Occurrence of Barley Yellow Dwarf Viruses in Small-Grain Cereals and in Alternative Hosts in Spain

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ABSTRACT

Moriones, E., and García-Arenal, F. 1991. Occurrence of barley yellow dwarf viruses in small-grain cereals and in alternative hosts in Spain. Plant Dis. 75:930-934.

The main small-grain cereal producing regions of Spain were surveyed for barley yellow dwarf viruses (BYDV) during the springs of 1987, 1988, and 1989. Barley yellow dwarf was found to be present in all regions of Spain, its incidence varying largely from year to year and among the different geographical regions. Both PAV- and RPV-like isolates were found in all surveyed regions; PAV-like isolates were largely more prevalent than RPV-like ones for cereals but not for weeds or forage grasses. The data on the distribution and relative frequencies of PAV- and RPV-like isolates and the different situations found for cereals and weeds may suggest that inoculum for spring epidemics of these viruses comes from distant sources rather than local reservoirs.

Barley yellow dwarf (BYD), a major disease of small grains occurring worldwide, is induced by different aphid-transmitted luteoviruses (barley yellow dwarf viruses, BYDV) with natural hosts in the Gramineae (20). The different BYDV can be differentiated antigenically (12) and have been classified according to their vector specificity and other characteristics (12,13,15,19).

BYDV were first detected in Spain in 1978 on rice grown in eastern Spain (14). Data from regional surveys showed that the more frequently found BYDV on small-grain cereals are of the RPV-specifically transmitted and, particularly, of the PAV-nonspecifically transmitted types (9,14). To obtain a more complete view of the occurrence and importance of BYD in small-grain cereals in Spain, we surveyed the main grain-producing regions in 1987, 1988, and 1989. Samples of small grain cereals and from alternative hosts (perennial weeds, forage grasses, and maize) were analyzed for the presence of PAV- and RPV-like BYDV. The data show both PAV- and RPV-like BYDV to be present in all surveyed regions. Their distribution and relative frequencies vary from year to year and differ among cereals and other hosts. The data suggest that inoculum for yearly epidemics comes from distant sources rather than from local reservoirs.

Accepted for publication 11 March 1991 (submitted for electronic processing).

MATERIALS AND METHODS

Survey. Barley (*Hordeum vulgare* L.), wheat (*Triticum aestivum* L. and *T. durum* Desf.), oat (*Avena sativa* L.), and triticale (× *Triticosecale* Wittmack) plants showing BYD-symptoms (when incidence of symptomatic plants did permit it) or random sampled (when symptomatic plants were not found or were at extremely low incidence) were collected in commercial fields in all the main grain-producing regions of Spain. An average of 20 plants of cereals or alternative hosts were collected at the indicated sites (Fig. 1), totaling 543 samples in 1987, 1,071 in 1988, and 934 in 1989. In addition to main (I–V) and marginal regions of cereal production, region VI (Fig. 1) in northern Spain, producing maize and forage grasses and having ecological conditions very different (an Atlantic climate with no or little hydric deficit in the summer) from the rest of Spain (a Mediterranean climate with a strong hydric deficit in the summer) was included in the survey. Sampling sites in the main cereal regions were chosen so that they represented different ecosystems/environments inside these regions (e.g., for region IV, irrigated crops [point 20], dry farming under low precipitation [≤400 mm per year, points 19 and 22], and dry farming under moderate precipitation [500–700 mm per year, points 21, 23, and 24]). Surveys were conducted during the 1986–1987, 1987–1988, and 1988–1989 growing seasons (hereafter 1987, 1988, and 1989, respectively) from March to late June depending on the sites. Plants were sampled at the expanded flag leaf growth stage (GS 4.7 of Zadoks' code [23]). Visual estimations of symptom incidence were recorded.

When present near the surveyed cereal fields, perennial weeds (Gramineae) and pasture grasses were randomly sampled. When possible, samples of maize (*Zea mays* L.) plants showing symptoms were also collected.

Detection of BYDV. BYDV infection in the collected samples was detected serologically by indirect enzyme-linked immunosorbent assay (ELISA) (3,15). Plates were coated with rabbit polyclonal antibodies to a BYDV isolate from Kentucky supplied by T. P. Pirone, Lexington, KY, reacting with either PAV- or RPV-like strains of BYDV (5). Antigens were detected with rat monoclonal antibodies (MAb) to RPV or PAV from L. Torrance, Harpenden, United Kingdom (22), and MAbs were detected with a commercial rabbit anti-rat IgG conjugated to alkaline phosphatase (Bio-Yeda, Israel). Extracts from healthy plants were used as negative controls, and extracts of plants infected with known RPV or PAV isolates from New York (19) (supplied by W. F. Rochow, Ithaca, NY) were used as positive controls. Field samples with A_{405nm} values $\geq 2\times$ negative controls in the same plate were considered positive.

