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Associations between three *ml-o* powdery mildew resistance genes and agronomic traits in barley

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Summary

A population of 198 chromosome-doubled haploid lines of spring barley was scored for segregation in locus *ml-o* (powdery mildew reaction) on chromosome 4 and in the linked loci *s* (rachilla hair length) and *ddt* (reaction to the insecticide DDT) on chromosome 7. They were also tested in a disease-free field trial for the agronomic traits: grain yield, thousand grain weight, lodging, and necrotic leaf spotting. The three mutagen–induced resistance genes *ml-o5, ml-o6* (from 'Carlsberg II') and *ml-10* (from 'Foma') showed no detectable differences with respect to effects on agronomic traits. They all conferred a four per cent reduction in grain yield caused mainly by lower thousand grain weight, and an increase in necrotic leaf spotting. The two original mutants of 'Carlsberg II' had additional mutant genes affecting agronomic traits. Lines with gene *S* (long hair) had on average a three per cent higher thousand grain weight than those with *s*. The alleles in locus *ddt* showed no association with the agronomic traits. It is concluded i) that the associations between the three *ml-o* alleles and agronomic traits are caused by pleiotropy, ii) that *ml-o* resistant, high-yielding lines may be selected, and iii) that the association between gene *s* and thousand grain weight may be due to genetic linkage.

Abbreviations: DH-lines = chromosome-doubled haploid lines

Introduction

Disease resistance genes and morphological marker genes are frequently, but sometimes unconsciously, manipulated in breeding programmes, and it is important to examine possible associations of such genes to agronomic traits. The associations may be due to pleiotropy or to genetic linkage.

Few investigations have been made on associations between disease resistance genes and agronomic traits in crop plants under disease-free conditions (Frey & Browing, 1971; Singh & Lambert, 1985; Webster et al., 1986). Associations between morphological marker genes and quantitative traits in barley have been reported in a few cases (Kjær et al., 1989; Suneson et al., 1952; Wexelsen, 1962).

Several mutagen-induced and spontaneously arisen powdery mildew resistance genes in the *ml-o* locus have been reported (cf. Jørgensen, 1984). Field trials with mother varieties and their *ml-o* mutants have shown that the resistant mutants have a lower yield than the susceptible mother varieties under disease-free conditions (Hänsel, 1966; Jørgensen, 1976a; Schwarzbach, 1976; Wi-

berg, 1973). It is not known whether this is also the case for spontaneously arisen *ml-o* genes.

The yield reduction ranges from about 5 per cent in mutants of 'Foma' barley (Wiberg, 1973) to about 15 per cent in mutants of 'Carlsberg II' barley (Jørgensen, 1976a). It has not been resolved, however, whether different *ml-o* resistance genes confer different yield reductions, or whether the differences between different pairs of mutants/mother varieties could be ascribed to other factors, particularly other simultaneously induced mutant genes, or interactions between the mutant genes and genetic background.

In the present study we have examined the effects of three *ml-o* powdery mildew resistance genes on quantitative characters in homozygous DH-lines having a randomized genetic background orignating from 'Carlsberg II' × 'Foma'. Furthermore, the effects of the genes *s* (short rachilla hair) and *ddt* (DDT resistance) occurring spontaneously in the material were studied.

Materials and methods

Plants

Two spring barley (*Hordeum vulgare* L.) varieties, 'Carlsberg II' and 'Foma' susceptible to the powdery mildew fungus *Erysiphe graminis* DC.: Fr. f.sp. *hordei* and three resistant mutants. Risø 5678 with resistance gene *ml-o5* and Risø 6018 with *ml-o6* induced in 'Carlsberg II' (cf. Jørgensen, 1976b), and 'SR7' with *ml-o10* induced in 'Foma' (Wiberg, 1973) were used. Locus *ml-o* is on barley chromosome 4 (cf. Jensen, 1988). The material also differs in alleles in locus *ddt* that confers reaction to the insecticide DDT, and locus *s* determining the length of rachilla hair (cf. Table 2) on chromosome 7 (cf. Jensen, 1981).

