Morphological Evaluation of the Trace of Grain Detachment in *Japonica* Rice Cultivars with Different Shattering Habits

Kazuo Okubo

(Research Institute for Agriculture, Okayama Prefectural Technology Center for Agriculture, Forestry and Fisheries, 1174-1 Kodori, Akaiwa 709-0801 Japan)

Abstract: Seed shattering is an important agronomic trait in rice as it directly affects the yield. Manipulation of the degree of shattering will maximize the yield potential. This study was performed to find an indicator for indirect selection to facilitate the selection of medium-shattering habit in *japonica* rice breeding. The grain shattering pattern and microscopic morphology of the separation zone on pedicels of five *japonica* rice cultivars with different shattering habits were compared. Almost all grains were separated between the sterile lemma and rudimentary glume in cultivars with medium-shattering, easily-shattering and very easily-shattering habits. On the other hand, approximately 50% of the grains of the cultivar with hardly-shattering habit were torn off at the bent portion of pedicel. A separation pileus was formed on the terminal of the pedicel. The pileuses were most prominent in cultivars with easily-shattering and very easily-shattering habits, while cultivars with a medium-shattering habit had more flat pileuses than prominent pileuses. Additionally, in the cultivar with a hardly-shattering habit all pileuses were flat. Development of fibrous cell walls on the separation pileus varied with degree of shattering habit. The easier the grain shattered, the poorer was the development of fibrous cell walls. These results strongly suggest that the shape of separation pileus and the development of fibrous cell walls are related to the shattering habit in *japonica* rice. Additionally, it is highly probable that the medium-shattering habit is characterized by the type of shattering that separates between sterile lemma and rudimentary glume with the flat shape of pileus.

Key words: Cultivar, *Japonica*, *Oryza sativa* L., Rice, Separation zone, Shattering habit.
shattering cultivars by the first and second methods based on the individual test of *japonica* rice (Okubo, 2013).

Fukuta et al. (1994) carried out conventional genetic analyses of shattering-resistant mutant lines based on the mean value of BTS that was calculated for 10 grains per individual panicle. However, the BTS is affected by the dryness of panicle. The BTS value of a dry panicle is considerably higher than that of a fresh panicle. The difference in BTS between dry and fresh panicles is often larger than the varietal difference under the same moisture condition (Ebata and Tashiro, 1990). Thus, the evaluation of shattering by BTS for panicle samples harvested under different conditions is complicated because it is imperative to synchronize the dryness of panicle samples from harvest to measurement. The medium-shattering habit is virtually impossible to select by conventional evaluation methods for shattering habit, and requires time-consuming line selection. Therefore, a simple marker is needed for individual selection of medium-shattering habit.

The type of grain shattering (Jin and Inoue, 1982) and morphological characteristic of separation zone (Ebata and Tashiro, 1990) have been suggested to control the grain shattering degree. However, Jin and Inoue (1982) used Korean *japonica-indica* hybrid varieties in addition to *japonica* rice cultivars. On the other hand, Ebata and Tashiro (1990) used three Asian cultivars *japonica*, *javonica* and *indica*, African cultivar of *Oryza glaberrima* Steud, and two wild species of *O. minuta* Presl. and *O. officinalis* Wall. *Japonica-indica* hybrid varieties and *indica* rice cultivars shatter more easily than *japonica* rice (Jin and Inoue, 1981; Lee and Huh, 1984; Fukuta, 1995). Wild species of rice shatter extremely easily. The grade of shattering habit is a varietal characteristic of *japonica* rice cultivars specific to Japan, so that the evaluation criteria of shattering habit of Japanese rice cultivars is different from the classification of shattering habit used in other countries (Fukuta and Fukui, 1995). Tikai and Nishitani (1976) and Kobayashi (1990) studied cultivars with a medium-shattering habit according to the Japanese classification.

Although Jin and Inoue (1982) and Ebata and Tashiro (1990) studied the relationship between the type of grain shattering, morphological characteristic of separation zone and shattering habit by using a considerably wide variety of materials, no medium-shattering cultivars according to the Japanese shattering classification were used as experimental materials in those studies. Thus, the simple morphological characteristics of the medium-shattering cultivars according to the Japanese shattering habit classification has not been studied.

