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Studies on cytoplasmic-genetic male sterility of cultivated rice (*Oryza sativa* L.)[1]

II. Morphological-histological investigation on functional male sterility

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Abstract : Anther indehiscence was the main cause of cytoplasmic-genetic male sterility for rices 65 P 2, 61 P 1 and KR 7. This type of male sterility, determined by cytoplasm and not by nucleus, was rather stable in a range of temperatures. The most significant difference of indehiscent anthers from normal ones is their strongly thickened-fibrous endothecium and their particular orientation pattern. The epidermal cells were also slightly thick-walled. Therefore the separation of intermicrosporangial stripe 1 (IMS 1) from the underlying parenchyma along each side of the connective tissue did not occur at anthesis. The outer surface of IMS 1 of indehiscent anther had some spurs or ridges whereas the surface of normal anthers was smooth. It may prevent the anthers to form anterior pore and pollen shedding. From these results, it is suggested that the anther wall structures and physical process of cohesion mechanism may be involved in anther dehiscence. The functional male sterility of rice is advantageous in that it can be propogated by compulsive self-pollination. Its possible use in developing hybrid rice was discussed.

In the previous paper [3], the present authors reported that anther indehiscence was the main cause of male sterility for rice plants having Pai-co cytoplasm (65 P 2, 61 P 1) and *O. rufipogon* cytoplasm (KR 7) regardless of temperature treatments. It is not determined by nuclear gene but is transmitted from generation to generation through egg cytoplasm. This type of sterility differs from other forms of sterility in that the plants produce normal amounts of viable pollen grains but the anthers do not open, and thus no pollen is shed as a result of defective dehiscence mechanism. Therefore it is called "functional male sterility".

The presence of viable pollens makes functional male sterility very attractive for hybrid breeding. The inbreeding of MS line or MS line propagation can be performed without any difficulties by compulsive-selfing of plants at anthesis. Using the functionally sterile parent as the seed line in the crossing block, the production of hybrid seeds can be ensured without manual operation.

Non-dehiscent anthers may be due to the absence of stomium [7,8,16]. Other possible

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explanations are that stomal cells may be tenacious and pressed by hooked petals which do not allow unfurling of corrolla [10], and anthers may be reflexed or hard and filaments are not able to elongate [12,14,20].

This paper reports the observations on morphological and histological features possibly related to anther indehiscence and also to its mechanism.

Materials and Methods

The materials used in this experiment were the cytoplasmic male sterile rices of TC 65 (P)MS or (Pai-co X TC 65/10), TNG 61 (P)MS or (Pai-co X TNG 61/10) which have the Pai-co cytoplasm, KR 7 MS or (*O. rufipogon* X KHS 1/9) which have *rufipogon* cytoplasm and their pollen parents. These plants were planted in a phytotron at two different day/night temperatures (25/20°, 30/25°C) and also under field conditions. For histological and scanning electron microscopic (SEM) observations, the spikelets of normal and CMS plants in the phytotron were collected at several stages from pre-anthesis to anther dehiscence.

Plastic, Paraffin Embeddings and Sectioning for Light Microscopy [1,2]

Freshly dissected samples were fixed in a mixture of 3% glutaraldehyde, 1% formalin and 0.1% Tween 20 prepared in a 0.05 M phosphate buffer (pH 7.2) for 4 hrs on ice and rinsed in three changes of cold buffer over a period of 2-3 hrs. Tissues were postfixed in 1% OsO_4 in 0.05 M phosphate buffer (pH 7.2) for 4 hrs on ice. Following washes with buffer, the tissue was dehydrated in a graduated series of alcohol and embedded in Spurr's medium ("Standard" formula) [21].

Semithin sections (0.7-1 μm)were cut on a MT 2 B ultramicrotome with glass knives. Plastic sections were floated on a drop of distilled water on slides coated with subbing solution (0.5% gelatin and 0.05% chrome alum). Slides with floated sections were heated at 60°C to dryness and stained according to one of the following schedules.

(a) Heamatoxylin-Safranin 0

The procedure of Warmke and Lee [25] was followed. All light microscopic figures except fig. 1a-b and 2e-f were prepared from sections stained by this routine.

(b) Periodic Acid-Schiff (PAS) procedure [5]

Slides were counterstained with methylene blue-Azure A [25]. Staining period of time was modified to 10 min. at 70°C. Starch localization was further confirmed with iodine-potassium iodide (I-KI) procedure.

For observations on the process of anthesis, mature anthers were fixed in Formalin-acetic alcohol, dehydrated in an ethyl-butyl alcohol series and embedded in paraffin in the usual manner. Sections were transversely cut at a thickness of 10-15 μ and stained with iron-heamatoxylin.

Scanning Electron Microscopy

Fixed anthers and spikelets were dehydrated in a graduated alcohol series followed by critical-point dry with liquid CO_2. The dried specimens were coated with gold. Surface details were observed with a Hitachi-SEM using accelerating voltage of 15 or 25 kv on the secondary electron emission mode.

