

Fine mapping of foxglove aphid (*Aulacorthum solani*) resistance gene *Raso1* in soybean and its effect on tolerance to *Soybean dwarf virus* transmitted by foxglove aphid

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Soybean dwarf virus (SbDV) causes serious dwarfing, yellowing and sterility in soybean (*Glycine max*). The soybean cv. Adams is tolerant to SbDV infection in the field and exhibits antibiosis to foxglove aphid (*Aulacorthum solani*), which transmits SbDV. This antibiosis (termed “aphid resistance”) is required for tolerance to SbDV in the field in segregated progenies of Adams. A major quantitative trait locus, *Raso1*, is reported for foxglove aphid resistance. Our objectives were to fine map *Raso1* and to reveal whether *Raso1* alone is sufficient to confer both aphid resistance and SbDV tolerance. We introduced *Raso1* into cv. Toyomusume by backcrossing and investigated the degree of aphid antibiosis to foxglove aphid and the degree of tolerance to SbDV in the field. All *Raso1*-introduced backcross lines showed aphid resistance. Interestingly, only one *Raso1*-introduced backcross line (TM-1386) showed tolerance to SbDV in the field. The results demonstrated *Raso1* alone is sufficient to confer aphid resistance but insufficient for SbDV tolerance. Tolerance to SbDV was indicated to require additional gene(s) to *Raso1*. Additionally, *Raso1* was mapped to a 63-kb interval on chromosome 3 of the Williams 82 sequence assembly (Glyma1). This interval includes a nucleotide-binding site–leucine-rich repeat encoding gene and two other genes in the Williams 82 soybean genome sequence.

Key Words: soybean, foxglove aphid, aphid resistance, *soybean dwarf virus*, NBS-LRR.

Introduction

Soybean dwarf virus (SbDV), a member of the *Luteoviridae*, is known to infect to soybean (*Glycine max*), red and white clovers (*Trifolium pratense* and *T. repens*) and other legume species (Tamada 1970). Infection of soybean by SbDV is widespread in northern Japan (Tamada 1975) and the United States (Thekkeveetil *et al.* 2007). In nature, SbDV is persistently transmitted by several aphid species (Gildow *et al.* 2000). In northern Japan, the foxglove aphid (*Aulacorthum solani*) transmits SbDV (Mikoshiha *et al.* 1995) from SbDV-infected red and white clovers to soybean during spring to summer. Infection by SbDV causes serious dwarfing, yellowing and sterility, and leads to significant yield losses in soybean production. To avoid damage induced by SbDV, soybean breeders have attempted to introduce SbDV resistant/tolerant germplasm. An old American culti-

var, ‘Adams’ (PI 548502), was found to show lower SbDV symptom incidence in the field. Adams suffers SbDV infection to a limited extent. However, the virus infection rate and symptom incidence are lower than other cultivars (Tanimura and Tamada 1976). In this paper, we termed this partial resistance to SbDV in the field “tolerance”. Interestingly, the number of foxglove aphids observed on Adams is lower than that on other cultivars in the field (Kanehira 1978). Moreover, young Adams plants exhibited antibiosis to the foxglove aphid in a no-choice test (Jinno *et al.* 1997). We termed this aphid antibiosis “aphid resistance”. Resistance to foxglove aphid was required for SbDV tolerance in the field when SbDV tolerance and aphid resistance were investigated in segregated progenies of Adams (Araki *et al.* 1997).

Aphid resistance is known among many plant species, including tomato (*Solanum lycopersicum*) (Rossi *et al.* 1998), wheat (*Triticum aestivum*) (Liu *et al.* 2005), barley (*Hordeum vulgare*) (Mittal *et al.* 2008), melon (*Cucumis melo*) (Brotman *et al.* 2002), barrel clover (*Medicago truncatula*) (Klingler *et al.* 2005), maize (*Zea mays*) (So *et al.* 2010) and soybean (Kim *et al.* 2010a, 2010b, Zhang *et al.*

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2010). Some aphid resistance genes have been cloned or fine mapped. In most cases, the resistance genes or the candidate of the resistance gene are a typical R-gene containing a leucine-rich repeat (Dogimont *et al.* 2010, Kim *et al.* 2010a, 2010b, Klingler *et al.* 2005, Milligan *et al.* 1998, Rossi *et al.* 1998, Smith and Boyko 2007). Thus aphid resistance in most plants seems to be controlled by the same mechanism as for other pest and disease resistance.

