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Review

Mapping and use of QTLs controlling pod dehiscence in soybean

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While the cultivated soybean, *Glycine max* (L.) Merr., is more recalcitrant to pod dehiscence (shattering-resistant) than wild soybean, *Glycine soja* Sieb. & Zucc., there is also significant genetic variation in shattering resistance among cultivated soybean cultivars. To reveal the genetic basis and develop DNA markers for pod dehiscence, several research groups have conducted quantitative trait locus (QTL) analysis using segregated populations derived from crosses between *G. max* accessions or between a *G. max* and *G. soja* accession. In the populations of *G. max*, a major QTL was repeatedly identified near SSR marker Sat_366 on linkage group J (chromosome 16). Minor QTLs were also detected in several studies, although less commonality was found for the magnitudes of effect and location. In *G. max* × *G. soja* populations, only QTLs with a relatively small effect were detected. The major QTL found in *G. max* was further fine-mapped, leading to the development of specific markers for the shattering resistance allele at this locus. The markers were used in a breeding program, resulting in the production of near-isogenic lines with shattering resistance and genetic backgrounds of Japanese elite cultivars. The markers and lines developed will hopefully contribute to the rapid production of a variety of shattering-resistant soybean cultivars.

Key Words: Soybean (*Glycine max*), wild soybean (*Glycine soja*), pod dehiscence, shattering resistance, quantitative trait loci (QTLs), marker-assisted selection (MAS).

Introduction

Shattering resistance is one of the primary traits that crops have acquired in the process of domestication (Fuller 2007). While wild soybean, *Glycine soja* Sieb. & Zucc., immediately scatters its seeds via pod dehiscence in response to drying after maturity as do many other wild legumes, cultivated soybean, *Glycine max* (L.) Merr., retains its seeds in pods after maturity. There is also significant genetic variation in the degree of pod dehiscence (shattering resistance) within cultivated species (Caviness 1965, Helms 1994, Romkaew and Umezaki 2006, Tsuchiya 1986). Highly shattering-resistant cultivars have been preferably developed and cultivated in some regions where soybean cultivation has been carried out on a large scale with the use of combine harvesters. In Japan, on the other hand, soybeans have traditionally been cultivated on a small scale. In addition, soybean seeds are generally harvested in cool and humid seasons. These factors have masked the problem of pod dehiscence in Japan; however, the recent unusual climatic fluctuations and the widespread use of combine harvesters are increasing the importance of breeding cultivars resistant to pod dehiscence.

Methods for evaluating pod dehiscence have been established (Jiang *et al.* 1991, Tsuchiya 1986, Tukamuhabwa *et al.* 2002) and have proven usable in breeding programs (Tsuchiya 1986); however, more efficient methods, such as marker-assisted selection (MAS), are desirable since conventional methods, involving heat treatment of pods, are not very convenient. For instance, these methods are not suitable for backcross breeding, since pod-shattering resistance has proven partially recessive (Tsuchiya 1986, 1987, Tukamuhabwa *et al.* 2002), which implies the need for progeny testing for selection.

Marked progress in soybean genomics has been made in

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the past two decades. Many restricted fragment length polymorphism (RFLP) markers had been developed by the early 1990s (e.g., Keim *et al.* 1990). Later, genome-wide simple sequence repeat (SSR) markers, with which more frequent polymorphism is generally found between closely related accessions, were reported by several groups (Cregan *et al.* 1999, Hisano *et al.* 2007, Hwang *et al.* 2009, Song *et al.* 2004, Xia *et al.* 2007, Yamanaka *et al.* 2001). Finally, the complete soybean genome sequences were released (Schmutz *et al.* 2010). These resources are useful for identifying or creating DNA markers for shattering resistance.

In this article, we overview recent advances in genetic and breeding studies on shattering resistance using DNA markers, focusing on the major quantitative trait locus (QTL) controlling shattering resistance in soybean.

Mapping of QTLs conditioning shattering resistance in cultivated soybean

Several groups conducted QTL analysis on shattering resistance in cultivated soybean. There is likely to be a major QTL and several minor QTLs.

