Theor Appl Genet (1993) 85:713–718

THEORETICAL AND APPLIED GENETICS

Genetical and RFLP studies at the *Mla* locus conferring powdery mildew resistance in barley

A. Jahoor, A. Jacobi, Christine M. E. Schüller, and G. Fischbeck

Lehrstuhl für Pflanzenbau und Pflanzenzüchtung, Technische Universität München, W-8050 Freising-Weihenstephan, Federal Republic of Germany

Received March 5, 1992; Accepted April 23, 1992
Communicated by G. Wenzel

Summary. The complex structure of the multigene family at the *Mla* locus conferring powdery mildew resistance in barley was studied by making diallel crosses between several near-isogenic lines carrying different *Mla* alleles. The mode of inheritance of the *Mla* alleles investigated was determined to be dominant for *Mla1*, *Mla6*, *Mla7* and *Mla13* and semidominant for *Mla3*, *Mla12* and *Mla20*. F_1 plants were backcrossed to the susceptible recurrent parent in order to identify susceptible and double-resistant recombinants in the BC_1F_1 generation. Out of 17605 progenies tested in the BC_1F_1 generation, two susceptible recombinants, one between *Mla1* and *Mla12* and one between *Mla13* and *Mla20* were confirmed. The former was also verified by RFLP analysis.

Key words: Barley – Multigene family – *Mla* locus – Recombination – RFLP marker

Introduction

The genes conferring resistance to plant diseases are not distributed randomly over the genome, rather they occur frequently in groups on particular chromosomes. In the case of barley powdery mildew, multiple allelism has been found on three loci, namely *Mla*, *Mlp* and *mlo* (Moseman and Jørgensen 1971; Giese et al. 1981; Jahoor et al. 1989; Hentrich 1979). The *Mla* locus of barley has been the focus of much interest because of its complex polymorphism; up to now 23 alleles or several closely linked loci have been confirmed for this locus (Jahoor et al. 1991a, b). Jørgensen and Moseman (1972) reported one susceptible recombinant plant originating from a cross involving the *Mla1* and *Mla3* alleles. Wise and Ellingboe (1985) studied the complex structure of the multigene family in the *Mla* region, a region which should allow intra-allelic recombination.

RFLP markers are phenotypically neutral and independent of allelic and nonallelic interaction. Due to this fact, they enable the investigator to detect the exact genetic constitution of an individual plant in a segregating population. RFLP-based genetic maps for barley are at present being developed at several laboratories (Heun et al. 1991; Jahoor et al. 1991a; Graner et al. 1991; Blake et al. 1991). Schüller et al. (1992) have been able to separate the *Mla* alleles into 11 different groups by polymorphism obtained with only one RFLP marker. This marker is very closely linked to the *Mla* locus (0.7 cM). In addition, two more markers have been identified that tightly flank the *Mla* locus on both sides.

The purpose of the study presented here was to detect the mode of inheritance and intralocus recombination at the *Mla* locus conferring powdery mildew resistance in barley.

Materials and methods

In order to minimise effects which might arise from the genetic background of the parental lines carrying different alleles of the *Mla* locus, near-isogenic lines (NILs) in the 'Pallas' background (Kølster et al. 1986) were used. For our study seven NILs carrying *Mla* alleles which originated from different geographic areas were chosen, together with one line derived from a *Hordeum spontaneum* collection from Israel that carried the *Mla20* allele (Table 1).

Single-spore isolates of powdery mildew which are able to distinguish individual resistance genes were selected from a

Correspondence to: A. Jahoor

Table 1. Near-isogenic lines of *Mla* alleles and geographic origin of their donors, including the recurrent parent Pallas

Mla allele	Near-isogenic line (Nil)	Donor	Geographic orgin	Reference
Mla8	Pallas	Hanna	Europe	Moseman (1955)
Mla1	P01	Algerian	Algeria	Moseman (1955)
Mla3	P02	Ricardo	Uruguay	Moseman (1955)
Mla6, *Mla14*	P03	*H. spontaneum* H204	Balkan	Honecker (1936)
Mla7	P04B	Lyallpur 3645	Pakistan	Hoffmann and Nover (1959)
Mla12	P10	Arabische	Arabia	Wiberg (1974a)
Mla13, *Ml(RU3)*	P11	Rupee	India	Moseman (1955)
Mla20	RS145-39 × Kiebitz[a]	*H. spontaneum* RS145-39	Israel	Jahoor and Fischbeck (1987)

