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A Major Soybean QTL, *qPDH1*, Controls Pod Dehiscence without Marked Morphological Change

Masaya Suzuki¹, Kaien Fujino² and Hideyuki Funatsuki³

¹Department of Crop Physiology, Faculty of Agriculture, Hokkaido University, 9 Kita 9 Nishi, Sapporo, Hokkaido, 060-8589, Japan;

²Department of Crop Physiology, Graduate School of Agriculture, Hokkaido University, 9 Kita 9 Nishi, Sapporo, Hokkaido, 060-8589, Japan;

³Crop Cold Tolerance Research Team, National Agricultural Research Center for Hokkaido Region (NARCH), Hitsujigaoka, Sapporo, Hokkaido, 062-8555, Japan)

Abstract : Pod dehiscence (shattering) is a major source of yield loss in the mechanically harvested soybean. We examined near-isogenic lines (NILs) for a major quantitative trait locus (QTL) controlling pod dehiscence, designated as *qPDH1*, to reveal the mechanism underlying the effect of this QTL on shattering resistance. The degree of shattering resistance differed among the NILs; as pod dehiscence percentage after 3 hr heat treatment was under 50% and over 90% for the genotypes resistant to shattering and those susceptible to shattering, respectively. On the other hand, there were no significant differences in the length, width and thickness of pods among the NILs. Anatomical analysis of the dorsal sutures of pods, at which pod dehiscence was found to commence most frequently, revealed no marked differences between the NILs. These results suggest that *qPDH1* controls pod dehiscence without markedly changing the morphology of the pods.

Key words : *Glycine max* (L.) Merr., Pod dehiscence, QTL, Near-isogenic lines (NILs), Pod morphology.

Seed shattering is an important trait for wild species to proliferate and adapt to the natural environment, while this trait would cause a significant yield loss in cultivated species. Therefore breeding efforts have been made to develop shattering-resistant cultivars. Soybean (*Glycine max* (L.) Merr.) is considered to have been domesticated from *Glycine soja* Sieb. & Zucc., which scatters its seeds via pod dehiscence (Hymowitz and Singh, 1987). Although in general, soybean (*G. max*) is more resistant to pod dehiscence (shattering-resistant) than *G. soja* (Liu et al., 2007), significant genetic variation has been found among soybean cultivars (e.g. Tsuchiya, 1986; Romkaew and Umezaki, 2006). Yield loss caused by a delay in harvest is a serious problem with shattering-susceptible cultivars (Philbrook and Oplinger, 1989).

In Japan, soybean seeds are generally harvested in cool and humid seasons, which have prevented the soybean breeders from the recognition of the importance of resistance to pod dehiscence. However, due to the recent, unusual climatic fluctuations and the widespread use of combine harvesters, soybean production systems now require shattering-resistant cultivars to ensure a stable yield.

Since the resistance to pod dehiscence is a quantitative trait, marker-assisted selection is considered to be a useful tool in breeding programs. To detect quantitative trait loci (QTLs) and the linked

molecular markers, we conducted QTL analysis using the progeny derived from a cross between a shattering-resistant cultivar, Hayahikari, and a susceptible one, Toyomusume (Funatsuki et al., 2006). A major QTL, *qPDH1*, was identified, and along with the linked markers it was suggested to be useful for Japanese soybean breeding (Funatsuki et al., 2008). Elucidation of the resistance to pod dehiscence conditioned by *qPDH1* is important in agronomy as well as plant science.

Tsuchiya (1986) compared cultivars/lines with different degrees of resistance to shattering in regard to pod morphology. He found a significant difference between susceptible and resistant cultivars and lines in the ratio of pod width to thickness, although it was unknown how the trait is associated with pod dehiscence. In addition, he found a difference in the morphology of suture between a cultivar and a related strain with contrasting shattering resistance. The wedge in the suture was determined to be longer in the susceptible cultivar. Tiwari and Bhatia (1995) also focused on the morphology of sutures. Their anatomical analyses suggested that the length and thickness of bundle caps could be associated with the degree of pod dehiscence. However, the direct association of the morphological variations observed with pod dehiscence was not clear since these studies used cultivars and lines differing in many characters as

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Abbreviations : QTL, quantitative trait locus; NIL, near-isogenic line; ANOVA, analysis of variance.

well as pod dehiscence.

In the present study, we morphologically characterized near-isogenic lines (NILs) segregating for *qPDHI* in order to determine whether the QTL controls pod morphology causing pod dehiscence.

