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ORIGINAL PAPER

# Detection of novel QTLs for foxglove aphid resistance in soybean

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**Abstract**

***Key message*** **The *Raso2*, novel QTL for Korea biotype foxglove aphid resistance in soybean from PI 366121 was identified on chromosome 7 using GoldenGate SNP microarray.**

*Abstract* Foxglove aphid, *Aulacorthum solani* (Kaltenbach), is a hemipteran insect that infects a wide variety of plants worldwide and causes serious yield losses in crops. The objective of this study was to identify the putative QTL for foxglove aphid resistance in wild soybean, PI 366121, (*Glycine soja* Sieb. and Zucc.). One hundred and forty-one $F_4$-derived $F_8$ recombinant inbred lines developed from a cross of susceptible Williams 82 and PI 366121 were used. The phenotyping of antibiosis and antixenosis resistance was done through choice and no-choice tests with total plant damage and primary infestation leaf damage; a genome-wide molecular linkage map was constructed with 504 single-nucleotide polymorphism markers utilizing a GoldenGate assay. Using inclusive composite interval mapping analysis for foxglove aphid resistance, one major candidate QTL on chromosome 7 and three minor QTL regions on chromosomes 3, 6 and 18 were identified. The major QTL on chromosome 7 showed both antixenosis and antibiosis resistance responses. However, the minor QTLs showed only antixenosis resistance response. The major QTL mapped to a different chromosome than the previously identified foxglove aphid resistance QTL, *Raso1*, from the cultivar Adams. Also, the responses to the Korea biotype foxglove aphid were different for *Raso1,* and the gene from PI 366121 against the Korea biotype foxglove aphid was different. Thus, the foxglove aphid resistance gene from PI 366121 was determined to be an independent gene from *Raso1* and was designated as *Raso2*. This result could be useful in breeding for new foxglove aphid-resistant soybean cultivars.

**Abbreviations**

| | |
|---|---|
| QTL | Quantitative trait loci |
| SNP | Single-nucleotide polymorphism |
| TPD | Total plant damage |
| PLD | Primary infestation leaf damage |
| RILs | Recombinant inbred lines |
| DAI | Days after infestation |

## Introduction

Soybean [*Glycine max* (L.) Merr.] is one of the major seed crops in the world with a wide range of its utilities, such as protein and oil sources for humans, feeds for livestock, and biofuels (Masuda and Goldsmith 2009). Even though soybean production has been dramatically increased in the last 20 years, about 19 % of actual yield losses were caused by animal pests, pathogens, and viruses (Oerke 2006). To avoid these significant yield losses, developing insect

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resistance soybean varieties is one of the most economic and promising strategies.

There are two types of resistance, antixenosis and antibiosis. Antixenosis is non-preference of insect pests for a host plant and refers to a host effect on insect behavior (Kogan and Ortman 1978). The choice test has been used to identify antixenosis without restriction of translocation of movements of insects among host plants to evaluate the preference. Antibiosis is defined by the way in which host plants have various adverse effects including biology, life cycle and abundance of the insects, if these are used for food of insects and refer to a host effect to insect physiological characteristic (Painter 1951). The no-choice test has been used to confirm the antibiosis effect by isolating each plant, and an individual plant was infested by insects. Their growth rate and change of life cycle was investigated (Mensah et al. 2005).

The major pests have drastically changed from foliage-feeding Lepidopteran and Coleopteran pests to sap-sucking hemipteran pests during the last few decades because of global warming and increasing temperature (Bansal et al. 2013; Hullé et al. 2010). The soybean aphids (*Aphis glycines* Matsumura), typical hemipteran pests, are significantly important economic pests which cause up to 58 % yield losses, or about $2.4 billion per year, in soybean in North America (Song et al. 2006; Tilmon et al. 2011; Wang et al. 1994). They feed on the underside of leaves; the aphids' withdrawal of sap from soybean leaves leads to loss of photosynthates and the possibility of transmitting the *soybean mosaic virus* (Ragsdale et al. 2011).

