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Identification and Inheritance of Leaf Rust Resistance Genes in the Wheat Cultivar 'Marvdasht'

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The objectives of this research were to examine the inheritance of leaf rust resistance genes in the Iranian wheat cultivar 'Marvdasht', which is highly resistant to leaf and stripe rusts, and to identify *Lr* genes present in this cultivar using molecular markers. The genetic basis of resistance to the leaf rust pathogen (*Puccinia triticina*) in 'Marvdasht' was studied in $F_{2:3}$ populations derived from crosses of Bolani (susceptible cultivar) × Marvdasht. Isolates 84-1 and 85-28 of *P. triticina*, which are the predominant isolates in Iran, were used to examine the segregation of resistance originating from 'Marvdasht'. The results indicated that resistance in 'Marvdasht' to *Puccinia triticina* isolate 84-1 was governed by two dominant seedling resistance genes *Lr1* and *Lr17a*. Allelism studies using an F_2 population derived from a cross between 'Falat' (Seri 82) and Marvdasht indicated that resistance in Marvdasht was not due to the resistance gene *Lr26* present in 'Falat'. With the application of a previously developed molecular marker for *Lr1*, the STS marker RGA-567-5, the presence of *Lr1* was verified in Marvdasht. Based on bulk segregant analysis, *Lr17a* was mapped to the distal end of chromosome 2AS and was closely linked to microsatellite marker *Xbarc212* at a distance of 3.7 cM. In conclusion, the presence of *Lr1* and *Lr17a* was confirmed in the cultivar Marvdasht.

Keywords: bulk segregation analysis, infection type, inheritance, near isogenic line

Introduction

Leaf rust, caused by *Puccinia triticina* (syn. *Puccinia recondite* f. sp. *tritici*), influences wheat production and quality throughout the world. Leaf rust and stripe rust *(P. striiformis* f. sp. *tritici),* are the most economically important wheat diseases in Iran. It is estimated that approximately 1.1 million hectares (20%) of land cultivated to wheat in Iran is prone to leaf rust infection (Singh et al. 2004). This is particularly noteworthy as wheat is the most critical crop in Iran grown on 5.47 million hectares (more than 50% of total cultivated land) (Singh et al. 2004).

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Leaf rust severity in wheat is directly related to the loss of effectiveness of rust resistance genes. Genetic diversity of leaf rust resistance in commonly grown wheat cultivars is currently the only practical method of managing leaf rust (Oelke and Kolmer 2005). To date, more than 60 major leaf rust resistance genes (*Lr* genes) have been identified and mapped onto wheat chromosomes (McIntosh et al. 2008). Many of these *Lr* genes have been deployed in commercial cultivars worldwide. The widespread cultivation of wheat cultivars with specific leaf rust resistance genes has resulted in an increase in pathotypes of *P. triticina* (Oelke and Kolmer 2005). Knowledge of the genetic basis of leaf rust resistance in wheat cultivars can be used to deploy cultivars with effective leaf rust resistance and to incorporate new resistance genes in breeding programs (Liu and Kolmer 1997; Oelke and Kolmer 2005). Numerous studies have used different pathotypes to examine the genetic basis of resistance to leaf rust in wheat cultivars worldwide (Barcellos et al. 1999; Kolmer and Liu 2002; Oelke and Kolmer 2005).

The cultivar 'Marvdasht', a CIMMYT wheat breeding cultivar, with the pedigree HD172/Bloundane//Azadi, was released in 1992. Marvdasht is highly resistance to leaf rust in southern, western and southwestern Iran and is one of the most important commercial wheat cultivars in these regions of Iran (Anonymous 2005). Marvdasht has effective resistance to the predominant isolates of *P. triticina* in Iran (Anonymous 2005).