Materials and Methods

1. Plant materials

A pair of NILs, HC1-85A and -85T, was used throughout the experiments except for the observation of starting point of pod dehiscence. Another pair of NILs, HC1-51A and -51T, was also used for the pod dehiscence test and the measurement of whole pod morphology. A pair of NILs is referred to as a family in this study. These families originated from RILs derived from a cross between a shattering-susceptible cultivar, Toyomusume, and a shattering-resistant cultivar, Hayahikari (Funatsuki et al., 2005), which is a progeny of a shattering-resistant Thai cultivar, SJ2 (Yumoto et al., 2000). The families were created from two independent residual heterozygous lines (Yamanaka et al., 2005), the marker loci of which were all fixed except for the genomic region around *qPDHI* according to the simple sequence repeat (SSR) marker genotype (Funatsuki et al., 2008). The two families had different genetic backgrounds, and the NILs within a family were supposed to be segregated only for the loci in the genomic region around *qPDHI*. Two shattering-susceptible cultivars, Toyomusume and Kitamusume, were used to determine where pod dehiscence commenced.

2. Growth conditions

Plants were grown at the experiment farm of National Agricultural Research Center for Hokkaido Region in Sapporo, Hokkaido, in 2006. The NILs and cultivars were seeded in a soil of Humus-rich Andosol on May 22. Fertilizer was applied prior to planting at the levels of 4-19-10 (N-P₂O₅-K₂O, g m⁻²). A rate of 16.7 plants m⁻², which was adjusted by over-seeding and thinning plants, was used in rows, 3 m long and spaced 60 cm apart. Plots were arranged in a randomized, complete block design with three and two replications for 85A/T and 51A/T, respectively. Toyomusume and Kitamusume were grown in a block consisting of ten rows, respectively. All plant samples of the NILs were grown to maturity and harvested. The plants harvested in the field were dried outside under a roof until used for experiments.

3. Measurement of whole pod morphology

Five plants per plot were randomly selected for analysis. Up to ten pods on the main stem of a plant were used for the measurement of whole pod morphology. Length, width and thickness of pods (Fig. 1) were measured using a vernier caliper. The values for each pod were used for statistical analysis.

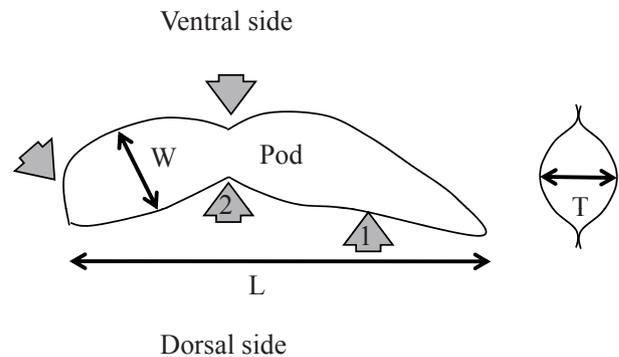


Fig. 1. Schematic illustration of mature soybean pod and parameters measured. L: length, W: width, T: thickness. Arrows indicate the positions at which pod dehiscence commenced. Numbers correspond to those in Table 3.

4. Evaluation of shattering resistance

To evaluate shattering resistance, we used heat treatment as in previous studies (Tsuchiya, 1986; Jiang et al., 1991; Tukamuhabwa et al., 2002; Funatsuki et al., 2006; Romkaew and Umezaki, 2006). The pods used for the measurement of whole pod morphology were also used for evaluation of shattering resistance. Shattering resistance degree was evaluated by monitoring the percentage of the dehiscent pods after heat treatment at 60°C for 1 hr and 3 hr (1 hr + 2 hr). The percentages of dehiscent pods were recorded for individual plants and the mean values of the percentages per plot and the arcsine-transformed values were used for statistical analysis. Since no significant difference in pod dehiscence percentage was found among pod types (one-, two- or three-seeded) (Tsuchiya, 1986), the data were pooled regardless of the pod type.

5. Determination of the start point of pod dehiscence

Approximately three weeks after maturity, we observed pods on the plants standing in the field. One hundred partially dehiscent pods were collected and the positions at which pod dehiscence started were determined (Fig. 1). Where pod dehiscence was observed at multiple sites in a pod, all the sites were recorded as starting points for the pod.

