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# Association between Grain Shattering Habit and Formation of Abscission Layer Controlled by Grain Shattering gene *sh-2* in Rice (*Oryza sativa* L.)

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**Abstract** : Rice garin shattering habit is closely associated with the abscission layer formed at the base of sterile lemmas (empty glumes). In the current study, the character expression of *sh-2*, one of the representative shattering genes, was investigated by comparing some agronomic parameters among Norin 29, a Japanese non-shattering cultivar, and its shattering near-isogenic line SH-AJNT, as well as Dee-geo-woo-gen, a shattering *indica* cultivar. After observation of longitudinal sections of sterile lemmas bases, the abscission layer was not found at the spikelet differentiation stage. However, at the reproductive cell formation stage, SH-AJNT faintly formed the abscission layer. No abscission layer, on the other hand, appeared in Norin 29 throughout the stage of panicle development. The breaking strength at the base of sterile lemmas was measured to compare the threshability among materials. Until 19 days after heading, both threshability on Norin 29 and SH-AJNT exhibited similarly high values, indicating non-shattering conditions. At 21 days after heading, the garin of SH-AJNT dropped more easily than those of previou stages, while Norin 29 kept its persistent character. This difference is important for the evaluation of SH-AJNT and Norin 29, shattering and non-shattering cultivars, respectively. The progressive decline in the breaking strength of SH-AJNT was thought to be associated with the ripening of the grain.
**Key words** : Abscission layer, Germination rate, Grain ripening, Rice, *Oryza sativa* L., Shattering gene.

**イネ (*Oryza sativa* L.) の脱粒性と脱粒性遺伝子 *sh-2* による離層組織との関係** : 大場伸哉・鷲見典子・藤本文弘・安江多輔 (岐阜大学農学部)

**要　旨** : イネの脱粒性は，護穎基部に形成される離層組織と密接な関連がある．本研究では，イネの代表的な脱粒性遺伝子である*sh-2*について，その形質発現を調べた．実験には，脱粒難の日本水稲品種農林29号とその脱粒性準同質遺伝子系統SH-AJNT，indicaの脱粒性品種低脚烏尖を用いた．脱粒性遺伝子 *sh-2* が形態に及ぼす作用を明らかにする目的で，農林29号とSH-AJNTの護穎基部のミクロトーム切片を作成し検鏡した．脱粒性遺伝子を持つSH-AJNTでは離層組織の形成が期待されたが，出穂19日前の穎花分化期には離層組織は認められなかった．また，脱粒難の農林29号においても離層は形成されていなかった．しかし，出穂17日前の生殖細胞形成期にはSH-AJNTに離層組織と思われる細胞層が観察された．その後，この組織は発達し出穂期には離層組織であることが確認できた．一方，農林29号では，穂の発育全期間を通じ離層組織は観察されなかった．出穂後の脱粒性程度の変化を調べる目的で，3種類・系統の穂を3日毎に採取し護穎基部の抗張強度と抗曲強度を測定した．また，胚乳の大きさと発芽率についても調べた．その結果，同じ遺伝的背景を持つ農林29号とSH-AJNTとの間の脱粒性強度に出穂後19日までは差はなかったが，その後SH-AJNTでは強度が急激に低下し脱粒易となった．この傾向は，脱粒性の低脚烏尖でも認められた．一方，開花・結実後の1000粒重と発芽率の変化を見ると，脱粒開始時には両形質とも大きな値を示し，種子の生長が完了しつつあることがわかった．このことから，脱粒開始には籾の生長が関係していることが推察された．
**キーワード** : イネ，脱粒性遺伝子，登熟，発芽率，離層組織．

Most of wild type plants and native cereal cultivars have easy grain shedding habit which favors wide seed dispersal. This character may be yield-limiting in cereal crops, because easy grain shattering habit causes high grain losses when harvesters are used. However, traditional harvesting methods have no such limitations on easy threshability. Therefore, the change of harvesting methods have required the improvement of threshability, thus non-shattering cultivars have been developed in areas where harvesters have been used and shattering cultivars have been maintained in areas where crops have been harvested by hand cutting.