[a] No NIL was available for *Mla20*

collection of mildew cultures maintained at the Institute of Agronomy and Plant Breeding, Weihenstephan; 9 out of the 13 isolates originated from European mildew populations and 4 originated from the wild population of *H. spontaneum* in Israel. For each of the two parents of the crosses that were made one virulent and one avirulent isolate was chosen to determine double-resistant as well as double-susceptible recombinant plants. Diallele crosses among lines carrying *Mla1*, *Mla3*, *Mla6*, *Mla7*, *Mla12*, *Mla13* and *Mla20* were made, and F_1 progenies were used to determine the mode of inheritance.

To study the fine structure of the *Mla* locus, F_1 plants of the diallel crosses were backcrossed to the susceptible recurrent parent of the near-isogenic lines, cv 'Pallas' (which carries the ineffective allele *Mla8*), in order to allow the identification of susceptible and double-resistant plants in the BC_1F_1 generation.

For the mildew tests, seedlings were grown under controlled conditions to exclude undesirable mildew infections. All experiments were carried out in vitro to avoid contamination. Detached leaves from the seedlings were placed upon agar containing 30 mg/l benzimidazol to delay leaf chlorosis. The inoculation technique, subsequent treatments after inoculation and reading of the infection type were similar to those described by Nover (1972). Type 0 denotes immune reactions showing no visible symptoms of infection, whereas reaction type IV indicates complete susceptibility, showing no visible defense mechanisms. In addition, infection severity of the leaf area covered with powdery mildew was classified in a 0.0–1.0 scale relative to the universal susceptible standard SM4142.

For Southern analysis, DNA from the recombinant plants and parents were isolated according to Graner et al. (1990). The DNA was digested with the restriction enzyme *Eco*RV. The restricted DNA (10 μg/lane) was subjected to electrophoresis in 0.75% agarose gels, and the resulting. DNA fragments were then transferred to nylon membranes as described by the supplier (Pall Crop, Dreieich). The inserts from the recombinant plasmids were labeled with ^{32}P-dCTP by random priming (Feinberg and Vogelstein 1983) and subsequently used as probes. Hybridisation and further treatments of the membranes were conducted as described by Jahoor et al. (1991a).

Results

Reaction pattern of parental lines

The reaction patterns of the parental lines are presented in Table 2. The mildew resistance genes included in the present investigation showed either highly resistant or highly susceptible reactions upon infection with European isolates but when exposed to infection by Israeli isolates most of them reacted in a susceptible manner. Only *Mla7* (P04B) developed highly resistant reactions against three Israeli isolates, which reaction type II scored from infection by Ar-4 and Al-1 indicated the presence of the *Mlk* gene in the near-isogenic line P04B.

Reaction pattern of heterozygous plants

The mode of inheritance of the mildew reactions conferred by 5 *Mla* alleles was determined by a comparison of the homozygous versus the heterozygous state of the *Mla* alleles (Table 2). Differences in the reaction pattern of heterozygous plants were considered significant if they deviated two scoring classes from the homozygous resistant parent, i.e. 0–II or I–III. The plants heterozygous for *Mla3* and *Mla12* showed incomplete dominance when exposed to avirulent isolates, whereas *Mla1* and *Mla7* heterozygotes reacted as being completely dominant. *Mla13* reacted dominantly in most cases, but upon inoculation with isolate PS-IS-2 incomplete dominant reactions were scored.