6. Anatomical analyses

Another five plants per plot of HC1-85A and -85T were selected randomly for analyses. To avoid pod dehiscence, we harvested the pods from the field were immediately stored in plastic bags. Pods were immersed in distilled water overnight to soften the pod walls, before hand sections were made. Cross sections were stained with phloroglucinol-HCl and observed using a microscope (E600 Nikon, Japan). The depth of the wedge of suture and the area of bundle cap were analyzed by Motic images plus 2.0S (Shimadzu, Japan).

7. Data analysis

Percentages of dehiscent pods were converted into arcsine-transformed values before three-way analysis of variance (ANOVA) was performed using the GLM procedure (SAS Institute, 1996). Comparison of mean

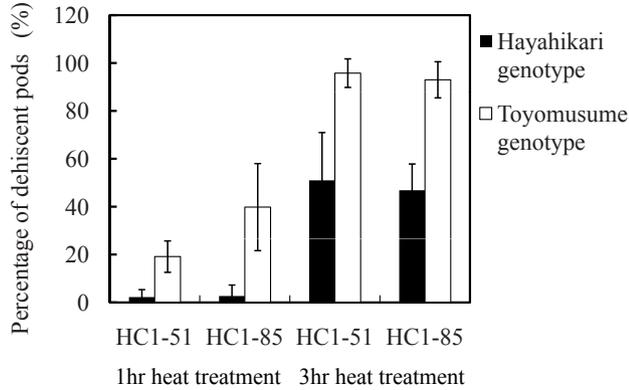


Fig. 2. Pod dehiscence percentages of NILs for *qPDH1* after 1hr and 3hr heat treatments. HC1-51 and -85 were families segregated for *qPDH1*, which were produced from RILs derived from a cross between shattering-susceptible Toyomusume and shattering-resistant Hayahikari.

values of parameters for suture analysis between the genotypes at *qPDH1* was performed by Student's *t*-test.

Results

1. Shattering resistance

The difference in shattering resistance between the genotypes at *qPDH1* was clear in both families (Fig. 2). The pods with the Hayahikari allele (resistance allele) at *qPDH1* hardly dehiscid after 1h heat treatment while those with the Toyomusume allele started to be open. After 3h treatment, most of the pods of the susceptible genotype had dehiscid while more than half of the pods of the resistant genotype remained indehiscid.

2. Whole pod morphology

The two pairs of NILs were compared in terms of morphology of whole pod using three parameters, length, width and thickness (Fig. 1). The mean values for pod type (one-, two-, or three-seeded) and family (derived from HC1-51 or HC1-85) were shown in Table 1. The results of the analysis of variance (ANOVA) with three sources of variance, family, genotype at *qPDH1* and pod type, are presented in Table 2. No significant

Table 1. Mean values of parameters for whole soybean pod morphology in NILs for *qPDH1*.

Family	Seed number	Number of pods		Length (mm)		Width (mm)		Thickness (mm)		Width/length		Width/thickness	
		HA ¹⁾	TM ²⁾	HA	TM	HA	TM	HA	TM	HA	TM	HA	TM
RIL-51	1	6	8	33.7	35.3	11.4	11.5	7.1	7.6	0.34	0.33	1.65	1.51
	2	48	53	43.7	44.0	11.5	11.7	7.4	7.5	0.27	0.27	1.57	1.56
	3	40	27	52.2	53.9	11.6	11.6	7.4	7.6	0.22	0.22	1.57	1.53
	Mean	–	–	43.2	44.4	11.5	11.6	7.3	7.6	0.28	0.27	1.60	1.53
RIL-85	1	21	20	35.3	35.0	12.0	11.5	7.7	7.4	0.34	0.33	1.56	1.58
	2	99	80	43.2	44.3	11.7	11.5	7.9	7.9	0.27	0.27	1.49	1.46
	3	21	30	52.3	51.3	12.2	11.4	8.0	7.6	0.23	0.22	1.47	1.52
	Mean	–	–	43.6	43.5	12.0	11.5	7.9	7.6	0.28	0.27	1.51	1.52
Mean	–	–	43.4	44.0	11.7	11.5	7.6	7.6	0.28	0.27	1.55	1.53	

¹⁾ Hayahikari (shattering-resistant) genotype at *qPDH1*.

²⁾ Toyomusume (shattering-susceptible) genotype at *qPDH1*.

Table 2. Summary of ANOVA of parameters for whole soybean pod morphology.

