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Molecular mapping and identification of QTL's associated to oat crown rust partial resistance

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Summary

Molecular mapping is a promising strategy for studying and understanding traits with complex genetic control, such as partial resistance to oat crown rust. The objectives of this research were to develop molecular maps from the progenies of the cross UFRGS7 (susceptible) × UFRGS910906 (partially resistant) and to identify QTLs (quantitative trait loci) associated to partial resistance to oat crown rust in two generations of that population. DNA of 86 genotypes of the F_2 and 90 genotypes of the F_6 UFRGS7 × UFRGS910906 population were used to generate AFLP markers. Molecular maps were constructed using Mapmaker Exp. 3.0 and QTLs for partial resistance to oat crown rust were identified with Mapmaker/QTL software. Five hundred and fifty seven markers in the F_2 and 243 markers in the F_6 generations were identified. The F_2 map integrated 250 markers in 37 linkage groups. The F_6 map integrated 86 markers in 17 linkage groups. Five QTLs were identified for partial resistance to oat crown rust in the F_2 generation and three QTLs in the F_6. The QTL identified on F_6 through the PaaaMctt340 AFLP marker showed consistency across two environments and two generations (F_4 and F_6), and appear to have potential for marker-assisted selection in oat.

Introduction

Cereal rusts are amongst the most harmful diseases. In particular, oat crown rust, caused by *Puccinia coronata* f. sp. *avenae*, results in great damages to the culture (Simons, 1985; Ohm & Shaner, 1992; Martinelli et al., 1994). One way to control this disease is through the use of resistant genotypes, which in general present qualitative resistance. This kind of resistance makes a high selection pressure on the fungus population, resulting in an evolution of races that quickly overcomes the resistance of the host, which shows, therefore, little durability. An alternative to increase the durability of the resistance is the use of host partial resistance (Luke et al., 1972; Wilcoxson, 1981; Johnson, 1984; Wang et al., 1994), which is characterized by its complexity, resulting from the interaction of several components: reduction of the number of lesions, increase of the latent period, smaller production of spores, smaller pustule's size and slow progress of the disease, which means a smaller rate of disease development (Parlevliet, 1979).

One of the strategies to study and understand traits with complex control is to develop molecular maps. Using these maps to identify genomic regions associated to traits of interest can aid mainly in the evaluation of diseases that are difficult to be interpreted, due to interactions of the genotype with the environment and different degrees of virulence of the pathogen (Young, 1996).

Oat molecular maps have been built for the diploid and hexaploid genomes. Maps related to the diploid genome AA, were developed from *Avena hirtula* X *A. atlantica* (O'Donoughue et al., 1992; Van Deynze et al., 1995) and *A. strigosa* X *A. wiestti* (Rayapati et al., 1994;

Kremer et al., 2001), presenting seven different linkage groups each. For the genome of the hexaploid oat, the first molecular map obtained was from *Avena byzantina* cv. Kanota by *A. sativa* cv. Ogle (O'Donoughue et al., 1995). New maps were developed from recombinant inbred lines (RILs) of the following crosses "Clintand 64" / "IL865698"; (Jin et al., 2000), "Ogle" / "TAM 0-301" (Portyanco et al., 2001) and "Kanota" / "Marion" (Groh et al., 2001). The "Ogle" / "TAM 0-301" map was used to identify QTLs for seven plant and two grain quality traits (Hoffman et al., 2000).

Mapping of disease resistance traits has been done for several crops as in barley for leaf blast (Sato et al., 2001) and leaf rust (Kicherer et al., 2000; Qi, et al., 1999), in soybean for *Sclerotinia sclerotiorum* (Arahana et al., 2001), in rice for rice blast (Guo-Liang et al., 1994), in oat for barley yellow dwarf virus (Jin et al., 1998) and in corn for *Puccinia polysora* (Brunelli, et al., 2002). Three QTL's for partial resistance to crown rust were identified in oat RILs from the cross "MN841801-1" (partially resistant) × "Noble-2" (susceptible) (Chen et al., 2000).

Mapping of the hexaploid cultivated oat is complicated due to the size of its genome and due to its polyploid nature ($2n = 6X = 42$). Besides being difficult to obtain a complete coverage of the genome, it is also difficult to solve the linkage groups in the 21 expected chromosomes. Part of this difficulty seems to be due to differences in translocations among parental lines of the mapping populations (O' Donoughue, 2000).

The objectives of this work were to develop F_2 and F_6 AFLP molecular maps from UFRGS7 × UFRGS910906 and to identify QTLs associated to partial resistance to crown rust in oat.

Material and methods

F_2 and F_6 generations of the UFRGS7 × UFRGS-910906 population were screened with AFLP markers, based in 86 F_2 and 90 F_6 individuals. The F_2 and F_6 maps generated were used for QTL identification of partial resistance to oat crown rust.

DNA was extracted according to the protocol described by Murray and Thompson (1980), quantified in spectrophotometer and diluted to 250 ng/ul.

Molecular mapping

AFLP markers were obtained following the protocol described by Vos et al. (1995), with some adaptations. Two hundred and fifty nanograms of DNA were first digested with the enzyme *Tru*9I (an isoschizomer of *MseI*) (Promega) for two hours at 60 °C and later with the enzyme *Pst*I (Gibco BRL), for two hours at 37 °C.

Specific forward and reverse adapters (MA 1.1 and 1.2; PA 1.1 and 1.2) (Gibco BRL) were annealed at 65 °C for 10′, 37 °C for 10′ and 25 °C for 10′. The adapters were added to the digested DNA and linked to it during two hours at room temperature, with the aid of the T4 DNA ligase enzyme (Gibco BRL).

