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Characterisation of BaYMV and BaMMV pathotypes in France

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Abstract

The reaction of thirty-four barley cultivars from European and Asiatic origin was analysed in six soils infected with barley yellow mosaic virus complex (BaYMV, BaMMV). These soils were selected from 16 sites for their differences in cultivar response. Amongst the six cultivars carrying the ym4 gene (Esterel, Express, Labéa, Majestic, Réjane, Vanoise), only cv Majestic was infected at one site with BaYMV and BaMMV. Concerning BaYMV, three cultivars were infected on all the soils and 19 on none of them. Twelve cultivars were differentially infected depending on the soil. In the case of BaMMV, four cultivars were infected on all the soils and 19 on none of them. Eleven cultivars were differentially infected depending on the soil. ELISA tests revealed the presence, in these soils, of variants of BaYMV and BaMMV that were able to overcome at least seven of the 12 known resistance genes (ym3, ym4, ym6, ym8, ym9, ym10, ym11) and the resistance of three varieties (Tosan Kawa 73, OU1 and Taihoku A) in which the genetic basis is unknown. Amplification by RT-PCR of the N-terminal region for three of BaYMV variants was performed. Nucleotide and amino acid sequences were determined and compared with the corresponding sequence of a common strain of BaYMV-G. A few nucleotide differences were detected between all the French isolates, but there were no strain specific amino acid differences.

Introduction

Barley yellow mosaic (BaYMV) and barley mild mosaic (BaMMV) bymovirus are vectored by *Polymyxa graminis* Led., and have the potential to cause important damage to winter barley crops. BaYMV and BaMMV have been reported in Europe (Huth and Lesemann, 1978; Lapierre, 1980; Hill and Evans, 1980; Maroquin et al., 1982; Proeseler et al., 1984; Langenberg and Van der Wal, 1986; Fantakhun et al., 1987; Rubies-Autonell et al., 1995; Katis et al., 1997) and East Asia (Ikata and Kawai, 1940; Kashiwazaki et al., 1989; Chen et al., 1992). The only effective means of controlling these viruses is through the use of resistant cultivars. Different biological and serological variants of BaYMV and BaMMV have been reported in Europe and Asia. In Europe the resistant gene ym4 issuing from the cv Ragusa, which was introduced in a number of European barley genotypes, has been overcome by BaYMV 2 and BaMMV 2 (Adams, 1989; Huth, 1989; Hariri et al., 1990; 1998). In Japan seven strains of BaYMV and two strains of BaMMV are described on the basis of pathogenicity towards barley cultivars (Kashiwazaki et al., 1989; Kashiwazaki and Hibino, 1995; Nomura et al., 1996). A Korean strain of BaMMV differing biologically and serologically from the Japanese and German isolates and several biological variants of BaYMV in China are also recognised (Chen et al., 1996; Lee et al., 1996).

In this study, we describe the existence in France of BaYMV and BaMMV variants overcoming the resistance genes ym3, ym4, ym6, ym8, ym9, ym10, ym11 as well as the resistance of varieties the genetic basis of which is unknown. The sequences of the N-terminal

region of the capsid protein for three of these BaYMV variants are compared.

Materials and methods

Plant material, soil transmission and serology

During the year 1996–1997, the study of behaviour of barley cultivars from European and Asiatic origin on 16 geographically different fields in France showed that in six of them the resistance of certain cultivars was overcome by BaYMV and/or BaMMV (unpublished data). The behaviour of the thirty-four cultivars carrying different resistance genes was therefore studied in 1997–1998 in these six soils at Versailles (Figure 1).

The soils were air-dried and mixed with a small portion of sterile sand to improve aeration and seedling emergence. Sowing was carried out at the end of September in pots of 12 cm with 10 plants per pot. The pots were placed in the cold frame on a 50-cm layer of sand to ensure better drainage. Symptoms on inoculated plants were noted from January and the presence of each virus was detected by DAS ELISA. The double-antibody sandwich was done essentially as described by Clark and Adams (1977), except that samples were prepared by grinding leaf tissue in citrate buffer. Polyclonal antisera to BaMMV and BaYMV were generously supplied by Dr. M.J. Adams. Either 10 plants or two bulks of five plants were analysed.