This study was conducted to determine the inheritance of resistance in 'Marvdasht' to isolates of *P. triticina* prevalent in Iran. Also, in different pathotype tests conducted in Iran, Marvdasht cultivar showed similar infection levels as those of the cultivar 'Falat' (Seri 82); pedigree analysis and gene postulation studies showed that 'Falat' carried resistance genes *Lr26* (due to the presence of 1RS.1BL translocation) and *Lr23* for resistance to leaf rust pathogen. Therefore, the allelic relationships between resistance gene(s) present in 'Falat' and those present in 'Marvdasht' also were examined. In addition to the genetic analysis for presence/absence of *Lr* gene(s) in Marvadasht, molecular markers were used to validate the presence of a given resistance gene.

Materials and Methods

Isolates and inoculations

Isolates 84-1 and 85-28 of *P. triticina* were used to examine the segregation of resistance in several cultivars. Isolates 84-1 and 85-28 originated from the Karaj and the Shiraz regions of Iran, respectively. The isolates represent the predominant contemporary isolates in Iran (Rafiei et al. unpublished data). In this study, the *P. triticina* isolates were increased on the susceptible cultivar 'Bolani' and were characterized for infection types on a set of differential cultivars. Differential sets were kindly provided by Prof. R.A. McIntosh, Sydney, Australia. The isolate 84-1 from the Karaj region, was avirulent on near-isogenic lines (NILs) of Thatcher wheat with *Lr1, Lr2a, Lr2b, Lr9, Lr14a, Lr15, Lr16, Lr17a, Lr18, Lr19, Lr23, Lr24, Lr25, Lr28, Lr29, Lr32, Lr33* and *Lr36* (Table 1) and Marvadsht (Table 2); and virulent to lines with *Lr2c, Lr3ka, Lr3bg, Lr10, Lr13, Lr14b, Lr20, Lr21, Lr26, Lr30*. The avirulence/virulence formula of isolate 85-28, which produced low infec-

tion types (ITs) on Marvdasht and Falat cultivars (Table 2) was: *Lr1, Lr9, Lr14a, Lr19, Lr20, Lr21, Lr24, Lr25, Lr26, Lr28, Lr29, Lr32, Lr36* / *Lr2a, Lr2b, Lr2c, Lr3ka, Lr3bg, Lr10, Lr13, Lr15, Lr17a, Lr18, Lr23* (Table 1).

Experiments were conducted in the greenhouse at the Cereal Pathology Institute, Karaj, Iran. For inoculation tests, four seeds were planted in plastic pots (55 mm in diameter) filled with a potting mix. Inoculations were performed at the two-leaf stage using urediniospores suspended in light mineral oil. The inoculated seedlings were placed in the dark at 18°C with a RH of 100% for 24 h, before being placed on greenhouse benches at 22±2°C. The seedling infection types were recorded according to the scale outlined by McIntosh et al. (1995). Based on this scale, the infection types 3–4 were regarded as susceptible or high infection type and infection types 0 to 2+ and heterogeneous mesothetic infection types were considered to be resistant responses or low infection type).

For each inoculation test, the near-isogenic wheat lines (NILS) of Thatcher each possessing different *Lr* genes were planted and included in the experiment as controls. Therefore, infection types of plants from the various populations were compared with those of their respective parents and the host differentials to assure proper classification and assignment to resistant and susceptible classes. The infection types of the NILs also allowed for the accurate identification of the isolates being examined.

Table 1. Avirulence/virulence formula of 3 tested isolates 84-1 and 85-28 on near-isogenic lines (NILs) of Thatcher wheat with different *Lr* genes

Leaf rust isolates	Avirulent on NILs	Virulent on NILs
84-1	*Lr1, Lr2a, Lr2b, Lr9, Lr14a, Lr15, Lr16, Lr17, Lr18, Lr19, Lr23, Lr24, Lr25, Lr28, Lr29, Lr32, Lr33, Lr36*	*Lr2c, Lr3ka, Lr3bg, Lr10, Lr13, Lr14b, Lr20, Lr21, Lr26, Lr30*
85-28	*Lr1, Lr9, Lr14a, Lr19, Lr20, Lr21, Lr24, Lr25, Lr26, Lr28, Lr29, Lr32, Lr36*	*Lr2a, Lr2b, Lr2c, Lr3ka, Lr3bg, Lr10, Lr13, Lr15, Lr17, Lr18, Lr23*

