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16. Genetic basis of breeding for resistance to barley yellow mosaic virus (BaYMV)

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SUMMARY

With the increasing acreage of winter barley, barley yellow mosaic virus (BaYMV) became one of the major diseases of winter barley in Europe where local yield losses of 70% or more have been realized. The resistant cultivars available now, e.g. 'Franka' (six-row) and 'Sonate' (two-row) are characterized by some unfavourable traits (e.g. small grain or susceptibility to fungal diseases) and are not fully accepted by agronomists and farmers. Furthermore, all of this resistant material has identical resistance gene(s); most probably derived from a Dalmatian spring barley land-race 'Ragusa'. Such a narrow basis of resistance may be dangerous because of an increasing likelihood that new virus pathotypes will evolve. The genetic basis of resistance therefore needs to be broadened urgently.

Although numerous stocks in various collections, particularly of Asian origin, are known to be resistant to BaYMV, only a few of them have yet been studied genetically. Two dominant genes were identified in 'Mokusekko 3' *(Ym1)* and 'Mihori hadaka' *(Ym2)*, respectively. Recently, it has been shown that another recessive gene *(ym3)* in mutant 'Ea52' of 'Chikurin Ibaraki 1' is not allelic to the other genes. Crosses of German cultivars to 'Mokusekko 3' are completely resistant in the F_2 generation implying that the recessive gene in German material and the dominant gene in 'Mokusekko 3' (and other Asian germplasm) are either allelic or very closely linked.

INTRODUCTION

Yellow mosaic disease of barley, caused by soil-borne barley yellow mosaic virus (BaYMV), is one of the most important cereal virus diseases in the Federal Republic of Germany and other European countries, such as France, Belgium, England and the German Democratic Republic. The present area of distribution in Germany mainly covers the central and northern parts of the country, although smaller areas in the south are also infested (Huth, 1984).

Barley yellow mosaic disease was first discovered in 1940 in Japan (Inouye & Saito, 1975) and became subsequently one of the major diseases of Japanese two-rowed malting barley (Usugi, p. 213, this volume). It is assumed and widely accepted now that the virus is naturally transmitted by a fungus, *Polymyxa graminis* (see p. 203 this volume). The disease frequently causes severe damage to susceptible winter barley crops (Plate 2) with corresponding substantial reductions of grain yield (Table 16-1; see also Friedt & Götz, 1987; Huth, 1984). Because of its soil-transmission, chemical measures against this virus disease are either inefficient or uneconomic. So far, yield losses can only be prevented by growing resistant cultivars.

Table 16-1 Grain yield of BaYMV-resistant as compared to susceptible winter barley cultivars in Northern Hesse, 1987

Cultivar	BaYMV-reaction	Grain yield*	
		dt/ha	relative
Six-row			
Franka	resistant or immune	48.2	100
Mammut	susceptible	19.8	41
Two-row			
Sonate	resistant or immune	46.1	100
Danilo	susceptible	24.9	54

*Gipper's Farm, Bellnhausen/Gilserberg: $10m^2$ plots, 3 replicates; LSD 5% = 7.8 dt/ha.

There is considerable variation among barley varieties with respect to disease symptoms, damage and resistance (immunity) to the disease. Several barley genotypes have been screened recently and numerous stocks found to be resistant or immune to BaYMV (Takahashi, 1983; Friedt, Huth, Mielke & Züchner, 1985) but only a few have yet been studied genetically (Table 16-2). Most of the immune genotypes originate from East Asia, but several have other provenances, e.g. the high-lysine barley 'Hiproly' from Ethiopia, 'Turkey Naked 2' (naked, black kernel) from Turkey, 'Anson Barley' (awnless) from the USA or the two-rowed barley cv. 'Palomino' from England (Table 16-2).

In Germany, several BaYMV-resistant cultivars are now commercially available, i.e. 'Banjo', 'Brunhild', 'Birgit', 'Franka', 'Ogra' (six-rowed) and 'Classica', 'Diana', 'Gloria', 'Sonate' (two-rowed). According to the nomenclature recommended by Cooper & Jones (1983), these cultivars may be considered as being immune to the sap-transmissible isolate (BaYMV-M) of the virus (see p. 61, this volume).

