THE UNIVERSITY OF MANITOBA

RESPONSES OF CEREALS TO BARLEY YELLOW DWARF VIRUS INFECTION INITIATED BY DIFFERENT NUMBERS OF VIRULIFEROUS APHIDS AND TO FEEDING BY NONVIRULIFEROUS APHIDS

by

Peter Alexander Burnett

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ENTOMOLOGY

WINNIPEG, MANITOBA

October 1974

RESPONSES OF CEREALS TO BARLEY YELLOW DWARF VIRUS INFECTION INITIATED BY DIFFERENT NUMBERS OF VIRULIFEROUS APHIDS AND TO FEEDING BY NONVIRULIFEROUS APHIDS

by

Peter Alexander Burnett

A dissertation submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

ABSTRACT

BY

Peter Alexander Burnett

RESPONSES OF CEREALS TO BARLEY YELLOW DWARF VIRUS INFECTION INITIATED BY DIFFERENT NUMBERS OF VIRULIFEROUS APHIDS AND TO FEEDING BY NONVIRULIFEROUS APHIDS

A study was made in the field and greenhouse of some responses of barley, oats and wheat to feeding by aphids, or infection by barley yellow dwarf virus (BYDV). The effect of dosage of BYDV, in the context of initiation of infection by different numbers of viruliferous aphids, was also examined.

In the field, yield of barley, oats and wheat was not affected by the feeding of nonviruliferous aphids, but yield reductions were associated with plots artificially infested with viruliferous aphids. Generally, losses increased when numbers of viruliferous aphids used to initiate infections were increased. In these experiments, only gross differences in plant response were detected because of limitations in experimental design, namely, the limited number of replicates. In experiments with small field plots where the coefficient of variation may be high, a large number of replicates are required. It is, therefore, essential to establish in advance the size of treatment differences to be detected so that the experiment may be designed accordingly.

In the greenhouse experiments, as in the field, plants were not affected, for any of the responses measured, by the feeding of non-viruliferous aphids, but marked adverse effects were observed for plants infected with BYDV. The effect of dosage was pronounced for most of the responses observed. In general, as the number of viruliferous aphids used to initiate infection was increased, plant height, head length and yield were decreased. There were some differences, among the cereals, in the response of some of the components of yield. In barley, number of fertile heads, number of seeds and kernel weight were all reduced. In oats, number of fertile heads and number of seeds were reduced, but kernel weight remained relatively constant. In wheat, number of fertile heads were increased and number of seeds remained constant, but kernel weight was reduced.

The results from the field and greenhouse studies supported a hypothesis of dosage effect that BYDV infections increase in severity when initiated by increased numbers of aphids.

ACKNOWLEDGEMENTS

This study was undertaken at the suggestion of Dr. A. G. Robinson of the Department of Entomology, University of Manitoba, Winnipeg, Manitoba. Grateful appreciation is extended to Dr. Robinson for his guidance and understanding while I was engaged on this project. Also sincere thanks are offered to Dr. P. H. Westdal and Dr. C. C. Gill of the Agriculture Canada, Research Station, Winnipeg, Manitoba for advice on and constructive criticism of my research work and writing. Dr. R. J. Baker also of the Agriculture Canada, Research Station, Winnipeg, Manitoba, is thanked for his invaluable assistance with the design of the experiments and analysis of the results.

I wish to thank Dr. W. C. McDonald, Director of the Agriculture Canada, Research Station, Winnipeg, Manitoba, for making available greenhouse space and facilities. Also Mr. Jerry Cox and all the other technicians too numerous to mention for all the help and laughter they gave me while I engaged on this study.

I wish also to express my gratitude to the Crop Research Division of the Department of Scientific and Industrial Research of New Zealand for awarding me a three year study leave.

Grateful acknowledgement is made of the financial assistance supplied by an Agriculture Canada operating grant awarded to Dr. Robinson.

I wish to thank Mrs. D. Romaniuk for her very capable typing of the manuscript.

Finally, I wish to thank my wife, Alison, for her love and understanding while I finished this study.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF APPENDICES

CHAPTER I

INTRODUCTION

Barley yellow dwarf (BYD) is a disease of cereals and grasses that is caused by a virus. The disease was discovered in California in 1951 and given the descriptive name of barley yellow dwarf; the causal agent was known as the barley yellow dwarf virus (BYDV), (Oswald and Houston, 1951). Oswald and Houston found that BYDV could not be mechanically transmitted to plants, that it was a yellow's type of disease, and that the virus had a circulative relationship with its aphid vector. Later, more detailed accounts of the disease were given by the same authors (1953a and 1953b).

By the late 1950's BYD was recognized as a disease of major importance in many areas of the world. In 1959, BYD was the most serious single disease of oats (Avena sativa L.) in the United States. In fact, a special supplement (No. 262) of the Plant Disease Reporter was published in that year on the disease.

BYDV has been reported to cause severe yield loss in cereals and to reduce severely the vegetative production of pasture species of grasses. Barley (Hordeum vulgare L.) and oats are the cereal crops that are most severely affected by BYDV. Although wheat [Triticum aestivum L. em Thell (Aestivum group)] and rye (Secale cereale L.) are also susceptible to this virus, they usually develop symptoms less readily than do barley and oats.

It has been observed in artificial infections that if the number of viruliferous aphids used to initiate an infection of BYDV was

increased then the severity of the resulting infection was greater. This applies both to the infection of field plots and of individual plants. With the infection of field plots it was usually the percentage of plants infected that was increased (Catherall, 1966b). When individual plants were infected it was thought that multiple infections may have led to a higher initial presence of virus and this may have caused more severe symptoms. This hypothesis was originally proposed by Smith and Richards (1963). At this time, the 'dosage' concept, as it was called was put forward to explain the difference in symptoms observed when different aphid vectors were used to transmit the same virus strain. Smith and Richards (1963) suggested that different vectors transmittted different doses of virus. Smith (1967) and Smith et al., (1968) gave further proof of the dosage hypothesis by showing that the severity of the BYDV infection increased as the number of viruliferous aphids used to initiate the infection increased. This increase in severity was expressed as a shorter incubation period to symptom development, more pronounced symptoms and a reduction in yield.

Purpose of this study

The purpose of this study was threefold. Firstly, to determine the yield losses that are associated with aphids in the field in Manitoba, either when they act as vectors of BYDV or when they do direct physical damage by feeding on the developing plant or grain. Secondly, to look at the relationship between different numbers of viruliferous aphids (BYDV), feeding on seedling plants, and some responses of these plants in the greenhouse. Thirdly, to examine the variability of yield loss

due to BYDV, in Selkirk wheat, in the greenhouse and to determine whether the measured loss had a genetic basis or was a function of the environment.

Definition of terms used

The terminology in this thesis is in general accord with that proposed by the Terminology Committee of the Canadian Phytopathological Society (Welsh,1961). However, it is felt that a definition of the following terms as defined by the terminology committee and/or as used in this thesis may be of assistance to the reader.

Virus isolate: "virus that is transferred in a successful inoculation from a diseased plant or in procedures designed to separate viruses or virus strains." All the virus isolates used in this study were obtained from C. C. Gill of Agriculture Canada, Research Station, Winnipeg, Manitoba. The numbering system is that of Dr. Gill's and refers to the year and sequence of collection, e.g. 6407 - refers to the seventh isolate collected in 1964.

Species-specific isolate: In this thesis the term refers to a virus isolate that is generally only transmitted by one species of aphid.

Species-nonspecific isolate: In this thesis the term refers to a virus isolate that may be transmitted by a number of species of aphids.

Viruliferous: "the condition of a vector having virus in those anatomical areas that render the vector potentially able to transmit that virus". In this thesis the term is used for aphids that have been given access to a virus.

Nonviruliferous: In this thesis the term refers to aphids that have never had access to virus.

Acquisition feed: "the feeding of a test vector on a virus source".

Inoculation feeding time: In this thesis the term refers to the time the vector is given access to a healthy plant.

Dosage concept: the severity of BYDV infection depends on the amount or dose of virus injected into the plant.

CHAPTER II

LITERATURE REVIEW

Although BYDV was not recognized as a virus disease until 1951 (Oswald and Houston, 1951) several workers had noted, much earlier, a disorder of plants that is now considered to have been BYDV. Possibly the earliest record of the disease in the United States was the observations of Galloway and Southwood (1890) in a paper entitled "Preliminary notes on a new and destructive oat disease." Manns, 1909 (Bruehl, 1961), in his review of red leaf of oats, said that he believed that red leaf was due to a simultaneous infection of the plant by two bacteria in a symbiotic relationship, and that this infection was aided by cool, moist weather. Thorne, 1907 and Grossard, 1907 (Bruehl, 1961), both in Ohio, noted that a large number of aphids and thrips were associated with oat crops that had these symptoms, but whether or not these insects had anything to do with the disease was unknown. These observations led Manns (Bruehl, 1961) to take English grain aphids, Macrosiphum (Sitobion) avenae (Fabricus), from diseased plants and cage them on healthy seedlings. He found that after 10-12 days, the oat plants inside the cage were showing symptoms of the disease while those outside were disease-free. He concluded that the aphid was acting as a vector of bacteria.

