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ORIGINAL PAPER

Quantitative trait loci mapping of partial resistance to Diamondback moth in cabbage (*Brassica oleracea* L)

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Abstract

Key message **The resistance to Diamondback moth insect in cabbage is governed by many minor loci in quantitative nature, and at least four genetic loci should be incorporated in marker-assisted breeding program for developing partially resistant DBM cabbage cultivars.**

Abstract The Diamondback moth (DBM), *Plutella xylostella* (L.), is the most destructive insect infesting cruciferous plants worldwide. Earlier studies have reported that the glossy leaves of cabbage are associated with resistance to this insect. However, until now, genetics of DBM resistance has not been studied in detail, and no QTL/gene mapping for this trait has been reported. In this paper, we report quantitative trait loci (QTL) mapping of DBM-resistant trait using 188 randomly selected segregating F_3 population derived from crossing a partially DBM-resistant glossy leaf cabbage (748) with a susceptible smooth cabbage line (747). Quantitative trait loci mapping using phenotypic data of four consecutive years (2008, 2009, 2010, and 2011) on DBM insect infestation detected a total of eight QTL on five linkage groups suggesting that DBM resistance is a quantitative in nature. Of these QTL, four QTL, i.e., *qDbm* 1 on LG1, *qDbm5* and *qDbm6* on LG7, and *qDbm8* on LG9, were detected in different tests and years. The QTL, *qDbm6* on LG7, was consecutively detected over 3 years. Tightly linked molecular markers have been developed for *qDbm8* QTL on LG9 which could be used in marker-assisted breeding program. Our research demonstrated that for desired DBM resistance cultivar breeding, those four genetic loci have to be taken into consideration. Furthermore, the comparative study revealed that DBM resistance QTL is conserved between close relative model plant *Arabidopsis thaliana* and *Brassica oleracea* genome.

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Introduction

The diamondback moth (DBM), *Plutella xylostella* L., is one of the most destructive insect pests known to attack cruciferous plants and major limiting factors for the production of cruciferous crops worldwide (Eigenbrode et al. 1991; Talekar and Shelton 1993). It is believed that glucosinolates, the sulfur containing secondary metabolites specifically found in crucifer plants, stimulate DBM infestation (Talekar and Shelton 1993). DBM causes severe damage

to all crucifer plants which includes cultivated vegetables crops *B. oleracea* (cabbage, broccoli, collard, brussels sprout), *B. rapa* (Turnip, Chinese cabbage, pakchoi), and oilseeds *B. napus* and *B. juncea* (Eigenbrode et al. 1991; Talekar and Shelton 1993). The newly hatch larvae starts feeding soon after emergence on spongy mesophyll tissues, and the older larvae generally feeds from the lower surface of the leaf leaving only the waxy layer on the upper surface (Talekar and Shelton 1993). The widespread damage caused by this insect started to become prominence after use of synthetic insecticides in 1950s. The ability to adapt rapidly by developing resistance to pesticides and absence of natural enemies (predators) which might have killed by widespread use of broad spectrum insecticides were reported to be possible reasons which helped DBM become more prominence in damaging crucifer crops. Therefore, the current strategy for controlling DBM with insecticides has been unsuccessful, and this insect has been listed second in the Arthropod Pesticide Resistance Database (APRD 2012; Gelernter and Lomer 2000; Talekar and Griggs 1986; Talekar and Shelton 1993). Furthermore, DBM has been reported as the first insect to become resistance to *Bacillus thuringiensis* (*Bt*) insecticides sprays in the open field (Tabashnik et al. 1990). Therefore, there is a need to diversify control measures of DBM and develop new strategies that are more environmentally sound and durable, thus minimizing our dependency on the use of pesticides (Dickson et al. 1986; Hasheela et al. 2010).

