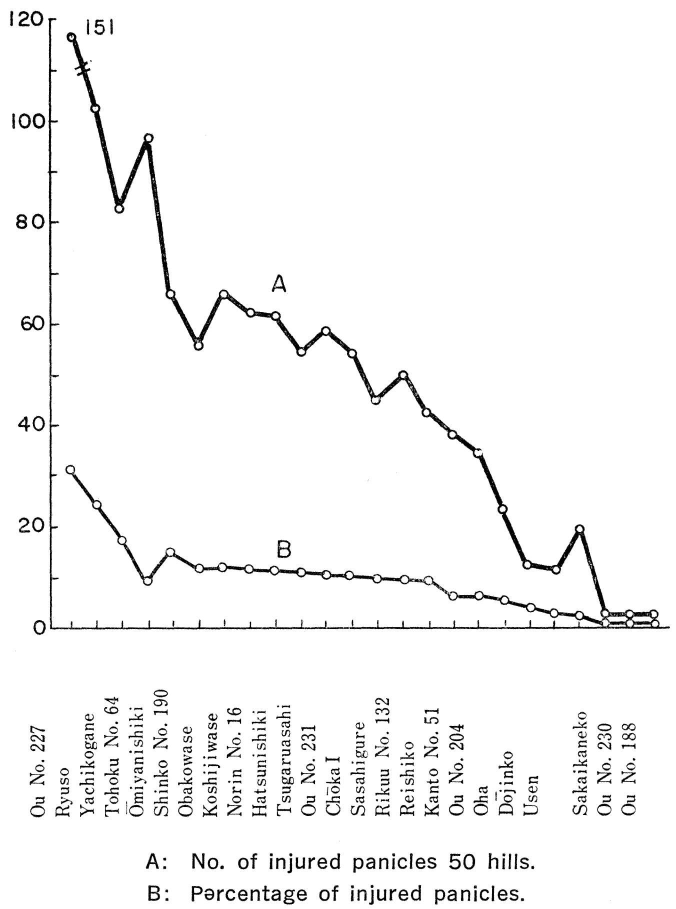


Fig. 2. Comparison of the number of injured panicles with the percentage of injured panicles. (Koyama, 1970)

Fuke and Koyama, 1955). The results indicated that the relative rank of each variety in the degree of infestatiion was consistent despite the differences in the insect population in years. Differences in infestatiion of the two selected varieties showed a marked contrast (Fig. 3). The incidence of injured panicles of Ou No. 227 closely corresponded with the insect abundance, suffering from severe damage. On the other hand, Ou No. 188 consistently had low infestation at any levels of the insect population.

Among the varieties with light infestation, there were some varieties with the low percentage of injured panicles to the total number of infested stems though the percentage of infested stems was high (Fig. 4). The varieties, Ou No. 230, Ou No. 188, Sakaikaneko, and Ou No. 204, belonged to this group. In contrast to this, there was another group of varieties such as Usen, Dôjinko, and Oha. These varieties had the low percentage of the iinfested stems and percentage of injured panicles to the total number of infested stems.

The above-mentioned results suggest that varietal differences in infestation are attributable to either the ovipositional preference or the larval death, or both of them.