A previous report showed that aphid resistance in Adams is controlled by a quantitative trait locus (QTL) named *Raso1* (Kamiya *et al.* 2008), which has a relatively high contribution rate ($r^2 = 0.32$). Using 204 RILs, *Raso1* was detected on the 3.7 cM region between Satt009 and Satt530 on chromosome 3 with a lod score of 16.0. The QTL analysis showed *Raso1* was essential for aphid resistance, but it is not clear whether *Raso1* is solely responsible for the aphid resistance. Similarly, based on previous reports, *Raso1* was deduced to be required for the SbDV tolerance phenotype of Adams, but it is not clear whether *Raso1* alone is sufficient to confer SbDV tolerance. In this study, we fine-mapped *Raso1* and investigated whether *Raso1* alone is sufficient to confer both aphid resistance and SbDV tolerance phenotype in Adams.

Materials and Methods

Plant material

Soybean cv. Adams (PI 548502) shows both foxglove aphid resistance and SbDV tolerance in the field (Jinno *et al.* 1997, Kanehira *et al.* 1978, Tanimura and Tamada 1976). Shokukei-10 is a breeding line which shows both foxglove aphid resistance and SbDV tolerance in the field (Fig. 1). Shokukei-10 was derived by crossing Adams with Mechita, a Russian cultivar (Fig. 1A). We introduced the aphid resistance QTL *Raso1* by backcrossing to Toyomusume, which is a commercial cultivar in northern Japan. Four backcrosses were performed using Toyomusume as the recurrent parent and Shokukei-10 as the donor of *Raso1*. A total of 9 backcross lines were developed from 9 BC₄F₁ plants. The Toyomusume backcrossed lines (TM-lines) were named TM-1382, TM-1386, TM-1387, TM-1388, TM-1394, TM-1397, TM-1402, TM-1404 and TM-1409. The simple sequence repeats (SSR) markers Satt152, Satt009 and Satt530 were used to introduce *Raso1* based on a previous report (Kamiya *et al.* 2008). Primer sequences and positions of SSR markers on the genome sequences are described in SoyBase (www.soybase.org). We started the backcrossing by crossing Toyomusume to F₁ plants generated from a cross between Shokukei-10 and Toyomusume. Then, Toyomusume was crossed to a population consisting of a mixture of 4 independent BC₁F₁ plants. To generate BC₃F₁ and BC₄F₁ plants, 12 randomly selected individual BC₂F₁ and BC₄F₁ plants were used. Thus, the final 9 BC₄ lines were partially independent. We used mapping populations C1905 and C1950, which were originally made for a breeding program and therefore have complex pedigrees. The

