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Present state and prospects of breeding for resistance or immunity to barley yellow mosaic virus[1]

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The BaYMV resistance of German cultivars like Diana, Franka, Gloria or Sonate is due to one recessive gene ('German gene'), located on barley chromosome 3. This gene and the gene *Ym1* are most probably allelic (or tightly linked). Resistance of the American cv. Anson barley is inherited independently of the 'German gene' and *Ym1*. The haploidy technique is an efficient means for approaching major breeding goals: (1) to improve quality characteristics of cultivars carrying 'German resistance'; (2) to adapt exotic germplasm carrying the gene *Ym1* to European growing conditions; (3) to broaden the genetic base of BaYMV resistance by incorporating additional 'new' resistance genes.

Introduction

Soil-borne barley yellow mosaic virus (BaYMV), transmitted by *Polymyxa graminis* and tentatively classed as a potyvirus, was first discovered in Japan in 1940 (Inouye & Saito, 1975) and was considered to be one of the major diseases of Japanese two-rowed malting barley (Usugi, 1988). Yellow mosaic disease of barley was first discovered in Germany 10 years ago (Huth & Lesemann, 1978) and is now one of the most important cereal virus diseases in Europe, where it frequently causes severe damage to susceptible winter barley crops with corresponding reductions of grain yield (Table 1; Friedt & Götz, 1987; Huth, 1984).

Because of its soil-borne nature, chemical measures against BaYMV are either inefficient or uneconomic. So far, yield losses can only be prevented by growing resistant cultivars.

After the virus was first reported in FRG (Huth & Lesemann, 1978), numerous barley entries were screened and many stocks from different parts of the world were found to be resistant or immune to BaYMV, e.g. cvs Turkey Naked 2, Anson barley or Palomino (Takahashi, 1983; Friedt *et al.*, 1985) (Table 2). Most of the identified, immune genetic stocks originate in East Asia, like cvs Mokusekko 3, Mihori hadaka 3, Chikurin Ibaraki 1, Muju covered 2, and Asahi 9 (Table 2).

In Germany, BaYMV-resistant cvs Banjo, Brunhild, Franka, Ogra (six-rowed), Diana and Sonate (two-rowed) are now available. According to the nomenclature recommended by Cooper & Jones (1983), these cultivars are considered to be immune to the virus.

Tests for resistance (immunity) to BaYMV are carried out by mechanical inoculation in the glasshouse and laboratory; details of inoculum preparation, plant inoculation and subsequent maintenance of inoculated plants were described by Friedt (1983, 1984a). To improve the mechanical inoculation technique regarding speed and simplicity of application for routine disease screening, an efficient and highly reliable method of air-brush (spray-gun) inoculation (Umbach, in Friedt *et al.*, 1988) is now used for laboratory testing of reaction to barley yellow mosaic virus type M (BaYMV-M).

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Table 1. Grain yield of BaYMV-resistant as compared to susceptible winter barley cultivars in Northern Hesse, 1987
Rendement en grains de cultivars d'orge d'hiver résistants ou sensibles au barley yellow mosaic virus, dans le nord de la Hesse, 1987

Cultivar	BaYMV-reaction	Grain yield*	
		t/ha	relative
Franka (6-row)	resistant (immune)	4.82	100
Mammut (6-row)	susceptible	1.98	41
Sonate (2-row)	resistant (immune)	4.61	100
Danilo (2-row)	susceptible	2.49	54

*Gipper's Farm, Bellnhausen/Gilserberg: 10-m2 plots, 3 replications; LSD 5% = 0.78 t/ha.