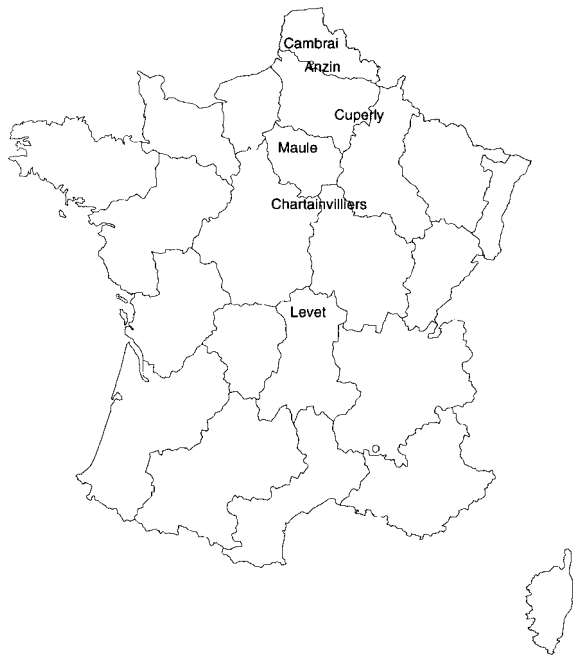

Figure 1. Location of six experimental sites.

Verification of the presence of the resistant genes ym4 and ym11

The RAPD marker OPZO4AH660, developed by Schiemann et al. (1997), is tightly linked to the ym4 resistance gene (0.7 cM). Four plants of cv Majestic from Chartainvilliers were tested to verify, in the multibanded pattern obtained with OPZO4A, the absence of the 660 bp band associated to the susceptible allele. The microsatellite HVM3 is localised at about 5.3 cM of the ym11 resistance gene (Bauer et al., 1997). Fourteen plants from four different sites (five from Levet, four from Maule, one from Anzin and four from Cambrai) were tested to verify the presence of the allele characteristic from Russia 57 (Le Gouis et al., 1999). Extractions and PCR reactions were carried out as in Bahrman et al. (1999).

Nucleic acid extraction, PCR amplification and sequence analysis

Total RNA was extracted from leaves (Schenk et al., 1995). PCR was performed (Dessens and Meyer, 1995) using two primers: 5′-ggtgatgatgaaatttggc 3′ (BaYMV-1 nt 6495–6512) and 5′-gtgcgccagcatcagtccaggc 3′ (complementary to BaYMV-1 nt 6906–6928) (Peerenboom et al., 1992). The PCR products were cloned in the plasmid pUC18 linearised at SmaI site. Dye terminator cycle sequencing was carried out with an Abi Prism TM 310 (Perkin-Elmer) automatic sequencer. At least, two independent cDNA clones were analysed for sequence determination. Nucleotide and amino acid comparisons were performed using the GCG package.

Results and discussion

Resistance against BaYMV

Results concerning BaYMV are presented in Table 1. Three cultivars were infected on all the soils and 19 on none of them. Twelve cultivars were differentially

Table 1. Proportion of infected plants barley cultivars after soil inoculation with barley yellow mosaic virus on six soils from France

