# Synergism in Cereals Between Corn Leaf Aphid-Specific and Aphid-Nonspecific Isolates of Barley Yellow Dwarf Virus

C. C. Gill and A. Comeau

Research Scientists, Agriculture Canada Research Stations, 195 Dafoe Road, Winnipeg, Manitoba, R3T 2M9; and 2560 Chemin Gomin, Sainte-Foy, Québec, Canada G1V 2J3.

Contribution No. 788, Agriculture Canada Research Station, Winnipeg.
Accepted for publication 16 May 1977.

ABSTRACT

GILL, C. C., and A. COMEAU. 1977. Synergism in cereals between corn leaf aphid-specific and aphid-nonspecific isolates of barley yellow dwarf virus. Phytopathology 67:1388-1392.

In greenhouse experiments with Rodney oats and Herta barley, seed yields from plants inoculated simultaneously (doubly inoculated) with an aphid-nonspecific (7410) and a *Rhopalosiphum maidis*-specific (7413) isolate of barley yellow dwarf virus were significantly lower than yields from plants inoculated with only one or the other isolate. Five cereals also were tested in a field experiment in which plants were doubly inoculated either simultaneously with both isolates early (late tillering stage) or with both late (jointing stage), or with one isolate early and the second late in reciprocal treatments. Seed yields from doubly inoculated Rodney, Hudson, and FF64-74 oats and from Bonanza barley were lower than yields from both of the relevant singly inoculated controls, except for one of the four double-inoculation treatments with the tolerant oat, FF64-74. The differences were significant for three of the four double inoculations with Rodney and for one with Hudson. Synergism was not evident on Herta barley. The results from double inoculation of this cultivar may have been affected by a stimulatory effect on seed yield when the plants were inoculated early with isolate 7413 (38% higher yield than on noninoculated plants). When Herta barley was inoculated in a growth cabinet with either one of the isolates first and then, after a period of 4 or 10 days, with the other, both isolates were recovered from the inoculated plants, indicating lack of protection between the isolates.

Interference or protection with isolates of barley yellow dwarf virus (BYDV) in cereals has been reported between *Macrosiphum avenae* (Fabricius)-specific and aphid-nonspecific isolates (1, 7, 8, 13), whereas either synergistic reactions or lack of protection were found between *M. avenae*-specific and *Rhopalosiphum padi* (Linnaeus)-specific isolates and between aphid-nonspecific and *R. padi*-specific isolates (1, 7, 11, 14, 15). Synergism also resulted between a *Schizaphis graminum* (Rondani)-specific isolate that caused severe and permanent stunting on oats (*Avena byzantina*, C. Koch 'Coast Black'), and one that was transmitted most efficiently by *S. graminum*, (but also by other aphids) and which caused only mild stunting of Coast Black oats (7).

*Rhopalosiphum maidis* (Fitch)-specific and aphid-nonspecific isolates of BYDV have been recovered frequently from cereals in Manitoba, particularly in years when BYDV was very common (4, 5, 6). Therefore, the probability was high that in some years individual plants in the field were infected with both types of isolate. In New York, individual plants of winter barley have been found infected with both *R. maidis*- and aphid-nonspecific isolates (12). Since there is no information on the reaction of cereals to mixed infections with these two variants of the virus, we have investigated this problem. The results obtained provide information on the relationship between these two variants and should be of value in predicting losses from BYDV in the field.



## MATERIALS AND METHODS

The two virus isolates used were collected from oats in Manitoba in 1974 (6) and were 7413 (*R. maidis*-specific) and 7410 (aphid-nonspecific). These produced mild and very severe symptoms, respectively, on Coast Black oats, when inoculated at the two-leaf stage. Viruliferous colonies of *R. maidis* and *R. padi* were reared, respectively, on caged barley, *Hordeum vulgare* L. 'Parkland', infected with isolate 7413; and on caged oats, *A. sativa* L. 'Rodney' infected with isolate 7410. Colonies of virus-free *R. maidis* and *R. padi* were maintained on caged Parkland barley. Samples of these aphids were tested at regular intervals on oats to check for freedom from virus.