The first cycle of amplification, called pre-amplification, was made in a MJ PCT 100 thermocycler for 20 cycles, at 94 °C for 30′, 56 °C for 1′ and 72 °C for 1′. This PCR reaction contained 10 ng of ligated DNA, 37.5 ng of primer P + A; 37.5 ng of primer M + C; 0.8 dNTP mM; 1X Taq DNA polymerase buffer; 1.5 mM of MgCl2; 1U of Taq DNA polymerase.

DNA fragments were amplified with 31 primer combinations for the F_2 and 18 combinations for the F_6 UFRGS7 × UFRGS910906 population (Table 1). The second cycle of DNA amplification, the selective amplification, was done using PCR touch down with cycles at 94 °C for 60′, 65 °C for 60′ and 72 °C for 90′. The annealing temperature started at 65 °C and was reduced 1 °C successively until it reached the temperature of 56 °C which was maintained for the remaining 23 cycles, totalizing 32 cycles. The selective PCR reaction contained 20 ng of pre-amplified DNA, 30 ng of the Pst I primer; 30 ng of the Mse I primer; 1.5 mM of $MgCl_2$; 0.8 dNTP mM; 1X Taq DNA polymerase buffer; and 1 U of Taq DNA polymerase.

The amplified fragments were separated by electrophoresis in 5% polyacrylamide gel (19 bis-acrylamide:1 acrylamide), at 80W, for approximately 2 hours and 30 minutes, accompanied with the marker pGEM (Promega) or DNA Ladder 100pb (Gibco BRL). Gels were silver-stained according to the Silver SequenceTM of Promega Corporation protocol (1996). Two independent readers did visual scoring of the bands on a table with fluorescent light.

Phenotypic analysis of partial resistance to crown rust

To identify marker-trait associations for partial resistance to crown rust in the present study, the F_2 generation (1998) was conducted to F_6 (2000) under natural field conditions for infection. For each generation (F_2 – 1998, F_4 – 1999 and F_6 – 2000) a row of each progeny and parents was sowed, using 20 seeds per row, spaced

Table 1. AFLP primer combinations used during selective PCR of the F_2 and F_6 generations of the UFRGS 7 × UFRGS 910906 population

Generation	Pst I Primer	Mse I Primer
F_2, F_6	P-ATT	M-CTT
F_2, F_6	P-ACA	M-CCC
F_2, F_6	P-ACC	M-CGG
F_2, F_6	P-AGA	M-CAC
F_2, F_6	P-ATT	M-CTC
F_2, F_6	P-AGA	M-CTG
F_2, F_6	P-AAT	M-CAG
F_2, F_6	P-AAA	M-CAC
F_2, F_6	P-ATG	M-CTC
F_2, F_6	P-AAA	M-CGA
F_2, F_6	P-AAC	M-CGA
F_2, F_6	P-ATC	M-CCG
F_2, F_6	P-AAA	M-CTT
F_2, F_6	P-ATT	M-CGA
F_2, F_6	P-ATC	M-CGA
F_2, F_6	P-ATC	M-CAC
F_2	P-AAA	M-CTG
F_2	P-AAT	M-CTG
F_2	P-AAT	M-CTT
F_2	P-AAG	M-CTT
F_2	P-ACC	M-CGA
F_2	P-ACC	M-CCA
F_2	P-AAT	M-CCA
F_2	P-AGG	M-CAC
F_2	P-ATT	M-CTG
F_2	P-AAG	M-CCC
F_2	P-AGC	M-CAC
F_2	P-AAG	M-CCT
F_2	P-AAG	M-CTC
F_2	P-AGG	M-CTG
F_2	P-ACT	M-CAT
F_6	P-AAA	M-CTC
F_6	P-ATC	M-CTC

20 cm between plants and 30cm between rows. Each generation was evaluated weekly during six successive weeks for disease on the main tiller, using the modified Cobb's scale (Peterson et al., 1948). Ten individual plants were scored for the F_4 generation and seven for the F_6.

QTL identification on the F_2 generation was based on individual plants phenotype and genotype. F_4 and F_6 phenotypic data was analyzed with molecular data collected from F_6 RILs for QTL identification on these generations.

Statistical analysis

Markers identified in the F_2 generation were tested for the 3:1 and in the F_6 for 1:1 segregation rate through the chi-square test at a significance level of 5% and one degree of freedom.

Mapmaker EXP 3.0 (Lander et al., 1987) was used for obtaining the F_2 and the F_6 maps. For the F_2 map a LOD 7 and maximum level of recombination 30 cM were used. Mapping of the F_6 was done in two stages: first using a LOD 10 and maximum recombination 30 cM to establish the main groups and, then, by grouping the remaining markers with LOD 7 and maximum recombination 30 cM.

Interval mapping analysis was used for QTL identification to partial resistance to oat crown rust and was accomplished through Mapmaker/QTL (Lander et al., 1987) statistical package.

Results and discussion

Molecular mapping of the F_2

Two hundred and forty three markers were identified in the F_2, giving an average of 7.8 markers per primer combination tested. From the total markers identified, 35 showed distortion of segregation with the χ-square test, representing 14.4% of total. This result agrees with those of Portyanco et al. (2001), which obtained 13% of markers with segregation distortion in the mapping population.