Table 2. Infection types of two isolates of *Puccinia triticina* on near-isogenic lines and wheat cultivars used in this study

Wheat lines	*P. triticina* isolates	
	84-1	85-28
Thatcher+*Lr1*	0;	0;
Thatcher+*Lr17a*	1–2	3+
Thatcher+*Lr26*	3+	0
Thatcher+*Lr23*	3+	3+
Marvdasht	0;	0
Falat	3+	0
Bolani	3+	3+

Infection types 0–2+ were considered as avirulent and 3–4 were considered as virulent (McIntosh et al. 1995).

Segregation of resistance in Bolani × Marvdasht

The analysis of the genetic segregation of resistance was conducted using the cross 'Bolani'×'Marvdasht'. 'Marvdasht' was used as the male parent and crossed with the leaf rust susceptible cultivar 'Bolani'. Twenty F_1 seed were sown and the F_2 seed harvested. The F_2 population of 'Bolani'×'Marvdasht' (BM-1), with 182 individual plants, was used to test phenotypic segregation against isolate 84-1. After scoring, F_2 plants were then transferred to pots (22 cm diameter) and grown to maturity and F_3 seed were harvested. A total of 125 plants in the BM-1 population produced F_3 seed. Twenty seedlings per F_3 line were tested for resistance to isolate 84-1. Infection types were recorded on each F_2 plant and individual progeny from each F_2 plants in corresponding F_3 families ($F_{2:3}$).

Allelism tests between 'Marvdasht' and 'Falat'

Based on similar responses of 'Marvdasht' and 'Falat' to the most prevalent Iranian leaf rust isolates it was hypothesized that *Lr26* was present in 'Marvdasht'. Pedigree analysis indicated that Falat was an Iranian name for breeding line Seri 82, which possesses resistance genes *Lr23* and *Lr26* to the leaf rust pathogen. An objective of the present study was to determine if the *Lr* resistance gene(s) present in Marvdasht cultivar are the same as those present in Falat cultivar. The isolate 85-28 which was avirulent on 'Marvdasht', 'Falat' and the Thatcher line with *Lr26,* was selected to examine the presence or absence of *Lr26* in 'Marvdasht'. If the resistant gene present in Marvdasht was the same as in 'Falat' (i.e. *Lr26*), no segregation would be found in the F_2 generation. Thus, a cross was made between 'Marvdasht' and 'Falat' and the infection type of the F_2 population to isolate 85-28 was determined. The goodness of fit to the expected segregation ratios for one and two independent genes was tested by chi-square analysis. Because F_2 progenies were derived from different F_1 plants, a chi-square test for homogeneity was used to determine whether different populations differed in segregation of resistance. Because of the homogeneous variance calculated among tested populations, the related data were pooled together.

Molecular studies

As part of this study, 160 F_2 plants derived from the cross Bolani×Marvdasht were assayed to confirm the presence of the postulated genes *Lr1* and *Lr17a* in Marvdasht. All individual F_2 plants were initially screened using by RGA-567-5, a sequence tagged site (STS) marker developed for the *Lr1* gene (Cloutier et al. 2007). Additionally, in order to map *Lr17a* a subset of F_2 plants, which did not possess *Lr1* in their genetic backgrounds, were selected to test microsatellite markers that mapped to wheat chromosome 2AS. Based on the Wheat Consensus SSR Map, seven microsatellite markers *Xbarc212, Xcfd36, Xgwm71, Xgwm296, Xgwm448, Xgwm614* and *Xwmc598* were used for genotyping the population. Bulk segregant analysis (BSA) was used to identify microsatellite marker(s) linked to the disease resistance genes (Somers et al. 2004). Each bulk consisted of DNA from five individual plants from homozygous resistance or susceptible $F_{2:3}$ families. Polymerase chain reaction (PCR) assays, were performed in 20 µl reaction volumes each con-