Results

Histological-morphological observations on normal male fertile anthers of rice revealed that initially the anther wall was consisted of an epidermis, an endothecium,

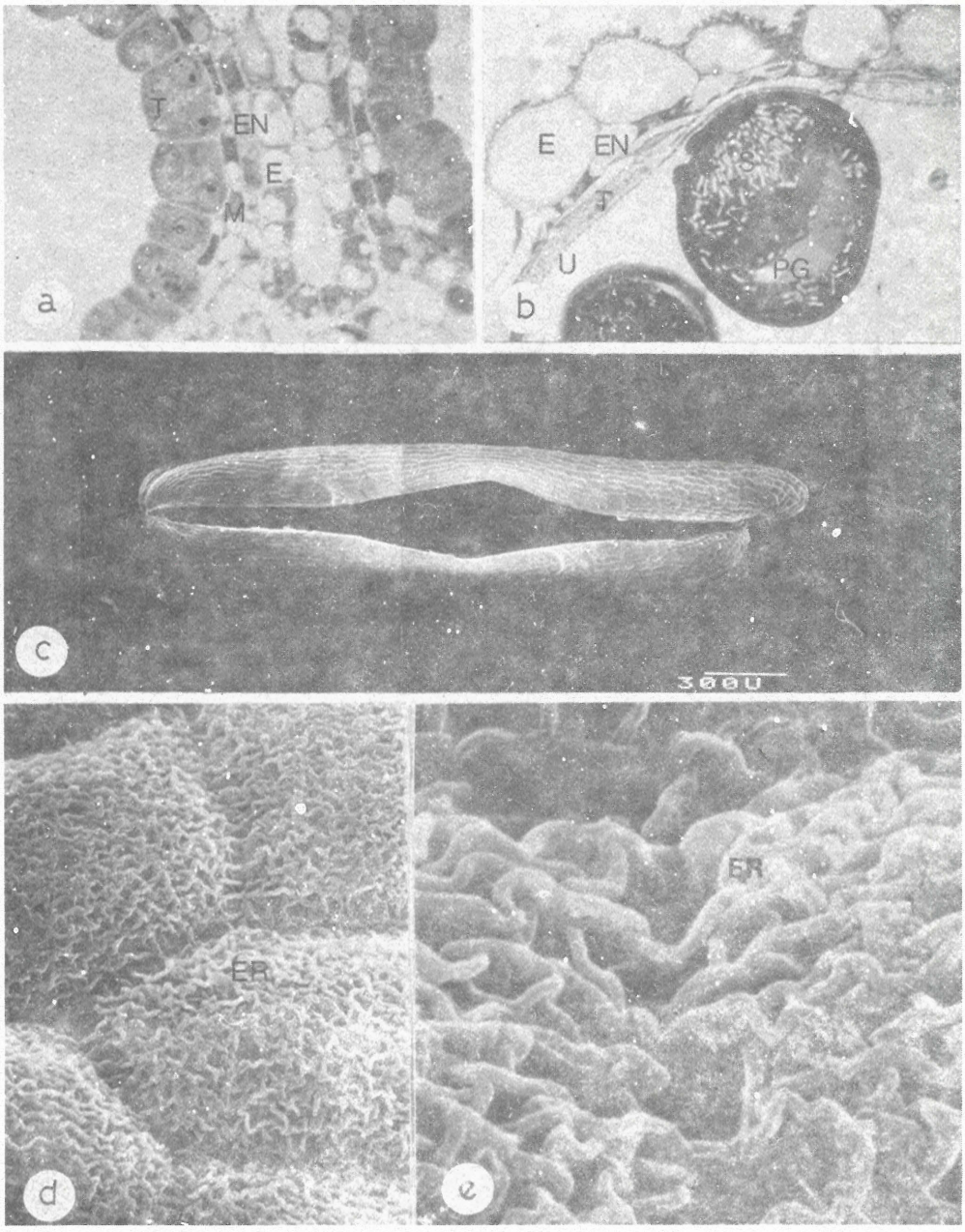


Fig. 1. a-e. LM (a-b) and SEM (c-e) views of normal anther development. a. At meiotic stage, the anther wall consists of epidermis (E), endothecium (EN), a middle layer cell (M), and tapetal cell (T), (600 X). b. At pollen ripening stage, tapetum has disintegrated, endothecium and middle layer are also degenerating. Pollen grain (PG) is filled with starch grains (S), (1,000 X). c. SEM view of whole mounts of dehiscent anther, (50X). d. Epidermal cell surface covered with ridges (ER), (1,500 X). e. Higher magnification of epidermal cells indicating the continuity of epidermal ridges between cells both in the long dimension and adjacent cells, (10,000 X).

one or more middle layers of cells and a singlelayered tapetum (Fig. 1 a). The middle layers degenerated quite early whereas tapetum and endothecium disintergrated later at pollen ripening stage (Fig. 1 b). At anthesis, the endothecium or subepidermal layers of cells is present only intermittently and shows a very feeble development of fibrous