Five hundred and fifty seven AFLP markers, 243 identified in this study and 314 from Thomé (1999), were used for mapping the F_2 UFRGS 7 × UFRGS 910906 population. From these, 250 were integrated into the F_2 map (44.9%), being distributed in 37 linkage groups (Figure 1). The large number of linkage groups found (37), in relation to the number of oat chromosomes ($n = 21$) can be explained due to the size of the oat genome, which requires large number of markers for full coverage and to consolidate smaller linkage groups into 21 expected linkage groups. The first map built for hexaploid oat ("Kanota" X "Ogle") placed markers in 38 linkage groups (O'Donoughue, et al., 1995), in spite of integrating a larger number of markers (532). In a second map built ("Ogle" X "TAM" 0–301) 426 markers were mapped in 34 linkage groups (Portyanco et al., 2001).

On the other hand, our map covered almost the totality of the oat genome extension, that is, according

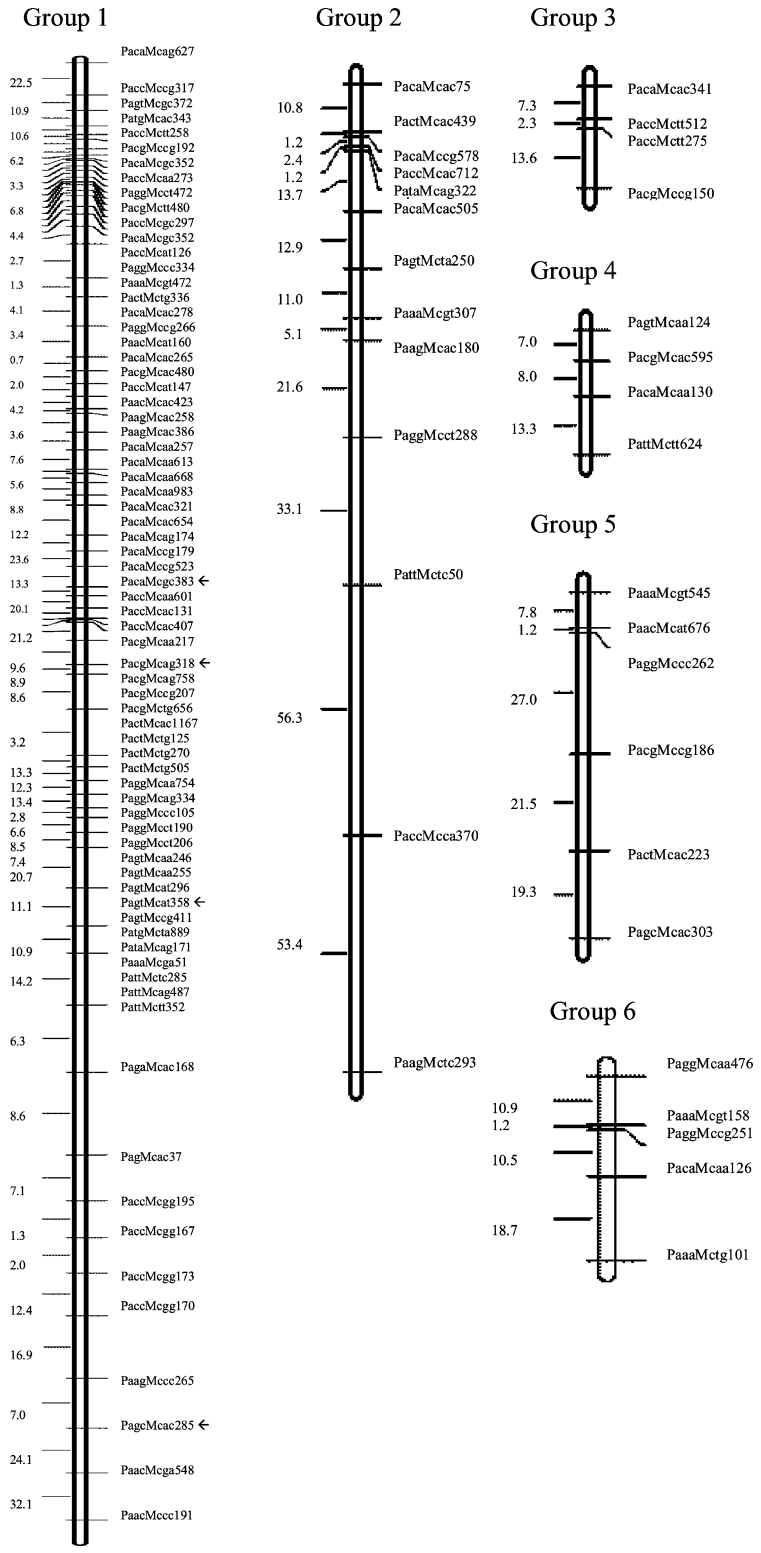

Figure 1. AFLP map of the UFRGS7 × UFRGS910906 F_2 population. The arrowheads indicate the QTL's identified in this generation.