The three mutants were crossed reciprocally with the non-parent variety. The three crosses are designated as follows:
Cross A: 'Risø 5678' × 'Foma',
Cross B: 'Risø 6018' × 'Foma',
Cross C: 'SR7' × 'Carlsberg II'
A total of 492 completely homozygous DH-lines with a random gene background from the common gene pool, 'Carlsberg II' × 'Foma' were produced by the Bulbosum technique (Jensen, 1976) from F_1 plants. Thirty-six DH-lines with Ml-o resistance and thirty without were taken randomly from each cross for the field trial. The reciprocal crosses are pooled in the following as no differences were found for the characters studied. The 66 DH-lines from each cross are designated population A, B, and C, respectively.

Powdery mildew reaction was determined before selection by using isolate A6 (290) of the powdery mildew fungus (cf. Torp et al., 1978). A test of DDT reaction was carried out using a modified method described by Jensen (1979). The classification for length of rachilla hair was done by visual examination of seeds.

Field trial

The 36 and 30 DH-lines per cross were divided into three groups each comprising twelve and ten lines. To each group were added the respective mutant line and the two mother varieties, 'Carlsberg II' and 'Foma'. The 25 lines per group were placed in a 5 × 5 square of field plots. Each plot was 5.3 m^2. The squares were replicated trice. The superior design of the trial was a 3 × 3 Latin square where three squares, one per cross, represented one 'treatment'.

The trial was conducted with normal agricultural practice and was treated with fungicides to control foliar plant diseases, in particular powdery mildew.

Four quantitative characters were measured in each plot. During the growing season *lodging* was scored on a 0 to 9 scale with 9 = completeley lodged, and *necrotic leaf spotting* was scored on a 0 to 10 scale with 10 = very severe necrotic spotting on leaves and stems (≧80% of the leaf area covered by necrotic spots). After harvest the *grain yield* was determined and adjusted to 15% water content, and the *thousand grain weight* was calculated from a random sample of 400–500 seeds per plot. The four quantitative characters were adjusted by the systematic effects of rows and columns in the Latin square. In the analyses of variance the

total degrees of freedom were reduced by four, and data for necrotic leaf spotting and lodging were transformed with ln (x + 1).

Results

Segregation of marker genes

The alleles in locus *ml-o* for the 492 DH-lines and the alleles in loci *s* and *ddt* for the 3 × 66 DH-lines in the yield trial segregated according to the expected 1 : 1 ratio in all three populations (Table 1). Segregations of marker genes were homogenous among the three populations.

The recombination percentages between loci *s* and *ddt* in the three populations of 21, 42 , and 30 per cent (Table 1) were barely significantly different at the 5% level ($\chi^2_{2df} = 7.23$).

Associations between ml-o genes and agronomic traits

The three *ml-o* mutants had lower grain yield, lower thousand grain weight and higher score of necrotic leaf spotting than their mother variety, whereas lodging scores did not differ (Table 2). Mutant Risø 6018 had the lowest grain yield, 23 per cent below that of the mother variety 'Carlsberg II', and a thousand grain weight reduced by 13 per cent. Mutant 'SR7' had only a three and five per cent reduction in grain yield and thousand grain weight, respectively, compared to 'Foma' (Table 2). The three *ml-o* mutants had high scores for necrotic leaf spotting (from 1.9 to 4.6), and 'Carlsberg II' and 'Foma' had low scores (from 0.2 to 0.3) (Table 2).

The means of the 66 DH-lines from each cross (Table 3) were in between the values of the parents (Table 2) for the quantitative characters. A comparison of the three populations showed that population B had a significantly higher variance for thousand grain weight than A and C, and that population A had a significantly higher mean for thousand grain weight than B and C (Table 3). Further, the mean values of the three populations differed significantly with respect to grain yield ($P < 0.001$) and necrotic leaf spotting ($P < 0.05$) (Table 3) but not for lodging. The lodging score mean for the 198 DH-lines was 2.1.

Within each of the three populations there were significant differences between DH-lines for the four agronomic traits, indicating a significant genetic variation for each of the four traits. Further, there was a negative correlation between leaf necrosis and grain yield and thousand grain weight, respectively, within each of the three populations. The three DH-populations subdivided into *Ml-o* (susceptible) and *ml-o* (resistant) subpopulations showed significant differences between subpopulations for grain yield, thousand grain weight and necrotic spotting (Tables 3 and 4), but not for lodging. The distribution and mean of the 3 × 2 subpopulations (Table 3) showed that the *ml-o* subpopulations had lower grain yield and thousand grain weight and more necrosis thant the *Ml-o* subpopulations.