Source of variance	F value				
	Length	Width	Thickness	Width/length	Width/thickness
Family (S1)	55.35***	0.45	29.57***	22.34***	22.00***
<i>qPDH1</i> (S2)	2.56	10.63**	0.16	1.63	2.01
Pod type (S3)	440.62***	0.17	3.32*	149.08***	5.39**
S1 × S2	0.21	12.98***	6.60**	0.38	0.97
S1 × S3	2.01	1.39	0.87	0.06	1.85
S2 × S3	0.19	1.96	1.81	0.40	0.53
S1 × S2 × S3	2.04	0.35	2.35	0.05	2.32

*, **, *** Significant at P=0.05, 0.01 and 0.001, respectively.

Table 3. Starting sites of pod dehiscence in soybean.

Cultivar	Pod type	No. of samples	Dorsal suture			Ventral suture
			Position 1 ¹⁾	Position 2	Others	
Toyomusume	2	60	49	37	2	11
	3	40	30	31	3	1
Kitamusume	2	45	9	38	2	6
	3	55	9	45	7	9

¹⁾Position numbers correspond to the arrow numbers in Fig. 1.

difference was found between the genotypes at *qPDH1* either in pod length or in thickness. On the other hand, the results of ANOVA indicated a significant difference in the effect of *qPDH1* on pod width, with the interaction between the effects of *qPDH1* and family also being significant. In fact, the difference was not obvious in the family derived from HC1-51. Where we analyzed the values normalized with length or thickness, the values did not significantly differ between the genotypes (Tables 1, 2).

3. Determination of the starting points of pod dehiscence

To determine where pod dehiscence commenced, we observed the pods of shattering-susceptible cultivars Toyomusume and Kitamusume that were partially dehiscent in the field (Table 3). In both cultivars, pod dehiscence started from dorsal sutures more frequently than from ventral ones regardless of the pod type. On some pods, dehiscence was observed at multiple sites. The most frequent site was the dorsal suture near the basal side (position 1 in Fig. 1) or between the first and the second seeds counted from the basal side (position 2 in Fig. 1).

4. Anatomical analyses of suture

The anatomical characteristics of sutures of pods were examined using transverse sections of dorsal sutures at position 1 in Fig. 1 (Fig. 3). The highly lignified tissues designated as bundle cap were developed between exo- and mesocarps. The bundle caps in the two halves of the carpel were separated by dehiscence zone, which had consisted of parenchyma cells, and were bound by fiber cap cells. No obvious qualitative difference in the anatomy of the sutures was observed between the genotypes (Fig. 3A, B). Lignification of vascular bundle and its adjacent tissues was evident and the dehiscence zone was observed equally in both genotypes. Abscission layers between the fiber cap cells and bundle caps appeared to be formed in both genotypes.

As shown in Table 4, quantitative characterization of the suture anatomy revealed no significant genotypic differences in the parameters examined. Fiber cap cells length (L1 in Fig. 3C), “perpendicular” length

