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H. El Attari · A. Rebai · P. M. Hayes
G. Barrault · G. Dechamp-Guillaume · A. Sarrafi

Potential of doubled-haploid lines and localization of quantitative trait loci (QTL) for partial resistance to bacterial leaf streak (*Xanthomonas campestris* pv. *hordei*) in barley

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Abstract Genetic variability for partial resistance to bacterial leaf streak in barley, caused by *Xanthomonas campestris* pv. *hordei*, was investigated in 119 doubled-haploid lines (DH) developed by the *Hordeum bulbosum* method from the F_1 progeny of the cross between two cultivars, 'Morex' (resistant) and 'Steptoe' (susceptible). Two experiments were undertaken in a randomized complete block design with three replicates, in a controlled growth chamber. Twenty seeds per replicate were planted in plastic containers ($60 \times 40 \times 8$ cm) containing moistened vermiculite. At the two-leaf stage seedlings were inoculated with an Iranian strain of the pathogen. Genetic variability was observed among the 119 DH lines for partial resistance to the disease. Some DH lines were significantly more resistant than 'Morex' (resistant parent) to bacterial leaf streak. Genetic gain in percentage of resistant parent for 5% of the selected DH lines was significant (47.70% and 33.72% in the first and the second experiment, respectively). A QTL analysis of bacterial leaf streak resistance showed that three QTLs were detected on chromosomes 3 and 7. Multilocus allelic effects of the three QTLs account for almost 54% of the mean difference between the parents and nearly 30% of the phenotypic variation of the trait in the mean experiment. The resistance locus on chromosome 3, near *ABG377*, apprears to be a major gene.

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H. El Attari · A. Rebai · G. Barrault
G. Dechamp-Guillaume · A. Sarrafi (✉)
Ecole Nationale Supérieure Agronomique de Toulouse,
Institut National Polytechnique (ENSAT-INP),
145, Avenue de Muret, F-31076 Toulouse-Cédex, France
Fax: + 33(0)562136564
E-Mail: sarrafi@ensat.fr.

P. M. Hayes
Department of Crop and Soil Science, Oregon State University,
Corvallis, OR 97331, USA

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Introduction

Pathovars of *Xanthomonas campestris* are the causal agents of bacterial leaf streak of cereals. The disease is found over a range of very different conditions such as irrigated fields in temperate climates, high-rainfall subtropical highlands and warm environments (Duveiller, 1994). The foliar expression of the disease is characterized by longitudinal stripes that extend between the leaf veins and by the production of milky exudates under humid conditions (Duveiller et al. 1993).

Bacterial leaf streak is present in many countries all over the world (Akhtar and Aslam, 1985). Under favourable conditions losses attributable to this disease can reach 40% in susceptible triticale (Schaad and Forster 1985) and wheat (Cunfer 1988) cultivars. The disease also reduces grain weight and protein content of the grain (Shane et al. 1987). Transmission of the disease on a large scale is due to the seed-borne nature of the pathogen (Sands et al. 1986; Duveiller 1989).

There are differences between wheat genotypes in their susceptibility to bacterial leaf streak, and resistance is incomplete (Duveiller 1990). The inheritance of resistance to *Xanthomonas campestris* pv. *translucens* from three resistant triticale lines showed that it was conferred by a single dominant gene (Johnson et al. 1987). A study of parental genotypes, F_1 plants and F_3 families showed that five genes were involved in resistance to *Xanthomonas campestris* pv. *undulosa* in bread wheat (Duveiller et al. 1993). Additive genetic effects, which are important in predicting the progeny performance of crosses, were reported in barley by Arabi et al. (1990) for partial resistance to net bloch and by Alizadeh et al. (1994) for resistance to bacterial leaf streak in barley. The susceptibility of wheat to bacterial

leaf streak is similar under field and greenhouse conditions (Akhtar and Aslam 1986).

Doubled-haploid (DH) plant production provides a fast way for obtaining completly homozygous progenies from selected crosses. Additionally, since all the alleles of DH lines are fixed, selection for quantitative characters is often more reliable than in conventional populations (Choo et al. 1985). Bedo et al. (1992) have reported that some DH lines derived from F_1 hybrids have surpassed the better parent for protein and gluten contents and gluten extention. Simmonds et al. (1993) have shown that approximately one-half of the DH lines from a cross between two varieties resistant and susceptible to Fusarium head blight were resistant to the disease. Steffenson et al. (1995) have reported that a few high yielding DH lines obtained from a cross between two genotypes resistant or susceptible to leaf rust, stem rust and powdery mildew were resistant to all of these diseases.