Barrus (1937) described a red leaf disease of oats that was prevalent and long known in New York State. The symptoms described were very similar to those described by Oswald and Houston (1951). Reports of similar types of symptoms in cereals were given by McKinney

(1950) and Johnston (1951). Moore (1952) reported aphid transmission of red leaf of oats, but Bantarri* (pers. com.) said that it was much earlier that Moore recognized the disease as one of virus etiology and also knew that it was transmitted by aphids but failed to make a formal report.

With one exception, the only known vectors of BYDV are aphids. Timian (1964) reported that BYDV was transmitted by dodder. Comprehensive lists of the aphid vectors of BYDV have been given by Bruehl (1961); Rochow (1961c); Kennedy et al., (1962) and Slykhuis (1967).

Aphid vectors may carry specific, semi-specific or non-specific strains or isolates of BYDV. Kennedy et al., (1962) refer to barley yellow dwarf virus as a group of viruses, to quote, "a group of viruses differing widely in transmissibility by the vectors listed."

Strains of BYDV have been recognized for over 16 years (Allen, 1957; Bruehl and Toko, 1957; Rochow, 1959a, b, 1961a, b; Takeshita, 1956; Toko and Bruehl, 1959; Watson and Mulligan,1960a, b). Gill (1967a) described four variants of BYDV from Manitoba and made mention of a fifth. Rochow (1969a, b) listed the same four variants as being the main ones found in New York. Gill (1969b) recorded a definite fifth variant in Manitoba and Rochow and Muller (1971) listed this variant from New York.

When working with BYDV, it must be remembered that the aphid vector is another biological variable. Rochow (1960), Saksena et al.,

---

*Bantarri, E. E., Associate Professor, Department of Plant Pathology, University of Minnesota, St. Paul, Minnesota.

(1964) and Rochow and Eastop (1966) found variations in the ability to transmit BYDV between clones of the same species of aphids. Other workers have found no differences between clones of aphids in their ability to transmit BYDV (Bruehl, 1958; Gill, 1967a; Rochow, 1958a, b; Rochow and Eastop, 1966; and Smith, 1963a).

The ability to transmit BYDV may differ with the life stage of the aphid. Orlob and Arny (1960) found that gynoparae, males, fundatrices and fundatrigeniae (alate) of the apple grain aphid Rhopalosiphum fitchii (Sanderson) did not transmit BYDV while oviparae and fundatrigeniae (alatoid) did. However, Orlob (1962) found that oviparae of non-migratory English grain aphids reared in the greenhouse transmitted BYDV as efficiently as apterous viviparous females. Nymphs are more efficient vectors of BYDV than are adult aphids especially with species-specific strains of BYDV (Gill, 1970a; Halstead and Gill, 1971a; Gill, 1972).

The presence of more than one strain of BYDV in a plant may influence vector specificity. Interactions of BYDV strains range from situations in which each virus in a mixed infection remains unaffected (Rochow, 1969b) to situations in which each strain protects against the other. This later case is called "cross protection" (Smith, 1963c; Jedlinski and Brown, 1965). Rochow (1969b) also points out that many workers have failed to find cross protection. Halstead and Gill (1971b) found interference with some strains of BYDV. This is a "mild" form of cross protection. In a third situation, the symptomatology and yield loss obtained with a mixed infection of BYDV is much more severe than with either single infection. This has been termed synergism (Aapola,

1968).

Rochow (1965) has detailed a case of apparent loss of vector specificity. In this case, the bird cherry oat aphid has been shown to transmit two species-specific strains--RPV, specific for the bird cherry oat aphid, Rhopalosiphum padi (Linnaeus), and MAV, specific for the English grain aphid--from doubly infected plants. The English grain aphid, however, will only transmit the MAV strain. This means that the vector specificity of the MAV strain of BYDV has broken down because it can be transmitted by the bird cherry oat aphid.

An explanation for the apparent loss of vector specificity is that from the doubly infected leaves, the bird cherry oat aphid transmitted unaltered MAV strain together with RPV strain in some form of complex. The bird cherry oat aphid can transmit MAV strains in the presence of RPV strain despite the inability to transmit the MAV strain alone (Rochow, 1965, 1969a, b). Rochow (1969b) postulates that the vector specificity results from the interaction of the protein capsid of a particular virus strain with the membranes surrounding the aphid salivary glands.

Rochow (1972) postulates two possible ways that loss of vector specificity may occur with BYDV. The first is that the relative quantity of the two virus strains in doubly infected plants may vary, that is, the concentration of one virus strain may increase when the two strains are in a mixture. Rochow (1972) has reported, however, that he found no proof of this with the mixing of RPV and MAV strains of BYDV.

A second way by which loss of vector specificity may come about involves the possible interaction of the two virus strains during the assembly stage of virus synthesis in doubly infected plants (Rochow, 1970). The theory is that during simultaneous synthesis of the two viruses some nucleic acid of one virus strain becomes incorporated into virus particles containing the protein capsid of the other virus strain. Such "mixed" virus particles can be transmitted by the appropriate vector species because the protein capsid is similar to that of the strain of virus regularly transmitted by the aphid.

More specifically, in the case of the MAV and RPV strains of BYDV the nucleic acid of MAV strain is incorporated into the protein capsid of the RPV strain and so the bird cherry oat aphid can transmit both strains. This does not work in reverse, i.e., the nucleic acid from the RPV being incorporated into the protein capsid of the MAV strain, because the English grain aphid can still only transmit the MAV strain from doubly infected plants.

Rochow (1970) and Rochow et al., (1971) have shown evidence for this when virus preparations made from doubly infected plants were treated with MAV antiserum, and aphids were allowed to feed through membranes on the treated preparation. The English grain aphid did not transmit. It was concluded that the MAV strain was neutralized in the preparation by the MAV antiserum. From the same preparation, however, the bird cherry oat aphid transmitted both RPV and MAV strains to about one third of the test plants. Perhaps the virus particles with mixed components function in the aphid like RPV strain because of the RPV protein capsid, and in the plant like MAV strain because of the MAV

nucleic acid. Studies of these interactions are in the very early stages (Rochow, 1972).

Brakke* (pers. com.) reported that the sedimentation coefficient and the molecular weights of the RNA of two strains of BYDV differed. At the present, he has only obtained this information for two strains but has raised the question--at what stage does one call a strain of virus a species? If strains of virus are, in fact, species of viruses, some of the current ideas on mixed infections may have to be altered.

In summary, it may be said that tests on field collected samples, made in different laboratories, have revealed a great range in vector specificity among isolates of BYDV. It is difficult to compare the results from all laboratories because of differences in methods, plants, and species of aphids used in transmission tests. It is often not possible to determine whether the variation encountered in one location results from properties of strains of the virus or from characteristics of clones of the species of aphids used in the transmission tests.

Rochow (1969b) sums up variations by saying:

"Because of changes in both strains of virus and in aphid species or even in aphid clones that predominate--coupled with interactions among host plants for both virus and aphids, with the weather and with the age and variety of crop plants--variations in the disease as it is observed in different locations are not surprising."

Paliwal and Sinha (1970) failed to find evidence that BYDV multiplied in its vector, the English grain aphid. They said this because:

a) They failed to transmit the virus serially from aphid to aphid.

---

*Brakke, M. K., Research Scientist, U.S.D.A., University of Nebraska, Lincoln, Nebraska.

b) The ability to inoculate plants with virus was eventually lost by most aphids.

c) The period of retention of the ability to inoculate plants with virus was dependent on the dose of virus given to the aphid.

Although symptoms may vary between species and varieties, in general, the symptoms for BYDV as with other "yellows" type diseases are discolouration and stunting of the host plant. Reduced tillering and distortions are also common, particularly with severe infections (Bruehl, 1961). Typically, the discolouration symptoms begin 7-20 days after inoculation. Among the cereals, the incubation time for the virus is usually shorter in oats than in barley and similarly shorter in barley than in wheat.