Cultivars	Resistance gene	Anzin	Cambrai	Chartainvilliers	Cuperly	Levet	Maule
Clarine		10/10[b]	8/10	7/10	2/10	8/10	10/10
Plaisant		10/10	8/10	6/10	10/10	10/10	10/10
Anson		7/10	6/10	10/10	5/10	7/10	7/10
Angora		2/2[a]	2/2	0/2	2/2	2/2	2/2
Hiberna	ym10	3/10	4/10	7/10	0/10	4/10	0/10
Tosan Kawa 73		2/2	1/2	0/2	0/2	1/2	2/2
10247	ym8	3/10	3/10	0/2	—	4/10	1/2
New golden		2/2	2/2	0/2	0/2	1/2	2/2
OU1		4/10	3/10	0/2	—	8/10	2/10
Ea 52	ym3	4/10	10/10	0/10	6/10	1/10	—
Prior	ym6	2/2	1/2	0/2	0/2	2/2	0/2
Bulgarian 347	ym9	8/10	0/10	0/10	0/10	4/10	7/10
Russia 57	ym11	6/10	8/10	0/2	0/2	0/2	10/10
Hagane Mugi	ym3	0/2	0/2	0/2	2/2	0/2	0/2
Majestic	ym4	0/10	0/10	4/10	0/10	0/10	0/10
Taihoku A		0/2	0/2	0/2	0/2	0/2	0/2
Iwate Omugi 1	ym5′	0/2	0/2	0/2	0/2	0/2	0/2
Kashimamugi		0/2	0/2	0/2	0/2	0/2	0/2
Chikurin Ibaraki 1		—	0/10	0/10	0/10	0/10	0/10
Kikai Hadaka		0/2	0/2	0/2	0/2	0/2	0/2
Mihori Hadaka	Ym2	0/2	0/2	0/2	0/2	0/2	0/2
Misato golden	ym5	0/2	0/2	0/2	0/2	0/2	0/2
Mokusekko 3	ym1 + ym5	0/2	0/2	0/2	0/2	0/2	0/2
Muju Covered	ym12	0/2	0/2	0/2	0/2	0/2	—
Resistant Ym No 1	ym5	0/2	0/2	0/2	0/2	0/2	0/2
Esterel	ym4	0/10	0/10	0/10	0/10	0/10	0/10
Express	ym4	0/10	0/10	0/10	0/10	0/10	0/10
Labéa	ym4	0/10	0/10	0/10	0/10	0/10	0/10
Réjane	ym4	0/10	0/10	0/10	0/10	0/10	0/10
Vanoise	ym4	0/10	0/10	0/10	0/10	0/10	0/10
Comte de serre	ym4+?	0/10	0/10	0/10	0/10	—	0/10
Marne	ym4+?	0/10	0/10	0/10	0/10	0/10	0/10
Superchampenois	ym4+?	0/10	0/10	0/10	0/10	0/10	0/10
Tokyo	ym5	0/10	0/10	0/10	0/10	0/10	0/10

A negative result is included for a absorbance values at 405 nm $< 3\times$ the healthy absorbance value at 405 nm.
[a]ELISA on two bulks of five plants; [b]ELISA on 10 plants; —: not tested.

infected depending on the soil. The most infectious soil was Anzin with 10 cultivars out of 12 infected, then Cambrai (9/12), Levet (8/12), Maule (7/11), Cuperly (3/10) and Chartainvilliers (2/12). Amongst the six cultivars carrying the ym4 gene (Esterel, Express, Labéa, Majestic, Réjane, Vanoise), only cv Majestic was infected and only at Chartainvilliers. The resistance of the other cultivars carrying the ym4 gene was not affected in this soil. The four infected plants of Majestic tested with the OPZ04A marker all showed the pattern expected for a ym4-carrying plant (absence of the 660 bp band). It is therefore unlikely that this result could be explained by seed impurity. Chen et al. (1992) also reported in China different behaviour for supposed ym4-carrying cultivars. Only cv Energy was resistant against all Chinese strains of BaYMV. Cvs Express, Franka or Gaulois were susceptible to at least one pathotype. Cv Hiberna (ym10) which is resistant to BaYMV-1 and BaYMV-2 in Germany was shown to be susceptible at four sites (Anzin, Cambrai, Chartainvilliers, and Levet). Cv Russia 57 (ym11) described as totally resistant (Ordon et al., 1997) was infected in three soils (Anzin, Cambrai, Maule). All the 14 infected plants tested with the HVM3 microsatellite showed the allele normally carried by Russia 57. The cv Prior (ym6) resistant to BaYMV-II in

Japan (Iida and Konishi, 1994) showed susceptibility at Anzin, Cambrai and Levet. At Cuperly, there seemed to exist a particular strain that can only infest ym3-carrying cultivars as only Ea52 and Haganemugi were susceptible. This strain may be related to the BaYMV-IV strain described in Japan by Kashiwazaki and Hibino (1995) which was isolated from a cultivar carrying ym3.

Resistance against BaMMV

Results concerning BaMMV are presented in Table 2. Four cultivars were infected on all the soils and 19 on none of them. Eleven cultivars were differentially infected depending on the soil. The most infectious soil was Anzin with eight cultivars out of 11 infected, then Chartainvilliers, Levet and Maule (5/11), Cuperly (3/11) and Cambrai (2/11). The difference between BaMMV and BaYMV is striking at Cambrai; Cambrai was highly infectious for BaYMV and least infectious for BaMMV. Chartainvilliers, on the other hand, was highly infectious for BaMMV and least infectious for BaYMV. Cvs Tosan Kawa 73 and Ou 1 were fully resistant to BaMMV but susceptible to BaYMV. BaMMV was detected in four cultivars previously described as resistant in Europe (Ordon et al., 1997). Cv Majestic was infected only in the site Chartainvilliers.