In breeding of *japonica* rice, shattering habit should be improved by using genetic variation in *japonica* cultivars, because useful variation of shattering habit obviously exists in *japonica* rice cultivars (Fukuta, 1995; Okubo, 2012). The main aim of the present study is to identify a morphological marker to facilitate the selection of medium-shattering habit in *japonica* rice breeding. In this study, the type of grain shattering and the microscopic morphology of separation zone on pedicels in *japonica* rice cultivars with different shattering habits were compared. In this study, I use the Japanese classification of shattering habit.

### Materials and Methods

#### 1. Plant materials and crop management

Five *japonica* rice cultivars, Asahi, Akebono, Omachi, Kibinohana and Setokogane were investigated in this study. Their shattering habit, origin and history are shown in Table 1. Akebono, Kibinohana and Setokogane are candidates of the donor parent for different shattering habits and Asahi is the recurrent parent in the backcrossing method in breeding programs of our institute. Brewers’ rice Omachi is not a candidate of donor parent, but it was used as experimental material for the medium grade of shattering habit, because this cultivar was used as experimental material in recent studies for shattering habit.

| Cultivar* | Grade of shattering habit** | Origin and history of the cultivar |
|-----------|-----------------------------|----------------------------------|
| Asahi     | Very easy                   | Pure line selected from native variety of Japan. Recommended variety in Okayama, Japan. For staple food. |
| Akebono   | Easy                        | Bred from crossing Norin 12 as seed parent with Asahi as pollen parent. Recommended variety in Okayama, Japan. For staple food. |
| Omachi    | Medium                      | Pure line selected from native variety of Japan. Recommended variety in Okayama, Japan. For brewers’ rice. |
| Kibinohana| Medium                      | Bred from crossing Asahi as seed parent with Shizuhikari as pollen parent. Recommended variety in Okayama, Japan. For staple food. |
| Setokogane| Hard                        | Bred from crossing Asahi as seed parent with Chubu 35 as pollen parent. Former recommended variety in Okayama, Japan. For staple food. |

* The cultivars are arranged in the order of easiness of grains to shatter from very easily-shattering to hardly-shattering in turn from the top.

** Grade of shattering habit is based on the studies by Hihara et al. (1991) and Okubo et al. (2012).
These cultivars were sown in nursery boxes on 20 May 2013. Seedlings at the 3.5-leaf stage were transplanted by hand to the paddy field in the Research Institute for Agriculture, Okayama Prefectural Technology Center for Agriculture, Forestry and Fisheries (Akaiwa, Japan; 34°47’N, 134°01’E) on 20 June 2013. Planting density was 18.3 hills m⁻² (at 26 cm row and 21 cm apart) and each hill had 3 seedlings. Each cultivar was transplanted on a fixed plot with a size of 3.4 m² (3 rows and 21 hills per row). Basal fertilizer was applied before puddling: 5.0, 6.2 and 4.7 g m⁻² of nitrogen (N), phosphate (P₂O₅) and potassium (K₂O), respectively. Topdressing was supplied at the panicle formation stage: 3.0 and 2.8 g m⁻² of N and K₂O, respectively.

Every cultivar was harvested at 55 days after heading, a panicle of the longest culm was selected per plant and 5 panicles without spontaneous grain shattering were selectively collected per cultivar for measurement.

2. Types of grain shattering

The grain shattering pattern was investigated on the day when the panicles of each cultivar were harvested. Three of the 5 panicles were used in this investigation. All grains of 3 panicles were pulled longitudinally to detach from pedicels and classified into 3 types of grain shattering (Jin and Inoue, 1982) as indicated in Fig. 1. Briefly, type A: grain was separated between sterile lemma and rudimentary glume, type B: grain was torn off at bent portion of pedicel, type C: separated between lemma and sterile lemma.

![Fig. 1. Three types of grain shattering.](image)

Type A: separated between sterile lemma and rudimentary glume.  
Type B: torn off at bent portion of pedicel.  
Type C: separated between lemma and sterile lemma.  
BP, bent portion of pedicel; L, lemma; RG, rudimentary glume; SL, sterile lemma; SP, separation pileus.