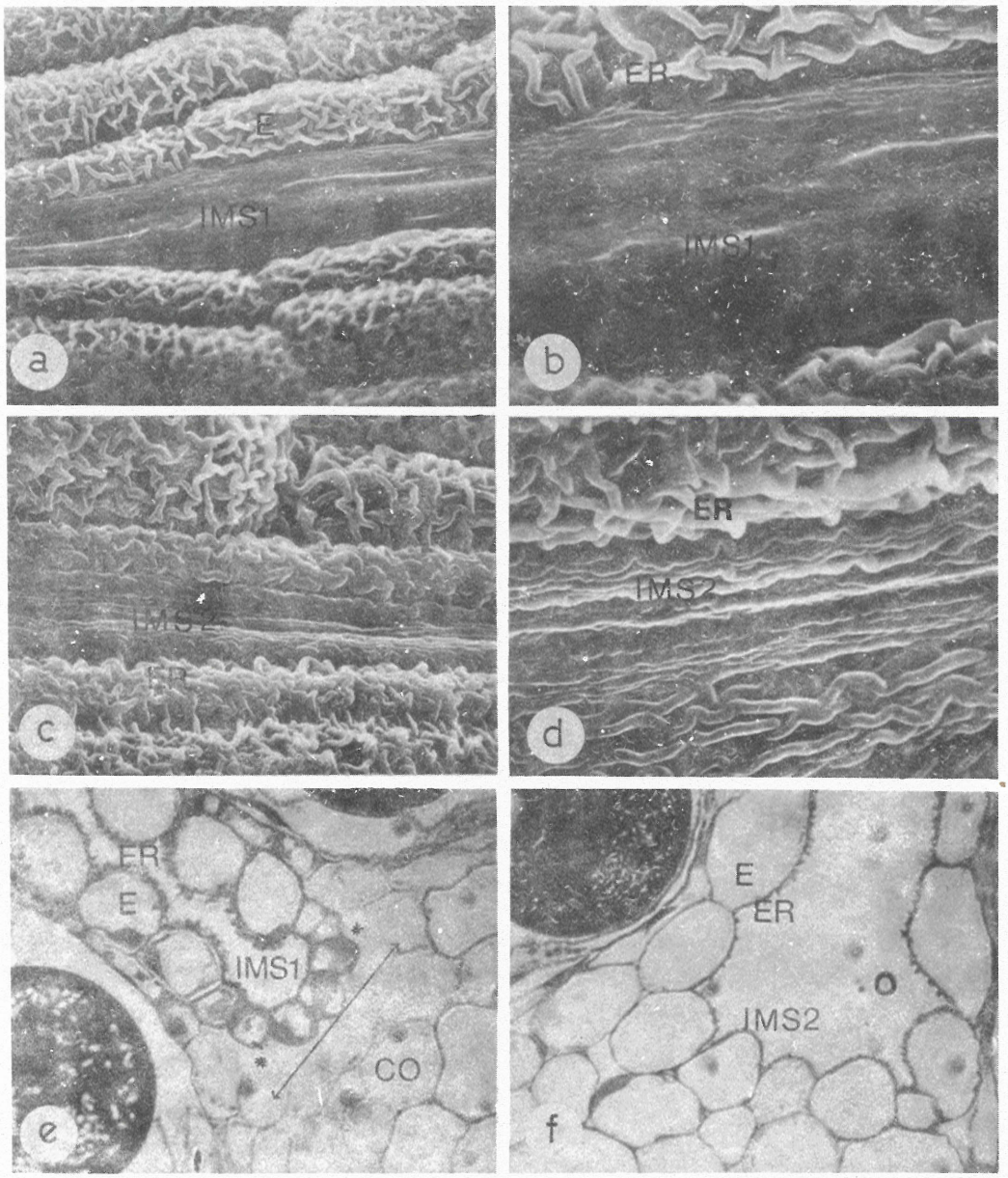


Fig. 2. a–f. SEM (a–d) and LM (e–f) views of intermicrosporangial stripe between microsporangia. a. Epidermal cells, along intermicrosporangial stripe 1 (IMS 1) which have no ridge and a few adjacent cells, (2,000 X). b. Higher magnification of IMS 1, (5,000 X). c. Epidermal cells along intermicrosporangial stripe 2 (IMS 2). Epidermal ridges on, IMS2 are straighter and parallel to each other, (3,000 X). d. Higher magnification of IMS 2, (5,000 X). e. Cross-section of IMS 1. The underlying parenchyma is indicated by a pair of arrows. Asterisk indicates the dehiscent site between IMS 1 and parenchyma cells, (1,000 X). f. The cross-section of IMS2, (1,000 X).

thickening on the cell walls. On the other hand, the epidermal cells have their inner and tangential walls slightly lignified and their outer walls cuticularized. The epidermis is thus the only layer enclosing the pollen grains when the anther mature. Surface view of whole anther at the onset of anthesis is shown in Fig. 1 c. Epidermal cells were covered with ridges which developed at the late young pollen stage and formed a highly ridged epidermal surface rapidly. Most epidermal ridges were crosswise and were oriented parallel to the long axis of the cells. They were not confined to a single cell but in most cases continued from cell to cell (Figs. 1 d-e). The cells of each anther wall layer possess