Currently, five soybean aphid resistance genes have been identified. A single dominant gene, *Rag1,* in soybean aphid-resistant cultivars, 'Dowling' and 'Jackson', was mapped to chromosome 7 (Kim et al. 2010b; Li et al. 2007). Another single dominant gene, *Rag2*, in plant introduction (PI) 200538 was fine mapped to a 54 kb region on chromosome 13 (Kim et al. 2010b). Similarly, a major antixenosis resistance gene, *Rag3* from PI 567543C, was mapped on chromosome 16 (Zhang et al. 2010). *Rag4* was isolated from PI 567541B and mapped on chromosome 13 (Zhang et al. 2009). A major QTL, *Rag5,* in PI 567301B was mapped on chromosome 13 (Jun et al. 2012). Interestingly, each gene showed a different contribution to soybean aphid resistance depending on three known biotypes, Illinois (biotype 1), Ohio (biotype 2), and Indiana (biotype 3) in North America (Kim et al. 2008).

The foxglove aphid (*Aulacorthum solani* Kaltenbach), one of the major hemipteran pests, has a wide range of host plants—95 different plants species from 25 families—and it causes significant damage to various crops in Europe and North America and recently worldwide (Jandricic et al. 2010). In soybean, it causes significant yield losses throughout the world, for example up to 90 % yield reduction in Japan (Nagano et al. 2001). In spite of its economic importance, research about foxglove aphid has been very limited compared to soybean aphid in terms of biology, ecology, and effective control methods. Previous reports suggested that foxglove aphid prefers fresh tissues; however, recent research indicated that mature leaves are preferred over growing tips or young leaves (Jandricic et al. 2014). *Raso1*, a foxglove aphid resistance QTL, was isolated from the cultivar 'Adams' (Weiss 1953) and mapped on chromosome 3 (Ohnishi et al. 2012). Sato et al. demonstrated that Tohoku 149 showed foxglove aphid resistance (Sato et al. 2013, 2014). They suggested that foxglove aphid resistance from Tohoku 149 was related to sulfur metabolism and methylation, since two methylated metabolites, S-methylmethionine and trigonelline, were not detected in foxglove aphid on Tohoku 149.

We discovered that wild soybean (*Glycine soja*) PI 366121 possessed foxglove aphid resistance. The objectives of this study were to position QTLs controlling foxglove aphid resistance from PI 366121 and develop single-nucleotide polymorphism (SNP) markers tightly linked to the genes.

## Materials and methods

### Plant materials

A population of 141 $F_{4:8}$ recombinant inbred lines (RILs) was developed from a cross between the susceptible cultivar 'Williams 82' (Bernard and Cremeens 1988) and PI 366121 (resistant) through the single seed descent method up to $F_4$ (Lenis 2011). These RILs and the two parental lines were used for this study. PI 366121 was originally collected from Fukushima, Japan, and it was highly susceptible to bean pod mottle virus infection (Zheng et al. 2005). Williams 82 was known as susceptible to foxglove aphid, and also recently, the whole genome sequence was published (Schmutz et al. 2010).

### Foxglove aphid

The foxglove aphids were collected at Suwon, Korea, in 2008, and reared continuously on soybean (*var.* Sowon) in the Crop Environment Research Division of National Institute of Crop Science, Korea. They were grown with isolated insect cages in growth chambers maintained at temperatures between 23 and 25 °C with 15 h of daily light and 60–80 % relative humidity with susceptible soybean (*var.* Sowon).