RESULTS

Distribution and incidence of BYD. Barley and wheat are the major small-grain cereals grown in Spain, barley representing about twice the hectareage of wheat. We considered the following symptoms at growth stage 4.7 characteristic of BYD: an intense yellowing (for barley), a dull yellowing (for bread wheat), or a yellowing wine reddening (for durum wheat) that develops from the apex to the base of the flag and upper leaves. Only spring-sown barley showed other BYD-like symptoms, such as dwarfing, general yellowing, increased tillering, or white heads (20). We have analyzed the correlation between the above symptoms and a positive reaction by ELISA—85% of symptomatic barley plants were BYDV positive, whereas only 40% of symptomatic wheat plants were BYDV positive. In contrast with other reports (4,17), no positives were found for asymptomatic plants of barley or wheat. According to these results, visual estimates of BYD incidence were done only for barley.

BYD was found in all surveyed regions for 1987, 1988, and 1989. During 1987, BYD incidence was low for all regions, never surpassing 20% in individual fields, whereas in 1988 and 1989, severe epidemics occurred. BYD incidences of 80% were frequent in individual fields in regions II, III, and IV (Fig. 1) and at isolated sites in other regions, such as Cazalla and Benavente (6 and 29 in Fig. 1) in 1988. In 1989, high incidences of BYD were registered in some fields of region III, such as Talavera and Alcala (10 and 17 in Fig. 1), and at most of region IV. The disease was particularly severe in spring-sown two-row barley, where severe dwarfing and/or white heads occurred in whole fields in regions III and IV. For all 3 yr, BYD incidence was lowest in regions I and V.

Distribution of RPV- and PAV-like isolates of BYDV. The results of the serological detection of PAV- and RPV-like BYDV isolates are presented in Tables 1 and 2. Both BYDV types were found in all surveyed regions during 1987–1989, both in crops and in gramineous weeds. For small-grain cereals, PAV-like isolates were clearly prevalent: They were found at all surveyed areas for all 3 yr, and, on average, were found in more than 90% of the ELISA-positive plants. In contrast, RPV-like isolates were much less frequent. In 1987, they were found in 22% of the ELISA-positive plants, and this proportion was less in 1988 (6.9%) and 1989 (3.4%). For each particular site, the ratio of PAV-like vs. RPV-like isolates varied from year to year (e.g., La Rambla and Lalín, 5 and 32 in Tables 1 and 2 and Fig. 1, respectively). Moreover, RPV-like isolates were not detected every year in all surveyed regions, but their distribution varied according to the year. A further relevant feature of BYDV-infection in cereals is that more than 50% of plants that were ELISA positive for RPV-like isolates were also ELISA positive for PAV-like isolates.

A completely different situation is found for BYDV detection in graminaceous weeds or forage grasses: For both 1987 and 1988 (the number of positives in 1989 was too small to draw any conclusion), RPV-like isolates were found in more than 40% of plants infected with BYDV. Although 77% of plants infected with RPV were also positive for PAV in 1987, only 7% of RPV-positive plants showed both PAV and RPV in 1988. For a given site, the ratio of plants positive for RPV-like isolates to PAV-like isolates was different for cereals and weeds (e.g., Tables 1 and 2, Alcalá, for 1987, 1988, 1989; Talavera, for 1988, etc.). Weeds or grasses that were ELISA positive for BYDV included *Elymus repens* (L.) Gould, *Elymus* spp., *Lolium perenne* L., *Brachypodium phoenicoides* (L.) Rochmer & Schulter, *Brachypodium* spp., *Festuca* spp., *Phragmites australis* (Cav.) Trin. ex Steudel and *Phalaris* spp.

DISCUSSION

BYDV was first found in Spain in the eastern rice-growing areas in 1978 (14); since then, BYDV has been recorded in other regions and on other crops as well as in weeds of the Gramineae (9,14). PAV- and RPV-like isolates were found to be prevalent on both cereals and weeds (9,14), although MAV-like (9) and RMV-like (E. Moriones and F. García-Arenal, *unpublished*) isolates have also been found sporadically.