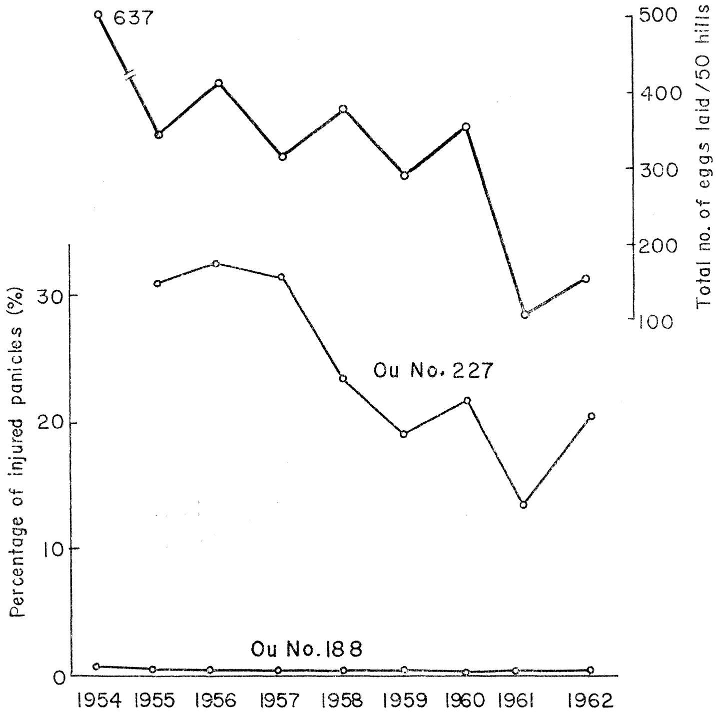
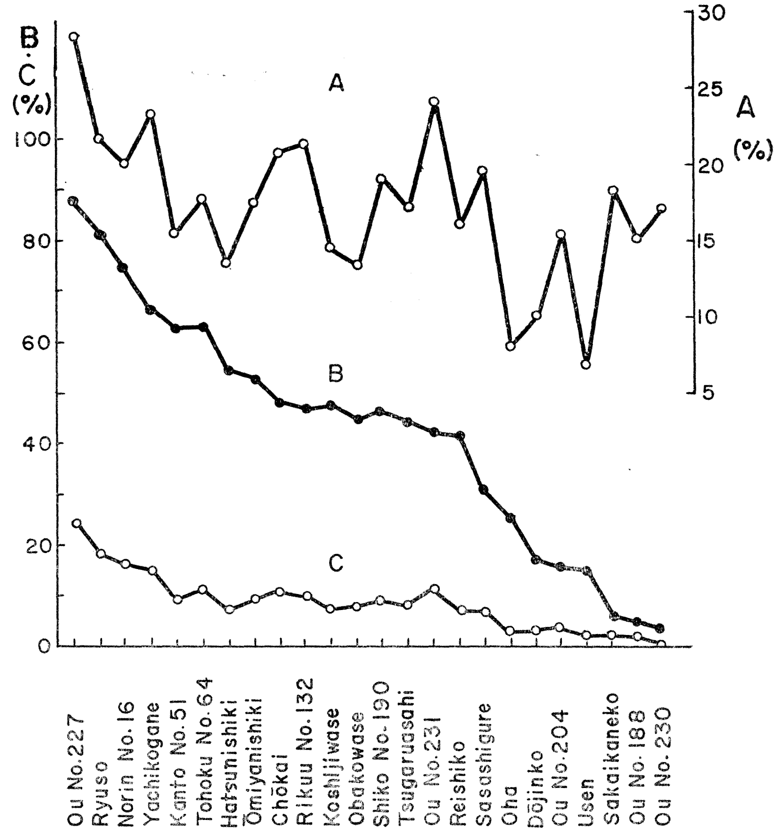


Fig. 3. Yearly incidence of the maggot population and infestation on the two selected varieties.



A: Percentage of infested stems.

B: Percentage of injured panicles to the total no. of infested stems.

C: Percentage of injured panicles.

Fig. 4. Comparison of three indexes for measuring the infestation. (Koyama, 1970)

Mechanisms of Resistance

Differences in Ovipositional Preference

Among 24 varieties tested in 1958, the number of eggs laid per 30 plants varied from 29 to 132, but most of the varieties had a range of 40-80 eggs. It was recorded that there were a few varieties whose number of eggs was markedly large or small. Observations on these varieties showed that the ovipositional preference was related to the leaf color; varieties with highly colored leaves such as Tohoku No. 64 and Ou No. 227, were more preferred, but those with lowly colored leaves, such foreign varieties as Oha and Dôjinko, were less preferred (Table 1).

Table 1. Differences in the number of eggs laid on the selected varieties and their leaf color (Koyama, 1970).

Variety	Leaf color	No. of eggs laid per 30 hills				No. of tillers per hill	Plant height (cm)
		A	B	C	Aver.		
Dōjinko	Light	31	34	30	32	11.3	48.0
Oha	Light	31	24	29	28	12.3	50.0
Ou No. 227	Dark	152	144	101	132	10.5	45.0
Tohoku No. 64	Dark	106	126	79	104	11.2	45.0

With the exception of these particular varieties the ovipositional preference was not significant among most of the commercial *Japonica* varieties. This statement is supported by other investigators in the different generations or localities (Okamoto, 1970). Thus it is evident that the ovipositional preference is not an important factor in the determination of resistance.

Differences in the Boring Rate of Hatched Larvae

When hatched, the infant larvae enter into the stem spirally through the slits of overlapping leaf sheaths. Then they bore one or two young leaves and reach the growth point.