Usually, the first symptom on plants in the greenhouse is "water soaking". This is an oil-like streak that appears on the leaf (Gill and Westdal, 1966; Burnett, unpublished). This symptom has not been widely recorded from the field although it may be present, particularly at certain times of the day. In the greenhouse, this symptom is more readily observed on dull days or early in the morning before plants have been exposed to direct sunlight. The water-soaking symptom tends to disappear after plants have been exposed to bright sunshine and high temperatures.

The green tissues of old leaves discolour along the leaf margins, the areas enlarging and coalescing in a basipetal direction until the whole leaf is discoloured. Young leaves show no unusual colour although they may be slightly chlorotic (Bruehl, 1961). A mild abaxial leaf rolling may occur in plants with severe leaf symptoms (Gill and Westdal,

1966). A symptom that is often overlooked is that the root system of an infected plant is often as retarded as the top growth (Oswald and Houston, 1953a).

The severity of the symptoms depends on the age of the plant when inoculated (Oswald and Houston, 1953a). Early infection generally produces the most severe symptoms--marked stunting and yellowing, failure to head and often premature death of the plant; later infections are less severe and after an initial setback, plants tend to recover although there may be a reduction in tillering and yield.

Oats develop the most distinct symptoms. They have very obvious and early "water soaking" followed by a colour change in the leaves. The most typical colour for infected oat leaves is red rather than yellow. For this reason the disease was, and still is on occasions, called "red leaf of oats". Yellowish-green blotches appear first near the leaf tip. These soon become red or reddish-brown and coalesce, leaving the entire tip of the leaf red (Oswald and Houston, 1953a). As the symptoms advance down the leaf, the leaf curls and takes on a spear-like appearance.

Barley infected with BYDV develops a "yellows" type of symptom. Plants tend to be stunted, and typically, the older leaves turn a brilliant yellow.

According to Oswald and Houston (1953a) wheat infected at the seedling stage is the most severely damaged of the three major cereal crops. At this stage of inoculation, the first indication of BYDV is a darker than normal green on the old leaves, a chlorosis of the new growth, and stunting. Wheat infected after tillering shows only a

yellowing starting at the tips of newly-formed leaves. There is little stunting and presumably little loss in yield (Oswald and Houston, 1953a).

The author has not found these symptoms to be typical in the greenhouse, nor has the yield of plants, infected in the seedling stage, been severely affected. In several experiments, wheat has been found to be the most difficult of the cereals to rate for symptoms, the only consistent symptom being stunting. However, this may be misleading because daily watering of the plants in the greenhouse may, in fact, lessen the effects of the reduction in size of the root system.

In the field, young plants infected in the early spring are subject to cooler temperatures, higher light intensities, and less adequate moisture than plants grown in the greenhouse. The sum of these factors could result in different symptoms and a higher yield loss in the field than in the greenhouse.

Although susceptible to BYDV, rye appears to be quite tolerant. The only symptom appears to be a slight stunting (Bruehl, 1961) and yield is not known to be affected. In contrast, in wheats, oats and barley, both the quality and the quantity of the grain produced are reduced.

Perennial ryegrass of several varieties is susceptible to BYDV and infected plants show stunting, and conspicuous yellowing and/or reddening of the foliage (Catherall, 1965). Bruehl and Toko (1957) and Watson and Mulligan (1960a) reported that ryegrasses act as symptomless carriers. Catherall (1966a) reported that in greenhouse trials, there was a substantial loss in yield three months after inoculation, but no apparent symptom until 12-15 months after inoculation. Catherall (1966a)

also reported that in simulated swards of ryegrass, survival of plants was not affected by infection with BYDV but that yield was markedly decreased.

There are many factors that influence the expression of symptoms: (1) Shading inhibits symptom expression (Wilson and Murphy, 1953). Orlob and Arny (1961) reduced light intensities from 5,600 foot-candles to 500 foot-candles and found that symptom expression was reduced. They also found that short days decreased the expression of symptoms. A possible exception is the water-soaking symptom which tends to be more pronounced in reduced light.

(2) Temperature is also important to symptom expression (Endo, 1957; Orlob and Arny, 1961). The ideal temperature for symptom development is thought to be 68°F (convenient that this should be exactly 20°C). Higher temperatures often mask the symptoms perhaps because of rapid plant growth.

(3) Different strains of BYDV may cause different symptoms (Allen, 1957; Bruehl, 1958; Rochow, 1959a; Toko and Bruehl, 1959).

(4) The age of the plant when it is infected may also affect symptom expression. Symptoms are less pronounced and yield losses less severe in plants infected at an advanced stage of development than in those infected at an early stage (Endo and Brown, 1957; Oswald and Houston, 1953a).

In very severe infections, plants may show the so-called "cut leaf" symptom which is a serration of the edge of the leaf. There is some doubt as to whether or not this is a true symptom of BYDV because this leaf defect has been observed on plants free of BYDV. In New

Zealand, cut leaf is accepted as a true symptom (Smith*, pers. com.).

Bruehl (1961) noted that severe infection of BYDV reduced internode length to the extent that heads failed to emerge, particularly in spring barley. He stated that these stunted plants often survived longer than normal plants in hot dry weather and acted as a food source of the aphids and a reservoir for the virus.

Esau (1957a, b) found the major internal symptom of BYDV-infected plants to be phloem necrosis both in the shoots and roots. She said that there was no direct stimulation of tillering. However, the author has found an increase in tillering in plants of Selkirk wheat infected with BYDV. This latter observation agrees with that of Doodson and Saunders (1970) regarding the English wheat variety, Rothwell Perdix. Also, Oswald and Houston (1953a) pointed out that the tillering of BYDV-infected barley may be increased.

Bruehl (1961) postulates that it is possible that the roots are deprived of carbohydrates because of the failure of the phloem to transport them downwards. Esau (1957a, b) classified BYDV as a virus that primarily attacks phloem tissue as does Jensen (1969a). Jensen (1969a) examined the mesophyll cells of BYDV-infected plants and found cytological abnormalities, but no particles of virus. He cautioned that this observation was of questionable value. In addition, Jensen (1968, 1969b and 1972) found that, in plants of wheat and barley infected with BYDV, there was a rapid and massive accumulation of

---

*Smith, H. C., Director, Crop Research Division, D.S.I.R. Lincoln, New Zealand.

soluble and storage carbohydrates in the leaves. This accumulation was accompanied by loss of chlorophyll and a reduction in the photosynthetic rate. He concluded that the basic effect of BYDV infection appeared to be the development of resistance to the translocation of photosynthate from the leaf blade to the leaf sheath, culm, or spike and the developing grain. This indicated that there was food production taking place in the plant, but because of phloem blockage, it could not be utilized by the developing grain.

Bruehl (1961) has recorded the presence of BYDV throughout North America from east to west and from Alaska to Mexico. BYDV has also been reported from the following European countries; Belgium, Britain, Czechoslovakia, Denmark, Finland, France, Germany, Netherlands, Norway and Sweden (Bremer, 1965; Bruehl, 1961; Kristensen and Engsbro, 1966; Oswald and Thung, 1955; Rochow, 1961c; Roland, 1960, 1962; Slykhuis, 1967; Vacke, 1964; Watson and Mulligan, 1957). It was first observed in New Zealand in 1954 (Smith, 1955) and recorded in Australia in 1956 and Tasmania in 1957 by Smith (1959). The disease has also been reported from India (Negaich and Vashisth, 1963), Israel (Harpaz and Klein, 1965) and South Africa (von Wechmar, 1965 from Slykhuis 1967). Slykhuis (1962) observed symptoms of the disease and noted that aphid vectors in cereal crops in Pakistan, Jordan, United Arab Republic and Italy as well as in New Zealand and Australia where the disease was already known. It has been described from Colombia by Lopez and Caluez (1969) and by Samborski* (pers. com.), who said that aphids are found infesting cereals

---

*Samborski, D. J., Research Scientist, Agriculture Canada, Research Station, Winnipeg, Manitoba.

commonly throughout Brazil and that symptoms of BYDV are common. The absence of reports from other areas of the world is probably more a reflection of lack of work on the disease rather than an indication that the disease is not present. It is probably correct to say that the disease has a world wide distribution.

Oswald and Houston (1951) reported that wheat, oats, and barley were susceptible to BYDV. Many workers have examined the host range of BYDV (Bruehl and Toko, 1957; Orlob, 1959; Oswald and Houston, 1953b; Rochow, 1959a; and Watson and Mulligan, 1960a). Bruehl (1961) summarized this work and produced a list of 97 species from 34 genera within the family Gramineae. His list includes rye, corn, sorghum, rice and most of the common grass species, e.g. Kentucky bluegrass, cocksfoot, timothy, perennial ryegrass and bromegrass. Rothman (1966) recorded five additional species of grasses. Slykhuis (1967) reported that about 100 species of grasses are susceptible to BYDV and warned that some are symptomless. He also stated that no dicotyledonous plants are known to be susceptible.

