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
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 descendents 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 (NIAS 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.

### 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 RHL, 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_3 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 function.
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Fig. 1

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/QTLCart.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:

\[ C = \frac{2A}{(2M + A)} \]  

(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

\[ C = \frac{2A}{(2M + A)} \]  

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.

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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.

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...
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. 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 | r² | a | Peak position (cM) | QTL region (cM)   |
|------------------------|------------|-----|----|---|-------------------|-------------------|
| Antixenosis resistance | 7          | 12.0| 0.25| 0.22| 28.2              | BARCSOYSSR_13_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 2015. 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).
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 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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