# The Response of Cereals to Increased Dosage with Barley Yellow Dwarf Virus

P. A. Burnett and C. C. Gill

Former Graduate Student, and Research Scientist, respectively, Department of Entomology, University of Manitoba, and Agriculture Canada Research Station, 25 Dafoe Rd., Winnipeg, Manitoba. Senior author's present address is Crop Research Division, DSIR, Private Bag, Christchurch, New Zealand.

The senior author thanks W. C. McDonald, Director of the Research Station, Winnipeg, for providing space and facilities, and P. H. Westdal and R. J. Baker for help and encouragement in this work.

Portion of a Ph.D. thesis submitted by the senior author to the University of Manitoba.

This study was supported in part by Agriculture Canada Grant No. 1003.

Contribution No. 630, Agriculture Canada Research Station, Winnipeg.

Accepted for publication 24 October 1975.

## ABSTRACT

BURNETT, P. A., and C. C. GILL. 1976. The response of cereals to increased dosage with barley yellow dwarf virus. Phytopathology 66: 646-651.

Herta barley, Rodney oats, and Selkirk wheat, were infested at the three-leaf stage for 2 days with 1, 20, or 100 individuals of *Rhopalosiphum padi* or *R. maidis* carrying, respectively, nonspecific barley yellow dwarf virus (BYDV) isolate 6801, and *R. maidis*-specific BYDV isolate 7005. Yield reductions were large and significant for the oats infected with either isolate and for the barley infected with isolate 6801, moderate for the barley infected with isolate 7005, and small for the wheat infected with either isolate. With increased numbers of aphids per plant, more plants became infected, the incubation period decreased progressively, and symptoms were more severe. Seed yield decreased progressively with increased numbers of aphids where yield reductions were large. Similar dosage-responses occurred in several other yield components such as number of seeds, mean seed weight, number of fertile heads, and length of the main culm and of its head. For barley infected with isolate 7005, and wheat infected with either virus isolate, trends in seed yield per plant with increased numbers of aphids were either small or absent, although for the wheat decreasing trends were observed in most of the variables measured on the main culm. The number of fertile heads on wheat increased progressively with larger numbers of aphids. Feeding by 1, 20, or 100 individuals of virus-free *R. padi* or *R. maidis* for 2 days caused no yield reductions.

*Additional key words*: *Hordeum distichum* L., *Avena sativa* L., *Triticum aestivum* L.

Inoculation of plants with a high concentration of virus usually results in more severe symptoms and a higher concentration of virus in the inoculated plants than in plants inoculated with a low concentration of virus (2, 14). Little, however, appears to have been published on the relationship between inoculum concentration and crop yield, particularly for viruses transmitted by insect vectors. Smith and Richards (12) found that symptoms on oats were more severe when an isolate of barley yellow dwarf virus (BYDV) was transmitted by the aphid vector *Rhopalosiphum padi* (Linnaeus) than by the less efficient vector *R. fitchii* (Sanderson). They proposed that this difference resulted from a difference in the amount of virus injected into the oats. This "dosage response" hypothesis was extended by Smith (10) and Smith et al. (11) to explain the increased losses that resulted from BYDV when cereals were infested with increased populations of viruliferous aphids. Jones and Catherall (7) also reported that the degree of stunting of barley from BYDV increased with larger numbers of viruliferous aphids per plant.

The present work with BYDV was designed to test the dosage response hypothesis more rigorously by measuring the seed yield and other responses of barley, oats, and wheat infested with different numbers of viruliferous aphids. Both a nonspecific isolate of BYDV and one specific for *R. maidis* (Fitch) were used because isolates of the nonspecific type have caused severe damage to barley and oats in Manitoba (5, 8) and isolates of the *R. maidis*-specific type are common in some years on barley in Manitoba (5).

## MATERIALS AND METHODS

Virus-free colonies of the cherry oat aphid, *R. padi*, and the corn leaf aphid, *R. maidis,* were each started from an original aphid collected in southern Manitoba in 1964, and maintained on caged barley, *Hordeum vulgare* L. 'Parkland.' These colonies were periodically restarted from a single unfed instar, and individuals of the colonies were regularly tested on oats as a precaution against virus contamination.