Bruehl (1961) pointed out that because of the extremely wide host range of this virus amongst long-lived grass species, there is very little chance of it being eradicated due to the lack of host. He cautioned, however, that most host range studies have been carried out in the greenhouse where the viruliferous aphids were forced to feed on the plant species under test and so this recorded range may not represent a true field host range. However, in most areas where BYDV occurs in cereals, non-cereal grasses play a role in the epidemiology of the disease (Bruehl, 1961; Oswald and Houston, 1953b). Smith and Wright

(1964) found that approximately 80% of ryegrasses in pastures in New Zealand had the virus. Doodson (1967) tested 112 samples of perennial ryegrass from the field in Great Britain and found that 104 of them were infected with BYDV.

Orlob (1959) grew dodder on infected barley plants and found that aphids, fed on the dodder, could transfer BYDV to healthy plants.

An understanding of the epidemiology of a disease implies a knowledge of the factors affecting disease development. Since BYDV can only be transmitted by aphids, these factors would include the development and dispersal of the aphid species, the strain of virus and the efficiency of the particular species of aphid as a vector of the strain. Because aphids are the sole vectors of the disease organism, their life cycle, migration and host specificity influence the epidemiology of the disease.

Oswald and Houston (1953b), after observing BYD for 2 years, said that this virus was only of economic importance in California following climatic conditions which:

(1) delayed planting of cereals

(2) induced rank cover of wild grasses on meadows and ranges

(3) encouraged the multiplication of aphid vectors on susceptible wild grasses

(4) brought about rapid dying of grass crops soon after the grain crops appear.

They concluded that BYDV would be important in California only when climatic conditions were such as to bring about a large movement of aphids to cereals in their early growth stage. This hypothesis assumes

that the grasses are acting as reservoirs for the inoculum.

Orlob (1961) questioned the importance of grasses because he failed to isolate BYDV from perennial grasses near oats in New Brunswick. He cautioned that his results may have been invalid because he used mature grass plants in his attempt to isolate the virus. Slykhuis et al., (1959b) recovered BYDV from winter rye and some perennial grasses, and suggested that these plant species were over-wintering hosts. In many parts of the world grasses are known to be important reservoirs for BYDV. For example, in New Zealand, Smith and Wright (1964) found that up to 80% of ryegrass tillers tested were infected with the virus. Doodson (1967) also found a very high percentage of a certain type of perennial ryegrass was infected in England and Wales.

Slykhuis et al., (1959b), noting the presence of English grain aphids in young oat crops before the aphids could be found in grasses, suggested that the aphids had flown or been carried in from a great distance rather than from an adjacent plant source. It is well known that many insects species remain active and breed throughout the winter in the warm temperate areas of North America, such as Texas and Oklahoma. These species migrate northwards in the spring on the warm south winds. Depending on weather conditions, these migrations may occur rapidly over very long distances (Bruehl, 1961). Chiykowski and Chapman (1965) have detailed the northward migration of the aster leafhopper and Westdal* (pers. com.) has shown that leafhoppers may move about 1000

---

*Westdal, P. H., Research Scientist, Agriculture Canada, Research Station, Winnipeg, Manitoba.

miles in 24 hours. This idea is supported by numerous reports of the occurrence of winged aphids on cereals in Manitoba early in the growing season (Gill*, Robinson* and Westdal, pers. com.). Many workers in North America have investigated the circumstances associated with the first appearance of aphids in the North Central States and Canada, and have shown that migration of aphids is widespread and frequent (Taylor, 1965; Jensen and Wallin, 1965; Wallin and Loonan, 1971). Alternatively, it is possible to have several short migrations. The short migrations are usually accomplished by successive generations of insects moving northwards over the land mass of central North America as crops and grasses develop.

Lowe (1968) reported on the flight patterns of the bird cherry oat aphid, the major virus vector found in New Zealand, from pastures into cereal crops. Slykhuis et al., (1959b) found that it took about two months for an infestation initiated by an aphid, hatching from an egg on a primary host, to occur in a field of grain.

The outbreak of BYDV in oats in the U.S.A. in 1959 was attributed largely to a northward migration of the greenbug on strong southerly winds in late April and early May (Orlob and Arny, 1959).

It is thought that the most important vectors of BYDV in Manitoba are the English grain aphid, the greenbug, Schizaphis (=Toxoptera) graminum (Rondani), the corn leaf aphid, Rhopalosiphum maidis (Fitch) and the

---

*Gill, C. C., Research Scientist, Agriculture Canada, Research Station, Winnipeg, Manitoba.

*Robinson, A. G., Professor, Entomology Department, University of Manitoba, Winnipeg, Manitoba.

bird cherry oat aphid (pers. com. Gill, Robinson and Westdal). These may migrate into Manitoba in late May or early June, the time of cereal emergence. Depending on the size of the migration population and the weather condition when the aphids arrive, large populations can develop rapidly. Usually, however, migrations do not occur until late June or early July and thus early seeded crops usually escape serious infections.

The percentage of viruliferous individuals among the incoming population is also an extremely important factor in the determination of whether or not an epidemic of BYDV may occur.

In Canada it is thought that the loss from BYDV may be very high in some years in localized areas which may have been seeded late and/or received a large influx of migrants, but that on a national scale the average loss may be very small as a percentage of the total crop. Nevertheless, a small percentage loss on a national scale may represent dollar losses of a high magnitude.

Another point is that vector specificity and host tolerance may be such that severity of outbreaks may vary from year to year even though climatic conditions and the abundance of aphids may appear to be very similar.

The author thinks that the epidemiology of BYD must be considered on a local scale and, like the symptomatology, it is very difficult to generalize and draw conclusions for a large area.

Literature on yield loss in cereals

The literature reviewed in this section will be presented in two

parts. The first section will deal with the literature pertaining to losses due to BYDV and the second section will deal with the literature pertaining to losses due to the damage by aphids.

BYDV is considered to be an important disease of cereals and many workers have attempted to estimate the losses in yield caused by this virus. Bruehl (1961) and Rochow (1961) both summarized the losses found in the U.S.A. up to 1961. Most of the information they presented may also be found in supplement 262 of the "Plant Disease Reporter" in a report entitled "The epidemic of barley yellow dwarf on oats in 1959". The occurrence and extent of the disease, area by area throughout the U.S.A. are presented in this report as are the estimated, or more rarely, the actual yield losses. These losses are extremely variable depending on the area involved. Some of the yield losses recorded in this publication are as follows: Slykhuis et al., (1959b) compared the yield of diseased oat plants to that of healthy oat plants and found a 31% loss. Sechler et al., (1959) estimated a yield loss of 37% for Missouri with a range of 2-70%. Caldwell et al., (1959) found a 27.5% loss in yield of the oat crop in Indiana. Browning et al., (1959) estimated a 12% loss of yield for oats in Iowa. Sill et al., (1959) estimated the yield loss in Kansas to be over 5 million bushels or 25% of the 1959 oat crop. So one could go on, quoting the whole report. Generally, however, losses in oats were estimated to range from 5-50%. Losses in barley and wheat were not thought to be as high, but were consistently about 25% of yield. However, caution should be exercised in accepting estimates of disease loss, as observers are prone to over-estimate disease incidence. Accurate estimates of disease loss can only

be obtained with the development of a good survey technique using adequate samples or by measuring actual losses in field trials.

Greenhouse studies have shown that a high percentage loss in yield (up to 100% in oats) may occur from infection with BYDV (Burnett,unpublished data; Doodson and Saunders, 1970; Gill, Buchannon and Westdal, 1969; Gill, Westdal and Richardson, 1961; Watson and Mulligan, 1960a; Westdal and Burnett,unpublished data).

Many workers have shown that it is possible to get large losses due to BYDV in the field. Two main methods for assessing yield loss due to BYDV have been used. Oswald and Houston (1953a) tagged individual plants in the field when symptoms appeared and then compared the yield of such plants to the yield of uninfected plants in the same field. In these tests yield losses in barley were 95% when infection occurred in the seedling stage but this loss was reduced to 15-25% when infection took place at the heading stage. Many other workers have shown the importance of plant age in relation to yield loss (Endo, 1957; Endo and Brown, 1957, 1963; Jenkins, 1966; Oppitz, 1970; Smith, 1967; Slykhuis et al., 1959a; Watson and Mulligan, 1957, 1960a). Rothman et al., (1959) used a similar method to record losses of 14-46% among different oat varieties. Gill (1970b) also used this method and recorded losses of 65%, by weight, of seed produced per plant in Herta barley. Martens and McDonald (1970) used a similar method and recorded losses of up to 69%, by weight, of seed produced by plots of oats.