### Foxglove aphid resistance evaluation

Both the choice and no-choice tests were conducted in growth chambers maintained at temperatures between

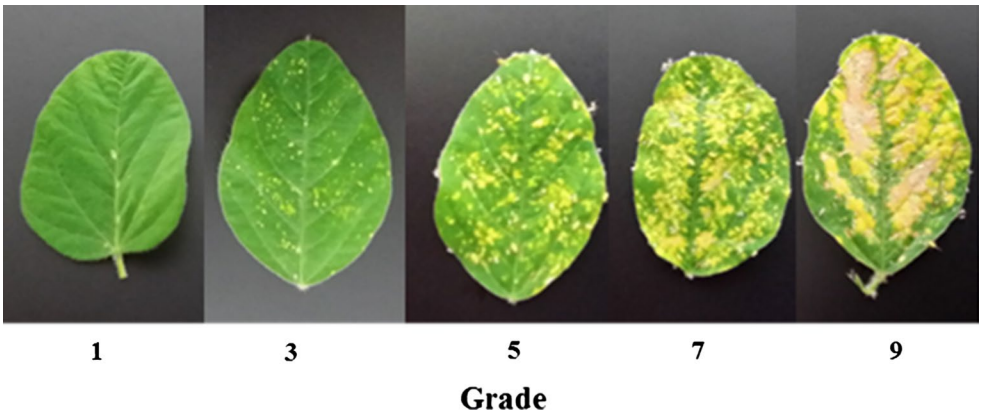


**Fig. 1** Damaged leaves and their damage grade. The *Leaf color* changes at 14 days after foxglove aphid infestation. According to area of changed *color* on the leaf, damage was graded from 1 to 9 (color figure online)

23 and 25 °C with 15 h of daily light and 60–80 % relative humidity with three biological replications. For the choice test, RILs were planted in 10 × 5 trays (550 L × 270 W × 120 H mm) with Sowon in the center column. For the non-choice test, RILs were planted in the same tray with an empty center column and covered with a 120-mesh cage to restrict movements of aphids among RILs. All of the trays included the parents, Williams 82 and PI 366121, as a control to evaluate the degree of resistance and infection damage. When soybean plants reached the V1 stage, four adult foxglove aphids were introduced on the upper side of the leaves of each plant using a paint brush. After 14 days (DAI-14) of infestation, total plant damage (TPD) and primary infestation leaf damage (PLD) were graded by assigning scores between 1 and 9, where 1 = no damage and 9 = severely damaged (Fig. 1). In soybean aphid research, the number of aphids per plant has been used to index plant damage grade (Xiao et al. 2013). However, for foxglove aphid, the number of foxglove aphids was not highly correlated with the total plant damage grade (Jandricic et al. 2014). Thus, these two damage grades, TPD and PLD, were used for further analysis.

To conduct the no-choice test, a small mesh cage was used; this condition restricts the plant growth, and plants in the no-choice test could not be scored at 14 days after infestation. However, the resistance degree evaluation at DAI-7 discriminated susceptible and resistance to foxglove aphid in the no-choice test.

### DNA extraction and GoldenGate assay

The non-expanded young trifoliate leaves from individual plants were harvested for the genomic DNA isolation. The genomic DNA was extracted with the modified CTAB (hexadecyltrimethylammonium bromide) method as previously described (Lenis 2011). For the construction of genetic map, 141 RILs and two parental lines were genotyped with 504 SNP markers using the GoldenGate assay, which contain well-distributed 1,536 SNP loci through 20 soybean chromosomes (Hyten et al. 2010). The selected 504 polymorphic SNP markers were evenly distributed to the whole soybean genome with about 25 markers per each chromosome.

### *Construction of genetic linkage map and QTL identification*

A linkage map was constructed using QTL IciMapping (version 4.0) according to the manufacturer's instructions with adjusted parameters; grouping by 3.0 of logarithm of odds (LOD) threshold, ordering algorithm by nnTwoOpt, which nearest neighbor was used for tour construction, and two-opt was used for tour improvement, and rippling by sum of adjacent recombination fractions (Li et al. 2008). QTL identification was conducted using inclusive composite interval mapping (ICIM) method with parameters: 1.0 cM of step and 3.0 of LOD threshold.

