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RFLP markers to identify the alleles on the *Mla* locus conferring powdery mildew resistance in barley

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Summary. To identify the mildew resistance locus *Mla* in barley with molecular markers, closely linked genomic RFLP clones were selected with the help of near-isogenic lines having the 'Pallas' and 'Siri' background. Out of 22 polymorphic clones 3 were located around the *Mla* locus on chromosome 5 with a distance of 5.1 ± 2.9 cM (MWG 1H068), 4.2 ± 1.7 cM (MWG 1H060) and 0.7 ± 0.7 cM (MWG 1H036), respectively. The polymorphic clone MWG 1H036 displayed the same RFLP pattern in both 'Pallas' and 'Siri' near-isogenic lines and in different varieties digested with six restriction enzymes possessing the same mildew resistance gene. The alleles of the *Mla* locus were grouped in 11 classes according to their specific RFLP patterns; 3 of these groups contain the majority of *Mla* alleles already used in barley breeding programs in Europe.

Key words: RFLP marker – Barley – Powdery mildew – *Mla* locus

Introduction

Erysiphe graminis f. sp. *hordei* is the causal organism for powdery mildew, which is one of the most important barley diseases in temperate climates. Many mildew resistance genes (or alleles) have been identified and localised either on chromosome 4 (4H) or on chromosome 5 (1H) of the barley genom. The *Mla* locus for mildew resistance located on chromosome 5 (1H) is known to be very complex. Since only eight of the known alleles from this locus have been used successfully in barley breeding programs in Europe, additional alleles from this locus will certainly be involved in future barley breeding programs. Based upon Flor's (1955) gene for gene hypothesis Moseman (1959) has demonstrated that the presence of a specific gene (or allele) for mildew resistance can be ascertained by an interaction with the mildew cultures that lack the corresponding gene for virulence. With an increasing number of resistance genes the use of this method will become difficult, since the disproportionate increase in the number of mildew cultures which will have to be employed in such analysis will become prohibitive. To overcome this difficulty, new methods involving RFLP analysis have recently been developed to determine genetic differentiation at the DNA level. RFLP-based maps have been established for a number of crop plants including tomato (Bernatzky and Tanksley 1986), potato (Bonierbale et al. 1988; Gebhardt et al. 1989), maize (Helentjaris 1987; Burr et al. 1988), lettuce (Landry et al. 1987) and barley (Heun et al. 1991; Graner et al. 1991; Jahoor et al. 1991 b). More specifically, a cyst nematode resistance gene in potato has been mapped with an RFLP marker (Barone et al. 1990). Jung et al. (1990) were able to determine RFLP marker linkage with resistance against cyst nematode (*Heterodera schachtii*) in sugar beet. Near-isogenic lines (NIL) carrying different genes/alleles for disease resistance are especially useful for identifying suitable RFLP markers for the resistance gene, as has been shown in tomato for the *I2* locus for resistance against *Fusarium oxysporum* (Sarfatti et al. 1989), the *Tm2* locus for resistance against tomato mosaic virus (Young et al. 1988) and the *Mi* locus for resistance against root knot nematode *Meloidogyne* spp. (Klein-Lankhorst et al. 1991; Messeguer et al. 1991); in barley for the *mlo* resistance gene against powdery mildew (Hinze et al. 1991); in maize for a gene for resistance against maize dwarf mosaic virus (MDMV); and in rice for the genes *Pi-2* (t) and *Pi-4* (t) against blast resistance (Yu et al. 1991).

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As long as the products of resistance genes are unknown (Manners et al. 1985), closely linked RFLP markers will also offer an alternative for the identification and isolation of these genes using one of the methods of "reverse genetics" (Orkin 1986).

In this communication, the identification of a *Mla*-linked RFLP marker using near-isogenic lines is described.

