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ORIGINAL PAPER

Molecular mapping of resistance gene to English grain aphid (*Sitobion avenae* F.) in *Triticum durum* wheat line C273

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Abstract The English grain aphid, *Sitobion avenae* (Fabricius), is one of the most important insect pests causing substantial yield losses in wheat production in China and other grain-growing areas in the world. The efficient utilization of wheat genes for resistance to English grain aphid (EGA) provides an efficient, economic and environmentally sound approach to reduce the yield losses. In the present study, the wheat line C273 (*Triticum durum* AABB, $2n = 4x = 28$), is resistant to EGA in greenhouse and field tests. To identify the resistance gene, designated RA-1 temporarily, C273 was crossed with susceptible genotype Poland 305 (*T. polonicum*, AABB, $2n = 4x = 28$). The F_1, F_2 and $F_{2:3}$ lines were tested with EGA in the field and greenhouse. The results indicated that *RA-1* is a single dominant gene, closely linked to the microsatellite markers (SSR) *Xwmc179*, *Xwmc553* and *Xwmc201* on chromosome 6AL at genetic distances of 3.47, 4.73 and 7.57 cM, respectively. The three SSR markers will be valuable in marker-assisted selection for resistance to EGA as well as for cloning this gene in the future.

Introduction

At present, five aphid races severely affect wheat production all over the world. They are Russian wheat aphid (RWA) [*Diuraphis noxia* (Kurdjumov)], English grain aphid (EGA) [*Sitobion avenae* (Fabricius)], greenbug [*Schizaphis graminam* (Rondani)], bird cherry-oat aphid [*Rhopalosiphum padi* (Linnaeus)], and *Acyrthosiphon dirhodum* (Walker). EGA is one of the most economically important species among cereal aphids in the wheat planting areas of China and in some other grain-growing areas worldwide (Johnston and Bishop 1987; Feng et al. 1991; Dedryver et al. 2008; Thackray et al. 2009; Alkhedir et al. 2010). It can cause considerable damages to grain production by direct feeding, excretion of honeydew and virus transmission (Budenberg et al. 1992; Longley and Jepson 1996; Dedryver et al. 2005; Yang et al. 2005; Tanguy and Dedryver 2009). EGA infestations may reduce wheat grain yield as much as 44.26% (Xu et al. 1998), and it causes significant yield losses in more than 90% of wheat production areas in China (Yang et al. 2005).

Chemical insecticides are often used to control aphid damage, but these result in severe environmental pollution (Flickinger et al. 1991; Daily et al. 1998). Use of resistant wheat cultivars can provide an efficient, economic and environmentally friendly approach to reduce the yield losses caused by the injury of EGA. There has been a worldwide effort to investigate EGA and identify EGA-resistant germplasm. Wheat resistance to the aphid is negatively correlated with the wax powdery and ear density (Watt 1979; Acreman and Dixon 1986; Zheng et al. 1999; Liu et al. 2006). In addition, resistance to this aphid in wheat is associated with the nutriments (Kazemi and Van Emden 1992; Havlickova 1996) and the secondary chemicals of wheat such as DIMBOA (the main hydroxamic acids in wheat) (Leszcynski et al. 1992; Nicol and Wratten 1997; Fuentes-contreras and Niemeyer 1998; Yin et al. 2005), alkaloids (Cai et al. 2009), and phenolics (Ciepiela 1989). More than 200 accessions of common wheat and its relatives have been evaluated for EGA resistance since