Table 2. Proportion of infected plants barley cultivars after soil inoculation with barley mild mosaic virus on six soils from France

Cultivars	Resistance gene	Anzin	Cambrai	Chartainvilliers	Cuperly	Levet	Maule
Clarine		6/10	10/10	10/10	7/10	10/10	5/10
Plaisant		7/10	6/10	8/10	7/10	3/10	10/10
New golden		2/2	2/2	2/2	2/2	2/2	2/2
Ea 52	ym3	7/10	6/10	10/10	10/10	5/10	—
Hiberna	ym10	10/10	2/10	8/10	7/10	1/10	0/10
Anson		1/10	0/10	0/10	6/10	5/10	0/10
Angora		2/2	0/2	2/2	1/2	0/2	2/2
Hagane Mugi	ym3	1/2	0/2	1/2	0/2	1/2	1/2
Chikurin Ibaraki 1		—	0/10	0/10	0/10	0/10	0/10
Prior	ym6	2/2	0/2	0/2	0/2	2/2	1/2
Taihoku A		2/2	1/2	0/2	0/2	0/2	2/2
10247	ym8	2/10	0/10	1/2	—	2/10	0/2
Bulgarian 347	ym9	2/10	0/10	0/10	0/10	0/10	0/10
Majestic	ym4	0/10	0/10	8/10	0/10	0/10	0/10
Russia 57	ym11	0/10	0/10	0/2	0/2	0/2	1/10
Tosan Kawa 73		0/2	0/2	0/2	0/2	0/2	0/2
OU1		0/10	0/10	0/2	—	0/10	0/10
Iwate Omugi 1	ym5′	0/2	0/2	0/2	0/2	0/2	0/2
Kashimamugi		0/2	0/2	0/2	0/2	0/2	0/2
Kikai Hadaka		0/2	0/2	0/2	0/2	0/2	0/2
Mihori Hadaka	Ym2	0/2	0/2	0/2	0/2	0/2	0/2
Misato golden	ym5	0/2	0/2	0/2	0/2	0/2	0/2
Mokusekko 3	ym1 + ym5	0/2	0/2	0/2	0/2	0/2	0/2
Muju Covered	ym12	0/2	0/2	0/2	0/2	0/2	—
Resistant Ym No 1	ym5	0/2	0/2	0/2	0/2	0/2	0/2
Esterel	ym4	0/10	0/10	0/10	0/10	0/10	0/10
Express	ym4	0/10	0/10	0/10	0/10	0/10	0/10
Labéa	ym4	0/10	0/10	0/10	0/10	0/10	0/10
Réjane	ym4	0/10	0/10	0/10	0/10	0/10	0/10
Vanoise	ym4	0/10	0/10	0/10	0/10	0/10	0/10
Comte de serre	ym4+?	0/10	0/10	0/10	0/10	—	0/10
Superchampenois	ym4+?	0/10	0/10	0/10	0/10	0/10	0/10
Marne	ym4+?	0/10	0/10	0/10	0/10	0/10	0/10
Tokyo	ym5	0/10	0/10	0/10	0/10	0/10	0/10

A negative result is included for a absorbance values at 405 nm $< 3\times$ the healthy absorbance value at 405 nm.
[a]ELISA on two bulks of five plants; [b]ELISA on 10 plants; —: not tested.

This variety and others carrying the ym4 gene are known to be infected by some variants of this virus (Hariri et al., 1990; Hariri, 1999). Cvs 10247 (ym8) and Taihoku A were infected in three sites (Anzin, Chartainvilliers, Levet and Anzin, Cambrai, Maule respectively). Cv Prior (ym6) showed susceptibility in the three soils Anzin, Levet and Maule. Cv Anson described as resistant to BaMMV was infected in three sites (Anzin, Cuperly and Levet). Finally a very low infection rate was found at Maule for Russia 57 (ym11).