Table 16-2 Various sources of resistance to BaYMV (Friedt & Foroughi-Wehr, 1987)

Variety	Origin	Characters	Gene(s)	Reference(s)
Mokusekko 3	China	6row, hulled	*Ym 1*[1]	Takahashi *et al.*, 1973
Resistant Ym No. 1	Japan	2row, hulled	*Ym 1*[1]	Muramatsu, 1976
Kanto nijo 19	Japan	2row, hulled	*Ym 1*[1]	Kitahara *et al.*, 1982
Tochigi-strains	Japan	2row, hulled	*Ym 1*[1]	Kitahara *et al.*, 1982
Mihori hadaka 3	Japan	6row, naked	*Ym 2*[2]	Takahashi *et al.*, 1973
Chikurin Ibar. 'Ea 52'	Japan	6row, hulled	*ym 3*	Ukai, 1984
Hiproly (CI 3947)	Ethiopia	2row, naked	dominant	Yoshikawa & Kato, 1983
Kagoshima Kobai	Japan	6row, naked	dominant	Friedt *et al.*, 1985
Muju covered 2	Japan	6row, hulled	dominant	Friedt *et al.*, 1985
Senbon hadaka	Japan	6row, naked	recessive	Kawada *et al.*, 1982
Asahi 9	Japan	2row, hulled	recessive	Sanada, pers. comm.
Nirasaki-strains	Japan	2row, hulled	recessive	Sanada, pers. comm.
Iwate Mensury 2	Japan	6row, hulled	recessive	Friedt *et al.*, 1985
Miyako A	Japan	6row, hulled	recessive	Friedt *et al.*, 1985
Taisho-mugi	Japan	6row, hulled	recessive	Kato, pers. comm.
Anson barley	USA	6row, hulled	recessive	Murphy, 1983
Turkey Naked 2	Turkey	2row, naked	dominant	Friedt *et al.*, 1985
Birgit, Franka, Ogra	FRG	6row, hulled	recessive[3]	Friedt *et al.*, 1985
Diana, Gloria, Sonate	FRG	2row, hulled	recessive[3]	Friedt *et al.*, 1985
Palomino	England	2row, hulled	recessive[3]	Friedt *et al.*, 1985

[1]Chromosome 4, [2]chromosome 1, [3]recessive or partially dominant.

SCREENING FOR BaYMV REACTION BY MECHANICAL INOCULATION

Tests for resistance (immunity) to BaYMV are carried out by mechanical inoculation in the greenhouse and laboratory; details of inoculum preparation, plant inoculation and subsequent maintenance of inoculated plants have already been described (Friedt, 1983; 1984).

In the last year, experiments were started to improve the speed and simplicity of the mechanical inoculation technique for routine disease screening. Particularly in segregating generations (e.g. F_2), large populations have to be screened and an efficient and highly reliable method of air-brush (spray-gun) inoculation (Umbach, 1987) is now used.

RESULTS OF GENETIC ANALYSES

Genetics of exotic sources of BaYMV-resistance or immunity. In earlier genetic analyses carried out in Japan, a completely dominant gene was identified in the immune Chinese spring barley 'Mokusekko 3' *(Ym1)*, and another partially dominant gene was found in the resistant Japanese naked spring barley 'Mihori Hadaka 3' (*Ym2;* Takahashi, Hayashi, Inouye, Moriya & Hirao, 1973). The resistance gene of 'Mokusekko 3' was introduced into the two-rowed malting type to produce 'Resistant Ym No. 1', a BaYMV-immune genotype with favourable agronomic characters and malting quality (Muramatsu, 1976). Gene *Ym1* was also transferred to 'Kanto Nijo 19' (Kitahara, Fujii, Kobayashi & Seko, 1982) and, at the Tochigi Agricultural Experiment Station, Seko & Fujii introduced the trait into numerous other breeding lines.

In addition, many resistant lines have been developed by the Kirin Brewery, using the recessive resistance of 'Asahi 9', an adapted Japanese malting barley. Other cultivars, e.g. 'Senbon Hadaka' (six-rowed, naked) and 'Taisho-mugi' (six-rowed, hulled), are currently used in Japanese breeding programmes as donors of resistance to BaYMV.

Ukai (1984) reported that a recessive mutation provides BaYMV-immunity in the early mutant 'Ea52' of the Japanese six-rowed cv. 'Chikurin Ibaraki 1'; its gene was shown to be not allelic to the genes *Ym1* and *Ym2*. Therefore, Ukai (1984) proposed the symbol *ym3* for this 'new' gene. However, *ym3* does not confer resistance to infection by field isolates of the virus in Western Germany, whereas the variety from which it came, 'Chikurin Ibaraki 1', is resistant (Friedt, 1985).