Over the years, there has been increasing interest in the identification and development of efficient, economic, and environmentally safe DBM-resistant *Brassica* cultivars (Dickson et al. 1986, 1990; Eckenrode et al. 1986; Eigenbrode et al. 1991; Talekar and Shelton 1993). Certain plant characteristics, including biochemical and morphological factors, have been reported to promote different kinds of resistance such as antibiosis, antixenosis, and tolerance (Eigenbrode and Espelie 1995; Li et al. 2000; Marazzi et al. 2004; Painter 1951; Reed et al. 1989; Sarfraz et al. 2006; Thorsteinson 1953). Antibiosis resistance reduces longevity and reproduction, and increases the mortality of insects, thereby significantly reducing insect damage. Antixenosis resistance is primarily owing to the non-preference of insects because of the presence of pubescences and surface waxes on plant organs such as leaves that adversely affect insect behavior, while in tolerance resistance, a plant can withstand or recover from damage caused by insect pest abundance (Painter 1951). Currently, limited information regarding the genetic control of DBM resistance in *Brassica* species is available. Earlier studies reported that Cauliflower Plant Introduction (PI) 234599 and its descendants showed the most promising resistance to DBM and other lepidopteron insects because of its glossy leaves (Dickson and Eckenrode 1980; Dickson et al. 1990; Eigenbrode and Shelton 1990; Eigenbrode et al. 1991). This glossy leaf characteristic is caused by a waxy layer and inherited as a single recessive gene, and DBM neonate larvae showed rapid movement and reduced feeding on glossy leaves (Eigenbrode and Shelton 1990; Eigenbrode et al. 1991). Subsequently, several genes for glossy leaf characteristics from diverse sources have been identified in *B. oleracea* (Eigenbrode et al. 1991; Stoner 1990). In all these glossy plants, reduced DBM larval survival until the four instar stage is directly correlated with neonates failing to establish on the leaves, leading to the observed resistance and reduced damage on crops (Eigenbrode et al. 1991). Although many glossy resistance sources have been identified in *B. oleracea* and used in breeding programs, no studies have been performed at the molecular level to identify QTL/genes or tightly linked molecular markers with DBM resistance or glossy traits. However, two previous studies reported the QTL mapping of DBM resistance loci in *B. napus* and *Arabidopsis thaliana* (Asghari et al. 2009; Kliebenstein et al. 2002). Kliebenstein et al. (2002) reported four QTL for resistance to DBM in *A. thaliana*, while three resistance QTL were reported in *B. napus* (Asghari et al. 2009).

The goal of the present study was to extend our current understanding of the genetic control of DBM resistance traits in cabbage by defining the genomic regions through QTL mapping. We identified a total of eight genomic regions in *B. oleracea* governing DBM resistance traits on five linkage groups. Furthermore, one QTL governing DBM resistance on LG7 was expressed over the three consecutive years. The above finding suggests that genetic control of DBM resistance trait was complex and governed by many genes, suggesting that breeding DBM resistance could be achieved with incorporation of multiple loci although few constitutively detected QTL could give success. We developed molecular markers linked to a constitutively expressed QTL which could be used in marker-assisted selection for developing varieties resistant to DBM. Furthermore, comparative analysis revealed that DBM resistance QTL/genetic locus is conserved between the closest relative *A. thaliana* and *B. oleracea* genomes.

Materials and methods

Plant materials

A total of 188 F_2 cabbage plants derived from the crossing between two diverse cabbage inbred lines 747 (DBM susceptible) and 748 (DBM resistance) were used for construction of a genetic linkage map in cabbage in another experiment. 747 cabbage line has smooth leaves, while 748 cabbage line has glossy leaves. Both the parental and F_2 lines were

provided by Nunhemp Company. The susceptible and resistant parental lines were found among the collected lines of cabbage germplasm by the Nunhemp Seed Company, Korea. F_3 families derived by selfing each F_2 plants were used for phenotypic screening of the DBM resistance trait and subsequently for QTL mapping of this trait in cabbage.

Diamondback insect infestation and measurement

Phenotypic screening of susceptibility and resistance traits for mapping was conducted for plants grown from March to July in 2008, 2009, 2010, and 2011. For insect infestation, 15 F_3 plants from each F_2 family and an equal number of resistant and susceptible parental lines were grown in pots in a glasshouse at Chungnam National University, Daejeon, South Korea in 2008, 2009, and 2010. Before infestation, the plants were covered with a net so as to exclude infestation by other insects until the DBM was supplied for the feeding assay. In 2008, plant infestation was achieved using 20 second-instar DBM larvae per plant inside the nylon net, which was specifically designed to isolate individual plants so that insects were forced to infest only a single plant. The observations of insect infestations were conducted 5 days after placement of the larvae in the netted cabbage plants. In the years 2009 and 2010, a mixture of 100 newly hatch adult moths and cocoons containing pupae, which were about to hatch adult moths, was maintained in Petridishes at a distance of 1 m inside the net covering the grown cabbage plants. Thus, after emergence of the adult moth from the cocoon, a suitable host plant could easily be found for laying eggs based on preference. In 2008 and 2009, 35-day-old cabbage plants were used for all insect infestation studies. In 2010, 60-day-old seedlings were used for insect infestations. In 2011, 31-day-old healthy seedlings were transplanted to the open field of Chungnam National University, which contained a natural population of DBM for field evaluations of the resistance trait along with the parental lines and F_1 plants. In 2010, for validation of linked molecular markers, 500 F_2 plants were grown and screened for resistance and susceptible traits in a green house, as described for the F_3 plants. In the greenhouse, the temperature was maintained between 20 and 25 °C. Insect damage or the infestation index (ID) was scored after 1 month of artificial infestation (after supply of adult moths) in green house-grown plants, while field-grown cabbage plants were evaluated for insect damage at maturity. The mean value of insect damage/feeding damage (ID) of ten plants was used for QTL mapping. The infestation scoring was conducted following Eckenrode et al. (1986). Feeding damage on whole plants was assessed using a rating scale from 1 to 5 as follows: 1 = <5 %, 2 = 5–20 %, 3 = 21–40 %, 4 = 41–60 %, and 5 = >60 % infestation of the leaf surface damage (Eckenrode et al. 1986).

