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Note

Evaluation of the resistance effect of QTLs derived from wild soybean (*Glycine soja*) to common cutworm (*Spodoptera litura* Fabricius)

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Common cutworm (CCW) is a serious herbivorous insect pest of soybean. Previously, we conducted an antixenosis bioassay (measuring feeding preference) with CCW using recombinant inbred lines (RILs) derived from a cross between a wild soybean (*Glycine soja*) collected in Hiroshima prefecture (JP110755) and the leading cultivar, Fukuyutaka. The analysis revealed quantitative trait loci (QTLs) for antixenosis resistance, *qRslx3* and *qRslx4*. In the present study we developed another RIL population using Fukuyutaka and a different *G. soja*, collected in Kumamoto prefecture (G406). An analysis revealed an antixenosis resistance QTL on chromosome 7, and the resistant allele of the QTL was derived from G406. The chromosomal position of the QTL was almost the same as that of *CCW-2*, a previously-reported antibiosis resistance QTL for CCW, detected in a F_2 population derived from a cross between Fukuyutaka and a resistant cultivar Himeshirazu. These QTLs could be the same locus; however, G406 and Himeshirazu are likely to possess different alleles, because Himeshirazu allele exhibits no antixenosis effect. We expect that pyramiding of the resistance QTLs derived from *G. soja* will contribute to the development of CCW resistant cultivars.

Key Words: soybean, common cutworm, quantitative trait locus, antixenosis resistance.

Introduction

Common cutworm (CCW) is one of the most serious herbivorous insect pests of soybean in Japan. Breeding of CCW-resistant cultivars would be beneficial for commercial soybean production. Screening of insect-resistant cultivars was conducted more than 40 years ago, and three Japanese landraces, Kosamame (PI 171451), Miyako white (PI 227687), and Sodendaizu (PI 229358), were reported to be resistant to Mexican bean beetle (*Epilachna varivestis* Mulsant) (Van Duyn *et al.* 1971). These landraces also exhibited resistance to CCW and other lepidopteran insects (Hatchett *et al.* 1976, Lambert and Kilen 1984, Van Duyn *et al.* 1972). Although these landraces were introduced into breeding programs, development of CCW-resistant cultivars has been unsuccessful. Selection of CCW-resistant breeding lines is difficult, because the density of CCW larvae tends to be high around the plants with oviposition, and feeding damage by CCW is uneven under field conditions. Another problem in the breeding of CCW resistance is undesirable agronomic traits of CCW-resistant cultivars, namely small seeds, colored hilum, late maturing, and low yield potential (Komatsu *et al.* 2004). These undesirable traits have hindered the breeding of high-yield elite cultivars with insect resistance.

Marker-assisted selection is useful for breeding CCW-resistant cultivars, because breeders can select individuals with resistance genes without any phenotypic investigations. Therefore, genetic analyses have been conducted to identify DNA markers linked with resistance genes for lepidopteran insects (Kim *et al.* 2014, Terry *et al.* 2000). Rector *et al.* (1998, 1999, 2000) identified a soybean QTL for resistance to corn earworm with both antixenosis (non-preference mechanism) and antibiosis (detrimental effect on pest development) effects. The resistant allele of the QTL was derived from PI 229358. This QTL on chromosome 7 (previously called linkage group M) was called QTL-M, and subsequent investigations revealed that the resistant allele of QTL-M exhibits resistance effects against other

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lepidopteran insects (Walker *et al.* 2002, 2004, Zhu *et al.* 2008). The detailed position of QTL-M was determined using fine-mapping and simple sequence repeat (SSR) markers that are tightly linked to QTL-M and which proved to be useful for breeding (Zhu *et al.* 2006).

Previously, we reported that a Japanese cultivar, Himeshirazu, shows strong CCW resistance (Komatsu *et al.* 2004). QTL analyses of CCW resistance using the descendants derived from a cross between Himeshirazu and the leading Japanese cultivar, Fukuyutaka, identified two antibiosis resistance QTLs, *CCW-1* and *CCW-2*, and two antixenosis resistance QTLs, *qRslx1* and *qRslx2* (Komatsu *et al.* 2005, Oki *et al.* 2012). Himeshirazu alleles of *CCW-1* and *CCW-2* were introduced into Fukuyutaka by recurrent backcrossing to develop near-isogenic lines (NILs), and the antibiosis effects of these genes were verified (Komatsu *et al.* 2008). *CCW-1* and *qRslx1* were likely to be the same locus because these QTLs were detected at almost the same position. Furthermore, Komatsu *et al.* (2008) verified by allelic test that *CCW-1* and QTL-M are the same locus. Comparison of the larval densities in the NILs possessing resistance genes with those in Fukuyutaka revealed that the resistant allele of *CCW-1* conferred significant resistance under field conditions and so was expected to be useful in breeding programs (Oki *et al.* 2015). However, the resistance of the NILs possessing Himeshirazu alleles of *CCW-1* and *CCW-2* was lower than that of Himeshirazu in antibiosis, antixenosis, and larval density. Therefore, additional resistance genes are required to develop cultivars with practically useful CCW resistance.