According to earlier analyses by Takahashi *et al.* (1973) and our own results (Table 16-3), BaYMV-immunity of the Chinese spring barley 'Mokusekko 3' is probably due to a single dominant gene. In order to identify the chromosomal location of this resistance gene of 'Mokusekko 3', Takahashi *et al.* (1973) studied genetic relationships between resistance gene *Ym1* and several marker genes on the individual barley chromosomes. Analyses were done on the F_2-generations of four hybrids between 'Mokusekko 3' and the susceptible genotypes with genetic markers, 'Nigrinudum', 'Orange lemma', Nikaku Chevalier' and 'Colsess IV'.

Table 16-3 BaYMV-reactions of crosses of resistant cultivars to the susceptible cultivar 'Igri' (Friedt & Foroughi-Wehr, 1987)

Cross 'Igri' ×	F_1	F_2	Total	No. susc.	No. resist.	χ^2	P
× Mokusekko (♀)	resist.	Obs.	69	15	54	0.39	>0.5
		Exp.**		17.25	51.75		
× Resist. Ym No. 1 (♂)	resist.	Obs.	94	13	81	6.25	<0.05
		Exp.**		23.50	70.50		
× Birgit (♀)	suscep.	Obs.	125	89	36	0.77	0.3–0.5
		Exp.*		93.75	31.25		
× Franka (♂)	suscep.	Obs.	129	95	34	0.12	0.7–0.8
		Exp.*		96.75	32.25		
× Ogra (♀)	suscep.	Obs.	124	90	34	0.39	0.5–0.7
		Exp.*		93.00	31.00		
× Sonate (♂)	suscep.	Obs.	128	92	36	0.67	0.3–0.7
		Exp.*		96.00	32.00		

*, ** Expected ratios based on monogenic dominant inheritance of susceptibility (*), or resistance (**), respectively.

Evidence of linkage of *Ym1* to *K* (hooded lemma) was found in the cross with 'Colsess IV', in which excessive numbers of parental character combinations were observed. The observed frequencies of the four phenotypes did not fit the calculated numbers for independent segregation (9:3:3:1), and therefore it was concluded that gene *Ym1* of 'Mokusekko 3' was located on chromosome 4.

Recent investigations in Japan (Kawada, Sasaki & Tsuru, 1986) have shown that other varieties also carry gene *Ym1*, e.g. 'Hakei I-41'. This gene was not derived from 'Mokusekko 3'. Moreover, it was shown that the Japanese varieties 'Ishukushirazu' and 'Hagane-mugi' carry the same resistance gene *(ym3)* as the mutant ('Ea52') of the susceptible variety 'Chikurin Ibaraki 1'. However, as mentioned above, *ym3* is ineffective in West Germany although 'Chikurin Ibaraki 1' is resistant.

Genetics of German BaYMV-immune cultivars. Previous genetic studies indicated that the immunity to BaYMV of German cultivars mentioned above is probably due to one recessive gene (Table 16-3). Resistance genes of the different cultivars seem identical, because progeny from crosses between them do not segregate in F_2, all being resistant (Table 16-4). This 'German gene' was probably derived from 'Ragusa', a Dalmatian land-race of spring-barley (Friedt, 1984).

Table 16-4 BaYMV-reactions of crosses among various resistant cultivars (Friedt & Foroughi-Wehr, 1987)

Cross			F_1	F_2: Total	No. susc.
Barbo	×	Franka	resistant	120	0
Franka	×	Birgit	resistant	74	0
Birgit	×	Franka	resistant	133	0
Birgit	×	Res.Ym1*	resistant	300	0
Dea	×	Res.Ym1	resistant	176	0
Franka	×	Res.Ym1	resistant	341	0
Ogra	×	Res.Ym1	resistant	405	0
Sonate	×	Res.Ym1	resistant	266	0
Wigo	×	Res.Ym1	resistant	285	0
Mokusekko	×	Res.Ym1**	resistant	216	0
Sonate	×	Kanto Nijo	resistant	140	0
Hakei I-41	×	Ogra	resistant	146	0
Hakei I-41	×	Mokusekko	resistant	124	0
Wigo	×	Mokusekko	resistant	487	0
Mokusekko	×	Esaw	resistant	485	0
Mokusekko	×	Bulgarian	resistant	269	0
Total				3,967	0

* Res.Ym1 = Resistant Ym No. 1 (Muramatsu, 1976).
**Both parents with identical gene *Ym1*.