## Results

### Phenotypic traits evaluation

The plant resistance responses to foxglove aphid of the 141 $F_4$-derived $F_8$ RILs and its parents, Williams 82 and PI 366121, are summarized in Table 1. To evaluate the antixenosis and antibiosis, choice and no-choice tests were conducted in the growth chamber using the RIL population and parents. The susceptible parent, Williams 82, was severely damaged by foxglove aphid, while the resistant parent, PI 366121, was not (Table 1). In the choice test, PLD of Williams 82 was scored to 8.1 and the TPD score was 6.0. However, both the TPD and PLD of PI 3661321 were scored to 1. The average PLD of RILs was 5.2, and TPD was 3.8. Damage score range was 1–9. In the no-choice test, PLD and TPD were graded at only DAI-7, since the isolated mesh cage inhibited optimal plant growth, and evaluation at 7 days after infestation was sufficient to discriminate

the resistant and susceptible responses to foxglove aphid. The PLD and TPD grade of Williams 82 were 5.8 and 5.6, respectively. PI 366121 showed no significant damage by foxglove aphid. RILs showed similar responses to foxglove aphid in the no-choice test. Transgressive segregants, which had higher damage scores than Williams 82, were observed.

A distribution of observed traits from choice and no-choice tests is shown in Fig. 2. In the choice test, the PLD has a bimodal shape that ranged from 1 to 9, instead of a normal distribution (Fig. 2a). The bimodal distribution indicates that the foxglove aphid resistance in PI 366121 is achieved by a limited number of major gene(s). In the no-choice test for antibiosis resistance in PI 366121, both PLD and TPD were graded at DAI-7 and frequency was evenly distributed from 1 to 9 (Fig. 2c, d). A total of 18 RILs showed grade 1 of PLD score, and 28, 33, and 11 RILs for grade 3, 5, and 9, respectively. The frequency distribution of TPD is similar to PLD. The phenotypic evaluation results indicated that both parents, PI 366121 and Williams 82, showed clear resistant and susceptible responses to foxglove aphid infestation, respectively; RILs from the cross between PI 366121 and Williams 82 showed appropriate frequency distribution for QTL analysis.

**Table 1** Primary infestation leaf damage grade (PLD) and total plant damage grade (TPD) of the $F_4$-derived $F_8$ mapping population and its parental lines, Williams 82 and PI 366121

| Trait | | Parents | | $F_{4:8}$ RILs | |
|---|---|---|---|---|---|
| | | PI 366121 | Williams 82 | Mean | Range |
| Choice test | PLD | 1 ± 0.0 | 8.1 ± 1.5 | 5.2 | 1–9 |
| | TPD | 1 ± 0.0 | 6.0 ± 0.9 | 3.8 | 1–9 |
| No-choice test | PLD | 1 ± 0.0 | 5.8 ± 1.2 | 3.9 | 1–9 |
| | TPD | 1 ± 0.0 | 5.6 ± 1.3 | 3.5 | 1–9 |

## QTL analysis

The QTL mapping with ICIM method was done using PLD and TPD phenotyping data from the choice and no-choice tests and genotyping data from GoldenGate assay (Lenis 2011). Five hundred and four SNP markers, which showed polymorphisms throughout the entire genome, were located with an average of 20-cM interval on each chromosome.

The QTL analysis for foxglove aphid resistance using PLD and TPD as phenotypic traits is summarized in