Table 2. Sources of resistance to BaYMV
Sources de résistance au BaYMV

Cultivar	Origin	Reference(s)
Mokusekko 3	China	Takahashi *et al.*, 1973
Resistant Ym No. 1	Japan	Muramatsu, 1976
Kanto nijo 19	Japan	Kitahara *et al.*, 1982
Tochigi-strains	Japan	Kitahara *et al.*, 1982
Mihori hadaka 3	Japan	Takahashi *et al.*, 1973
Chikurin Ib. Mut. Ea52	Japan	Ukai, 1984
Kagoshima Kobai 1	Japan	Friedt *et al.*, 1985
Muju covered 2	Japan	Friedt *et al.*, 1985
Senbon hadaka	Japan	Kawada *et al.*, 1982
Asahi 9	Japan	Sanada, pers. comm.
Nirasaki-strains	Japan	Sanada, pers. comm.
Iwate Mensury 2	Japan	Friedt *et al.*, 1985
Miyako A	Japan	Friedt *et al.*, 1985
Taisho-mugi	Japan	Kato, pers. comm.
Anson barley	USA	Murphy, 1983
Turkey Naked 2	Turkey	Friedt *et al.*, 1985
Birgit, Franka, Ogra	FRG	Friedt *et al.*, 1985
Diana, Gloria, Sonate	FRG	Friedt *et al.*, 1985
Palomino	England	Friedt *et al.*, 1985

Results of genetic analyses

Genetic interactions between established sources of resistance

Previous genetic studies have indicated that immunity to BaYMV in German cultivars is probably due to one identical recessive gene, because their crosses do not segregate in F_2, where all plants are resistant. This 'German gene' was probably derived from a common parent, a Dalmatian land-race of spring barley, Ragusa (Friedt, 1984b). However, according to earlier

analyses by Takahashi *et al.* (1973) and our own results, BaYMV immunity in the Chinese spring barley cv. Mokusekko 3 is probably due to a single gene.

Crosses of German cultivars with Asian resistant parents carrying the gene *Ym1*, like cv. Mokusekko 3, are all resistant in F_1 and no segregation of susceptible individuals is observed in the F_2 generations (Friedt & Foroughi-Wehr, 1987). Therefore, the resistance genes must be either allelic or very tightly linked.

Chromosomal localization of resistance genes

Takahashi *et al.* (1973) studied genetic relationships between the resistance genes mentioned above and several marker genes on different barley chromosomes in order to identify the chromosomal location of resistances of cvs Mokusekko 3 (*Ym1*) and Mihori Hadaka 3 (*Ym2*). Evidence for linkage was found between resistance gene *Ym1* and marker gene *K* (hooded lemma) as well as between genes *Ym2* and *n* (naked kernel). Therefore, it was concluded that gene *Ym1* must be located on chromosome 4 and gene *Ym2* on chromosome 1.

Recently, we have carried out marker and trisomic analyses in order to localize the gene for resistance of the German cultivars. For marker analyses, multiple genetic markers, Nigrinudum and Colsess orange lemma, kindly provided by the Institute of Agricultural and Biological Sciences, Okayama University (JP) were used. Nigrinudum carries alleles *n* (naked kernel, chrom. 1), *V* (two-rowed spike, chrom. 2) and *B* (black kernel, chrom. 5). Colsess orange lemma has *K* for hooded lemma (chrom. 4) and *o* for orange lemma base and nodes (chrom. 6).

Cv. Franka was crossed to the mentioned multiple genetic marker stocks. As expected, the F_1-generation was susceptible to BaYMV. Segregation in the F_2-generation (Table 3) indicates that the 'German resistance' is inherited independently of genes *n*, *V*, *B* and *o*; the results in F_2 also

Table 3. Linkage analyses of 'German' BaYMV-M resistance by the use of genetic markers (Kaiser, 1989)
Analyse des liaisons génétiques de la résistance 'allemande' au BaYMV-M, à l'aide de marqueurs (Kaiser, 1989)