Table 1. Segregation in three populations of DH-lines for alleles in locus *ml-o* (reaction to powdery mildew) in 492 DH-lines, and for alleles in loci *ddt* (reaction to the insecticide DDT) and *s* (length of rachilla hair) in 3 × 66 DH-lines tested in field trial

Population	Powdery mildew			DDT-reaction and length of rachilla hair				χ^2 1 : 1		Per cent recombination between loci *ddt* and *s*
	Ml-o	ml-o	χ^2 1 : 1	S, Ddt	S, ddt	s, Ddt	s, ddt	ddt	s	
A: Risø 5678 × Foma	66	71	0.18	6	21	31	8	0.97	2.18	21.2 ± 5.0
B: Risø 6018 × Foma	85	74	0.76	15	17	21	13	0.55	0.06	42.4 ± 6.1
C: SR7 × Carlsberg II	108	88	2.04	9	23	23	11	0.06	0.06	30.3 ± 5.7
Total	259	233	1.37	30	61	75	32	0.73	1.29	31.3 ± 3.3

The variance of grain yield was greater within the susceptible lines than within the resistant ones. In the C population the variances of the subpopulations were significantly different for grain yield ($P < 0.05$). The variation in the necrotic leaf spotting score was larger for the resistant subpopulations than for the susceptible subpopulations, but with statistical significance within populations A and C only ($P < 0.01$ and $P < 0.001$, respectively).

On average the three *ml-o* mutant genes reduced the grain yield and thousand grain weight and increased the necrotic leaf spotting to an equal extent (Table 4). The presence of anyone of the three *ml-o* genes reduced the grain yield with about 2.1 hkg/ha and the thousand grain weight with about 2.5 grammes, both equal to 4–5 per cent, and increased the necrotic leaf spotting score by 1.5–2.0 points.

These values are very close to those obtained from comparing 'Foma' and its mutant 'SR7' (Table 2). This suggests that all the differences between these two barleys may be ascribed to the presence of mutant gene *ml-o10* in 'SR7'. The differences between 'Carlsberg II' and its mutants 'Risø 5678' and 'Risø 6018', with respect to grain yield and necrotic leaf spotting, plus thousand grain weight for 'Risø 6018' only, (Table 2), were much greater than what can be ascribed to the presence of the *ml-o* genes. This is probably caused by the presence of simultaneously induced mutant genes affecting grain yield, thousand grain weight and necrotic leaf spotting. The presence of other induced genes for necrotic leaf spotting in population B is supported by the significant negative correlation ($r = -0.60$, $P < 0.001$) between thousand grain weight and necrotic leaf spotting that occurs within the susceptible lines.

Associations of the marker genes s and ddt with agronomic traits

The two marker genes and the four quantitative traits determined in the field trial provide eight possible pairwise combinations of markers and traits. One of these, between locus *s* and thousand grain weight was significant in population B in which the thousand grain weight of DH-lines with allele *S* was 44.3 ± 0.4 g, and with allele *s* 41.2 ± 0.4 g. However, when the thousand grain weight of the DH-lines within subpopulations *S* and *s* was distributed on interval classes within the three populations, A through C, the subsequent heterogeneity test showed that all three DH-populations were equal with respect to that portion of thousand grain weight that was affected by locus *s*. Therefore, we assume that the effect of alleles in locus *s* was present in all three populations. The three populations were then adjusted for the effect of cross and that of *ml-o* locus.

In the entire material (198 DH-lines) the mean thousand grain weight of DH-lines with allele *S* was 44.1 ± 0.3 g and that of lines with allele *s* was

Table 2. Genotypes of three loci and mean plus standard deviation for four quantitative traits of the parental material

