HISTOLOGICAL AND GENETIC STUDIES ON SHEDDING AND LODGING HABITS OF RICE PLANTS

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Grain shedding and lodging are serious problems in rice breeding. Generally, *indica* varieties are easier to lodge and shed than *japonicas*. In India, the loss of yield due to grain shedding was estimated to be 3–30% (Bhalerao, 1930; Ramiah and Rao, 1936), and the losses caused by lodging came up to about 60% (before heading) and 18% (dough to ripening stages) (Parthasarathy, 1956).

In Taiwan, both the 'Ponlai' varieties (*japonica* type; about 60%) and the 'native' ones (*indica* type; about 40%) are grown. Hybridization between the 'Ponlai' and the 'native' varieties has been made in the past, but it was generally unsuccessful in improving shedding and lodging habits of native varieties. The writers have engaged in radiation-breeding of rice, since 1957 under the leadership of Dr. H. W. Li, Academia Sinica (Hu, *et al.*, 1960; Li, *et al.*, 1962). We have found a few non-shedding and non-lodging mutants of *indica* varieties, and attempted to look into the genetic basis of these characters.

Materials and Methods

The strains used are shown in Table 1.

For investigating the development of the abscission layer between spikelet basis and pedicel, materials were collected at the interval of 5 days starting from the flowering date, and were fixed in Farmer's fluid for 24 hours. They were then imbedded in paraffin, sectioned longitudinally at the thickness of 11 micra, and were stained with Delafield's haematoxylin.

For testing shedding resistance, panicles were placed on a board inclined at 5° (Hanumantha Rao 1935), and were run over three times by a roller weight 1 kg. Then, the number of grains which dropped from the panicles were recorded in percentage of the total grain number.

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Table 1. *Brief description of materials*

Strain	Type	Character	Origin
1) Pai-mi-fen	*indica*	Easily shedding	A 'native' variety of Taiwan.
2) P-30-98-15	*indica*	Non-shedding	A mutant obtained from X-rayed progeny (30 kr) of Pai-mi-fen.
3) Taichung 65	*japonica*	Shed. resist.	A 'Ponlai' variety.
4) W107	wild type (*O. sativa* f. *spont.*)	Very easily shedding	Collected from Cuttack, Orissa, India.
5) Taichung native 1	*indica*	Easily shed.	An improved 'native' variety; dwarf type.
6) Nan-teh-hau	*indica*	Easily shed.	A 'native' variety of the Chinese mainland.
8) Liu-chow	*indica*	Lodging	A 'native' variety of Taiwan.
9) L-25-87	*indica*	Erect and non-lodging	A mutant obtained from X-rayed progeny (25 kr) of Liu-chow.

Regarding lodging resitance, cross sections of the culm were observed. Also the breaking strength of the third internode (from top) at maturiy was measured by using the Holdefleiss' straw tester.

The F_1 and F_2 plants between mutant and their original strains were also observed.

Results of Observations

1. Shedding

The longitudinal sections between spikelet basis and pedicel of different strains are illustrated in Figures 1–4 and Plate figures 1–4. The induced non-shedding mutant of Pai-mi-fen (P-30-98-15) was found to have no abscission layer (figure 1 and plate figure 1). The other three strains, Pai-mi-fen (figure 2 and plate figure 2), Taichung 65 (figure 3 and plate figure 3), and W107 (figure 4 and plate figure 4), had abscission layer developed in different degrees. The highly shedding wild strain (W107) had the most developed abscission layer which adhered very closely to the central vascular bundle. The relatively non-shedding strain Taichung 65 showed poor development of the abscission layer. The F_1 hybrid between Pai-mi-fen and non-shedding mutant showed an incomplete development of the abscission layer, as shown in plate figure 5.

The mode of abscission layer development also differed between strains. In the wild strains, cracks were found at the central part of the abscission layer 10 to 15 days after flowering. Pai-mi-fen showed such cracks 30 days after flowering. Taichung 65 showed no cracks until maturity. The F_1 hybrid between Pai-mi-fen and non-shedding mutant exhibited no crack in its poorly developed abscission layer. The occurrence of cracks in the abscission layer