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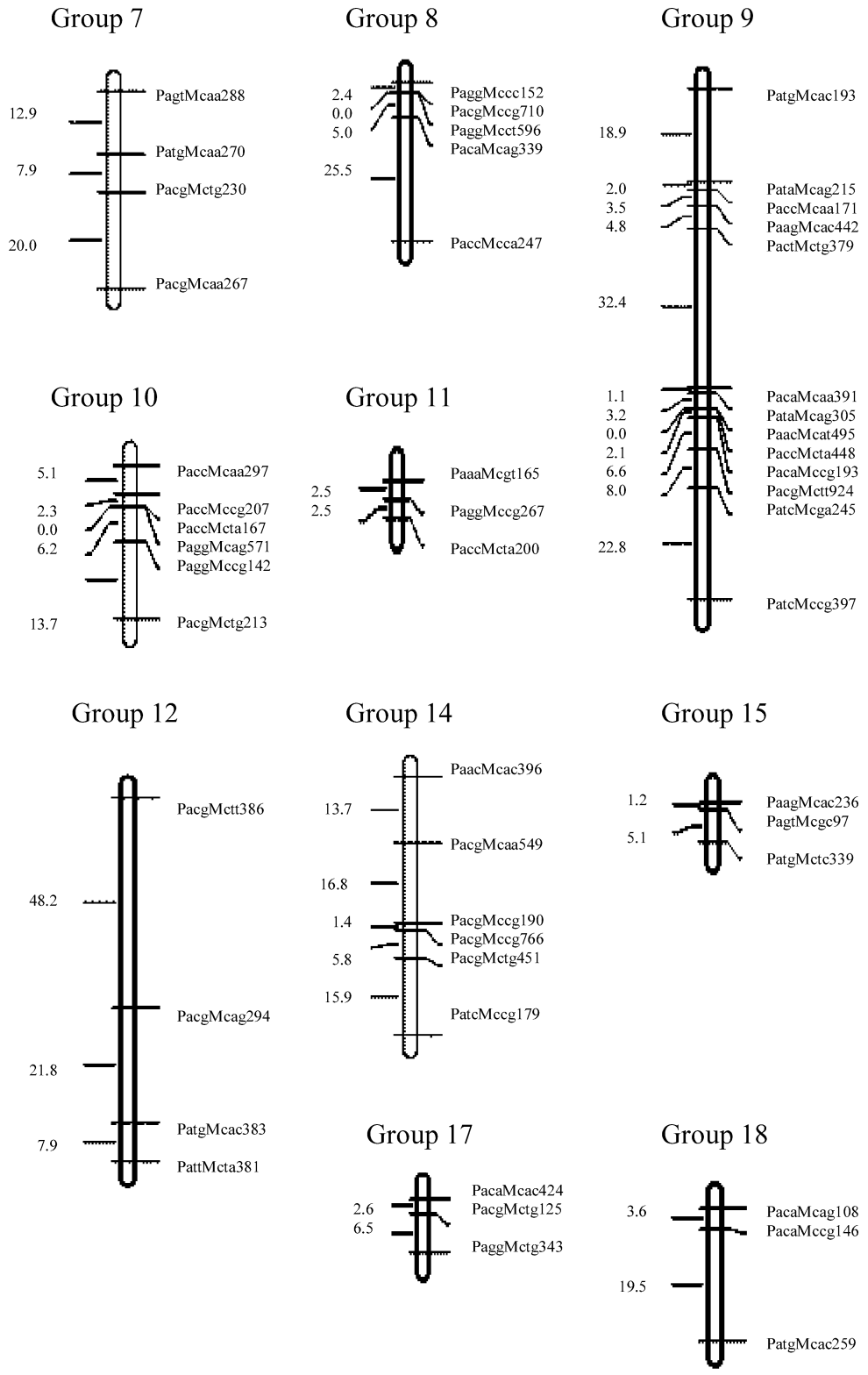

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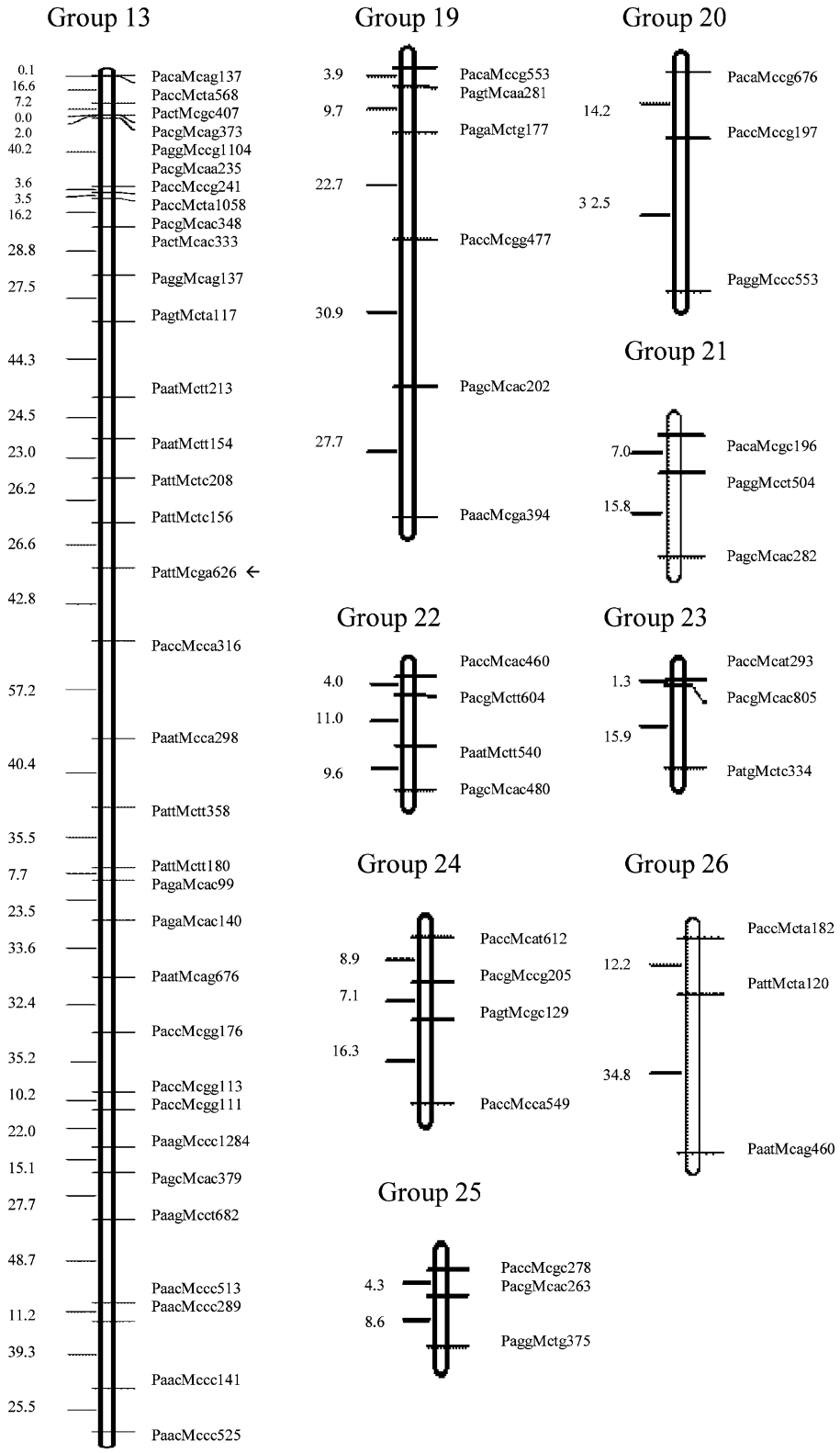