We found BYD in all surveyed regions, although its incidence and economic importance varied largely according to the year and region. Although the high incidence of the disease in 1988 and 1989 could be related to unusually mild winters and high aphid populations in spring, it is not obvious why disease incidence in regions I and V was consistently lower than in regions II, III, and IV. A possible explanation is that eco-

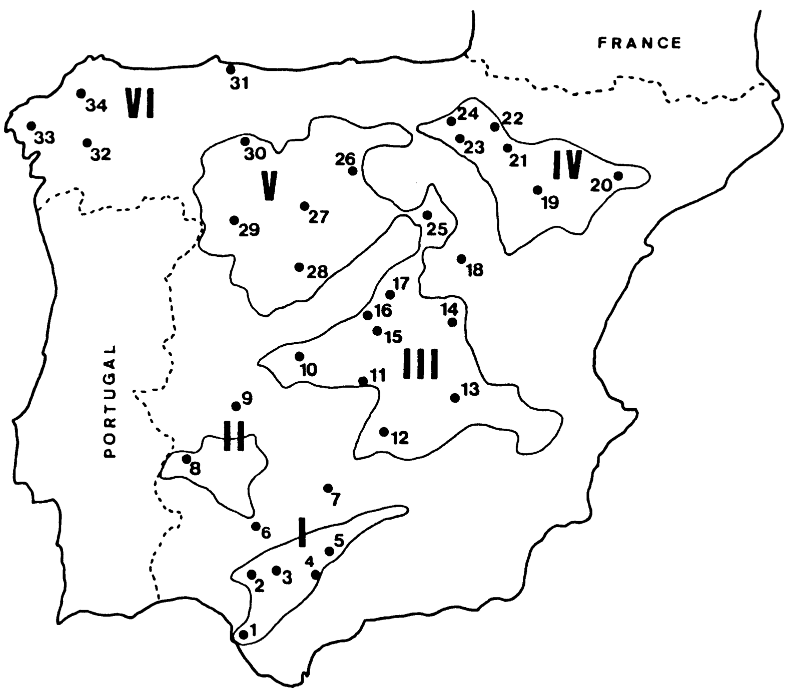

Fig. 1. Map of Spain showing the major producing areas of small grain (I–V) and maize and forage grasses (VI), and the sites where samples were collected (1–34).

logical conditions in those regions will favor the escape of the crop from the disease—in region I by the earliness of the growing season (wheat being harvested since May) and in region IV, severely cold temperatures in winter and spring may delay aphid dispersal of the BYDV.

As reported by other authors (9,14), serological analysis of BYD-affected plants showed PAV-like isolates to be largely prevalent on cereals in all surveyed regions, a situation comparable to that reported for other countries with similar (6,11) or different (4,10) ecological conditions. Cereal plants were not randomly sampled, because an effort to collect symptomatic plants was made. Nevertheless, because PAV- and RPV-like isolates induce similarly severe symptoms (11) (our own greenhouse controls), we are confident that our data reflect the true structure of BYDV populations in the field. At odds with other reports (9), RPV-like isolates were also found in all surveyed regions, although in cereals they were comparatively infrequent, and their frequency decreased from 1987 to 1989. This may reflect a fluctuation in structure of BYDV populations, as had been reported in New York (21), California (11), and Sweden (7), the causes of which remain to be established.

Two main features stand out from our data and are common to all surveyed regions: 1) the frequency of RPV-like isolates varies according to years, both in relation to the frequency of PAV-like isolates at a certain site and in its apparent geographical distribution and 2) for weeds, RPV- and PAV-like isolates are nearly as frequent. These two features could be explained in terms of the vector populations. Detailed analyses of the population dynamics of cereal aphids have been reported only for Alcalá (17 in Fig.1) and Lérida (20 in Fig.1), whereas both *Rhopalosiphum padi* L. and *Sitobion avenae* (Fabricius) behave as anholocyclic species with population maxima in the fall (on weeds, forage grasses, and volunteers) and spring (on cereals), overwintering locally (2,18).

The prevalence of PAV-like isolates over RPV-like isolates in cereals, but not in weeds, has been related to *R. padi* having been the most abundant species in the fall, transmitting both PAV- and RPV-like isolates (hence, the high percentage of mixed infections), whereas *S. avenae* was the most abundant species in the spring, thus favoring the dispersal of PAV-like isolates in cereals (9).