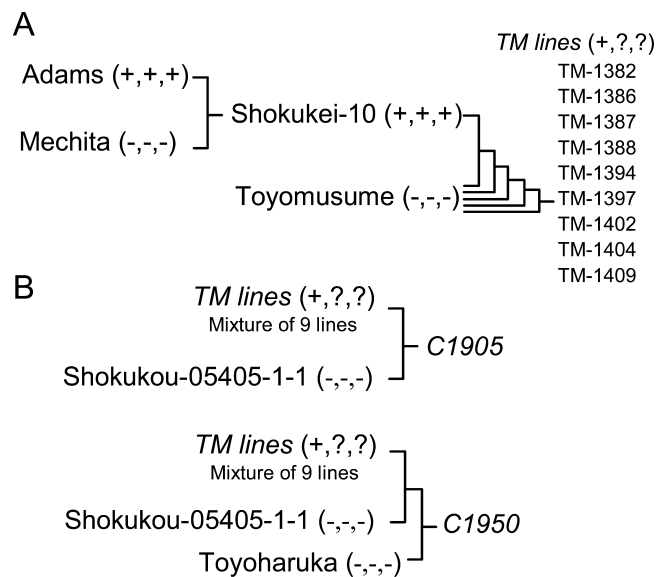


Fig. 1. Schematic representation of development of experimental lines. The plus (+) or minus (-) signs in parentheses represent the presence or absence of QTL *Raso1*, aphid resistance, and SbDV tolerance, respectively, derived from Adams. Question marks represent “determined in this paper”. (A) TM-lines are Toyomusume-backcrossed lines with the putative aphid resistance QTL *Raso1*. (B) C1905 and C1950 are mapping populations. C1905 and C1950 were originally made for a breeding program, but we used them for fine mapping. C1950 was derived from a 3-way crossing of F₁ plants of C1905 and Toyoharuka.

population C1905 was derived by crossing the population derived from mixing the 9 TM-lines described above in the F₄ generation to an experimental line, Shokukou-05405-1-1 (Fig. 1B). Shokukou-05405-1-1 is a breeding line derived from backcrossing Tyokomachi, a cultivar in northern Japan, to an Indonesian cultivar, Wilis. The mapping population C1950 was generated by crossing F₁ plants of C1905 and Toyoharuka, a cultivar in northern Japan. Crossing Toyoharuka was for breeding purposes and not essential for mapping. Shokukou-05405-1-1 and Toyoharuka do not exhibit aphid resistance.

Evaluation of aphid resistance

For nine TM-lines (TM-1382, TM-1386, TM-1387, TM-1388, TM-1394, TM-1397, TM-1402, TM-1404 and TM-1409), a no-choice test was performed according to a previous report (Jinno *et al.* 1997) to determine the degree of aphid antibiosis. Foxglove aphids (*Acyrtosiphon solani*) were collected at Naganuma, Japan (43.017°N, 141.695°E), and were maintained on fresh leaves of the aphid-susceptible soybean cultivar Chusei-hikarikuro. Three soybean seeds were sown in unglazed pots (height 12 cm; diameter 10 cm) filled with potting soil. Seedlings were thinned to one per pot to synchronize the plant growth stage. A single seven-day-old aphid was settled per plant when the first true leaf was 3–5 mm long (cotyledons were not completely opened). After settlement, plants were grown in a plant incubator

Table 1. Primer sequences and location of markers on chromosome 3 of the Williams 82 soybean genome sequence assembly (Glyma1)

Marker Name	Location ^a	Forward primer	Reverse primer
Gm03-01	4,811,664	AACCGTCGCTTAATCGTGATA	CCCTGAAAGCATAAAAAAGTGG
Gm03-03	5,448,257	CATAAACTTTGGTCATGCTTAACTG	ACCTTGACCAAACATTCTTGA
Gm03-06	4,683,586	CTTGTATATATTACATTAATAATTGGAG	TGATGAAGAGTGACTACAGTTGAG
Gm03-07	4,697,806	AAAAACCTTGATTTGTTCTTCA	CAAAGGTTGTTACAGAAATTCAA
Gm03-09	4,613,933	CCATTCTAAGATGATTATTTACCTG	GACGCATGAAGACGATTTT
Gm03-10	4,637,354	CGGACAACCAAATCTCAAT	GAAAGCATGGAATAAACGAA
Gm03-11	4,661,084	GTGGCCACATGAAAATACAG	TCCTGGTGGACTTGCTAATA
Gm03-12	4,724,159	AAAAAGGCTAAAAAGTATATTTCTGT	TGATACCATGATGTTTATATTTTT

^a Nucleotide numbers from the end of chromosome to the forward primer.

maintained at 15°C with a 16 h/8 h (light/dark) photoperiod. Each plant was covered with a mesh cage. The number of aphids on each plant was counted 14 days after settlement. The same procedure was adopted for fine mapping of *Rasol*.