Material and methods

Plant material

Two sets of near-isogenic lines for mildew resistance with the background of 'Pallas' and 'Siri' developed by Kølster et al. (1986) and Kølster and Stølen et al. (1987) were employed to isolate polymorphic clones. Donor lines for *Mla* alleles and several cultivars carrying different *Mla* alleles were also included in this study. A set of wheat/barley addition lines carrying single pairs of individual barley chromosomes originating from var 'Betzes', developed by Islam and Shepherd (1981), was used to locate the polymorphic clones on specific chromosomes. F_2 progenies from the cross between '1B-87' × 'Vada', a mildew-resistant *Hordeum spontaneum* line collected from Israel and an European barley cultivar, respectively, were used to construct a linkage map of RFLP markers. Linkage analysis between RFLP markers located on chromosome 5 (1H) and the *Mla* locus were carried out on a set of double-haploid anther culture progenies derived from F_1 plants from the cross between 'Franka' and 'Igri', kindly supplied by B. Foroughi-Wehr (Institute of Resistance Genetics, Grünbach, FRG).

RFlP analysis

Methods of extraction of DNA, restriction digestion and Southern analysis are described elsewhere (Graner et al. 1990; Jahoor et al. 1991 a). Three to five probes were pooled and tested on NIL-DNA filters in order to accelerate the screening process (Young et al. 1988).

Powdery mildew test

Powdery mildew tests were carried out at the seedling stage using detached leaves placed on agar containing 30 mg/l benzimidazol. The seedlings were raised in a growth chamber in order to prevent contamination. Mildew infections were carried out according to the method described by Aslam and Schwarzbach (1980). The powdery mildew isolates used in this study originated from a collection of single-spore progenies which differ in virulence and which are maintained at the Institute of Agronomy and Plant Breeding, TUM Weihenstephan. After inoculation, the agar plates were kept under controlled conditions for 9 days until disease readings were carried out as described by Jahoor and Fischbeck (1987).

Results

Identification of polymorphic RFLP markers with the help of near-isogenic lines

Out of 664 tested plasmids a total of 474 genomic clones detecting single and low-copy sequences were screened by hybridisation on DNA filters made up from four NILs and the recurrent parent 'Pallas'. Only 22 probes were identified which displayed RFLPs between the DNA of 'Pallas' and at least one of the tested *Mla*-NILs.

Localisation of polymorphic RFLP markers

To locate informative probes on specific chromosomes, hybridisations with wheat/barley addition lines were carried out. Only 3 informative probes (MWG 1H036, MWG 1H060, MWG 1H068) turned out to be located on chromosome 5 (1H), while the other 19 were found to be distributed among all the other barley chromosomes (data not presented), which indicates the incomplete status of recovery of the recurrent parent genotype after six backcrosses. Linkage studies with the RFLP markers located on chromosome 5 (1H) were conducted on a set of F_2 progenies from the cross '1B-87' × 'Vada'. As will be seen from the data shown in Fig. 1 all 3 probes are located in the region between the *Hor1* and *Hor2* genes, which are known to flank the *Mla* locus.

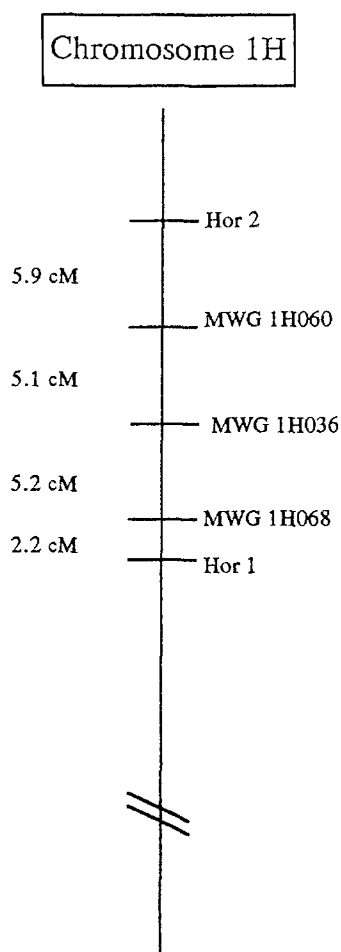

Fig. 1. Location of 3 polymorphic RFLP clones MWG 1H036, MWG 1H060 and MWG 1H068 between *Hor1* and *Hor2* on the short arm of barley chromosome 5