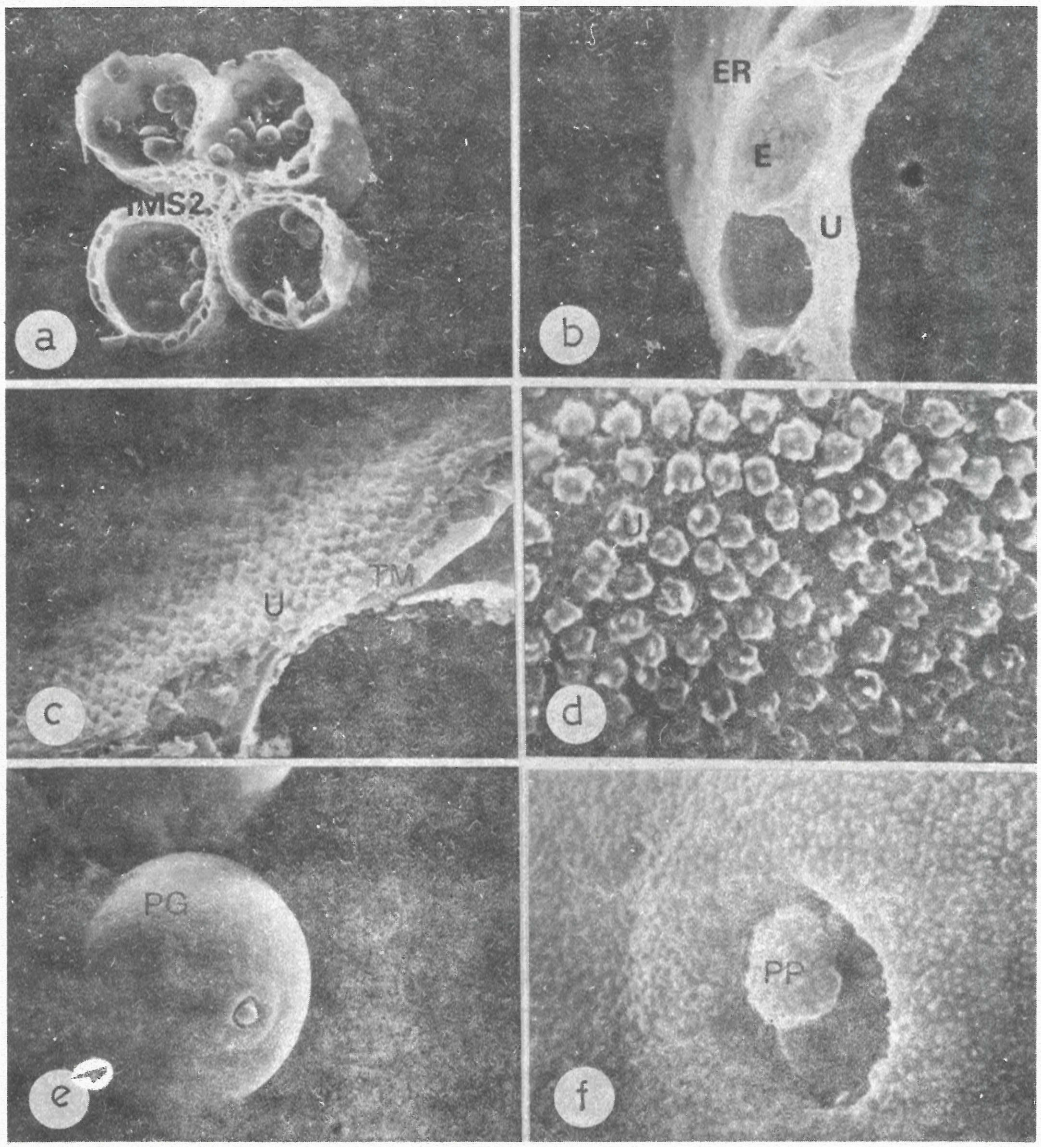


Fig. 3. a-f. SEM views of inner morphology in mature normal anthers. a. Cross-section of anther, (150X). b. Mature anther wall consists of epidermis, degenerated endothecium and tapetum with Ubisch bodies (U), (1,500 X). c. The inner surface of tapetum (TM) with U bodies, (5,000 X). d. Higher magnification of U bodies, (10,000 X). e. Mature pollen grain (PG), (1,500 X). f. The pollen grain surface and pollen pore (PP), (10,000 X).

their own particular orientation pattern. Epidermal cells are arranged parallel to the microsporangium circumference. The orientations of epidermal and endothecial cells are related to the mechanism of anther dehiscence (Figs. 1, a-c).

Another feature of the surface structure of mature anthers was the intermicrosporangial stripes existed between two microsporangia. Epidermal cells lacking ridges on the surface formed longitudinal stripes called intermicrosporangial stripe 1 (IMS 1)