We have focused on CCW resistance in wild soybean (*Glycine soja*), which is found in eastern and northeastern China, Japan, Korea and far eastern Russia (Carter *et al.* 2004). In Japan, *G. soja* is distributed broadly in disturbed habitats, such as riverbanks, roadsides and at the edges of fields (Kaga *et al.* 2005, Kuroda *et al.* 2005, 2006, 2007). *G. soja* can be used as a genetic resource for soybean breeding programs, because *G. soja* and soybean can be crossed and the progeny are fertile. More than 2000 *G. soja* lines have been collected and preserved in the NARO Genebank Project (http://www.gene.affrc.go.jp/index_j.php). In a previous report, we revealed that the antixenosis resistance of *G. soja* (NARO Genebank accession JP110755) collected in Hiroshima prefecture was higher than that of Fukuyutaka (Oki *et al.* 2017). A QTL analysis identified novel antixenosis resistance QTLs, *qRslx3* and *qRslx4* (Oki *et al.* 2017).

Although the QTLs *qRslx3* and *qRslx4* are expected to be useful for breeding programs, the genetic basis of CCW resistance in *G. soja* is unclear. We used only one *G. soja* line for the previous investigation, and it remains unknown whether the resistance of other *G. soja* lines is also controlled by these genes. Here we report investigating the resistance of another wild soybean line, G406, to clarify whether or not the resistant alleles of *qRslx3* and *qRslx4* are possessed by another wild soybean line, and to identify novel resistance QTLs.

Materials and Methods

Plant materials

A *G. soja* line, G406 (NIAS Genebank accession JP267519), collected in Kumamoto prefecture, was randomly chosen as a source of potential CCW resistance genes, because we have already developed a population of RILs derived from a cross between G406 and Fukuyutaka (JP29668), which is a leading cultivar in western Japan and susceptible to CCW. We crossed Fukuyutaka and G406 and developed a RIL population using single seed descendants of F_2 segregants.

The RILs and their parents were grown in a field (andosol soil) at the Kyushu Okinawa Agricultural Research Center (located at 32°52′ N, 130°44′ E) in 2014. The planting date was June 24. Inter-row spacing and in-hill plant spacing were 70 cm and 42 cm, respectively. Three individuals were grown for each RIL, and leaflets were sampled from all three plants. Stakes were used to support each plant, because *G. soja* and the RILs have long stems. Approximately three stems per plant were guided to the stakes and other stems were cut because they might twine to the stakes of other lines. No pesticides were applied over the experimental period.

The effect of the detected antixenosis resistance QTL was confirmed using a residual heterozygous line (RHL). Investigation of the SSR markers Satt150, BARCSOYSSR_07_0173, Satt567 and Satt540 revealed a RIL, RIL104, with heterozygous genotype for the antixenosis resistance QTL. The genotypes for these SSR markers of the RIL104 descendants were investigated; two RHLs, RHL104-F and RHL104-G, were developed, which possessed homozygous allele of the antixenosis resistance QTL from Fukuyutaka and G406, respectively. The antixenosis resistance of these RHLs were investigated in 2016 to clarify the effect of the antixenosis resistance QTL. The planting date was July 20. Inter-row spacing and in-hill plant spacing were 70 cm and 28 cm, respectively.

DNA extraction and genotyping of SSR loci

We constructed a linkage map based on the segregation data using SSR markers in the F_7 generation. A total of 288 SSR markers were analyzed using the whole-genome SSR panel system developed by Sayama *et al.* (2011). Of the 288 SSR markers, 236 exhibited unambiguous polymorphism between Fukuyutaka and G406, and 229 of them were used to construct a linkage map. SSR markers, BARCSOYSSR_07_0010, BARCSOYSSR_07_0057, BARCSOYSSR_07_0090 and BARCSOYSSR_07_0173 were used to increase the marker density around the QTL detected on chromosome 7. The sequence of these SSR markers are available at Soybase (http://soybase.org/). In total, 233 SSR markers were used to construct a linkage map.