Statistical analysis and QTL mapping

Correlation coefficient analysis of phenotypic traits was done using SPSS program. Quantitative trait loci mapping of DBM resistance was conducted using the composite interval mapping function in WinQTL Cartographer version 2.5 (Wang et al. 2005). For declaring the presence of a QTL, genome-wide threshold values were estimated from 1000 permutations of trait data across all genetic intervals. Tests for the presence of QTL were performed at 2-cM intervals using a 5-cM window and five background cofactors, which were selected via forward regression analysis following Ramchiary et al. (2007).

Results

Quantitative trait loci (QTL) mapping of the diamondback resistance trait

The parental lines and segregating populations showed substantial variation for insect resistance (Figs. 1, 2). Susceptible line 747 showed an infestation index ranging from 4.10 to 4.6, while resistance ranged from 1.33 to 2.5 in different years of the experiment (Table 1). The F_1 showed partial resistance to DBM insects/larvae which was comparable with resistance parental line (748) suggesting dominance inheritance. The F_3 plants exhibited variation in degree of insect infestation index ranging from 1 to 5 in different years of trials (Table 1). The phenotypic score of the insect infestation did not show a clear-cut segregation pattern, indicating that this trait is governed by many loci (Fig. 3). Furthermore, it was observed that 748 (resistance line) and glossy leaf segregating plants showed more resistance when infested in a large netted bed containing many plants compared to infestation of a single plant in a net individually with insect larvae (Figs. 1, 2). The more damage was observed in 747 (susceptible lines) and its inherited smooth leaf segregating cabbage plants. Therefore, the resistance observed might be due to the preference of adult moth to smooth leaf over glossy leaf. Furthermore, when 30-day-old cabbage plants were infested with insects, damage to the resistant parents was less than that to the 1 month old seedlings when used for infestation. Previously developed genetic map (unpublished) was used for DBM-resistant QTL mapping in cabbage using the phenotypic data scored in 2008, 2009, 2010, and 2011. The genetic map was based on 188 randomly selected segregating F_2 lines derived from crossing between 747 and 748 cabbage lines. The map consists of a total of 276 marker loci, majority drawn from earlier *B. rapa* map (Ramchiary et al. 2011), of which 158 are cnu, nia, BrgMS, and BRPGM simple sequence repeat markers, 8 *B. juncea* Intron polymorphic marker (IP), 51

Fig. 1 The damage due to insect infestation in susceptible (747) and resistant (748) *lines* of cabbage (**a**–**d**). Resistant and susceptible *lines* observed in 115-(**a, b**) and 150-(**c**, **d**) day-old cabbage plants, respectively. Figures **a** and **b** are from glasshouse infestations, and **c** and **d** are from field-grown plants infestation. **a** and **c** are resistant (748) parental *lines*, and **b** and **d** are susceptible parental (747) *lines*

ACMP EST-SSRs, and 59 public SSR markers covering a total distance of 1028.7 cM in nine linkage groups of the cabbage genome (communicated for another publication).

QTL mapping detected a total of eight QTL conferring resistance to DBM in five linkage groups (Fig. 4; Table 2). The highest number of QTL (i.e., 5) was detected for the phenotypic data scored in 2010, whereas the lowest number of QTL (i.e., 2) was detected in the year 2011. The percentage of phenotypic variance explained by individual QTL ranged from 4 to 15. The five linkage groups showing resistance QTL were LG1, LG2, LG3, LG7, and LG9 (Fig. 4; Table 2). Four DBM resistance QTL i.e. *qDbm1* on LG1, *qDbm5* and *qDbm6* on LG7, and *qDbm7* on LG9 were detected in more than one experiment and year. Of these, QTL *qDbm6* which was consecutively detected in 3 years from 2009 to 2011 showed a comparatively higher logarithm of odds (LOD) value. Although *qDbm8* detected in 2008 showed a high LOD value of 10, it was not detected in any other experiments. *qDbm1* showed the highest LOD value of 10.5 in 2010, which was again detected in 2011, with an LOD value of 5.55. As expected, the majority of resistance QTL was contributed by resistance parent, 748.