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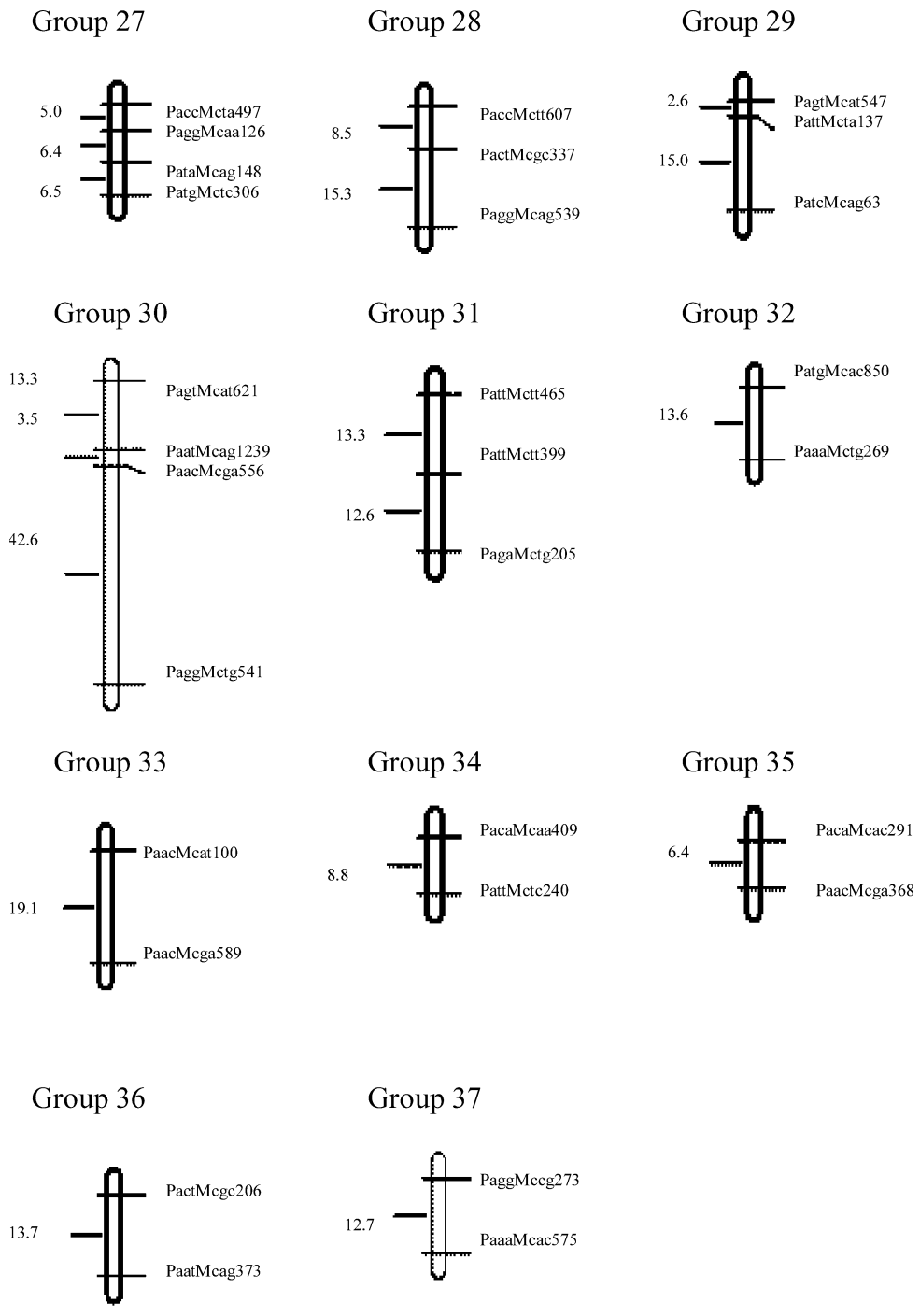

Figure 1. (*Continued*)

to O'Donoughue et al. (1995), approximately 3000 cM. However, more markers are still necessary to fill out the intervals among those already grouped so it would make possible to determine precisely the linkage groups and to enlarge genome coverage of those populations.