As the resistance to BaYMV and BaMMV was not overcome in an identical manner in all soils, this suggests that this heterogeneity of behaviour could be linked to the presence of several variants of these viruses.

Molecular characterisation of BaYMV variants

In order to better characterise the French BaYMV variants, an analysis was performed on the sequences of the N-terminal region of their capsid protein. This region was chosen because it shows a high variability. Two amino acids in positions 56 (Thr/Asn) and 64 (Thr/Ala) were found different between a common strain and a BaYMV pathotype overcoming the ym4 resistant gene in Germany (Bendiek et al., 1993). For three soils, the cloning and sequencing were carried out for the BaYMV strain infecting the susceptible cv Plaisant and one of the three resistant varieties showing a different behaviour (10247, OU1, Russia 57). The nucleotide sequences varied from 0.2% to 3.3%. Differences were found to be as great between BaYMV variants coming from different soils infecting the same susceptible cultivar as between BaYMV variants infecting either susceptible or resistant cultivars in the same soil. At the protein level, except for two cases, the sequences were similar to the common German strain of BaYMV-1 except for the amino acid 56 (Asn) which corresponded to that found for the German BaYMV-2 (Figure 2). The first exception concerned the BaYMV infecting the cv 10247 at Anzin for which the amino acid 46 (Lys/Arg) differed from the German BaYMV-1. The second exception concerned the BaYMV infecting the cv Plaisant at Cambrai which apart from the change in position 56 also showed a second difference at position 67 (Asp/Glu). These results showed the presence of different populations of BaYMV distinguishable by their nucleotide profile in different soils and indicate that the pathogenicity of these isolates towards the cvs 10247, OU1 and Russia 57 was not directly related to a mutation of amino acid 56. This study confirms a previous report on English BaYMV 1 and BaYMV 2 isolates for which the same change of amino acid at position 56 (Asn) was noticed indicating that this amino acid was not the determining factor of pathogenicity towards the gene ym4 (Shi et al., 1995).

Conclusion

This study showed the presence of variants of BaYMV and BaMMV in France able to overcome at least seven of the 12 known resistance genes (ym3, ym4, ym6, ym8, ym9, ym10, ym11) (Bauer et al., 1997) and the resistance of three varieties (Tosan Kawa 73, OU1 and Taihoku A) the genetic basis of which is unknown. These variants are quite frequent since they are found in five soils in the north and the central parts of France. For BaMMV and BaYMV, variants at Anzin overcame the resistances of ym3, ym6, ym8, ym9, ym10, ym11, Taihoku A, OU1 and Tosan Kawa 73. Three of the known resistance genes were never overcome in the six soils: Ym2, ym5 and ym12. As ym1 is associated to ym5 in Mokusekko 3 it was not possible to determine exactly its action.

The French variants of BaYMV and BaMMV could correspond either to a single pathotype capable of overcoming the resistance conferred by all of these genes or to different pathotypes each one capable of overcoming one of these resistant genes. The fact that the resistances were not overcome in all the soils favour the hypothesis that different viral variants exist in France. In Japan and China, the analysis of different cultivars in several infected soils showed the presence of pathotypic variants of BaYMV (Kashiwazaki et al.,1989; Chen et al., 1996). The variant present at Maule has the same characteristics to that BaYMVII-1 (Kashiwazaki et al., 1989). These results reinforce the hypothesis that different variants of BaYMV occur in France. For BaMMV, none of the French variants showed a behaviour similar to the Korean and Japanese variants (Lee et al., 1996). Verification of the presence of the PCR patterns corresponding to ym4-carrying plants in cv Majestic and ym11-carrying plants in cv Russia 57 limited the possibility of seed impurity.

The sequences obtained for the N-terminal region of the capsid protein of three BaYMV variants indicate that this region is not directly involved in the pathogenicity of this virus. Such a situation is reminescent of the results reported for other