Development of molecular markers linked to Diamondback moth resistance loci

With the aim to develop tightly linked molecular markers to the four DBM QTL, which were detected in more than one experiment (i.e., *qDbm1* on LG1, *qDbm5* and *qDbm6* on LG7, and *qDbm7* on LG9), many markers which fall within the confidence interval of those QTL were screened so that tightly linked marker once developed could be utilized in the marker-assisted breeding of the four loci for DBM resistance cabbage cultivar. A total of 23 markers (i.e., five from LG1, 13 from LG7, and six from LG9) were used for screening tightly linked molecular markers in 94

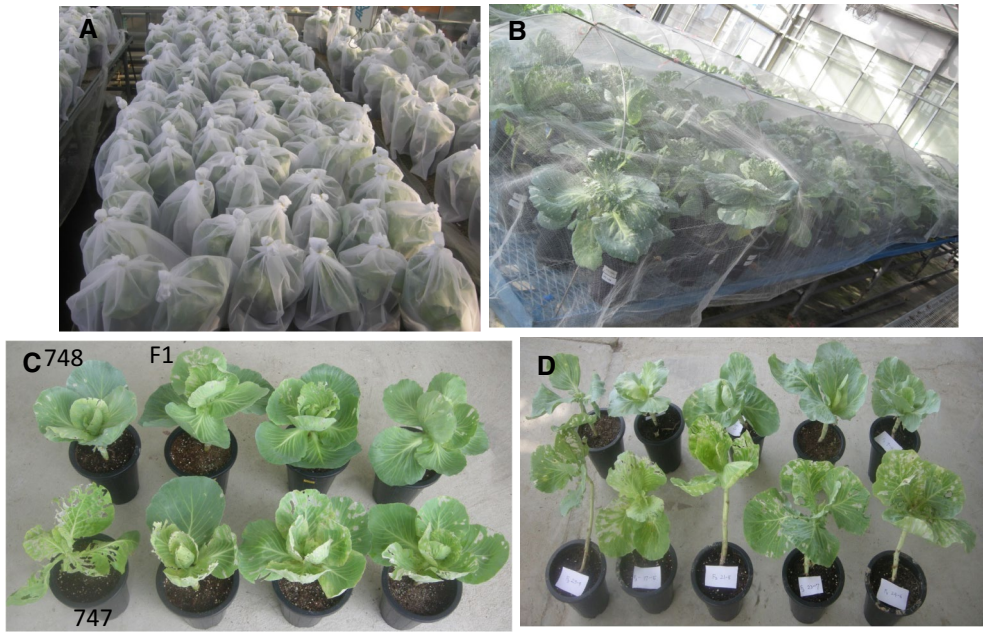

Fig. 2 Single plant and multiple plant insect infestation of cabbage plants by Diamondback moth. **a** shows infestation of a single cabbage plant by DBM larvae, while **b** shows insect infestation of a large number of cabbage plants under common net using DBM pupae. **c** and **d** show susceptible (747), resistant (748), F_1 and F_3 segregating population showing contrasting insect damage

Table 1 Mean and range of DBM resistance traits in cabbage parents and segregating F_3 lines

Year	747	748	F_3 lines		
			Range		
			Mean	Minimum	Maximum
2008	4.33	1.33	2.69	1.0	5.00
2009	4.60	1.90	2.32	1.0	5.00
2010	4.50	2.40	2.53	0.67	4.68
2011	4.10	2.50	2.78	0.33	4.45

randomly selected F_2 and F_3 plants showing resistance to DBM insects (i.e., showing a phenotypic score ID of <2.5 and ≥4.0). Of the 23 markers tested in the 47 susceptible and 47 resistance lines, along with the 747 (susceptible) and 748 (resistance) lines, two SSR markers (i.e., BRPGM0157 and ACMP00635) tightly linked with *qDbm8* on LG9 were detected (Fig. 5). However, for the remaining three QTL, we observed numerous recombination sites in the individuals tested, suggesting that more individuals and markers need to be tested as the resistance traits are governed by many loci.