Molecular mapping of the F_6

Two hundred forty three markers were also identified in the F_6, giving an average of 13.5 polymorphic bands per primer combination. From the total polymorphic bands identified, 60 presented distortion in segregation for the χ-square test, representing 24.6%. From these, 22 segregated towards UFRGS7 and 38 towards UFRGS910906. It is possible that some percentage of heterozygosis in F_6 has contributed to a larger distortion in segregation than expected. Another problem that might have happened was an incomplete digestion of some samples, although this was not visible from the gels.

From the 243 identified markers, 86 (35.3%) were integrated into the map, being distributed in 17 linkage groups (Figure 2). The linkage groups presented from 2 to 22 markers (average = 5.4 markers per linkage group) and varied in size from 22.1cM to 616.7cM with an average of 117.3 cM, with a total extension map of 1994 cM.

Groups that concentrated larger number of markers were Group 1, with 22 markers and 616.7 cM of extension and Group 2, with 17 markers and 460.1 cM of extension. The other groups presented number of markers varying between 2 and 6.

Identification of QTL's associated to partial resistance to oat crown rust in the F_2

Five QTL's were identified by the Mapmaker/QTL program in the F_2 population. Four of these are in linkage Group 1 and one in linkage Group 13 (Table 2). The first QTL identified (Group 1) was located in the region of the marker PacaMcgc383 at 0.0 cM from it, explaining 12.5% of the phenotypic variation for this trait. That QTL is in repulsion to the character of interest, in other words, absence of the band in individuals with smaller disease severity and presence in individuals with larger severity. The second QTL was located closer to the marker PacgMcag318, at 2.0 cM of distance, explaining 16.8% of the phenotypic variation and also showing repulsion to the character of interest. The third QTL was located at 0.0 cM of distance of the marker PagtMcat358, explaining 19.5% of the variation and also in repulsion to the character of interest. The fourth QRL was located at 14.3 cM from the marker PagcMcac285, being linked in repulsion to the character of interest and explaining 27.6% of its variation. The fifth QTL, identified in linkage Group 13, was located closer to the PattMcga626 marker, at a distance of 8.0 cM. This QTL explained 38.2% of the variation and, unlike the others identified in F_2, was in association to the character of interest, what means that the band appeared in individuals with smaller disease severity and was absent in individuals with larger disease severity.

Three QTL's associated to oat crown rust partial resistance trait have been identified by Chen et al. (2000) in the "MN841801-1" (partially resistant) x "Noble" (susceptible) American RIL population under field conditions, explaining together 27% of the trait variation. However, because the oat populations were different, it is not possible to conclude that the QTL's identified in this studied correspond to QTLs found by Chen and co-workers.

Identification of QTL's associated to partial resistance to oat crown rust in the F_6

Three QTL's were identified in the F_6 mapping population by Mapmaker/QTL program. One of these (PaaaMctt340) was detected in two generations, in other words, with phenotypic data collected from the F_6 and F_4 generations in two distinct years (1999 and 2000, respectively) (Table 2).

None of the five QTLs identified in the F_2 generation was identified in the F_6. This is due, mainly, to the ephemeral nature of QTL's that, when with small effects, have the expression varied in different environments and from highly heterozygous F_2 to more homozygous F_4 and F_6 generations. The conditions of the environment for cropping in the years of 1998, 1999 and 2000 were very different amongst themselves, what interfered in the expression of the partial resistance. Besides, it is possible that, during the recombination through the successive generations, linkage breaks had occurred, which avoided the identification of QTL's from F_2 to F_6.

The first identified QTL in the F_6 UFRGS 7 $\times$ UFRGS 910906 population was located in the linkage Group 1, closer to the marker PatgMctc322, at 12 cM distance from it. This QTL explained 26.5% of the phenotypic variation for this trait and is in association with the character of interest, that is, smaller