The second method involves the inoculation of field plots by artificial infestation with aphids carrying BYDV and then comparing yields of such plots with yields of plots not infested with aphids.

Often these infested plots are also compared to plots that are sprayed with an insecticide. Endo and Brown (1957) grew three varieties of oats and infested these at two different stages of plant growth. Yield reductions for the three varieties inoculated at the three leaf and boot stages, respectively, were: Fayette, 92.5 and 10.1%; Clintland, 94.4 and 21.8% and Rodney, 75.8 and 15.0%. Many other workers have carried out yield loss studies in this way or with slight modifications (Burnett and Robinson, 1972; Burnett, unpublished data; Endo and Brown, 1963; Close, 1969; Gill, 1967b; Gill, Buchannon and Westdal, 1969; Gill, Westdal and Richardson, 1969; Jenkins, 1966; Oppitz, 1970; Palmer and Sill, 1966; Slykhuis et al., 1959a; Suneson and Ramage, 1957; Watson and Mulligan, 1957, 1960a; Westdal and Burnett, unpublished data). This is not a complete list but it gives an indication of the amount of work done in this area. The yield losses obtained ranged from 0-90% depending on the plant species, the plant cultivar or variety, the aphid species, the strain of BYDV, the age of the plants at the time of infection, and the experimental design.

There are three other methods that have been used periodically in attempts to estimate losses due to BYDV in the field. In the first method plots are caged in the field, to prevent infection and yields of caged plots are compared with those of plots open to natural infection. Using this method Bruehl and Damsteegt (1959) reported a loss of 10 bushels per acre due to BYDV in oats. However, the method is open to question since plants in caged plots are not exposed to the same conditions of weather as plants outside the cages.

In the second method, yields of a given variety are compared, in a year of high disease incidence, with yield of the same variety in a year of low disease incidence. Browning et al., (1959) compared yields of oats in 1959, a year of high BYDV incidence with yields for the same variety at the same location in 1958, when the disease was not present. Supposedly both years were good for oat production, and other diseases did not complicate the comparison so that their results may be assumed to be reasonable measurements of the effect of disease on yield. Bruehl et al., (1959) similarly used 1956, a year reportedly free of BYDV, as a basis for the estimation of the losses due to BYDV from natural infection in 1959. It is the opinion of the author that great care must be exercised in estimating yield loss by this method because factors other than disease may contribute greatly to fluctuations in yield from year to year.

In the third and possibly the best method plots are treated with insecticide to prevent infestations by aphids, and yields are compared with those of untreated plots subject to natural infestations. Smith (1963b) and Smith and Wright (1964) have used this method with field plots of several acres. The use of large plots may give an accurate estimate of field losses but has the disadvantage of limiting tests to one variety. Also, replication is usually limited, but may be compensated for by the size of the plots.

Another important factor, especially where aphids are added to plots, is the number of viruliferous aphids per plant. In many cases, large numbers of viruliferous aphids per plant are used and consequently all the plants in "treated plots" become infected. In nature, 100%

infection seldom occurs and healthy plants may compensate for the loss in yield of adjacent infected plants. This cannot happen when all plants are infected. Loss estimates under these conditions may thus be exaggerated.

Smith and Wright (1964) reported severe losses, up to 25%, due to natural infections of BYDV in New Zealand. However, there is now doubt as to whether the losses were due entirely to BYDV or whether they were due partly to aphids feeding on the developing grain.

In England, losses due to BYDV in cereals have been estimated at 3-10% (Doodson and Saunders, 1970). Palmer and Sill (1966) say that severe losses from natural infections of BYDV in wheat have never been observed in Kansas. They also state,

"Thus far, BYDV has not been severely damaging to wheat in the great plains."

Large losses due to BYDV have been reported with oats and barley, but some of the reported losses may be exaggerated since these crops may react similarly to many other conditions. Orlob and Arny (1959) warned that BYDV symptoms may be confused with a plant reaction in response to drought and Westdal (pers. com.) suggested that originally a good deal of what was diagnosed as BYDV in North America was in fact a disease known as "aster yellows" caused by a mycoplasma that is transmitted by a leafhopper. The symptoms of BYD and aster yellows are often very similar (Gill and Westdal, 1966) and so the disease could easily be incorrectly diagnosed.

A second aspect that must be highlighted in this review is the yield loss that is due to the direct physical effect of aphid feeding

on the plants or developing grain. Kolbe (1969) reviewed reports of losses that have been experienced due to direct aphid damage. He states that the longest series of studies in this area have been carried out in Denmark between 1906 and 1966 and have been reported on by Stapel. He quotes Stapel as saying that a decade of heavy infestation (1910 to 1919) was followed by a 35-year period from 1920 to 1955 in which infestation was severe only in 7 of the years. During the 12 years from 1955 to 1966, there were heavy infestations in 8 years, with an extremely high peak in 1963. Stapel from (Kolbe 1969) says that aphid species that occurred during the study period were the bird cherry oat aphid, the English grain aphid and the rose grass aphid Metopolophium dirhodum (Walker). Also that in 1964 a yield increase was obtained by spraying the English grain aphid on the heads of barley, wheat and oats with parathion. No mention was made of whether or not these aphids had been tested to ascertain if they were transmitters of BYDV. Therefore, the loss recorded could be due to aphid feeding or BYDV.

Rautapää (1966), reported that, in Finland, the English grain aphid, which chiefly attacks the ears of grain caused up to 30% loss in yield in wheat fields where ear infestation persisted for 4 weeks. The greatest losses were found to occur if the infestation occurred at flowering. A population of 200 aphids per ear could reduce the 1000 kernel weight from 27 g to 11 g. In these experiments, the aphids were caged on the wheat plots and an aphid index, the sum of the average daily number of aphids on a shoot during the test period, was calculated.

Rautapää (1968) also reported on work with the English grain aphid and barley. In this study he again caged the aphids on the crops and calculated an aphid index. He noted that the grain yield per cage and per head, the weight of 1000 kernels and the number of heads per cage were inversely proportional to the aphid index. He noted that the yield loss corresponding to an index of 1000 was about 25%. There was a significant negative correlation between the aphid index and both percentage protein and the total beta-amylase of the grain. Also, there was a significant positive correlation between the alpha-amylase activity of the malt and the aphid index. He found that the changes shown to occur in the grain and in the malt were too small to reduce the quality of the grain.

Raatikainen and Tinnita (1961) said that in Finland there have been large losses of barley, oats and wheat due to the complex of aphids composed of the bird cherry oat aphid, the English grain aphid and the rose grass aphid. He noted that the application of organophosphorus compounds had prevented losses of about 8% for barley, 12% for oats, and 3% for wheat. However, it is not clear whether these losses were due to aphid feeding or virus.

Kolbe (1969) also noted that in Rhineland, in 1968, the bird cherry oat aphid, the English grain aphid and the rose grass aphid caused losses in wheat and oats amounting to 25% of yield, at an infestation density of 25-50 aphids per shoot or ear. The yield losses incurred were much greater if the infesting aphids carried virus diseases. It was found that the critical economic level for chemical control was when the field population of aphids reached 25-50 per ear, but if virus

diseases occurred, the vectors had to be controlled at a far lower level per ear.

Kolbe (1970) found that the most important aphids attacking cereal crops in Germany were the bird cherry oat aphid, the English grain aphid and the rose grass aphid. He found that the grain yield of oats could be increased by 15% by spraying for aphid control and that of winter wheat by 14%. In other trials with winter wheat he found that a loss of 10% in yield of grain was experienced when there were 35 aphids per stem and a loss of 5% in yield was experienced when there was 27 aphids per stem. In plots where there was a density of 20 aphids per stem no loss in grain yield could be measured.

Kolbe (1970) concluded his article by saying:

> "It is pointed out that the critical infestation density level and the profitability of controlling aphids in cereal crops depend upon the time of spraying and upon the course of infection before and after spraying. If crops are sprayed before, during or shortly after blossom, and infestation in Untreated continues to increase or remains constant for several weeks after spraying, an appreciable yield increase can be expected."

He cautioned, however, that if there is any suspicion of cereal crops being infected by yield-reducing virus diseases, it is essential to control the vectors immediately.