Material	Genotypes[1]			Quantitative traits							
				Grain yield		Thousand grain wgt		Necrosis		Lodging	
				kg/plot	relative	grammes	relative	ln (x + 1)	x	ln (x + 1)	x
Carlsberg II	Ml-o	ddt	S	2.89 ± 0.02	100	46.2 ± 0.2	100	0.27 ± 0.07	0.3	1.27 ± 0.07	2.5
Risø 5678	ml-o5	ddt	S	2.52 ± 0.04	87	44.2 ± 0.4	96	1.71 ± 0.13	4.5	1.28 ± 0.13	2.6
Risø 6018	ml-o6	ddt	S	2.22 ± 0.04	77	40.0 ± 0.4	87	1.72 ± 0.13	4.6	1.43 ± 0.13	3.2
Foma	Ml-o	Ddt	s	2.75 ± 0.02	100	45.3 ± 0.2	100	0.19 ± 0.07	0.2	0.74 ± 0.07	1.1
SR7	ml-o10	Ddt	s	2.68 ± 0.04	97	42.9 ± 0.4	95	1.06 ± 0.13	1.9	0.57 ± 0.13	0.8

[1] ml-o/ML-o = resistant/susceptible powdery mildew reaction.
ddt/Ddt = resistant/susceptible DDT reaction.
s/S = short/long rachilla hair.

Table 3. Distribution of DH-lines in the Ml-o/ml-o subpopulations with respect to grain yield, thousand grain weight and necrotic leaf spotting. The means of the populations and Ml-o/ml-o subpopulations are given

a. Grain yield. (Interval means are in kg per plot)

	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	3.1	$\bar{X}$
A: Risø 5678 × Foma														
ml-o5			2	1	2	8	8	7	6	1	1			2.52
Ml-o				1	1	1	10	6	2	4	5			2.61
Total			2	2	3	9	18	13	8	5	6			2.56
B: Risø 6018 × Foma														
ml-o6	1		1	3	7	7	12	3	2					2.41
Ml-o			1	2	1	8	6	2	6	3			1	2.54
Total	1		2	5	8	15	18	5	8	3			1	2.46
C: SR7 × Carlsberg II														
ml-o10						4	3	8	4	13	4			2.68
Ml-o					1	3		3	4	8	2	6	3	2.79
Total					1	7	3	11	8	21	6	6	3	2.73

b. Thousand grain weight. (Interval means are in g)

	34	36	38	40	42	44	46	48	50	$\bar{X}$
A: Risø 5678 × Foma										
ml-o5				2	12	10	11		1	43.9
Ml-o					4	11	9	3	3	45.4
Total				2	16	21	20	3	4	44.6
B: Risø 6018 × Foma										
ml-o6	1	2	8	10	4	6	3	1	1	41.1
Ml-o			1	4	2	11	4	5	3	44.5
Total	1	2	9	14	6	17	7	6	4	42.7
C: SR7 × Carlsberg II										
ml-o10			2	12	12	7	2	1		41.9
Ml-o			1	2	5	12	6	3	1	44.2
Total			3	14	17	19	8	4	1	42.9

c. Necrotic leaf spotting score. Interval means on scale 0-10 and transformed with ln(x + 1)

ln(x + 1)	0	0.3	0.6	0.9	1.2	1.5	1.8	2.1	Mean value	
x	0	0.3	0.8	1.5	2.3	3.5	5.1	7.2	ln (x + 1)	x
A: Risø 5678 × Foma										
ml-o5	1	4	3	3	8	5	5	7	1.26	2.5
Ml-o	12	9	4	5					0.33	0.4
Total	13	13	7	8	8	5	5	7	0.84	1.3
B: Risø 6018 × Foma										
ml-o6		3	4	4	7	11	7		1.23	2.4
Ml-o	13	6	2	6	2	1			0.40	0.5
Total	13	9	6	10	9	12	7		0.85	1.4
C: SR7 × Carlsberg II										
ml-o10	2	5	10	2	6	3	8		0.97	1.6
Ml-o	24	3	3						0.09	0.1
Total	26	8	13	2	6	3	8		0.57	0.8

42.8 ± 0.3 g (Table 5). These two means were significantly different ($P < 0.001$). This association was also present in the two parent varieties 'Carlsberg II' and 'Foma' (Table 2). These findings suggest that one or more genetic factors for thousand grain weight are on chromosome 7. Associations between alleles in locus *ddt* and the four agronomic traits could not be found, suggesting that these two alleles are neutral in relation to the four traits measured here, and that the genetic factors affecting thousand grain weight may be near or at locus *s*.