Evaluation of *SbDV* tolerance in the field

To evaluate *SbDV* tolerance, we selected 3 TM-lines (TM-1394, TM-1382 and TM-1386) that differ in degree of aphid antibiosis. Field evaluations of *SbDV* tolerance were performed in Date City, Japan (42.505°N, 140.889°E), a region with a severe *SbDV* endemic infection. There are two virus strains *SbDV*-D and *SbDV*-Y, which cause yellowing and dwarfing symptoms in soybean (Tamada 1973). Both strains are observed in Date. In this region, no viral disease except *SbDV* was observed in soybean, and thus the dwarfing or yellowing symptoms were likely caused by *SbDV*. Soybean lines were sown on 13 May 2008 and 8 May 2009. Soybean fields were managed according to the local custom except that pesticide applications for control of aphids were omitted. Endemic *SbDV* symptoms on soybean were first observed about 50 days after sowing. Soybean plants with dwarfing or yellowing symptoms were counted and the incidence rate against the total number of the tested plants was calculated as “virus symptom incidence”. Four replications of each line were grown and each 1.32 m² plot contained 22 plants. Virus symptom severity was scored according to a previous report (Mikoshiha *et al.* 1990) on 3 November 2009, 113 days after sowing.

Mapping and marker assay

From the mapping populations described above, a total of 669 F₂ plants for C1905 and 576 F₂ plants for C1950 were screened with the SSR markers Satt009 and Satt530, which flank the QTL *Rasol* (Kamiya *et al.* 2008). We selected 59 plants for C1905 and 34 plants for C1950 in which a recombination event between the markers was confirmed. The harvested plants were used to produce the next generation in a greenhouse and one homozygous plant per recombination event was selected and grown to produce seed. For further genotyping between Satt009 and Satt530, SSR were identified from the Williams 82 soybean genome sequence Glyma01 (Schmutz *et al.* 2010) and primers were designed. After PCR amplification, the SSRs that showed

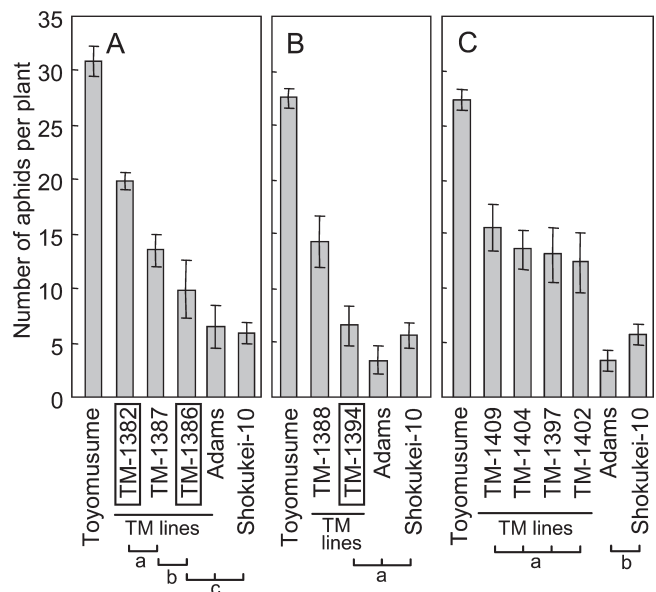


Fig. 2. Aphid resistance phenotype of *Rasol*-introduced Toyomusume-backcrossed lines (represented by TM lines). (A), (B) and (C) show the results of three independent experiments. Shokukei-10 is an Adams-derived breeding line that shows both foxglove aphid-resistant and *SbDV*-tolerant phenotypes. Vertical axis indicates the number of aphids per plant 14 days after settlement in a no-choice test. TM lines highlighted in a box were evaluated for their virus tolerance phenotype (see Figs. 2, 3). Vertical bars indicate the standard error of the means ($n=8$). Static comparisons were carried out independently for each experiment. Grouping by the square brackets below the line names indicates there was no significant difference within the group at the 5% level using the Tukey-Kramer multiple comparison test.