In rice plant, grain shattering habit was reported to be induced by the formation of abscission layer at the sterile lemmas

base[4,5,9,18,21]. The abscission layer is classified into two types ; namely presence and absence of cracks in the abscission layer. The cracked abscission layer is found in some *indica* cultivars and wild strains, which shed their grains easier than *japonica* cultivars have non-cracked abscission layer. These shattering habit was reported to be controlled by a few genes[9,10,13,15], and one of them, *sh-2* is thought to control the shattering habit of most cultivars in both *indica* and *Japonica* sub-species[14]. In this reason, to understand the mechanism of grain shattering habit in rice, the investigation of shattering gene *sh-2* may play an important role.

As described above, the grain shattering habit is an important character which widely control seeds dispersal. For this purpose, it is advantageous to keep the seed attached to the mother plant until the seed is well ripen, because in this way seeds can store up much nutrients for germination and competition with other plants. Indeed, as grain weight increases during ripening period, plants are liable to shed more grains[8]. However, the relationships between the grain ripening and the shattering process has not been well investigated into ; that is to say, the germination ability of shed grain has been completely ignored.

The shattering gene *sh-2* was reported to govern the formation of abscission layer[12]. However, the time when this gene forms the abscission layer is unknown, although the abscission layer have been observed already on the emerging stage of panicles. Detecting the expression stage of this gene is necessary to clarify the formation and the grain shattering process of rice abscission layer. In the current study, we investigated into how and when the grain shattering gene *sh-2* initiate to organize the abscission layer.

Furthermore, the changes in the degree of grain shattering was also investigated during the grain ripening period. In some plant organs such as leaves, fruits, and flower bud, etc., the formation of abscission layer is induced by ethylene and abscissic acid, which are associated with senescence and maturation of plant organs. Therefore, in the case of rice, the growth of grain is assumed to influence the maturation of abscission layer through some physiological changes.

## Materials and Methods

Japanese rice cultivar Norin 29 and its near-isogenic line SH-AJNT were used to compare the differences in shattering habit. Norin 29 is non-shattering while SH-AJNT have the shattering gene *sh-2* inherited from Chinese *indica* cultivar Ai-jio-nan-te to genetic background of Norin 29 through six times of recurrent back-crossing. In addition, Chinese cultivar Dee-geo-woo-gen with shattering habit was also used as representative of *indica*. Dee-geo-woo-gen also carries the shattering gene *sh-2*[14].

### 1. Observation of longitudinal sections of sterile lemmas base

Norin 29 and SH-AJNT were transplanted to paddy field at Gifu University on 9 June 1992 and young panicles of Norin 29 and SH-AJNT were collected every three days. Longitudinal microtome sections of their sterile lemmas bases were made by fixing them in acetic acid : alcohol (3 : 1) and then embedding in paraffin. Thickness of the microtome sections was about 10 $\mu$m. After staining with hematoxyline, safranine and first-green, these microtome sections were searched to compare the morphological differences between Norin 29 and SH-AJNT under a light microscope.

### 2. Changes in shattering habit during the grain ripening period

Norin 29, SH-AJNT, and Dee-geo-woo-gen were transplanted to the paddy field on 6 June 1993 and the heading days of their panicles were recorded. After panicles emergence, three panicles of each cultivars and line were collected every three days to measure the degree of grain shattering, such as breaking tensile strength and breaking bending strength at sterile lemmas base. In this measurement, five grains per panicle were sampled from the top portion of panicle, and the two breaking strength were measured by a modified method of Jin and Inouye[7].

In addition to the grain shattering habit, we investigated the growth of seed during the ripening period to find the kind of association between grain shattering and maturation. 50 grains were collected from the same panicles as the measurements of shattering degree, and then dry weight of kernel, endosperm length and seed germination were measured as indices of grain growth. 1000-kernel-weight was