In 1956, investigations were conducted on the varietal differences in the boring rate of hatched larvae on the main stems by inspecting the oviposited stems and subsequently the infested stems with injured leaves. The boring rate of hatched larvae, thus obtained, ranged from 65 to 88% on 24 varieties. In this case the following factors would be concerned with the ineffectiveness of eggs and the failure of hatched larvae in reaching the growth point: death of eggs caused by parasites and predators, not yet ascertained, and by falling down from the leaves; and death of hatched larvae before and immediately after boring into the stems. In addition, some of hatched larvae failed to enter into the main stems, because the oviposited leaf of the main stem was attached to other new tillers which emerged close to the main stem within the incubation period. In this case the hatched larvae were forced to enter into the new tiller.

More detailed investigations indicated the boring rate of 70–80% on four selected varieties with different degrees of resistance. No significant differences in the boring rate were observed when the plant age advanced. A similar result was also obtained when the infant larvae were artificially placed on the stems (Yushima and Tomisawa, 1957).

It is suggested that there are no difficulties met by the hatched larvae in entering into the stem when inherent morphological characters exist on each variety. Thus it is concluded that the death of larvae before reaching the growth point of the stem is not related to the varietal resistance.

Differences in the Larval Mortality during the Feeding Period

In the 2-generation region, several types of infested stems are observed (Fig. 5). The occurrence of these types is closely related to resistance. The number of injured leaves vary depending on the time of larval feeding and the plant maturity. The appearance of healthy leaves or a panicle after the occurrence of injured leaves indicates the larval death prematurely. In this case, one or two upper injured leaves usually have the discolored patches of various forms. The discolored patch is probably caused by the secretion or excrement of living larva or decayed substances from the dead body of larva. The appearance of an injured panicle indicates the complete growth of larva therein. Consequently, the percentage of injured panicles to the total number of infested stems represents the survival rate of larvae during their feeding period.

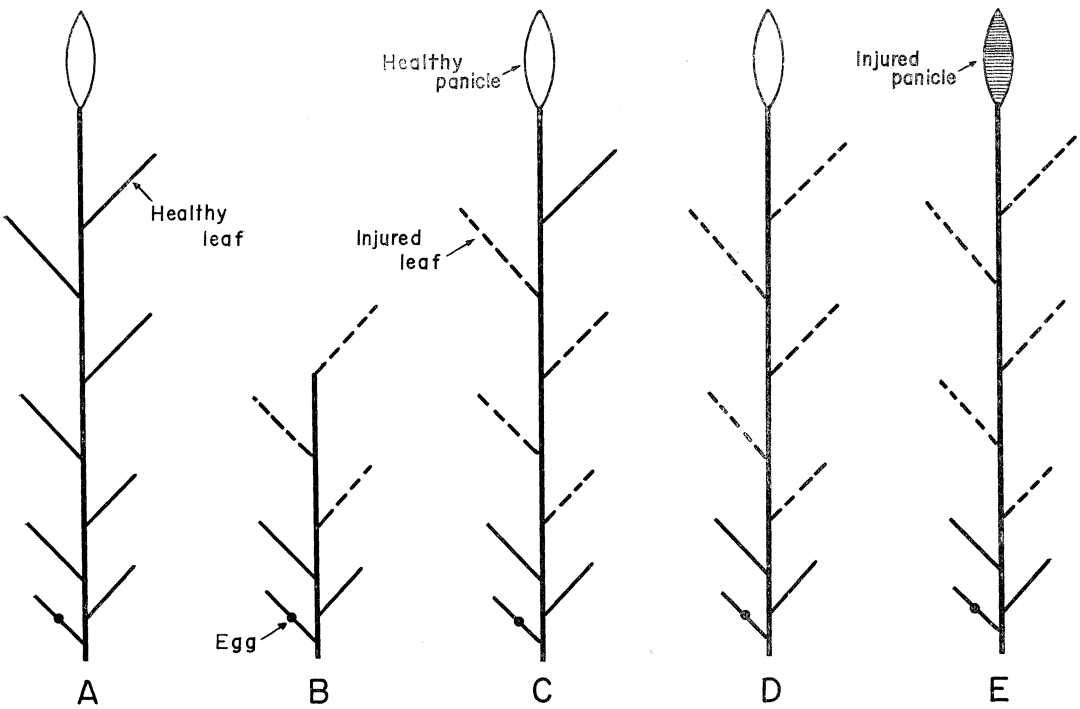


Fig. 5. Diagram showing the types of occurrence of injured leaves and panicle in the 2-generation region.

From this point of view, the larval mortality during the feeding period was investigated on the main stems of 23 varieties in 1956. Simultaneously, the time of larval death was recorded by observing the number of injured leaves, and the period of larval death was divided into three stages: early, medium, and late.