polymorphism between Adams and Shokukou-05405-1-1 or Toyoharuka, the parents of the mapping populations, were used as SSR markers. The position of the SSR markers on chromosome 3 and the sequences of the primers are shown in Table 1. The genotype of Satt641 and the newly developed SSR markers were assessed for 42 selected lines from 93 plants in which the recombination event was confirmed. For genotype data, 15 informative lines were used to evaluate the degree of aphid antibiosis. For screening of the mapping population, DNA extraction and SSR marker assay were performed as described previously (Sayama *et al.*

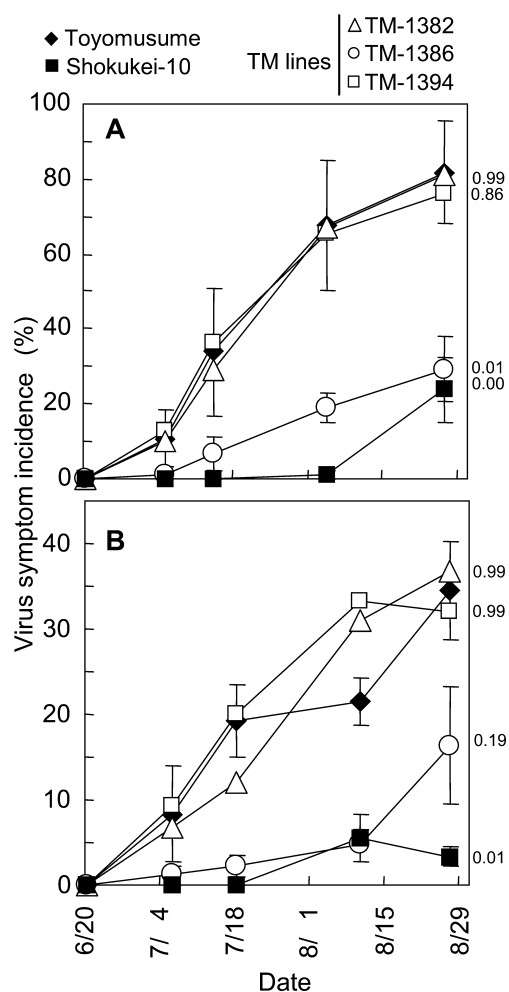


Fig. 3. SbDV tolerance phenotype of Toyomusume-backcrossed (TM) lines in the field. Virus symptom incidence in 2008 (A) and 2009 (B) are shown. Dwarfing or yellowing symptoms induced by SbDV were examined in the field. The X-axis represents the assessment date. Vertical bars indicate the standard error of the means ($n=4$). The standard errors for TM-1382 and TM-1394 are of the same level as Toyomusume and its display are omitted. The p-values by Dunnett's test are indicated on the right side of each panel. Dunnett's test was performed for the final observations in each year using Toyomusume as the reference.

2011). To obtain the sequence and gene annotation data of Williams 82, Phytozome v7.0 was used (Schmutz *et al.* 2010).

Results

Aphid resistance of *Ras1*-introduced backcross lines

Adams and its derivatives demonstrated antibiosis to foxglove. We used the term "aphid resistance" for this antibiosis. The foxglove aphid resistance QTL, *Ras1*, localized to a 3.7 cM interval between Satt009 and Satt530 (Kamiya *et al.* 2008), was introduced into Toyomusume by backcrossing (Fig. 1). In all TM-lines tested, the number of aphids per plant was significantly lower than that observed on

