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Note

Development and validation of DNA markers linked to *Sdvy-1*, a common bean gene conferring resistance to the yellowing strain of *Soybean dwarf virus*

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The yellowing strain of *Soybean dwarf virus* (SbDV-YS) causes yellowing and yield loss in common bean (*Phaseolus vulgaris*). The most effective control is achieved through breeding for resistance. An indeterminate climbing cultivar with a white seed coat, 'Oofuku', is resistant to SbDV-YS in inoculation tests. We crossed 'Oofuku' with an elite cultivar, 'Taisho-Kintoki', which is SbDV-YS-susceptible, determinate dwarf with a red-purple seed coat, and performed amplified-fragment-length polymorphism analysis of F_3 lines. From nucleotide sequences of the resistant-specific fragments and their flanking regions, we developed five DNA markers, of which DV86, DV386, and DV398 were closely linked to *Sdvy-1*, a resistance gene. Using the markers, we developed 'Toiku-B79' and 'Toiku-B80', the near-isogenic lines (NILs) incorporating *Sdvy-1* in the background of 'Taisho-Kintoki'. The NILs had similar growth habit, maturity date and seed shape to those of 'Taisho-Kintoki'. The quality of boiled beans was also similar, except that the NILs had more seed coat cracking than 'Taisho-Kintoki'. The NILs showed no SbDV-YS infection in inoculation tests. We suggest that *Sdvy-1* is a useful source of SbDV-YS resistance in common bean.

Key Words: AFLP, disease resistance, kidney bean, *Phaseolus vulgaris*, SCAR marker, seed coat color.

Introduction

Soybean dwarf virus (SbDV), in the family *Luteoviridae*, is persistently transmitted by the foxglove aphid, *Aulacorthum solani*. SbDV was first reported in soybean (*Glycine max*) in Japan (Tamada *et al.* 1969) and has been found in various legumes worldwide, including those in Australia, Ethiopia, Germany, Japan, New Zealand, Tunisia, and the USA (Abraham *et al.* 2007, Johnstone and McLean 1987, Najar *et al.* 2003, Tadesse *et al.* 1999, Tamada 1973, Wilson and Close 1973).

SbDV infection in common bean (*Phaseolus vulgaris*) was first reported in Hokkaido, the northernmost island of Japan. In this region, the dwarfing strain, SbDV-DS and the yellowing strain, SbDV-YS, are prevalent. Only SbDV-YS is infectious to common bean, whereas both strains can infect other legumes, such as soybean (Tamada 1973). SbDV-YS-infected common bean plants show interveinal chlorosis and produce few or no seeds.

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'Taisho-Kintoki', a leading common bean cultivar planted in Hokkaido for more than 60 years, is popular for its red-purple seed coat and fine cooking qualities. However, its susceptibility to SbDV-YS hinders its stable production. Insecticides and reflective plastic film control the foxglove aphid but are costly (Mizukoshi *et al.* 1991, 1992). The most effective way to prevent SbDV-YS infection is through breeding for resistance.

Differences in resistance to SbDV-YS among common bean cultivars have been reported (Onodera and Ebe 2003, Tamada 1975). When inoculated with SbDV-YS, 'Taisho-Kintoki' showed severe symptoms, whereas the white-seeded indeterminate climber 'Oofuku' remained symptomless. Segregation analysis of crosses between the two cultivars revealed that the SbDV-YS resistance derived from 'Oofuku' is controlled by a single dominant gene, *Sdvy-1* (*Soybean dwarf virus*, the yellowing strain) (Ebe *et al.* 2002).

Amplified-fragment-length polymorphism (AFLP) analysis is a powerful tool used to identify genomic regions linked to a trait; it is highly reliable, and no prior sequence knowledge is necessary (Vos *et al.* 1995). In this study, we performed AFLP analysis of a cross between 'Taisho-Kintoki' and 'Oofuku' to identify fragments specific to

Sdvy-1 in common bean, whose genome sequence was not available until 2013. We designed sequence-characterized amplified region (SCAR) markers linked to *Sdvy-1* and used them to develop near-isogenic lines incorporating *Sdvy-1* (*Sdvy-1*-NILs) in the background of 'Taisho-Kintoki', which we then evaluated for resistance to SbDV-YS. The ultimate goal is to develop SbDV-YS-resistant cultivars with similar agronomic traits and eating qualities to those of 'Taisho-Kintoki'.