![Fig. 2. Evaluation criteria of shape of separation pileus.](image)

A, B and C = flat shape; D, E, F and G = prominent shape. Separation pileuses were stained with safranin solution in order to accentuate the shape of them.
Plant Production Science Vol.17, 2014

2. Type of grain shattering

The type of grain shattering is shown in Table 2. Almost all grains except for Setokogane were categorized as type A. Only grains from Setokogane were divided into type A and type B sub-equally. None of the grains in any cultivar were categorized as type C.

| Cultivar  | Repetition of panicle | Number of grains investigated | Type of grain shattering* |
|-----------|-----------------------|------------------------------|----------------------------|
|           |                       |                              | A  | B  | C  |
| Asahi     | 1                     | 159                          | 159 | 0  | 0  |
|           | 2                     | 143                          | 143 | 0  | 0  |
|           | 3                     | 139                          | 139 | 0  | 0  |
| Akebono   | 1                     | 170                          | 169 | 1  | 0  |
|           | 2                     | 151                          | 151 | 0  | 0  |
|           | 3                     | 150                          | 148 | 2  | 0  |
| Omachi    | 1                     | 170                          | 168 | 2  | 0  |
|           | 2                     | 162                          | 160 | 2  | 0  |
|           | 3                     | 163                          | 158 | 5  | 0  |
| Kibinohana| 1                     | 120                          | 119 | 1  | 0  |
|           | 2                     | 116                          | 115 | 1  | 0  |
|           | 3                     | 112                          | 112 | 0  | 0  |
| Setokogane| 1                     | 118                          | 60  | 58 | 0  |
|           | 2                     | 115                          | 57  | 58 | 0  |
|           | 3                     | 116                          | 57  | 59 | 0  |

* Types of grain shattering are shown in Fig. 1.

---

3. Microscopic analysis of the morphology of separation zone

Microscopic observation was performed with a stereo microscope (SteREO Discovery V8, Carl Zeiss Microscopy GmbH, Jena, Germany) and an environmental scanning electron microscope (ESEM: Mini scope TM-1000, Hitachi, Ltd., Tokyo, Japan) on 30 October 2013. In observation with a stereo microscope, terminals of pedicels with type A shattering pattern were investigated using another 2 panicles and classified into two groups i.e., flat and prominent, according to the shape of separation pileus (Ebata and Tashiro, 1990) as indicated in Fig. 2. Separation pileuses were observed from two observation directions: the tip side of rudimentary glumes. The pileus recognized to be flat from either observation direction was classified as flat (Figs. 2A, 2B). On the other hand, the pileus recognized to be prominent independent of the degree from both observation sides was classified as prominent (Figs. 2D, 2E, 2F, 2G). Furthermore, a partly flat pileus (Fig. 2C) in which the brim of separation pileus was recognized to be flat but center of pileus was recognized to be barely prominent, was classified as flat pileus. A violently damaged pileus was not scored.

Additionally, the fine structure of the separation pileus was analyzed under ESEM. Each sample was observed with neither fixation nor sputter coating.

Results

1. Type of grain shattering

The type of grain shattering is shown in Table 2. Almost all grains except for Setokogane were categorized as type A. Only grains from Setokogane were divided into type A and type B sub-equally. None of the grains in any cultivar were categorized as type C.

---

Table 2. Number of grains according to the type of grain shattering.

| Cultivar  | Repetition of panicle | Number of grains investigated | Type of grain shattering* |
|-----------|-----------------------|------------------------------|----------------------------|
|           |                       |                              | A  | B  | C  |
| Asahi     | 1                     | 159                          | 159 | 0  | 0  |
|           | 2                     | 143                          | 143 | 0  | 0  |
|           | 3                     | 139                          | 139 | 0  | 0  |
| Akebono   | 1                     | 170                          | 169 | 1  | 0  |
|           | 2                     | 151                          | 151 | 0  | 0  |
|           | 3                     | 150                          | 148 | 2  | 0  |
| Omachi    | 1                     | 170                          | 168 | 2  | 0  |
|           | 2                     | 162                          | 160 | 2  | 0  |
|           | 3                     | 163                          | 158 | 5  | 0  |
| Kibinohana| 1                     | 120                          | 119 | 1  | 0  |
|           | 2                     | 116                          | 115 | 1  | 0  |
|           | 3                     | 112                          | 112 | 0  | 0  |
| Setokogane| 1                     | 118                          | 60  | 58 | 0  |
|           | 2                     | 115                          | 57  | 58 | 0  |
|           | 3                     | 116                          | 57  | 59 | 0  |

* Types of grain shattering are shown in Fig. 1.