EcoRV

MWG 1H036

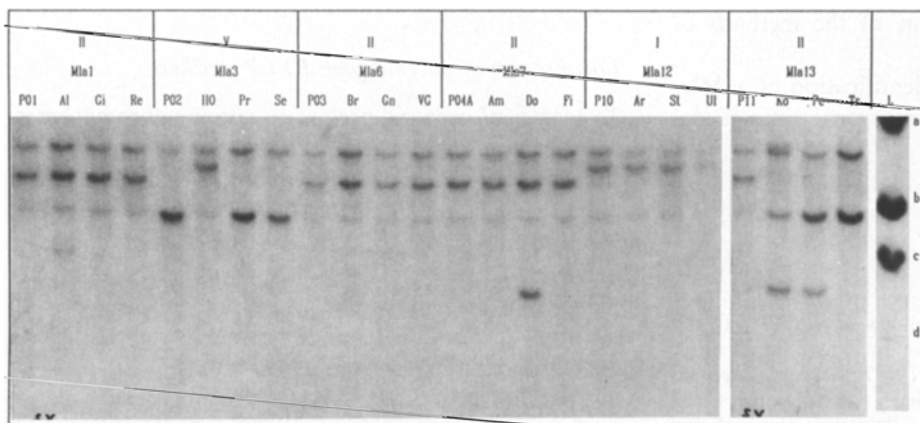

Fig. 2. Southern blot of near-isogenic lines and 3 varieties of different origins possessing corresponding *Mla* alleles. DNA was digested with the restriction enzyme *Eco*RV and hybridised to clone MWG 1H036. *Al* Algerian, *Gi* Gitte, *Re* Regatta, *HO* HOR 1036, *Pr* Princess, *Se* Sewa, *Br* Brunhild, *Gn* Ginso, *VG* Vogelsanger-Gold, *Am* Amsel, *Do* Dorett, *Fi* Fink, *Ar* Aramir, *St* Steina, *Ul* Ultra, *Ko*, Koral, *Pe* Perun, *Tr Triton*. *L* Length standard, Lambda/*Hin*dIII, *a* 23 130 bp, *b* 9416 bp, *c* 6557 bp, *d* 4361 bp

BamHI

MWG 1H036

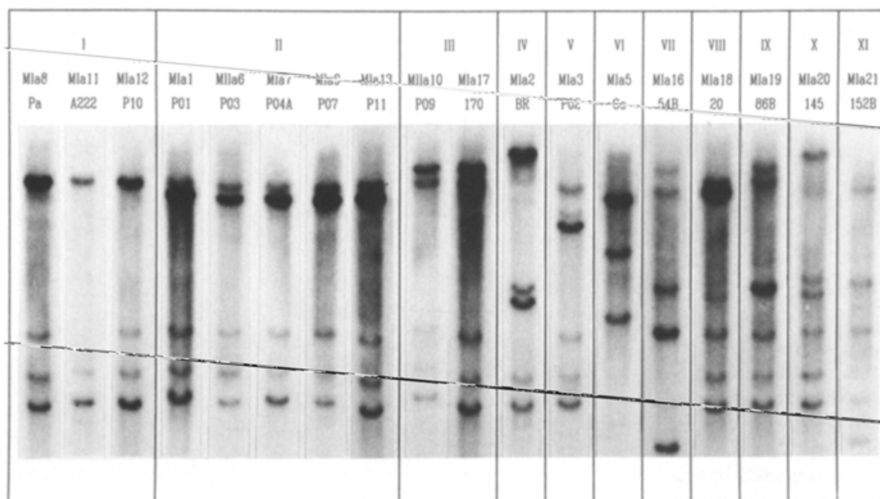

Fig. 3. Comparison of 11 different RFLP patterns obtained with clone MWG 1H036 and the restriction enzyme *Bam*HI. Bands in the *lower part* of the autoradiography are considered to be unspecific. *Pa* Pallas, *BR* Black Russian, *Go* Gopal *170* RS170-47 × Kiebitz, *54B* Diamant × 1B-54B, *20* RS20-1 × Kiebitz, *86B* Diamant × 1B-86B, *145* RS145-39 × Kiebitz, *152B* Diamant × 1B-152B

Analysis of the Mla locus

For a more detailed study about the relationship between these 3 RFLP markers and the *Mla* locus, the markers were tested against NILs carrying different *Mla* alleles. Polymorphisms among 'Pallas' and 'Pallas' NILs were detected with all 3 probes, but the patterns from 'Pallas' and 'Siri' NILs carrying the same *Mla* allele differed with probe MWG 1H060 and probe MWG 1H068. On the contrary, probe MWG 1H036 detected a complex of polymorphisms among the *Mla* alleles, but the patterns were the same between the NILs carrying the same allele in the 'Pallas' and 'Siri' background, respectively.