A nonspecific isolate of BYDV [isolate 6801 (6)] and an isolate specific for *R. maidis* (isolate 7005) obtained in 1968 and 1970, respectively, from southern Manitoba, were maintained on oats, *Avena byzantina* K. Koch 'Coast Black.' Results of previously described (3) characterization tests showed that the percentage of individual aphids that transmitted isolate 7005 from oats to oats was 67, 6, 0, and 0% for *R. maidis, Schizaphis graminum* (Rondani), *R. padi,* and *Macrosiphum avenae* (Fabricius), respectively, (Gill, *unpublished*). These values were averages for a total of 18 individuals of each aphid species tested in three trials. Viruliferous colonies

TABLE 1. Mean responses[a] per plant of three cereal cultivars to infestation with different numbers of virus-free *Rhopalosiphum padi*, or *R. padi* carrying barley yellow dwarf virus isolate 6801

| | Herta barley | | | | Rodney oats | | | | Selkirk wheat | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Treatment | Fertile heads (no.) | Seeds (no.) | 1,000-kernel weight[b] (g) | Seed yield (g) | Fertile heads (no.) | Seeds (no.) | 1,000-kernel weight (g) | Seed yield (g) | Fertile heads (no.) | Seeds (no.) | 1,000-kernel weight (g) | Seed yield (g) |
| Control (no aphids) | 5.6 | 88.2 | 37.1 | 3.28 | 3.5 | 124.5 | 33.9 | 4.19 | 4.2 | 77.8 | 35.1 | 2.74 |
| Nonviruliferous aphids | | | | | | | | | | | | |
| 1 | 5.1 | 84.5 | 37.3 | 3.14 | 3.2 | 121.6 | 31.4* | 3.82 | 4.1 | 79.7 | 36.2 | 2.88 |
| 20 | 5.1 | 87.8 | 35.7 | 3.14 | 3.4 | 119.3 | 30.9** | 3.69 | 4.3 | 81.0 | 35.6 | 2.87 |
| 100 | 5.3 | 81.2 | 36.7 | 2.96 | 3.2 | 114.7 | 33.3 | 3.83 | 4.2 | 78.6 | 35.5 | 2.76 |
| Viruliferous aphids | | | | | | | | | | | | |
| 1 | 3.0**A[c] | 34.4**A | 33.3 A | 1.26**A | 2.1**A | 16.1**A | 36.5* A | 0.58**A | 4.6 A | 75.8 A | 30.7* A | 2.30 A |
| 20 | 3.8* A | 28.3**A | 32.0 A | 0.88**A | 2.6**B | 13.9**AB | 33.7 B | 0.46**AB | 5.2* AB | 76.7 A | 28.8**A | 2.19**A |
| 100 | 1.4**B | 7.6**B | 16.2**B | 0.16**B | 2.3**AB | 11.1**B | 35.3 AB | 0.39**B | 5.7**B | 76.7 A | 30.1**A | 2.28* A |

[a]Infected plants that produced no seed were excluded when calculating the mean values for the number and weight of seeds per plant.

[b]Calculated only for plants that yielded 10 or more seeds.

[c]Asterisks * and ** indicate values significantly different from the "no aphids" treatment at $P = 0.05$ and 0.01, respectively. Values within a column with the same letter behind them are not significantly different from each other ($P = 0.05$).

TABLE 2. Mean responses[a] per plant of three cereal cultivars to infestation with different numbers of virus-free *Rhopalosiphum maidis*, or *R. maidis* carrying barley yellow dwarf virus isolate 7005