The total mortality of larvae during their feeding period varied markedlly from 2 to 100% on different varieties (Table 2). On the resistant varieties a high mortality

Table 2. Larval mortality or survival rate during the feeding period (Koyama, 1970).

Variety	Mortality in the (%)				Survival (%)
	Early stage	Medium stage	Late stage	Total	
Ou No. 188	74	18	8	100	0
Sakaikaneko	60	25	15	100	0
Oha	62	19	13	94	6
Ou No. 230	42	37	12	91	9
Ou No. 204	50	21	12	83	17
Dōjinko	17	25	33	75	25
Koshijiwase	37	17	11	65	35
Sasashigure	32	14	22	68	32
Reishiko	7	35	10	52	48
Rikuu No. 132	18	13	16	47	53
Hatsunishiki	27	5	8	40	60
Ou No. 231	11	17	22	50	50
Shinko No. 190	17	12	14	43	57
Ōmiyanishiki	17	11	17	45	55
Tsugaruasahi	15	26	10	51	49
Chōkai	21	13	13	47	53
Kanto No. 51	19	8	14	41	59
Obakowase	6	14	20	40	60
Yachikogane	17	6	9	32	68
Norin No. 16	2	0	16	18	82
Tohoku No. 64	1	13	6	20	80
Ou No. 227	2	2	2	6	94
Ryuso	2	0	0	2	98

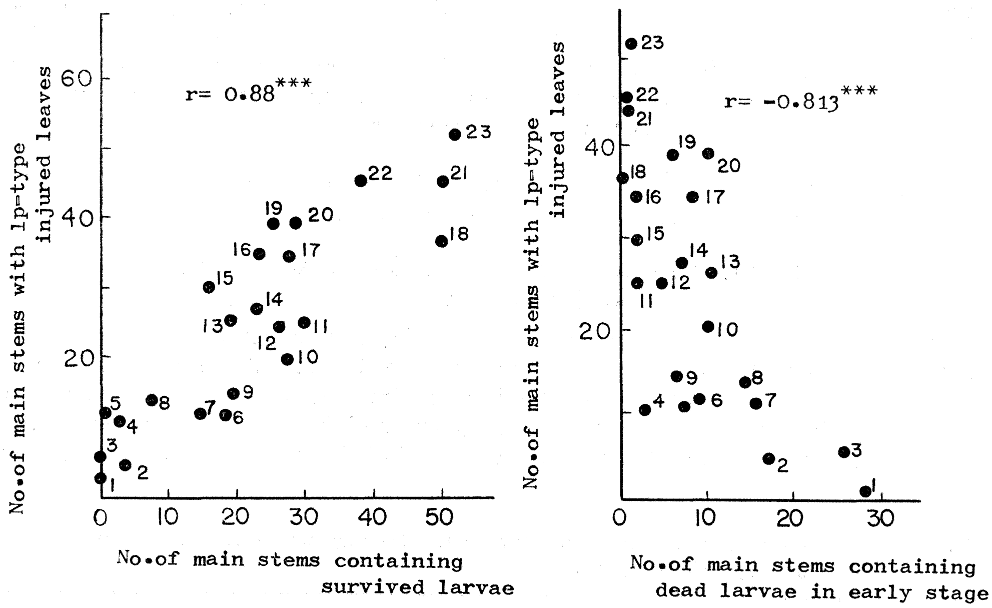
of 50–74% occurred in the early stage of larval growth. Some of the moderately resistant and susceptible varieties had an uniform mortality in all stages, but others relatively high mortality in the medium or the late stage. The results were in good agreement with those obtained from a total 121 varieties tested for three years. Thus it is difficult to measure the varietal differences in resistance exactly by the time of larval death.

As to the larval growth, an interesting result was reported in the first generation of the 3-generation region (Yushima and Tomisawa, 1957). When the oldest larvae were artificially placed on the seedlings of the resistant variety (Norin No. 25), the survival rate was significantly higher, in contrast to the lower rate of the younger larvae (Table 3). This means that the resistant factor must have affected the younger larvae but not affected the older ones.

Infestation results in several types of injured leaves, depending on the varieties and the leaf positiion on the stems. Concerning the types of injured leaves, it was generally said that susceptible varieties had more number of injured leaves with holes and large punctured feeding scars (1p-type in Fig. 6), and that resistant varieties had the injured leaves with discolored patches though the number of injured leaves was smaller because of larvaal death in the early stage. In case of some resistant varieties, however, there was no relation between the resistance and the appearance of the injured leaves with discolored patches.