Additional tests were made using 18 barley cultivars carrying six different *Mla* alleles that have been developed in different countries. Allele-specific RFLP patterns were again verified in most cases (Fig. 2). An exception, however, was observed with genotypes carrying the allele *Mla 13*. While the near-isogenic *Mla 13* lines from 'Pallas' and 'Siri' showed the same specific RFLP pat-

EcoRV

MWG 1H036

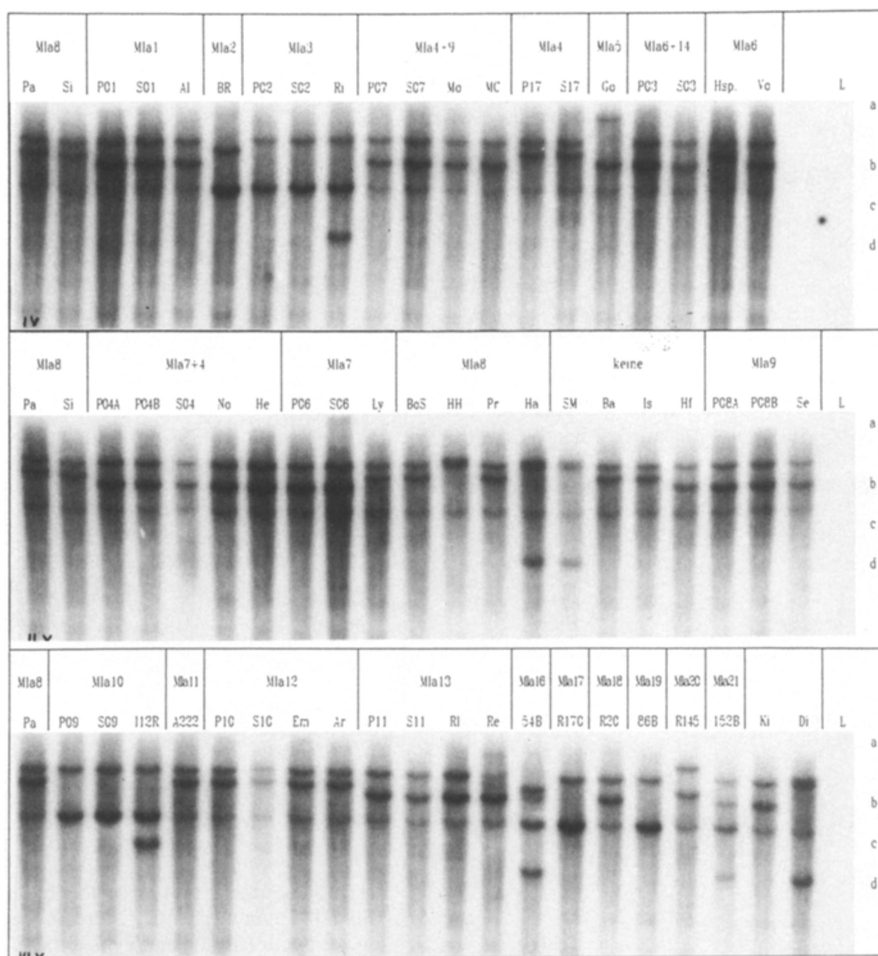

Fig. 4. Southern blot of all *Mla* alleles represented by near-isogenic lines, their donor lines and different varieties. DNA was digested with *Eco*RV and hybridised to clone MWG 1H036. *Pa* Pallas, *Si* Siri, *Al* Algerian, *BR* Black Russian, *Ri* Ricardo, *Mo* Mona, *MC* Monte Cristo, *Go* Gopal, *Hsp H. spontaneum nigrum*, *Vo* Voldagsen, *No* Nordal, *Ly* Lyallpur, *BoS* Bonus sensitiv, *HH* Heils Hanna, *Pr* Proctor, *Ha* Hanna, *SM* SM4142, *Ba* Bavaria, *Is* Isaria, *Hf* Hafnia, *Se* Senat, I12R *Iso* 12R, *Em* Emir, *Ar* Arabische, *Rl* Rupal, *Re* Rupee, *54B* Diamant × 1B-54B, *170* RS170-47 × Kiebitz, *20* RS20-1 × Kiebitz, *86B* Diamant × 1B-86B, *145* RS145-39 × Kiebitz, *152B* Diamant × 1B-152B; *Ki* Kiebitz, *Di* Diamant. *L* Length standard Lambda/*Hin*dIII, *a* 23 130 bp, *b* 9416 bp, *c* 6557 bp, *d* 4361 bp

tern, this pattern differed from the pattern consistantly obtained from three cultivars carrying the *Mla 13* allele.