Interaction between Mla alleles

F_1 plants derived from the diallele crosses between NILs carrying different *Mla* alleles were infected with isolates that were virulent against one parent and avirulent against the other, and vice versa. The results agreed with the information obtained from crosses between the near-isogenic lines and the recurrent parent 'Pallas'. A dominant mode of inheritance was also observed shown for *Mla6*, for which heterozygous plants from a cross with 'Pallas' were not available. Most of the *Mla* alleles involved in this study maintained a stable mode of inheritance against different avirulent isolates, with the exception of *Mla13*

Table 2. Reaction patterns of lines carrying different *Mla* alleles in the homozygous and in heterozygous state

Isolate	P01 (*Mla1*)	P01 × Pallas	P02 (*Mla3*)	P02 × Pallas	P03 (*Mla6/14*)	P04B (*Mla7*)	P04B × Pallas	P11 (*Mla13*)	P11 × Pallas	*Mla20*[b]	*Mla20*[b] × Pallas	Pallas
RU3	$I_{0.1}$[a]	$I–II_{0.3}$	$I_{0.1}$	$III_{0.5}$	0	0	$I_{0.1}$	$IV_{0.5}$	$IV_{0.6}$	$I_{0.1}$	–	$IV_{0.5}$
201/60	$IV_{0.6}$	$IV_{0.6}$	$I–II_{0.4}$	$II–III_{0.5}$	$IV_{0.6}$	$IV_{0.6}$	$IV_{0.5}$	I	II	II	–	$IV_{0.5}$
131/13	$I_{0.2}$	$I_{0.2}$	$I–II_{0.2}$	$II_{0.5}$	$IV_{0.6}$	$IV_{0.7}$	$IV_{0.5}$	$I_{0.3}$	$I–II_{0.4}$	$I–II_{0.2}$	–	$IV_{0.5}$
184/21	$I_{0.2}$	$I–II_{0.3}$	$I–II_{0.3}$	$III_{0.6}$	$I_{0.1}$	$IV_{0.5}$	$IV_{0.5}$	$I_{0.2}$	$I–II_{0.4}$	$I_{0.1}$	–	$IV_{0.4}$
OR-4	0	$I_{0.2}$	$I_{0.1}$	$II–III_{0.7}$	$IV_{0.5}$	$IV_{0.5}$	$IV_{0.6}$	$I_{0.1}$	$I–II_{0.4}$	$I–II_{0.3}$	–	$IV_{0.4}$
D-44	$I_{0.1}$	$I–II_{0.3}$	$I–II_{0.4}$	$III_{0.7}$	$I_{0.1}$	$IV_{0.6}$	$IV_{0.6}$	$IV_{0.7}$	$IV_{0.6}$	$I_{0.2}$	–	$IV_{0.6}$
AR-4	$I_{0.1}$	$I–II_{0.4}$	$I_{0.2}$	$II–III_{0.6}$	$IV_{0.6}$	$II_{0.4}$	$III–IV_{0.6}$	$I_{0.1}$	$I–II_{0.3}$	$I_{0.1}$	–	$IV_{0.6}$
D-40	$I_{0.1}$	$I–II_{0.4}$	$IV_{0.6}$	$IV_{0.7}$	0	$IV_{0.6}$	$IV_{0.7}$	$I_{0.2}$	$I–II_{0.5}$	$II_{0.3}$	–	$IV_{0.5}$
A1-1	$IV_{0.5}$	$IV_{0.4}$	$I_{0.2}$	$III_{0.4}$	0	$I–II_{0.2}$	$III_{0.2}$	$I_{0.2}$	$I–II_{0.3}$	0	–	$IV_{0.4}$
129-13	$I_{0.1}$	$I_{0.3}$	$IV_{0.7}$	$IV_{0.6}$	$IV_{0.6}$	$IV_{0.6}$	$IV_{0.4}$	$I_{0.3}$	$I–II_{0.4}$	$I–II_{0.4}$	–	$IV_{0.6}$
501-IS-b	$IV_{0.5}$	$IV_{0.6}$	$IV_{0.5}$	$IV_{0.6}$	$III_{0.4}$	0	$I_{0.1}$	$I_{0.4}$	$II_{0.4}$	$IV_{0.6}$	–	$III–IV_{0.5}$
PS-IS-2	$III–IV_{0.6}$	$III–IV_{0.6}$	$III–IV_{0.5}$	$III–IV_{0.6}$	$III–IV_{0.6}$	0	$I_{0.3}$	$I_{0.3}$	$II–III_{0.3}$	$III–IV_{0.6}$	–	$III–IV_{0.6}$
EI-IS-1	$II_{0.6}$	$III_{0.6}$	$III–IV_{0.6}$	$III–IV_{0.7}$	$I–II_{0.2}$	$I–II_{0.3}$	$II_{0.4}$	$III–IV_{0.6}$	$III–IV_{0.5}$	$III–IV_{0.6}$	$III–IV_{0.7}$	$III–IV_{0.5}$