Table 3. Comparison of resistance between the resistant and the susceptible varieties in the first generation of the 3-generation region (Yushima and Tomisawa, 1957).

Variety	Larval instar placed	No. of larvae placed	Boring rate of larvae (%)	Pupal formation (%)
Norin No. 25 (R)	1st	51	80.4	0
	2nd	51	80.4	9.8
	3rd	18	100	72.2
Norin No. 8 (S)	1st	51	60.0	58.1
	3rd	50	80.0	57.5



1:Ou No.188; 2:Sakaikaneko; 3:Ou No.230; 4:Dōjinko; 5:Oha; 6:Hatsunishiki; 7:Koshijiwase; 8:Ou No.204; 9:Rikuu No.132; 10:Chōkai; 11:Obakowase; 12:Tsugaruasahi; 13:Sasashigure; 14:Ōmiyanishiki; 15:Reishiko; 16:Ou No.231; 17:Shinko No.190; 18:Tohoku No.64; 19:Yachikogane; 20:Kanto No.51; 21:Ou No.227; 22:Norin No.16; 23:Ryuso.

Fig. 6. Relation between the types of injured leaves and larval growth. (Koyama, 1970)

The above results indicate that the larval mortality during the feeding period plays an important role in the determination of resistance. The larval mortality of the resistant varieties was significantly high in the early stage of larval growth, and it corresponded to the spikelet-differentiation stage of pancles. It is evident that resistance to the rice stem maggot in the rice plants is expressed as antibiosis.

Thus the survival rate of larvae during the feeding period indicates the substantial resistance. Here we call it "resistance index." The resistance index is represented by the percentage of injured panicles to the total number of infested stems.

Reaction of the Plant Growth Against the Infestation

In the first generation of the 3-generation region, the infested plants had slightly increased the number of stems at the early growth stage. There was no difference, however, in the number of panicles between the infested and uninfested plants at the heading stage. In the second generation when the infestation occurred at the panicle-forming stage, there was no difference in the number of panicles between the infested and uninfested plants. Occasionally among some of the susceptible varieties, the stem with an injured panicle branched a new stem from the upper node. This is considered as a result of compensation for the infestation. Most of the branched stems emerged unseasonally so late that they were fruitless (Okamoto, 1970).

In the 2-generation region, a certain number of infested stems were stunted and died prematurely without bearing the panicles (Fig. 5). The percentage of stunted stems was high among the resistant varieties. This is considered as a sensitive reaction of the plants against the infestation. In case of the susceptible variety, Rikuu No. 132, an increase of the secondary and the tertiary tillers was observed at harvest in the infested plants, though this is considered to be an exceptional case (Yuasa, 1952).

The above results indicate that the rice plants have no distinct tolerance for the maggot infestation from the view point of yield production.

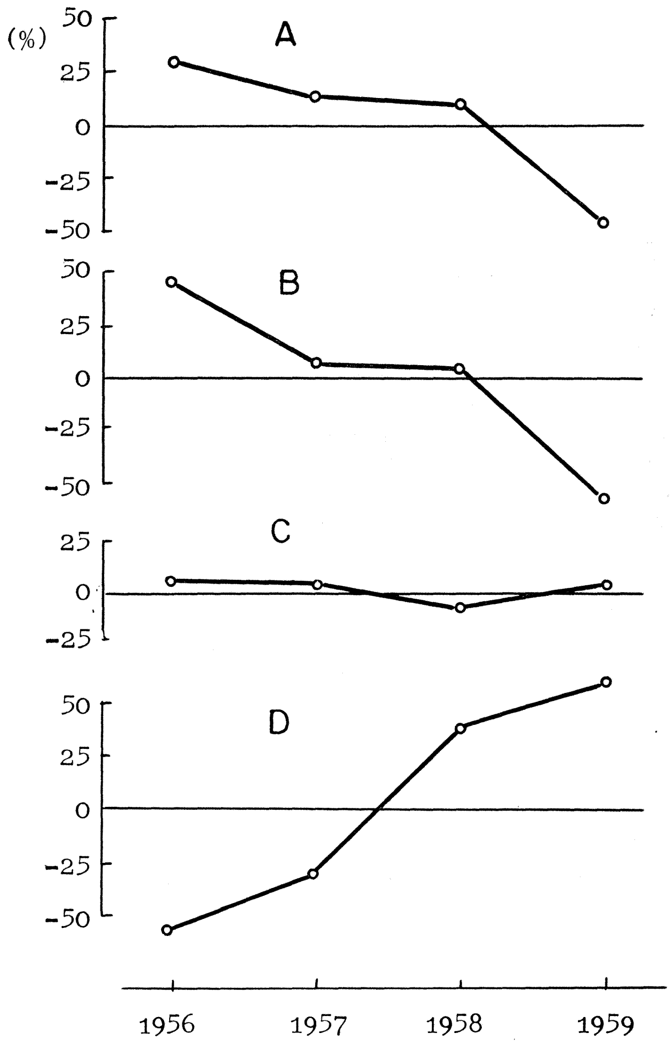
Consistency and Validity of Resistance Index as a Measure of Resistance