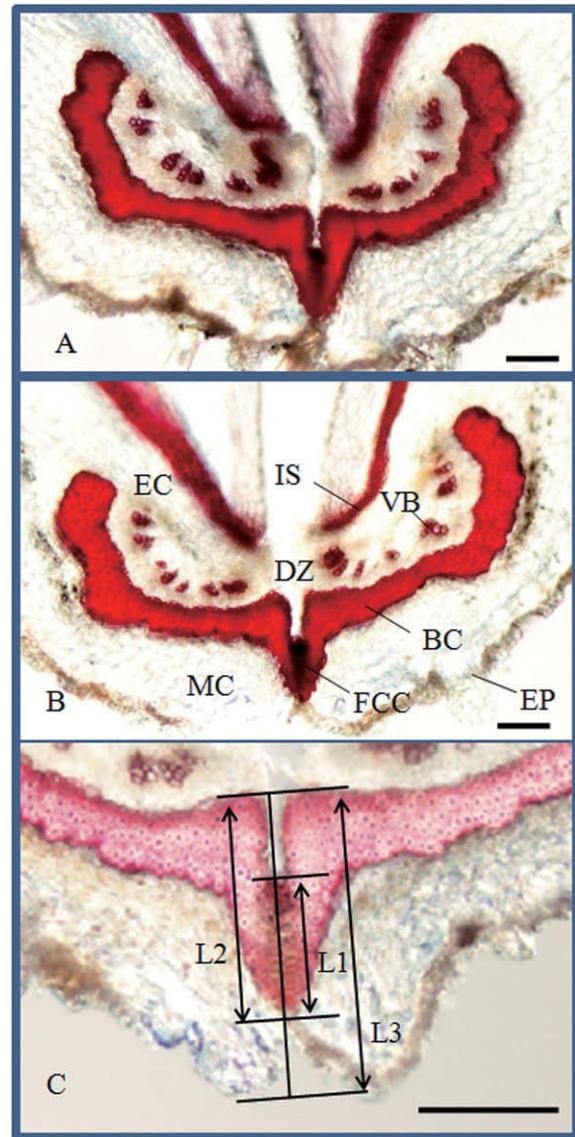


Fig. 3. Light micrographs of cross-sections of dorsal suture at position 1 in Fig. 1 of soybean pods at maturity. A: NIL of shattering-resistant genotype, B: NIL of shattering-susceptible genotype. C: Magnified figure of suture. BC, bundle cap; DZ, dehiscence zone; EC, endocarp; EP, epidermis; FCC, fiber cap cells; IS, inner sclerenchyma; MC, mesocarp; VB, vascular bundle. L1, L2 and L3 were measured to estimate the depth of the “wedge” of suture. Bar=100 μ m.

Table 4. Morphology of dorsal suture of soybean pods.

Parameter	qPDH1		P
	HA ¹⁾	TM ²⁾	
L1 (μm)	128.3 \pm 10.6	127.3 \pm 11.4	N.S.
L2 (μm)	227.1 \pm 19.1	226.8 \pm 18.0	N.S.
L3 (μm)	319.8 \pm 25.8	330.4 \pm 32.2	N.S.
L1/L2	0.57 \pm 0.05	0.56 \pm 0.04	N.S.
L1/L3	0.40 \pm 0.05	0.39 \pm 0.05	N.S.
Bundle cap area ($\times 10^3 \mu\text{m}^2$)	61.1 \pm 10.2	63.9 \pm 7.9	N.S.

¹⁾ Hayahikari (shattering-resistant) genotype at *qPDH1*.

²⁾ Toyomusume (shattering-susceptible) genotype at *qPDH1*.

of bundle cap (L2 in Fig. 3C), thickness of suture (L3 in Fig. 3C) and the ratios of L1 to L2 and L1 to L3, which may indicate the depth of wedge, were similar in both genotypes. There was no significant difference in bundle cap area between the genotypes, either.

Discussion

Previous studies suggested the presence of differences in pod morphology between shattering-resistant and -susceptible soybean cultivars/accessions (Tsuchiya, 1986; Tiwari and Bhatia, 1995). Recent findings with *Arabidopsis* mutants also indicated the involvement of genes controlling pod tissue development in shattering resistance (for review, Dinnyeny and Yanofsky, 2005). In the present study, however, no dramatic difference in pod morphology was found between the NILs segregating for a major QTL, *qPDH1*, in soybean.

The effect of *qPDH1* was demonstrated to be so large that this QTL accounted for more than 50% of total variance for pod dehiscence percentage in the populations of recombinant inbred lines (RILs) and F₂ plants (Funatsuki et al., 2006). A QTL that is presumed to be identical to *qPDH1* also explained nearly 50% of total variance in another RIL population (Bailey et al., 1997). The NILs segregating for *qPDH1* exhibited a more than 80% difference in pod dehiscence percentage (Funatsuki et al., 2008). In the present study, the difference in pod dehiscence percentage seen between the NILs of each family was not as pronounced as in the previous study. This was probably due to a prolonged drying period prior to heat treatment. Nevertheless, the degree of pod dehiscence after heat treatment was evidently different between the NILs. Therefore the relationship between pod morphology and shattering resistance was examined using these lines.

Tsuchiya (1986) found that the ratio of width to thickness of pod was significantly smaller in shattering-resistant cultivars although he doubted the direct association of this trait with shattering resistance. In the present study, the result of ANOVA suggests a

significant effect of *qPDH1* on pod width. However, the interaction effect of family and *qPDH1* genotype was also significant, and in fact, the difference was observed only for the HC1-85 family. This is in contrast with the result that the degree of pod dehiscence after heat treatment was similar in the two families. In addition, the difference found in the HC1-85 family resulted in a larger value of the ratio of width to thickness of pod in the shattering-resistant genotype, which is contrary to the result by Tsuchiya (1986). Taken together, pod width seems not to be associated with shattering resistance.