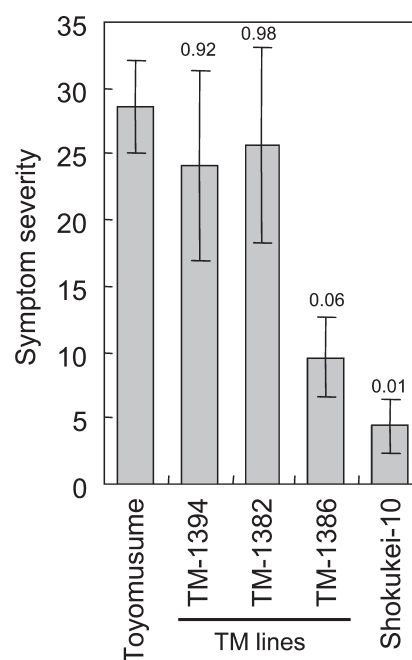


Fig. 4. Virus symptom severity of Toyomusume-backcrossed (TM) lines 118 days after sowing in 2009. Dwarfing or yellowing symptoms induced by SbDV in the field were assessed using the scoring system of Mikoshiba *et al.* (1990). Each plant was scored on a scale between 0 (no symptom) and 4 (severe symptoms) with increments of 1. The symptom severity was calculated by $[100(\text{Sum of the score of plant}/4(\text{total number of plant}))]$. Vertical bars indicate the standard error of the means ($n=4$). The p-values by Dunnett's test using Toyomusume as the reference are indicated at the top of the bars.

Toyomusume 14 days after aphid settlement (Fig. 2). However, the degree of aphid antibiosis varied among lines. TM-1386 and TM-1394 exhibited a similar number of aphids per plant as compared to Adams and Shokukei-10, from which the aphid resistance originated, whereas the other TM-lines exhibited a higher number of aphids than Adams did (Fig. 2). However, we concluded that the aphid-resistance QTL *Ras1* solely confers the aphid resistance phenotype when it is introduced by backcrossing.

SbDV tolerance of *Ras1*-introduced backcross lines

Adams and its derivatives demonstrated lower incidences of SbDV symptoms in the field. We used the term "SbDV tolerance" for this partial resistance in the field. The SbDV tolerance of 3 independent backcross lines differing in aphid resistance phenotype (TM-1382, TM-1386 and TM-1394, highlighted in boxes in Fig. 2) was tested. Only TM-1386 demonstrated virus tolerance equal to that of Shokukei-10, and TM-1382 and TM-1394 exhibited similar levels of virus symptom incidence as Toyomusume, the recurrent parent of both lines. Similar results were obtained in consecutive years (Fig. 3A, 3B) and when tolerance was evaluated as severity of virus symptoms (Fig. 4).