– = missing data

[a] 0–IV indicates severity of immune reaction with 0 indicating no visible symptoms of infection and IV indicating index values 0.1–1.0 added to reaction type score indicate quantitative level of disease incidence as compared with susceptible standard SM4142 = $IV_{1.0}$

[b] Line RS 145-39 × Kiebitz was used because no NIL for *Mla20* was available

and *Mla20*. The tests for the mildew reaction of *Mla20* in the heterozygous state indicated that in crosses with *Mla1*, *Mla3*, *Mla12* and *Mla20* had a semidominant mode of inheritance, while against isolates used in the crosses with *Mla6*, *Mla7* and *Mla13* the reaction of *Mla20* appeared to be recessively inherited (Table 3). As indicated in Tables 2 and 3 the differences in the mode of inheritance of the resistant reaction observed in some host-pathogen combinations with *Mla13* and *Mla20* were independent of the presence of another *Mla* allele, e.g. the semidominant inheritance of *Mla13* was always clearly present upon infection with isolate PS-IS-2. This also holds true with all other cross combinations: no transposition interaction was found between the *Mla* alleles included in this study. It therefore appears that the gene-for-gene interactions which determine the reaction type between a given *Mla* allele and corresponding genes for avirulence present in different test cultures are not affected by the presence of other *Mla* alleles in the heterozygous state, irrespective of the mode of inheritance of the effective *Mla* gene.

Recombination at the Mla locus

A total of 17 605 progenies obtained from the BC_1F_1 generation were inoculated with two appropriate powdery mildew isolates in order to identify recombinant plants. A rather large number of potential recombinants were found (data not shown), mainly originating from those backcross populations involving semidominant alleles. Since the heterozygous plants crosses do not always express clear reaction types, self-pollinated progenies of potential recombinants were tested in order to verify the presence of recombinant plants. From each potential recombinant plant, the BC_1F_2 generation was raised in the greenhouse, and 60 progenies were tested in the seedling stage with the same powdery mildew isolate used in BC_1F_1 generation. With this test two susceptible recombinants were confirmed. These originated from a cross between the *Mla1* and *Mla12* near-isogenic lines and from the cross between *Mla13* and *Mla20*.

An attempt was made to link conclusively the underlying recombination effect at the *Mla* locus to corresponding changes in the RFLP pattern. For this purpose the recombinant progeny from the cross *Mla1* × *Mla12* was chosen, since *Mla1* and *Mla12* are characterized by different RFLP patterns, as shown by Schüller et al. (1992).

Three RFLP markers, MWG 1H036, MWG 1H060 and MWG 1H068, were used. They are located in the *Mla* region within genetical distances of 0.7 cM, 4.2 cM and 5.1 cM, respectively, as described by Schüller et al. (1992). The recurrent parent 'Pallas' and NIL P10, which carries the *Mla12* gene, do not show

Table 3. Different modes of inheritance of mildew reaction conditioned by *Mla20*

	Semidominant[a]				Recessive[b]		
Isolate	*Mla20*	F_1	*Mla12*	Isolate	*Mla20*	F_1	*Mla13*
184/21	$I_{0.1}$	$II–III_{0.7}$	$IV_{0.6}$	Ru-3	$I_{0.2}$	$IV_{0.7}$	$IV_{0.5}$