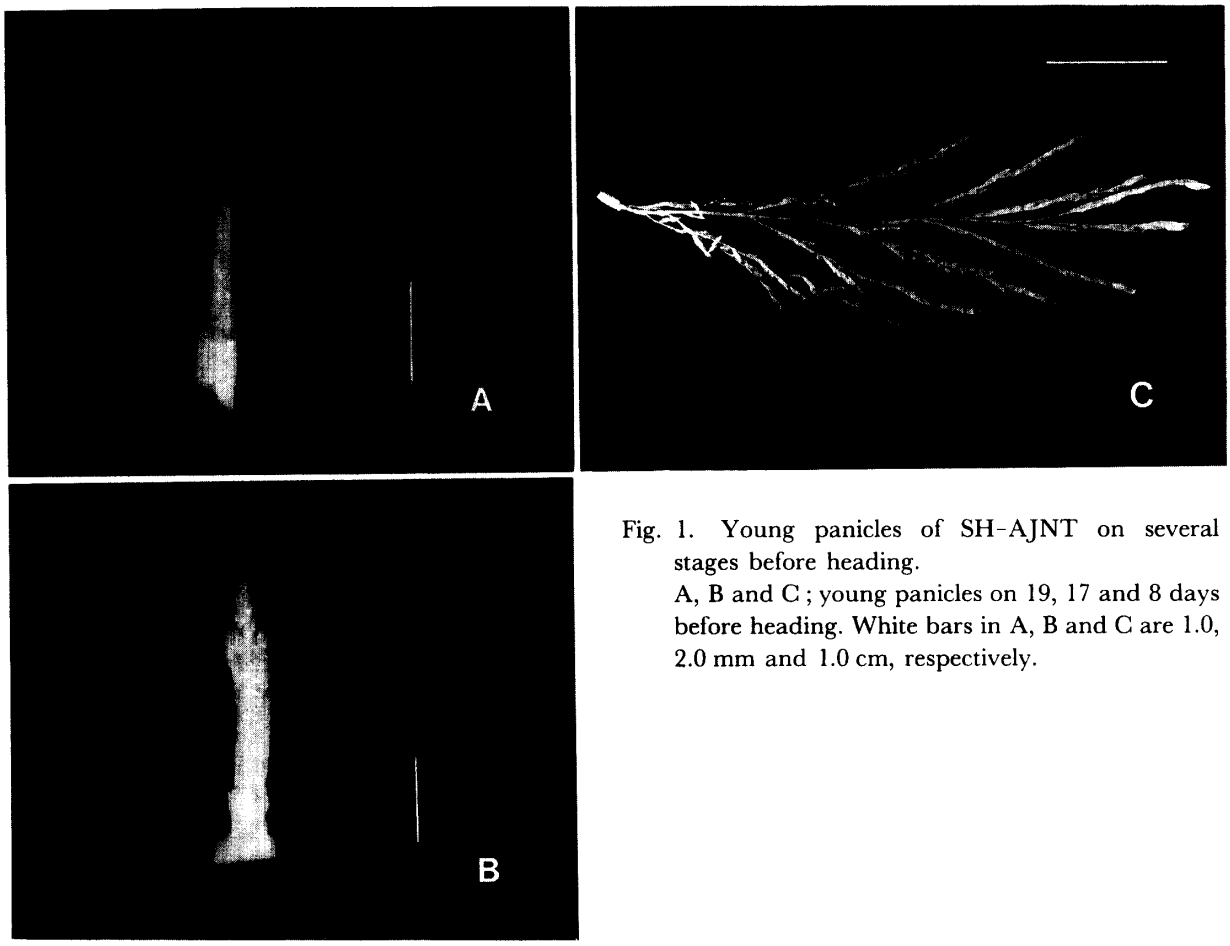


Fig. 1. Young panicles of SH-AJNT on several stages before heading.
A, B and C ; young panicles on 19, 17 and 8 days before heading. White bars in A, B and C are 1.0, 2.0 mm and 1.0 cm, respectively.

estimated from the value of 20 times the 50 kernel weight. The grains were stored at 50°C for a week to break their dormancy, since germination has been reported to be influenced by seed dormancy[5]. After the break of seed dormancy, seeds were sown on wet filter papers and incubated at 30°C. The number of germinated seeds were counted every day and their germination rate and germination energy were estimated from the number of germinated seeds within ten and four days, respectively.

## Results

### 1. Observation of longitudinal sections of sterile lemmas base

In 1992, heading date of Norin 29 and SH -AJNT were on 20 August and 14 August, respectively.