	Marker[1]		Susceptible		Resistant				
Cross	X	x	X	x	X	x	Total	X^2	P
	Chromosome 1								
Franka x	*N*	n^2	299	121	118	44	582	6.07	0.20–0.10
	Chromosome 2								
Franka x	*V*	v^3	312	108	126	36	582	3.35	0.50–0.30
	Chromosome 4								
Franka x	*K*	k^4	190	72	68	29	359	2.96	0.50–0.30
x Franka	*K*	*k*	263	98	91	34	486	1.35	0.80–0.70
	Chromosome 5								
Franka x	*B*	b^5	305	115	120	42	582	3.80	0.30–0.20
	Chromosome 6								
Franka x	*O*	o^6	190	72	67	30	359	3.58	0.50–0.30
x Franka	*O*	*o*	258	103	99	26	486	3.72	0.30–0.20

[1] Colsess-orange lemma or Nigrinudum; [2] *N*-hulled, *n* = naked; [3] *V* = two-rowed, *v* = six-rowed; [4] *K* = Kapuze (hood), *k* = awned; [5] *B* = black, *b*-yellow lemma & pericarp; [6] *O* = yellow, *o* = orange lemma.

indicate, that the German resistance gene is inherited independently of gene *K* for hooded lemma on chromosome 4 (Table 3).

This result is in contradiction with earlier results where the gene *Ym1* was reported to be linked to gene *K* on chromosome 4 (Takahashi *et al.*, 1973) and the 'German gene' was shown to be allelic to gene *Ym1* (Friedt & Foroughi-Wehr, 1986).

However, the definite genetic location of the German resistance gene still remained to be determined. Therefore, trisomic analyses were started with a complete trisomic set of the cultivated spring barley cv. Shin Ebisu 16 kindly provided by Dr T. Tsuchiya, Colorado State University, Fort Collins (US). Trisomic plants of each barley chromosome were crossed as females to the German resistant cvs Sonate and Ogra. Trisomic plants of each cross combination were identified in F_1 by morphological and cytological examinations according to Tsuchiya (1963) and grown to maturity. In F_2, the plants were morphologically classified as disomics or trisomics twice (one day before and one month after infection); F_2 populations were heterogeneous because of the expected presence of disomic and trisomic plants. Heterogeneity was also evident between F_2 populations due to the different trisomic chromosomes.

F_2 plants were mechanically infected with BaYMV-M in the 4- to 5-leaf stage. Transmission was not always complete, because of the heterogeneous populations and the weak growth habit of some trisomics. Based on previous classification, it was possible to evaluate the segregation for reaction to BaYMV-M for trisomics and disomics separately. F_2 populations with less than 80% infection rate in the control plants (cv. Gerbel) were excluded and populations with less than 100% infection were corrected arithmetically.

In the trisomic fractions, especially of the weakest trisomics (Slender, Pale and Semi-erect), unexpected segregations with an excess of resistant plants were found (Kaiser & Friedt, 1989); this finding may be explained by deleterious effects of the severe inoculation procedure on the weak trisomic plants. However, for the disomic fractions, which were more uniform and vigorous, clear results were obtained. For example, in all disomic F_2 populations of Ogra crosses except the one with cv. Pale as a parent, a good fit to the uncritical segregation (3:1) was found; the disomic F_2 derived from the cross to cv. Pale (trisomic for chromosome 3) showed good fit to the critical segregation of 8:1 (Table 4).

Identical results were obtained in disomic F_2's of crosses to cv. Sonate. Data for all F_2 populations, except Pale, again indicate good fits to an expected uncritical segregation. Fit to the critical segregation (8:1) in disomic F_2's of cv. Pale was also demonstrated (Kaiser, 1989).