[a] Semidominant mode of inheritance has also been found with mildew isolates D-44, AR-4 and A1-1
[b] Recessive mode of inheritance was confirmed with mildew cultures 201/60, 131/13, OR-4 and 129-13

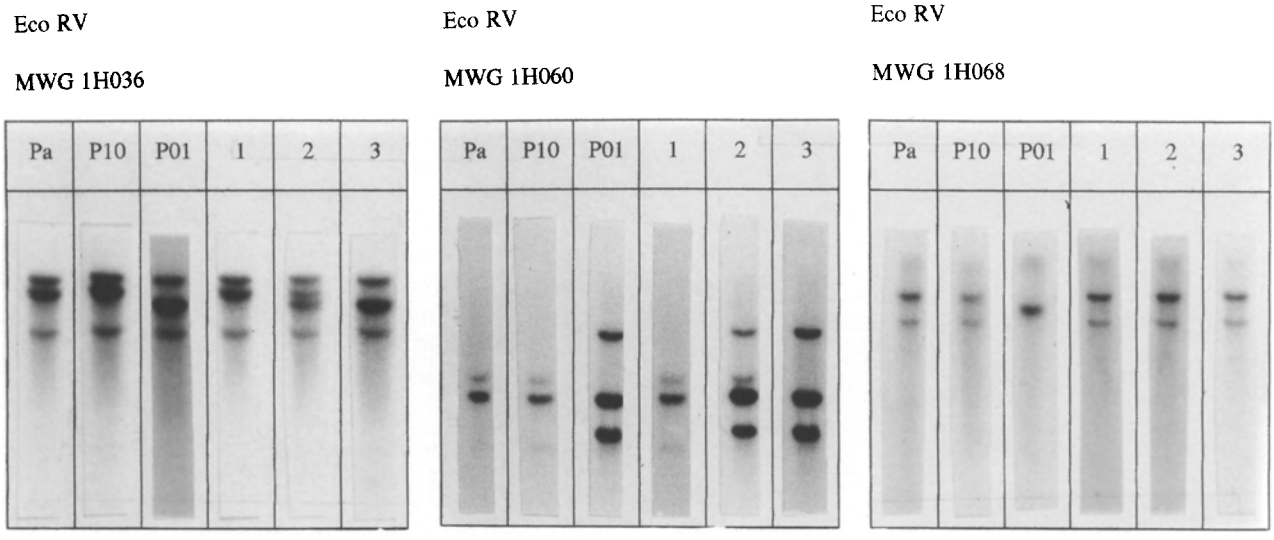

Fig. 1. Southern blot of the *Eco*RV-digested DNA of parental lines and three different progenies of a recombinant BC_1F_1 plant probed with RFLP markers MWG 1H036, MWG 1H060 and MWG 1H068, respectively. *Pa* 'Pallas', *P10* NIL for *Mla12*, *P01* NIL for *Mla1*, *1* homozygous line like 'Pallas', *2* heterozygous recombinant line, *3* homozygous recombinant line

polymorphism with any of the three RFLP markers, but RFLP patterns in NIL P01, which carries *Mla1*, differ from 'Pallas' in all three cases (Fig. 1). RFLP analysis of the recombinant plants reveals a pattern which shows that the fragment distal to the *Mla* locus originates from P01 (*Mla1*) and that fragment proximal to it, from P10 (*Mla12*). Therefore, a cross-over event must have taken place between the RFLP loci MWG 1H036 and MWG 1H068 that caused both *Mla* alleles to become ineffective. Figure 2 presents the genetic constitution of the parent lines and the origin of the fragment associated with the *Mla* locus in the homozygous and heterozygous state.

Discussion

The mode of inheritance of genes for disease resistance in host plants is mostly reported in the literature as being dominant (Wiberg 1974b; Crute 1985; Islam et al. 1989) with only a few exceptions (Schwarzbach 1967). However, F_2 progenies do not give clear indications about the mode of inheritance because they do not exclusively segregate into parental types; in addition, different frequencies of non-parental types of reaction also occur (Jahoor 1987). Therefore, it is often difficult to build segregation classes into the F_2 generation. In the investigation reported here, F_1 plants were used to determine the mode of inheritance of several *Mla* alleles. The results obtained are largely in agreement with those of Giese et al. (1981) with the exception that the latter authors reported *Mla7* as being semidominant, whereas we determined that it clearly belongs to the dominant group. As was shown recently by Islam et al. (1992) the mode of inheritance will not be stable in all cases if a very large number of mildew isolates is used.