Panicle length of both cultivar and line measured 19 days before heading were shorter than 5 mm. Observation of young glumes in details was difficult without a microscope (Fig. 1). The anatomical organization of both glumes and pedicels were observed by the microscopic technique to clarify the histological differences between Norin 29 and its isogenic line. At this stage, the glumes of both Norin 29 and SH-AJNT renged between 300 and 400 $\mu$m ; differentiation of anther were also observed (Fig. 2). We have already reported that the shattering gene *sh-2* carried by SH-AJNT controls the formation of abscission layer, while Norin 29 have no abscission layer[11]. Therefore, it was not surprising to find the presence of abscission layer in SH-AJNT and its absence in Norin 29. However, at this stage no morphological differences between Norin 29 and SH-AJNT were discernible, as band of smaller cells which constitute the abscission layer were completely absent.

On 17 days before heading, the panicle length of both cultivar and line were about 1 cm and the length of spikelets were about 700 —1000 $\mu$m (Fig. 1 and Fig. 2). These glumes were visible even with the naked eye, and the pollen mother cells, on the other hand, were observed inside the anther organs using the microscope. Furthermore, the abscission layers were also observed in the microtome sections

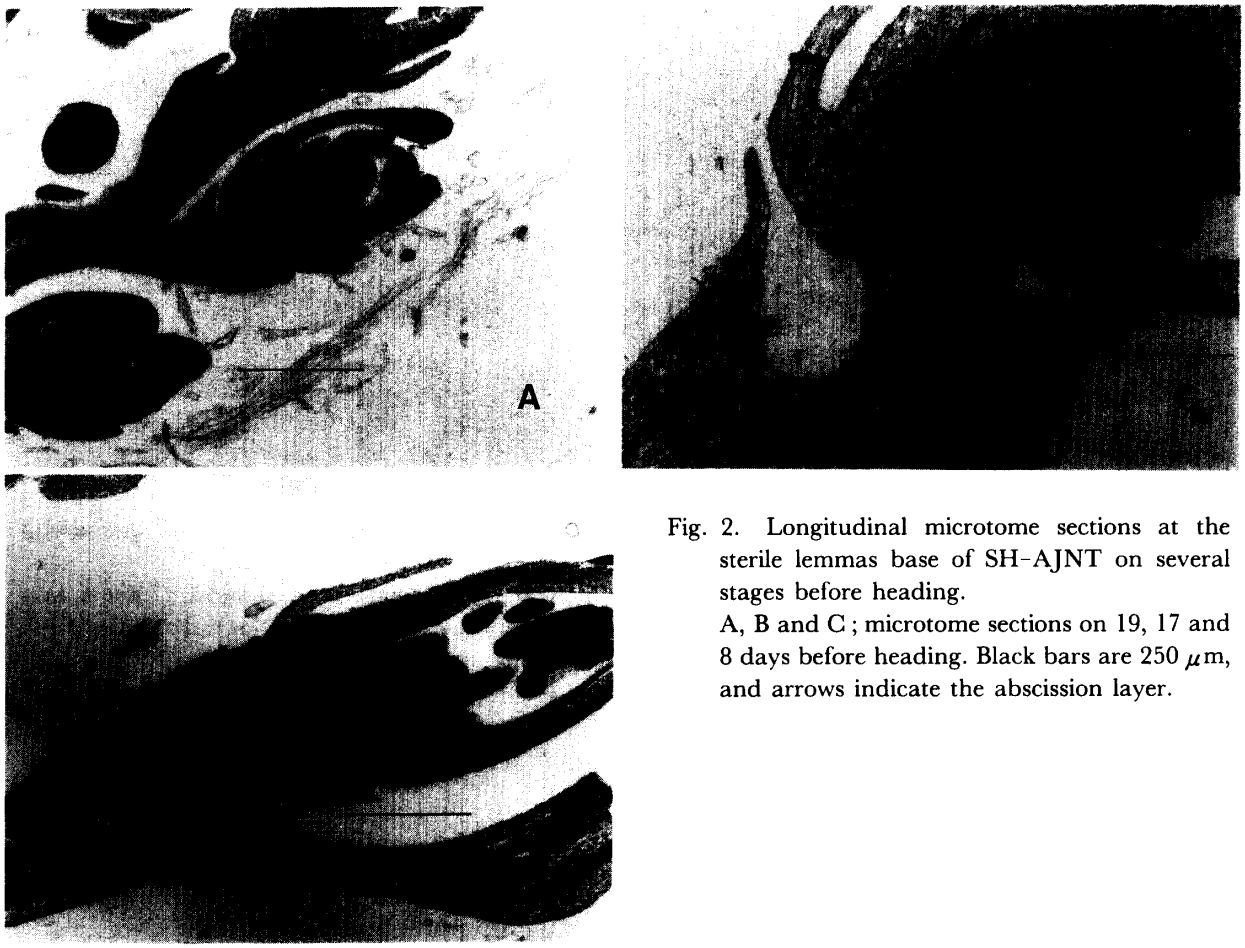


Fig. 2. Longitudinal microtome sections at the sterile lemmas base of SH-AJNT on several stages before heading.
A, B and C; microtome sections on 19, 17 and 8 days before heading. Black bars are 250 $\mu$m, and arrows indicate the abscission layer.