From the data presented above, it can be concluded that the recessive gene for resistance

Table 4. Segregation for reaction to BaYMV-M in F_2 disomics of crosses of Shin Ebisu 16 trisomics with the resistant cv. Ogra (Kaiser, 1989; Kaiser & Friedt, 1989)
Ségrégation pour réaction au BaYMV-M chez des F_2 disomiques provenant du croisement de trisomiques Shin Ebisu 16 avec le cultivar résistant Ogra (Kaiser, 1989; Kaiser & Fried, 1989)

Trisomic type	Extra chromosomes	Infection rate (%)	Susceptible *n*	Resistant *n*	Total *n*	X^2 (3:1)	P
Bush	1	92	113	55	168	0.237	0.70–0.50
Slender	2	89	126	60	186	0.083	0.80–0.70
Pale	3	89	69	17	86	7.044	<0.01*
Robust	4	96	109	39	148	0.199	0.70–0.50
Pseudo-*n.*	5	100	125	46	171	0.329	0.70–0.50
Purple	6	100	65	20	85	0.098	0.80–0.70
Semi-erect	7	96	113	39	152	0.414	0.70–0.50

Test of 8:1 ratio for Pale (chrom. 3): $X^2 = 0.0649$; $P = 0.90–0.80$.

against BaYMV-M of German cultivars is located on barley chromosome 3. This conclusion is supported by recent results of Konishi & Matsuura (1987). They found, that the Chinese landrace Mokusekko 3 and some resistant cultivars derived from crosses to Mokusekko 3 always show the same esterase isozyme pattern. These results indicate that a minor resistance gene of Mokusekko 3 may be linked to an esterase isozyme gene block at the terminal end of the long arm of chromosome 3.

In conclusion, our own results together with those of Takahashi *et al.* (1973) and Konishi & Matsuura (1987) can be interpreted as follows: either the 'German gene' for resistance is allelic to a minor gene of Mokusekko 3 on chromosome 3, or it is allelic to the gene *Ym1* of Mokusekko 3, which then must also be located on chromosome 3.

Summary of genetic diversity of BaYMV-resistance

In order to obtain a complete picture of genetic diversity of BaYMV-resistance in barley, German resistant cultivars were crossed in various combinations to additional foreign carriers of BaYMV-resistance (Table 2). By analyzing such crosses, different linked and unlinked resistance genes can be identified.

Hybrid plants (F_1) from crosses of German cultivars like Ogra to Asian resistant parents carrying the gene *Ym1*, like Mokusekko 3, Resistant Ym No. 1 or Hakei I-41, were all resistant and the respective F_2 populations did not segregate susceptible individuals (Table 5), as mentioned above. Therefore, the respective resistance genes must be either allelic or very tightly linked.

Several other resistant stocks, like Iwate Mensury 2, Nirakei 31 and Turkey Naked 2, were crossed to German cultivars. These crosses also did not segregate susceptible plants in F_2 and, therefore, the respective resistance genes must also be allelic to the 'German gene'.

The cross between Diana and Anson barley was the first between a German and a foreign resistant cultivar which segregated susceptible plants in the F_2 (Table 5). The observed

Table 5. Genetics of BaYMV-M resistance: results in F_2 of crosses of German cvs and donors of *Ym1* (Götz, 1989)
Génétique de la résistance au BaYMV-M: résultats en F_2 des croisements entre des cultivars allemands et des plantes porteuses de *Ym1* (Götz, 1989).

	Genetic relationship with	
Cultivar	'German resistance'	*Ym1*
Birgit	identical	allelic
Diana	identical	allelic
Franka	identical	allelic
Mokusekko 3	allelic	identical
Kanto Nijo 19	allelic	identical
Hakei I-41	allelic	allelic or identical
Nirakei 31	allelic	allelic or identical
Iwate Mensury 2	allelic	allelic or identical
Kagoshima Kobai 1	allelic	allelic or identical
S-1001	allelic	allelic or identical
Turkey Naked 2	allelic	allelic or identical
Anson barley	7:9	13:3?

segregation (7:9) indicates that the respective genes for resistance are unlinked and that both act recessively.