taining 2 µl genomic DNA (50 ng). The PCR products were separated by 2% agarose gel. The gels were visualized by ethidium bromide solution and were read by Biometra Gel Documentation Model UVsolo. Thatcher and the Thatcher line with *Lr17a* were used as negative and positive controls, respectively. To map *Lr17a*, the SSR markers that were polymorphic between parents and two bulks were run on capillary fragment analysis system. Twenty microliters of the reaction consisted of 2 µl genomic DNA (50 ng/µl), 2 µl 10× PCR buffer, 2 mM dNTPs, 1 pmol of M13-tailed forward primer, 5 pmol of reverse primer, 5 pmol of M13 primers labeled with 6-FAM (6-carboxyfluorescein) were run on ABI (Applied Biosystems). A touch-down PCR program was applied by initial denaturation at 95°C for 10 min, followed by 10 cycles of touch down program of denaturation at 94°C for 1 min, annealling at 60°C for 1 min and extension at 72°C for 1 min. Each cycle reduced the anealling temperature by 0.5°C with the final 30 cycles at 55°C annealing temperatures. A final elongation step in which temperature was set at 72°C for 5 min completed the reaction. The correct amplicon size of the polymorphic marker for the parents and the control lines was determined using an ABI system and Gene Mapper software.

For the allelism test, the presence/absence of *Lr26* in Marvdasht was determined using *Iag95,* a STS marker which was developed to identify *Lr26* (Mago et al. 2005). The marker was tested on Marvdasht and bulked DNA of resistant and susceptible F_2 plants. The Thatcher line with *Lr26* and Thatcher were used as positive and negative controls, respectively.

Results

Segregation of resistance in Bolani × Marvdasht

Among 182 F_2 plants tested with 84-1 in the BM-1 population, 165 were resistant and 17 were susceptible (Table 3). Chi-square analysis of the phenotypic disease reactions fit a segregation ratio of 15 resistant : 1 susceptible in this F_2 population (χ^2= 2.97; P < 0.05). This result indicated the presence of two dominant genes in the cultivar 'Marvdasht' conferring resistance to *P. triticina* isolate 84-1. Among 125 F_3 families, 61 were homozy-

Table 3. Goodness-of-fit of F_2 progeny of Bolani × Marvdasht and F_2 progeny of Falat × Marvdasht. Segregating for infection type to pathotypes 84-1 and 85-28 of *Puccinia triticina*

Parent / Cross	Generation	Tested pathotype	No. plants/families			Ratio	χ^2
			Res	Seg.	Susc.		
Marvdasht	P1	84-1	35				
Bolani	P2	84-1			40		
Bolani × Marvdasht	F2	84-1	165		17	15:1	2.97*
Bolani × Marvdasht	F3	84-1	61	52	12	7:8:1	4.75**
Marvdasht	P1	85-28	32				
Falat	P2	85-28	28				
Falat × Marvdasht	F2	85-28	199		19	15:1	2.62**

*= non-significant in α = 5%
**= non-significant in α = 1%

gous resistant, 52 were segregating and 12 were homozygous susceptible. Chi-square test fit a genotypic segregation ratio of 7 homozygous resistant, 8 heterozygous: 1 homozygous susceptible in this F_2 population (Table 3). This result suggested a digenic inheritance model for resistance to isolate 84-1 in the population of Marvdasht × Bolani.

Allelism tests between 'Marvdasht' and 'Falat'

An allelic test was conducted to determine the relationship between the resistance gene(s) in 'Marvdasht' and *Lr26* that is present in 'Falat' (Table 3). The segregation pattern observed for the reaction of the F_2 population derived from the cross 'Marvdasht' (R) × 'Falat' (R) to isolate 85-28 fit a 15 resistant : 1 susceptible segregation ratio (Table 3) indicating the presence of two dominant genes segregating for resistance. Thus, both of the resistance genes present in 'Marvdasht' are independent of *Lr26* in 'Falat'.