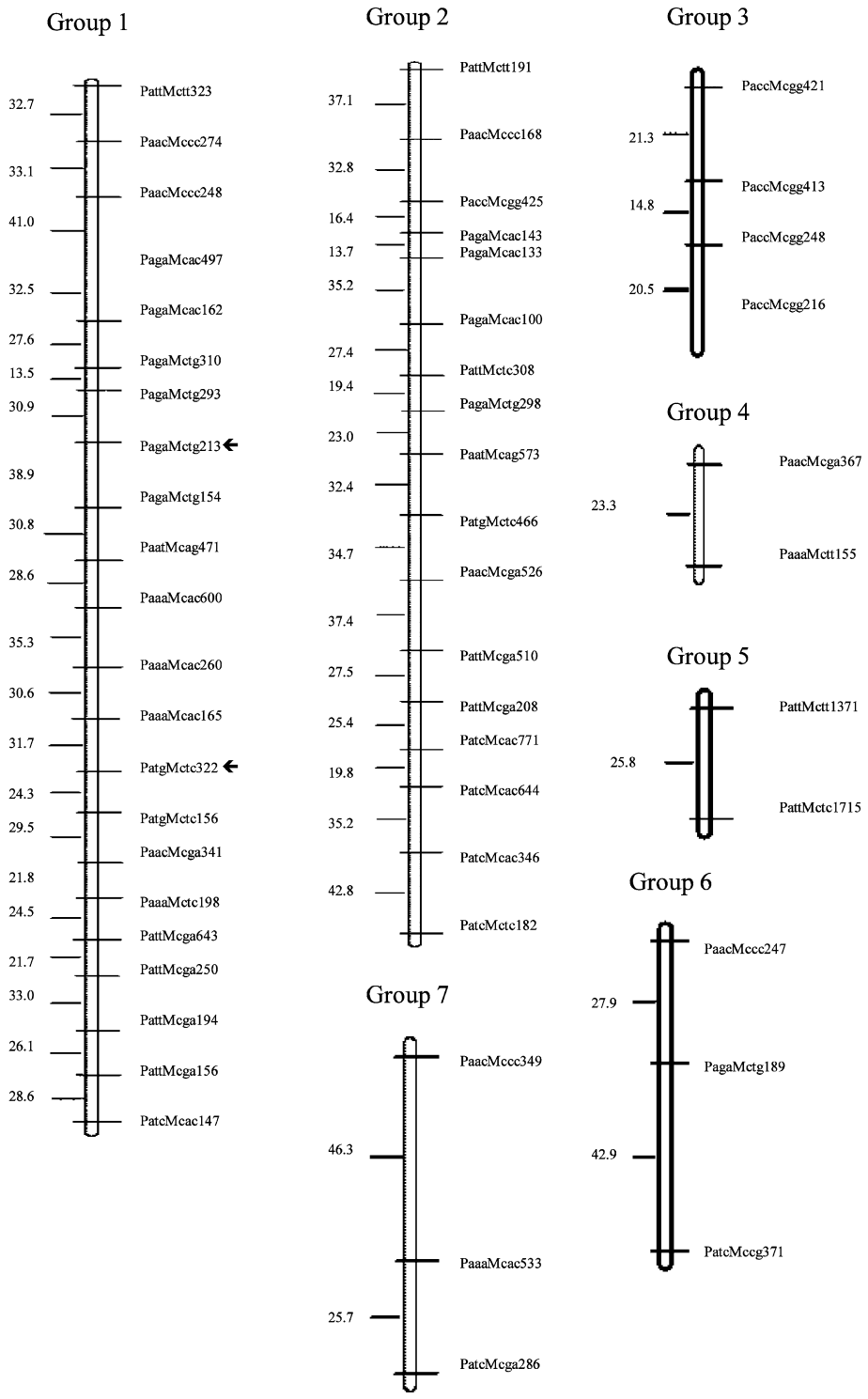

Figure 2. AFLP map of the F_6 recombinant inbred line UFRGS7 × UFRGS910906 population. The arrowheads indicate the QTL's identified in this generation.

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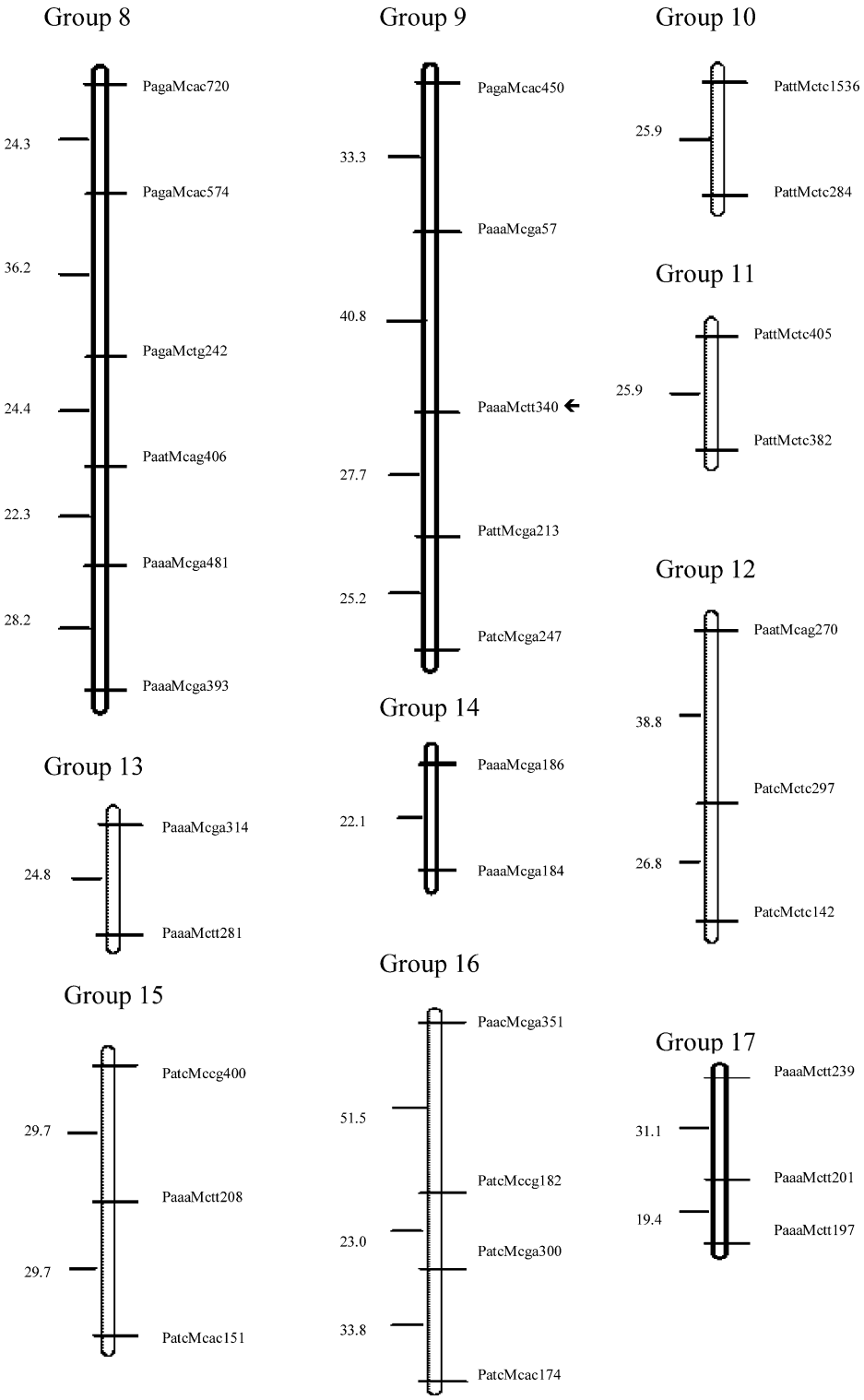