Progeny of crosses of several resistant genetic stocks to either *Ym1* or German cultivars lead to identical results, i.e. no segregation in F_2 (Table 5). This confirms the above conclusion that the 'German gene' and *Ym1* are either allelic or tightly linked.

Finally, the F_2 segregation of crosses of German resistant cultivars and *Ym1*, respectively, to Anson barley (Table 5) clearly indicates that resistance of the latter cultivar is inherited independently of the former genes.

Breeding for BaYMV-resistance

Goals of resistance-breeding

Breeding for BaYMV-resistance focuses on three major goals: (1) to improve the agronomic performance of germplasm carrying the 'German gene', (2) to improve agronomic performance of new breeding material carrying gene *Ym1*, and (3) to broaden the genetic basis of BaYMV-resistance by incorporating additional, 'new' resistance genes. As mentioned above, several resistant German cultivars are available. However, they carry an identical recessive gene and, in addition, show unsatisfactory agronomic characters like small grain or insufficient yield potential. Therefore, breeding programmes were initiated in order to incorporate different resistances into highly productive, adapted cultivars like Igri.

Application of androgenetic haploids

In self-pollinating barley, new breeding lines and cultivars are developed by conventional selfing over several generations, i.e. pedigree, bulk or family selection procedures. Haploidy techniques (e.g. via androgenesis, i.e. anther or microspore culture) were applied in order to accelerate and facilitate the breeding procedure through the production of doubled haploid, i.e. homozygous diploid lines. In the case of monogenic recessive resistance, as many as 50% of homozygous

Table 6. Combination of favourable agronomic characters in doubled haploid lines (DH) from a cross of Franka × Igri as compared to the parents (2 years, 2 locations)
Combinaison de caractères agronomiques favorables dans des lignées haploïdes doublées (DH) provenant d'un croisement entre Franka et Igri, par rapport aux parents (2 années, 2 sites)

Parents DH	Row no.	Mildew (1–9)*	BaYMV	Lodging (1–9)*	Grain yield**	
					total	marketable
Igri	2	7.0	s	5.4	110.5	91.5
DH1	2	7.5	r	7.4	100.0	84.0
DH2	2	6.5	r	6.5	111.5	92.0
DH3	6	7.0	r	4.6	104.0	78.5
DH4	6	7.5	r	4.4	114.5	85.5
DH5	6	7.0	r	5.5	110.0	74.0
DH6	6	7.0	s	6.2	106.5	74·0
DH7	6	7.5	r	6.7	109.5	78.0
Franka	6	4.0	r	6.3	105.5	80.5

* Scale 1–9 (1 = most favourable character expression).
** % of trial average.

Table 7. Results of anther culture from different crosses (Foroughi-Wehr & Wenzel, 1988)
Résultats de la culture d'anthères après divers croisements

Cross	Green plants (%)**	BaYMV-resistant plants (%)
P22427* × Ginso	0.2	54.5
P91367* × Ester	0.6	52.9
Igri × 521D2	1.8	53.6
Franka × Igri	1.4	56.1
(P22488* × P28657*) × Igri	2.3	28.2
(P91376* × P22488*) × Igri	4.8	28.2

* Derived from crosses involving *Yml*.
** % of numbers of cultured anthers.

resistant doubled haploids can be expected from an F_1 hybrid derived from a cross of a resistant and a susceptible parent; the corresponding selfed F_1-progeny yields only 25% homozygous recessive BaYMV-resistant plants in F_2. Numerous doubled haploid lines have already been tested in field trials for agronomic performance. Some are agronomically competitive with highly productive susceptible cultivars like Igri (Table 6). Thus, the haploidy technique has been demonstrated to be an efficient means of improving the efficiency of breeding self-pollinated winter barley for resistance to yellow mosaic disease.