Fig. 1

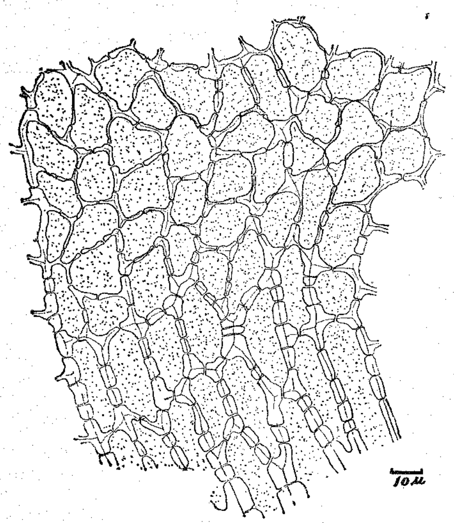
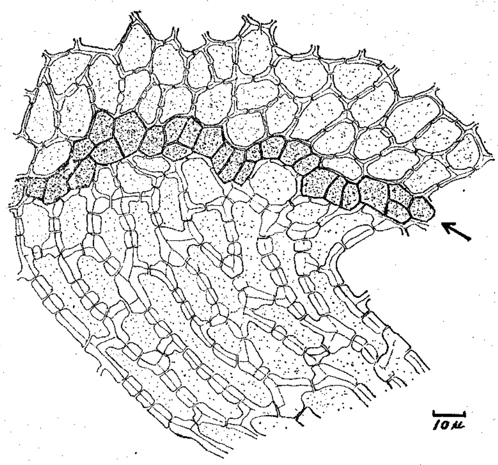


Fig. 2



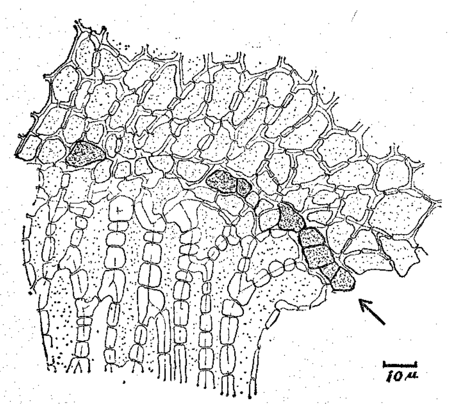


Fig. 3

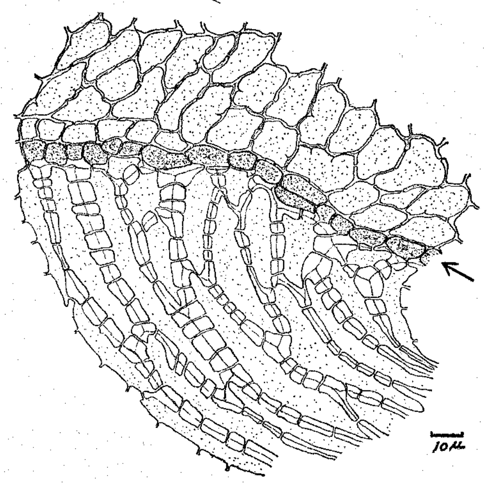


Fig. 4

Fig. 1-4. Camera-lucida drawing showings the structure of abscission layer (indicated by an arrow),

Fig. 1. Non-shedding mutant from Pai-mi-fen, with no abscission layer.

Fig. 2. A shedding variety, Pai-me-fen (*indica* type).

Fig. 3. A shedding resistant variety, Taichung 65 (*japonica* type). The abscission layer cells are not much developed.

Fig. 4. A wild strain (*Oryza sativa* f. *spontanea*, W107).

was parallel with that of grain shedding in field observations. Moreover, the degree of shedding resistance by the roller method (Table 2 and 3) seemed to be in close agreement with the degree of abscission layer development.

The measurements of shedding resistance and other characters in non-shedding mutant, Pai-mi-fen and their F_1 hybrid are shown in Table 2.

Table 2. *Measurement of characters in Pai-mi-fen; the non-shedding mutant and their F_1 hybrid.*

Strain	Shedding grains per panicle	Abscission layer		Plant height (cm)	Panicle length (cm)	No. of grains per panicle
		at flowering date	30th day			
Pai-mi-fen	22.4±5.1	+	+ (with cracks)	122±5.9	20±0.9	87.3
Non-shed. mutant	0.2±0.3	—	—	79±4.8	14±0.9	58.7
F_1	2.6±1.5	+	+	114±4.6	20±0.9	100.6

Table 3. *F_2 segregation in crosses between non-shedding mutant and other strains.*