of SH-AJNT by the same method. This organs were located at the junction between the pedicel and the sterile lemmas and were intensively stained by safranine dye. Compared with the other organs of spikelet, this layer was constructed on one or two layer of smaller cells which size was about 6.3 $\mu$m (Table 1). By contrast, cells of Norin 29 were similar in size across the organs of pedicels and sterile lemmas, and the region which was intensively dyed with safranine as in SH-AJNT were not shown.

The length of panicle and spikelet continued to elongate irrespective of their genotypes. The size of panicle and spikelet reached about 15 cm and 3 mm, respectively 8 days before heading (Fig. 1). At this stage, the abscission layer of SH-AJNT was clearly distinguished from other organs of spikelet, because this region was mainly made up of small cells with an average size of 6.72 $\mu$m and were brightly stained red (Fig. 2). On the other hand, the cells size of other tissues were larger than the cells of abscission layer. Their average size was 10.49 $\mu$m in the spikelet and 34.16 $\mu$m in the pedicel sides.

On heading date, cell size of abscission layer in SH-AJNT was about 7.80 $\mu$m, while those on the spikelet and pedicel side were about 11.83 $\mu$m and 34.40 $\mu$m, respectively. Therefore, the cells on the latter organs were longer than the cells of former by about 4 $\mu$m and 27 $\mu$m, respectively (Table 1). Thus, the abscission layer stood out clearly from the other regions owing to its unique smaller cell size.

**2. Changes in the shattering degree**

Heading date of Norin 29 and SH-AJNT were on 18 and 14 August 1993. Heading date of Dee-geo-woo-gen was on 21 August.

Breaking bending strength of the shattering cultivar Dee-geo-woo-gen averaged 125 g on the day of heading (Fig. 3). This strength decreased from day to day and was zero gram 15 day after heading. SH-AJNT also traced similar time course to that of Dee-geo-woo-gen and the strength of SH-AJNT decreased from 85 g on heading to zero gram 21 days after heading. Comparing the shattering cultivar and line, the non-shattering cultivar, Norin 29, showed a different time course. During a

Table 1. Cell size of three portion in sterile lemmas base at several stages before heading.

| Cultivar and line | Tissues in sterile lemmas base | Days before heading | | | |
|---|---|---|---|---|---|
| | | 19 | 17 | 8 | 0 |
| | | μm | μm | μm | μm |
| Norin 29 | Abscission layer | ——[1)] | —— | —— | —— |
| | Tissue in the side of kernel | 6.11±0.22[2)] | 7.52±0.24 | 8.78±0.30 | 9.39±0.41 |
| | Tissue in the side of pedicel | 7.47±0.31 | 11.83±0.65 | 45.63±0.19 | 32.94±1.84 |
| SH-AJNT | Abscission layer | —— | 6.26±0.15 | 6.72±0.21 | 7.80±0.21 |
| | Tissue in the side of kernel | 6.02±0.27 | 6.65±0.12 | 10.49±0.38 | 11.83±0.23 |
| | Tissue in the side of pedicel | 6.65±0.17 | 9.22±0.26 | 34.16±2.25 | 34.40±1.20 |

1) Abscission layer was not observed. 2) Mean±S.E.