One trial each with barley, *H. distichum* L. 'Herta' and Rodney oats, was performed in the greenhouse to determine the reactions of these cereals when inoculated simultaneously with the two virus isolates at the three-leaf stage. The cereals, seeded in March, were grown singly in 12.7-cm-diam clay pots containing a 3:1 mixture of soil and "Turface" (processed montmorillonite clay) at about 18 C with supplementary, cool-white, fluorescent lighting for 16 hr/day. Seedlings to be infected as controls with one isolate were inoculated by caging either six individuals of *R. padi*, or 12 of *R. maidis* from viruliferous colonies on each plant. Seedlings to be infected with both isolates (hereafter called doubly inoculated) were infested with six *R. padi* and 12 *R. maidis*. More individuals of *R. maidis* were used because the transmission of isolate 7413 by *R. maidis* is less

efficient than that of isolate 7410 by *R. padi*. Three days later the aphids were sprayed with tetraethylpyrophosphate (TEPP) insecticide. In the trial with oats, some plants, as additional controls, were caged with virus-free aphids and then sprayed as above. Five wk after inoculation, the plants were tested for the ability of aphids to recover virus. A leaf detached from the plant was placed in a petri dish and infested with virus-free aphids of the requisite species. After 2 days at 15 C, aphids were removed from the leaves and 15 *R. maidis* or 10 *R. padi*, depending on the isolate concerned, were caged on each of three Coast Black oat test seedlings. After 5 days, the plants were sprayed with TEPP and were observed for BYDV symptoms for 4 wk. When the barley and oats used in the double inoculation trial were mature, the dry weight of the plant (excluding roots) and the number of heads and seeds and weight of seeds per plant were recorded.

Two more trials were performed in a growth cabinet to determine whether virus could be recovered from Herta barley, after inoculation first with one isolate, then, after a period of either 4 or 10 days, with the other. The plants were grown in flats of soil at 18 ± 1.5 C with 15,000 lux of fluorescent lighting for 18 hr/day. The method of inoculation of the seedlings with virus was the same as described for the greenhouse trials. Control plants were inoculated at the same time as the doubly inoculated plants but with only one or the other of the isolates. Four-to-seven plants were inoculated for each treatment. Transfer of isolate 7410 from the inoculated plants was attempted 15 days after each inoculation with this isolate, and 20 days after each inoculation with isolate 7413. The method of transfer was the same as that for recovery of virus from plants in the greenhouse trials, except that four Coast Black oat test seedlings were used per virus source plant.

A field plot trial at Winnipeg was performed in 1976 to study the reactions of five cereals inoculated either simultaneously with the two isolates or sequentially with a time interval between inoculations. Herta and Bonanza barley, and Rodney, Hudson, and FF64-74 oats, the latter a line from Sainte Foy, Québec, were seeded on May 20, using a five-replicate split-plot design with the five cereals as main plots and the nine treatments as sub-plots. Each sub-plot was a 2.74-m row and was separated on all sides from other sub-plots by three or four guard rows of a mixture of oats, barley, and wheat. Rows were spaced 22.9 cm apart. Sub-plots were treated as follows: no inoculation; single inoculation with one or the other isolate, early or late; double inoculation with both isolates, early or late; and double inoculation with one isolate early and the other late in reciprocal fashion. The early and late inoculations were made 27 and 39 days after seeding, at the late tillering or jointing growth stages, respectively. Viruliferous aphids, *R. maidis* with isolate 7413, and *R. padi* with isolate 7410, were reared in separate greenhouse sections on a mixture of barley, oats, and wheat grown in beds of soil. Tests with the aphids sampled from each greenhouse at the time of inoculation in the field demonstrated that they were carrying the requisite isolates. Aphids harvested from these plants, mixed with a small amount of talcum powder, were taken to the field in plastic boxes and distributed in the sub-plots to be inoculated, at the rate of about five aphids per plant. A special inoculation device was used (3) in which the mixture of aphids and talcum powder was applied to the bases of the plants through a tube from a plastic box carried by the operator. The talcum powder served to reduce agglomeration of the aphids. The plots were sprayed with Pirimor insecticide 7 days after the second inoculation. Symptoms were rated 21 days after each inoculation on a scale of 0-5 for increasing amounts of leaf discoloration. The plants were harvested on 9 August and the mean dry weight of the plants (excluding roots), the mean seed yield, and 1,000-kernel weight per sub-plot were recorded.