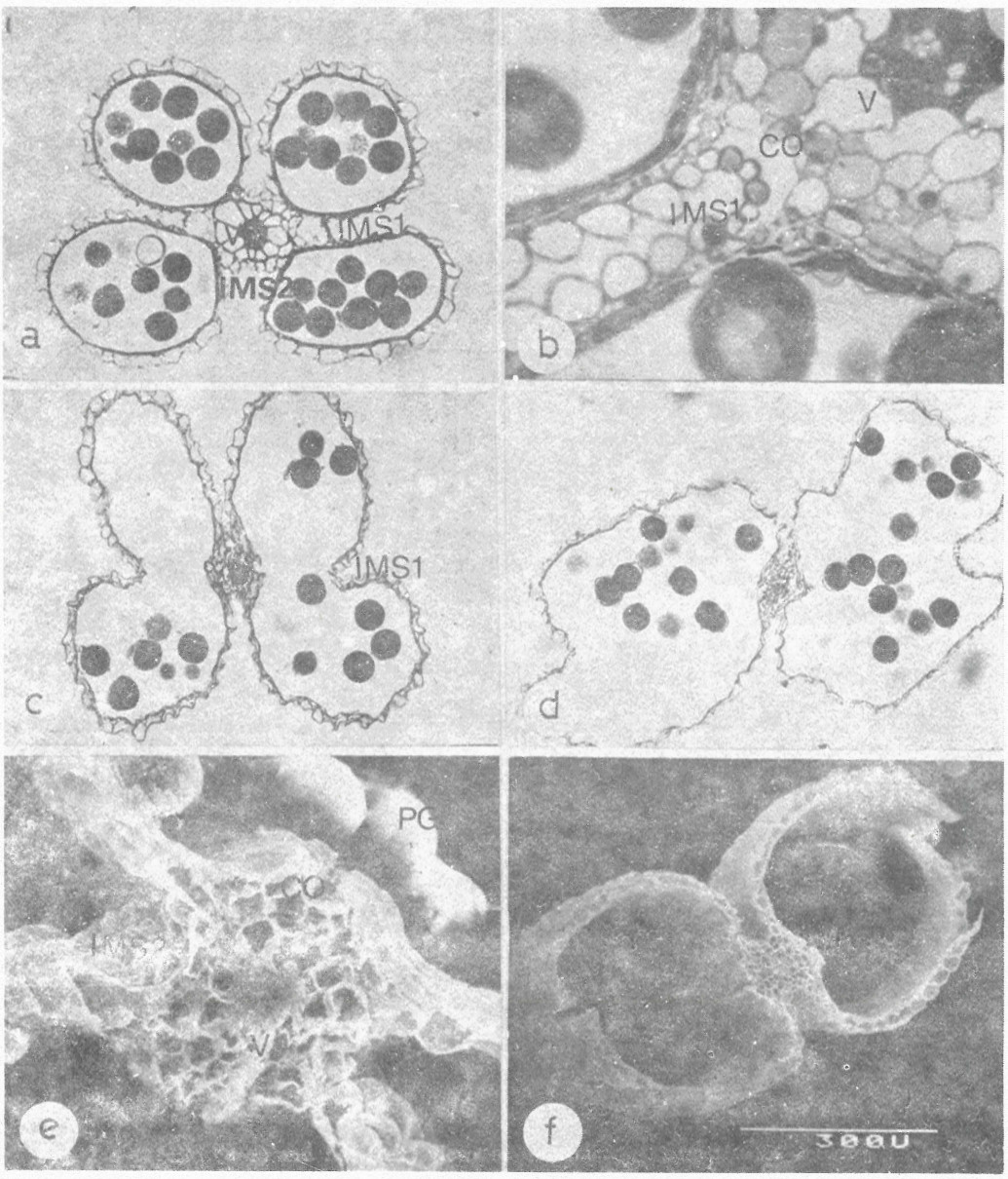


Fig. 4. a-f. LM (a-d) and SEM (e-f) views of anther dehiscent process. a. IMS1 was partially separated from connective tissue (CO) ; V, vascular bundle, (200X). b. Higher magnification of IMS1 separation from CO, (600X). c-d. Two microsporangial locules join into a single pollen cavity at pollen ripening stage, (200X). e. SEM view of two microsporangial locules joining into a single pollen cavity at pollen ripening stage, (500X). f. Anther dehiscence at anthesis, (150X).

where the locules fused through the separation of intervening connective cells (Figs. 2 a-b). These stripes were usually three to six cells wide. At anthesis, the mature anther dehisced from this pair of stripes (IMS 1). Another pair of stripes having ridges were called intermicrosporangial stripe 2 (IMS 2) (Figs. 2c-d) which were located along the connective cells and contained 10-20 cells, much wider than IMS 1. The ridges on IMS 2 were oriented parallel to each other and also to the long axis of the cell. The results of cross section observation (Figs. 2e-f) coincided with those of SEM observations regarding the presence of IMS 1 and IMS 2.

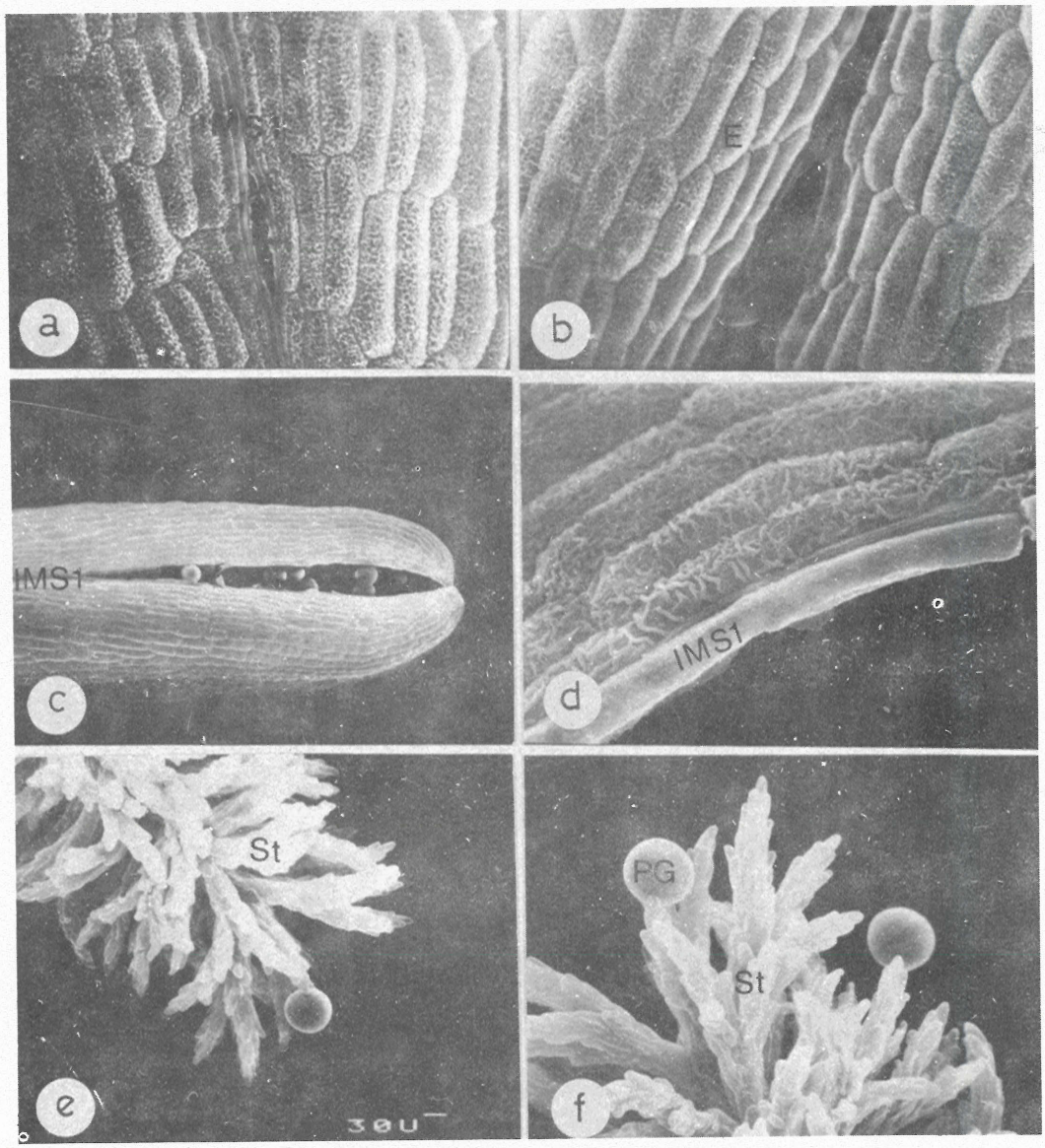


Fig. 5. a-f. SEM views of anther dehicence process. a. Anterior formation on IMS 1, (75 X). b-c. Anther dehisced along IMS 1, (75X, 50 X). d. Higher magnification of IMS 1 and a few epidermal cells after dehiscence, (1,000X). e-f. Pollen grains shed and adhered to stigma, (200X, 300X).