A major QTL was repeatedly identified on the linkage group (LG) J (chromosome 16) in independent studies using segregating populations derived from a cross between shattering-resistant (SR) and -susceptible (SS) parents. The first evidence was provided by Bailey *et al.* (1997), who used a population of recombinant inbred lines (RILs) created from a cross between a shattering-resistant, North American cultivar Young and a shattering-susceptible accession introduced from Japan (PI 416937). They mapped a major QTL on LG J (Table 1), although the position was inaccurate because of the sparseness of RFLP markers used and no use of interval mapping. Subsequently, a QTL with a large effect was identified also on LG J in populations of RILs and F_2 plants, derived from a cross between SS and SR Japanese cultivars, Toyomusume and Hayahikari (Table 1, Funatsuki *et al.* 2005, 2006). The shattering resistance of Hayahikari was derived from a Thai cultivar, SJ2. Since all of the SSR markers available were used in that study, the position of the QTL could be narrowed down to <5 cM genetic distance, which was included in the region of the major QTL suggested by Bailey *et al.* (1997). Furthermore, Kang *et al.* (2009) found a major QTL on LG J in a population involving Korean cultivars, Keunolkong (SS) and Sinpaldalkong (SR) (Table 1). The candidate position overlapped those identified previously by Bailey *et al.* (1997) and Funatsuki *et al.* (2006). Finally, Yamada *et al.* (2009) conducted allelism tests using two crosses between SR and SS cultivars, Kariyutaka (SS) × Hayahikari (SR) and Wasekogane (SR) × Yukihomare (SS). The two resistant cultivars had no common ancestors. Major QTLs were found in almost the same position of LG J as the previously-detected QTLs (Bailey *et al.* 1997, Funatsuki *et al.* 2006), suggesting that the resistance in the two parents was controlled by the same QTLs. These findings suggest a QTL on LG J (chromosome 16) in cultivated soybean that roughly determines whether the cultivar is SR. This locus was designated *qPDH1* by Funatsuki *et al.* (2008)

In contrast, relatively little commonality was found among the positions for minor QTLs (Table 1). Bailey *et al.* (1997) found QTLs on LGs D1b, E, L and N in a cross between Young and PI416937. Kang *et al.* (2009) identified QTLs on LGs A1, B2, D1b, L and O in crosses between Keunolkong (SS) and Sinpaldalkong (SR) and between Keunolkong (SS) and Iksan 10 (SR). Yamada *et al.* (2009) showed the possible presence of a QTL on LG A2 in a cross between Toyomusume (SS) and Harosoy (SR). Since these studies differed in cross combination, growth conditions and method for evaluating shattering resistance, the minor QTLs might be dependent on the genetic background and/or the environment for plant growth and drying the pods. These QTLs may be useful for fine-tuning shattering resistance, since in some cases moderate shattering resistance is required. In addition, in the segregating population derived from an SS cultivar, Keunolkong, and an SR cultivar, Iksan 10, only minor QTLs were identified; no major QTL was detected either on LG J, or on other LGs (Kang *et al.* 2009). This suggests that an SR cultivar could be developed by pyramiding shattering resistance alleles at minor QTLs.

QTLs found in progeny derived from crosses between cultivated and wild soybeans

As mentioned above, elimination or reduction of natural seed dispersal is regarded as the single most important domestication trait (Fuller 2007); therefore, to study the domestication process of soybean, it is of importance to dissect the trait of pod dehiscence genetically by comparing cultivated and wild soybeans. Saxe *et al.* (1996) found three QTLs, two on LG J and one on LG D1b (Table 1). Both QTLs on LG J were mapped quite far from *qPDH1* (Table 1 and Fig. 1). These QTLs are likely to differ from *qPDH*, although mapping accuracy might not be very high because of the limited numbers of markers used. A QTL was also detected on LG J in another study (Liu *et al.* 2007). The locus was, in contrast, mapped near *qPDH1* (Table 1 and Fig. 1), indicating that it is possibly identical to *qPDH1*; however, its effect was relatively small (Table 1). The line used in the latter study, Tokei 780, is SS in common cultivated soybean lines (Y. Tanaka unpublished data) and is presumed to have an SS allele at *qPDH1*, although the genotype of this line at the locus on LG J was determined to be SR in the *G. max* × *G. soja* population. These findings suggest the presence of multiple alleles at *qPDH1* or the presence of another QTL near *qPDH1*. No other significant QTLs for pod dehiscence were detected in the study by Liu *et al.* (2007), although the difference between cultivated and wild soybeans seen in shattering resistance was considerably large. This suggests the presence of a number of QTLs for pod dehiscence. Taken together, several loci are likely to be involved in the domestication of wild soybean.