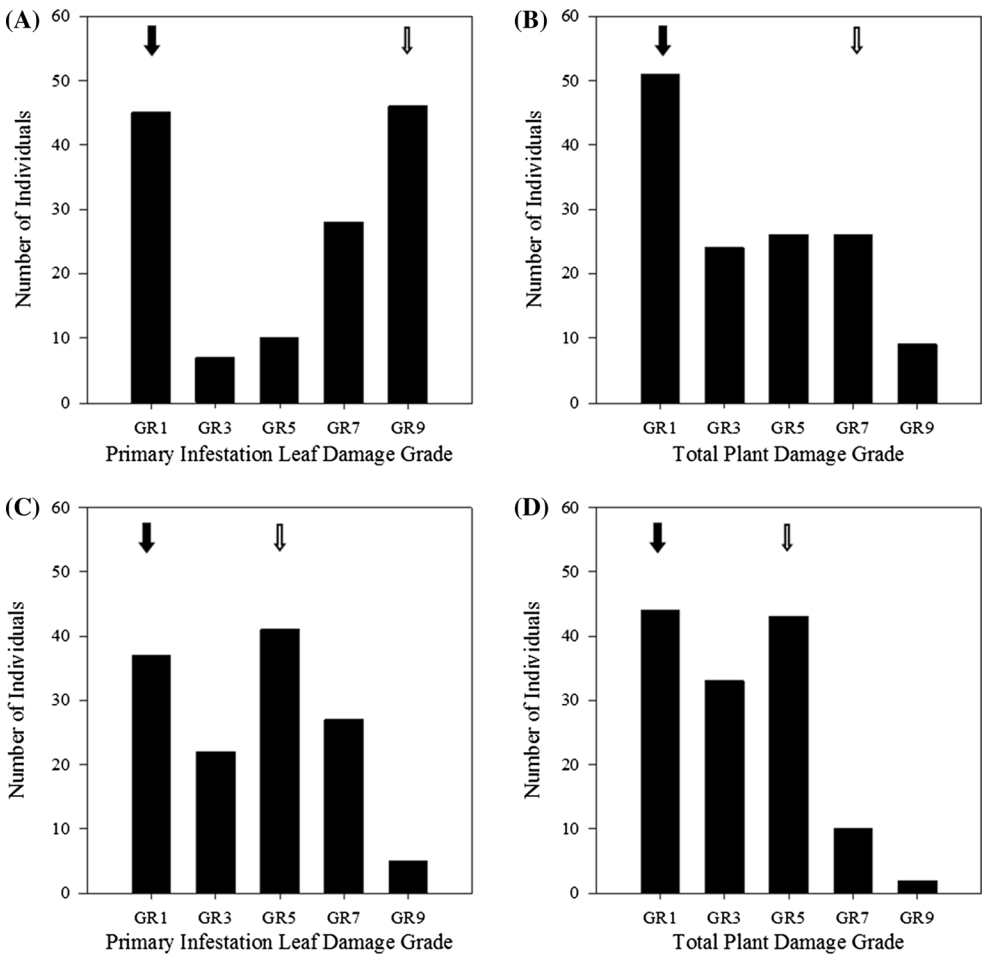


**Fig. 2** Phenotype frequency distribution in the mapping population. The distribution of primary infestation leaf damage grade and total plant damage grade in choice test (*top panel*) and no-choice test (*bottom panel*) are presented, where GR1 = no damage and GR9 = severely damaged. The location of both parents, Williams 82 (*open arrow*) and PI 366121 (*closed arrow*) were marked with *arrows*

**Table 2** Significant QTLs of foxglove aphid resistance with $F_4$-derived $F_8$ mapping population from a cross between Williams 82 and PI 366121, using inclusive composite interval mapping