We used version 3.0b of MAPMAKER/EXP (Lander *et al.* 1987) to group and order the SSR marker loci. The linkage distances were estimated using the Kosambi mapping

Breeding Science
Vol. 69 No. 3 BS

function (Kosambi 1943). The minimum logarithm of odds (LOD) score and the maximum distance for linkage map construction were adjusted to 3.0 and 37.2 cM, respectively. To estimate the QTL locations and effects, we used the composite interval mapping method (Zeng 1993, 1994) implemented by version 2.5 of the Windows QTL Cartographer software (Wang *et al.* 2010, http://statgen.ncsu.edu/qtlcart/WQTLCart.htm). The setting for the cross type was recombinant inbred line and the walk speed was 1 cM. The LOD score criterion for QTL significance was estimated by means of a permutation test (Churchill and Doerge 1994) with 1000 permutations. The threshold of the LOD score was set at 3.86 for antixenosis (equivalent to a 5% genome-wide type I error rate).

Evaluation of antixenosis resistance to CCW

The antixenosis resistance bioassays were performed as described by Oki *et al.* (2012, 2017). Briefly, third instar CCW larvae reared on an artificial diet (Insecta LF S; Nippon Nousan Kougyo Co., Yokohama, Japan) were used for paired comparison tests of feeding preferences in Petri dish arenas. The bottom of each dish was covered with a moist filter paper, and a square segment (approximately 25 × 25 mm) of fully expanded mature leaflet of the standard cultivar, Akisengoku, and one of the RILs or parents were laid with the abaxial side facing up. Akisengoku was used as a standard cultivar for bioassay because it exhibited intermediate antixenosis resistance between *G. soja* and Fukuyutaka. A single CCW larva was placed on the dish and after approximately 14 hours at 23.5 ± 1°C, defoliation was assessed visually and rated on a scale of 0–10 for each leaflet segment. A rating of 0 indicated that the leaflet segment was not defoliated, whereas a rating of 10 indicated the leaflet was fully defoliated. The antixenosis resistance was evaluated for each RIL and the parents using 12 and 72 leaflet segments, respectively. The following formula (1) was used to calculate the antixenosis index (*C*), which we used to compare the test plants with the standard plant:

$$C = 2\,\Sigma A/(\Sigma M + \Sigma A) \quad (1)$$

where A = the defoliation score of the sample leaf segment and M = the defoliation score of the standard leaf segment (Akisengoku). A *C* value was calculated from 12 replicate leaflet segments. A *C* value of 1 indicates that the feeding on the test plant equaled the feeding on the standard plant. A *C* value >1 indicates a preference for the test plant (more defoliation than the standard), whereas a *C* value <1 indicates that the test plant had higher antixenosis resistance (less defoliation) than the standard cultivar.

Results

C values of a wild soybean line, G406, and Fukuyutaka were 0.84 and 1.42, respectively, signifying that the antixenosis resistance of G406 was significantly higher than that of Fukuyutaka (**Fig. 1**, $p < 0.001$). The frequency distribution of the *C* values of the RILs was continuous and extended beyond the ranges of the parents, from 0.13 to 1.91. The mean *C* value of the RILs was 1.09; the *C* values of 30% of the RILs were smaller than *G. soja* and 25% were larger than Fukuyutaka.

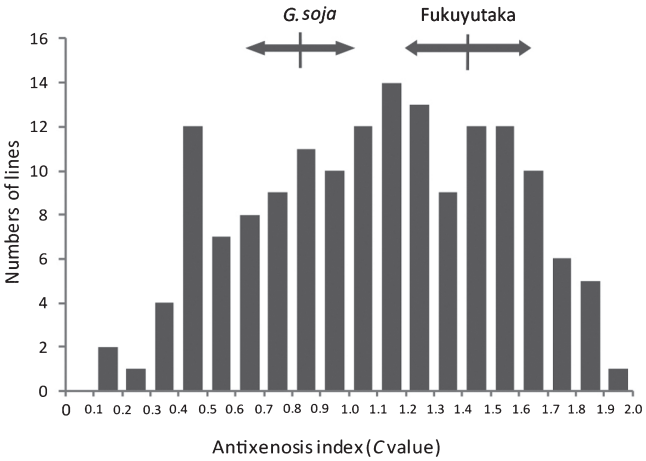

Fig. 1. Frequency distributions of the antixenosis indices of the recombinant-inbred lines derived from a cross between Fukuyutaka and *G. soja*, grown in 2014. Antixenosis resistance to common cutworm larvae was evaluated using *C* values (calculated using Equation 1), which represent the extent of larval feeding relative to that in a standard cultivar, Akisengoku ($C = 1.0$). The antixenosis resistance was evaluated for each RIL and the parents using 12 and 72 leaflet segments, respectively. Arrows and vertical lines represent the standard deviations and mean values of the parents, respectively.