As a measure of resistance, the percentage of injured panicles has been usually used in the first and the second generations of the 2- and 3-generation regions, respectively. The percentage of injured panicles is influenced by the differences in the maggot population of the same variety in years and in the total number of the stems of varieties. In addition, this percentage is affected by the levels of fertilizer

Table 4. Survival rate of late of larvae during the feeding period in relation to the plant age (Koyama, 1970).

Resistance	Variety	Date, larvae placed	No. of stems with		Larval survival* (B/A×100) (%)
			Injured leaves (A)	Injured panicles (B)	
R	Ou No. 188	June 24	64	2	3.1
		July 8	35	1	2.9
	Sakaikaneko	June 24	127	3	2.4
		July 8	55	2	3.6
M	Shinko No. 190	June 24	100	24	24.0
		July 8	36	11	30.6
	Hatsunishiki	June 20—21	154	42	27.3
		July 8	61	23	37.7
S	Norin No. 16	June 18—20	98	76	77.6
		July 8	82	74	90.3
	Ou No. 227	June 18	80	80	85.0
		July 8	114	103	90.5

* Obtained from the percentage of injured panicles to the total No. of infested stems.



A: Percentage of infested stems.
B: Percentage of injured panicles.
C: Percentage of injured panicles to the total no. of infested stems.
D: Percentage of infested stems stunted.

Fig. 7. Deviation of indexes from the average of 4-year measurements on 24 varieties. (Koyama, 1970)

application and dates of planting due to the differences in the number of eggs laid. In the strict sense, therefore, the percentage of injured panicles does not indicate the true resistant value exactly.

In contrast to the percentage of injured panicles, the resistance index shown by the survival rate of larvae during their feeding period, is consistent under the above-mentioned insect and plant conditions (Fig. 7 and Table 4). Therefore, the resistance index is valid to measure the degrees of resistance exactly. It ranges from 0 to 100%, and is rated as follows: resistant; 0–33, moderately resistant; 34–66, and susceptible; 67–100.

Test Methods for Evaluating Resistance

In the 3-generation region, the varietal difference can be tested in the first generation in the early sown nursery bed, where severe maggot infestation occurs (Okamoto, 1970). As a measure of resistance, the percentage of infested plants was proved to be reliable. The percentage of infested plants should be recorded when most of injured leaves have appeard. In this case, the plants with large punctured leaves were only recorded as being infested since these leaves were caused by the attack of old larvae and indicated the complete larval growth. The degree of varietal resistance of the first generation obtained in this method corresponded to the percentage of injured panicles in the second generation. However, such close relation between the two generations could not be observed among some varieties.

A new modified method was tested in the nursery bed (Yushima and Tomisawa, 1957). The results indicated that the time-mortality curve of larvae in the seedlings was more useful to measure the absolute value of resistance than the percentage of infested plants.

Furthermore, the experiments showed the possibilities in testing the varietal resistance by using the young rice seedlings in an incubator (25°C) (Tamura and Suzuki, 1958). The hatched larvae were artificially placed onto the seedlings at the

Table 5. Tests for resistance on the rice seedlings using with overwintered larvae in early spring in the 2-generation region. (Koyama, 1970)

Year	Resistance	Variety	No. of seedlings used	No. of seedlings with injured leaves	Larval survival (%)
1958	R	Ou. No. 188	74	30	0
		Sakaikaneko	67	26	0
	M	Rikuu No. 132	88	18	5.6
		Shinko No. 190	106	33	9.1
	S	Ou. No. 227	85	27	29.1
		Ryuso	69	26	46.1
1963	R	Ou. No. 188	66	46	2.4
		Sakikaneko	68	40	0
		Ou. No. 230	69	50	6.0
	M	Rikuu No. 132	66	41	14.6
		Shink No. 190	69	59	6.9
		Chōkai	66	48	25.0
	S	Ou. No. 227	62	46	71.7
		Norin No. 16	59	48	85.0
		Kanto No. 51	62	45	75.6

1-leaf stage and grew to the last instar for 10 days. The results indicated that the survival rate of larvae on the seedlings of 38 varieties was in accordance with the number of injured panicles in the field. The size of larvae recovered from the susceptible varieties was large.