| Traits | Chromosome | Position (cM) | Left marker | Right marker | LOD[c] | PVE (%)[d] | Add[e] |
|---|---|---|---|---|---|---|---|
| Choice test | | | | | | | |
| PLD[a] | 3 | 124 | BARC-044643-08744 | BARC-062759-18042 | 3.4 | 4.9 | −0.7 |
| | 6 | 33 | BARC-031337-07051 | BARC-064115-18558 | 6.1 | 9.1 | 1.1 |
| | 7 | 69 | BARC-039383-07310 | BARC-042815-08424 | 22.3 | 54.7 | −2.5 |
| | 7 | 74 | BARC-042815-08424 | BARC-015945-02020 | 33.2 | 71.8 | −2.9 |
| | 18 | 14 | BARC-048095-10484 | BARC-037195-06738 | 3.2 | 5.2 | −0.8 |
| | 18 | 35 | BARC-016867-02359 | BARC-040429-07735 | 5.5 | 11.2 | 1.1 |
| | 18 | 40 | BARC-040429-07735 | BARC-015633-02774 | 6.2 | 10.6 | 1.1 |
| TPD[b] | 7 | 69 | BARC-039383-07310 | BARC-042815-08424 | 9.9 | 35.8 | −1.7 |
| | 7 | 74 | BARC-042815-08424 | BARC-015945-02020 | 16.7 | 66.2 | −2.3 |
| | 18 | 102 | BARC-030493-06880 | BARC-049989-09280 | 3.8 | 29.4 | 2.0 |
| No-choice test | | | | | | | |
| PLD | 7 | 69 | BARC-039383-07310 | BARC-042815-08424 | 10.0 | 36.4 | −1.4 |
| | 7 | 74 | BARC-042815-08424 | BARC-015945-02020 | 11.8 | 60.7 | −1.9 |
| | 18 | 123 | BARC-049989-09280 | BARC-052957-11678 | 4.3 | 39.9 | 1.7 |
| TPD | 7 | 69 | BARC-039383-07310 | BARC-042815-08424 | 11.5 | 39.0 | −1.3 |
| | 7 | 73 | BARC-042815-08424 | BARC-015945-02020 | 11.5 | 47.4 | −1.4 |

[a] Primary infestation leaf damage grade

[b] Total plant damage grade

[c] Log of odds

[d] Phenotypic variance explained

[e] Additive effect

Table 2. Overall, the analysis identified a major QTL region on chromosome 7 that accounted for 60–72 % of the phenotypic variation for all tests except the no-choice TPD test. In the choice test with PLD, QTLs were identified on chromosomes 3, 6, 7, and 18. Chromosomes 3 and 6 each have one QTL, and there were two QTLs on chromosome 7 and three QTLs on chromosome 18. There are two QTLs on chromosome 7 with high LOD score, 22.3 and 33.2, respectively These two most significant QTL peaks are closely located to each other on chromosome 7 (3.97 cM distance between the closest markers) and accounted for nearly 72 % of the phenotypic variation. For TPD, three QTLs were identified: Two QTLs peaks were on chromosome 7 and corresponded to the position of QTLs for PLD on chromosome 7, and another QTL peak was located on chromosome 18. In the no-choice test, for PLD, three QTLs were also detected, and the two on chromosome 7 were identical to the QTLs for TPD in the choice test. For TPD, the two QTLs on chromosome 7 corresponding to the QTLs for in the other tests were again detected. The identified QTLs on chromosome 7 have the highest phenotypic variance explained value (PVE %), which is the genetic variation caused by the QTL (25 % is commonly used as criterion to determine major QTL) (Bradshaw et al. 1998). The additive effect (Add) of QTLs on chromosome 7 showed negative values, indicating the effect originated from the resistant parent, PI 366121. The other QTLs on chromosomes 3, 6, and 18 had low LOD and PVE % values. According to the LOD and PVE % value, the major resistance QTLs for antixenosis and antibiosis are located on chromosome 7, and the others could be considered as minor QTLs. The major QTL on chromosome 7 is displayed between two SNP markers in 13 cM distance corresponding to the region between 71 cM and 84 cM on chromosome 7, BARC-042815-08424 and BARC-015945-02020, as shown in Fig. 3. Based on the result, this major QTL on chromosome 7 appears to play a key role for increasing resistance to foxglove aphid for both antixenosis and antibiosis in PI 366121.

## Discussion

Soybean is the most important legume to feed humans and livestock, but its yield loss by insect pests is significant. Recently, because of global climate change following temperature fluctuation, the major pest species have been changed from Lepidopteran and Coleopteran pests to sap-sucking hemipteran pests, and soybean aphid is one of the critical damaging pests to soybean with economic impact.