Discussion

Segregation of marker genes

Loci *ml-o, s,* and *ddt* segregated as expected in 1 : 1 ratio supporting the belief that haploids produced by the Bulbosum method are random gametes of F_1 plants (Choo et al., 1985; Kjær et al., 1989).

The recombination frequencies between loci *s* and *ddt* are somewhat heterogenous for the three populations (Table 1). Jensen (1979) found a recombination frequency of 41.45 ± 3.44 per cent. The recombination frequency of population A alone is in disagreement with the results of Jensen (1979). This deviation may be ascribed to random variation.

Asssociations between ml-o genes and quantitative traits

The present results did not disclose any differences between the effects of the three alleles *ml-o5, ml-o6,* and *ml-o10* on reduction in grain yield and thousand grain weight, and on increase in necrotic leaf spotting (Table 4). Anyone of the alleles reduced grain yield and thousand grain weight with four or five per cent. The grain yield reduction is considerably smaller and the thousand grain weight reduction is similar to those reported by Schwarzbach (1976) from a study on F_2 plant progenies. The effects of the *ml-o* genes on the three agronomic traits probably originates from one common cause, necrotic leaf spotting. It is expressed particularly after heading in the field, and this reduces the effective photosynthesis leaf area and the translocation of photosynthesis products from the leaves to the spike during grain filling. This will cause reduced grain yield particularly through reduced grain size.

The associations between *ml-o* genes and agronomic traits are probably due to pleiotropic effects of the *ml-o* genes rather than genes linked to the *ml-o* locus. It is most unlikely that three independently induced *ml-o* mutant genes should carry simultaneously induced mutant genes which cause identical effects on agronomic traits in other loci close to *ml-o*. Further, the low frequency of resistant lines with no necrotic leaf spotting in the present material (Table 3) also suggest pleiotropy. Finally, a hypothesis of a deletion covering locus *ml-o* and several other loci can be rejected because the *ml-o* genes which segregate in a Mendelian pattern, can undergo intra-locus recombination (cf. Jørgensen & Jensen, 1979). Another quantitatively expressed trait associated with Mlo resistance is the occasional powdery mildew colonies occurring on inoculated plants. Resistant barleys with different *ml-o* alleles may differ in frequency of colonies, but it has not been possible to ascribe any differences in this trait to different *ml-o* alleles (Jørgensen & Mortensen, 1977). This leads us to

Table 4. Effects of the three *ml-o* alleles on three quantitative traits. Given as $(\bar{X}_{ml\text{-}o} - \bar{X}_{Ml\text{-}o}) \pm$ deviation

	ml-o5	ml-o6	ml-o10
Grain yield (kg per plot)	− 0.098* ± 0.044	− 0.129** ± 0.047	− 0.109** ± 0.047
Thousand grain weight (g)	− 1.49** ± 0.54	− 3.43*** ± 0.83	− 2.37*** ± 0.11
Necrosis (ln (x + 1))	+ 0.93*** ± 0.12	+ 0.84*** ± 0.12	+ 0.87*** ± 0.11

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

the conclusion that the agronomic traits and the resistance traits studied are affected equally and pleiotropically by different *ml-o* alleles. Other authors (Hentrich, 1979; Heun & Röbbelen, 1984) have described different pleiotropic effects of different *ml-o* mutant genes disclosed in populations of F_2 plants or F_2 plants progenies.

The differences between the three *ml-o* mutants employed in this study (Table 2) must be ascribed to other mutant genes induced simultaneously with the *ml-o* mutations. In mutant 'SR7' it was not possible to detect other mutant genes, whereas 'Risø 5678' and 'Risø 6018' must possess probably several mutant genes that affect the agronomic traits. This explains the differences between the three populations of DH-lines (Table 3), and, most likely, the negative correlation between thousand grain weight and necrotic leaf spotting in the susceptible lines in population B. This population includes mutant 'Risø 6018' that carries the heaviest mutational load. The statistically significant higher variance of thousand grain weight in population B may be due to the simultaneous segregation of other induced mutant genes.