Materials and Methods

Plant materials

For AFLP analysis, we used 102 F_3 lines derived from a cross between 'Taisho-Kintoki' × 'Oofuku' (*Sdvy-1* donor). By backcrossing against 'Taisho-Kintoki', we developed two *Sdvy-1*-NILs, 'Toiku-B79' (BC_5F_7) and 'Toiku-B80' (BC_6F_7). The NILs were selected based on their genotypes at SCAR markers DV86, DV386, and DV398 (Table 1) and agronomic traits (growth habit and seed coat color).

AFLP analysis

DNA was extracted from fresh leaves by a modified CTAB method (Suzuki *et al.* 2012). We used two bulked samples, one from 12 resistant F_3 plants and the other from 12 susceptible F_3 plants, all plants from different lines. AFLP analysis was performed following the method of Vos *et al.* (1995) as modified by Suzuki *et al.* (2013). *Eco*RI (E) primers were labeled with fluorescent dye (6-FAM or VIC). Selective amplification was performed using combinations of E primers with three selective nucleotides and *Mse*I (M) primers with three selective nucleotides (E-NNN/M-NNN). The amplification products were analyzed on an ABI Prism 310 Genetic Analyzer (Applied Biosystems, USA) with GeneScan software and a GeneScan-500 LIZ size standard.

Development of DNA markers

Amplified fragments specific to the resistant bulk were extracted, purified, concentrated (Suzuki *et al.* 2013), and sequenced by inverse PCR (Ochman *et al.* 1988). We designed SCAR markers 18 to 28 nucleotides long with a GC content of 28% to 56% (Table 1). PCR was performed following the protocol of Suzuki *et al.* (2013).

Evaluation of SbDV-YS resistance

We evaluated SbDV-YS resistance following inoculation of plants by SbDV-YS-infected aphids (Onodera and Ebe 2003). Inoculated plants were grown either in a greenhouse (F_3 lines) or in an experimental field of Tokachi Agricultural Experiment Station (AES) (Shikaoi, Japan; 43°05′N, 142°59′E). Approximately two months after SbDV-YS inoculation, plants with yellowing symptoms were counted and the percentage of symptomatic plants (%SP) was calculated. SbDV-YS infection was further confirmed by triple antibody sandwich enzyme-linked immunosorbent assay using monoclonal antibodies (Mikoshiba and Honda 2000).

Agronomic trait analysis

The *Sdvy-1*-NILs were grown in the field of Tokachi AES (Memuro, Japan; 42°53′N, 143°04′E) and Kitami AES (Kunneppu, Japan; 43°45′N, 143°43′E). Seeds were sown on 26 May (Memuro) and 22 May 2009 (Kunneppu) at 20-cm intervals in rows 60 cm apart. In Memuro, each line was grown in four 12.0-m^2 plots, with 200 plants per plot. In Kunneppu, each line was grown in three 9.6-m^2 plots, with 160 plants per plot. We recorded and evaluated flowering and maturity dates, plant height, number of pods per plant, 100-seed weight, seed yield, and %SP in each plot.

Evaluation of seed appearance and boiled bean quality

We measured the length, width, and thickness of 60 seeds of the two NILs and 'Taisho-Kintoki' harvested from the Memuro field. The seed coat color of 20 to 30 raw or boiled seeds was measured by a CM-3500d spectrophotometer (Konica Minolta, Tokyo, Japan), and L*, a* and b* were calculated. For evaluation of boiled bean quality, three replicates of 100 seeds were soaked in 350 mL water at 25°C for 18 h and then boiled at 98°C for 20 min. The

Table 1. SCAR markers developed in this study

Marker	Type	Primer	Sense	Sequence (5′ to 3′)	Reference sequences[a]	Specificity
DV86	Co-dominant	DV86-11	Forward	CGTTTAGAAACACCATGAATTCA	AB897684, AB897685	Oofuku
		DV86-12	Reverse	CACTTTCTTTCATAAATTTAATGGACTG		Common
		DV86-13	Forward	GTGTTCGAAGTTGTTTAAACGAC		Taisho-Kintoki
DV309	Co-dominant	DV309-11	Forward	GGGTTGAAAACTAAATGGTAG	AB897686, AB897687	Taisho-Kintoki
		DV309-15	Forward	CTAAAACTAGTAATCTGAGACAGATG		Oofuku
		DV309-20	Reverse	GTTTTTGAAAGAGCAGAAAGGTG		Common
DV353	Co-dominant	DV353-06A	Reverse	CCATTAATTTATCTCTTTATGAGTG	AB897691, AB897692	Common
		DV353-07	Forward	CAGGTGAATCAGTGATGAAG		Taisho-Kintoki
		DV353-13	Forward	GCATGGACCATCATCTCG		Oofuku
DV386	Co-dominant	DV386-16	Reverse	CAATACGTCCTCCACATAGAGA	AB897688, AB897689	Oofuku
		DV386-27	Forward	GGATGGAAGGATGCTCTC		Common
		DV386-28	Reverse	GATGATTCCTTGATCATAACG		Taisho-Kintoki
DV398	Dominant	DV398-05	Forward	GGAGATTGAGGTAGCAGAAAG	AB897690	Oofuku
		DV398-16	Reverse	CCTGTAGATGTATAATACACATGCTTG		Oofuku