The seven *Mla* alleles included in this study were selected as being representative of a large range of geographic origins in the hope of increasing chances for intralocus recombination. The results indicate that only susceptible recombinants were recovered, both of which resulted from test crosses between semidominant and dominant *Mla* alleles. In many cases, other apparently susceptible recombinants could not be verified in later generations. This may

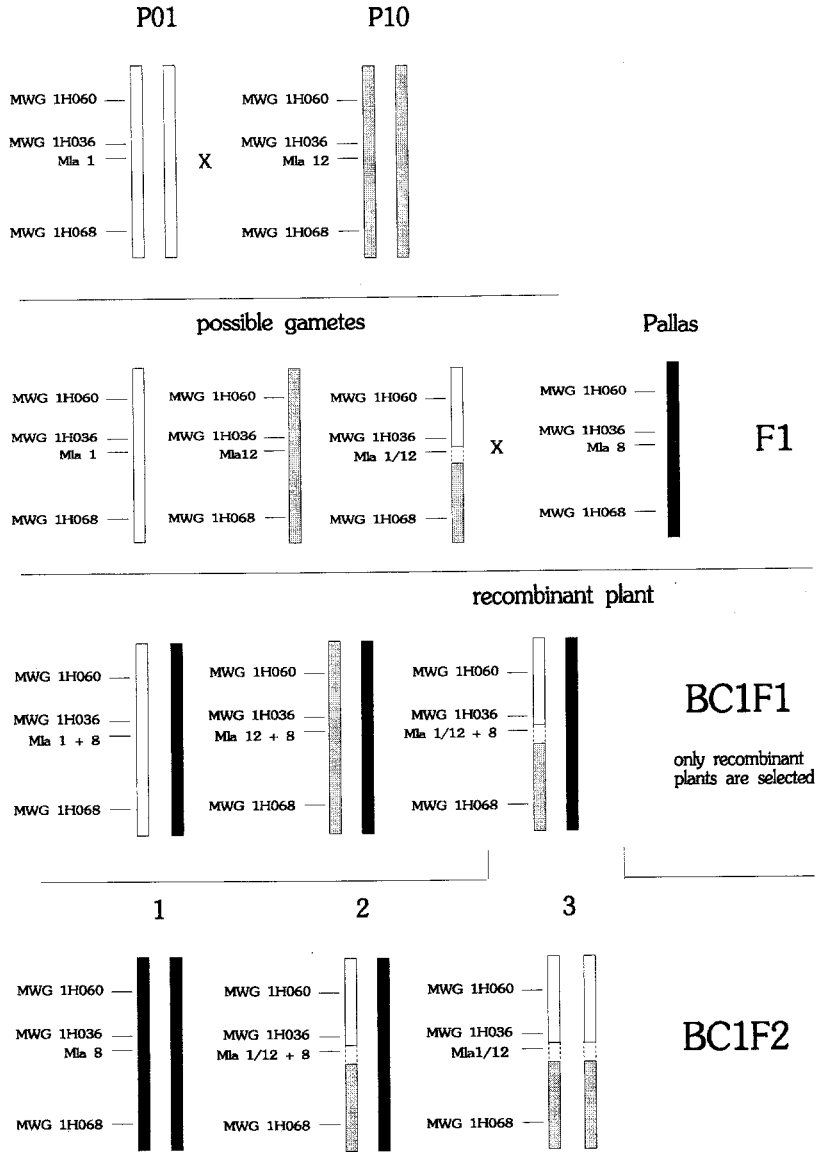

Fig. 2. Occurrence and genetical constitution of the double susceptible recombinant progeny originating from the cross between NILs carrying *Mla1* and *Mla12*. The mapping positions of all three hybridisation probes, MWG 1H036, MWG 1H060, MWG 1H068, and the *Mla* locus on chromosome 5 (1*H*) are indicated. *P01* NIL for *Mla1*, *P10* NIL for *Mla12*