We constructed a linkage map of the RILs using the segregation data for 233 loci in 161 RILs. The total map length was 2282.8 cM. A QTL associated with *C* values was detected on chromosome 7 (linkage group M) (**Fig. 2**, **Table 1**). The resistance allele of the QTL was derived from *G. soja*, and the r^2 value (proportion of variance explained) and the additive effect (a) were 0.25 and –0.22, respectively.

To validate the effect of the QTL, we searched for RHLs from the RILs. An investigation of SSR markers Satt150, BARCSOYSSR_07_0173, Satt567 and Satt540 revealed that RIL104 possessed a heterozygous genotype at the QTL (**Fig. 3**). The lines RHL104-F and RHL104-G, which possess the homozygous allele of the QTL from Fukuyutaka and G406, respectively, were selected from the progenies of RIL 104, based on the marker genotypes, and were evaluated for *C* value (**Fig. 4**). A significant difference ($p < 0.001$) was observed between the *C* values of RHL104-F (1.09) and RHL104-G (0.67).

Discussion

Previously, we identified novel CCW resistance QTLs, *qRslx3* and *qRslx4*, using a RIL population derived from a cross between *G. soja* (JP110755) collected in Hiroshima prefecture and Fukuyutaka, revealing that *G. soja* can be used as a source of resistance genes. Therefore, we conducted a QTL analysis using a *G. soja* line collected from a

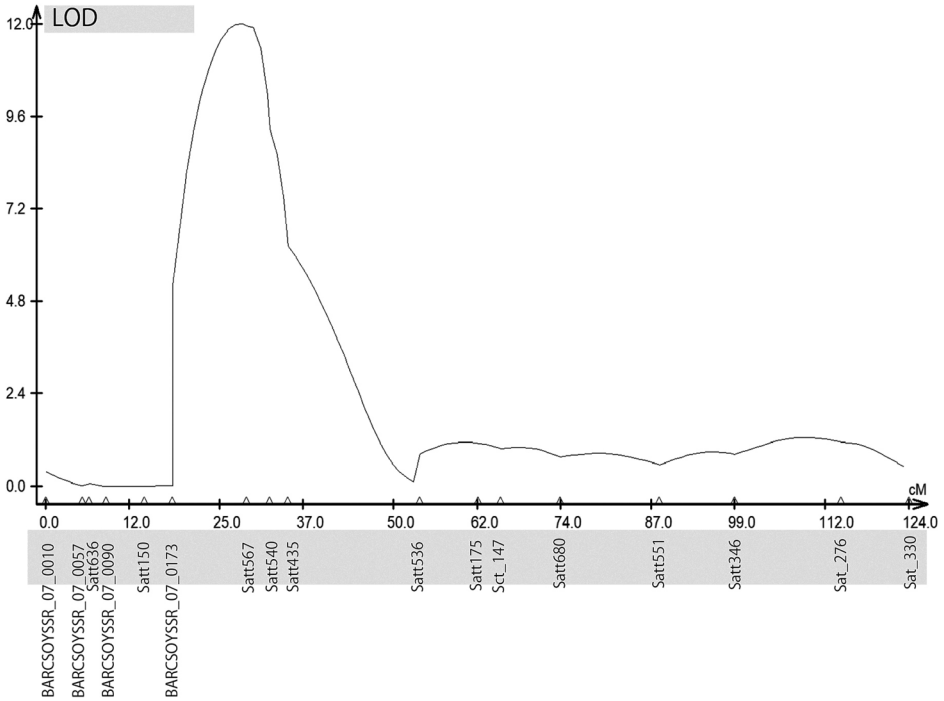

Fig. 2. Logarithm of odds (LOD) scores associated with antixenosis index (*C* value) of common cutworm on chromosome 7, estimated by means of the composite interval mapping method. An LOD score of 3.86 for the QTL detection threshold was associated with a Type I error of 5% from a 1000-permutation test.