Molecular studies

Molecular marker analysis was done to further validate the presence of the postulated leaf rust resistance gene *Lr1*, and to map *Lr17a*, another candidate conferring resistance to leaf rust in Marvadasht. Initially, to find the molecular marker linked to gene *Lr17a*, a total of 160 F_2 plants from Bolani × Marvdasht were screened for the presence/absence of *Lr1* using STS marker *RGA-567-5* (Fig. 1). In the second step, a subset of 54 F_3 families including 42 resistant and segregating families without *Lr1*, and 12 susceptible families (without *Lr1* and *Lr17a*) were selected to map *Lr17a*. Using nine SSR markers tested on DNA of Marvdasht, Bolani, bulked DNA of 5 F_3 resistant plants, bulked DNA of 5 susceptible F_3 plants, Thatcher (as negative control) and the Thatcher line with *Lr17a* (as positive control), resistance gene *Lr17a* was mapped to the distal end of chromosome 2AS. Microsatellite marker *Xbarc212* was linked to *Lr17a* (Fig. 2). In a subset of population BM-2, *Xbarc212* was 3.7 cM distal to *Lr17a* gene. Analysis of the results of ABI 3730 fragment analyzer, by means of Gene Mapper software, showed that Marvdasht and

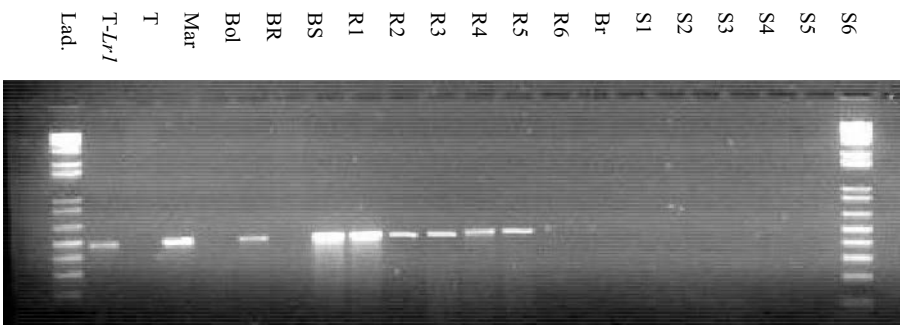

Figure 1. The results of 2% agarose gel electrophoresis of the amplification products obtained from DNAs of T-*Lr1* (Thatcher+*Lr1*), T (Thatcher), Mar (Marvdasht), Bol (Bolani), BR (bulked of resistant families), BS (bulked of susceptible families), individual resistant plants (R1–R6) and individual susceptible plants (S1–S6) with the use of *RGA-567-5*

Bolani cultivars amplified *Xbarc212*$_{235}$ and *Xbarc212*$_{245}$, respectively. However, Thatcher and the Thatcher line with *Lr17a* amplified *Xbarc212*$_{243}$ and *Xbarc212*$_{227}$, respectively.

The STS marker *Iag95* was used to reconfirm the presence/absence of *Lr26* in Marvdasht. DNA of Thatcher (negative control), Marvdasht and bulked DNA derived from Falat × Marvdasht did not amplify any band but the specific band was amplified in the Thatcher line with *Lr26* used as positive control (Fig. 3).