Sanderson and Mulholland (1969, 1970) carried out yield loss studies in wheat with the grain aphid, Macrosiphum miscanthi (Takahashi), a species which is very similar in appearance and habit to the English grain aphid. They found, in 1967-1968, that control of aphids with chemicals prevented a loss of 10 bushels/acre, and similarly, in 1968-1969, prevented a loss of 20% in yield. Although the grain aphid can act as a vector of BYDV (Butler et al., 1959), most of the losses found

by Sanderson and Mulholland (1970) were due to actual feeding damage by the aphid. In small, caged, field trials, which provided nearly ideal conditions for the development of populations of the grain aphid, grain yields were consistently reduced by 32 to 82% depending on the time of infestation in relation to the flowering time of the wheat plants. Aphids present at flowering suppressed yields by reducing the number of seeds set per spikelet and by decreasing the weight of individual seeds. A significant correlation between yield and the number of aphids was shown. As in the work of Rautapää (1968), an increase in the amylase activity in ripe grain was noted from areas of high aphid infestation. This increase in activity occurred only when the plants were grown under natural conditions and not when they were grown in a greenhouse or in cages.

Wright (1970) reported that there is strong evidence that isogenic lines of wheat may vary in their susceptibility to the grain aphid and that the losses in yield may be as high as 44%.

Aphids have been known for many decades as pests of cereals. In the Scandinavian countries most of the losses reported have been attributed to feeding damage of aphids. In New Zealand and Australia aphids are recognized as having two roles; firstly, as vectors of viruses, and secondly, as causing damage by feeding. In Britain and Canada the aphids of cereals have been mainly considered important as vectors of viruses.

In North America it is recognized that aphids may cause losses in grain crops by direct feeding damage as well as by spreading viruses. One of the best known examples is the greenbug, Schizaphis (=Toxoptera)

graminum, which causes plant damage and yield loss due to a toxic salivary secretion (Chatters and Schlehuber, 1961 from Wood 1965).

There are a number of reports in the literature, not associated with BYDV, on the effects of aphid control on crop yield. Forbes (1962), reporting on 4 years of observations and experiments on oats (1957-1960) in British Columbia, found that, among aphid species, the order of importance was the English grain aphid, the rose grass aphid, and the bird cherry oat aphid. In the 4 years, the aphid populations were 10 individuals per shoot in 1957, four per shoot in 1958, 11 per shoot in 1959 and 47 per shoot in 1960. According to the report there were no differences in yield from plots treated with insecticides and those that were not treated. Therefore, under conditions similar to those that prevailed during the period of the tests, the level of aphid population at which economic injury would be expected would be in excess of 47 per shoot. The use of insecticides for the control of aphids in oats in British Columbia was not recommended.

Wood (1965) studied the effect of foliage infestations of the English grain aphid on the yield of Triumph wheat and found that even with 200 aphids per linear foot of row it was not economically practical to apply insecticides for the control of aphids since the increase in yield was only 0.9 bushels/acre.

Adams and Drew (1965) found that, starting with similar initial populations, aphid infestations became higher in herbicide treated areas in oat fields than in similar untreated areas possibly because fewer coccinellids were present in the areas treated. Their data showed that coccinellid larvae were susceptible to herbicides such as

2,4-D-amine and that if these larvae were killed it gave an unnatural advantage to the aphids. They found that if an aphidicide was applied with the herbicide the level of subsequent aphid populations was similar to that in untreated plots. Even though there were as many as 250 aphids per tiller or shoot, no reduction in grain yield or straw was detected in tests conducted in 1962 or in 1963.

Jacob-Haupt (1969) also carried out spray trials in Rhineland (Western Germany) on wheat and oats with populations of 231 and 39 aphids/ear, respectively. The English grain aphid was predominant, but there were also some Macrosiphum fragariae (Walker), bird cherry oat, corn leaf, Rhopalosiphum maidis (Fitch), and rose grass aphids. The use of chemicals for the control of the aphids was associated with an increase in yield, which although indicating that the aphids had been causing economically important damage, was not large enough to compensate for the high cost of spraying. No toxic residues could be detected 21 days after spraying, and the research showed further that although chemical control of aphids on cereals appeared to be economically desirable and medically safe, the timing and cost of methods of treatment are important.

Harwood and Bruehl (1961) applied systemic compounds to the seed of cereals and found that, in the laboratory, considerable protection against Macrosiphum species was achieved, but there was slight plant stunting due to the phytotoxicity of the chemicals. In field tests, two compounds controlled aphids at 10 days but not at 21 days and it was noted that there was no significant reduction in incidence of the virus.

Wilson et al., (1960) used phorate to control the apple grain aphid, and the English grain aphid and the Hessian fly, Phytophaga destructor. The phorate caused significant losses in the stand through reduced germination, but these losses were not reflected in reduced yields. Highly significant increases in yield were obtained with all treatments where insects were controlled.

Stern (1967) conducted a study to determine if chemicals could be used to control the incidence of BYDV and to see if direct feeding losses caused by the bird cherry oat aphid and the corn leaf aphid were sufficiently severe to warrant the use of chemical control. Unfortunately, only a few plants with BYDV were discovered so this part of the study was dropped, but it was found that yield increases with a value greater than the cost of treatment were to be expected when aphids, at a level of about 25-30 aphids per tiller were controlled. At populations above this level, increased yields may be expected when aphids are controlled.

Adams and Drew (1969) carried out studies on the effects of malathion and 2,4-D amine on aphid populations in relation to yields of oats and barley. The bird cherry oat aphid and the English grain aphid were the only species involved. The authors found that one application of malathion, applied when the aphids were dispersing in the field, reduced ensuing aphid numbers on oats by 29% and on barley by 64%. Yields of oats were increased by 47% and of barley by 32% when malathion alone was used. These were the highest grain yields obtained. Treatments of 2,4-D amine alone decreased the yield of oats by 20% but increased the barley yield by 12%. Adding malathion to the treatment

increased the yield of oats by nearly 50% but its addition had little effect on the yield of barley.

Harper (1973), in Alberta, sprayed plots of wheat that had an average of 74 English grain aphids per head with dimethoate. Samples were harvested from these plots 7 and 22 days after spraying and it was found that the only difference was that the 1000 kernel weight of grain from the check plots was 8% less than the treated plots that were harvested 22 days after spraying.

Fehn (1970), in Brazil, treated plots of wheat with insecticides for the control of the rose grass aphid and the greenbug. Since the plants in both the treated and untreated plots were affected by virus disease, the increase in yield obtained was attributed to a decrease in the amount of mechanical damage done by the aphids. The increases ranged from 13-33% depending on the treatment. None of the treatments was phytotoxic and the increase in yield more than compensated for the cost of the treatment.

Wells and McDonald (1961) noted that little yield loss was caused on barley by the corn leaf aphid when infestation occurred at the late stage of stem elongation. On the other hand, when infestation occurred during the tillering stage, marked reductions in yield occurred. The magnitude of this reduction depended, to some extent, on the variety of barley. The authors suggested spraying the barley at the tillering stage with malathion to control the aphids until the crop had reached the tolerant stage.

Literature on the dosage effect of the aphid

The proportion of plants that become systemically infected with virus may be used as a measure of the proportion of insects that are capable of transmitting virus, if single insects are used to initiate the infection. Swenson (1969) has pointed out that there is no way of knowing whether infection was established at one site or several sites and this is especially true if more than one insect was used.

Throughout the literature on insect transmission of plant viruses there are many reports in which small and large groups of aphid vectors have been used in transmission tests (Jensen et al., 1952; Sheffield, 1957; Watson, 1946; Bindra and Sylvester, 1961), but since individual aphids were not used it is extremely difficult to evaluate the influence of insect numbers on infectivity from these reports. There are also many studies where individual insects and insects in groups of varying sizes have been used, but the experiments have not been designed in such a way that the results of the different experiments can be compared (Sylvester, 1954; Bindra and Sylvester, 1961). Nevertheless, in all cases reported, there was an increase in the percent infection as the number of vectors was increased.

This type of result has, in the past, led to a theory of "Mass-action". This hypothesis was put forward by Carsner and Lackey (1929) and it implied that each of several insects (vectors) could inject a subminimal dose of virus into a plant and that when the plant received several of these injections, which individually were incapable of causing infection, they could combine within the plant tissue to cause infection. Severin (1931) supported a mass-action hypothesis for the

transmission of sugar beet curly top virus by the beet leafhopper, Circulifer tennellus (Baker), but his work was far from conclusive. Giddings (1946) also postulated a mass-action hypothesis with the same virus and vector, but his idea of mass-action appeared to be different than that put forward by the previous author because he worked with single inoculation feeds of leafhoppers that had fed on virus source plants for different periods of time. Carter and Schmidt (1935), in studies on mass-action of mealy bug wilt of pineapple, said that they could not distinguish between toxic effects of mealybugs and mass action. Bindra and Sylvester (1961) concluded that there was no proof for the mass-action theory and have presented strong evidence against it.