In order to obtain a more complete picture of genetic diversity of BaYMV-resistance in barley, German immune cultivars were crossed in various combinations to foreign carriers of BaYMV-resistance. By analyzing such crosses different (non-allelic) resistance genes can be identified. Hybrid plants (F_1) from crosses of German cultivars like 'Ogra' to Asian resistant parents, which carry the gene *Yml*, 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 16-4). Since German varieties possess recessive resistance gene(s), segregation into 3 susceptible and 13 resistant F_2-plants would be expected, provided that the genes were unlinked. The fact, that not one susceptible individual occurred among almost 4000 F_2-plants (Table 16-4) indicates, therefore, that the respective resistance genes are either allelic or very tightly linked. Studies of crosses between German cultivars and 'Mihori Hadaka 3' or 'Chikurin Ibaraki 1' have been initiated, but genetic data are not yet available.

To prove the former provisional conclusion, resistant cultivars, e.g. 'Birgit' or 'Franka' were crossed to genetic marker stocks such as 'Colsess-orange lemma' *(KKoo)* and 'Nigrinudum *(nnBB)* obtained from the Institute of Agricultural and Biological Sciences, Okayama University, Japan. The F_1-generation was susceptible to BaYMV, as expected. However, segregation in the F_2-generation (Table 16-5) and the absence of significant chi-square values indicated that the 'German resistance gene' may be inherited independently of gene *K* for hooded lemma on chromosome 4. This result could be explained as follows. If the 'German gene' for resistance and the gene *Yml* of 'Mokusekko 3' were allelic or tightly linked, as indicated above (Table 16-4), it might be possible that gene *Yml* is not located on chromosome 4, which would be in contradiction to earlier results of Takahashi *et al.* (1973). Our results could

Table 16-5 Linkage analysis of BaYMV-resistance of German winter barley cultivar 'Franka' (Kaiser, 1988)

Cross: Marker × cv	Marker[1] X	Marker[1] x	Susceptible X	Susceptible x	Resistant X	Resistant x	Total	χ^2_L	P
	Chromosome 1								
Franka ×	N	n	314	106	118	44	582	2.96	.50–.30
	Chromosome 4								
Franka ×	K	k	185	70	73	31	363	5.26	.20–.10
× Franka	K	k	263	98	91	34	486	1.35	.80–.70
	Chromosome 5								
Franka ×	B	b	305	115	120	42	582	3.80	.30–.20

[1]'Colsess-orange lemma' or 'Nigrinudum', N = hulled, n = naked, K = Kapuze (hooded), k = awned, B = black, b = yellow lemma & pericarp, χ^2 = chi-square value for linkage test, P = probability value.

also be explained by the presence of an additional, recessive gene in 'Mokusekko 3', which then should be allelic to the gene in the German cultivars.

This latter resistance gene is also independent of the genes *n* (naked karyopsis) on chromosome 1 and *B* (black lemma and pericarp) on chromosome 5. However, these results have to be confirmed by further studies of F_2-generations of crosses of German immune cultivars to other markers and to trisomic ($2n = 2x + 1 = 15$) strains for each chromosome.

BREEDING FOR BaYMV-RESISTANCE

Since various sources of monogenically inherited resistance or immunity are available (Table 16-2), rapid progress in breeding for BaYMV-resistance has been made in recent years and further advances can be expected in the near future. Unfortunately, many of the resistant genotypes have undesirable agronomic characters, such as proneness to lodging, or insufficient grain yield (Friedt & Götz, 1987). Therefore, extensive breeding activities are required to improve the agronomic value of these resistant lines.