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1982. The ancient wheat species Einkorn and Emmer, and the modern Sicco exhibited resistance to the cereal aphids EGA, in terms of non-preference and antibiosis on plants at three growth stages in laboratory (Sotherton and VanEmden 1982). Of 3,516 wheat germplasm investigated, Nongda-4356, Yanda-1817, Nongda-198 and Nongda-6085 showed resistance to EGA (Zhou et al. 1982). Of the 91 spring wheat breeding lines tested, 26 showed some resistance to EGA in the greenhouse (Lowe 1984). Duan et al. (2006) reported that Sigeasson, Zhongpin 1818, PI262660 and PI243781 displayed resistance to EGA by combining seedling and adult plant resistance tests. Using the electrical penetration graph (EPG) technique (Caillaud et al. 1995) and the intrinsic rate of natural increase (r_m) (Di Pietro et al. 1993), *T. monococcum* line Tm44 was identified as a highly resistant wheat genotype to EGA. Five species among 41 wild and cultivated wheat lines showed antibiosis to EGA estimated by the plant biomass lose due to aphid infestation (Migui and Lamb 2003). Ou et al. (2005) reported resistance to EGA in Bainong64 and Yanzhan-1 by reduction ratio of wheat weight per 1,000 grains. Liu et al. (2006) reported *T. durum* line C273 and *T. turgidum* S894 were highly resistant to EGA by the method of aphid number ratio.

Development of new varieties with resistance to EGA is urgently needed to reduce further losses caused by EGA. However, conventional breeding methods via phenotypic selection are cumbersome, time consuming and sometimes inconclusive, particularly in the breeding of aphid-resistant wheat varieties. Aphid density may be affected by environmental conditions, such as heavy rainfall and strong wind, suggesting that more efficient techniques are needed to identify EGA-resistant genes or genotypes. The identification of molecular markers closely linked to the resistance genes not only facilitates the identification and mapping of insect-resistant genes, but also allows the marker-assisted selection (MAS) of resistant lines in the wheat breeding programs. The MAS approach particularly enhances the prospect of pyramiding traits in desired germplasm and varieties, leading to a fast process of breeding for multiple and durable resistance.

Several molecular markers systems (e.g., RAPD, RFLP, AFLP and SSR) have been used in MAS for breeding RWA-resistant lines (Myburg et al. 1998; Venter and Botha 2000; Matsioloko and Botha 2003; Liu et al. 2001) and greenbug-resistant lines (Weng and Lazar 2002; Boyko et al. 2002; Zhu et al. 2004, 2005). Among these markers, SSRs are reliable, highly polymorphic and can link a gene to a specific chromosome or arm. SSRs are easy to use and have been widely adopted for locating RWA- and greenbug-resistant genes. It was reported that the RWA-resistant genes *Dn0, Dn1, Dn2, Dn5, Dn6*, and *DnX* were closely linked to SSR marker *Xgwm111* on chromosome 7DS (Saidi and Quick 1996; Liu et al. 2001, 2005), and *Dn9* was associated with *Xgwm642* on chromosome 1DL (Liu et al. 2001). A greenbug-resistant gene *Gbz* co-segregated with the SSR marker *Xwmc157* on chromosome 7DL (Zhu et al. 2004), and another greenbug-resistant gene *Gb3* was placed in the same chromosome (Weng and Lazar 2002). However, at present, no molecular markers linked to EGA-resistant genes have been reported.

The aims of the present study were to identify the EGA-resistant gene in *Triticum durum* wheat line C273 and its closely linked SSR markers. We mapped the accurate location of these markers for practical use in the development of wheat varieties for resistance to EGA.

Materials and methods

Plant materials

To study the resistance to EGA in the durum wheat line C273 (*T. durum* AABB, $2n = 4x = 28$), an aphid-susceptible wheat variety. Poland 305 (*T. polonicum*, AABB, $2n = 4x = 28$) was used as the female parent to cross with the aphid-resistant wheat line C273 (Liu et al. 2006). The F_1, F_2 and $F_{2:3}$ populations derived from the cross were used for mapping the resistance gene to EGA. A bread wheat cultivar Xiaoyan 6, highly susceptible to EGA, was used as a control in the present study.