Watson (1936) demonstrated that the percentage of plants infected increased when the number of viruliferous aphids used for the infestation was increased. She also found that the relationship between the number of plants infected and the number of viruliferous aphids used for the infestation indicated that the infections were local and independent. The probability of infection with a group of insects was the probability that the group contained one or more individuals that could cause the infection. She adapted the binomial theory to her data and using this and the maximum likelihood estimator, she found that the calculated values for transmission agreed with those actually found. Storey (1938) and Watson and Roberts (1939) also found that calculated values agreed very closely with actual values. Bindra and Sylvester (1961) summed up Watson's findings as follows:

"In other words a group will transmit if at least one of its members would have transmitted alone. Accordingly, subinfective doses of virus, if inoculated at different foci into a plant, would not combine to give an infective dose."

Bindra and Sylvester (1961) summarized much of the work done and pointed out that the hypothesis of independence of infections by individuals of a group is now accepted.

Kirkpatrick and Ross (1952) and Williams and Ross (1957) suggested from their work that the ability of a single aphid to transmit virus was decreased as the number of aphids was increased. That is, the observed transmissions were less than the expected transmissions based on the expansion of the binomial theorem. These results were in conflict with those of Watson (1936), Storey (1938) and Watson and Roberts (1939). Williams and Ross (1957) theorized that these differences were caused by the colony interfering with the feeding of the individual aphids. Also, they felt that the susceptibility of the plants was lessened when nonviruliferous aphids were allowed to feed before viruliferous aphids. Another hypothesis was that there was great plant variability among the test plants used.

Bindra and Sylvester (1961), as already mentioned, carried out extensive work on the effect of insect numbers on aphid transmission of potato leafroll virus and they concluded that prolonged feeding by large numbers of nonviruliferous green peach aphids, Myzus persicae (Sulzer), on Physalis floridana plants before infestation with a single viruliferous green peach aphid decreased the probability of success of virus transmission. The results of this work agree with those of Williams and Ross (1957). Bindra and Sylvester (1961) found that if

they contained the aphids for this prefeed on one side of the leaf and put the infective viruliferous aphid on the other side of the leaf, no interference could be detected.

Bindra and Sylvester (1961) found that group feeding interfered with inoculative feeding only in a few specific cases, usually when there were 10 aphids or more on the plant. These workers did discover a departure from the expected values that could be determined by the traditional use of the binomial theorem, but they pointed out and justified a modification in calculation and interpretation, and concluded that the lower probability values obtained for five and 10 aphids should not be construed as a departure from the binomial theorem.

The transfer of several insects to one plant is essentially a form of the multiple transfer method (Gibbs and Gower, 1960). The proportion of insects which transmit virus in such cases can be estimated by the use of the binomial theorem adapted to the maximum likelihood estimation. This is calculated as follows:

$$p^* = 1-(1-R/N)^{1/i}$$

N - is the number of test plants used

i - is the number of insects transferred to each test plant

R - is the number of test plants which became infected

p - is the proportion of infective insects in the population being studied, and p^* is the maximum likelihood estimate of p

$q = 1-p$ is the proportion of uninfected insects in the population and $q^* = 1-p^*$ is the estimate of q

The probability that none of i insects is infected is q^i. Therefore, the probability that a test plant becomes infected when virus

is transferred from i insects to it is $1-q^i$. The estimate q* is then given by

$$R/N = 1-q^{*i}$$

Therefore, $p^* = 1-q^* = 1-(1-R/N)^{1/i}$

This method is good when p is low because then not more than one insect of a group placed on a test plant is likely to transmit virus. When p is high, however, more than one insect may transmit to a test plant. This may lead to a bias in the estimate of p. For low values of p, i may be high, but for high values of p, i may be low. If p is high then there is little use in using multiple transfer if infectivity is the only interest.

Swenson (1967) stressed that systemic infection of a plant may arise from infection at any one site and that as plant susceptibility increased the possibility of infection at more than one site increased. If transmission is judged by the number of plants that become systemically infected, plants infected at a single site cannot be separated from plants infected at several sites. It must also be remembered that an individual insect may probe or feed at several locations, thus creating a situation similar to the multiple transfer method.

The response of plants to multiple infections is of particular interest, as it has been observed that plants respond differently to different numbers of viruliferous insects (Smith, 1967; Smith et al., 1968; Westdal and Burnett, unpublished; Westdal, unpublished). This response has been considered a dosage effect and was proposed by Smith and Richards (1963) as a dosage hypothesis to explain the difference, in ability to transmit BYDV, between the bird cherry oat aphid and the

apple grain aphid. Smith and Richards stated:

> "A 'dosage' concept is based on the hypothesis that the severity of BYDV infection resulting from an infection feed depends on the amount or dose of virus injected."

They pointed out that this concept has not been favored by many workers and they go on to discuss the work Storey (1938) referred to earlier in this review. Storey (1938) suggested that a high rate of transmission with a large number of aphids was due to an increase in the probability of a certain minimal necessary dose or unit of virus reaching the right infection site. Smith and Richards (1963) pointed out that the concept of a minimal infective dose was useful to explain differences in the efficiency of transmission as a plus (positive) or minus (negative) recording but it was not sufficient to explain the differences in severity of infection which they had frequently observed. They noted from their work that a relationship between symptom severity and dosage of BYDV was indicated. Symptoms were more severe when the bird cherry oat aphid rather than the apple grain aphid was used as a vector. They stated that comparative transmission tests with longer acquisition feeding periods and larger numbers of aphids also caused greater losses in yield. They obtained consistently severe infections with BYDV transmitted by the bird cherry oat aphid but the symptoms were less severe when the same BYDV isolate was transmitted by the apple grain aphid. They proposed that this could be most reasonably explained on the basis of dosage of virus. However, they conceded, in their closing remarks, that a selection of different types of virus particles by the different aphid species could also account for the observed differences in severity of symptoms.

From further studies Smith (1963a) concluded

"It is considered that the evidence on increasing severity of infection with different species of aphids and quicker symptom development with longer acquisition periods or larger aphid numbers presented in this paper supports a dosage hypothesis of infection for BYDV."

Tetrault et al., (1963) in their work on the effect of population levels of three aphid species on BYDV transmission pointed out that generally, virus incubation periods in the plant were reduced when populations of infective aphids were increased. They concluded that the greater the efficiency in transmission by the aphids, the shorter the incubation period required in the plants.

In further studies Smith (1967) showed that the severity of a specific strain of BYDV was modified by varying the number of aphids used for inoculation. This was based on a wide range of trials using different varieties of cereals and inoculating at different stages of plant growth in both Canada and New Zealand. This supports the earlier work of Smith and Richards (1963).

The main value of this hypothesis is in relation to breeding for high levels of BYDV resistance in cereals. Although cereal varieties moderately tolerant to BYDV may suffer only a slight reduction in yield when infected with BYDV by a low number of aphids at a late stage of growth, they may suffer severe losses in yield when the plants are infected with a large number of aphids at the same stage. A low number of viruliferous aphids may be used in screening for resistance in seedlings but high numbers may have to be used at a later stage of plant development. It should be noted that there are some isolates of BYDV that are virulent on plants in the late stage of development.

Smith (1967) used the dosage hypothesis to explain the high yield losses, with late infections, in New Zealand. He maintained that the high yield losses were related to high levels of aphid infestations. He cautioned that apparent tolerance in wheat may break down when plants are subjected to high levels of infestation.

Smith et al., (1968) noted that symptoms of BYDV on oats were more severe when plants were exposed to large numbers of viruliferous aphids than when they were exposed to small numbers of aphids. They also found that as the number of aphids per plant was increased, the yield decreased. This was attributed to the dosage effect.

Gill (1969a) found that when virus-free aphids were allowed access to source plants that had been inoculated with 12 viruliferous aphids there was a higher % transmission and symptoms occurred earlier than with aphids that had been given access to source plants that had been inoculated with three viruliferous aphids.

Jones and Catherall (1970) also reported that the severity of symptoms was proportional to the number of aphids used for inoculation. The bird cherry oat aphid fed on a source of BYDV for 24 h and then on test seedlings of Blenda oats for 24 h using five, 10 and 15 aphids per plant caused the test plants to be stunted by 11.2, 21.8 and 27.0% respectively. They suggested that these results showed that the severity of BYDV might be proportional to the amount of virus injected into the plant. They postulated that if this was so and a similar number of aphids were used to inoculate each plant then the symptoms obtained would depend on the virus source used. They tested this hypothesis and found that oat seedlings were stunted 6.2, 8.6 and 17.2%

when early, intermediate and late-maturing barley plants respectively were used as the source of virus. They postulated that if the amount of stunting in the oat plants may be taken as an indication of the amount of virus the aphids acquired, then the concentration of virus in the barley plants must have been inversely proportional to the rate of maturity. They summed up by saying:

> "However, if, as has been suggested, the severity of BYDV is proportional to virus concentration, the low virus concentration resulting from a rapid rate of plant growth would enhance, and the high virus concentration resulting from a slow rate of plant growth would reduce, the benefits to be derived from the possession of a tolerance gene which provides a specific reduction in the rate of virus multiplication."