| Treatment | Herta barley | | | | Rodney oats | | | | Selkirk wheat | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Fertile heads (no.) | Seeds (no.) | 1,000-kernel weight[b] (g) | Seed yield (g) | Fertile heads (no.) | Seeds (no.) | 1,000-kernel weight (g) | Seed yield (g) | Fertile heads (no.) | Seeds (no.) | 1,000-kernel weight (g) | Seed yield (g) |
| Control (no aphids) | 6.3 | 78.5 | 37.9 | 3.02 | 2.7 | 77.9 | 35.5 | 2.75 | 2.9 | 53.4 | 35.0 | 1.85 |
| Nonviruliferous aphids | | | | | | | | | | | | |
| 1 | 5.8 | 71.7 | 37.7 | 2.73 | 2.8 | 87.0 | 35.1 | 3.06 | 2.9 | 55.0 | 34.8 | 1.89 |
| 20 | 5.5 | 71.0 | 36.8 | 2.72 | 2.7 | 81.6 | 34.3 | 2.81 | 2.7 | 52.8 | 33.7 | 1.75 |
| 100 | 6.5 | 87.0 | 37.2 | 3.30 | 2.9 | 82.0 | 34.3 | 2.79 | 2.5* | 50.9 | 35.8 | 1.80 |
| Viruliferous aphids | | | | | | | | | | | | |
| 1 | 5.0*A[c] | 57.1*A | 38.4 A | 2.23 A | 1.5**A | 35.3**A | 41.8 AB | 1.37**A | 2.8 A | 49.6 A | 36.2 A | 1.80 A |
| 20 | 6.3 A | 72.1 A | 35.8 A | 2.60 A | 1.9**A | 27.9**B | 39.7**A | 1.10**B | 3.6**A | 52.7 A | 30.7**A | 1.64 A |
| 100 | 6.0 A | 68.4 A | 35.3*A | 2.40 A | 1.4**A | 23.2**BC | 34.0 B | 0.80**C | 3.4* A | 47.7 A | 32.0* A | 1.51**A |

[a]Infected plants that produced no seed were excluded when calculating the mean values for the number and weight of seeds per plant.
[b]Calculated only for plants that yielded 10 or more seeds.
[c]Asterisks * and ** indicate values significantly different from the "no aphids" treatment at $P = 0.05$ and 0.01, respectively. Values within a column followed by the same letter are not significantly different ($P = 0.05$).

TABLE 3. Percentage of cereals that became infected after infestation[a] with different numbers of aphids carrying barley yellow dwarf virus isolate 6801 or 7005[b] and percentage of the infected plants that produced no seed

| Aphids per plant | Herta barley | | | | Rodney oats | | | | Selkirk wheat | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 6801 | | 7005 | | 6801 | | 7005 | | 6801 | | 7005 | |
| | inf.[c] | ster.[d] | inf. | ster. | inf. | ster. | inf. | ster. | inf. | ster. | inf. | ster. |
| 1 | 16 | 19 | 7 | 0 | 73 | 3 | 19 | 0 | 19 | 0 | 5 | 0 |
| 20 | 45 | 50 | 70 | 0 | 100 | 0 | 90 | 0 | 87 | 0 | 78 | 0 |
| 100 | 92 | 62 | 83 | 0 | 100 | 0 | 83 | 0 | 92 | 3 | 93 | 0 |

[a]For each cereal and isolate 100 plants were infested with one aphid and 40 plants each with 20 and 100 aphids.
[b]*Rhopalosiphum padi* was the vector for isolate 6801 and *R. maidis* for isolate 7005.
[c]Percentage of plants proved infected out of total infested with viruliferous aphids.
[d]Percentage of infected plants that produced no seed.

were obtained by allowing the respective aphids, *R. padi* for isolate 6801, and *R. maidis* for isolate 7005, a 2-day acquisition feed on the infected oats, and then transferring about 50 of these aphids to the respective virus-free aphid colonies 2 weeks after the colonies were started. One week later these colonies were used as a source of viruliferous aphids. At the time of use, five 10-aphid groups from each colony were tested on Coast Black oats to determine whether the aphids were viruliferous or virus-free as desired.

Barley (*H. distichum* L. 'Herta'), oats (*A. sativa* L. 'Rodney'), and wheat (*Triticum aestivum* L. 'Selkirk') when tested for their response to BYDV were grown one plant per 12.7 cm diameter pot in a greenhouse at 20 ± 2 C with supplemental cool-white fluorescent lighting for 16 hours per day. At the three-leaf stage (23 days after seeding), 1, 20, or 100 viruliferous or virus-free aphids were caged on individual plants. Some plants also were caged without aphids. Forty plants were used for each treatment except for treatments with one viruliferous aphid in which 100 plants were used to compensate for the expected low percentage of infected plants. Treatments were randomized. After a 2-day feeding period, all plants were sprayed with tetraethylpyrophosphate (TEPP) insecticide and then twice weekly thereafter to control stray aphids.

Just before leaf senescence, inoculated plants were tested to determine whether they were infected. One end of a portion of a leaf detached from the plant was inserted in moist sand in a petri dish and the leaf was infested with virus-free aphids of the requisite species. After 2 days at 15 C the aphids were removed and caged on Coast Black oat test seedlings for a 3-day inoculation feed. After elimination of the aphids by spraying with TEPP, the oat test plants were observed for BYDV symptoms for 4 weeks.