Strain		No. of shedding per panicle	F_2 segregation non—easy	Total plants observ.	χ^2	P
Non-shed. mutant (P_1)		2.2±0.3				
Pai-mi-fen (P_2)		22.4±5.1				
Nan-teh-hau (P_3)		24.2±3.4				
Taichung native 1 (P_4)		11.7±7.4				
$P_1 \times P_2$	F_1	2.6±1.5				
	F_2	8.4±8.6	217: 62 (3) (1)	279	1.15	0.20–0.30
$P_1 \times P_3$	F_1	—				
	F_2	20.2±25.9	98: 38: 21; 8 (9) (3) (3) (1)	165	5.72	0.10–0.20
$P_1 \times P_4$	F_1	4.0± 2.2				
	F_2	18.7±19.5	102: 31: 32: 20 (9) (3) (3) (1)	185	7.74	0.05–0.10

The modes of F_2 segregation of shedding habit in different crosses are shown in Table 3 and Fig. 5. The abscission layer development of hybrid plants seemed to be controlled by one or two dominant genes. The F_1s had non-shedding habit though they had abscission layers. Thus, the non-shedding mutant seems to be dominant in shedding habit, and recessive in the formation of the abscission layer. A 3:1 ratio was clearly seen in the F_2 between the non-shedding mutant and its original strain, Pai-mi-fen. On the contrary a 9 (non-shedding): 3: 3: 1 (highly shedding) ratio appeared when the non-shedding mutant was crossed with other strains, Nan-teh-hau and Taichung native 1.

The non-shedding mutant was a dwarf type as shown in Table 2. The F_1 showed normal plant height, and the F_2 segregated into 3 (normal) to 1 (dwarf or short) regarding plant height and panicle length. An observation of F_3 progeny indicated that dwarf plants with short panicles were a non-shedding type and the normal height with non-shedding habit again segregated into 3 normal and 1 dwarf, while the normal plant height with shedding habit were like the parent strain Pai-mi-fen. It seems that the dwarfness and the non-shedding habit are due to pleiotropic effects of the same recessive mutation.

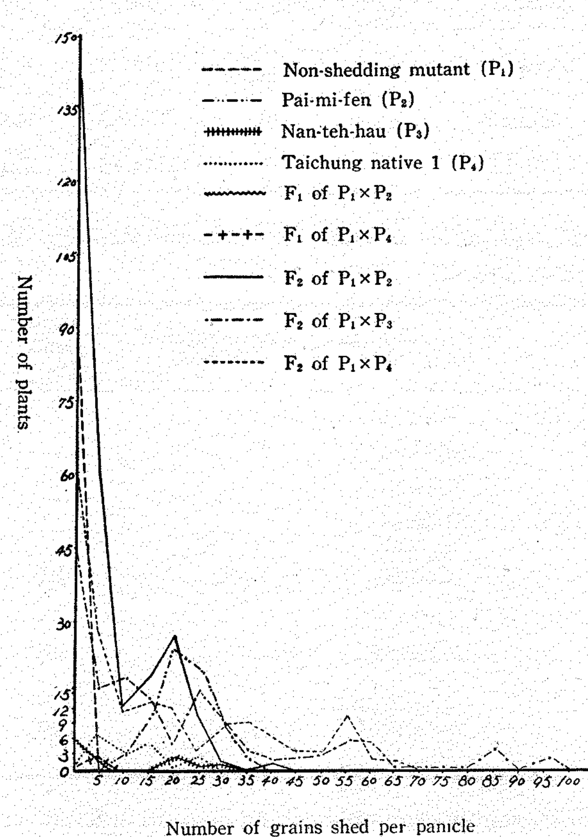


Fig. 5. Frequency distributions of the number of grains shed per panicle in three crosses

2, *Lodging*

Liu-chow is an easily lodging *indica* type variety. We have obtained several erect type of non-lodging mutants from this variety. One of these strains L–25–87 was used for this study. Measurement of various charcters of the mutant and original strains are given in Table 4, the erect mutant showed smaller plant height and shorter panicle length, but larger diameter and breaking strength of the culm than the original strain. The mutant also had more and larger vascular bundles, and shorter internode than the control, and the panicles did not completely extrude from the top leaf-sheath. In field observation, the mutant did not lodge until ripening and even in quite dead ripening stage.

Table 4. *Measurements of characters in Liu-chow; the erect mutant and their F_1 hybrid.*

Strain	Plant height (cm)	Panicle length (cm)	No. of panicle	Culm diameter (mm)	Breaking strength of culm (gr)	No. of vascular bundles		Thickness of sclerenchyma layer (μ)	Diameter of vassel (μ)
						inside	outside		
Liu-chow	125±5.3	19±3.6	15	4.1±0.4	232±43.0	30±1.7	29±1.8	6.5±0.7	35.4±3.5
Erect mut.	93±3.5	15±2.7	13	5.3±0.5	384±94.9	34±1.7	38±5.7	7.3±1.1	39.1±1.9
F_1	127±6.7	19±2.6	—	4.4±0.6	249±41.3	31±1.6	31±1.6	6.5±0.8	35.4±4.6

The F_1 hybrid resembles its original strain in the histological structure of the stem as well as in other characters. The F_2 ratio appeared to be 3 normal to 1 erect. This suggests that the erect character is controlled by a recessive gene. But there were some exceptions; a few plants had normal plant type but their panicle extraction was incomplete, and a few dwarf plants had slender and stiff culms.