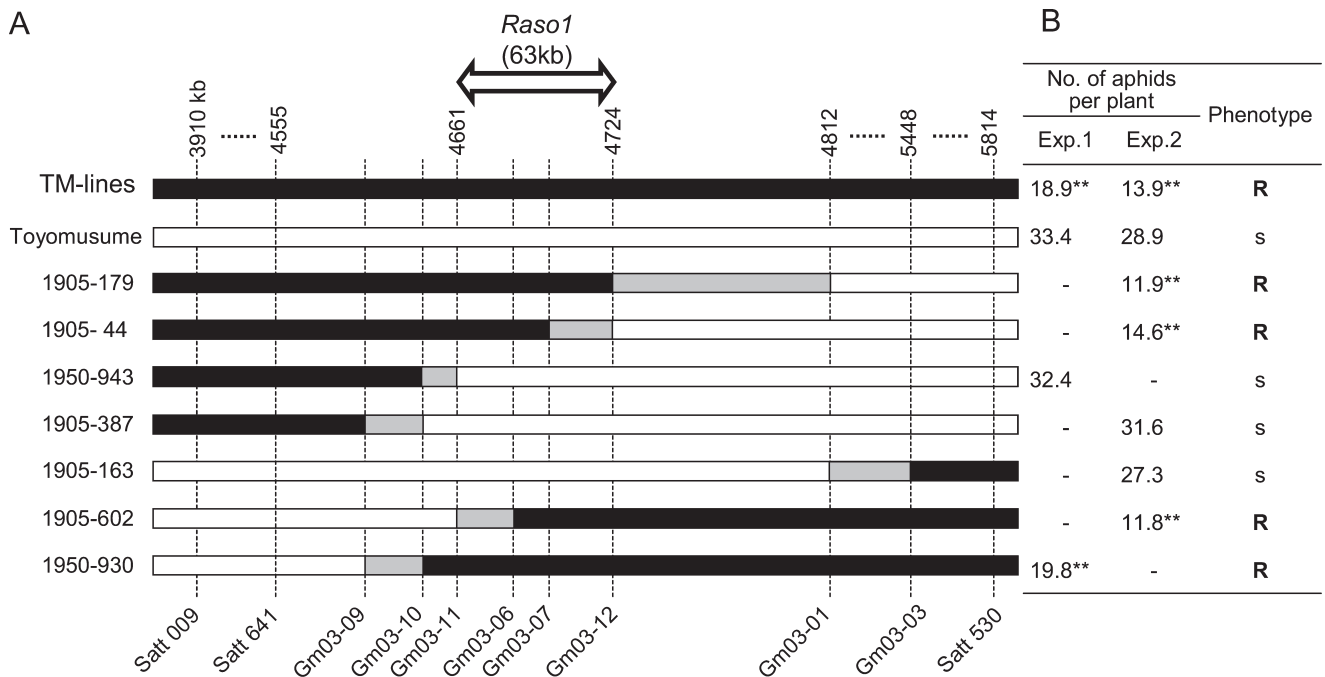


Fig. 5. Fine mapping of *Raso1* to a 63-kb interval of chromosome 3. (A) Summary of the informative seven lines used to fine-map the location of *Raso1*. Line names beginning with 1905 and 1950 indicate their derivation from the mapping populations C1905 and C1950, respectively. TM-lines represent Toyomusume-backcrossed lines. Solid bars represent the genomic region derived from Adams, the source of aphid resistance. Open bars indicate the genomic region derived from Toyomusume or Toyoharuka or Shokukou-05405-1-1, the parent of the populations. Gray bars indicate intervals in which recombination events might occur. The scale at the top shows positions in the soybean genome sequence assembly (Glyma1) on chromosome 3. Intervals marked with horizontal dotted lines are greatly reduced in scale. Markers used for mapping (shown at the bottom) are described in Table 1. (B) Phenotype data of lines used for fine-mapping. The data represent the number of aphids per plant 14 days after settlement. For TM-lines, the results of bulked Toyomusume-backcrossed lines are shown. Jugged phenotype by aphid numbers are drawn at the rightmost column. Susceptible and resistant phenotype are abbreviate to 's' and 'R' respectively. Significant differences from Toyomusume obtained with Dunnett's test at the 1% level are indicated by **.

Fine mapping of *Raso1*

Because *Raso1* solely showed the aphid resistance, fine-mapping of *Raso1* was undertaken. A total of 1245 F₂ lines were screened for recombination events between the markers Satt009 and Satt530. Recombination events were confirmed in 93 lines, from which 42 lines were selected. The marker genotype for Satt641 and additional SSR markers located between Satt009 and Satt530 (Table 1) were determined for the 42 lines. For genotyping, Satt641 and additional SSR markers listed in Table 1 were used. Fifteen informative lines were selected and the degree of aphid antibiosis was investigated. The results for the seven most-informative lines is presented in Fig. 5. *Raso1* was located between markers Gm03-11 and Gm03-12, comprising a 63 kb interval in the Williams 82 genome sequence. This interval contains three predicted genes in the Williams 82 genome sequence, namely Glyma03g04500 (TATA-box binding protein), Glyma03g04510 (calcium/calmodulin-dependent protein kinase-related) and Glyma03g04530 (NB-ARC domain and leucine-rich repeat-containing protein, a member of the nucleotide-binding site-leucine-rich repeat [NBS-LRR] gene family) based on Phytozome v7.0.