[a] Accession no. assigned from DDBJ (http://www.ddbj.nig.ac.jp).

Table 2. Growth habit, seed coat color and genotypes of *Sdvy-1*-NILs

Cultivar		Growth habit	Seed coat color	Genotype[a]		
				DV86	DV386	DV398
Toiku-B79	BC_5F_7	Determinate dwarf	Red-purple	T	O	O
Toiku-B80	BC_6F_7	Determinate dwarf	Red-purple	T	O	O
Taisho-Kintoki	–	Determinate dwarf	Red-purple	T	T	T
Oofuku	–	Indeterminate climber	White	O	O	O

[a] O ('Oofuku' type), T ('Taisho-Kintoki' type).

hardness of the whole seed and of the seed coat was measured by a TA-XT2 texture analyzer (Stable Micro Systems, UK), and means of 20 seeds in each replicate were determined.

Results

Development of DNA markers linked to Sdvy-1

We selected five AFLP fragments that were specific to the SbDV-YS-resistant bulk (E-AGT/M-ACC-86, E-AGC/M-TGC-309, E-ATG/M-CTC-353, E-AGT/M-TTA-386 and E-AAA/M-TTA-398). We developed SCAR markers on the basis of differences in the nucleotide sequences of the AFLP fragments and their flanking regions between the resistant and susceptible bulks, and designed the co-dominant markers DV309, DV86, DV386, and DV353, and the dominant selectable marker DV398, which amplified the resistant 'Oofuku' genotype (Table 1). Recombination among the SCAR markers was found in 5 of the 102 F_3 lines. Comparison of the genotypes and SbDV-YS resistance identified DV86, DV386, and DV398 as the more closely linked to *Sdvy-1* than DV309 and DV353.

Development of Sdvy-1-NILs 'Toiku-B79' and 'Toiku-B80'

To develop *Sdvy-1*-NILs in the background of 'Taisho-Kintoki', we screened 600 BC_nF_2 (n = 1–6) plants with SCAR markers DV86, DV386, and DV398, and selected plants with the 'Oofuku' genotype at two or three markers. We evaluated the growth habit and seed coat color of the selected plants in BC_nF_3 lines and chose only dwarf lines with a red-purple seed coat. We obtained only two *Sdvy-1*-NILs with a red-purple seed coat, which were later named 'Toiku-B79' and 'Toiku-B80'. The NILs carried the 'Oofuku' genotype at markers DV386 and DV398 and the 'Taisho-Kintoki' genotype at DV86 (Table 2).

Table 3. SbDV-YS resistance of *Sdvy-1*-NILs

Cultivar	% Symptomatic plants
Toiku-B79	0.0 (n = 26)
Toiku-B80	0.0 (n = 23)
Taisho-Kintoki	76.9 (n = 26)

Plants were inoculated with SbDV-YS before planting in the field.

SbDV-YS resistance and agronomic traits of Sdvy-1-NILs

In the inoculation test, no SbDV-YS infection was observed in either NIL, but 76.9% of 'Taisho-Kintoki' plants were symptomatic (Table 3). In the field, no symptoms were observed in either NIL, but %SP of 'Taisho-Kintoki' was 0.2% in Memuro and 7.3% in Kunneppu (Table 4). Both 'Toiku-B79' and 'Toiku-B80' were close to 'Taisho-Kintoki' in flowering and maturity dates and plant height. However, 'Toiku-B79' had significantly more pods and 'Toiku-B80' had higher 100-seed weight than 'Taisho-Kintoki' in both Memuro and Kunneppu. The yields of the NILs were 4%–5% higher in Memuro and 21%–23% higher in Kunneppu than those of 'Taisho-Kintoki'.