## RESULTS

**Greenhouse and growth cabinet experiments.**—In the yield trials in the greenhouse in which oats or barley were inoculated simultaneously with the two virus isolates, all inoculated plants became infected and both aphid species recovered virus in tests from the doubly inoculated plants. Symptoms on test plants of Coast Black oats were mild and severe, respectively, when *R. maidis* or *R. padi* transmitted virus. The aphid-nonspecific isolate 7410 also was more severe than the *R. maidis*-specific isolate 7413 both on Rodney oats and Herta barley in all parameters measured (Table 1), and in the symptoms. Symptoms on

TABLE 1. The effect on the yield of Rodney oats and Herta barley inoculated in the greenhouse with *Rhopalosiphum maidis*-specific isolate 7413, or aphid-nonspecific isolate 7410, of barley yellow dwarf virus, or with both isolates

| | | | Mean values per plant | | | |
|---|---|---|---|---|---|---|
| Cereal | Treatment | Plants (no.) | Heads (no.) | Plant weight (g) | Seeds (no.) | Weight of seeds (g) |
| Rodney oats | Uninoculated | 8 | 8.7 a[y] | 54.2 a | 568.5 a | 15.5 a |
| | Isolate 7413 | 40 | 4.9 a | 25.6 a | 62.9 b | 5.0 b |
| | Isolate 7410 | 30 | 4.5 a | 23.6 a | 14.2 c | 0.5 c |
| | Both isolates[z] | 30 | 0 b | 2.1 b | 0 d | 0 d |
| Herta barley | Isolate 7413 | 28 | 36.8 a | 47.9 a | 505.5 a | 17.5 a |
| | Isolate 7410 | 30 | 4.7 b | 12.6 b | 32.3 b | 1.2 b |
| | Both isolates | 30 | 1.7 c | 7.8 c | 9.3 c | 0.3 c |

[y]Values with the same letter per column and per cereal are not significantly different from each other ($P = 0.05$) (Student's $t$-test).
[z]Inoculations were made simultaneously.

barley infected with isolate 7413 were mild on some plants and masked on others.

Symptoms on doubly inoculated plants were usually more severe than on the singly inoculated controls. Also, the mean values for plant weight, number of heads, number of seeds, and weight of seeds for doubly inoculated plants were all significantly lower than the values for the corresponding controls (Table 1). With

TABLE 2. The response of five cereals inoculated in a field plot with *R. maidis*-specific isolate 7413, or aphid-nonspecific isolate 7410, of barley yellow dwarf virus, or with both isolates