The responses of the barley, oats, and wheat to the different treatments were determined at maturity by determining the following variables: 1,000-kernel weight (for all heads that produced 10 or more seeds), the number and weight of seeds, and the number of fertile tillers per plant; the number and weight of seeds from the main culm, and the lengths of the main culm and its head. Values for the main culm were excluded from the results, and only general trends are reported here. Infected plants or main culms that produced no seed were excluded when calculating the mean values for the number and weight of seeds per plant or per main culm. Tests of statistical significance were carried out according to Steel and Torrie (13).

## RESULTS

**Effect of aphid feeding.**—There were no pronounced differences in the responses between plants without aphids (referred to as "control" plants) and plants infested with 1, 20, or 100 virus-free aphids (Tables 1 and 2). Only three of the 72 values were significantly different from those of the controls. Two of these exceptions were values for the 1,000-kernel weight of oats infested with 1 or 20 virus-free *R. padi* (Table 1). These values were both less than the value for the control. The third exception was the number of fertile heads on Selkirk wheat infested with 100 virus-free *R. maidis* (Table 2); in that treatment group there appeared to be a trend to fewer tillers with increased numbers of aphids. In the subsequent sections of this report the responses of infected plants are compared with those of the control plants.

**Susceptibility of the cereals to infection.**—More plants were infected when larger numbers of viruliferous aphids were placed on them (Table 3). The incubation period decreased progressively and symptoms were more severe with increased numbers of viruliferous aphids.

**Responses to infection with isolate 6801.**—*Barley.*—A striking response with Herta barley and isolate 6801, which was largely absent from the other cereal-virus combinations, was the high percentage of infected plants that produced no seed. This percentage increased with increased numbers of viruliferous aphids per plant (Table 3).

Seed yield, number of seeds, and number of fertile heads per infected plant (Table 1) were each significantly less than the controls. These values, except for the number of fertile heads, also decreased with an increase in the number of viruliferous aphids. Nevertheless, for all three variables, differences between values for one and 100, and between 20 and 100 viruliferous aphids were significant, indicating a dosage response. If the plants that produced no seed had been included in the results, the differences, and hence the dosage response, between individual values for the three treatments with viruliferous aphids would have been larger. With seed yield, for instance, values for 20 and 100 viruliferous aphids were, respectively, 30 and 87% less than those for one viruliferous aphid when seedless plants were excluded, but were 60 and 95% less when seedless plants were included.

Although 1,000-kernel weights for infected plants were significantly lower than the control only when infested with 100 viruliferous aphids, 1,000-kernel weight decreased progressively with increased numbers of viruliferous aphids. Also, there was a significant dosage response between the values for 1 and 100, and between 20 and 100 viruliferous aphids (Table 1).

The differences between treatments for the number of seeds, 1,000-kernel weight, and seed yield from the main culm strongly supported the evidence for the dosage response effects found for the whole plant. Also, the length of the main culm and of its head were significantly shorter in the treatments that had received viruliferous aphids than those from the control treatment (except for head length of plants infested with one viruliferous aphid). These lengths also decreased with increased numbers of viruliferous aphids, though differences between treatments with increasing numbers of viruliferous aphids were not significant.

*Oats.*—The number of fertile heads, number of seeds, and seed yield for plants infested with 1, 20, or 100 viruliferous aphids were significantly lower than for the control plants (Table 1). Also, the number of seeds and the seed yield were progressively less from treatments with larger numbers of viruliferous aphids, though differences were significant only between treatments with 1 and 100 viruliferous aphids. The 1,000-kernel weight of seed from infected plants was the same or higher than that of the controls, and, like the number of fertile tillers, was unaffected by differences in numbers of aphids.

A dosage-response effect, similar to that found for the number of seeds and the seed yield for the whole plant, was also found in the main culm. Also, head length and height of the main culm were significantly less than those of the controls, but only head length decreased progressively with increasing aphid numbers.

*Wheat*.—There were two main differences between the responses of wheat and those of barley and oats. First, losses of the wheat were low. Second, instead of fewer fertile heads per plant, wheat responded with an increased number of heads, and the increase became progressively larger with larger numbers of aphids (Table 1). This increase was significant between treatments with 1 and 20 viruliferous aphids.