Conservation of Diamondback moth resistance QTL in the same genomic blocks of Cabbage and *Arabidopsis*

In our previous study, we identified five major crucifer blocks in *B. rapa* (E, R, F, J, and W) harboring genetic loci for yield and leaf-related traits (Li et al. 2013). In the present study, when we compared DBM resistance QTL with earlier studies, conservation of cabbage DBM QTL with that of a previous DBM QTL mapping study in *A. thaliana* was found. Kliebenstein et al. (2002) mapped DBM resistance QTL in *A. thaliana* using L*er* × Col and L*er* × Cvi recombinant inbred line populations. They detected two QTL for DBM resistance, one each on chromosomes II and V. On chromosome II, the DBM resistance QTL was mapped near the *erecta* locus, which belongs to block I, one of the 24 ancestral crucifer blocks reported by Schranz et al. (2006). A homology search using sequence-informative markers showed that LG7 (chromosome 4) in our cabbage map contained markers showing synteny to block I containing the *erecta* locus, which encodes a leucine-rich repeat receptor-like kinase (LRR-RLK) and is involved in the specification of organs originating from the shoot apical meristem. A DBM resistance locus, *qDbm6*, detected in this syntenic locus in 2009, 2010, and 2011 explained 9–12 % of the phenotypic variation in different years (Table 2). Furthermore, a comparative map of DBM resistance between *B. oleracea* and *B. napus* could not be created because of a lack of common markers between these two species.

Discussion

The present study was designed to map partial diamondback moth resistance traits in cabbage. The cabbage