Table 1. QTLs associated with pod dehiscence in soybean

Linkage group	Chromosome	Marker[a]	PVE (%)[b]	Parent[c]		Ref[d]
				Resistant	Susceptible	
A1	5	Satt385	7.2	Sinpaldalkong	Keunolkong	3
A2	8	Satt409	11.0	Harosoy	Toyomusume	4
B2	14	Satt126	7.3	Sinpaldalkong	Keunolkong	3
D1b	2	A725	6.5	Young	PI 416937	1
		Satt350	5.0	Sinpaldalkong	Keunolkong	3
		Satt296	6.8	Iksan 10	Keunolkong	3
		B194-2	23.7	A81-3560222	PI468916 (soja)	5
E	15	cr274-1	7.3	Young	PI 416937	1
		Sat_124	9.6	Tokei 780	Hidaka 4 (soja)	6
J	16	B122-1	44.4	Young	PI 416937	1
		Sat_366	>50	Hayahikari	Toyomusume	2
		Satt183	42.3	Sinpaldalkong	Keunolkong	3
		Satt621	31.0	Harosoy	Toyomusume	4
		Sct_065	34.7	A81-3560222	PI468916 (soja)	5
		A724	21.6	A81-3560222	PI468916 (soja)	5
		Satt215	16.3-21.8	Tokei 780	Hidaka 4 (soja)	6
L	19	A489-1	5.7	Young	PI 416937	1
		Sct_010	3.7	Sinpaldalkong	Keunolkong	3
		Satt238	10.4	Iksan 10	Keunolkong	3
N	3	A808n	5.1	Young	PI 416937	1
O	10	Satt243	4.3	Iksan 10	Keunolkong	3

[a] The marker linked most tightly to the QTL or the marker displaying the highest R^2 value.

[b] Percentage of variance explained.

[c] "Resistant" and "Susceptible" are determined by comparison of the two parents. "soja" indicates *Glycine soja*.

[d] Bailey *et al.* (1997), Funatsuki *et al.* (1996), Kang *et al.* (2009), Liu *et al.* (2007), Saxe *et al.* (1996), Yamada *et al.* (2009).

Fine mapping and development of DNA markers for the major QTL

Since the major QTL, *qPDH1*, had a marked effect and a recessive allele controlled shattering resistance (Funatsuki *et al.* 2006), the development of useful DNA markers linked with *qPDH1* was desired for the establishment of MAS for shattering resistance. Using a residual heterozygous line (RHL), which was first defined and used for fine mapping of a QTL for flowering time by Yamanaka *et al.* (2005), Funatsuki *et al.* (2008) confirmed that the major QTL was located between SSR markers Sat_093 and Sat_366 on LG J. Furthermore, a large segregating population was screened for recombinants between Sat_093 and Sat.366 (Suzuki *et al.* 2010). The genotypes of the recombinants were determined with SSR markers designed using the Williams 82 genome sequence (Phytozome). Analysis of the genotype and the phenotype of each recombinant narrowed down the candidate region of *qPDH1* to 134 kb (Suzuki *et al.* 2010). In this region, Suzuki *et al.* (2010) found several insertion/deletion (In/Del) variations between SR and SS parents, which were used to develop three DNA markers (SRM0, SRM1 and SRM2) for *qPDH1*. A survey of the genotype of various SR and SS accessions at these markers revealed that all shattering-resistant accessions had an identical genotype at these markers, which was distinct to those of SS accessions with a few exceptions at SRM2. These findings suggest that the markers developed can be used to select progeny derived from various cross combinations between SR and SS lines.

In addition, successful narrowing down of the genomic region of *qPDH1* allows us to discuss the candidate gene underlying the QTL. In the 134-kb region, 10 putative open reading frames (ORFs) were predicted to be present (Suzuki *et al.* 2010), based on the published genome sequence (Schmutz *et al.* 2010). Interestingly, no ORF showed sequence homology to the genes that have previously been identified as pod dehiscence-related genes in *Arabidopsis*, such as *SHATTERPROOF1* and *SHATTERPROOF2* (Liljegren *et al.* 2000), *FRUITFULL* (Ferrandiz *et al.* 2000), *ALCATRAZ* (Rajani and Sundaresan 2001), *INDEHISCENT* (Liljegren *et al.* 2004) and *NST1* and *NST3* (Mitsuda and Ohme-Takagi 2008). In addition, while mutants of these genes exhibited distinct phenotypes in terms of fruit patterning in comparison with the wild types in *Arabidopsis*, anatomical observation of the pods of near-isogenic lines derived from an RHL for *qPDH1* revealed no apparent difference between the genotypes with regard to fruit patterning (Suzuki *et al.* 2009). These results suggested that a novel gene and an unknown mechanism are likely to underlie pod dehiscence in soybean.