In the 2-generation region, methods with seedlings in the nursery bed or in an incubator can not be applied, because the larval periiod of the 2-generation ecotype is three times as long as that of the 3-generation one, therefore, the tests should be conducted in the paddy field. The resistance index, as mentioned before, can be obtained from the percentage of injured panicles to the total number of infested stems. The infested stems should be marked individually with a wool thread or other materials.

An attempt was made to simplify the testing method in the 2-generatiion region. In early spring overwintered larvae in the first or the second instar were transferred artificially from the winter grasses to the rice seedlings bred in a glasshouse. The infested seedlings were allowed to grow for 20 or 30 days, and then they were dissected. The survival rate of larvae was in accordance with the degrees of resistance. There was, however, an annual variation in the value of the survival rate on the moderately resistant and the susceptible varieties (Table 5). It is required to test a greater number of varieties before concluding the practical use of this method.

Inheritance of Resistance

In the study of inheritance, the degree of resistance in the F_1 hybrids was intermediate between the parents or somewhat susceptible than the intermediate position, probably because heading was promoted by hybrid vigor (Table 6). Crosses of

Table 6. Degrees of resistance in the F_1 hybrids. (Fuke and Koyama, 1955)

Cross combination (Injured panicles, %; date of heading)		Injured panicles (%)	Date of heading in Aug.	F_1 hybrid	
				Injured panicles (%)	Date of heading in Aug.
Somewake× (40.0, Aug.)	Norin No. 1	19.4	8	39.0	7
	Ou. No. 187	2.1	11	35.0	5
	Rikuu No. 132	15.0	12	30.0	11
	Ayashi No. 1	8.9	13	24.8	10
Tohoku No. 27× (30.0, Aug. 12)	Ou No. 189	0	11	26.2	11
	Kamenoo No. 4	11.5	11	21.9	12
	Norin No. 1	19.4	9	19.6	12
	Tono No. 1	17.0	1	18.2	5
	Ayashi No. 1	8.9	15	15.9	15
	Kuhei No. 2	6.0	4	11.1	11
Ou No. 187× (2.1, Aug. 11)	Somewake	40.0	9	35.2	5
	Norin No. 1	19.4	10	14.1	10
	C S No. 310	13.8	12	13.1	10
	L C No. 8	8.3	15	8.1	14
	Kanto No. 13	13.8	17	5.9	15
	C S No. 304	6.6	16	3.9	14
	Ou No. 202	2.1	20	3.6	16
	Ou No. 204	2.3	18	3.4	14

Table 7. Segregation in the F_3 generation of crosses of the resistant and the susceptible varieties. (Fuke and Koyama, 1955)

Cross combination	No. of lines			χ^2 (1 : 2 : 1)	P
	R	M	S		
Ou No. 188×Rikuu No. 132 (R) (S)	20	50	21	0.02	>0.9
Ou No. 195×Ou No. 191 (S) (R)	23	45	22	0.91	0.9–0.8

resistant parents produced the resistant F_3, and the susceptible parents the susceptible F_3. In crosses of the resistant variety with the susceptible variety, resulting segregation for resistance in the F_3 generation was a 1:2:1 ratio (Table 7). Consequently, the resistance to the rice stem maggot is inherited, indicating monogenic incomplete dominance. On the inheritance of resistance the result obtained in the first generation of the 2-generaton region was in good agreement with that in the first generation of the 3-generation region (Okamoto, 1970). The investigation showed no substantial difference in resistance between the two ecotypes (Hirao, 1970).

Concerning the relationship of resistance between the parents and their progenies in the present main varieties in Tohoku region, it is interesting to note that the resistant factor has been derived from the old resistant variety, Jôshu, and the susceptible factor from the two susceptible varieties, Fujisaka No. 3 and Ginbozu (Fig. 8).