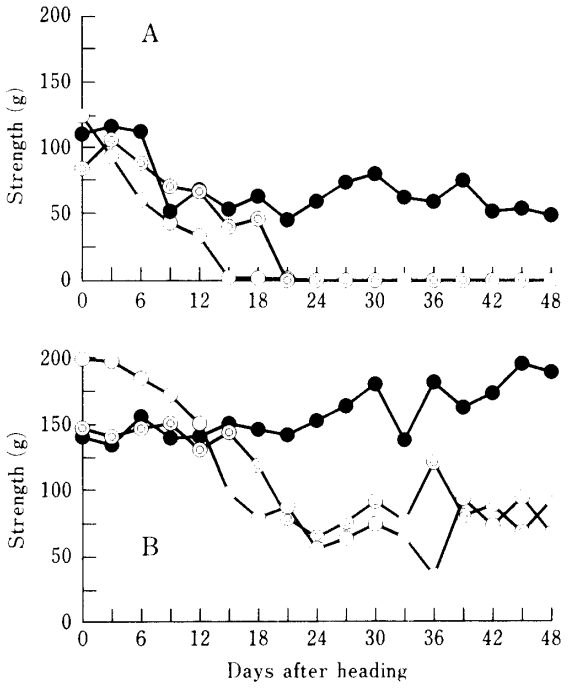


Fig. 3. Changes in the breaking bending strength (A) and the breaking tensile strength (B) of sterile lemmas base after heading.
●; Norin 29, ◎; SH-AJNT, ○; Dee-geo-woo-gen.

period from the heading date to nine days after heading, the strength of Norin 29 decreased from about 110 g until 50 g. Thereafter, this strength fluctuated narrowly between the range of 50 g and 80 g until 48 days after heading, but did not drop to zero as observed in the cases of SH-AJNT and Dee-geo-woo-gen.

The change of breaking tensile strength in each cultivars and line showed similar tendency to the results of breaking bending strength, although there was a little difference between two results (Fig. 3). The breaking tensile strength as well as the breaking bending strength of Norin 29 did not decrease during the ripening period. The breaking tensile strength of Norin 29 increased from 140 g at the heading date to about 190 g 48 days after heading. The breaking tensile strength of SH-AJNT rapidly decreased from 143 g on 15 days to 78 g on 21 days, although it held similar strength to that of Norin 29 until 15 days. However, after 21 days, the strength of SH-AJNT almost stopped decreasing and kept its value with little variation. Here we noticed that around 21 days after heading it corresponded to the day when the breaking bending strength fall to about zero gram. The breaking tensile strength of Dee-geo-woo-gen (200 g) at the heading date was no doubt the highest among three cultivars and line. However, this strength also decreased as grain ripening proceeded, attaining to 97 g around 15 days after heading. After this day the strength of Dee-geo-woo-gen did not decrease, although there were fluctuations in its strength. Here the 15 days after heading corresponded to the day when the breaking bending strength fell on about zero gram.

### 3. Change of grain ripening

Size of hulled grain was too small to measure without a microscope for the first six days (Fig. 4). However, growth of the endosperm length initiated on six days after heading and both grain of Norin 29 and SH-AJNT showed similar growth pattern and reached about 5 mm on the ninth day. The grain of Dee-geo-woo-gen also elongated and reached about 5.3 mm on 18 days after heading, although its rate was smaller than those of the two *japonica* cultivar and line.

For the first six days after heading, 1000-kernel-weights of the three cultivars and line

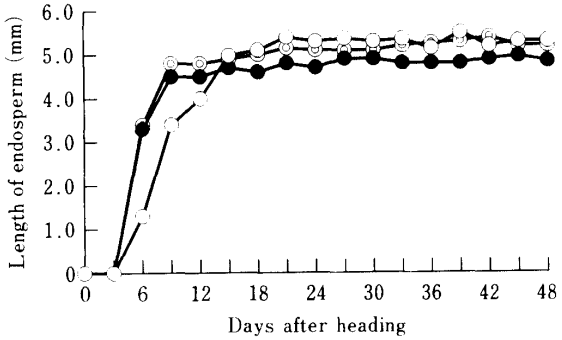


Fig. 4. Changes of endosperm length during ripening.
●; Norin 29, ◎; SH-AJNT, ○; Dee-geo-woo-gen.

were about three gram, and the changes in kernel weight were little (Fig. 5). However, from six days after heading onwards, the increase of kernel weight was clearly observed and the weight of Dee-geo-woo-gen over about eight gram, and those of Norin 29 and SH-AJNT were over about seven gram. These grains continued to grow at a high rate. The kernel weight of Norin 29 and Dee-geo-woo-gen attained 23 g and 21 g, respectively, on 27 days after heading; however, the growth stopped after grain filling in the kernel. The kernel weight of SH-AJNT also increased at a high rate until 18 days and then peak up about 23 g on 27 days.