Evaluation of EGA resistance in field and greenhouse

F_1 plants, and F_2 and $F_{2:3}$ segregating populations were evaluated for their resistance to EGA in the field and greenhouse in Northwest A & F University during 2005–2009 cropping seasons.

For the field evaluation, about 20 seeds of each parent and F_1 were planted in a 1-m row and 130 F_2 seeds were planted in 1-m rows with 10 seeds in each row and 24 cm between rows. The plots were surrounded by the susceptible control Xiaoyan 6 as a spreader. We used conventional management without the application of pesticide during the whole growth period. At the jointing-booting stage, each plant of Xiaoyan 6 in source of infection was artificially infested with 50 EGAs and the above-tested wheat materials were subsequently infected. The number of aphids was determined at the milky stage when the outbreak of the aphid occurred. Ten severely infested parental and F_1 plants were examined and the absolute number of aphids was recorded if it was below 50 per stem. The average resistance score with stems was determined for each of the F_2 plants. $F_{2:3}$ seeds were harvested from the F_2 plants for testing $F_{2:3}$ lines in the field as described above.

For the greenhouse evaluation, about 20 seeds of each parent and F_1 and Xiaoyan 6, and 160 F_2 seeds were planted in plastic pots filled with a potting mixture. Seedlings grew in the greenhouse at 16 h light and 8 h dark with diurnal temperatures 20–22°C. At the three-leaf stage, each plant was artificially infested with 5 same size EGAs and evaluated for resistance in 7 and 14 days after treatment, respectively.

The aphid resistance was scored according to the Painter's (1951) method as described. Infestation severity was scored from 0 to 6 in which scores of 0–3 represented aphid-resistance while scores 4–6 represented aphid-susceptibility (Table 1).

DNA extraction, PCR amplification, electrophoresis and gel visualization

At the three-leaf stage, the second leaf from each of the F_2 progenies and parents was harvested for DNA extraction. Genomic DNA was extracted using the CTAB procedure. DNA was quantified using the mini-gel method and a spectrophotometer. DNA concentrations were adjusted to 30 ng/μL for the use in PCR.

SSR markers (Roeder et al. 1998; Somers et al. 2004) were used to map the resistance gene. The primer sequences, chromosomal locations and PCR protocols were obtained from the GrainGenes Database available at http://www.wheat.pw.usda.gov/. Primers were synthesized by SBS Sangon (Shanghai, China). Amplification reactions were performed in a total volume of 10 μL containing 20–40 ng of genomic DNA, 250 nM of each primer, 2 mM of $MgCl_2$, 200 μM of dNTPs, 5.5 μL of 1× Buffer, 0.25 U of *Taq* DNA polymerase (Dongsheng, Guangdong, China). The microsatellite PCR was carried out as described by Wang et al. (2007) using a Perkin Elmer 480 thermocycler.

PCR products were analyzed by polyacrylamide gel electrophoresis (PAGE). Banding patterns were visualized with silver staining. Briefly, the gel on a glass plate was pretreated with fix/stop solution [10% alcohol and 0.5% acetic acid (v/v)] for 10 min, and then stained in the 0.2% $AgNO_3$ solution for 15 min. After a brief rinse in distilled H_2O for 1 min, the gel was transferred into a solution containing 0.002% (w/v) sodium thiosulfate for 1 min followed by incubation in the well-chilled developer solution (15% (w/v) sodium hydrate and 0.4% (v/v) formaldehyde) for 3–8 min. The reaction was stopped by incubating the gel in distilled water with shaking for 5 min.