Irrigated maize crops cannot be direct sources of inoculum for small grains in most of the surveyed sites, at odds with other reported situations (1), because late sowing of barley and wheat in the fall prevents overlapping the crops, although it cannot be dismissed that aphids carrying BYDV from maize may survive in alternative weed hosts. Also, it could be that in high disease incidence years, weeds and cereals behave as partially separate systems. Although weeds may be the inoculum source for a minor RPV- and PAV-like infection of cereals in the

Table 1. PAV and RPV barley yellow dwarf viruses (BYDV) detected in cereal host[z] plants by enzyme-linked immunosorbent assay (ELISA)

	1987				1988				1989			
Location	**Total**	**PAV**	**RPV**	**Mix**	**Total**	**PAV**	**RPV**	**Mix**	**Total**	**PAV**	**RPV**	**Mix**
Region I												
1. Jerez	13(B,W)	4	0	0	15(W)	5	0	0	18(W)	12	0	0
2. Sevilla	...	...	...	...	17(B)	12	0	0	...	...	...	...
3. Carmona	14(W)	3	0	0	20(W)	11	0	0	32(W)	30	0	1
4. Estepa	...	...	...	...	10(W)	0	0	0	13(W)	9	2	0
5. La Rambla	33(W)	18	0	0	30(W)	1	1	0	15(W)	12	0	0
6. Cazalla	...	...	...	...	20(B,T)	13	0	0	...	...	...	..
7. Ademuz	...	...	...	...	30(O)	1	8	5	15(W)	1	1	0
Region II												
8. Lobon	...	...	...	...	48(W,B)	38	1	1	35(W,B)	26	0	0
9. Trujillo	...	...	...	...	15(W,O)	9	0	0	20(B,O)	7	0	0
Region III												
10. Talavera	37(W,B)	13	0	1	20(W)	19	0	0	20(W,B)	18	0	0
11. Arisgotas	10(B)	3	0	0	...	...	...	...	10(W)	9	0	0
12. Almagro	...	...	...	...	20(B)	16	0	0	24(B)	3	0	0
13. S. Clemente	10(W,B)	1	0	0	20(B)	18	0	0	25(B)	1	0	0
14. Olivares	...	...	...	...	20(B)	0	0	0	...	...	...	...
15. Aranjuez	27(O,W)	10	2	1	...	...	...	...	...	...	...	...
16. Madrid	19(W)	9	1	1	24(W,O)	19	0	0	...	...	...	...
17. Alcalá	82(W,B)	12	2	0	17(W,B)	7	0	1	96(W,B)	46	0	2
18. Molina Aragón	...	...	...	...	20(W)	9	0	3	25(W,B)	20	0	0
Region IV												
19. Zaragoza	21(B)	1	1	3	30(W,B)	25	0	0	17(W,B)	10	0	0
20. Lérida	21(W,B)	6	0	1	19(W,B)	11	0	2	43(W,B)	12	0	0
21. Egea	...	...	...	...	19(W)	5	0	0	10(B)	0	0	0
22. Sofuentes	...	...	...	...	...	...	...	...	22(B)	18	0	0
23. S. Adrián	29(B)	2	0	2	5(B)	3	0	0	10(B)	9	0	1
24. Peralta	...	...	...	...	29(W,B)	26	0	0	25(B)	9	0	0
Region V												
25. Almazán	...	...	...	...	20(B)	0	0	0	...	...	...	...
26. Lerma	...	...	...	...	...	...	...	...	16(B)	1	0	0
27. Valladolid	25(W,B)	2	0	2	20(W,B)	18	0	0	23(B)	2	0	1
28. Arevalo	16(W,B)	1	1	0	20(W,B)	12	0	0	22(B)	6	2	0
29. Benavente	...	...	...	...	15(B)	12	0	0	26(W)	18	0	0
30. Stas. Martas	...	...	...	...	16(B)	10	0	0	15(B)	1	0	0
Region VI												
31. Gijón	...	...	...	...	...	...	...	...	...	...	...	...
32. Lalín	12(W)	1	2	5	28(W)	10	1	0	30(W)	0	0	0
33. Cee	...	...	...	...	...	...	...	...	...	...	...	...
34. Mabegondo	...	...	...	...	...	...	...	...	...	...	...	...
Total	369	86	9	16	567	310	11	12	607	280	5	5
Percent over ELISA-Positive	...	78	8	14	...	93	3	4	...	97	2	2

[z] Cereal hosts include barley (B), wheat (W), oat (O), and triticale (T).