Furthermore, the RFLP patterns of the NILs carrying different alleles of *Mla* were compared with their respective donor lines. If no near-isogenic line was available, only the donor lines were used ('Black Russian' for *Mla 2*, 'Gopal' for *Mla 5*, A222 for *Mla 11* and several *H. spontaneum* lines collected in Israel that carry *Mla 16–21*). The DNA of all lines was restricted with the enzymes *Bam*HI, *Eco*RV, *Eco*RI, *Hin*dIII and *Xba*I, and different degrees of polymorphism were detected.

On the basis of the data obtained with clone MWG 1H036 and the most informative restriction enzyme, *Bam*HI, RFLP patterns for different alleles of the *Mla* locus were divided into 11 groups (Fig. 3). Group II is the largest and includes the alleles *Mla 1*, *Mla 6/14*, *Mla 7*, *Mla 9*, and *Mla 13;* group I is made up to 3 different alleles (*Mla 8*, *Mla 11* and *Mla 12*); group III includes *Mla 10* and *Mla 17*; and each of the remaining 8 patterns characterized just 1 different *Mla* allele (Table 1). It is interesting to note that the majority of the *Mla* alleles already used in barley breeding programs in Europe, often having been introduced from landraces of different origin, are included in the first 3 groups of RFLP patterns, whereas none of the *Mla* alleles from the other 8 RFLP patterns are present in any barley cultivar until now and many of these are found in mildew-resistant lines of *H. spontaneum* collected in Israel.

An inconsistency was observed for varieties possessing the *Mla 8* allele or no *Mla* allele at all, respectively (see Fig. 4). Varieties 'Pallas', 'Siri', 'Bonus S' and 'Proctor' (*Mla 8*) show the same pattern as 'Bavaria' and 'Isaria' (no *Mla* allele). A second group with an identical, RFLP pattern consists of 'Hanna' (*Mla 8*) and 'SM4142' (no *Mla* allele); 'Heils Hanna' (*Mla 8*) and 'Hafnia' (no *Mla* allele) each possess specific bands. Because all known