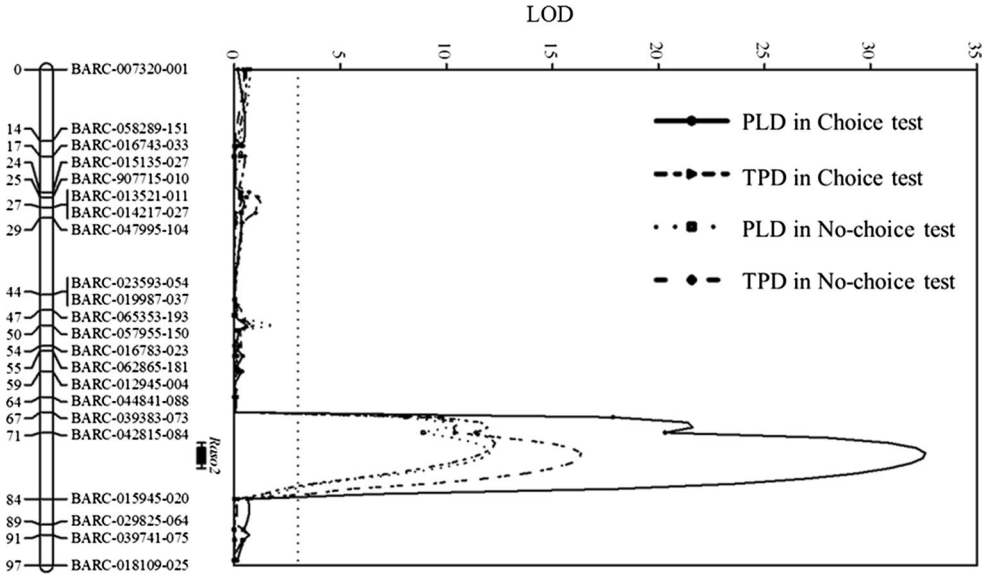


**Fig. 3** Inclusive composite interval mapping for QTLs conferring primary infestation leaf damage grade (PLD) and total plant damage grade (TPD) from choice and no-choice test. *Raso2* is mapped in the region between BARC-042815-08424 and BARC-015945-02020 with high LOD value from PLD and TPD in both choice and no-choice test

Currently, five soybean aphid resistance genes, *Rag1* on chromosome 7 from 'Dowling' (Li et al. 2007), *Rag2* on chromosome 13 from PI 243540 (Mian et al. 2008), *Rag3* on chromosome 16 from PI 567543C (Zhang et al. 2010), *Rag4* on chromosome 13 from PI 567541B (Zhang et al. 2009), and *Rag5* on chromosome 13 from PI 567301B (Jun et al. 2012), have been identified, and their biotype-specific characteristic was evaluated (Kim et al. 2008).

The foxglove aphid can feed wide range of host plants, and this makes it one of the important economic hemipteran pests worldwide, even though very limited information is known about its ecology and biology. Thus, developing foxglove aphid resistance plant is an economically efficient strategy to avoid yield losses by foxglove aphid. Currently, only one resistance gene, *Raso1* from Adams, has been identified in soybean, which is responsible for the foxglove aphid resistance and mapped on chromosome 3 (Ohnishi et al. 2012). Also, metabolite research showed that foxglove aphid resistance from Tohoku 149 was related to sulfur metabolism and methylation due to two methylated metabolites, S-methylmethionine and trigonelline (Ohnishi et al. 2012).