Table 1 Evaluation of wheat resistance to EGA

Resistance scale	Resistance	Ratio of aphid quantity[a]
0	Immunity	0
1	HR	0.01–0.30
2	MR	0.31–0.6
3	LR	0.61–0.9
4	LS	0.91–1.2
5	MS	1.21–1.5
6	HS	>1.5

[a] Ratio of aphid quantity = A/B

A The average aphid number per stem of each tested material, *B* The average aphid number per stem of all tested materials

Bulked segregant analysis

SSR markers linked to EGA-resistant genes were initially identified through bulked segregant analysis (BSA) (Michelmore et al. 1991). Two DNA bulks were assembled by equal amounts of DNA from eight most resistant and eight most susceptible F_2 plants, respectively, which were confirmed as homozygous resistant or homozygous, susceptible by testing the $F_{2:3}$ lines in the field. A total of 565 microsatellite primer pairs specific for wheat chromosomes A and B, were used to screen the parents and bulks. Primer pairs generating bands specific to both C273 and the resistant bulk, were used to genotype all F_2 plants.

Statistical analysis and genetic mapping

Chi-squared ($\chi 2$) test was used to evaluate the goodness of fit of observed and expected segregation ratios for EGA reactions and molecular markers. The "chi-test" procedure in the Excel data analysis of Microsoft Office 2007 was used to calculate *P* values. Recombination frequency (RF) or linkage relationship between microsatellite markers and EGA-resistant gene were calculated using maximum-likelihood equations with F_2 data for marker genotype and plant phenotype of the EGA reaction. The linkage maps were constructed using the software MapMaker3.0 (Lincoln et al. 1992). A LOD threshold of 3.0 was set to declare markers as significant. The Kosambi function (Kosambi 1944) was applied to convert RF into genetic map distance (cM).

Results

Inheritance of EGA resistance in C273

C273 was highly resistant to EGA in the 2006 seedling test and the 2005–2006, 2006–2007 field tests whereas Poland 305 was susceptible, and the F_1 plants from the cross between C273 and Poland 305 were resistant to EGA (Table 2).

As shown in Table 3, the F_2 segregation ratio indicated that resistance to EGA was controlled by a single dominant

Table 2 EGA resistance in parental and F_1 plants from the cross of Poland 305 × C273

Plant material	Ratio of aphid quantity		Resistance	Resistance scale
	Seedling stage in the greenhouse	Grain filling stage in the field		
Xiaoyan 6	1.85	1.87	HS	6
C273	0.27	0.25	HR	1
Poland 305	1.11	1.49	S	4/5
F_1	0.78	0.23	R	3/1

Table 3 EGA resistance in F_2 population from the cross of Poland 305 × C273

F_2 Progeny	Population							Expected ratio	$\chi 2$	*P*
	R				*S*					
	I	HR	MR	LR	LS	MS	HS			
Seedling stage in the greenhouse	3	31	34	27	13	13	17	3:1	1.09	0.32
	95				43					
Grain filling stage in the field	0	14	20	27	6	6	7	3:1	0.03	0.85
	61				19					

Table 4 Molecular markers linked to the gene for resistance to EGA in C273, size and presence or absence in C273 and Poland 305, number of F_2 plants with or without the makers, and $\chi 2$ tests

Marker	Size (bp)[a]	Presence (+) and absence (−) of the marker		Number of F_2-resistant plants with or without the marker		Number of F_2 susceptible plants with or without the marker		Number of F_2 plants with or without the marker			
		C273	Poland 305	With	Without	With	Without	With	Without	$\chi 2$	*P*
Xgwm570	100	+	−	52	9	2	17	54	26	0.76	0.38
Xwmc179	245, 220	+	−	58	3	3	16	61	19	0.03	0.85
Xwmc553	400, 360	+	−	56	5	2	17	58	22	0.03	0.85
Xwmc201	250, 300	+	−	54	7	2	17	56	24	0.28	0.59
Xwmc580	150	+	−	55	6	10	9	65	15	0.59	0.44

[a] The sizes of markers were estimated using DNA size markers

gene. In the 2007 seedling test, the spaced planting of about 160 F_2 seeds produced 138 F_2 plants for recording resistance to EGA, of which 95 were resistant and 43 susceptible, fitting to 3:1 ratio ($\chi 2 = 1.29$, $df = 1$, $P = 0.25$) (Table 3). In the 2007–2008 field test, the spaced planting of about 130 F_2 seeds produced 80 F_2 plants for recording resistance to EGA, of which 61 were resistant and 19 susceptible, fitting to 3:1 ratio ($\chi 2 = 0.03$, $df = 1$, $P = 0.85$) (Table 3). Therefore, it is likely a single dominant gene conferred the resistance to EGA in C273.