In self-pollinating barley, new breeding lines and cultivars can either be developed by conventional selfing over several generations, i.e pedigree-, bulk- or family-selection procedures (Fig. 16-1), or by using haploidy-techniques (e.g. androgenesis, via anther- or microspore-culture, Fig. 16-2) to produce doubled-haploid, homozygous lines. In the case of monogenic recessive immunity, as many as 50% of homozygous resistant doubled haploids can be expected from an F_1-hybrid derived from an immune and a susceptible parent, whereas the selfed F_1-progeny yields only 25% homozygous recessive, i.e. BaYMV-immune plants in the F_2. This expectation has been confirmed by progeny testing after culturing anthers of various F_1-hybrids including German immune parents. A sample of results of eight crosses is given in Table 16-6. Numerous doubled haploid lines have already been tested in field trials for agronomic performance and some have been given to breeding companies for further propagation and testing.

CONCLUSIONS

Barley yellow mosaic virus is widely distributed in Central and Western Europe, where it locally causes severe damage resulting in considerable yield losses in susceptible winter barley crops. The effects of the vector fungus have not been unambiguously distinguished from those of the virus but it is presumed that all cereal land is infested by *P. graminis*.

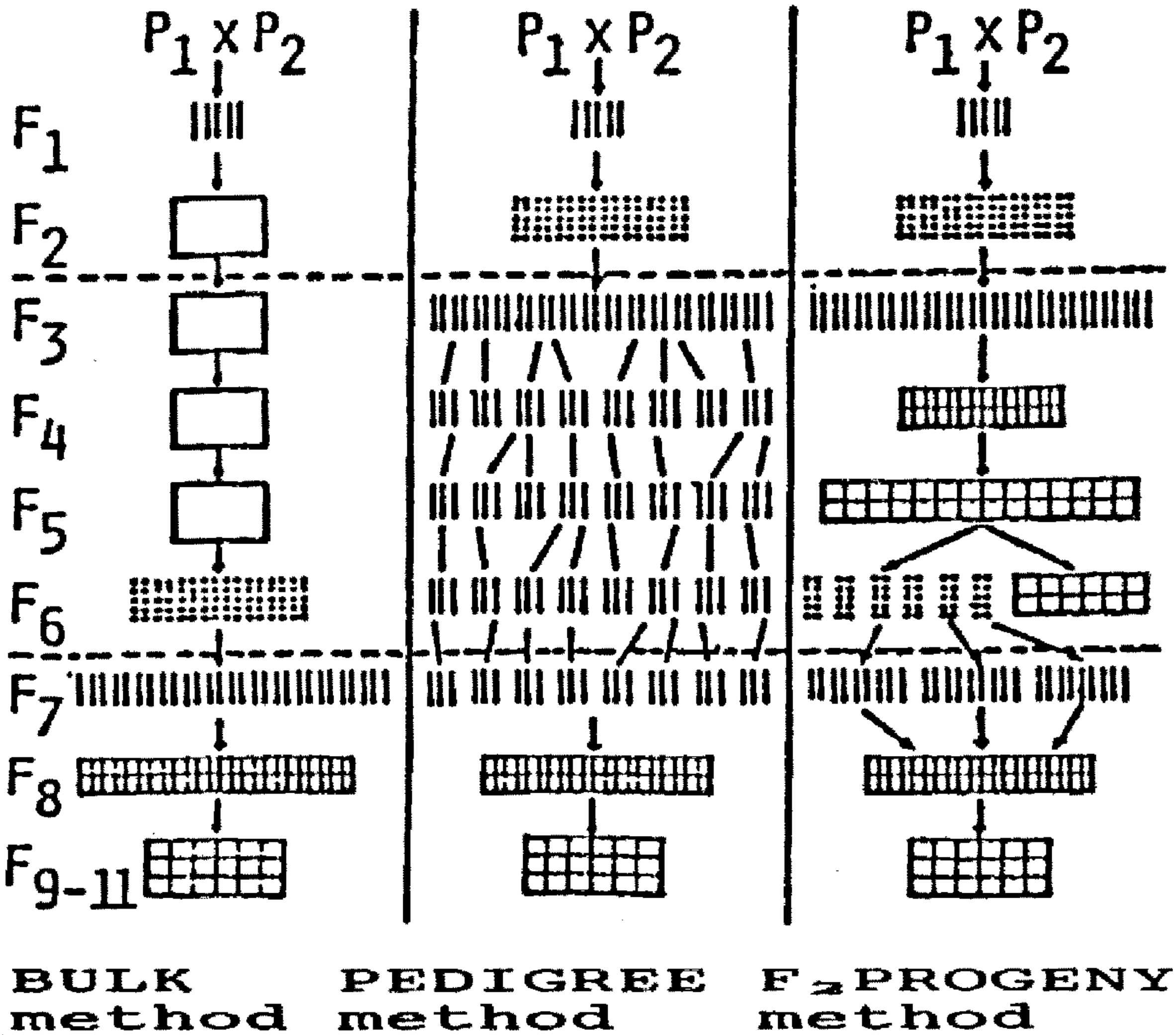

Fig. 16-1 Schemes of typical breeding procedures for self-pollinating crops such as barley.