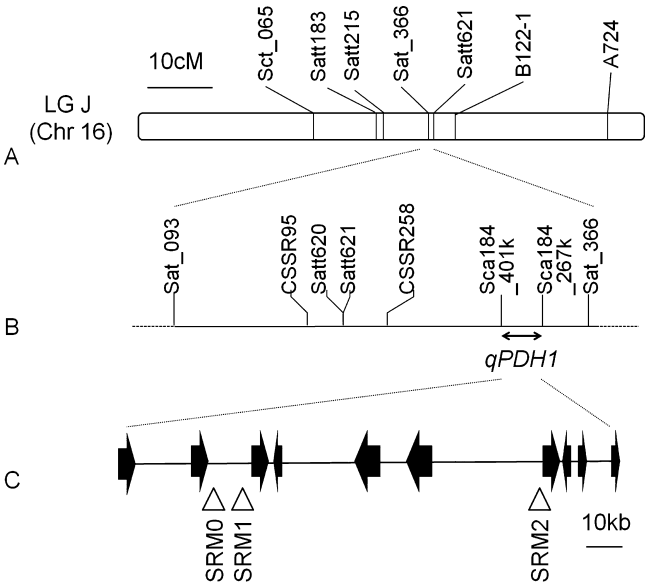

Fig. 1. Genetic and physical maps of the genomic region including *qPDH1*. A, Genetic map of molecular markers linked to QTLs for shattering resistance on linkage group (LG) J, or chromosome 16, based on the consensus map by Song *et al.* (2004). B, Genetic map of SSR markers in the vicinity of *qPDH1*. C, Physical map of open reading frames (ORFs), shown as arrows, and DNA markers linked tightly to *qPDH1*, shown as triangles, based on the genome sequence published on the Phytozome web site (http://www.phytozome.net/soybean).

Use of *qPDH1* for soybean breeding

In general, the effect of a QTL is influenced by environmental conditions and the genetic background; therefore, the stability of the effect of the SR allele from SJ2 was examined against various genetic backgrounds and multiple test locations (Funatsuki *et al.* 2006, 2008, Yamada *et al.* 2009). Under these conditions, the SR allele improved SR of the genotype compared with the SS genotype(s), although the difference in the degree of SR seen between the two genotypes varied.

The stable effect of *qPDH1* has encouraged breeders to use this QTL for breeding SR soybean lines. Yamada *et al.* (2010) introduced the SR allele from SJ2 to 11 Japanese soybean cultivars. They first used Sat_366 and Sat_093 as selection markers since *qPDH1* existed between them, and more tightly linked markers later became available. Five to seven consecutive processes of backcrossing and marker selection for three years resulted in near-isogenic lines of all cultivars used. As for these lines, primary agronomic traits other than shattering resistance were subsequently shown to be almost the same as those of the recipient parents. Conventional breeding methods could not produce near-isogenic lines so rapidly, demonstrating the usefulness of DNA markers for *qPDH1*.

Future prospects

The eleven SR lines developed possess genetic backgrounds of representative cultivars grown on the main island, and Kyushu and Shikoku regions of Japan (Yamada *et al.* 2010). These cultivars are frequently used as parents for crossing, indicating that we now have a variety of breeding materials with shattering resistance in Japan. Since the shattering resistance of these lines is basically granted by the *qPDH1* locus, half of the progeny in advanced generations should be shattering-resistant in the case of the cross combination of SR and SS lines, suggesting the relatively straightforward selection of SR lines with other favorable traits even without MAS. In addition, rapid and efficient MAS systems are available in soybean (e.g., Sayama *et al.* 2011), enabling us to treat shattering resistance as a target trait of MAS along with other important traits such as disease resistance. We expect that many SR cultivars will be released in the near future using these lines and markers, resulting in a steep increase in the growing area of SR cultivars and a marked reduction of yield loss due to pod dehiscence in Japan.

The genomic region in which *qPDH1* is located has been narrowed down to 134 kb, where no more than 10 candidate genes are presumably present (Suzuki *et al.* 2010). A large segregating population and a complementation test may allow us to identify the gene underlying *qPDH1*. As mentioned above, no sequence showed any homology to the genes associated with pod dehiscence that have been revealed in *Arabidopsis*. Characterization of *qPDH1* at the molecular level will lead to an understanding of the mechanism of pod dehiscence specific to soybean or legumes. This information may also be useful for breeding other legumes since pod dehiscence is also a problem in the breeding of legume crops such as cowpea and lupin, especially when using SS wild relatives (e.g., Li *et al.* 2010, Mohammed *et al.* 2010).

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