be explained by the assumption that in BC_1F_1 progenies involving a semidominant resistance gene the resistant and susceptible reactions are difficult to score. Probably due to this fact, Wise and Ellingboe (1985) also reported many susceptible recombinants, a result paralleling that of the present investigation. These authors discussed the presence of transposable-like elements in this region, but this hypothesis could not be verified in the work of Jahoor et al. (1991). Nevertheless, in the present study two wild-type recombinants originating from crosses between *Mla1* and *Mla12* and between *Mla13* and *Mla20*, respectively, were confirmed in the BC_1F_2 generation. Jørgensen and Moseman (1972) reported one susceptible recombinant from a cross involving the *Mla1* and *Mla3* alleles, and Giese et al. (1981) also observed one susceptible recombinant between the *Mla12* and *Mla13* alleles. Due to the lack of closely linked markers, however, it has not been possible to distinguish between true recombinations and possible mutations. It is interesting to note that all of the recombinants found so far originated from crosses involving one parent carrying a dominant and another parent carrying a semidominant *Mla* allele. This could lead to the assumption that the *Mla* region may include at least two very closely linked loci. However, the persistent lack of double-resistant recombinants does not support this hypothesis. It still may be assumed that all of the alleles of the *Mla* region belong to the same locus. Thus, if a crossover takes place between two alleles located at the same position of the chromosome only susceptible recombinant plants

will occur because in the *cis* position of the recombinant alleles disturbances in the open reading frame do not allow the expression of both of the parental allele specificties. At the same time, such intra-allelic crossover events may give rise to new alleles, which would display entirely different patterns of reactions against powdery mildew isolates. This would agree with the origin of new alleles from the reorganisation of the DNA sequence in a particular region of a chromosome, which has been suggested by different authors in other cases (Shepherd and Mayo 1972). As Shepherd and Mayo (1972) have pointed out, functional recombination of different genes requires that both the *cis* and *trans* positions produce the same reaction pattern, which can only be proven if double-resistant recombinant plants occur or if an allele-specific RFLP marker for the *Mla* locus becomes available.

Acknowledgements. The helpful technical assistance of C. Stockenreiter for mildew infections and of S. Erhard for DNA isolation is greatly appreciated. The authors also thank Dr. A. Graner for reading the manuscript. This study was supported by the Federal Ministry for Research and Technology (Grant Nr. 0318990 G).

References

Blake T, Dahleen L, Dvorak J, Gustafson P, Hayes P, Hoffman D, Kasha K, Procunier S, Kim W, Kleinhofs A, Lapitan N, LaRoche A, Saghai Maroof MA, Molnar S, Fedak G, Scoles G, Skadsen R, Sorrels M, Tanksley S (1991) An RFLP map of barley – North American genome mapping project. In: Munck L (ed) Proc VIth Int Barley Genet Symp (Barley Genetics VI). Helsingborg, pp 245–248

Crute IR (1985) The genetic basis of relationships between microbial parasites and their hosts. In: Fraser RSS (ed) Mechanisms of resistance to plant diseases. Martinius Nijhoff/ Dr. W. Junk, Dordrecht Boston Lancaster, pp 80–142

Feinberg AP, Vogelstein B (1983) A technique for radiolabeling DNA restriction endonuclease fragments to high specific activity. Anal Biochem 132:6–13

Giese H, Jørgensen JH, Jensen HP, Jensen J (1981) Linkage relationship of ten powdery mildew resistance genes on barley chromosome 5. Hereditas 95:43–50

Graner A, Siedler H, Jahoor A, Herrmann RG, Wenzel G (1990) Assessment of the degree and the type of restriction fragment length polymorphism in barley (*Hordeum vulgare*). Theor Appl Genet 80:826–832