Since various sources of monogenically inherited resistance or immunity are available in foreign germplasm (Table 2), it is immediately possible to use them in a barley breeding programme. However, many of these resistant stocks exhibit inferior agronomic performance, due to susceptibility to lodging or various diseases or, in total, insufficient grain yield (Friedt & Götz, 1987). Therefore, intensive breeding work is required for an improvement of agronomic value of these resistant materials. The anther culture technique has been applied again in this programme. Some results obtained from culturing anthers of various F_1 hybrids including *Yml* as a parent are given in Table 7.

First results of field trials indicate that, by selection for agronomic characters, it is definitely possible to recover lines which are BaYMV-resistant and high-yielding, even from crosses including an unadapted cultivar.

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Situation actuelle et perspectives pour la sélection de résistance ou d'immunité envers le barley yellow mosaic virus

Chez les cultivars d'orge allemands comme Diana, Franka, Gloria ou Sonate, la résistance au BaYMV est due à un seul gène récessif (le gène dit allemand), situé sur le chromosome 3. Ce gène est probablement allèle du gène *Yml* (ou étroitement lié). La résistance du cultivar américain Anson barley se transmet indépendamment du 'gène allemand' ou de *Yml*. L'utilisation de la technique d'haploïdisation permet au sélectionneur d'atteindre plusieurs objectifs importants: (1) amélioration de la qualité des cultivars portant la résistance 'allemande'; (2) adaptation aux

conditions européennes du matériel génétique exotique portant le gène *Ym1*; (3) élargissement de la base génétique de la résistance au BaYMV par introduction de 'nouveaux' gènes de résistance.

Текущее состояние и перспективы селекции на сопротивляемость по отношению к *barley yellow mosaic virus*

На таких немецких селекционных сортах ячменя как Диана, Франка, Глория или Соната, сопротивляемость по отношению к *barley yellow mosaic virus* объясняется только одним рецессивным геном (так называемым «немецким»), находящимся в 3-ей хромосоме. Этот ген, по всей вероятности, аллеличен с геном Ym1 (или тесно связан с ним). Сопротивляемость американского селекционного сорта ячменя Ансон передается независимо от «немецкого гена» или Ym1. Использование метода гаплоидизации позволяет селекционеру достичь целого ряда важных задач : (1) улучшение качества селекционных сортов, имеющих «немецкую» сопротивляемость, (2) адаптация к европейским условиям экзотического генетического материала с доминантным геном Ym1, (3) расширение генетической базы сопротивляемости по отношению к *barley yellow mosaic virus* для введения «новых» генов сопротивляемости.

References

Cooper, J.I. & Jones, A.T. (1983) Responses of plants to pathogens: proposals for the use of terms. *Phytopathology* **73,** 127–128.

Foroughi-Wehr, B. & Wenzel, G. (1988) [Anther culture for solution of the yellow mosaic problem in winter barley]. *Gesunde Pflanzen* **40,** 233–238 (in German).

Friedt, W. (1983) Mechanical transmission of soil-borne barley yellow mosaic virus. *Phytopathologische Zeitschrift* **106,** 16–22.

Friedt, W. (1984a) [Early selection for resistance to barley yellow mosaic virus by mechanical inoculation]. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes* **36,** 179–182 (in German).

Friedt, W. (1984b) The genetic basis of breeding winter barley for resistance to barley yellow mosaic virus. *Vorträge für Pflanzenzüchtung* **6,** 145–155.

Friedt, W. & Foroughi-Wehr, B. (1986) [Origin, properties and use in breeding of sources of resistance to barley yellow mosaic virus]. *Vorträge für Pflanzenzüchtung* **10,** 82–93 (in German).

Friedt, W. & Foroughi-Wehr, B. (1987) Genetics of resistance to barley yellow mosaic virus. In *Barley Genetics V*, pp. 659–664. Okayama (JP)

Friedt, W. & Götz, R. (1987) [Prospect for winter barley with the additional problem of barley yellow mosaic virus]. *Ergebnisse Landwirtschaftlicher Forschung an der Justus Liebig-Universität* **18,** 31–40 (in German).