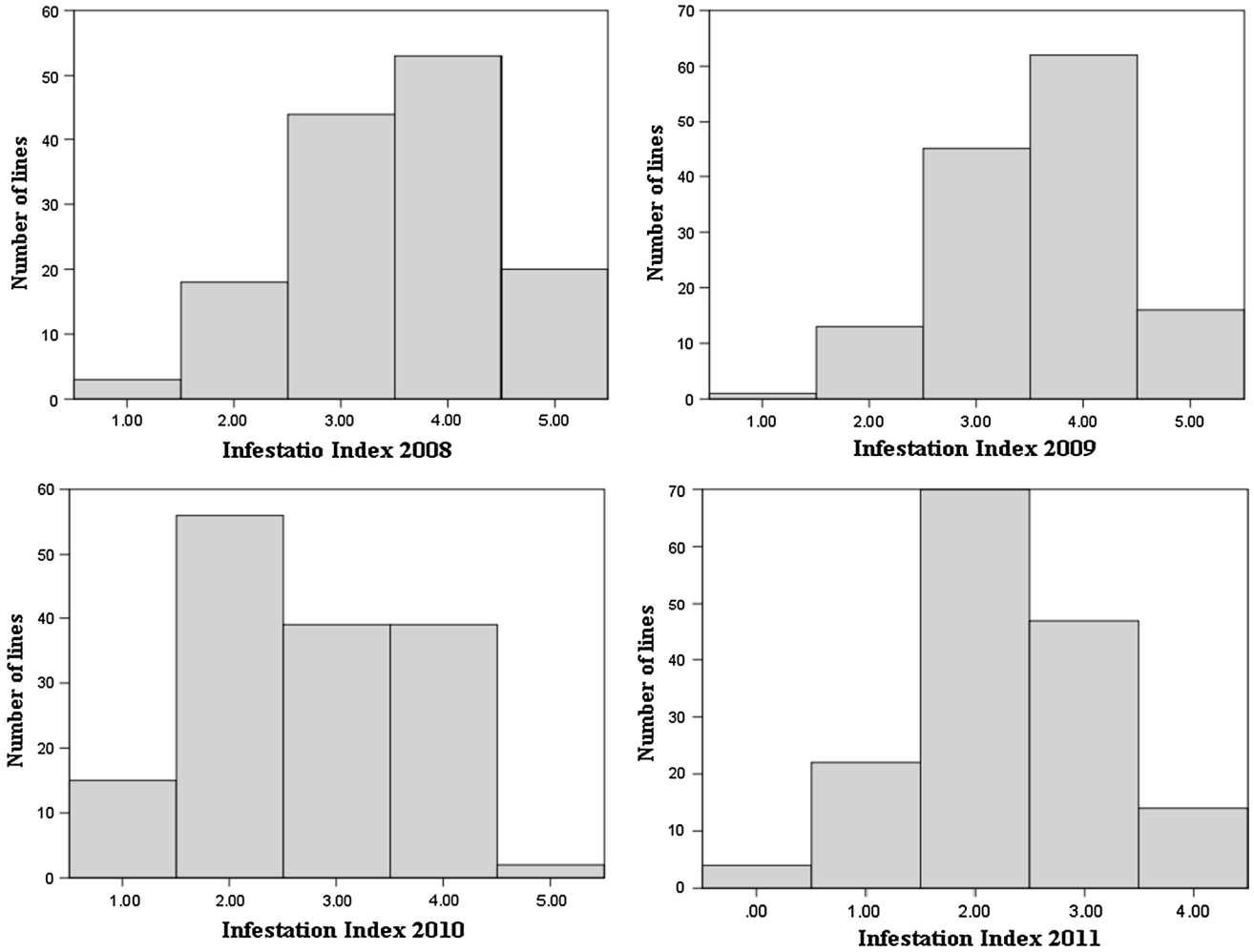

Fig. 3 Frequency distribution of Diamondback moth resistance trait in cabbage F_3 segregating population in different years

genetic map was earlier developed in the lab using mainly *B. rapa* markers so that complete alignment of C genome of *B. oleracea* could be done with A genome of *B. rapa* for future comparative QTL mapping study for economically important traits. Previous studies identified a few DBM resistance glossy leaf cabbage collections (Dickson et al. 1986, 1990; Eigenbrode et al. 1991). Eigenbrode et al. (1991) studied resistance mechanism conferred by glossy leaf cabbage genotypes compared to smooth open bloom genotypes. They reported that glossy resistance is associated with reduced wax and reduced density of wax crystalline structures on leaf surfaces. Furthermore, they opined that glossy leaf waxes apparently elicit non acceptance behaviors in neonate larvae resulting in their failure to successfully establish on resistant glossy plants. They observed reduced larval survival of Diamondback moth on glossy wax genotypes as low as 1 %, compared with standard cultivars and polar extracts of the resistant plants reduced larval survival when added to an artificial diet. Neonate larvae also moved significantly faster on glossy-resistant plants and rejected glossy plants and failed to establish on them, leading to the observed resistance. Our result of getting more resistance in glossy leaf parent 748 and glossy leaf segregating lines while releasing adult moth in a netted bed containing many plants compared to single plant infestation also confirms their finding.

Although breeding DBM resistance cabbage cultivars has been the objectives of many breeders, detailed genetic study by employing QTL mapping and genomics approach has been still lacking in *B. oleracea*. In this paper, we report the first QTL mapping in *B. oleracea* for DBM resistance. We identified a total of eight QTL showing resistance to DBM infestation in cabbage. As expected, we also observed that majority of favorable alleles for Diamondback moth resistance QTL were contributed by cabbage parental line 748. Our results indicate that DBM resistance is not simply an inherited trait, although earlier studies reported it to be governed by a single gene. In the