The kernels obtained within the first six days after heading completely failed to germinate in all the three cultivars and line (Fig. 6). However, ninth day after heading, some seeds of Dee-geo-woo-gen showed signs of germination. After this stage the germination rate of Dee-geo-woo-gen increased rapidly to 94% 24 days after heading and reached its maximum of 100% at its final stages of growth. Germination in Norin 29 were also observed nine days after heading, but its germination rate was relatively lower, 0.67%. The germination rate of Norin 29 increased rapidly 12 days after heading onwards and was over 90% around 24 days after heading. In the case of SH-AJNT, germination was first observed 12 days after heading and then its rate increased rapidly to over 90% 18 days after heading. These germination in the three cultivars and line occurred within four days of treatment, following the germination energy which coincided with the results of the germination rates (data is not shown).

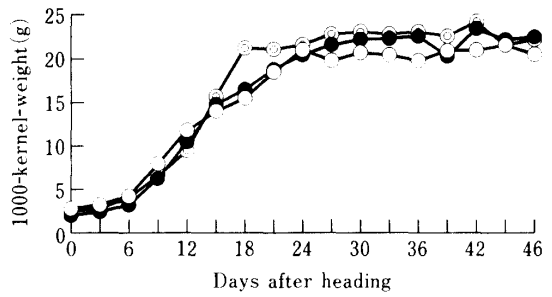


Fig. 5. Changes in 1000-kernel weight during ripening.
●; Norin 29, ◎; SH-AJNT, ○; Dee-geo-woo-gen.

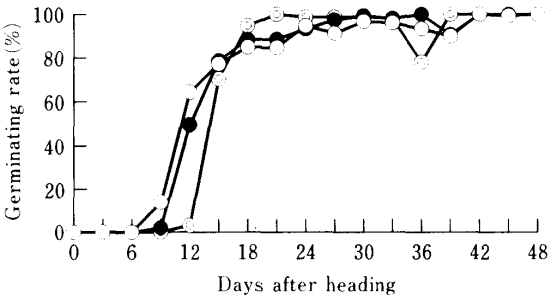


Fig. 6. Changes in germination rates of grain during ripening.
●; Norin 29, ◎; SH-AJNT, ○; Dee-geo-woo-gen.

## Discussion

Most higher plants have the abscission trait by which the plants detach some organs such as the petiole of a leaf, the pedicel of a flower and a fruit. Usually, this abscission layer are formed at the joint portion between the organs and the stalk prior to abscission and then cell wall degradation enzymes are induced to separate these organs from the stalk.

Also in rice, grain shattering habit is associated with the formation of abscission layer and the crack of this layer. The shattering gene *sh-2* is thought to control the abscission of grain in many rice cultivars[14]. Therefore, the character expression of this gene is very important to understand the mechanism of rice grain shedding. In the current study, we demonstrated that the shattering gene *sh-2* promotes the formation of abscission layer. However, on earlier stages of the young panicle formation, the figure of abscission layer did not appear at the sterile lemmas base of both Norin 29 without *sh-2* and SH-AJNT with *sh*

*-2*. Morphological differences were not found between the two cultivar and line, indicating that the shattering gene does not express its characters on morphological level in this stage. This time was 19 days before heading, the length of young glumes were about 300—400 $\mu$m and young panicles were shorter than 5 mm in length. Inside the glumes, anther organs initiated to differentiate.

Generally, rice plants initiate the differentiation of young panicles 34 or 35 days before heading[2]. The young panicles over 1 mm of length begin to develop spikelets, and the length of young panicles reach 2 mm around 24 days before heading. On around 16 days before heading, the length of young panicles are about 1.5 cm, and reproductive cells are formed inside anthers. In following stage, young panicles elongated with high rate and complete the several organs such as pollen, embryosac and spikelet etc. According to this classification, the stage of small panicles, in which no morphological difference between Norin 29 and SH-AJNT was observed, was thought to be the spikelet differentiation stage.

A faint figure of abscission layer were found in the case of SH-AJNT with the *sh-2* 17 days before heading. This stage was thought to be a reproductive cell formation stage, because pollen mother cells were observed in anthers. The early abscission layer developed as panicle elongated and the figure of abscission layer was clearly observed under the microscope owing to its blight red color than other tissues around the abscission layer. The intensive red color of abscission layer was attributed to the safranine dyeing lignin.