The inner and outer morphology of mature normal anther is shown in Fig. 3. It is consisted of an epidermis with ridges, a degenerated thin layer endothecium, Ubisch bodies on the surface of inner wall of tapetum and mature pollen grains (Figs. 3 a-b). The Ubisch bodies developed on tapetum cell wall after the tetrad stage and remained contact at anthesis (Figs. 3 c-d). The attachment of pollen grains to Ubisch bodies indicated that the spherical U bodies seemed to serve as channels of nutrient transport between tapetum and microspores. The surface of pollen grain also had similar structure to the Ubisch bodies (Figs. 2e-f). Pollen pore (Fig. 3 f) was conspicuous on the mature pollen grain and a pollen tube could emerge from this pore when pollen germination occured.

The process involved in the dehiscence of the normal male fertile anthers is shown in Fig. 4. Initially, there was a separation of lip cells (IMS 1) from the underlying parenchyma cells between the microsporangia along each side of the connective tissue (Figs. 4 a-b). This separation resulted in a join of two microsporangial locules into a

Table 1. Percentages of stainable pollens and seedset of functional male-sterile rices and their recurrent parents in different growth environments.

Entry	Treatment[a]	Pollen fertility Mean±SE (%)	Seedset Mean±SE (%)
TC 65	A	92.1 ± 0.8	96.3 ± 1.2
	B	86.0 ± 5.2	95.0 ± 2.1
	C	90.1 ± 1.2	92.3 ± 2.0
65 P 2	A	88.7 ± 4.4	1.1 ± 0.8
	B	12.2 ± 7.9	0.2 ± 0.4
	C	85.6 ± 3.8	1.5 ± 0.6
TNG 61	A	95.1 ± 2.0	95.6 ± 1.8
	B	79.3 ± 4.9	98.1 ± 1.2
	C	89.5 ± 4.8	93.2 ± 2.2
61 P 1	A	89.3 ± 5.2	1.5 ± 0.8
	B	27.5 ± 10.3	0.2 ± 0.2
	C	90.2 ± 5.6	1.8 ± 0.6
KHS 1	A	96.0 ± 2.0	95.4 ± 1.2
	B	93.4 ± 2.3	94.5 ± 1.0
	C	92.0 ± 3.0	92.6 ± 1.3
KR 7	A	88.8 ± 8.0	2.9 ± 2.1
	B	60.8 ± 8.9	0.6 ± 0.5
	C	78.5 ± 9.2	3.4 ± 2.6

[a] A : in the phytotron at 30/25° C.
B : in the phytotron at 25/20° C.
C : in the field condition.

single pollen cavity. Consequently four pollen sacs formed two pollen cavities (Figs. 4 c-f). The anthers of rice plant started to dehisce from the tip and base to the center, i. e. in a centripetal motion, along IMS 1 to form the anterior pore (Figs. 5 a-b). The separation of anterior epidermal cells from the underlying parenchyma cells along IMS 1, although initially for a short distance (Fig. 5 b), would proceed gradually to the full length (Fig. 1c and Fig. 5 c). After the opening of pelea and lemma, the anthers swang on the top of elongated filaments and the pollens shed on the stigma (Fig. 5, e-f).

The indehiscent character of functional male sterile anthers was first checked with a hand lens and was found to remain indehiscent until the anther dried up. When the anthers were smeared and treated with an 1% I-KI solution, 85% or more pollen grains were stainable although seedset percentage was consistently low under different weather conditions (Table 1). The compulsive self-pollination gave a seedset as high as 90% and their self-progenies were also anther indehiscence (funtional male sterility). The stainable pollen and seedset percentages are shown in Table 2.

Table 2. Percentages of stainable pollens and seedset of the progenies derived from compulsive self-pollination of functional male sterile rice.

Entry	Pollen fertility Mean±SE (%)	Seedset Mean±SE (%)
TC 65	93.6 ± 2.6	91.3 ± 1.2
65 P 2	86.4 ± 3.1	2.1 ± 1.6
65 P 2 S	88.2 ± 3.4	1.6 ± 0.9
TNG 61	91.8 ± 2.2	92.2 ± 2.0
61 P 1	85.4 ± 3.1	1.1 ± 0.8
61 P 1 S	86.4 ± 3.5	1.4 ± 0.8
KHS 1	90.4 ± 1.9	93.3 ± 2.8
KR 7	85.7 ± 3.4	2.1 ± 1.1
KR 7 S	86.2 ± 3.6	2.3 ± 1.4

Compared to normal anthers, the functonal male sterile anthers have well developed endothecial cells with strong fibrous thickenings at pollen ripening stage. These endothecial cells have their long axes arranged perpendicularly to the microsporangium circumference (Figs. 6 a-b). The epidermal cells were also slightly thick-walled. Another difference was that the surface structure of epidermal cells at IMS 1 seemed to be lignified and cuticularized. As mentioned before, the surface of epidermal cells that form longitudinal stripes between the microsporangia in the dehiscent anther were lacking of ridges, but ridges or spurs were found on the indehiscent anthers (Figs. 6cd). In addition, the ridges frequently showed more straight figures and were parallel more closely to each other. Therefore, the separation of IMS 1 from the underlying parenchyma between the microsporangia or separation from each other along the IMS 1 did not occur as it did in the dehiscent type, and the anther possessed two or four locules

after anthesis. As the anther wall of the individual lobe was quite strong, it did not rupture and thus the anthers remained indehiscent and pollination could not take place (Fig. 6 e-f). At anthesis, the filaments could elongate as usual in this type of male sterility, and the anthers remained outside of the spikelet after flowering.