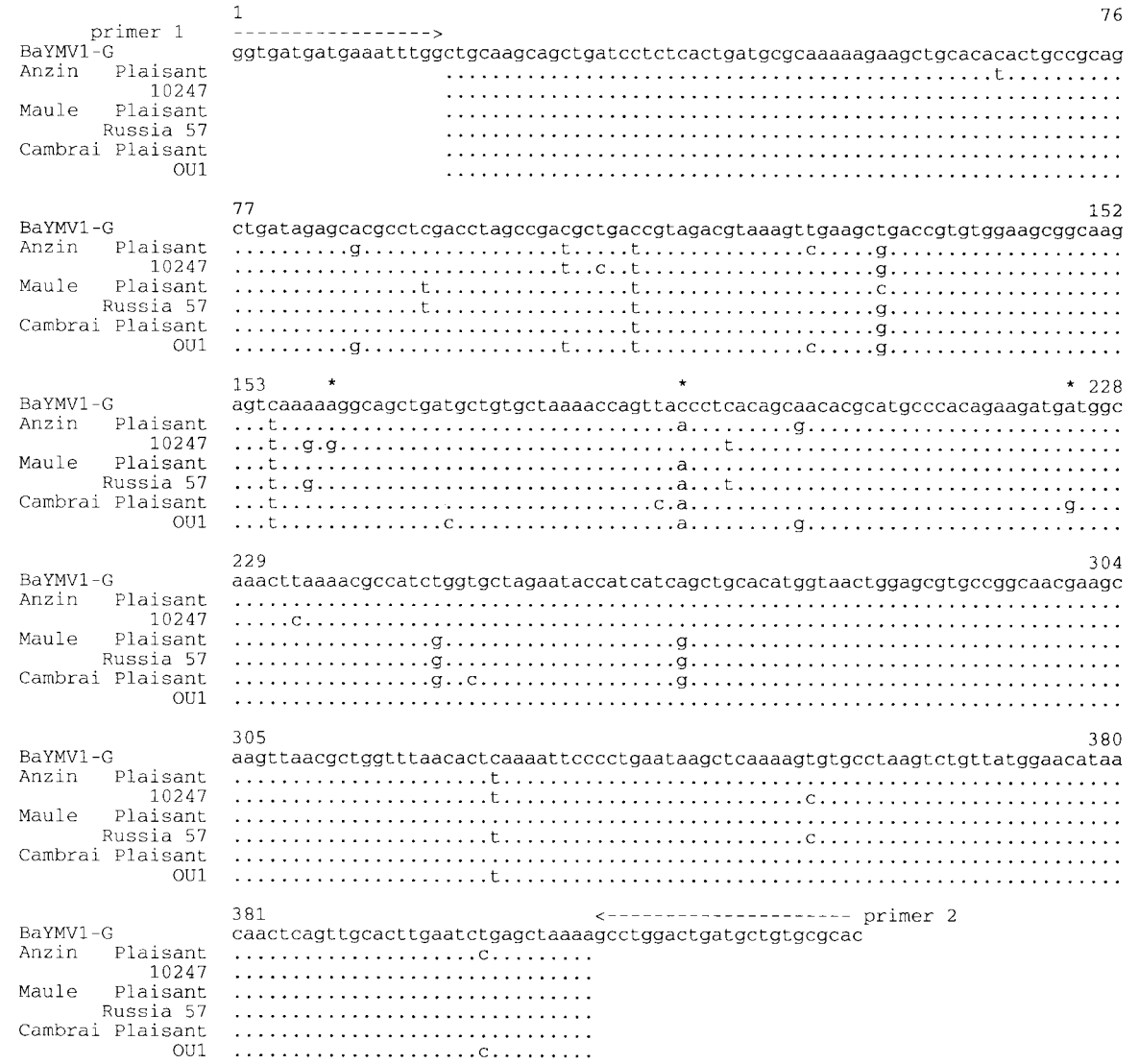

Figure 2. Nucleotide sequence comparisons of the 5′ N-terminal region of the capsid protein of French isolates with the published sequence of a German isolate of BaYMV. Only those nucleotides which differ from the sequence of the German isolate are shown. The positions of the virus-sense and minus-sense primers (arrows), and residues corresponding to different amino acids between BaYMV 1-G and the French isolates (asterisks) are included.

Potyviridae, particularly potyviruses, (Pacot-Hiriart et al., 1997). Other regions known to be variable such as the N-terminal domain of the P2 protein could be studied.

For BaMMV, insofar as an infectious clone was obtained recently (Meyer and Dessens, 1997), the construction of viral hybrids from pathotypic and serotypic variants already described in France (Hariri et al., 1998; Hariri, 1999), as well as from the variants characterised in this study, will allow us to determine which viral regions are implicated in the pathogenicity.

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