Various sources of BaYMV-resistance or immunity are available now from different parts of the world. Recessive resistance genes are present in a number of German and European winter barley cultivars, like 'Franka' (six-row) or 'Sonate' (two-row). The genetic basis of resistance or immunity is still not completely clear. Inter-crossing different cultivars, with either recessively or dominantly inherited resistances, resulted in completely resistant (immune) F_1- and F_2-generations. Therefore, the gene(s) involved must be either allelic or very tightly linked.

Newly occurring virulent strains of BaYMV may be able to 'break' resistances described above, so that constant and careful observation of the cultivars' behaviour in infested areas should be made. Some Japanese barley stocks are field immune in Japan but infectible in West Germany (mechanically and in the field) and some cultivars (e.g. 'Franka' and 'Mokusekko', or derivatives) seem to be field resistant in different countries to different virus types.

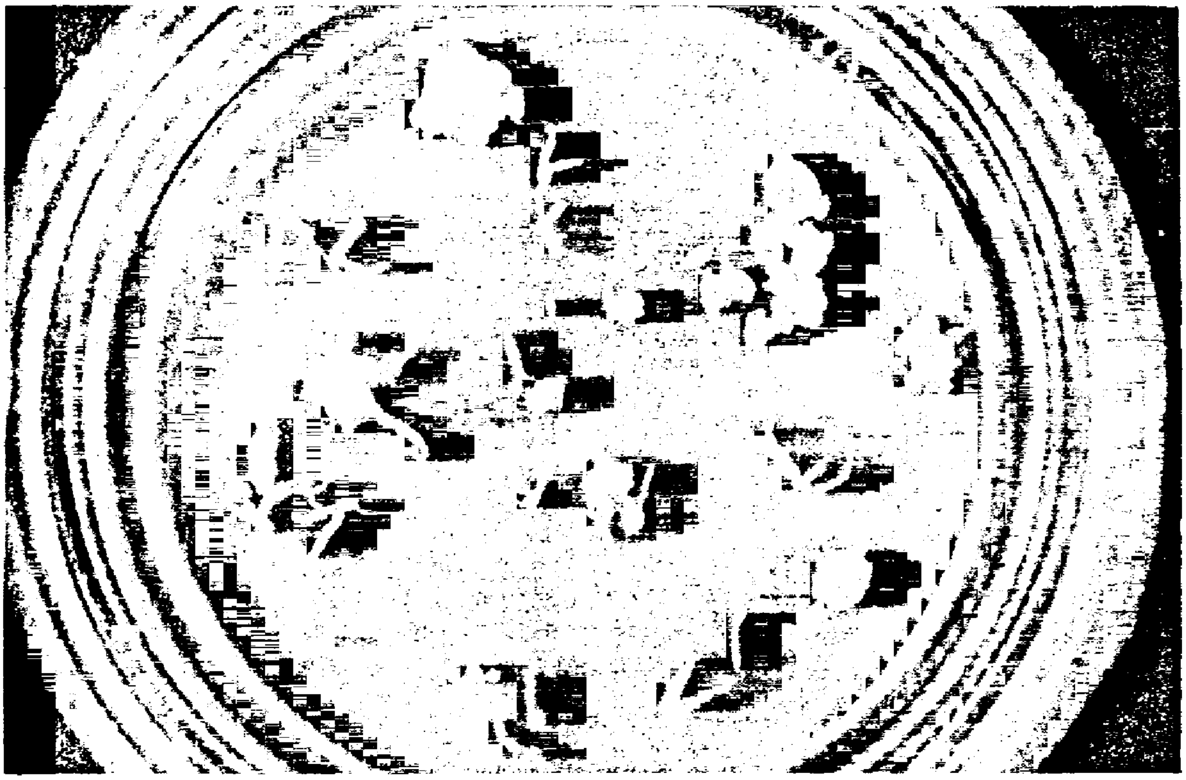

Fig. 16-2 Petri-dish with cultured anthers of winter barley showing formation of androgenetic (microspore-derived) calluses and plantlet.