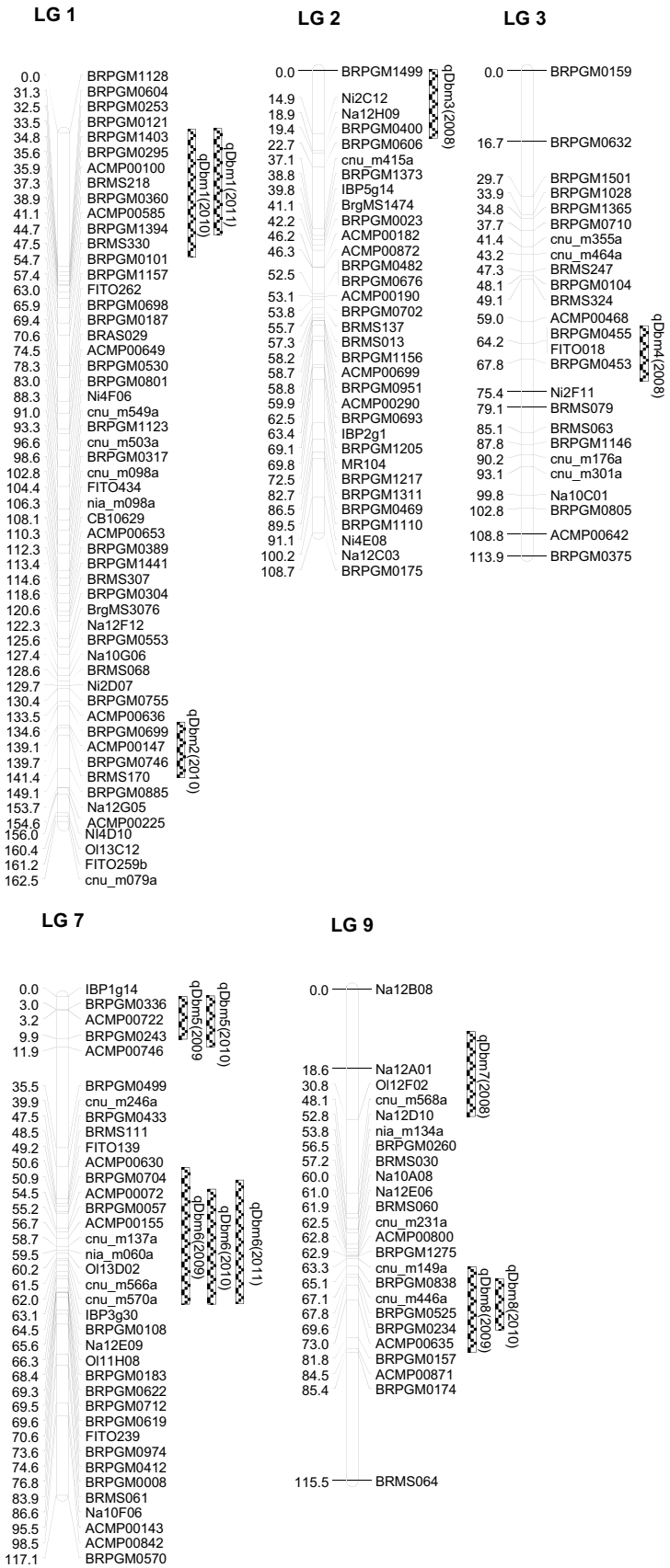

Fig. 4 Distribution of Quantitative trait loci for Diamondback moth resistance trait on five linkage groups of cabbage. QTL names are indicated by abbreviations of trait names, and the number indicates the QTL number. The *numbers* in *parenthesis* indicate the year of QTL detection. Trait abbreviation, *Dbm* Diamondback moth resistance trait

Table 2 Details of Diamondback moth resistance QTL detected in different linkage groups of cabbage

QTL	LG	Year of detection	LOD	CI	Flanking markers	Additive effect	Dominance effect	R^2
qDbm1	1	2010	10.5	0–30	BRPGM1128-BRPGM0604	−0.21	−0.16	17
		2011	5.55	0–25	BRPGM1128-BRPGM0604	−0.90	0.66	7
qDbm2	1	2010	8.55	139–152	ACMP00147-Na12G05	−0.55	0.34	12
qDbm3	2	2008	7.75	0–16	BRPGM1499-Na12H09	0.14	−1.86	9
qDbm4	3	2008	4.53	60–73	ACMP00468-BRMS079	−0.53	−1.35	5
qDbm5	7	2009	4.49	0–10	IBP1g14-BRPGM0243	0.34	−0.74	5
		2010	4.50	0–12	IBP1g14- ACMP00746	0.25	−0.13	4
qDbm6	7	2009	7.32	40–72	cnu_m246a-BRPGM0974	−0.79	0.23	16
		2010	6.22	45–72	cnu_m246a-BRPGM0974	−0.43	−0.24	9
		2011	8.55	43–72	cnu_m246a-BRPGM0974	−0.67	0.30	13
qDbm7	9	2008	10.00	10.1–30.33	Na12B08-Ol12F02	0.32	1.08	15
QDbm8	9	2009	5.50	65–85	BRPGM0838-BRPGM0174	−0.87	0.52	6
		2010	4.82	68–80	BRPGM0525-BRPGM0157	−0.70	0.41	5