Discussion

We introduced the aphid resistance QTL *Raso1* into a Toyomusume background by backcrossing. All *Raso1*-introduced lines showed the aphid resistance (Fig. 2). Hence we conclude *Raso1* represents a resistance gene(s) effective against foxglove aphid. However, most backcross lines showed a lower degree of aphid antibiosis compared with the donor of *Raso1*, Shokukei-10, or Adams. While we observed less than 7 aphids per plant 14 days after settlement in Shokukei-10 and Adams, we observed more than 13 aphids in most TM-lines (Fig. 2). These observations imply the presence of additional minor gene(s) that modify the degree of aphid antibiosis in Adams.

In contrast to aphid resistance, introduction of *Raso1* by backcrossing was insufficient to exhibit the SbDV tolerance phenotype. Two backcross lines (TM-1382 and TM-1394) showed virus symptom incidence similar to that of the recurrent parent Toyomusume, even though they harbor *Raso1* (Fig. 3). Interestingly, only one line (TM-1386) exhibited a SbDV-tolerant phenotype (Fig. 3). Araki *et al.* (1997) reported that resistance to foxglove aphids was necessary for SbDV tolerance in segregated progenies of Adams. Our observations, together with those of Araki *et al.* (1997), suggest

that an additional gene(s) is required for SbDV tolerance. Nevertheless, because the SbDV-tolerant line TM-1386 showed similar agricultural traits as the recurrent parent Toyomusume, it is useful for breeding programs in northern Japan.

Rasol was fine-mapped to a 63-kb fragment containing three gene candidates in the Williams 82 sequence assembly (Glyma1). One of the three gene candidates is a NB-ARC domain and leucine-rich repeat-containing gene (NBS-LRR), a typical type of so-called R-gene. In this study only sequence data for the soybean Williams 82 was utilized. The corresponding genomic sequence in Adams is unknown, hence we cannot discuss further. However, this NBS-LRR gene is a most likely candidate of *Rasol* because the previously cloned aphid resistance genes *Mi* (Milligan *et al.* 1998, Rossi *et al.* 1998) and *Vat* (Dogimont *et al.* 2010), and candidates of the aphid resistance genes *AKR* (Klingler *et al.* 2005), *Rag1* (Kim *et al.* 2010a) and *Rag2* (Kim *et al.* 2010b), are members of the NBS-LRR gene family.

In soybean, three resistance genes for soybean aphid (*Aphis glycines*) are reported, namely *Rag1* on chromosome 7 (Kim *et al.* 2010a), *Rag2* (Kim *et al.* 2010b) and *Rag3* (Zahng *et al.* 2010) on chromosome 13. We mapped *Rasol* on chromosome 3, therefore *Rasol* represents a gene independent from *Rag1*, *Rag2* and *Rag3*. Moreover, previous reports demonstrate Adams does not show resistance to soybean aphid (Honda 1999), for which *Rag1*, *Rag2* and *Rag3* show resistance. Interestingly, candidates of *Rag1* and *Rag2* are NBS-LRR genes, the same type of gene as one of the candidates of *Rasol*. Thus soybean might evolve novel NBS-LRR genes for resistance to different aphid species. Comparisons among *Rasol*, *Rag1* and *Rag2* will help to improve our understanding of aphid resistance effected by the NBS-LRR gene family.

In the case of Adams, aphid resistance and tolerance to the virus transmitted by the aphid are closely related. A similar case was reported in melon with melon-cotton aphid (*Aphis gossypii*) and *Cucumber mosaic virus* (CMV) (Boissot *et al.* 2010, Pitrat *et al.* 1980, Sarria *et al.* 2008). In this case, the causal gene *Vat*, which shows both aphid resistance and the resistance to aphid transmission of CMV, was cloned and demonstrated to be a member of the NBS-LRR gene family (Dogimont *et al.* 2010). It is interesting to determine whether the aphid resistance manifested by NBS-LRR proteins will basically beside the resistance to virus transmission by the aphid or not.

Acknowledgments

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