The development of quantitative trait loci (QTL) mapping analyses has provided an alternative approach to locating and subsequently manipulating resistance genes related to powdery mildew and stripe rust in barley (Huen 1992; Chen et al. 1994, respectively), powdery mildew in mungbean (Young et al. 1993), downy mildew in sunflower (Mouzeyar et al. 1995) and important agronomic characters in barley (Backes et al. 1995).

The objective of the investigation presented here was to evaluate the variability and genetic gain for partial resistance to bacterial leaf streak due to *Xanthomonas campestris* pv. *hordei* in doubled-haploid lines obtained from F_1 progeny of a cross between two barley varieties resistant and susceptible to the disease. We also carried out a QTL mapping analysis to characterize genomic regions involved in bacterial leaf streak. The locations of detected QTLs were compared to those of QTLs influencing agronomic, quality and disease resistance traits mapped in other studies.

Materials and methods

A population of 119 doubled-haploid lines developed by the *Hordeum bulbosum* method (Chen and Hayes 1989) from the F_1 progeny of the 'Steptoe' × 'Morex' cross were used in this experiment. 'Steptoe' is a high-yielding, broadly adapted six-row feed-type barley developed at the Washington State University (Seattle, Wash., USA). 'Morex' is a six-row spring malting barley released by the Minnesota Agricultural Experiment Station in 1978. Our preliminary experiments showed that 'Steptoe' is susceptible to bacterial leaf streak caused by *Xanthomonas campestris* pv. *hordei* and 'Morex' is resistant to this disease. Two successive experiments, each in a randomized complete block design with three replicates, were performed in a growth chamber. Twenty seeds per replication per genotype were sterilized with sodium hypochlorite solution (6 chlorimetric degrees) for 5 min, washed several times in sterile distilled water and then planted in plastic containers ($60 \times 40 \times 8$ cm) containing moistened vermiculite. At the two-leaf stage, seedlings were enclosed in a special transparent cover (plexiglass) for 24 h in order to create saturating moisture favourable for bacterial inoculation. The inoculation was then carried out by spraying bacterial suspension of an Iranian strain of the pathogen (IBLS8) standarized at about 10^8 colony-forming units per milliliter. This strain was isolated from a barley variety grown in southeastern Iran and identified as *Xanthomonas campestris* pv. *hordei* (Alizadeh and Rahimian, 1989). In order to maintain the high activity of the strain, we maintained the colonies on nutrient agar medium (Difco) with transfers being made every 4 days at $25^\circ \pm 1^\circ$C and keeping cultures in the dark for 24 h. The cultures were used directly or stored under optimal conditions of virulence at $4^\circ \pm 1^\circ$C.

Scoring was performed 12 days after inoculation. The first leaf of the seedling was stored to determine the proportion of diseased leaf area (water-soaking and translucent spots or stripes). The host reaction was rated from 1 (resistant) to 9 (susceptible) in proportion to the leaf area showing symptoms, as proposed by Alizadeh et al. (1994). Intensity values did not require any transformation to normalize the distribution. Statistical analyses were carried out in order to determine the effect of genotype on partial resistance in both experiments. The Newman – Keuls test was used for comparing the means of parents and DH lines. The mean of the 119 DH lines and that of the parents was also compared. The most resistant DH line as well as the 5% of DH lines showing the highest partial resistance to the pathogen (low values) were compared with the resistant parent. Genetic gain in percentage of the resistant parent was also determined for the above-mentioned selected lines.

For QTL analyses we used 223 marker loci which had (previously) been mapped in the 'Steptoe' × 'Morex' populations by Mather (1995). The map, having an average marker density of 6 cM, is available under the Graingenes database. The reader is referred to this database and to Kleinhofs et al. (1993) for a comprehensive discussion and presentation of the map.

The MQTL software (Tinker and Mather 1995) was used for QTL mapping. We performed simple interval mapping (SIM) and simplified composite interval mapping (sCIM) on both experiments and on their means. SCIM uses background markers to account for other QTLs on the genome and thus gives a better resolution of multiple-linked QTLs. For sCIM, a single set of 48 (5–8 per chromosome) uniformly spaced background markers were chosen and used throughout the analysis, with a marker each 25 cM on average. Significance thresholds for SIM and sCIM tests were calculated by permutations using MQTL.