HindIII

MWG 1H036

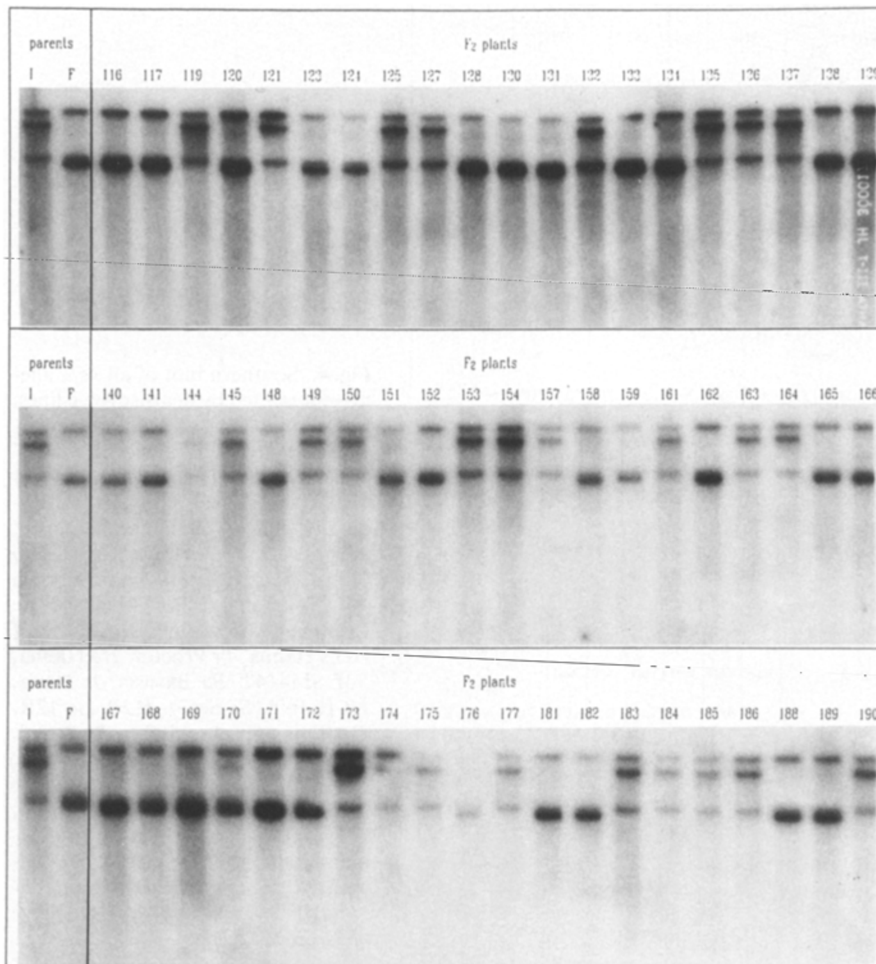

Fig. 5. Southern blot of double haploid F_2 plants and their parents digested with *Hind*III and hybridised to clone MWG 1H036. *I* Igri, *F Franka*

mildew isolates are virulent against *Mla 8*, the identification of this allele in a variety is very difficult. Therefore, a grouping according to mildew infection is risky, as has been shown in this RFLP study.

The above data very strongly indicate that clone MWG 1H036 may have either originated from, or should be very closely linked to the *Mla* locus.

Linkage analysis between RFLP probes and the Mla locus

While conducting our analysis on the linkage of the *Mla* locus with probe MWG 1H036 and other informative clones, we observed that the F_2 populations of barley do not clearly segregate into susceptible and resistant groups (Jahoor and Fischbeck 1987). Possible misclassifications could interfere with the correct estimates of genetic distances between different loci. Therefore we based detailed analysis of linkage upon a set of DH (double haploid) lines that originated from a cross between 'Igri' and 'Franka', which carry the *Mlra* and *Mla 6* alleles, respectively. Since virulence against *Mlra* is generally present in the European population of barley mildew (Limpert et al. 1990), it was not possible to select isolates that are avirulent on *Mlra 8* plants. Therefore, two mildew isolates avirulent against *Mla 6* and virulent against *Mlra* were used to study the segregation of mildew reaction in the 'Igri' × 'Franka'-derived DH lines. After infection with these two isolates a 1:1 ratio (susceptible: resistant) was confirmed, as was expected in DH progeny (Table 2). The RFLP patterns obtained from these DH lines using different probes (as shown in Fig. 5 for probe MWG 1H036) were also examined and both data sets subjected to linkage analysis. Out of the 144 DH lines tested six crossover events occurred between the *Mla* locus and probe MWG 1H060 (Table 2). With probe MWG 1H036 only 1 DH line showed recombination following the

Table 1. Alleles of the *Mla* locus grouped on the basis of RFLP pattern by means of the genomic clone MWG 1H036 and *Bam*HI-restricted DNA of near-isogenic lines (NIL) and some commercial varieties

Pattern	*Mla* allele	Origin	NIL	Commercial varieties
0	*Mla 8*		Pallas/Siri	Bonus S, Proctor
	None			Bavaria, Isaria
	Mla 11	A222		
	Mla 12	Arabische	P10/S10	Steina, Hockey, Emir
II	*Mla 1*	Algerian	P01/S01	Regatta, Gitte
	Mla 6/14	Voldagsen	P03/S03	Brunhild, Ginso, Vogelsanger-Gold
	Mla 7	Nordal	P04A/S04/P06/S06/P04B	Amsel, Dorett, Fink, Heine, Kiebitz
	Mla 9	Monte Cristo	P07/S07/P08A/P08B	Mona, Senat
	Mla 13	Rupal	P11/S11	Koral [c], Perun [c], Triton [c]
III	*Mla 10*	Durani	P09/S09	
	Mla 17	RS170-47 × Kiebitz [b]		
IV	*Mla 2*	Black Russian		
V	*Mla 3*	Ricardo	P02/S02	Princess, Sewa
VI	*Mla 5*	Gopal		
VII	*Mla 16*	Diamant × 1 B-54B [b]		
VIII	*Mla 18*	RS20-1 × Kiebitz [b]		
IX	*Mla 19*	Diamant × 1B-86B [b]		
X	*Mla 20*	RS145-39 × Kiebitz [b]		
XI	*Mla 21*	Diamant × 1B-152B [b]		