In addition to pleiotropism and simultaneously induced mutant genes in *ml-o* mutants, a third component, namely gene background, has to be considered. It is a common experience that the phenotypic expression of mutant genes is affected by the genetic background (cf. Gaul & Lind, 1976). Genetic modification of necrotic leaf spotting on *ml-o* mutants has been described by Schwarzbach (1976), Hentrich (1979), and Jørgensen (1976a), and modifications of the number of occasional mildew colonies on inoculated plants by Jørgensen and Mortensen (1977). High-yielding *ml-o* DH-lines selected in the present material showed in yield trials over two years yield capacity around the average of the two susceptible parents, 'Carlsberg II' and 'Foma'. The highest frequency of high-yielding lines was from population C (mutant 'SR7') without any other mutant genes, and the lowest frequency was from B (mutant 'Risø 6018') with many other mutant genes.

The commercial spring barley varieties 'Atem', 'Apex', 'Salome', 'Alexis', and 'Grosso' with Mlo resistance from Ethiopian barley have been released in Europe. At Risø these barleys have little or some necrotic leaf spotting, whereas Ethiopian barleys with gene *ml-o11* have severe spotting. Further, a population of spring barley lines with gene *ml-o5* from a cross between a line (no. 42) selected for low necrotic spotting at Risø (Jørgensen, 1976a) and the Swedish spring barley variety 'Agneta' has much reduced necrotic leaf spotting (K. Aastveit, pers. comm.). These observations indicate that high-yielding spring barley lines with spontaneously arisen or mutagen-induced Mlo resistance can be produced provided that appropriate adjustments are made of the genetic background. Furthermore, it suggest that absence of necrotic leaf spotting may be the easiest selection criterion for removing undesirable pleiotropic effects of Mlo resistance.

Associations of the marker genes s and ddt with agronomic traits

An association between locus *s* and thousand grain weight was found. DH-lines with long rachilla hair (allele *S*) had a three per cent higher thousand grain weight than DH-lines with short rachilla hair

Table 5. Distribution of DH-lines in *S* and *s* subpopulations when classified with respect to thousand grain weight (interval means are given), and means of subpopulations and of the 198 DH-lines

S/s subpopulation	Thousand grain weight (g)									$\bar{X}$
	36	38	40	42	44	46	48	50	52	
S	1	0	8	22	30	17	9	4	0	44.1
s	0	5	22	33	23	20	2	1	1	42.8
Total	1	5	30	55	53	37	11	5	1	43.4

(allele *s*). No association between alleles in locus *ddt* and thousand grain weight was found, suggesting that genetic factor(s) for thousand grain weight is close to or at locus *s* on chromosome 7.

Jensen (1989) has estimated the recombination percentage between locus *s* and the genetic factor (s) for thousand grain weight. 'Carlsberg II' with long rachilla hair is a malting variety with a relatively high thousand grain weight. A connection may exist between malting barley and a gene (block) on chromosome 7 affecting thousand grain weight. The great majority of modern barley varieties in Denmark have long rachilla hair. The selection for large seeds has apparently been an unconscious one for long rachilla hair (allele *S*). Genetic factors of thousand grain weight on chromosome 7 have been reported earlier. Bal et al. (1959) found an association between long rachilla hair (allele *S*) and light kernels. The reversed association has been found in the 198 DH-lines. This discrepancy can be explained be a reversed linkage phase.

The results presented here show that DH-lines are well suited to investigations of associations between genetic markers and agronomic traits as found by Bjørnstad (1987); Kjær et al. (1989); and Powell et al. (1985). The main advantages of DH-lines are that the plants are completely homozygous, so that an unlimited number of plants can be produced of each genotype, thus allowing each genotype to be evaluated in field trials under normal agricultural practice.

References

Bal, B.S., C.A. Suneson & R.T. Ramage, 1959. Genetic shift during 30 generations of natural selection in barley. Agron. J. 51: 555–557.

Bjørnstad, A., 1987. The role of linkage and pleiotropy in doubled haploid lines from a barley cross. Hereditas 106: 155–168.

Choo, T.M., E. Reinbergs & K.J. Kasha, 1985. Use of haploids in breeding barley. Plant Breed. Rev. 3: 219–252.

Frey, K.J. & J.A. Browning, 1971. Association between genetic factors for crown rust resistance and yield in oats. Crop Sci. 11: 757–760.

Gaul, H. & V. Lind, 1976. Variation of the pleiotropy effect in a changed genetic background demonstrated with barley mutants. In: Induced Mutations in Cross Breeding, pp. 55–69. IAEA, Vienna.