Results and discussion

Analyses of variance of the 119 DH lines and their parental varieties 'Morex' and 'Steptoe' showed a high significant genotype effect in both experiments (data not presented). The genetic variability of the parental genotypes and DH lines for partial resistance to *Xanthomonas campestris* pv. *hordei* in two experiments are presented in Table 1. In both experiments 'Morex' showed a high level of partial resistance when compared with 'Steptoe', the other parental genotype, which confirms a previous finding (Alizadeh et al. 1994). Some DH lines like DH-11 and DH-30 were highly resistant to bacterial leaf streak in both experiments and others like DH-112 and DH-126 were highly susceptible. These results indicate that genotype is thus a major determinant of resistance to bacterial leaf streak. Several reports have also shown the genetic variability of partial resistance to bacterial leaf streak in wheat (Milus and Kirkpartick 1990; Duveiller et al.

Table 1 Partial resistance[a] of parental genotypes and DH lines to *Xanthomonas campestris* pv. *hordei*

Variety or DH	Experiment 1	Experiment 2	Variety or DH	Experiment 1	Experiment 2
Morex	2.83c	2.53c	DH-112	7.73i	7.02k
Septoe	6.46h	6.38i	DH-116	6.87h	6.47j
DH-1	5.30f	4.90g	DH-120	7.37i	6.88k
DH-2	6.36g	6.25j	DH-124	2.44b	2.30c
DH-3	4.60e	4.46f	DH-125	5.73g	6.51i
DH-5	5.75g	5.87i	DH-126	7.31i	7.07k
DH-7	2.49b	3.09b	DH-127	3.17f	3.00b
DH-10	7.89i	6.94k	DH-129	5.17f	5.67g
DH-11	1.39a	1.23a	DH-130	3.53d	2.93b
DH-12	5.90g	5.70i	DH-132	3.48d	3.27c
DH-14	4.98f	4.05f	DH-133	3.26c	4.40e
DH-16	3.53d	3.75d	DH-134	3.36c	3.19d
DH-20	2.78c	3.19c	DH-135	4.79e	5.69i
DH-21	4.33e	3.98d	DH-136	7.16h	6.76k
DH-22	5.94g	5.52h	DH-137	3.53d	4.06f
DH-23	7.57I	6.73j	DH-139	6.71h	6.24j
DH-24	2.68b	2.63c	DH 141	5.50f	5.28h
DH-25	3.69d	4.46e	DH-143	2.22b	2.33c
DH-27	6.21g	5.57h	DH-144	6.20g	6.56j
DH-30	1.27a	1.16a	DH 145	7.20i	7.01j
DH-31	5.00f	5.54g	DH-146	5.13f	4.78g
DH-32	6.19g	6.16i	DH-147	3.55d	3.97d
DH-35	6.66h	5.90i	DH-149	1.93a	1.59a
DH-40	6.17g	5.61h	DH-150	4.96f	4.72g
DH-41	5.44f	5.00g	DH-151	7.99j	8.12k
DH-42	6.98h	6.27j	DH-152	7.10i	6.45h
DH-43	6.13g	6.84k	DH-153	5.62g	6.39h
DH-50	1.66a	2.83b	DH-154	4.94f	5.78g
DH-54	5.31f	5.40g	DH-155	5.51f	4.47e
DH-55	5.29f	5.53g	DH-156	7.07i	6.51i
DH-56	7.04h	6.75j	DH 157	5.13f	6.70i
DH-57	1.40a	2.05a	DH-158	2.99c	2.93b
DH-58	5.56f	6.35j	DH-159	6.05g	7.05i
DH-59	5.40f	5.66i	DH-160	5.43f	5.39h
DH-61	1.37a	2.12a	DH-162	6.18g	6.69i
DH-63	4.46e	4.50f	DH-164	1.78a	1.91b
DH-64	6.14h	6.89i	DH-166	4.01d	3.81d
DH-67	3.78d	3.51c	DH-167	5.38f	6.37h
DH-68	5.00f	5.26f	DH-168	3.20c	3.58c
DH-69	5.97g	5.13f	DH-169	3.50d	4.60e
DH-70	7.19i	7.26k	DH-170	2.66b	3.04b
DH-71	6.38h	7.13j	DH-171	6.07g	6.19h
DH-72	6.02g	6.62j	DH-172	1.40a	2.18a
DH-74	3.50d	3.61e	DH-173	6.81h	6.86i
DH-75	5.58f	6.24j	DH-174	3.03c	3.48c
DH-76	4.77e	4.88g	DH-176	6.37h	6.45h
DH-78	2.77c	3.44c	DH-179	7.03i	7.10j
DH-79	2.87c	4.17d	DH-180	6.52h	7.39j
DH-81	5.03f	6.03i	DH-181	7.22i	6.77i
DH-82	4.90e	5.57i	DH-182	6.15g	6.73i
DH-83	6.23g	5.82i	DH-184	3.37c	2.28a
DH-85	4.76e	5.29h	DH-185	5.40f	6.29h
DH-87	5.95g	6.07i	DH186	6.64h	7.05i
DH-88	8.18j	7.14k	DH-187	6.09g	6.71i
DH-89	7.61j	6.30j	DH-188	4.06d	3.77d
DH-91	3.12c	4.68g	DH-194	5.37f	6.70i
DH-92	7.02h	5.63i	DH-196	6.87h	6.63j
DH-93	6.32g	5.86i	DH-197	7.28i	7.83k
DH-103	2.42b	3.50c	DH-198	6.33h	6.37h
DH-105	4.65e	4.56e	DH-200	3.56d	4.13f
DH-110	5.29f	7.28j			