Figure 2. (*Continued*)

Table 2. QTL's associated to partial resistance to oat crown rust identified in the F_2, F_4 and F_6 generations of the UFRGS7 × UFRGS910906 population

QTL's	Linkage Group	Markers in the interval (position in cM)[1]	Minor Partial Resistance Score (Absence$^-$ or presence$^+$ of band)	Parent inherited	Aditivity	Dominance	% of Variation	LOD[2]
$F_2 - 1$		PacaMcgc383	6.0^-	Ufrgs 910906	−0.332	0.793		2.5
	1	PaccMcaa601 (0.0)	5.9^+	Ufrgs 7			12.5	
$F_2 - 2$		PacgMcag318	5.9^-	Ufrgs 910906	−0.390	0.721		2.7
	1	PacgMcag758 (2.0)	5.9^-	Ufrgs 910906			16.8	
$F_2 - 3$		PagtMcat358	6.2^-	Ufrgs 7	−0.455	0.782		4.0
	1	PagtMcgc411 (0.0)	5.6^-	Ufrgs 7			19.5	
$F_2 - 4$		PaagMccc265	5.8^-	Ufrgs 910906	−1.198	−0.153		2.2
	1	PagcMcac285 (14.3)	5.6^-	Ufrgs 910906			27.6	
$F_2 - 5$		PattMcga626	5.4^+	Ufrgs 910906	−0.455	1.904		3.4
	13	PaccMcca316 (8.0)	5.8^+	Ufrgs 910906			38.2	
$F_6 - 1$		PatgMctc322	13.7^+	Ufrgs 910906	0.965	−1.577		2.24
	1	PatgMctc156 (12.0)	12.5^+	Ufrgs 910906			26.5	
$F_4 - 2$		PagaMctg293	2.3^+	Ufrgs 910906	1.519	−1.257		2.50
	1	PagaMctg213 (14.8)	2.2^+	Ufrgs 910906			39.3	
F_4 and F_6-3	9	PaaaMcag57	$F_4 - 2.3^+$ $F_6 - 13.90^+$	Ufrgs 910906	0.439	−1.046	38.1	2.56
		PaaaMctt340 (16.8)	$F_4 - 2.4^+$ $F_6 - 14.10^+$	Ufrgs 910906				

[1] Position of the LOD peak of the QTL in relation to the first marker of the given interval.
[2]Log of the odd probability of detecting a QTL in a particular place.

disease severity. The second identified QTL in the F_6 was located in linkage Group 1, closer to the marker PagaMctg213, at 14.8 cM of distance and explaining 39.3% of the variation, being in association to the trait of interest. Such QTL was identified when the phenotypic data of the F_4 generation were used, but was not further identified in the F_6 generation. Probably, the interaction with the environment masked the expression of this QTL in F_6 or it could be due to the loss of the marker by the linkage break from one generation to the other. The third QTL was identified in linkage Group 9, located closer to the marker PaaaMctt340, at 16.8 cM of distance. This QTL explained 38% of the phenotypic variation and is in association to the character of interest. It was also identified when the molecular data collected from the F_6 generation were analyzed with the phenotypic data of the F_4 generation, obtained in the previous year (1999).

The evidence that the QTL linked to the marker PaaaMctt340 was identified in the two distinct F_4 (1999) and F_6 (2000) generations indicates that this QTL presents good consistence, since it was identified in two different environments and through two generations of recombination. As mentioned previously, the severities of the rust were very different in both years for collecting the phenotypic data for the F_4 (1999) and F_6 (2000) generations due to the high environmental variation in Southern Brazil. The consistence of these data, combined to the reasonable effect on the expression of the resistance (38%) and the linkage in association to the character of interest, makes the marker PaaaMctt340 potentially useful for marker-assisted selection of partial resistance to oat crown rust. Further studies to validate the effect of this QTL across different genetic backgrounds and environments will further elucidate the importance of this genomic region in controlling partial resistance to oat crown rust.

The results of the molecular data indicated QTL's explaining larger percentage of phenotypic variation in advanced generations (26.5%, 38% and 39.3%). In this sense, molecular maps based on recombinant inbred lines can be more efficient in the search of more consistent and stronger QTL effects, which could be more useful to breeding programs. Besides, these molecular maps facilitate the tests for validation of QTL's in different environments, due to a higher genetic stability and immortalized seed source of these advanced populations what also allow the use of replications.

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