Discussion

The development of the abscission layer in relation to sheddng in rice was investigated first by Takeuchi (1922). Using native varieties of Taiwan and Japan, he found that the abscission layer had a thinner cell wall than the other tissues, and that easily shedding and non-shedding varieties differed in the number and size of abscission cells. At maturity, Taiwan native varieties showed separation of the grains at the abscission layer, which was considered to be due to dehydration of the cells.

As to the inheritance of the shedding habit, Onotera (1929) reported the occurrence of a highly shedding plant from a cross between shedding and non-shedding strains, assuming three pairs of genes. Bhalerao (1930) also considered that more than one gene were involved in the inheritance of this character. Kato (quoted by Nagai, 1959) reported that F_2 between shedding resistant and easily shedding strains of Japanese varieties gave 3 (shedding resistance): 1 (easily shedding) ratio. On the other hand, Kadam (1936) found that shedding character was dominant in hybrids between a wild rice (*O. sativa* var. *fatua*?) and a non-shedding strain of Burmese origin; the F_1 showed the same degree of shedding as the wild parent, and the F_2 gave a 15: 1 ratio. He assumed that non-shedding was probably controlled by two recessive genes (sh_1 sh_2). Ramiah and Hanumantha Rao (1936) have studied this character quantitatively, they could not come to definite conclusion about the gene nature of shedding (Ghose *et al.* 1960).

According to our observations, the non-shedding mutant had no abscission layer, and the degree of shedding appeared to be closely correlated with the development of the abscission layer. However, in its hybrids with the original strain, the non-shedding mutation was found to be dominant in the shedding habit, and was recessive in the abscission layer formation. This suggests that shedding is due not only to the formation of abscission layer but also, possibly, to the occurrence of cracks in the abscission layer, while both characters have dominant relationships controlled by one gene pair. In other crosses, further, a 9 (non-shedding): 3: 3: 1 (highly shedding) ratio was found. There might be another gene controlling the varietal difference in shedding habits.

Previous genetic studies cited above suggest that there might be several genes concerned with this character. The mutant gene we have found might be due to a change or loss of the basic one which is responsible for the formation of abscission layer.

Regarding lodging, Ramiah and Dharmalingam (1934) have observed a number of varieties, and pointed out that among lodging varieties, various type of lodging could be found, though no single factor could be used as an index. They further made several crosses on the lodging and erect type strains, and considered that the lodging habit is controlled by a single Mendel factor, but the degree of lodging was much affected by environmental condition. Latterly Ramiah designated this gene pair Ld-ld (Ghose *et al.* 1960). Matsuo (1952) further recognized two type of varieties, one lodging at dense spacing and other at heavy fertilization. Recently, Bollich (1963) has calculated a number of correlation coeffi-

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Explanation of Plates

Longitudinal sections of the abscission layer are shown. The materials were taken on flowering day(a) and after flowering(b).

Sp: spikelet. G: glume (empty glume). Pe: pedicel. F: facet. V: vascular bundle.

Plate fig. 1. Non-shedding mutant of Pai-mi-fen. No abscission layer is found, on both flowering day(a) and 35 days after flowering(b).

Plate fig. 2. A shedding variety, Pai-mi-fen (*indica* type). a: Clear abscission layer is seen at flowering date. b: 30 days after flowering, a crack occurs in the central part of the abscission layer as shown by an arrow.

Plate fig. 3. A shedding resistant variety, Taichung 65 (*japonica* type). a: The abscission layer was less developed than Pai-mi-fen, and b: no crack on 35 day (in maturity) after flowering is seen.

Plate fig. 4. An easily shedding wild strain (*Oryza sativa* f. *spontauta*). The well-developed abscission layer is attached to the central vascular bundle. a: Flowering day. b: 10 days after flowering (the spikelets shed about 12–15 days after flowering).

Plate fig. 5. The F_1 between shedding mutant and its original strain. The abscission layer is not so clearly seen as in the original strain, on both flowering day (a) and 35 days after flowering(b).