[a] Means with the same letter do not differ significantly at $P = 0.05$. The values represent the mean of the host reaction rate, scale range 1 to 9, from three replications

Table 2 Genetic gain for partial resistance to bacterial leaf streak in DH lines of barley. The values represent the mean of the host reaction rate, scale range 1 to 9, from three replications

Parent or DH lines	Experiment 1	Experiment 2
Steptoe (P1)	6.46	6.38
Morex (P2)	2.83	2.53
P1-P2	3.63*	3.85*
$\bar{X}P = (P1 + P2/2)$	4.64	4.45
$\bar{X}DH$[a]	5.06	5.2
$\bar{X}DH$-$\bar{X}P$	0.42 NS	0.75*
Best DH (BDH)	1.27	1.16
BDH-Best parent (BP)[b]	− 1.56*	− 1.37*
100(BDH-BP)/BP = GG[c]	− 55.12*	− 54.15*
5% Selected DH (5% SDH)	1.48	1.67
5% SDH-BP	− 1.35*	− 0.85*
100(5%SDH-BP)/BP = GG	− 47.70*	− 33.72*
Least significant difference LSD	0.71	0.55

* Significant at P, 0.05; NS, not significant
[a] $\bar{X}DH$, Mean of all doubled-haploid lines
[b] BP, Best parent ('Morex')
[c] GG, Genetic gain when the best DH line or 5% of the selected DH lines are compared with the best parent ('Morex')

1993) and in barley (Kim et al. 1982; Noval 1989; Alizadeh et al. 1994).

The difference between DH lines and their parents was not significant in the first experiment but significant in the second one, showing that the 119 randomized DH lines used in these experiments are not quite representative of the total number of DH lines of the cross 'Morex' × 'Steptoe'.

The comparison between the best parent and the best DH line showed a significant difference for resistance to bacterial leaf streak in both experiments with genetic gains of 55.12% and 54.13% in the first and second experiment, respectively (Table 2). This phenomenon might be due to the accumulation of favourable alleles for resistance in this DH line. The same phenomenon was observed when the best parent was compared with the mean of 5% selected DH lines; the genetic gains are 47.70% and 33.72% in the first and second experiment, respectively.

The use of DH lines in plant breeding has been already reported by several authors. For example, favourable DH lines resistant to Fusarium head blight in wheat (Simmonds et al. 1993) and DH lines resistant to leaf rust, stem rust and powdery mildew in barley (Steffenson et al. 1995) have been mentioned. The present results indicate that a high genetic variability for partial resistance to bacterial leaf streak caused by *Xanthomonas campestris* pv. *hordei* can be obtained in DH lines coming from F_1 progeny of resistant and susceptible genotypes and that significant genetic gain can be obtained by selecting the most partial resistant lines. Finally, doubled-haploid production can be considered as an efficient method for breeding disease-resistant genotypes.

As far as QTL analyses are concerned, the threshold values at a 5% significance level computed over 10,000 permutations were very similar for both experiments. Values of 12.7 and 36.8 were used for SIM and sCIM tests, respectively.