Friedt, W., Huth, W., Mielke, H. & Züchner, S. (1985) [Carriers of resistance to barley yellow mosaic virus]. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes* **37,** 129–135 (in German).

Friedt, W., Kaiser, R., Götz, R., Umbach, H. & Foroughi-Wehr, B. (1988) Viruses with fungal vectors. In *Developments in Applied Biology 2* (eds Copper, J.I. & Asher, M.J.C.), pp. 227–237. AAB, Wellesbourne (GB).

Götz, R. (1989) [Genetic studies on diversity for BaYMV resistance in the world assortment of barley]. *Ph.D. Thesis*. Universität Giessen (DE).

Huth, W. (1984) [Barley yellow mosaic virus in FRG since 1978]. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes* **36,** 49–54 (in German).

Huth, W. & Lesemann, D. (1978) [A new virus of winter barley in FRG]. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes* **30,** 184–185 (in German).

Inouye, T. & Saito, Y. (1975) Barley yellow mosaic virus. *CMI/AAB Descriptions of Plant Viruses* no. 143. AAB, Wellesbourne (GB).

Kaiser, R. (1989) [Studies on the genetics of barley yellow mosaic resistance in winter barley cultivars]. *Ph.D.Thesis*. Universität Giessen (DE).

Kaiser, R. & Friedt, W. (1989) Chromosomal location of resistance to barley yellow mosaic virus in German winter-barley identified by trisomic analysis. *Theoretical and Applied Genetics* **77,** 241–245.

Kawada, N., Sasaki, A. & Tsuru, M. (1982) [Selection of resistance varieties to barley yellow mosaic disease and their agronomic characters]. *Japanese Journal of Breeding* **32,** suppl. 2, 158–159 (in Japanese).

KITAHARA, S., FUJII, T., KOBAYASHI, S. & SEKO, H. (1982) [Studies on breeding of malting barley which is resistant to barley yellow mosaic. 2. Yields of resistant lines in the infected field]. *Japanese Journal of Breeding* **32,** suppl. 2, 34–35 (in Japanese).

KONISHI, T. & MATSUURA, S. (1987) [Variation of esterase isozyme genotypes in a pedigree of Japanese two-rowed barley]. *Japanese Journal of Breeding* **37,** 412–420 (in Japanese, English summary).

MURAMATSU, M. (1976) Breeding of malting barley variety which is resistant to barley yellow mosaic. In *Barley Genetics III*, pp. 476–485. Thiemig, München (DE).

MURPHY, R.P. (1983) Registration of Anson barley (Reg. no. 182). *Crop Science* **23,** 181.

TAKAHASHI, R. (1983) *Catalogue of Barley Germplasm preserved in Okayama University*. Institute of Agricultural and Biological Sciences, Okayama University, Kurashiki (JP).

TAKAHASHI, R., HAYASHI, J., INOUYE, T., MORIYA, I. & HIRAO, C. (1973) Studies on resistance to yellow mosaic disease in barley. I. Tests for varietal reactions and genetic analysis of resistance to the disease. *Berichte der Ohara Instituts für Landwirtschaftliche Biologie, Okayama Universität* **16,** 1–17.

TSUCHIYA, T. (1963) Chromosome aberrations and their use in genetics and breeding in barley—trisomics and aneuploids. In *Barley Genetics I*, pp. 116–150. PUDOC, Wageningen (NL).

UKAI, Y. (1984) Genetic analysis of a mutant resistant to barley yellow mosaic virus. *Barley Genetics Newsletter* **14,** 31–33.

USUGI, T. (1988) Epidemiology and management in Japan of soil-borne cereal mosaic viruses with filamentous particles. In *Viruses with Fungal Vectors, Developments in Applied Biology 2* (eds Cooper, J.I. & Asher, M.J.C.), pp. 227–237. AAB, Wellesbourne (GB).