| Cereal | Cultivar or line | Treatment[x] | Mean symptom rating per plot[y] | Mean dry plant weight per plot (g) | 1,000-kernel weight (g) | Mean seed yield per plot (g) | Seed yield as % of uninoculated |
|---|---|---|---|---|---|---|---|
| Oat | Rodney | 0,-0 | 0.1 | 745 a[z] | 31.2 a | 271 a | 100 |
| | | 0,-A | 3.0 | 455 c | 25.6 b | 129 c | 48 |
| | | 0,-B | 1.2 | 576 b | 28.9 a | 180 b | 66 |
| | | A,-0 | 4.2 | 285 d | 30.2 a | 74 d | 27 |
| | | B,-0 | 4.2 | 334 d | 25.0 b | 69 d | 25 |
| | | A,-B | 4.3 | 256 d | 30.2 a | 56 de | 21 |
| | | B,-A | 4.5 | 255 d | 29.0 a | 34 ef | 13 |
| | | 0,-A+B | 3.6 | 505 bc | 25.0 b | 90 d | 33 |
| | | A+B,-0 | 4.9 | 160 e | 28.7 a | 17 f | 6 |
| | Hudson | 0,-0 | 0 | 902 a | 30.2 ab | 294 a | 100 |
| | | 0,-A | 2.2 | 690 b | 28.9 abc | 143 b | 49 |
| | | 0,-B | 2.4 | 566 c | 28.3 bc | 159 b | 54 |
| | | A,-0 | 4.2 | 456 cd | 31.0 a | 61 cd | 21 |
| | | B,-0 | 3.9 | 265 e | 26.6 cd | 65 cd | 22 |
| | | A,-B | 4.6 | 307 e | 28.2 bc | 31 de | 11 |
| | | B,-A | 4.2 | 272 e | 23.8 e | 57 cd | 19 |
| | | 0,-A+B | 3.3 | 432 d | 25.4 de | 95 c | 32 |
| | | A+B,-0 | 4.6 | 211 e | 26.6 cd | 19 de | 6 |
| | FF64-74 | 0,-0 | 0 | 639 a | 19.4 a | 243 abc | 100 |
| | | 0,-A | 0 | 602 a | 24.3 a | 235 abc | 97 |
| | | 0,-B | 0 | 627 a | 23.7 a | 221 bc | 91 |
| | | A,-0 | 0 | 672 a | 23.4 a | 287 a | 118 |
| | | B,-0 | 1.9 | 570 a | 23.0 a | 208 bc | 86 |
| | | A,-B | 0 | 626 a | 22.6 a | 248 ab | 102 |
| | | B,-A | 1.7 | 486 a | 23.0 a | 193 c | 79 |
| | | 0,-A+B | 0 | 566 a | 23.8 a | 213 bc | 88 |
| | | A+B,-0 | 2.7 | 566 a | 22.7 a | 205 bc | 84 |
| Barley | Bonanza | 0,-0 | 2.2 | 343 a | 33.2 a | 136 a | 100 |
| | | 0,-A | 2.8 | 310 a | 28.9 b | 106 ab | 78 |
| | | 0,-B | 3.3 | 338 a | 23.8 c | 70 bc | 51 |
| | | A,-0 | 3.3 | 351 a | 29.9 b | 127 a | 93 |
| | | B,-0 | 4.6 | 211 a | 25.6 c | 49 c | 36 |
| | | A,-B | 4.2 | 195 a | 24.7 c | 44 c | 32 |
| | | B,-A | 4.8 | 231 a | 19.9 d | 28 c | 21 |
| | | 0,-A+B | 4.4 | 218 a | 23.3 c | 44 c | 32 |
| | | A+B,-0 | 4.8 | 233 a | 23.2 c | 41 c | 30 |
| | Herta | 0,-0 | 0.3 | 383 b | 36.9 a | 134 b | 100 |
| | | 0,-A | 1.1 | 364 b | 34.8 a | 125 b | 93 |
| | | 0,-B | 3.1 | 156 d | 26.8 b | 38 d | 28 |
| | | A,-0 | 1.2 | 525 a | 37.3 a | 180 a | 134 |
| | | B,-0 | 3.7 | 127 d | 25.8 b | 11 d | 8 |
| | | A,-B | 2.1 | 315 bc | 29.2 b | 84 c | 63 |
| | | B,-A | 3.8 | 160 d | 25.3 b | 6 d | 4 |
| | | 0,-A+B | 3.5 | 195 cd | 26.6 b | 34 d | 25 |
| | | A+B,-0 | 3.8 | 133 d | 29.0 b | 16 d | 12 |

[x]Symbols: 0 = no inoculation; A = inoculation with isolate 7413 (*R. maidis*-specific); B = inoculation with isolate 7410 (aphid-nonspecific). Relevant singly inoculated controls for double inoculation A-B would be A,-0, and 0,-B, respectively, for example, while those for 0,-A+B, would be 0,-A and 0,-B. The first inoculation was made 27 days after seeding, and the second inoculation 12 days later.