Table 1. QTL for antixenosis index (*C* value) in recombinant inbred lines derived from Fukuyutaka and wild soybean

Trait	Chromosome	LOD	r^{2a}	a^b	Peak position (cM)	QTL region (cM)
Antixenosis resistance	7	12.0	0.25	0.22	28.2	BARCSOYSSR_07_0173 (18.2) – Satt567 (28.8)

[a] Proportion of variance explained.
[b] Additive effect of the allele of Fukuyutaka.

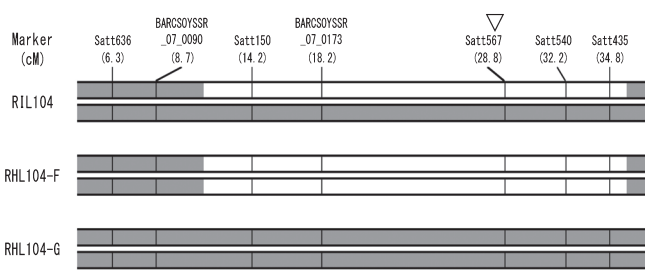

Fig. 3. Graphical genotypes of the residual heterozygous lines of the antixenosis resistance QTL detected using a RIL population derived from a cross between Fukuyutaka and G406. The lines RHL104-F and RHL104-G possess homozygous alleles of the QTL from Fukuyutaka and *G. soja*, respectively. The white and gray bars indicate regions from Fukuyutaka and G406, respectively. The white triangle represents the position of the QTL.

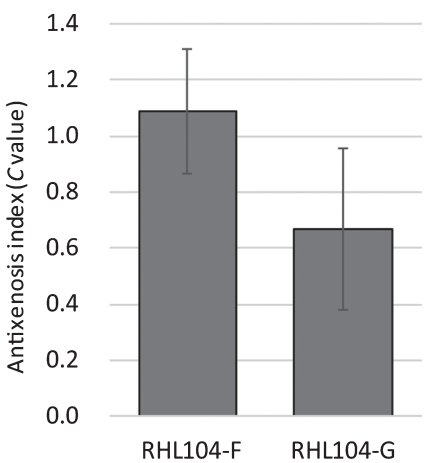

Fig. 4. Antixenosis index (*C* value) of residual heterozygous lines of the antixenosis resistance QTL detected using a RIL population derived from a cross between Fukuyutaka and G406, grown in 2016. The lines RHL104-F and RHL104-G possess homozygous alleles of the QTL from Fukuyutaka and *G. soja*, respectively. Values represent means ± standard errors. The means were significantly different ($p < 0.001$).

different location for further investigation of the CCW resistance of *G. soja*.

We developed a RIL population derived from a cross between a leading Japanese cultivar, Fukuyutaka, and G406, which is a *G. soja* line collected in Kumamoto prefecture.