Breeding of BaYMV-resistant or immune winter barley stocks with improved general agronomic performance is needed and the use of haploidy-techniques can help to accelerate and facilitate the breeding procedure.

Table 16-6 Reactions to BaYMV-M of androgenetic DH-lines derived from crosses of a resistant (italics) to a susceptible parent (Friedt & Foroughi-Wehr, 1987)

Hybrid F_1	BaYMV-reactions No. susceptible	No. resistant	% resistant
Sonate × 75/1312/43	42	52	55
Sonate × 75/456/12	37	35	38
817338 × *Diana*	110	110	50
822528 × *Diana*	10	12	54
847939 × *Diana*	101	84	45
Sonja × *Diana*	51	56	52
Igri × *Diana*	213	214	50
Igri × *521d2*	311	297	49
Total	845	830	49.6
Grand total		1,675	

REFERENCES

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

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

FRIEDT, W. (1984a). Frühselektion auf Resistenz gegen Barley Yellow Mosaic Virus durch mechanische Inokulation. *Nachrichtenblatt für den Deutschen Pflanzenschutzdienst* **36** 179–182.

FRIEDT, W. (1984b). The genetic basis of breeding winter barley for resistance to barley yellow mosaic virus. In: *Breeding for disease resistance and oat breeding*. Proceedings EUCARPIA Cereals Section Meeting, Freising. *Vorträge Pflanzenzüchtung* **6**, 145–155.

FRIEDT, W. (1985). Genetic studies of resistance to barley yellow mosaic virus of German winter barley cultivars. *Barley Genetics Newsletter* **15**, 58–61.

FRIEDT, W. & FOROUGHI-WEHR, B. (1987). Genetics of resistance to barley yellow mosaic virus. *Barley Genetics V*, Proceedings of the Fifth International Barley Genetics Symposium, Okayama, Japan (in press).

FRIEDT, W. & GÖTZ, R. (1987). Perspektiven des Wintergerstenanbaues bei zunehmender Gefährdung durch das Gelbmosaikvirus. *Ergebnisse Landwirtschaftlicher Forschung* **18**, 31–40.

FRIEDT, W., HUTH, W., MIELKE, H. & ZÜCHNER, S. (1985). Resistenzträger gegen Barley Yellow Mosaic Virus. *Nachrichtenblatt für den Deutschen Pflanzenschutzdienst* **37**, 129–135.

HUTH, W. (1984). Die Gelbmosaikvirose der Gerste in der Bundesrepublik Deutschland – Beobachtungen seit 1978. *Nachrichtenblatt für den Deutschen Pflanzenschutzdienst* **37**, 129–135.

INOUYE, T. & SAITO, Y. (1975). Barley yellow mosaic virus. *CMI/AAB Descriptions of Plant Viruses* No. 143, 3pp.

KAISER, R. (1988). Untersuchungen zur Genetik der BaYMV-Resistenz bei einheimischen Wintergerste-Sorten. *PhD Thesis, Universität Giessen* (in prep.).

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.

KAWADA, N. & TSURU, M. (1986). Genetics and breeding of the resistance to barley yellow mosaic virus. *Barley Genetics V*, Proceedings of the Fifth International Barley Genetics Symposium, Okayama, Japan (in press).

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.

MURAMATSU, M. (1976). Breeding of malting barley variety which is resistant to barley yellow mosaic. In *Barley Genetics III*, 476–485. Proceedings of the Third International Barley Genetics Symposium, Garching, 1975.

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, Kurashiki, Japan, 217p.

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 Ohara Institut für Landwirtschaftliche Biologie Okayama Universität* **16**, 1–17.

UKAI, Y. (1984). Genetic analysis of a mutant resistant to barley yellow mosaic virus. *Barley Genetics Newsletter* **14**, 31–33.
UMBACH, H. (1987). Entwicklung einer effizienten Sprüh-Methode zur mechanischen Inokulation von BaYMV. *Dipl. Thesis, Unversität Giessen.*
YOSHIKAWA, R. & KATO, I. (1983). Inheritance of barley yellow mosaic resistance in naked barley (*Hordeum vulgare* L. emend. Lam.). *Japanese Journal of Breeding* **33** (Suppl. 1), 232–233.