---

Table 3. Shape of separation pileus under a stereo microscope.

| Cultivar  | Number of pedicels* | Shape of separation pileus |
|-----------|---------------------|----------------------------|
|           |                     | Flat shape | Prominent shape |
| Asahi     | 293                 | 57 (19%)   | 236 (81%)       |
| Akebono   | 316                 | 102 (32%)  | 214 (68%)       |
| Omachi    | 326                 | 191 (59%)  | 135 (41%)       |
| Kibinohana| 229                 | 149 (65%)  | 80 (35%)        |
| Setokogane| 116                 | 116 (100%) | 0 (0%)          |

* Pedicels which were separated between sterile lemma and rudimentary glume were investigated.
2. Microscopic morphology of separation zone

Shapes of the separation pileuses observed under a stereo microscope are shown in Table 3. In Asahi and Akebono, only 19% and 32% pedicels were classified as flat in shape, respectively. In Omachi and Kibinohana, 59% and 65% pedicels were categorized as flat in shape, respectively. Flat pileuses of these two cultivars were mainly observed on the basal side of their panicles. All pedicles of Setokogane were categorized as flat in shape.

Fig. 3 shows the fine structure of typical separation pileus observed by ESEM in five cultivars. The separation pileus had an elliptical frustum shape in Asahi and Akebono (Figs. 3A, 3B). However, in Omachi, Kibinohana and Setokogane, the separation pileus was comparatively flat (Figs. 3C, 3D, 3E). In Setokogane, clear-cut separation pileuses were rare because the tissue of sterile lemma was adhered to most of the separated surface (Fig. 3F). The diameter of the pileus was approximately 350 to 450 μm.

The enlarged views of the surface of the separation pileuses by ESEM in five cultivars are shown in Fig. 4. As the outcome of detachment of grain, tissue of the vascular bundle either came out (Figs. 4A, 4B, 4C, 4E) or was damaged (Fig. 4D). The fibrous structure of cell walls mentioned by Ebata and Tashiro (1990) was observed around the vascular bundle. This structure had string-shaped tissue inside the cell wall. The fibrous structure was sparse in relatively easily-shattering cultivars, i.e. Asahi (Fig. 4A), Akebono (Fig. 4B), Omachi (Fig. 4C) and Kibinohana (Fig. 4D). The development of the fibrous cell wall was remarkable in the hardly-shattering cultivar, Setokogane (Fig. 4E). In addition, the development of the fibrous cell wall in the relatively easily-shattering cultivars became poorer in association with degree of shattering. The easier the grain shattered, the poorer was the development of fibrous cell wall (Table 1, Figs. 4A, 4B, 4C, 4D).

Discussion

The present study was performed in an attempt to find a simple marker trait to facilitate the selection of medium-shattering habit in *japonica* rice breeding. The results clarified the relationships between simple morphological characteristics and shattering habit using several *japonica* rice cultivars.

The cultivars used in this study were classified into the cultivars shattering relatively easily or hardly-shattering by the ratio of type A to type B grain shattering type (Table 2). The ratio of the flat shape of separation pileus to the prominent shape also varied with the grade of shattering habit of cultivars (Table 3).

A few studies on the relationship between simple morphological features and degree of grain shattering have been reported. However, the medium-shattering grade of *japonica* rice was not the subject of research in these studies. Jin and Inoue (1982) showed that an easily-shattering Korean *japonica-indica* hybrid variety had a type A shattering pattern and hardly-shattering *japonica* variety had not only type A but also type B shattering pattern.
Ebata and Tashiro (1990) investigated the relationship between the shattering resistance and the morphology of separation pileus in *indica*, *japonica* and *javanica* rice cultivars, and showed that the shattering-resistant variety had a flat-shape separation pileus.

Ebata and Tashiro (1990) pointed out that the development of the fibrous cell wall around the vascular bundle i.e., sclerenchymatous fiber tissue, was remarkable in shattering-resistant varieties, whereas in the wild species of rice, the development of the fibrous tissue was very poor. Similarly, many fibrous cell walls were observed on the surface of the separation pileus in the hardly-shattering cultivar Setokogane (Fig. 4E), while it was hardly observed in the very easily-shattering cultivar Asahi (Fig. 4A). The easier the grain shattered, the poorer the development of sclerenchymatous fiber tissue (Table 1, Fig. 4). In Asahi and Akebono, development of the fibrous cell wall was poor in both prominent and flat pileuses. On the other hand, development of the fibrous cell wall was more extensive on the flat pileus in comparison with prominent pileus in Omachi and Kibinohana (data not shown). The fibrous cell wall i.e., sclerenchymatous fiber tissue, was considered a secondary cell wall. These observations showed that the secondary cell walls on the surface of the separation pileus would be molten down in association with the disorganization of abscission layer. It is likely that the degree of survival of fibrous cell walls on the surface of the separation pileus also relates to shattering habit.