[y]Symptoms were rated 21 days after the second inoculation, on a scale of 0-5 for increasing amounts of leaf discoloration.

[z]Values followed by the same letter are not significantly different from each other ($P = 0.05$) (Duncan's multiple-range test).

Rodney oats, five doubly inoculated plants died in the seedling stage and there was no seed yield from the remaining plants. Only one oat plant inoculated singly with isolate 7410 died and four other plants yielded no seed. After double inoculation of Herta barley, nine of 30 and 15 of 30 plants produced no heads and no seed, respectively. When inoculated singly with isolate 7410, two of 30 plants produced no heads and four plants produced no seed.

In the growth cabinet trials where initial inoculations of barley with one isolate were subsequently challenged by inoculation with the second isolate, no protection occurred between the isolates. In the transmission tests from doubly inoculated source plants, both aphid species transmitted virus from each of 21 plants. All of the 84 test plants infested with *R. padi* became infected and 74 of 80 test plants infested with *R. maidis* became infected. In transmission tests from the singly inoculated controls, *R. padi* transmitted virus from each of 22 plants inoculated with isolate 7410 to a total of 88 test plants that were infested, and *R. maidis* transmitted virus from each of 22 plants inoculated with isolate 7413, to a total of 83 of 88 test plants infested. None of 30 individuals each of *R. padi* and *R. maidis* placed directly on test plants from the aphid colonies transmitted virus. Results in a second trial were similar to those in the first trial. As with the greenhouse trials, virus transmitted from doubly inoculated plants by *R. maidis* was mild on Coast Black oats, and that transmitted by *R. padi* was severe.

**Field experiment.**—Aphids distributed in the early inoculation became scarce on the infested plants after a few days presumably because of rain and predators. Nevertheless, judged by symptoms, all plants appeared to have become infected. Mean symptom ratings of all doubly inoculated sub-plots except those of FF64-74 oats, were higher than on the relevant singly inoculated controls (Table 2). The small amount of leaf discoloration which occurred on noninoculated plants with three of the cereals was caused by senescence of the lower leaves. Natural infection with BYDV and the incidence of other diseases was not more than a trace.

According to the seed yield from singly inoculated plants (Table 2), Rodney and Hudson oats were sensitive to both isolates. The overall data showed that Hudson was slightly more sensitive than Rodney. Losses in both were higher with early inoculation than with late inoculation. They were equally sensitive to both isolates with early inoculation, but with the late inoculation, isolate 7413 was the more severe. Plants of FF64-74 oats showed a high degree of tolerance to both isolates, though yields were slightly lower with isolate 7410 than with isolate 7413. When inoculated early with isolate 7413, the yield of seed from this oat was 18% higher than the yield from uninoculated plants, but the difference was not significant. The severity of isolate 7413 on Rodney and Hudson oats contrasts with its mildness on Coast Black oats and on most barley lines tested. In another experiment, this isolate was also rather mild on 16 of 20 oat lines tested, but was very severe on O.A. 236 and Hudson oats (Comeau and Gill, *unpublished*).

Herta barley was highly sensitive to isolate 7410, but was tolerant to isolate 7413. Indeed, early inoculation with isolate 7413 resulted in 34% higher seed yield and 37% higher dry plant weight than noninoculated plants. Also, the 1,000-kernel weight was highest with this treatment. Bonanza barley also showed tolerance to isolate 7413 but was moderately sensitive to isolate 7410. With both cultivars, yields were higher when inoculated early with isolate 7413 than when inoculated late. The reverse was true with isolate 7410.