Graner A, Jahoor A, Schondelmaier J, Siedler H, Pillen K, Fischbeck G, Wenzel G, Herrmann RG (1991) Construction of an RFLP map of barley. Theor Appl Genet 83:250–256

Hentrich W (1979) Allelwirkung und Pleiotropie mehltauresistenter Mutanten des *mlo* Locus der Gerste. Arch Zeuchtungsforschung 9:283–291

Heun M, Kennedy AE, Anderson JA, Lapitan NLV, Sorrells ME, Tanksley SD (1991) Construction of a restriction fragment length polymorphism map for barley (*Hordeum vulgare*) Genome 34:437–447

Hoffmann W, Nover I (1959) Ausgangsmaterial für die Züchtung mehltauresistenter Gersten. Z Pflanzenzeucht 42: 68–78

Honecker L (1936) Über den derzeitigen Stand und die Aussichten der Bekämpfung des Mehltaubefalles der Gerste durch Züchtung. Prakt Bl Pflanzenbau Pflanzenschutz 13: 309–320

Islam MR, Jahoor A, Fischbeck G (1992) Analysis of powdery mildew reaction on barley F_1 plants involving different *Mla* alleles. Physiol Mol Plant Path 40:353–358

Islam MR, Shepherd KW, Mayo GM (1989) Recombination among genes at the L group in flax conferring resistance to rust. Theor Appl Genet 77:540–546

Jahoor A (1987) Mehltauresistenz israelischer Wildgersten–Resistenzspektrum, Vererbung und Lokalisierung. (PhD thesis) Technische Universität München

Jahoor A, Fischbeck G (1987) Source of resistance to powdery mildew in barley lines derived from Hordeum spontaneum collected in Israel. Plant Breed 99:274–281

Jahoor A, Ludwig A, Fischbeck G (1989) New genes for powdery mildew resistance in *Hordeum spontaneum*-derived lines allelic or closely linked to the *Mlp* locus. Barley Genet Newle 19:23–26

Jahoor A, Backes G, Graner A, Herrmann RG, Fischbeck G (1991a) Development of RFLP markers for the barley genome. Plant Breed 107:73–76

Jahoor A, Stephan U, Fischbeck G (1991b) Study of powdery mildew resistance genes from 'Engledow India'. Barley Genet Newsl 20:41–42

Jørgensen JH, Moseman JG (1972) Recombination at the *Mla* locus in barley conditioning resistance to *Erysiphe graminis* f. sp. *hordei*. Can J Genet Cytol 14:43–48

Kølster P, Munk L, Stølen O, Lohde J (1986) Near-isogenic barley lines with genes for resistance to powdery mildew. Crop Sci 26:903–907

Moseman JG (1955) Sources of resistance to powdery mildew of barley. Plant Dis Rep 39:967–972

Moseman JG, Jørgensen JH (1971) Identification of genes at the *Mla* locus in barley for resistance to *Erysiphe graminis* f. sp. *hordei*. Crop Sci 2:547–550

Nover I (1972) Untersuchungen mit einer gegen den Resistenzträger 'Lyallpur-3645' virulenten Rasse von *Erysiphe graminis* D.C. f. sp. *hordei* Marchal. Arch Pflanzenschutz 8: 439–445

Schüller C, Backes G, Fischbeck G, Jahoor A (1992) RFLP markers to identify the alleles on the *Mla* locus conferring powdery mildew resistance in barley. Theor Appl Genet 84:330–338

Schwarzbach E (1967) Recessive total resistance of barley to mildew (*Erysiphe graminis* D.C. f. sp. *hordei* Marchal) as a mutation induced by Ethylmethansulfonate. Genet a šlechténi 3:159–162

Sheperd KW, Mayo GME (1972) Genes conferring specific plant disease resistance. Science 175:375–380

Wiberg A (1974a) Sources of resistance to powdery mildew in barley. Hereditas 78:1–40

Wiberg A (1974b) Genetical studies of spontaneous sources of resistance to powdery mildew in barley. Hereditas 77:89–148

Wise PR, Ellingboe AH (1985) Fine structure and instability of the *Mla* locus in barley. Genetics 111:113–130