According to these findings, the medium-shattering habit of *japonica* rice appears to be related with type A grain shattering pattern, the flat shape of separation pileus and the moderated development of the fibrous cell wall. On the other hand, easily-shattering habit of *japonica* rice is related to type A grain shattering pattern, the prominent shape of separation pileus and poor development of the fibrous cell wall.

From the size of separation pileus, it is difficult to distinguish flat shape from prominent shape even with a magnifying lens. However, it is easy to distinguish the two shapes with a stereo microscope. Microscopic observation of the separation pileus was useful for assessing the grain shattering degree. Additionally, the grasping panicle method appears to be helpful in estimating the type of shattering because it is possible to classify the shattering habit into two groups, i.e., hard and others, but it is difficult to distinguish among medium-shattering, easily-shattering and very easily-shattering habit by the grasping panicle method on an individual plant basis (Okubo, 2013).

This study strongly suggests that the medium-shattering habit is characterized by the type A shattering pattern with the flat shape of pileus. It is highly probable that these traits can be useful for the selection of medium-shattering habit for *japonica* rice breeding which may adapt better in combine harvest as mentioned by Kobayashi (1990).

Jin and Inoue (1982) demonstrated that the grain shattering degree is related to the formation of abscission layer, occurrence of splitting and the size of central vascular bundle with sclerenchyma tissue around it. Ebata and Tashiro (1990) reported that the shattering habit may be regulated by the relative extent of the abscission layer formation and the development of sclerenchymatous fiber tissue.
Recently, the rice-shattering genes, qSH1 and sh4, which influence the formation of abscission layers in pedicels, have been isolated. The sh4 gene was shown to be involved in the degradation of abscission layer (Li et al., 2006). The qSH1 gene is a major quantitative trait locus of grain shattering in rice and a single-nucleotide polymorphism in the promoter region of qSH1 gene causes loss of grain shattering owing to the absence of abscission layer formation (Konishi et al., 2006). Four rice cultivars with a relatively easily-shattering habit, Asahi, Akebono, Kibinohana and Omachi were reported to carry a functional qSH1 allele and a non-functional sh4 allele (Akasaka et al., 2011). In the present study, Asahi, Akebono, Kibinohana and Omachi showed the type A grain-shattering pattern dominantly. This result may be related to the formation of abscission layers caused by the functional qSH1 allele. On the other hand, tissue of the vascular bundle either came out or was damaged with detaching of grains in these four cultivars (Fig. 4). It is likely that the formation of abscission layers did not extend to the vascular bundle in these four cultivars. Furthermore, a medium-shattering cultivar has more sclerenchymatous fiber tissues around the vascular bundle as compared with the easily-shattering cultivar. Akasaka et al. (2011) presumed that extremely easily-shattering trait of weedy rice accessions is mediated by unidentified genes other than qSH1 and sh4. Additionally, the data of Akasaka et al. (2011) indicates that differences of grain shattering habit among these four cultivars (Asahi, Akebono, Kibinohana and Omachi) in Okayama are also mediated by unidentified genes other than qSH1, sh4 and other genes that regulate weedy shattering trait. In the present study, it is suggested that the shape of separation pileus and development of sclerenchymatous fiber tissue affected the grain-shattering degree. It is currently not clear whether these two morphological characters are independent genetic characters or pleiotropism. Investigation of the genes that regulate these phenotypes is required.

Acknowledgements
I wish to thank Prof. Kazuhiro Sato, Institute of Plant Science and Resources, Okayama University and Dr. Ryo Ishikawa, Graduate School of Agricultural Science, Kobe University for critical reading of this manuscript.