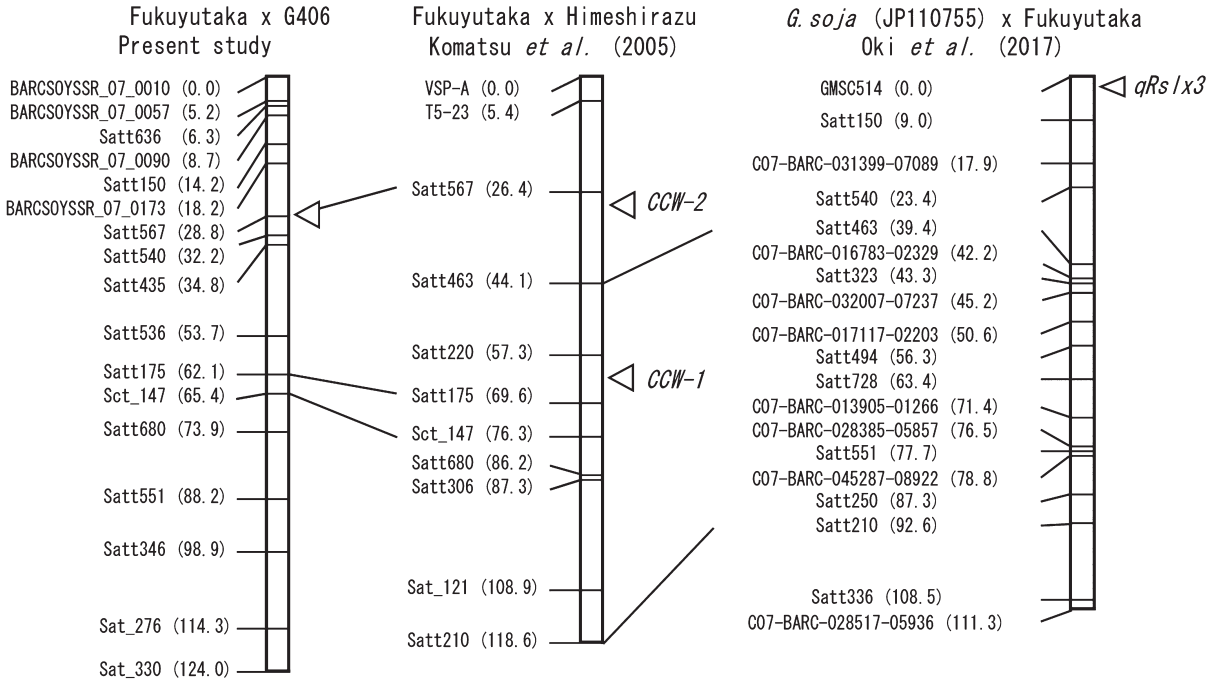

Fig. 5. Location of the quantitative trait loci (QTLs) for CCW resistance, *CCW-1*, *CCW-2*, *qRslx3* and the QTL detected in the present study, on chromosome 7 in three different recombinant inbred line populations. Labels to the left of the bars show the marker names and positions (cM). The triangles represent the locations of the QTLs for CCW resistance.

An analysis revealed a QTL for antixenosis resistance on chromosome 7. The effect of the QTL was confirmed using RHLs. *qRslx3*, which was detected in a previous study (Oki *et al.* 2017), and the QTL detected in the present study were both detected on chromosome 7 using different RIL populations and could be the same locus (**Fig. 5**). The peak position of *qRslx3* was detected approximately 5 cM upstream from Satt150, and the QTL detected in the present study was detected 0.4 cM upstream of Satt567, which is located 14.6 cM downstream of Satt150. The LOD score was below 0.1 in the upstream region of Satt150, and no peak was observed in this study (**Fig. 2**). These results suggested that these QTLs were likely to be different loci. However, the peak positions of the QTLs are often affected by environmental and experimental errors. We are developing NILs of the QTL detected in the present study to investigate the detailed chromosomal position and whether the QTL and *qRslx3* are the same locus or not. Komatsu *et al.* (2005) detected an antibiosis resistance QTL, *CCW-2*, in the vicinity of Satt567 using a F_2 population derived from a cross between Fukuyutaka and a CCW-resistant cultivar Himeshirazu (**Fig. 5**). These QTLs might possibly be the same locus because they were both detected around Satt567. However, G406 and Himeshirazu likely possess different alleles, because Himeshirazu allele exhibits no antixenosis effect (Oki *et al.* 2012). The development of the NIL of the QTL detected in the present study is expected to clarify the relationship between the QTL and *CCW-2*. Moreover, the position of the QTL detected in the present study is estimated to be approximately 30 cM apart from *CCW-1* (Komatsu *et al.* 2005), suggesting that these QTLs are different loci. Kim *et al.* (2014) detected an antibiosis CCW resistance QTL, *qCCW7-1*, on chromosome 7 at a position close to the QTL detected in the present study. Similar to *CCW-2*, *qCCW7-1* exhibited no antixenosis effect. Therefore, the resistant allele of the QTL detected in the present study is likely to be a different from the reported resistant allele of *qCCW7-1*.

No additional QTL was detected in the vicinity of the antixenosis QTLs, *qRslx3* and *qRslx4*, in the present study (**Fig. 5**). Interestingly, the results of our analyses using two different *G. soja* lines suggest that antixenosis resistance genes of *G. soja* differ among different lines. More than 2000 *G. soja* lines have been collected and preserved in NARO Genebank project (http://www.gene.affrc.go.jp/index_j.php) and could be used as a genetic resource for CCW resistance. Global warming is predicted to threaten the stability of soybean production, because high temperatures will cause more frequent outbreaks of lepidopteran insects (Jepsen *et al.* 2008, Parmesan *et al.* 1999). We expect that the resistant allele of the QTL detected in the present study will play an important role in breeding programs and that pyramiding of resistance QTLs derived from *G. soja* will contribute to the development of elite cultivars with high CCW resistance.

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