[a] One the basis of RFLP pattern 'Pallas', 'Siri', 'Bonus S' and 'Proctor' seem not to possess any resistance allele at the *Mla* locus
[b] Jahoor and Fischbeck (1987)
[c] They have the distinct RFLP pattern from P11 and S11, but among temselve they are equal

Table 2. Linkage analysis between RFLP clones MWG 1H036, MWG 1H060, MWG 1H068, *Hor1* and *Hor2* and the *Mla* locus

Igri × Franka		Parent phenotype		*n*	Segregation [a]				Expected ratio	Chi [2]	*P*	Recombination ratio
RFLP probe	Mildew culture	P1	P2		FR	IR	FS	IS				
MWG 1H036	184-21	IS	FR	142	70	1	0	71	1:1:1:1	138.06	<0.05	0.70 ± 0.70
	Ru3	IS	FR									
MWG 1H060	184-21	IS	FR	144	70	2	4	68	1:1:1:1	121.09	<0.05	4.17 ± 1.67
	Ru3	IS	FR									
MWG 1H068	184-21	IS	FR	59	24	3	0	32	1:1:1:1	47.95	<0.05	5.08 ± 2.86
	Ru3	IS	FR									
Hor1	184-21	IS	FR	142	64	7	7	64	1:1:1:1	98.53	<0.05	4.98 ± 1.97
	Ru3	IS	FR									
Hor2	184-21	IS	FR	121	62	1	5	53	1:1:1:1	91.52	<0.05	9.99 ± 2.51
	Ru3	IS	FR									

[a] S, Susceptible genotype, R, resistant genotype; F, RFLP pattern of the var 'Franka'; I, RFLP pattern of the var 'Igri'

mildew reaction from 'Igri', but the RFLP pattern from 'Franka' was determined. From linkage analysis of these data using maximum likelihood methods the genetic distances between the *Mla* locus and these probes have been calculated. The linkage of probe MWG 1H036 amounts to 0.7 ± 0.7 cM while for probe MWG 1H060 and MWG 1H068 distances were estimated to be 4.2 ± 1.7 cM and 5.1 ± 2.9 cM units, respectively.

Discussion

In a previous study 43% single or low-copy DNA clones revealed polymorphism among cultivated barley varieties (Graner et al. 1990); this increased to 65% after a *H. spontaneum* line was included in the analysis (Weiss 1991). Since the donors of mildew resistance genes in the available near-isogenic lines originated mostly from lan-

Table 3. Comparison of the grouping of *Mla* alleles according to infection type and degree of dominance (Giese et al. 1981) or RFLP pattern

A. Infection type and degree of dominance		B. RFLP pattern	
		Mla 3	V
0/semidominant	*Mla 3* *Mla 10* *Mla 8* *Mla 12*	*Mla 10* *Mla 17*	III
2 unknown	*Mla 11*	*Mla 8*[a] *Mla 12* *Mla 11*	I
0/dominant	*Mla 1* *Mla 6* *Mla 9* *Mla 13*	*Mla 1* *Mla 6+14* *Mla 9* *Mla 13* *Mla 7*	II
0-1 n/semidominant	*Mla 7*		
2/dominant	*Mla 5* *Ma 14*	*Mla 5*	VI
2/semidominant	*Mla 2*	*Mla 2*	IV

[a] Based upon RFLP pattern of 'Pallas'

draces of different origin (Kølster et al. 1986; Jahoor 1987), a lower level of polymorphism among donor lines might be expected. Therefore, from 474 single-copy probes randomly and uniformly distributed over the barley genome about 284 (60%) should have been able to detect polymorphism among donor lines and recurrent parents, and 40 of these on chromosome 5 (1H). According to Muehlbauer et al. (1988), the donor fragment remaining on the marker chromosome in a near-isogenic line after five backcrosses and one selfing (BC_5S_1) would cover $22.0 \pm 2.2\%$ of the recurrent parent genome (Michalek 1991). This would amount to 9 polymorphic probes instead of the 3 which actually have been found on chromosome 5 (1H). This discrepancy can be explained by selection in favor of the phenotype of the recurrent parent throughout the backcrosses made during NIL development (Kølster et al. 1986).