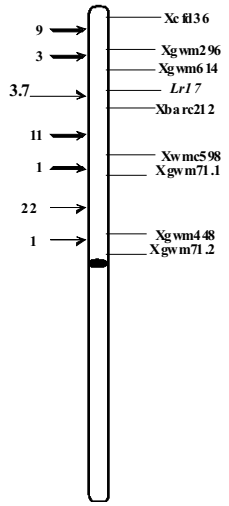

Figure 2. Mapping of *Lr17a* on the short arm of chromosome 2A. The linkage map shows SSR marker *Xbarc212* at the distance of 3.7 cM from *Lr17a* locus. Map distances are according to wheat consensus SSR maps (Somers et al. 2004)

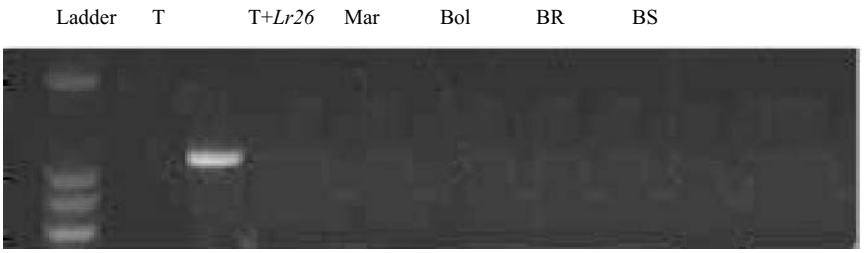

Figure 3. The results of 2% agarose gel electrophoresis of the amplification products obtained from DNAs of T (Thatcher), T+*Lr26* (Thatcher+*Lr26*), Mar (Marvdasht), Bol (Bolani), BR (bulked of resistance families) and BS (bulked of susceptible families) with the use of *Iag-95* marker

Discussion

Information on the genetics of resistance to *Puccinia triticina* in *T. aestivum* L. can facilitate efficient *Lr* gene exploitation leading to the development of wheat cultivars with

broad based resistance. Combination of several effective resistance genes into a single cultivar can extend the period of rust resistance since mutation at several avirulence loci would be required to produce new virulent isolates (Mesterházy et al. 2000). Although it is possible to hypothesize which *Lr* resistance genes may be present in a given wheat cultivar based on pedigree analysis and field disease reactions, the specific number and identity of resistance genes in wheat cultivars only be determined conclusively by genetic analysis (Kolmer 1996). Basically, genetic studies and analysis of breeding generations such as F_2, F_3 or back-cross populations are conducted to identify the resistance gene(s) present in different cultivars. They are also useful to determine if the resistance gene(s) carried by a specific cultivar represents a newly identified resistance gene or is allelic with a previously identified resistance gene. Marvdasht, an Iranian wheat cultivar released in 1992, has been hypothesized to possess *Lr1* and *Lr17a*, two seedling genes for resistance to *P. triticina* (Rafiei et al. 2007). The $F_{2:3}$ genetic analyses indicated that Marvdasht carried two dominant *Lr* genes conferring resistance to pathotype 84-1 of *P. triticina*. According of the gene-for-gene hypothesis complementary pairs of dominant genes must be present in the host and pathogen (Flor 1971). These data suggested that resistance was determined by *Lr1* and *Lr17a* to isolate 84-1. The result is consistent with the result of Gupta et al. (1995) and Khanna and et al. (2005) who reported a15 (R):1 (S) phenotypic ratio and 7:8:1 ratio for resistance to leaf rust pathogen in F2 and F3 populations, respectively.

The rust resistance genes in the Petkus-derived 1RS chromosome are *Lr26, Sr31* and *Yr9* that impart resistance to leaf rust, stem rust and stripe rust, respectively (McIntosh et al. 2005). Chi-square analysis in the study of allelism in the cross Marvdasht × Falat fit a phenotypic segregation ratio of 15 resistant : 1 susceptible for the reaction to pathotype 85-28 of *P. triticina* indicating that the resistance genes present in Marvdasht are different from *Lr26* that is present in Falat. Lack of any amplified DNA using *Iag95,* an STS marker developed to identify *Lr26* (Mago et al. 2005) in Marvdasht and bulked DNA of resistant F_2 plants, confirmed the absence of this widely distributed gene in Marvdasht (Fig. 3).