References
Akasaka, M., Konishi, S., Izawa, T. and Ushiki, J. 2011. Histological and genetic characteristics associated with the seed-shattering habit of weedy rice (Oryza sativa L.) from Okayama, Japan. *Breed. Sci.* 61: 168-175.
Alizadeh, M.R. and Allameh, A. 2011. Threshing force of paddy as affected by loading manner and grain position on the panicle. *Res. Agric. Eng.* 57: 8-12.

Ebata, M. and Tashiro, T. 1990. Studies on shedding habit of rice plant: I. Morphology of separation zone. *Jpn. J. Crop Sci.* 59: 63-71*.
Fukuta, Y., Yano, M. and Kobayashi, A. 1994. Genetic analysis of shattering-resistant mutant lines induced from an indica rice (*Oryza sativa* L.) variety, “Nan-jing 11”. *Breed. Sci.* 44: 325-331**.
Fukuta, Y. 1995. Genetic and breeding analysis of shattering habit using the resistant mutant lines in rice (*Oryza sativa* L.). *Bull. Hokuriku Natl. Agric. Exp. Stn.* 37: 67-105**.
Fukuta, Y. and Fukui, K. 1995. Shattering habit. *Misc. Natl. Agric. Res. Cent.* 30: 114-115***.
Hihara, S., Okatake, S., Tomihisa, Y., Ishida, K., Omori, N., Nakano, Y., Fujii, S., Hitomi, S. and Tsuibo, H. 1991. A new rice variety “Setokogane”. *Bull. Okayama Pref. Agric. Exp. Stn.* 9: 23-31***.
Ichikawa, T., Sugiyama, T., Takahashi, H. and Miyahara, S. 1990. Equipment for quantitative measurement of shattering habit of paddy. *JARQ* 24: 37-42.
Ito, K., Inoue, J. and Tikai, K. 1969. Studies on the grain shedding in some crops: On the measuring method of grain shedding in rice plants. *Proc. Crop Sci. Soc. Jpn.* 38: 247-252**.
Jin, L.D. and Inoue, J. 1981. On the degree of grain shedding of japonica-indica hybrid rice bred in Korea. *Jpn. J. Crop Sci.* 50: 181-185**.
Jin, L.D. and Inoue, J. 1982. Relationship between grain shedding and abscission layer in pedicel of japonica-indica hybrid rice in Korea. *Jpn. J. Crop Sci.* 51: 43-50**.
Kikuchi, F., Itakura, N., Ikehashi, H., Yokoo, M., Nakane, A. and Maruyama, K. 1985. Genetic analysis of semi-waifur in high-yielding rice varieties in Japan. *Bull. Natl. Inst. Agric. Sci., Ser. D* 36: 125-145**.
Kobayashi, A. 1990. Varietal adaptability for mechanized rice cultivation: Direct seeding adaptability, shattering habit, smoothness. *J. Agric. Sci.* 45: 186-189***.
Konishi, S., Izawa, T., Lin, S.Y., Ebata, K., Fukuta, Y., Sasaki, T. and Yano, M. 2006. An SNP caused loss of seed shattering during rice domestication. *Science* 312: 1392-1396.
Lee, S.W. and Huh, Y.K. 1984. Threshing and cutting force for Korean rice. *Trans. ASAE* 27: 1654-1657, 1660.
Li, C., Zhou, A. and Sang, T. 2006. Rice domestication by reducing shattering. *Science* 311: 1936-1939.
Oba, S., Kikuchi, F. and Maruyama, K. 1990. Genetic analysis of semi-waifur and grain shattering of Chinese rice variety “Ai-Jio-Nan-Te”. *Jpn. J. Breed.* 40: 13-20.
Okubo, K., Watanabe, T., Miyatake, N., Maeda, S. and Inoue, T. 2012. Evaluation method for threshability of rice varieties by grasping the panicle with hand. *Jpn. J. Crop Sci.* 81: 201-206*.
Okubo, K. 2013. The effect of the number of plants used for grasping the panicles in one hand on the evaluation of threshability of rice cultivars. *Jpn. J. Crop Sci.* 82: 283-288*.
Ozaki, K. 1993. Effect of the application of growth retardant on the shedding of rice grain. *Jpn. J. Crop Sci.* 62 (Extra 1): 224-225***.
Tikai, K. and Nishitani, H. 1976. The degree and classification of shedding habit in rice varieties. *J. Agric. Sci.* 31: 172-173***.

* In Japanese with English abstract.
** In Japanese with English summary.
*** In Japanese. Title was translated by the author.