Seventy-five $F_{2:3}$ lines were tested with EGA in the field in 2008–2009. The tests produced identical results with F_2 population confirming segregation at a single locus. The 19 homozygous susceptible lines were derived from susceptible F_2 plants and 15 resistant and 41 segregating lines were from resistant F_2 plants. Resistant lines, segregating lines and susceptible lines accorded with a ratio of 1:2:1 ($\chi 2 = 0.57$, $df = 2$, $P = 0.44$). The results indicated that a single dominant gene in C273 conferred resistance to EGA and the phenotypic data were reliable for molecular mapping.

Molecular mapping of the EGA-resistant gene in C273

Of the 565 SSR primer pairs evaluated, 76 amplified polymorphic fragments between the resistant parent C273 and the susceptible parent Poland 305. Five of the seventy-six primer pairs generated nine robust and repeatable polymorphic bands in bulked segregant analysis and were selected to test the eighty F_2 plants (Table 4). As an example, SSR WMC553 amplified 400 and 360 bp fragments from DNA of the resistant parent C273 and resistant bulk, absent in the susceptible parent and susceptible bulk, and 390 and 350 bp fragments from DNA of the susceptible parent Poland 305 and susceptible bulk.

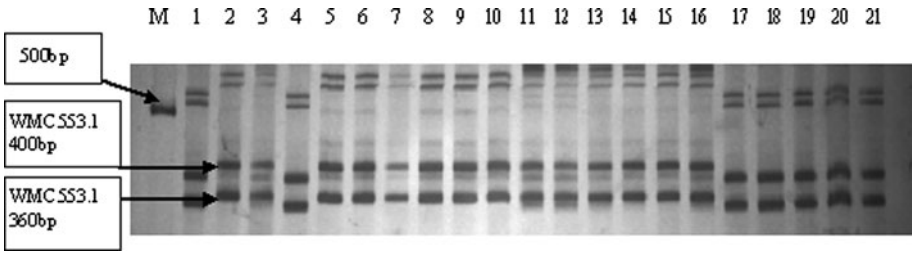

Fig. 1 PCR amplification patterns by primer *Xwmc553* in F_2 segregating population of Poland 305 × C273. *M* represents DNA ladder DL 2000, line *1* Poland 305, *2* C273, *3* resistant bulk, *4* susceptible bulk, *5–16* aphid-resistant plants, *17–21* susceptible plants

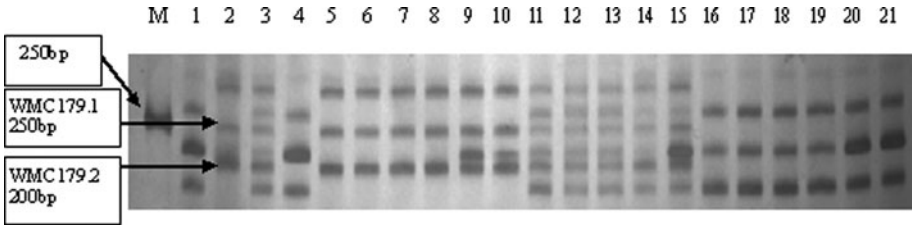

Fig. 2 PCR amplification patterns by primer *Xwmc179* in F_2 segregating population of Poland 305 × C273. *M* represents DNA ladder DL2000, line *1* Poland 305, *2* C273, *3* resistant bulk, *4* susceptible bulk, *5–15* aphid-resistant plants, *16–21* susceptible plants