During the growth period of panicle and glume before emergency, cell size of abscission layer actively developed at first, attaining their maximum sizes around the heading stage. This results corresponded to the report of Jin, that the cells of abscission layer were at first found 20 days before heading and the size of cells were about 5 $\mu$m of diameter[11]. These cells continued to increase in size until the panicle emerged and reached about 6 $\mu$m-8 $\mu$m. Therefore, the abscission layer of rice was thought to almost complete its growth on morphological level at the heading date.

On the other hand, pulling the glumes from pedicels on the heading date required strong force, i.e. over 130 g in all materials, although variable shattering degree are to be observed among these cultivars and line due to the presence and the absence of *sh-2*. This hard threshability on the heading date supposed that the grain shedding is not directly attributable to the existence of abscission layer, because the abscission layer have been formed in SH-AJNT and probably Dee-geo-woo-gen already. However at harvesting time, SH-AJNT and Dee-geo-woo-gen showed the grain shattering habit, while the recurrent parent, Norin 29, kept their persistent habit.

Generally, to produce seeds with high competitive ability, plant must transport adequate nutrient to the developing seeds until the seeds secure the potentiality for germination. Then, the seeds with their germination potentiality are separated from the mother plants for seed dispersal. In this reason, seed dropping before the completion of ripening is thought to be disadvantageous for reproduction of plants and shattering is assumed to occur after grains ripen well on the mother plant.

Therefore, we also investigated the change in seed size and germination ability as the index of seed growth during the grain ripening period, involving the grain shattering habit as well. To consider the relationship between the grain ripening and the grain shattering, we compared the values indicating seed growth between the initiation time and a harvesting time of grain shattering. The initiation time of grain shattering was thought to be 15 days after heading in Dee-geo-woo-gen and 21 days after heading in SH-AJNT, provided on criteria that was the day when the breaking bending strength fell to zero gram. The length of endosperms on the criteria days indicated that the endosperms of SH-AJNT and Dee-geo-woo-gen have completed their elongation three or six days earlier (Fig. 4). However, the 1000-kernel-weight and the germination rate of SH-AJNT on 21 days neared the value around harvesting (Fig. 5 and Fig. 6). In addition, those of Dee-geo-woo-gen were also over 65% of the value at harvesting, while these values compared unfavorably with the results of SH-AJNT. Thus, rice grain was difficult to drop from the mother plant before the completion of seed ripening, although the abscission layer have formed already. This outcome suppose that physiological change in grain ripening leads breaking of abscission

layer.

Most scientific reports on the physiology of leaf abscission and fruit abscission have indicated that the abscission are influenced by phytohormones such as abscissic acid, auxin and ethylene. The ethylene and the abscissic acid are produced in aging leaves and mature fruits etc., and these phytohormones are thought to stimulate the formation of abscission layer[3,16,17]. On the relationship between the ripening of rice grain and the phytohormones, we may imagine similar mechanisms of leaf and fruit abscission, although the physiology of grain shattering in most of cereal plants have been rarely investigated.

Cell wall degradation enzymes such as cellulase and pectinase are also associated with the process separating the organs from the stalk of plant[1,19,20]. These enzymes digest the cell wall in the abscission layer so that the organs break away from the stalk of plant. In rice, existence of cracked abscission layer has been reported. This crack may be associated with the cell wall degradation enzymes, although these enzyme activity have never been investigated in rice. Jin *et al.* showed that the formation of abscission layer and the crack of the layer were controlled by two independent genes[6]. The current study show that the rice grain shattering gene *sh-2* controls the formation of abscission layer, but do not crack this layer.

Physiological change caused by the cell wall degradation enzyme may influence the resistance of the breaking strength of the abscission zone and then induce some organs to drop from the plant. As described above, our result indicated that any physiological changes in the ripening grain may affect the abscission layer, so that the grain will shed easily. The shattering gene *sh-2* was clarified to govern the formation of abscission layer. however, it is not quite clear how these changes in the abscission layer may cause grain shedding. Therefore, to clarify this physiological and morphological change of abscission layer after seed set, further studies are required.

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* In Japanese.
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