Table 2. PAV and RPV barley yellow dwarf viruses (BYDV) detected in host plants[z] by enzyme-linked immunosorbent assay (ELISA)

Location	1987				1988				1989			
	Total	PAV	RPV	Mix	Total	PAV	RPV	Mix	Total	PAV	RPV	Mix
Region I												
1. Jerez	...	...	...	...	15(G)	0	0	0	...	...	...	...
2. Sevilla	...	...	...	...	12(G)	0	1	0	...	...	...	...
3. Carmona	...	...	...	...	15(G)	0	1	0	15(G)	0	0	0
4. Estepa	...	...	...	...	...	...	...	...	...	...	...	...
5. La Rambla	...	...	...	...	20(G)	0	0	0	20(G)	2	0	0
6. Cazalla	...	...	...	...	21(G,F)	2	0	0	...	...	...	...
7. Ademuz	...	...	...	...	...	...	...	...	...	...	...	...
Region II												
8. Lobon	...	...	...	...	11(G)	1	0	1	...	...	...	...
9. Trujillo	...	...	...	...	15(G)	0	0	0	15(G)	0	0	0
Region III												
10. Talavera	...	...	...	...	10(G)	0	1	0	...	...	...	...
11. Arisgotas	...	...	...	...	...	...	...	...	...	...	...	...
12. Almagro	...	...	...	...	10(G)	0	0	0	...	...	...	...
13. S. Clemente	...	...	...	...	10(G)	1	0	0	...	...	...	...
14. Olivares	...	...	...	...	15(G)	0	0	0	...	...	...	...
15. Aranjuez	...	...	...	...	...	...	...	...	...	...	...	...
16. Madrid	...	...	...	...	...	...	...	...	...	...	...	...
17. Alcalá	77(G)	2	4	10	106(G)	0	1	0	87(G)	2	0	0
18. Molina Aragón	...	...	...	...	15(G)	2	0	0	20(G)	2	0	0
Region IV												
19. Zaragoza	...	...	...	...	15(F)	2	0	0	15(F)	0	0	1
20. Lérida	...	...	...	...	10(G)	0	0	0	33(G)	1	0	0
21. Egea	...	...	...	...	11(G)	1	1	0	...	...	...	...
22. Sofuentes	...	...	...	...	...	...	...	...	15(G)	0	0	0
23. S. Adrián	...	...	...	...	15(G)	0	0	0	10(G)	1	0	0
24. Peralta	...	...	...	...	...	...	...	...	...	...	...	...
Region V												
25. Almazán	...	...	...	...	20(G)	0	0	0	...	...	...	...
26. Lerma	...	...	...	...	...	...	...	...	...	...	...	...
27. Valladolid	16(G)	0	0	0	20(G)	0	0	0	20(G)	0	0	0
28. Arevalo	...	...	...	...	15(G)	0	4	0	...	...	...	...
29. Benavente	...	...	...	...	15(G)	0	2	0	17(G)	0	0	0
30. Stas. Martas	...	...	...	...	20(G)	0	0	0	...	...	...	...
Region VI												
31. Gijón	20(F)	1	0	0	4(F)	0	0	0	...	...	...	...
32. Lalín	18(F)	0	1	0	14(F)	1	0	0	15(G)	0	0	0
33. Cee	18(F)	0	1	1	40(F,M)	10	2	0	45(M)	1	0	0
34. Mabegondo	25(F)	0	0	9	30(F,M)	2	0	0	...	...	...	...
Total	174	3	6	20	504	22	13	1	327	9	0	1
Percent over ELISA-Positive	...	7	21	71	...	59	38	3	...	90	0	10

[z] Hosts include graminaceons weeds (G), forage grasses (F), and maize (M).

fall, the major spring-dispersed epidemic of PAV-like isolates could come from distant sources as has been suggested for similar situations (4,8). Our data seem to favor this second hypothesis for the following reasons: 1) the critical moment for BYDV epidemics seems to be the spring—severe symptoms are observed only in spring-sown barley, not in fall-sown barley or wheat; 2) in the high disease incidence years 1988 and 1989, the prevalence of PAV-like isolates over RPV-like isolates in cereals was more dramatic than in 1987; and 3) there were no unusually high spring populations of *S. avenae* in these years—for 1987, fall and spring populations of both aphid species have been similar (16) (E. Moriones and F. García-Arenal, *unpublished*). In any case, until more information on population dynamics and long-range migrations of cereal aphids in Spain is available, a hypothesis on the inoculum source for epidemics of BYDV will remain largely speculative.

ACKNOWLEDGMENTS

This work was supported by grant CCA-8309/155 of the U.S.-Spain Joint Comittee for Scientific and Technological Cooperation; Enrique Moriones received a fellowship from INIA, Spain. We thank T. P. Pirone and L. Torrance for providing sera, W. F. Rochow for providing BYDV isolates, and L.Martínez-Vassallo, ISPV, Spain, for the use of his laboratory facilities. We also thank the many people who helped us with the field surveys.

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