Hentrich, W., 1979. Allelwirkung und Pleiotropie mehltauresistenter Mutanten des *ml-o* Locus der Gerste. Arch. Züchtungsforsch. 9: 283–291.

Heun, M. & G. Röbbelen, 1984. Heteroallelism in the *ml-o* locus of barley. Z. Pflanzenzüchtg. 92: 281–288.

Hänsel, H., 1966. Induction of mutations in barley: Some practical and theoretical results. In: Mutations in Plant Breeding, pp. 117–137. IAEA, Vienna.

Jensen, C.J., 1976. Barley monoploids and doubled monoploids: Techniques and experience. In: H. Gaul (Ed.), Barley Genetics III, pp. 316–345. Karl Thiemig, Munich.

Jensen, J., 1979. Location of a high-lysine gene and the DDT-resistance gene on barley chromosome 7. Euphytica 28: 47–56.

Jensen, J., 1981. Construction of a barley chromosome 7 linkage map. In: M.J.C. Asher, R.P. Ellis, A.M. Hayter & R.N.H. Whitehouse (Eds), Barley Genetics IV, pp. 921–939. Edingburgh Univ. Press, Edingburgh.

Jensen, J., 1988. Linkage map of barley chromosome 4. In: T. Konishi & S. Yasuda (Eds), Barley Genetics V, pp. 189–199. Okayama Univ.

Jensen, J., 1989. Estimation of recombination parameters between a quantitative trait locus (QTL) and two marker gene loci. Theor. Appl. Genet. (in press).

Jørgensen, J.H., 1976a. Studies on recombination between alleles in the *ml-o* locus of barley and on pleiotropic effects of the alleles. In: Induced Mutations for Disease Resistance in Crop Plants (1975), pp. 129–140. IAEA, Vienna.

Jørgensen, J.H., 1976b. Identificaction of powdery mildew resistant barley mutants and their allelic relationship. In: H. Gaul (Ed.), Barley Genetics III, pp. 446–455. Karl Thiemig, Munich.

Jørgensen, J.H., 1984. Durability of the *ml-o* powdery mildew resistance genes in barley. Vortr. Pflanzenzüchtg. 6: 22–31.

Jørgensen, J.H. & K. Mortensen, 1977. Primary infection by *Erysiphe graminis* f.sp. *hordei* of barley mutants with resistance genes in the *ml-o* locus. Phytopath. 67: 678–684.

Jørgensen, J.H. & H.P. Jensen, 1979. Interallelic recombination in the *ml-o* locus in barley. Barley Genet. Newsl. 9: 37–39.

Kjær, B., V. Haahr & J. Jensen, 1989. Associations in a barley cross between ten genetic markers and twentythree quantitative traits. Plant Breeding (in press).

Powell, W., W.T.B. Thomas, P.D.S. Caligari & J.L. Jinks, 1985. The effects of major genes on quantitatively varying characters in barley. 1. The GP-ert locus. Heredity 54: 343–348.

Schwarzbach, E., 1976. The pleiotropic effects of the *ml-o* gene and their implications in breeding. In: H. Gaul (Ed.), Barley Genetics III, pp. 440–445. Karl Thiemig, Munich.

Singh, N.B. & J.W. Lambert, 1985. Effect of gene Rps_1 for resistance to *Phytophtora* rot on yield and other characteristics of soybean. Crop Sci. 25: 494–496.

Suneson, C.A., C.W. Schaller & E.H. Everson, 1952. An Association Affecting Yield in Barley. Agron. J. 44: 584–586.

Torp, J., H.P. Jensen & J.H. Jørgensen, 1978. Powdery mildew resistance genes in 106 North-West European spring barley varieties. Kgl. Vet.- og Landbohøjsk. Årsskr. 75–102.

Webster, R.K., M.A. Saghai-Maroog & R.W. Allard, 1986. Evolutionary response of barley composite cross II to *Rhynchosporium secalis* analysed by pathogenic complexity and gene-by-race relationships. Phytopath. 76: 662–668.

Wexelsen, H., 1962. Quantitative inheritance in barley. Association of quantitative and qualitative characters. Meldinger fra Norges Landbrukshøgskole 41 (6): 1–29.

Wiberg, A., 1973. Mutants of barley with induced resistance to powdery mildew. Hereditas 75: 83–100.