Pedigree analysis showed that Falat cultivar possesses *Lr23* as another source of resistance to leaf rust pathogen. Based on multipathotype tests it was concluded that *Lr23* could not be present in Marvdasht cultivar. Because during greenhouse tests, an isolate of *P. triticina* was found which was virulent on the Thatcher line with *Lr26* and Marvdasht but avirulent on Falat and Thatcher line with *Lr23* (Rafiei et al. unpublished data).

The information of inheritance patterns of resistance genes is useful to breeders in applying special schemes in breeding programs. In breeding for resistance, backcrossing is the major approach for introducing resistance into an otherwise superior cultivar. The result of present study revealed the dominant inheritance of all of the *Lr* resistance genes identified in Marvdasht and Falat cultivars. This dominant inheritance will facilitate introgression of *Lr* genes present in these cultivars.

The *Lr1* gene, which originated from cv. Malakoff was located on the long arm of chromosome 5D and is currently found in many wheat cultivars. Although this gene is not highly effective against currently existing races of the pathogen, it can be successfully used in breeding programs in combination with other *Lr* genes (McIntosh et al. 1995; Singh and Rajaram 1991).

Exploitation of the resistance gene *Lr17a* is more desirable compared to *Lr1* and *Lr26* which conferred low protection and moderate resistance to leaf rust populations present in Iran, respectively.

The *Lr17* resistance gene was mapped on the short arm of wheat chromosome 2AS in 1977 (Dyck and Kerber 1985; McIntosh et al. 1995). Monosomic analysis revealed that the Australian wheat cultivar Harrier carried a seedling leaf rust resistance gene (tentatively designated *LrH*) which was located on chromosome 2A (Singh et al. 2001). *LrH* failed to segregate independently from *Lr17*. Therefore, *Lr17* was re-designated *Lr17a* and the new allele designated as *Lr17b*. The seedling resistance gene *Lr17a* was attributed to resistance of a number of wheat cultivars in Australia, CIMMYT, the Indian continent, South America, UK and the hard red winter wheat region of the United States (McIntosh et al. 1995).

Up to now, the near-isogenic line carrying *Lr17a* had a high level of resistance to leaf rust populations distributed in different parts of Iran (Rafiei et al. unpublished data). Also, wheat cultivars carrying *Lr17a* displayed adequate protection against wheat leaf rust pathogen in some other Middle East countries (Al-Maaroof et al. 2005). Genetic analysis conducted in this study determined that *Lr17a* is likely present in Marvdasht. The BSA and microsatellite primer screens (located on three different deletion bands of chromosome 2AS) of the F_2 subpopulation of Marvdasht × Bolani *Lr17a* was mapped to the distal region of chromosome 2AS. The SSR marker-*Xbarc212* was found to be linked to *Lr17a* with genetic distance of 3.7 cM. Near-isogenic lines (NILs) of Thatcher and the Thatcher line with *Lr17a* as negative and positive controls, respectively, produced different size of amplification by *Xbarc212* marker. Polymorphic fragments which were amplified between NILs Thatcher and the Thatcher with *Lr17a* by using *Xbarc212* showed that this PCR-based microsatellite marker can be applied in wheat breeding programs effectively. Recently two separate studies have been reported linked SSR markers to *Lr17*a gene (Zhang et al. 2008; Bremenkamp-Barrett et al. 2008). Zhang et al. (2008) showed *Lr17a* is closely linked to SSR marker *Xgwm636* at a distance of 4 cM. Bremenkamp-Barrett et al. (2008) using SSR markers on F_2 lines made from a cross of Chinese Spring and Thatcher-*Lr17a* showed that SSR markers *Xgwm614* and *Xwmac407* flanked *Lr17a* at genetic distances of 0.7 and 2.5 cM, respectively.

Field and molecular studies showed Marvdasht cultivar carries *Lr13* and *Lr46* as source of adult plant resistance to leaf rust pathogen (Rafiei et al. unpublished data). Conclusively, Marvdasht could be a suitable candidate in breeding programs conducted for resistance to leaf rust in Iran.

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