The experiments for three years, 1953–1955, indicated that the pedigree selectiion for resistance had the possibilities of adding the resistance as a supplemental character

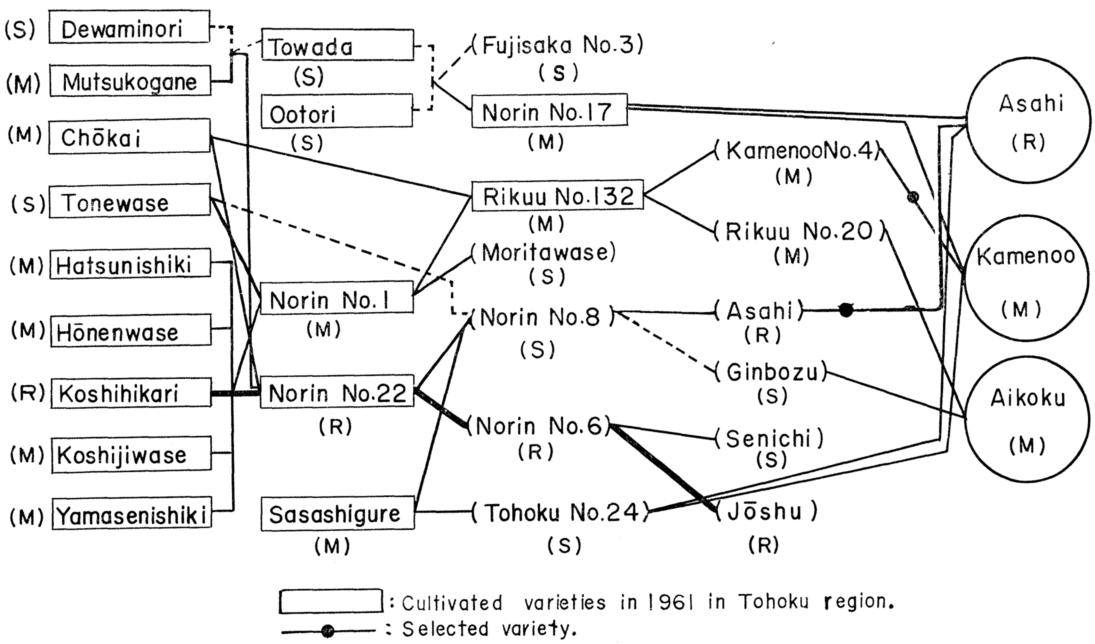


Fig. 8. Parentage relation of resistance in the main varieties in Tohoku region.

to some of the varieties. This method is applied to some of the newly-bred varieties, and varieties which have not yet received selection for resistance during their breeding generations.

Conclusions

Of the three mechanisms of resistance (Painter, 1951), resistance to the rice stem maggot in the rice plants is expressed as an antibiosis, where the maggot dies after it begins to feed. This form of resistance is more desirable for protection of the rice plants effectively from the maggot infestation. Suppresson of the maggot population and damage through the cultivation of the resistant varieties is considered to be an ideal control measure. Resistance is consistent and inherited simply so that it is desirable to use resistant parental varieties to breed a new variety in the breeding program.

No data have been given on the resistant factor. However, a toxic substance(s) may be concerned. For this purpose, biochemical studies are required with the development of an artificial diet.

Discussion

M. D. Pathak, IRRI: Your results showed that non-preferred varieties were lighter in color. Was there similar relationship between the leaf color and antibiosis?

Answer: There is no relationship between the leaf color and antibiosis.

C. Kaneda, Japan: Degenerated florets are caused by low temperatures (minimum 19°C in 1970) even in the Philippines which attack the early stage of spikelet formation (around three weeks before heading). 1) Please point out other factors causing injured panicles, and how do you differentiate them from one another? 2) The low temperature also causes injured panicles. What about the difference of injured panicles?

Answer: 1) The paddy stem maggot, *Hydrellia sasakii,* sometimes injures the panicles, and also we can see unfilled panicles caused by the physiological factor. It is difficult to distinguish each other the injured panicles caused by both factors but symptoms of the injury on the leaves are different. 2) Abnormal lower temperature also causes white glumes. In case of the rice stem maggot, there are a certain number of kernels fed away and injured directly by larvae other than white glumes.

T. Saito, Japan: Have treed to extract the toxic substance in resistant rice plant varieties?

Answer: I have not yet tried it.

T. Saito, Japan (Comment): High populatiion density of the insect causes not only toxic substance but also deficiency of the nutrient materials.

Soenardi, Indonesia: So far the rice stem maggot has not been recorded in Indonesia. From which rice growing countries has this insect been recorded?

Answer: Distribution of the rice stem maggot is restricted only to Japan. (A Japanese entomologist recorded to occurrence of the rice stem maggot in Korea about 40 years ago, but the recorded pest is Hydrelia griseola F. (Smaller rice leaf minor).

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