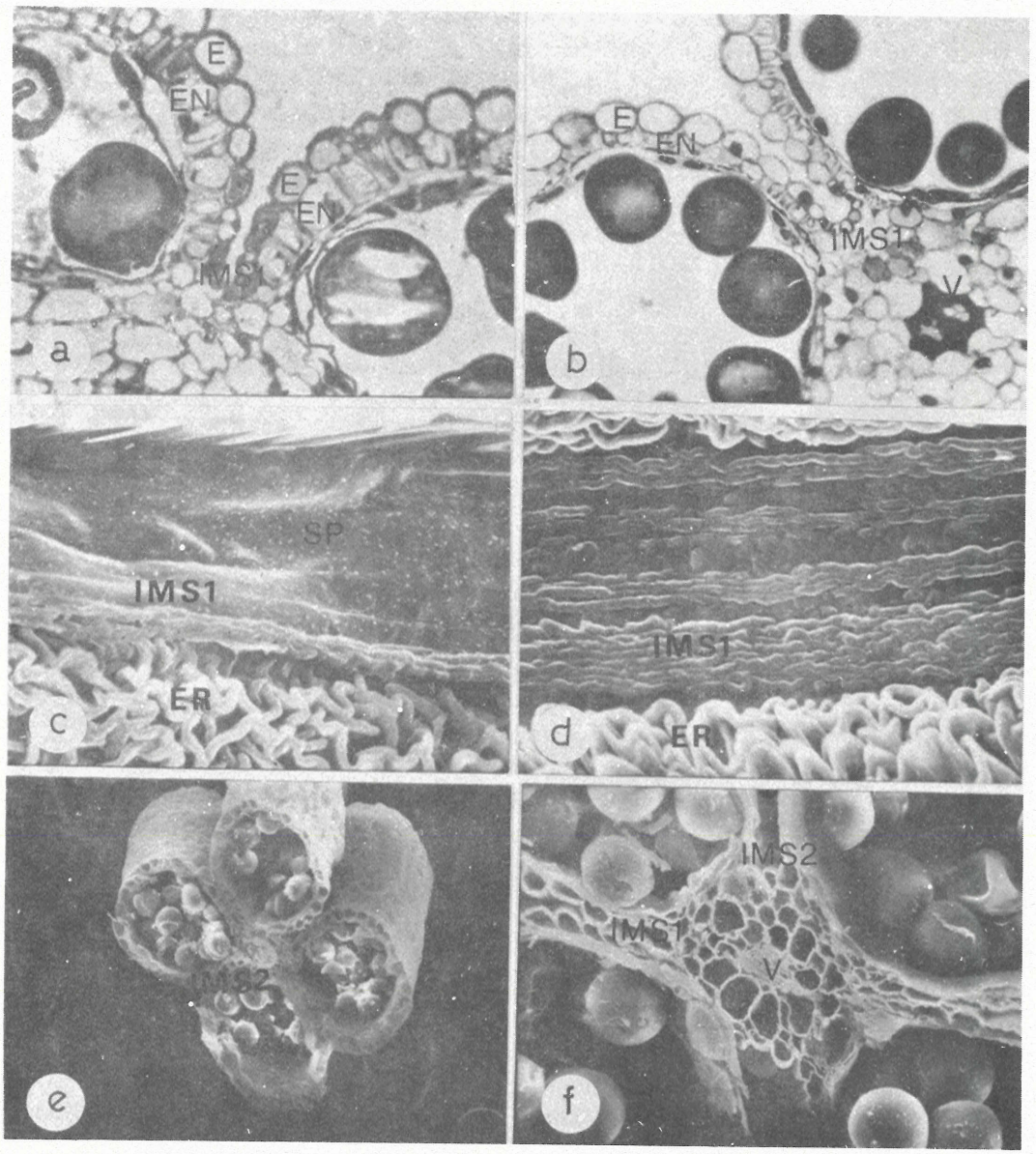


Fig. 6. a-f. Effect of cytoplasm on the development of dehiscent site. a-b. Cross-sections of indehiscent anther at pollen ripening stage. The endothecium layer is well developed and slightly thickening, and their long axes are perpendicular to the microsporangium circumference. The IMS 1 is slightly lignified, thus no separation occur between IMS 1 and CO, (400 X). c-d. SEM views of IMS 1 surface on indehiscent anther, noting spurs (SP) and ridges, (5,000X). e-f. The indehiscent anther at anthesis. Dehiscent site is not formed. The pollens in pollen sacs were not shed, (150 X, 500X).

Discussion

The mechanism of anther dehiscence or opening of microstrobili and the release of pollen vary according to different plant families. The stamens of the vast majority of the appoximately 225,000 species are dehiscent. Their anthers release pollen grains by valves, by terminal pores or, typically by lateral longitudinal (rarly transverse) slits [13,19]. Forrice plante, the anther starts dehiscing from the tip and the base toward the center after opening of pelea and lemma, then proceeding gradually to the full length. It is a longitudinal dehiscence or a slit-like opening, the most common form in angiosperms.