Double inoculation affected the seed yield of both Rodney and Hudson oats in a similar way (Table 2). Yield loss was highest when both inoculations were made early. Inoculations separated by a time interval caused a moderate loss, and those performed simultaneously and late had the least effect. All four double inoculations resulted in lower yields than either of their relevant singly inoculated controls. Differences between double and single inoculations were significant for three of the treatments with Rodney and for one for Hudson. With FF64-74 oats, yields in three of the four double inoculations were lower than the relevant controls, but the differences were not significant.

All four double inoculations of Bonanza resulted in yields lower than those of the controls, though differences again were not significant. With Herta, yields from two of the four double inoculations were lower than both relevant controls, whereas in the other two, yields were lower than only one of the controls. The most damaging double inoculation for FF64-74, Bonanza, and Herta was with isolate 7410 early and 7413 late.

Dry-plant weights of the doubly inoculated plots of all three oats were usually lower than the relevant controls (Table 2), and the differences were significant with Rodney for early inoculation with both isolates and for Hudson with isolate 7413 followed by 7410. Dry plant weights of doubly inoculated Herta were intermediate between those of the controls.

All eight inoculations of FF64-74 oats resulted in 1,000-kernel weights higher than those of uninoculated plants, though the differences were not significant (Table 2). Three of the double inoculations with Hudson oats and Bonanza barley resulted in 1,000-kernel weights that were lower than those of the singly inoculated controls. Differences were significant for two of the treatments with Hudson (isolate 7410 early and 7413 late; and both isolates late), and for one of the treatments with Bonanza (isolate 7410 early and 7413 late).

## DISCUSSION

Synergistic effects were clearly evident with Herta barley and Rodney oats when individual plants were inoculated with both isolates in the greenhouse trials. The effect of the virus was more severe in the greenhouse than in the field, probably because the plants were inoculated at the most susceptible growth stage in the greenhouse, although other factors may have contributed.

Symptom ratings in both greenhouse and field also pointed strongly to synergism except for the tolerant oat, FF64-74. When comparing seed yields in the field, synergism was most apparent on Rodney oats, in which differences between the yield from doubly inoculated plants and the yields from the two relevant controls were significant for three of the four double-inoculation treatments. Seed yields from doubly inoculated plants of Hudson and FF64-74 oats and Bonanza barley were also

lower than those of the relevant controls, except for one double inoculation of FF64-74 oats. Differences, however, were only significant for one of the double-inoculation treatments with Hudson. Results with two of the four double inoculations of Herta barley in which yields were higher than one of the two controls may have resulted from the increased seed yield induced by the early infection with the *R. maidis*-specific isolate. This stimulatory effect on seed yield may, therefore, have obscured possible synergistic effects. The increase in seed yield on barley induced by a *R. maidis*-specific isolate does not appear to have been reported before. The mechanism of this yield increase is obscure, but the significantly higher dry weight of the inoculated plants suggests that either additional fertile tillers or fertile heads per plant were produced. In a previous study, evidence was found for increases in the number of fertile heads per plant on Selkirk wheat when inoculated with a moderate or high inoculum dosage of either aphid-nonspecific isolate 6801 or *R. maidis*-specific isolate 7005 of BYDV (2).

In the field, the presence or absence of significant synergistic responses as judged by seed yield appeared to be associated with the relative severity of the two virus isolates on the cultivar. Thus, the response was evident with Rodney oats and to a lesser extent with Hudson where both isolates were severe. Evidence for the response was less clear or absent with Bonanza in which one isolate was mild and the other severe; with FF64-74, in which both isolates were very mild, and with Herta in which one isolate was very severe and the other was either very mild or induced an increase in yield.