Sp
G
F
G
V
Pe
1a
1b
2a
2b
3a
3b
4a
4b
5a
5b

cient among rice characters in several varieties and F_2 populations. He indicated only two characters, culm diameter and culm weight, were significantly and positively correlated in all populations, while other characters differed in years and were not always significant. The value of coefficicient of variability was alike to the number of tillers, the breaking strength and unit culm weight were subject to a strong degree of environmental variation. Chang (1964) also recognized the correlation breakig strength and culm density was highly significant ($r=0.607$); whereas, the correlation between culm density and the lodging resistance factor (cLr) appeared to be poor, and indicated that the breaking strength of culm did not appear to index closely the lodging behavior of variety. However, the character of culm thickness, percent of vascular bundles fused with schlerenchyma, relative thickness of schlerenchyma, pattern of internode elongation, and sheath wrapping and cover age, related to lodging habit.

Lodging is a difficult character to evaluate, since it is influenced by plant height, weight of grains, culm strength especially histological structure and other genetic and environmental factors. For studying the inheritance of the lodging resistance, it is better to consider the whole genetic background concerning the above-mentioned characters. From this viewpoint, the erect mutant derived from X-ray treatment might be useful, as it would differ from the original strain only in a particular locus which control lodging resistance, and is affected by the same pattern of environment.

Our genetic study showed that the erect mutant was non-lodging and a single recessive mutation. The same gene also induced various morphological characters pleiotropically, those unfavorable effects of this gene may be removed by inserting modifiers. A preliminary investigation on the hybrid population of the erect mutant x Pai-mi-fen for breeding purpose, was sucessful in selecting a number of non-lodging type strains which combined the characters of Pai-mi-fen with the erect trait of mutant. But it was found that less tillering, stiffness and larger diameter of culm and incomplete extrution of panicle were associated with th the non-lodging habit.

The results of our experiments suggest that induced mutants are useful materials for obtaining non-shedding as well as non-lodging strains, which cannot be easily selected from conventional hybrid populations, and that induced materials are useful for further hybridization breeding. Induced mutants are often accompanied by unfavorable effects. Those undesirable characters may be to some extent improved by readjusting the genetic background. Further studies will be directed to this point.

Summary

Two X-ray induced mutants of *indica* type and several other rice varieties with different degrees of shedding and lodging resistance were studied anatomically and genetically. It was found that:

1. The non-shedding mutant had no abscission layer. Comparison among various varieties showed that the degree of shedding was parallel to the development of the abscission layer. A highly shedding wild strarin (*O. sativa* f. *spontanea*) showed well-developed abscission layer which adhered closely to the central vascular bundle. The occurrence of cracks in the abscission layer also differed among those strains, in close assoiation with the degree of shedding.

2. In hybrids between non-shedding mutant and shedding varieties, the absence of the abscission layer was a simple recessive character, while non-shedding was dominant. The F_2 gave 3:1 or 9:3:3:1 ratios, in latter ratio cross a few very easily shedding plants turned up probably due to interaction of two genes.

3. The erect mutant obtained from a lodging variety was a simple recessive. It differed not only in culm histologically but also in various other culm characters from the original strain.

稻之脫粒性及倒伏性組織學及遺傳學的研究

胡 兆 華　高 國 楠　張 家 成

本文報告印度型水稻二品種經 X 光線處理後獲得的不脫粒突變及直立抗倒伏系統，與其他脫粒性程度相異的稻種行脫粒性，稻稈組織比較及遺傳學研究，結果如後:

1. 稻穀之脫落難易與穀粒基部有無離層組織及是否發達有平行關係 。 不脫粒突變系統無離層組織，而其原種（印度型）的離層組織頗爲發達，日本型品種則離層組織細胞發育不完全，野生稻的離層組織極發達且橫斷小枝梗直達中央部維管束。又於穀粒成熟時日本型品種離層細胞間未見開裂，而印度型品種於開花後 30 日，野生稻則於開花後 10–15 日見離層細胞間開裂。

2. 不脫粒突變系統與易脫粒品種行雜交，無離層爲隱性，F_1 爲不脫粒但見有類似離層的細胞，F_2 脫粒之難易分離比爲 3:1 及 9:3:3:1。後一分離比少數較原親本更易脫落植株之出現推測爲兩對遺傳因子之相互作用。

3. 自印度型伏倒品種中獲得的抗倒伏突變體 ， 稻稈組織比原品種維管束數增加直徑增大外，同時亦見有稈其他性狀的改變。抗倒伏爲隱性突變。（摘要）

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