The seed yield, number of seeds per plant, and the 1,000-kernel weight for each treatment with viruliferous aphids were uniformly smaller than the controls. This reduction was least for the number of seeds (Table 1). There was a decrease in seed yield, number of seeds, culm height, and the length of the head of the main culm with increasing numbers of viruliferous aphids. The difference in head length between the treatments with 1 and 20 viruliferous aphids was significant.

**Responses to infection with isolate 7005**.—The responses of the cereals to isolate 7005 were milder than with isolate 6801, the difference being largest with barley and smallest with wheat.

*Barley*.—With barley and isolate 7005, few of the treatments with viruliferous aphids resulted in significantly lower values than those for controls, but seed yield losses per plant, for example, were appreciable and ranged from 14 to 26% (Table 2). There was a tendency for decreased weights with increased numbers of viruliferous aphids for 1,000-kernel weight per plant (Table 2) and per main culm, but no trends between these aphid treatments were apparent for the other variables.

*Oats*.—Values for infected plants in all variables except 1,000-kernel weight were significantly below those of the controls (Table 2). Also, seed yield and number of seeds per plant decreased progressively for treatments with larger numbers of viruliferous aphids. The difference in seed yield was significant between treatments with 1 and 20, and 20 and 100 viruliferous aphids. The number of seeds differed significantly between treatments with 1 and 20, and 1 and 100 viruliferous aphids. Both variables illustrate the dosage effect. There was no trend in the number of fertile heads with different numbers of viruliferous aphids. Kernel weights (1,000-kernel weights) per plant (Table 2) and per main culm were lower with larger numbers of aphids.

Number of seeds and seed yield for the main culm were similar to those for the whole plant. The length of the main culm and of the head, and values obtained for treatments with 20 and with 100 viruliferous aphids were significantly less than those for the controls. Differences were significant between treatments of 1 and 100, and 20 and 100 viruliferous aphids for head length.

*Wheat*.—The effect of isolates 7005 and 6801 were similar. Seed yield per plant (Tables 1 and 2), decreased with larger numbers of viruliferous aphids, the value for the treatment with 100 viruliferous aphids being significantly less than the value for the controls. The same response was obtained from the main culm, except that the seed yield obtained from treatments with 20 or 100 viruliferous aphids were both significantly lower than the control. The numbers of fertile heads per plant for treatments with 20 and 100 viruliferous aphids were significantly larger than the controls. The number of seeds per plant was scarcely altered, but there was a significant reduction for treatments with 20 and 100 viruliferous aphids in the number of seeds per main culm. The main culm and its head were progressively shorter with increased numbers of viruliferous aphids, values for treatments with 20 and 100 viruliferous aphids being significantly less than those for the controls. Although trends were obvious in the values of some of the variables (Tables 1 and 2) with increasing numbers of aphids, none of the differences between the aphid treatments was significant.

## DISCUSSION

Disease severity as judged by total seed yield usually increased with increased dosage of the inoculum. An exception with Selkirk wheat and isolate 6801 appeared to result from a stimulation by the virus of the number of fertile tillers. This is also a form of dosage-response, since the number of tillers increased with increasing numbers of aphids, and this effect partially compensated for a reduction in other yield components, notably 1,000-kernel weight. Therefore, the increased tillering could be considered as a form of resistance to the virus by this cultivar. No reason for the second exception with Herta barley and isolate 7005 was apparent. Isolate 7005 was mild on barley both in the greenhouse trial and in a field trial (1). Also symptoms were mild or masked in barley naturally infected with *R. maidis*-specific isolates (5), and the concentration of an *R. maidis*-specific isolate in infected barley was low (9). The factor involved in the apparent mildness of this type of isolate in barley may also regulate the lack of response to increased inoculum concentration. Nevertheless, if with Herta barley and isolate 7005, individual yield components were considered, a dosage-response was discernible in the decrease of kernel weight, both per plant and per main culm. Results of the limited number of virus-host combinations examined in the greenhouse, therefore, confirm the dosage-response hypothesis (10, 12) for severity of symptoms and incubation period, but with seed yield, exceptions occurred depending on the virus-host combination. Field trials with Selkirk wheat and Rodney oats and an isolate of BYDV specific for *Macrosiphum avenae* also showed that seed yield reductions were greater with 100 viruliferous aphids per plant than with ten (1).