The number of polymorphic bands which were obtained from restricted DNA from *Mla 1* through *Mla 13* near-isogenic lines after hybridisation with probe MWG 1H036 is low and mainly expressed by rather small differences in fragment length based upon shifts in the recognition sites of the restriction enzymes. Moreover, within this set of data 6 groups of RFLP patterns are formed, each group including 1–5 *Mla* alleles (Figs. 3, 4 and Table 1). On the contrary, the banding patterns from *Bam*HI-restricted DNA, obtained from the newly identified alleles *Mla16–Mla 21* (Jahoor and Fischbeck 1987), generally show a larger number of bands together with more drastic changes in their position. Each allele showed a distinct banding pattern and no grouping occurred (Figs. 3, 4 and Table 1).

Since the banding pattern observed with the *Mla 1–Mla 13* alleles has been shown to be independent of genetic background, it seems reasonable to apply these results to other *Mla* alleles for which near-isogenic lines are not available. If the speculative assumption is made that larger differences in banding pattern are based on a higher degree of DNA differentiation at the *Mla* locus, it may be assumed that a higher degree of complexity will also be needed for the corresponding genes of virulence, which at present only occur in mildew populations in Israel (Jahoor and Fischbeck 1987). Therefore, it will be very interesting to observe if any differences in the durability of mildew resistance conferred by these alleles will be noted when they eventually are introduced in future barley cultivars.

In the landrace 'Hanna' from Bohemia *Mla 8* was first identified with the help of a Japanese isolate (Hiura 1960). Therefore, the RFLP pattern of this variety should be specific for *Mla 8*. Varieties 'Bavaria' and 'Isaria', early descendants from the landrace population 'Lower Bavaria', do not carry known genes for mildew resistance; thus, the RFLP patterns of these varieties can be concluded for *Mla* locus (no resistance allele). Varieties of a more recent origin such as 'Pallas', 'Siri', 'Proctor' and 'Bonus S' often involve 'Hanna' in their pedigrees (Fischbeck 1991). Due to the absence of a virulence against *Mla 8* in the European powdery mildew population, this allele is difficult to identify by mildew infections and the RFLP pattern seems to be a better test.

Giese (1981) made an attempt to divide the *Mla* region into 6 very closely linked loci based upon differences in infection type and degree of dominance. In spite of the fact that Islam et al. (1991) have recently been able to show that the degree of dominance of mildew resistance in segregating populations depends not only on the host gene and its background but also an the pathogen culture used for it, the grouping of *Mla* alleles in Giese's study coincides to some degree with the results of the present investigation as can be seen from Table 3. The largest group in both studies consists of the same alleles, with the exception of *Mla 7*. The remaining groups from Giese's study are divided into subgroups by the RFLP patterns obtained in this study.

Although the agreement between both groupings is not perfect and there seems to be no way to integrate the additional RFLP patterns which have been found in this study into a more detailed hypothesis about the structure of the *Mla* locus, the overall picture justifies the expectation that this locus will consist of a rather large DNA fragment of chromosome 5 (1H). As has been shown by Sørensen (1989) and Siedler and Graner (1991) the loci *Hor B* and *Hor C*, which are known to flank both sides of the *Mla* locus, are located on large DNA fragments comprising more than 100 kb, respectively. Large-sized complex loci have also been reported from th human genome (Worton and Thompson 1988). Furthermore, present knowledge seems to indicate that existing complex loci are not randomly distributed but may be concentrated upon certain chromosomes, as exemplified by the sequence of *Hor B* and *Hor C*, and there may be others on the short arm of chromosome 5 (1H).

The patterns of polymorphism which have been obtained with probe MWG 1H036 provide new means for characterizing genetic differences at the *Mla* locus that often coincide with the different reaction patterns against powdery mildew obtained from the high number of different alleles of this locus. Even at is stage of development this information may usefully be applied to check for the presence of new alleles of the *Mla* locus in a barley breeding program. This may be of increasing importance with further increases in the number of *Mla* alleles. The close linkage of probe MWG 1H036 to the *Mla* locus also provides favorable conditions for new efforts to identify the molecular basis of the *Mla* locus and its alleles.

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