The dehiscence of anther is a desiccatory process. The process has been characterized as being affected by a hygroscopic and/or a cohesion mechanism. Hygroscopic (imbibition) mechanisms depend entirely upon volumetric changes in cell walls, whereas cohesion mechanisms involve volumetric changes in cell lumina, the cell walls undergoing largely passive deformation. Many workers now accept a cohision mechanism for anther dehiscence [15,19,22,24]. Some features of the stamen such as open stomata, a weakly developed cuticule, a prominent intercellular-space system and xylem lacunae may play a role in anther dehiscence, since such features would tend to promote a rapid loss of water or a disruption of the water supply to the anther [19]. We also suggest that some additional force and ridged epidermal layer would be necessary to accomplish the separation of IMS 1 from the underlying parenchyma. The formation of anterior pore may be the result of deformation of the endothecial wall thickening.

The change of atomospheric humidity is the most frequent causative agent leading to anther wall rupture. Temperatures also affect dehiscent characteristics [17,18,23]. In the phytotron and field experiments, we obtained that there were no significant difference in seedset percentage of functional male sterile plants. Therefore, this type of male sterility is stable under such environmental conditions. It is also showed that these weather conditions did not affect anther indehiscence.

One of the most significant aspects of indehiscent anthers of functional male sterile plants is that the separation of IMS 1 from the underlying parenchyma does not occur. This may be due to the well developed endothecium and their particular orientation pattern. Another difference from those of mormal fertile plant was the spurs or ridges on the surfce of IMS 1 of epidermal cells. Those ridges may be the products of epidermal cell wall and their outer walls are cuticularized. It may be suggested that the constructive force on such IMS 1 may tend to prevent separation from each other along the IMS 1. Therefore, well developed endothecium and spurs or ridges at IMS 1 may prevent the anthers to form anterior pore and pollen shedding.

A number of male sterility genes are known to prevent pollen release by modifying normal differentiation or functioning of the stomium and thus prevent release of fertile pollen through failure of anther dehiscence. These functional male sterile types leave the option of forced pollen release open. They are found not only as recessive traits in tomato [4] but also as dominant traits in potato [6]. A genetic nondehiscent anther cha-

racter in sorghum [26] and a similar situation in cotton [11] have been reported. In this paper, the anther indehiscence was transimitted from generation to generation through egg cytoplasm rather than nuclear genes.

Kitamura [9] found that all F_1's of Japanese varieties X "Ta-strain" were normal in both seed-setting and pollen fertililes, whereas F_1's of the reciprocal crosses showed a wide range of seedset percentages in spite of their good pollen fertility. The sterility was connected with the difficulty in anther dehiscence caused by Tadukan cytoplasm. Yabuno [27] reported that the *glaberrima* strain of substitution lines having the cytoplasm of japonica variety Akebono was associated with cytoplasmic male sterility and anther indehiscence. The pollen fertility restoring gene Rf_i also functioned in homozygous condition as a restorer of anther dehiscence.

Since the selfing progenies of indehiscent anther plants were also anther indehiscent and pollens of these plants were full fertile, it may be suggested that this type of male sterility can be maintained by hand pollination or compulsive-selfing. To search for stable fertility restoring (gametoficant) chemical will be helpful. If gametoficants were available, there would be no need to develop R-lines. Unstable genetic restoration of fertility would be trouble some to hybrid variety breeders. A systemic chemical of this kind would be ideal. Therefore, from the agronomic point of view, functional male sterile lines are very attractive for hybrid breeding. Unfortunately this attractive sterility occurs only in a limited number of crops. The crop which has been mostly investigated so far is tomato [10]. It is also found in eggplant, cabbage and *Streptocarpus* [8]. The use of functional male sterility in tomato is limited by two factors. One is that the indehiscence is sensitive to environment. Depending on weather condition up to 50% self-fertilization may occur in the seed lines. The second factor is that the stigmas of tomato are hidden within a cone of connate stamen. Hence cross pollination is severely impeded. This problem can be bypassed, however, by the use of mutants having exserted stigmas.

In the functional male sterility of rice, several problems in hybrid breeding need to be solved. The presence of widespread hybrid sterility in rice species is disadvantageous for hybrid-variety breeding. We need more information regarding the effect of genetic and environmental interaction on male sterility and fertility restoration. Perhaps the most importatn problem is how to modify the floral structure of male sterile rice to increase its outcrossing potential.

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水稻細胞質—遺傳因子雄不稔性之研究[1]

Ⅱ、構造雄不稔花藥之形態及組織學的研究

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摘 要

具有白殼細胞質之「臺中 65 (白殼) MS」與「臺農 61 (白殼) MS」以及具有 *O. rufipogon* 細胞質之「高雄選 1 (R) MS」等細胞質雄不稔系統，其不稔之主要原因爲花藥不能裂開，但花粉發育卻皆正常，此型雄不稔稱之爲構造性雄不稔性。利用掃描電子顯微鏡與光學顯微鏡觀察構造性雄不稔花藥與正常花藥之結果得知，不裂開花藥與正常花藥間最顯著之差異爲內皮細胞之强靱纖維化與其長軸方向的組成及輕微角質化之表皮細胞，因此開花時花粉囊間帶 I (IMS 1) 與藥隔薄壁組織間不發生分離。另外在不裂開花藥之 IMS 1 表面上發現有部分刺狀物或表皮脊狀凸起，與正常花藥 IMS 1 表面光滑不同。因此開花後構造性雄不稔之花藥經常維持着四個或兩個花粉囊，故花藥之藥壁結構及黏接 (Cohesion) 機制之物理過程與花藥裂開似有密切關係。

在水稻，此種構造性雄不稔性，可以用强迫自交或其他方法來繁殖後代而不須要代代回交其輪迴親，因此在發展雜種水稻上，此種雄不稔性具有很大的功用。

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