Evidence that maximum virus levels in a systemically infected plant are reached more rapidly with high than with low inoculum dosages was found with alfalfa mosaic virus in tobacco (14) and with BYDV in oats (4). In the former case the maximum virus concentration in the plant was also higher with increased dosage of inoculum. These effects could result in earlier and more severe damage to tissues, which in turn could cause greater seed loss.

The contribution of the yield components to the total seed yield of the cereals infected with BYDV varied according to the host, and sometimes also to the virus isolate. Thus, with the oats, both viruses caused a reduction in the number of fertile heads and the number of seeds per plant, but the average weight per seed was constant. With the barley and isolate 6801 the number of seeds, the average weight per seed, and the number of fertile heads were all reduced, but with isolate 7005 the number of fertile heads remained constant. With the wheat the average weight per seed was reduced, the number of fertile tillers was increased, while the number of seeds remained constant.

The effect of virus dosage on yield has a number of implications. Crops infested with large populations of viruliferous aphids could suffer severely, not only because more plants become infected, but also because of the larger number of viruliferous aphids per plant. In breeding programs aimed at developing resistant cultivars, inoculum levels should be matched with those found in the field. Thus, as with BYDV in New Zealand, although small aphid populations may be adequate for inoculation at an early growth stage, larger populations may be required for testing at a later stage (10). The same principles would also hold true when attempting to estimate yield losses by artificial inoculation of plants with virus in test plots.

## LITERATURE CITED


1. BURNETT, P. A., I. ALLEN, and A. G. ROBINSON. 1974. Some effects of barley yellow dwarf virus on cereals infested with different numbers of viruliferous aphids. Can. J. Plant. Sci. 55:621-623.
2. FRANCKI, R. I. B. 1972. Purification of viruses. Pages 295-335 *in* C. I. Kado, and H. O. Agrawal, eds. Principles and techniques in plant virology. Van Nostrand-Reinhold Company, New York.
3. GILL, C. C. 1967. Transmission of barley yellow dwarf virus isolates from Manitoba by five species of aphids. Phytopathology 57:713-718.
4. GILL, C. C. 1969. Cyclical transmissibility of barley yellow dwarf virus from oats with increasing age of infection. Phytopathology 59:23-28.
5. GILL, C. C. 1970. Epidemiology of barley yellow dwarf in Manitoba and effect of the virus on yield on cereals. Phytopathology 60:1826-1830.
6. 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.
7. JONES, A. T., and P. L. CATHERALL. 1970. The relationship between growth rate and the expression of tolerance to barley yellow dwarf virus in barley. Ann. Appl. Biol. 65: 137-145.
8. MARTENS, J. W., and W. C. MC DONALD. 1970. Assessment of yield losses from barley yellow dwarf in oats. Can. Plant Dis. Survey. 50:88-89.
9. ROCHOW, W. F., A. I. E. AAPOLA, M. K. BRAKKE, and L. E. CARMICHAEL. 1971. Purification and antigenicity of three isolates of barley yellow dwarf virus. Virology 46:117-126.
10. SMITH, H. C. 1967. The effect of aphid numbers and stage of plant growth in determining tolerance to barley yellow dwarf virus in cereals. N. Z. J. Agric. Res. 10:445-466.
11. SMITH, H. C., R. W. HART, L. C. HURNDELL, and M. SMITH. 1968. Transmission of barley yellow dwarf virus (BYDV) in cereals by two aphid species, Rhopalosiphum padi (L.) and Macrosiphum miscanthi (Tak.). N. Z. J. Agric. Res. 11:500-505.
12. SMITH, H. C., and W. R. RICHARDS. 1963. A comparison of Rhopalosiphum padi (L.) and R. fitchii (Sand.) as vectors of barley yellow dwarf virus. Can. Entomol. 95:537-547.
13. STEEL, R. G. C., and J. H. TORRIE. 1960. Principles and procedures of statistics: with special reference to the biological sciences. McGraw-Hill, New York, 481 p.
14. VERHOYEN, M. 1966. Effect of the concentration of inoculum on the multiplication and in vivo inactivation of alfalfa mosaic virus. Pages 22-27 *in* A. B. R. Beemster, and J. Dijkstra, ed. Viruses of plants. North-Holland, Amsterdam, The Netherlands. 342 p.