In this research, we tried to identify the foxglove aphid resistance QTL in soybean with the Korea biotype foxglove aphid and detected a major QTL region located on chromosome 7 with several minor QTLs. The foxglove aphid resistance gene from PI 366121 mapped to a different chromosome than a previously reported foxglove aphid resistance QTL, *Raso1* on chromosome 3. Also, the responses of Adams to the Korean biotype foxglove aphid were different from that of PI 366121 (data not shown). Although Adams and Tohoku 149 showed resistance to the Japanese biotype foxglove aphid, it did not exhibit the resistance response to the Korean biotype foxglove aphid. Thus, the QTL region on chromosome 7, which was identified in this research, is named *Raso2*. The total map distance of 20 cM per each chromosome of the linkage map constructed in this study considerably narrows down the region to identify the highly responsible QTLs for the target phenotype. The physical distance between the two flanking SNP markers, BARC-042815-08424 and BARC-015945-02020, is about 2.2 Mbp and there are 275 annotated putative genes based on the Williams 82 reference genome according to USDA-ARS soybean genetic database (Grant et al. 2010). Most plant disease resistance (R) genes, including *Rag1* and *Rag2*, are known to encode nucleotide-binding proteins, which are termed nucleotide-binding site–leucine-rich repeats (NBS-LRRs) (Pan et al. 2000). The NBS-LRR family is homologous to the animal innate immunity protein, NB-ARC family, which has two subfamilies according to the domain in the N-terminus. One subfamily contains toll and interleukin-1-receptor (TIR) domains, and the other subfamily contains a putative coiled coil (CC) or a leucine zipper (LZ). Currently, about 319 NBS-containing putative R genes have been reported in soybean (Kang et al. 2012). The genomic region between the two flanking SNP makers for *Raso2* has several putative R genes. It is very interesting that several R genes are located in the very limited 2.2 Mbp region. This could be caused by genome duplication during evolution. Thus, these putative R genes could be strong candidates for the major foxglove aphid resistance gene, *Raso2*. Among the previously reported soybean R genes, *Rag1*, soybean aphid resistance gene, was mapped to 115 kbp on chromosome 7 that corresponds to *Raso2,* and there are two candidate NBS-LRR genes in the *Rag1* interval (Kim et al. 2010a). However, the gene source of *Rag1*, cultivars 'Jackson' and 'Dowling', did not show the resistance responses to Korea biotype foxglove aphid in

our germplasm screening (data now shown). Based on this result, we conclude that *Raso2* is a novel and newly identified resistance gene to Korea biotype foxglove aphid in soybean.

In summary, a newly identified QTL, *Raso2*, for strong antibiosis and antixenosis foxglove aphid resistance in soybean has been identified with 504 SNP markers, corresponding to 14–39 SNP markers for each chromosome with an average 20 cM distance. *Raso2* was positioned on chromosome 7 between two flanking SNP markers, BARC-042815-08424 and BARC-015945-02020, located at 71 cM and 84 cM, respectively. *Raso2* shows different responses to foxglove aphid and is located on an independent locus from the previously reported foxglove aphid resistance QTL, *Raso1*, from Adams, or other soybean aphid resistance genes, *Rag1, Rag2, Rag3, Rag4,* and *Rag5*. This could be reasonable, since previous studies have shown that different resistance genes can be responsible for effects against the typical foxglove aphids from different location (i.e., different biotypes); *Raso1* from Adams, was identified in Japan, and *Raso2* was identified from the Korean biotype foxglove aphid (Kim et al. 2008). According to the intrinsic characteristic of resistance genes, which is typical resistance to different biotypes, pyramiding of a wide range of resistance genes to various biotypes is required to achieve broad resistance to foxglove aphid, and the two linked SNP markers will be useful for marker-assisted selection of this gene.

**Author contribution statement** JSL and YMH contributed equally to this research. JSL and YMH designed and conducted field tests and drafted the manuscript. JKJ provided foxglove aphid. KDB and JDL developed mapping population and genotyping. STK designed the experiment, organized manuscript. All authors read and approved the final manuscript. Authors state that the experiments comply with the current laws of the country in which they were performed.

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**Conflict of interest** The authors declare that they have no conflict of interest.

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