Pod dehiscence occurs along the suture, but, the site where exactly pods start dehiscing has not been reported. The shattering-susceptible cultivars used in the present study started pod dehiscence at dorsal sutures more frequently than at ventral ones. Interestingly, the concave sites near the base or between the seeds were found to be "hot spots". Since no apparent difference in morphology between the concave and the convex sites of sutures was recognized in our preliminary experiment (data not shown), the force to dehiscence pods may be concentrated at those sites due to the undulating shape of pod.

At the starting point of pod dehiscence, we made cross sections for anatomical analyses of sutures. Based on the observation of the suture, bundle caps and fiber cap cells appeared to play a role in preventing the two halves of the pericarp from separating. Tiwari and Bhati (1995) reported an inverse correlation of the length and thickness of bundle cap and shattering-resistance among cultivars. In the present study, instead, the areas of bundle caps were calculated using an image analysis system since the non-flat shape of bundle caps made it difficult to measure the length and the thickness precisely. In contrast to the result of the previous study, there was no significant difference in the area of bundle cap between the NILs. We consider that the length and thickness of bundle cap are not correlated with the shattering resistance conditioned by *qPDH1*. Tsuchiya (1986) reported that the shattering-resistant line had a tendency of

harboring a shallow wedge in suture. However, we found no significant difference in any parameter related to the depth of wedge in suture.

This discrepancy could be explained by the difference in plant materials compared. We used NILs for a QTL controlling pod shattering. The use of these lines had an advantage of less influence of genetic backgrounds on any trait as compared with the use of cultivar/accession groups displaying differential shattering resistance, which were used in previous studies (Tsuchiya, 1986; Tiwari and Bhatia, 1995). Therefore, the previous findings of the association of shattering resistance degree with pod morphology may be due to a biased distribution of genes that were not associated with shattering resistance but affected pod morphology. For example, extremely shattering-susceptible *Glycine soya*, which was included in the plant materials in the study by Tiwari and Bhatia (1995), has much smaller pods than the cultivated species, *Glycine max*. Small pods are presumed to be composed of thin pod walls and short and thin bundle caps, and they found close correlations among all characters examined. Therefore, the inverse correlation between the small sizes of these characters and the shattering resistance, which was found by Tiwari and Bhatia (1995), might reflect no more than the differences between the wild and cultivated species. Another plausible explanation is that other QTLs conditioning shattering resistance were involved in the genotypic differences found in the previous studies, although several shattering-resistant cultivars besides Hayahikari-related ones are likely to harbor shattering-resistance alleles at *qPDH1* as well (Bailey et al., 1997; Funatsuki et al., unpublished results) and this QTL seems to have played a role in the domestication process (Liu et al., 2007).

In *Arabidopsis thaliana*, a model plant species, several mutants with indehiscent pods were isolated and the responsible genes were identified (Liljegren et al., 2000; Ferrándiz et al., 2000; Rajani and Sundaresan, 2001; Liljegren et al., 2004). All the genes were involved in patterning of pod (Dinneny and Yanofsky, 2005) and the anatomical analyses revealed obvious differences between the shattering-resistant mutants and the wild-type (Liljegren et al., 2000; Ferrándiz et al., 2000; Rajani and Sundaresan, 2001; Liljegren et al., 2004). Therefore we envisaged the presence of a similar mechanism associated with *qPDH1*, which was, in fact, not the case. While the knowledge obtained with model plants using artificial mutants is sometimes useful for understanding the genetic and physiological mechanisms underlying natural variations in agronomically important traits in crops (e.g. Yano et al., 2000), our results suggest the importance of the investigation with the trait using the crop of interest.

The present study show that the major QTL, *qPDH1*, controls soybean pod dehiscence without any marked

morphological change in pods. Some factors other than pod morphology could be associated with pod dehiscence, such as a cell wall-degrading enzyme (Christiansen et al., 2002) and twist strength of pod wall (Isemura et al., 2007), which is presumed to be a force to dehisce pods. Very recently, the chemical composition of the pod wall in cultivars susceptible to shattering was found to differ from that in the shattering-resistant cultivars (Romkaew et al., 2008). In addition, secondary cell wall thickening has been found to play a critical role in dehiscence of anthers (Mitsuda et al., 2005). These factors should be examined in the future to elucidate the mechanism underlying shattering resistance controlled by *qPDH1*.

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