Seed appearance and boiled bean quality of Sdvy-1-NILs

'Toiku-B79' had similar seed dimensions to those of 'Taisho-Kintoki', whereas 'Toiku-B80' had longer, wider, thicker seeds, but in the same proportions as those of 'Taisho-Kintoki' (Table 5, Fig. 1). The seed coat color of the raw NIL beans was close to that of 'Taisho-Kintoki' beans, except that the NIL beans had higher L* values (Table 6, Fig. 1). The L*, a* and b* values of the boiled NIL beans were not significantly different from those of 'Taisho-Kintoki' beans. The hardness of the whole seed and of the seed coat was not significantly different between the NILs and 'Taisho-Kintoki'. However, 24.7–27.7% of the *Sdvy-1*-NILs had a cracked seed coat after boiling, versus 8.7% of 'Taisho-Kintoki' (Table 6).

Table 4. Agronomic traits of *Sdvy-1*-NILs

Location	Cultivar	Flowering date	Maturity date	Plant height (cm)	No. of pods (per plant)	100-seed weight (g)	Yield (kg/1000 m^2)[a]	% Symptomatic plants
Memuro	Toiku-B79	14-Jul	12-Sep	53.5	18.5**	71.8	312 (104)	0.0
	Toiku-B80	14-Jul	12-Sep	57.0	17.4	75.0*	313 (105)	0.0
	Taisho-Kintoki	14-Jul	11-Sep	53.0	16.3	72.8	299 (100)	0.2
Kunneppu	Toiku-B79	11-Jul	10-Sep	49.0	22.1**	77.8	403 (123)*	0.0**
	Toiku-B80	11-Jul	10-Sep	50.0	19.3	80.2	398 (121)*	0.0**
	Taisho-Kintoki	10-Jul	9-Sep	50.0	19.6	77.2	328 (100)	7.3

Asterisks indicate significant differences from 'Taisho-Kintoki' by Dunnett's test at *5%, **1%.

[a] Numbers in parentheses are % yields relative to 'Taisho-Kintoki'.

Table 5. Seed size and shape of *Sdvy-1*-NILs

Cultivar	Length (mm, L)	Width (mm, W)	Thickness (mm, T)	L/W	W/T
Toiku-B79	14.66	9.41	7.40	1.56	1.27
Toiku-B80	15.20**	9.69**	7.61**	1.57	1.27
Taisho-Kintoki	14.60	9.32	7.31	1.57	1.27

Asterisks indicate significant differences from 'Taisho-Kintoki' by Dunnett's test at **1%.

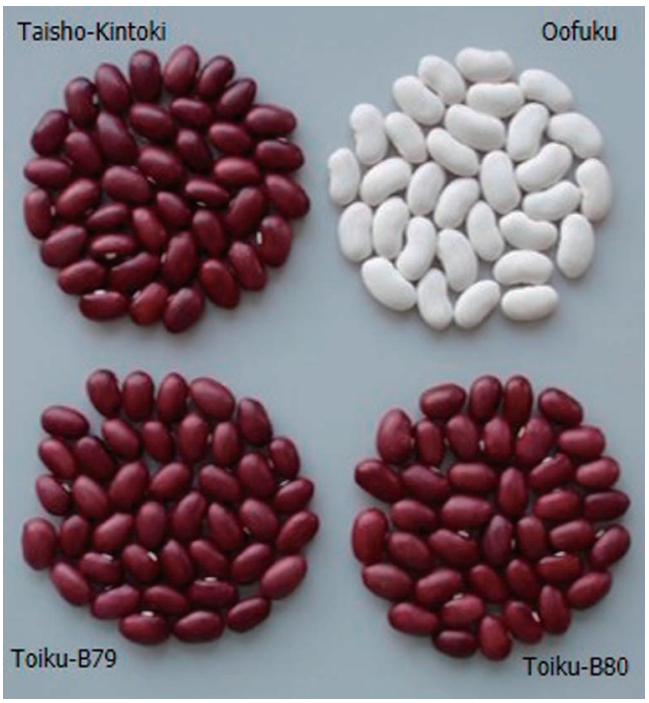

Fig. 1. Seed appearance of *Sdvy-1*-NILs 'Toiku-B79' and 'Toiku-B80' and their parents 'Taisho-Kintoki' (recurrent parent) and 'Oofuku' (*Sdvy-1* donor).