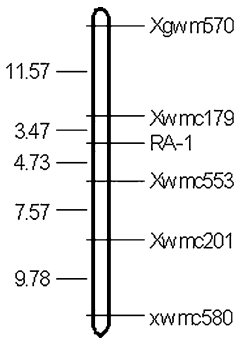

Fig. 3 Genetic linkage map of wheat chromosome 6AL consisting of a EGA-resistant gene *RA-1* based on 80 F_2 plants from Poland 305 × C273

Segregation in the F_2 population is shown in Fig. 1. Microsatellite primer WMC179 amplified 245 and 220 bp fragments from DNA of the resistant parent C273 and resistant bulk, absent in the susceptible parent and susceptible bulk, and 210, 230 and 255 bp fragments from DNA of the susceptible parent Poland 305 and susceptible bulk. Segregation in the F_2 population is shown in Fig. 2.

Five markers segregated in 3:1 ratios for the presence and absence (Table 4), indicating that these markers were single-locus markers. The results of linkage analyses indicated that microsatellite markers *Xgwm570*, *Xwmc179*, *Xwmc553*, *Xwmc201* and *Xwmc580* on chromosome 6AL were linked to *RA-1* with genetic distances of 15.04, 3.47, 4.73, 7.57 and 22.07 cM, respectively (Fig. 3).

Discussion

There have been different arguments on the inheritance of EGA resistance in wheat. For example, Wu et al. (1999) reported that EGA resistance was a quantitative trait controlled by minor polygenes and affected by environmental condition and adaptation of the aphids, whereas Ou et al. (2005) showed that the resistance to EGA was largely correlated with the genetic background of the parental plants. The progeny plants of resistant parents had a strong resistance to EGA while the progeny plants of susceptible parents were susceptible to EGA, indicating that the resistance to EGA was strongly inheritable. Diallel crossing tests among three EGA-resistant and susceptible cultivars showed that EGA resistance was consistent with the incomplete dominant model in which resistance was controlled by a single gene (Yin et al. 2003). The genetic analysis of resistance evaluated by aphid number ratio method, using the F_1 plants and F_2 populations derived from the cross between the resistant Linyuan 207 and susceptible Witchita (Duan et al. 2006), those from crossing the resistant line J231 and susceptible line J239, and from the cross between the resistant line J248 and susceptible line J239 (Hu et al. 2009), showed that EGA resistance in the resistant lines Linyuan 207, J231 and J248 were controlled by a single dominant gene. In this current study, genetic analysis showed that a single dominant gene was responsible for resistance to EGA in C273 consistent with those reported previously (Duan et al. 2006; Hu et al. 2009). But the resistance gene to EGA in Linyuan 207, J231 and J248 were not localized on a specific chromosome locus.

Based on breeding records, we cannot pinpoint the exact original genetic material for C273. But C273 is a tetraploid wheat line, whereas Linyuan 207, J231 and J248 are

hexaploid wheat lines, indicating that C273 may provide another useful independent-resistant gene to EGA, origination from the A genome. Our results indicated that *RA-1* is closely linked to two microsatellite markers located on the long arm of wheat chromosome 6A (Daryl et al. 2004), *Xwmc553* and *Xwmc179* at distances of 4.73 and 3.47 cM, respectively. This is the first report on gene location and molecular mapping of resistance to EGA in wheat.

To date, there are more than 20 designated resistance genes to greenbug (Zhu et al. 2004; Weng and Lazar 2002) and RWA (Anderson et al. 2003; Liu et al. 2001, 2005; Heyns et al. 2006), and many others genes with temporary designations. We identified an effective EGA-resistant gene in wheat line C273 and mapped it to the long arm of chromosome 6A. This gene should be useful in developing cultivars with an effective resistance to EGA, and the linked SSR markers *Xwmc553* and *Xwmc179* could be used in marker-assisted selection for EGA resistance in wheat breeding programs.

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