The growth stage at which the cultivar is inoculated also may constitute an important factor in the results, as evidenced by the reactions of doubly inoculated Herta. Synergism occurred with inoculation at the seedling stage, but not with inoculation at later stages. The importance of this factor was previously demonstrated when mutual exclusion of three isolates of BYDV occurred in oats when inoculation was made at the one-leaf stage, but not when plants were inoculated at a more advanced stage (8).

The present work also has indicated that the *R. maidis*-specific isolate was mild on the two barley cultivars, and in a previous study (2), another *R. maidis*-specific isolate, 7005, also was mild on Herta barley when inoculated at the three-leaf stage. This evidence, coupled with observations in the field, seems to indicate that *R. maidis*-specific isolates may, in general, be mild on barley in Manitoba, and it would be interesting to know whether this stimulatory effect would occur also from an early infection with this BYDV variant on certain cultivars in commercial barley fields. Unexpectedly, yield losses were higher on Herta and Bonanza barley when inoculated late with isolate 7413 than when inoculated early. Jones and Catherall (9) found similar responses on tolerant barley when inoculated with an isolate transmitted by *M. avenae*.

The evidence for synergism obtained with the two isolates on Rodney and Herta in the greenhouse and on Rodney and to a more limited degree on Hudson in the field, coupled with the lack of cross-protection in the challenge experiments suggest that the *R. maidis*-specific and aphid-nonspecific isolates used in this work may not be closely related (10).

## LITERATURE CITED


1. AAPOLA, A. I. E., and W. F. ROCHOW. 1971. Relationships among three isolates of barley yellow dwarf virus. Virology 46:127-141.
2. BURNETT, P. A., and C. C. GILL. 1976. The response of cereals to increased dosage with barley yellow dwarf virus. Phytopathology 66:646-651.
3. COMEAU, A. 1976. Élevage en masse, cueillette et épandage sur le terrain des pucerons (Aphidae) vecteurs du virus du nanisme jaune de l'orge (BYDV). Can Entomol. 108:373-378.
4. GILL, C. C. 1969. Annual variation in strains of barley yellow dwarf virus in Manitoba, and the occurrence of greenbug-specific isolates. Can. J. Bot. 47:1277-1283.
5. GILL, C. C. 1970. Epidemiology of barley yellow dwarf in Manitoba and effect of the virus on yield of cereals. Phytopathology 60:1826-1830.
6. GILL, C. C. 1975. An epidemic of barley yellow dwarf in Manitoba and Saskatchewan in 1974. Plant Dis. Rep. 59:814-818.
7. HALSTEAD, B. E., and C. C. GILL. 1971. Effect of inoculation of oats with paired combinations of barley yellow dwarf virus isolates. Can. J. Bot. 49:577-581.
8. JEDLINSKI, H., and C. M. BROWN. 1965. Cross protection and mutual exclusion by three strains of barley yellow dwarf virus in Avena sativa L. Virology 26:613-621.
9. JONES, A. T., and P. L. CATHERALL. 1970. The effect of different virus isolates on the expression of tolerance to barley yellow dwarf virus in barley. Ann. Appl. Biol. 65:147-152.
10. KASSANIS, B. 1963. Interactions of viruses in plants. Adv. Virus Res. 10:219-255.
11. ROCHOW, W. F. 1959. Transmission of strains of barley yellow dwarf virus by two aphid species. Phytopathology 49:744-748.
12. ROCHOW, W. F., and I. MULLER. 1974. Mixed infections of barley yellow dwarf virus isolates in winter grains. Plant Dis. Rep. 58:472-475.
13. SMITH, H. C. 1963. Interaction between isolates of barley yellow dwarf virus. N. Z. J. Agric. Res. 6:343-353.
14. TOKO, H. V., and G. W. BRUEHL. 1959. Some host and vector relationships of strains of the barley yellow dwarf virus. Phytopathology 49:343-347.
15. WATSON, M. A., and T. E. MULLIGAN. 1960. Comparison of two barley yellow dwarf viruses in glasshouse and field experiments. Ann. Appl. Biol. 48:559-574.