Discussion

As it was unclear which marker was the most closely linked to *Sdvy-1*, we used three markers to introduce *Sdvy-1* into 'Taisho-Kintoki'. The *Sdvy-1*-NILs with the 'Oofuku' genotype at DV86 had a wide range of seed coat colors, including black, tan, pale tan, purple, and mottled. 'Toiku-B79' and 'Toiku-B80', which were selected for their red-purple seed coat, possessed the 'Oofuku' genotype at DV386 and DV398 but not at DV86 (Table 2). Several molecular markers linked to genes controlling seed coat color and pattern have been mapped (Kyle and Dickson 1988, McClean *et al.* 2002). We speculate that one of those genes is closely linked to *Sdvy-1* and is located closer to DV86 than DV386 and DV398.

'Toiku-B79' and 'Toiku-B80' were similar to 'Taisho-Kintoki' in most of the agronomic traits, except a greater number of pods in 'Toiku-B79' and higher 100-seed weight in 'Toiku-B80', which may have greatly contributed to the higher yields than in 'Taisho-Kintoki' in Memuro, where the incidence of SbDV-YS was low (Table 4). 'Toiku-B80' had larger seeds, in agreement with its higher 100-seed weight (Table 5).

The inoculation test revealed that *Sdvy-1* is necessary and sufficient for SbDV-YS resistance (Table 3). Because infected plants suffer yield loss, the SbDV-YS resistance explains most of the significantly higher yields of the NILs than of 'Taisho-Kintoki' in Kunneppu, where the incidence of SbDV-YS was high (Table 4). These findings support our contention that the SCAR markers DV386 and DV398 are useful for breeding SbDV-YS-resistant common bean. Of the two, DV386 is particularly favorable because of its ability to distinguish heterozygous genotypes from homozygous resistant ones (Table 1).

The coat color of the raw *Sdvy-1*-NIL seeds had higher L* values than that of 'Taisho-Kintoki' (Table 6), but similar to that of 'Fukumasari', another elite 'Kintoki'-brand cultivar (data not shown). The boiled NIL seeds had significantly more seed coat cracking than 'Taisho-Kintoki' (Table 6). Because seed coat cracking greatly lowers the cooking quality, neither NIL was registered as a cultivar, despite their similarity to 'Taisho-Kintoki' in other aspects of seed appearance and eating quality. Further study is required to elucidate whether seed coat cracking is linked to *Sdvy-1*.

Rsdv1 is a major soybean gene controlling SbDV resistance derived from the Indonesian cultivar 'Wilis' (Tazawa *et al.* 2008, Uchibori *et al.* 2009, Yamashita *et al.* 2013). Although SbDV-YS does not infect common bean carrying *Sdvy-1*, it infects soybean carrying *Rsdv1* although the symptoms develop slowly and are mild (Tazawa *et al.* 2008). Despite this difference, *Rsdv1* shares common characteristics with *Sdvy-1*: both are major single loci conferring SbDV resistance and are not recessively inherited; i.e., plants carrying *Sdvy-1* or *Rsdv1* are fully or partially resistant to SbDV. We hypothesize that *Sdvy-1* and *Rsdv1* are

Table 6. Boiled bean quality of *Sdvy-1*-NILs

Cultivar	Seed coat color						Hardness (g)		Seed coat cracking (%)
	Raw			Boiled					
	L*	a*	b*	L*	a*	b*	Whole seed	Seed coat	
Toiku-B79	29.3*	19.2	4.6	49.0	9.3	9.9	3249.0	113.2	24.7**
Toiku-B80	29.6*	20.0	4.9	49.5	7.5	9.2	3155.0	99.5	27.7**
Taisho-Kintoki	28.1	19.4	5.0	49.5	8.4	9.5	3497.0	105.9	8.7

Asterisks indicate significant differences from 'Taisho-Kintoki' by Dunnett's test at *5%, **1%.

homologs and play similar roles in SbDV resistance. This hypothesis can be tested in further research using the genomic sequence database of both soybean and common bean (http://www.phytozome.net) and the results of synteny studies (McClean *et al.* 2010).

Genes controlling gene-for-gene resistance in plants encode proteins with distinct motifs such as nucleotide-binding sites (NBS) and leucine-rich repeats (LRR). In common bean, several disease resistance genes encode NBS-LRR motifs. Such genes include the *I* locus for resistance to *Bean common mosaic virus*, *Bean common mosaic necrosis virus* and several other viruses, and the *Co-2* locus for anthracnose resistance (Creusot *et al.* 1999, Vallejos *et al.* 2006). Further research is necessary to establish whether *Sdvy-1* is one of the more than 400 NBS resistance genes in the common bean genome (Garzón *et al.* 2013).

Acknowledgments

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