In both experiments we found strong evidence for the presence of two QTLs, about 60 cM apart, on chromosome 3. These QTLs were detected with almost the same effects and positions in the two experiments (Table 3) and are in coupling phase. Figure 1 shows the test profile for the mean over the two experiments, the profiles for each experiment being very similar. The sCIM method gives two major peaks, indicating the likely positions of the QTLs, whereas SIM gives three peaks. The peak located at position 43.3 cM (midway between the two QTLs) is very likely to be a 'ghost' QTL.

Allele substitution effects and positions relative to markers of the two QTLs on chromosome 3 are given in Table 3. Both QTLs had relatively strong effects, accounting for about 13% and 20% (respectively) of the variation in disease severity in the entire population. As expected, the susceptible parent ('Steptoe') contributed the positive value allele; QTL allele values are 0.64 and 0.80 in rating units (for the mean

Table 3 Mapping positions and effect of QTL detected on chromosome 3

Experiments	Position in centiMorgans[a]	sCIM test	QTL effect[b]	Marker interval[c]
1	13.6	39.6	0.68	ABA307B-**ABC171**
	76	55.3	0.81	**ABG377**-MWG555B
2	13.6	43.0	0.61	ABA307B-**ABC171**
	77	68.6	0.82	**ABG377**-MWG555B
1 + 2	13.6	44.2	0.64	ABA307B-**ABC171**
	77	63.9	0.80	**ABG377**-MWG555B

[a] From the leftmost marker of the chromosome
[b] Allele substitution effect of 'Steptoe' in rating units
[c] Nearest marker in *boldface*

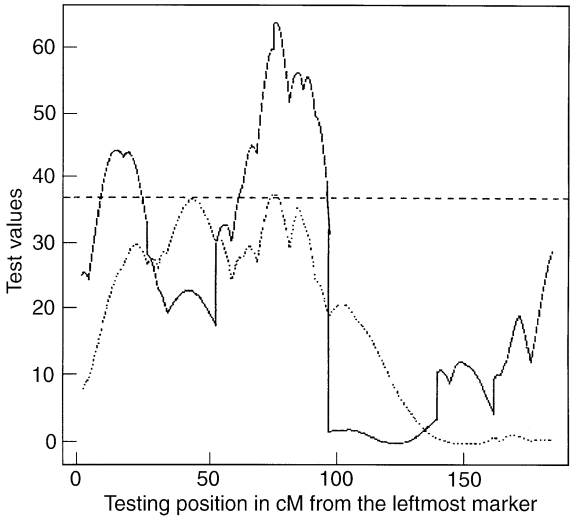

Fig. 1 Profiles of test values for sCIM (*solid line*) and SIM (*dashed line* for *chromosome* 3). The *straight line* is the threshold value for sCIM test

experiments). The estimated location of the first QTL is 3 cM from marker *ABC171* in a region where QTLs have been detected (in the 'Steptoe' × 'Morex' population) for tiller number rand malt extract (near marker *ABG471*, 17 cM from marker *ABC171*, Han et al. 1995; Hayes et al. 1996). The second QTL is located in the long arm of chromosome 3 (4 cM from marker *MWG555B*) in the vicinity of QTLs acting on grain weight and about 60 cM far from a net blotch resistance QTL.

Another QTL was detected for experiment 2 on chromosome 7 at position 167.1 cM, 2 cM from marker *ABC155*. For the mean of the two experiments, a peak was found at position 167.1 cM, but the sCIM test value was 35.4 (one unit under the threshold) and the QTL substitution effect was -0.55. Experiment 1 gave a non-significant peak at 177.6 cM, near marker *ABG391*. Note that this QTL was not detected in either experiments (nor the mean) by the SIM method (low test values). This putative QTL mapped to a chromosome region in the vicinity of marker *ABG495A* (10 cM from it), where QTLs have been reported for kernel weight, and 80 cM from a marker (*CDO057*) linked to a major QTL of stripe rust resistance (Chen et al. 1994).

We calculated the multilocus allelic effects of the three QTLs and found that they accounted for almost 54% of the mean difference between the parents and nearly 30% of the phenotypic variation of the trait in the mean experiment. The resistance locus on chromosome 3, near *ABG377*, appears to be a major gene. Further investigations with additional markers in the region and measurements of other traits are needed to characterize the action of these QTLs and to assess the importance of their linkage with agronomic, quality and other disease resistance QTLs.

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