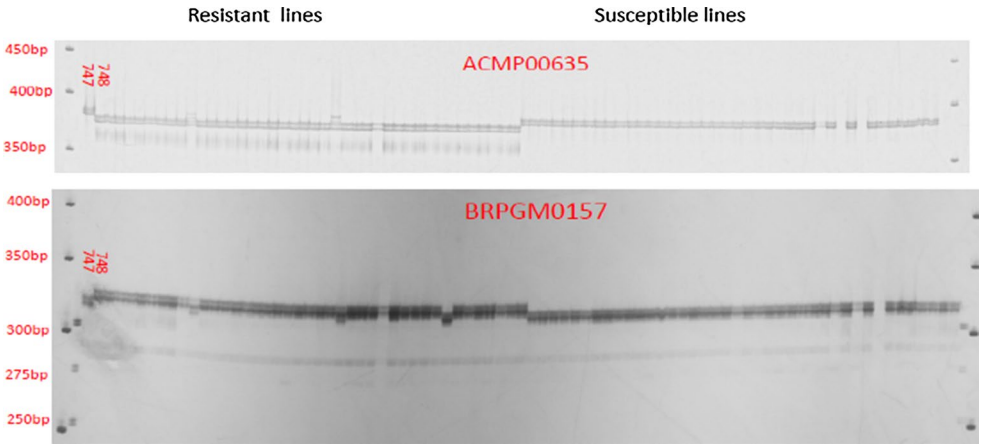

Fig. 5 The genotyping of two SSR markers, i.e., BRPGM0157 and ACMP00635, showing tight linkage with the DBM resistance QTL *qDbm8* on linkage group 9 in 94 randomly selected F_2 and F_3 cabbage segregating *lines*; line no. 747 is the susceptible parent, no. 748 is the resistant parent, while 47 *lines* after 748 are resistant *lines,* and the remaining 47 *lines* are susceptible

present study, no QTL explaining more than 25 % phenotypic variation was detected. This might be due to the partial resistance observed in one of the parental lines. Our study also indicated that the resistance shown by 748 and glossy segregating lines was more related to preference type than to resistance type, which was supported by showing a greater infestation when insect larvae was placed in a net containing only a single plant compared to the experiment where adult moths could choose among many plants. On the basis of the glossy (resistance) and smooth (susceptible) leaf surfaces, adult DBM moths seemed to prefer the smooth leaves rather than the glossy leaves for laying eggs. Furthermore, the detection of eight DBM resistance QTL also supports the argument that DBM resistance is a complex trait, and manipulation of at least four loci (*qDbm1*, *qDbm5, qDbm6*, and *qDbm8*), which were detected more than once, must be conducted for developing DBM-resistant cultivars. We did, however, identify two markers, BRPGM0157 and ACMP00635, linked with *qDbm8* on linkage group 9. The identification of tightly linked markers, at least for the remaining three DBM resistance QTL (i.e., *qDbm1* on LG1, and *qDbm5* and *qDbm6* on LG7), should be conducted using additional markers and other segregating populations.

Tightly linked markers with one resistance locus in a particular resistant line may not be linked to other resistant lines because resistance is governed by many loci, as was determined in the present study. Therefore, fine mapping using large segregating populations and additional markers would be helpful in the development of tightly linked molecular markers for incorporation of DBM resistance loci in commercial cultivars though marker-assisted breeding. This is the first report of DBM resistance QTL mapping in *B. oleracea*, although earlier studies reported the mapping of three QTL in *B. napus* (Asghari et al. 2009).

The observations of synteny between the DBM resistance QTL (*qDbm6* on LG 7) in the present study with that of *A. thaliana* (Kliebenstein et al. 2002) would be helpful for the identification of orthologous genes in *B. oleracea* which might have originated from the ancestral genome

and govern by the same loci or different loci. The mapping of DBM-resistant QTL on chromosome II near *ERECTA*, a receptor kinase gene, indicated that this locus might be involved in conferring resistant to this insect although further experiments need to be done for validating it (Kliebenstein et al. 2002). The involvement of *ERECTA* locus in conferring resistance to diseases such as bacterium wilt caused by *Ralstonia Solanacearum* and verticilium wilt caused by *Verticillium longisporum* has been shown in *A. thaliana* (Godiard et al. 2003; Häffner et al. 2014). However, further research to validate this locus in insect resistance needs to be done, and no such study at gene level has been reported in any crops including in *B. oleracea*. Due to the unavailability of common markers, we could not make a comparison with the DBM resistance QTL map in *B. napus* reported by Asghari et al. (2009). As the marker density in our map was lower, fine mapping to dissect the genomic region and comparative analyses with *B. rapa* and *A. thaliana* should be conducted to develop molecular markers for all loci, especially for QTL *qDbm1* on LG1, and *qDbm5* and *qDbm*6 on LG7.

Author contribution statement WP and VDN did genotyping and phenotyping works. XL and SRC helped in data analysis. MK and JN provided the parental lines and reared Diamondback moth (DBM) larvae and adult moths used for infestation. HYS and SB helped in phenotype screening in 2008. AK, MKY, and MK helped in manuscript preparation. NR involved in designing, genotyping, phenotyping, data analysis, and manuscript writing. YPL conceived the project and supervised all the experiments and helped in manuscript preparation. All authors read and approved the final manuscript.

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

Ethical statement The experiments comply with the current laws of the Republic of Korea.

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