Burnett (unpublished) found that the time from inoculation to symptom expression was longer when tolerant plants were used as a BYDV source, than when susceptible plants were used as the BYDV source.

Price and Birkenhead (1971) and Westdal and Burnett (unpublished) have evidence, with BYDV, that as the number of viruliferous aphids used for infesting the plants is increased then the plant yield obtained is decreased. Holmes (1929) showed that the numbers of local lesions produced on test plants infected with tobacco mosaic virus (TMV) was dependent on the concentration of the inoculum. Hooker and Benson (1960) found that when serial dilutions of potato X virus were mechanically inoculated to leaves of Datura tatula L., the test plants that were inoculated with high concentrations of the virus developed systemic symptoms within the minimum time. As the virus concentration was decreased the time from inoculation to symptom appearance increased. The influence of low virus concentration was

reduced as the incubation temperature was raised.

Verhoyen (1966) studied the "Effect of the concentration of inoculum on the multiplication and *in vivo* inactivation of alfalfa mosaic virus." He found that all virus growth curves seemed to have the same sigmoidal pattern. Also that virus production, during the same period, was higher when the concentration of inoculum used was higher and lower when the concentration of inoculum was lower. Therefore, in the latter case it took a longer time for the virus concentration to reach a certain point on the growth curve. In his discussion it is summed up as follows:

> "At given intervals of time after inoculation, different values were obtained, virus production being faster and the maximum concentration of virus and infectivity more rapidly reached with increasing concentrations of inoculum."

Kemeny *et al.*, (1971) in their paper entitled "Titrations of equine infectious anemic virus: Effect of dosage on incubation time and clinical signs" stated that as the concentration of virus in the inoculum was increased, the incubation period was reduced and more of the experimental ponies were killed.

CHAPTER III

MATERIALS AND METHODS

This study was conducted in the field and in the greenhouse. The methods differed considerably for the two areas of work except for one aspect, the care and maintenance of aphid colonies, which was common to both.

Colonies of virus-free aphids of each of the bird cherry oat aphid, the English grain aphid and the corn leaf aphid were started from an unfed first instar nymph taken from appropriate clonal colonies obtained from C. C. Gill. These colonies were reared on caged Parkland barley plants in a growth cabinet, maintained at 20 $\pm$ 1°C at 16 hours of light, at the Agriculture Canada, Research Station, Winnipeg, Manitoba. The barley was grown in sterilized soil in disposable composition pots, 12.7 cm in diameter, in a greenhouse maintained at 20 $\pm$ 2°C and with supplementary fluorescent lighting for 16 hours per day. There were five plants per pot. The plants were caged from the time of emergence with plastic cylinders 10 cm x 25 cm with 54 gauge nylon cloth over ventilation holes in the sides and the top. When the plants were two weeks old or at the 2-3 leaf stage they were changed for larger ones, 10 cm x 35 cm, of the same type to allow for plant growth. New colonies were established by transferring 30-40 aphids from old colonies to young caged plants. At this time, the colonies were placed in the growth cabinet. The aphid colonies survived 4-5 weeks from the time of establishment. Normally the aphids were used 3 weeks after colony

establishment.

Periodically throughout these studies, colonies were reinitiated from a single unfed aphid as a further precaution against virus contamination. Regularly throughout the study, aphids from these colonies were tested on Clintland oats or Coast black oats to check that they were free of BYDV.

The bird cherry oat aphid was used for greenhouse studies only and the English grain aphid was used for field studies only but the corn leaf aphid was used for both greenhouse and field studies.

Viruliferous aphids were obtained by allowing virus-free aphids to feed for 2 days at 15°C on leaf cuttings taken from virus-infected oat plants. This 2-day acquisition feed was carried out in disposable plastic Petri dishes 9 cm in diameter and 1 cm deep. A teaspoon of sand was placed in these dishes. The dishes were then sloped so that the sand would accumulate against one side and the leaf cuts were slipped into the sand so that they lay flat against the bottom of the Petri dish. The sand was then moistened with distilled water. Generally, two leaf sections, each about 8 cm long, were used in each Petri dish. These were cut from young leaves of the infected oat plants. About 50 of these aphids were added to aphid colonies that had been established for about 2 weeks. After 1 week these colonies were considered viruliferous and used for transmission work. At the time of use, five groups of 10 aphids each were tested from each colony to check that the colonies were viruliferous or virus-free, whichever was the case.

The leaf cuttings used in the initial virus feed were obtained from stock plants of Clintland oats maintained in a greenhouse by C. C. Gill.

Three isolates, as follows, were used throughout this study:

6801 - a non specific isolate of BYDV--the bird cherry oat aphid was used as a vector (Halstead and Gill, 1971b).

6407 - a specific isolate of BYDV transmitted by the English grain aphid (Gill, 1967a).

7005 - a specific isolate of BYDV transmitted by the corn leaf aphid. The transmission obtained with this isolate was as follows:

Out of two groups of 18 Clintland oat plants, one group being infested with the cherry oat aphid and the other being infested with the English grain aphid none became infected with BYDV. Out of a group of 18 Clintland oat plants infested with the greenbug only one plant became infected with BYDV. On the other hand out of the 18 Clintland oat plants that were infested with the corn leaf aphid 12 became infected with BYDV. All aphids used in these tests were nymphs that had a 2-day acquisition feed of virus infected leaf-cuts and a 3-day infection feed on the Clintland oat plants that were used as test plants.

The transfer of aphids was generally carried out with a moist sable-hair brush, either directly from the plant or from a sheet of foolscap paper. In the latter case the cage was removed and the aphids dislodged by shaking the plant.

These general methods of handling aphids were used throughout all of the experiments carried out during this study. Except where otherwise stated all aphids used in this study were healthy apterous adults.

Field trials

Field trials were carried out in the summers of 1971, 1972 and

1973 at the University of Manitoba Research Station, Glenlea, Manitoba.

Throughout the 3 years of field trials the cereal varieties grown were those recommended by the publication of the Manitoba Agronomists Conference in the "Field crop recommendations for Manitoba" for the appropriate year.

In 1971 and 1972 the English grain aphid was used in the trials and the virus isolate was 6407, specific for this species of aphid. The aphids, reared in the growth cabinets, as described, were transported to the field in circular pill boxes 7.5 cm in diameter and 6 cm deep. One pill box, containing about 100 aphids was used to infest each row to be treated.

In 1971, Conquest barley and Harmon oats were seeded in plots consisting of four rod rows, arranged in blocks that were replicated six times. Each block was composed of eight plots--four for each of barley and oats--arranged in a line. The crops were seeded on June 14. There were four treatments as follows allotted at random to the plots in each block: Metasystox R (Oxydemeton-methyl) sprayed at the rate of 0.024 kg/ha, at six weekly intervals beginning 32 days after seeding; untreated to allow a natural infestation of aphids; viruliferous aphids distributed along the middle two rows of a plot at the rate of about two aphids per three plants; and nonviruliferous aphids similarly distributed. The aphids were distributed when most plants in the plots were beginning to head, about 50 days after seeding.

The barley was harvested on September 4 and the oats on September 16. Weights were taken for the grain from the middle two rows, the

four rows and 1000 kernels for each plot.

In 1972, the experiment differed from that of 1971 in that Manitou wheat was added and the seeding date was May 31. The blocks were composed of eight plots of the same variety, arranged in a line and each block was replicated 12 times. Viruliferous and nonviruliferous aphids were placed in the appropriate plots at two stages of plant growth--the 2-3 leaf stage and when the plants were tillering. This was on June 28 and July 11, 28 and 41 days, respectively, after seeding. Two plots in every block were sprayed with Metasystox R and two were untreated to allow natural infestations of aphids.

Barley was harvested on August 25, wheat on August 30 and oats on September 8. Weights were taken for the grain from the middle rows and 1000 kernels for each plot.

In 1973 it was decided to use two species of aphids, the English grain aphid and the corn leaf aphid in the field studies. As in 1971 and 1972 BYDV isolate 6407 was used with the English grain aphid, but isolate 7005 was used with the corn leaf aphid. Pill boxes were again used to transport the aphids to the field.

In 1973 hill plots were sown. There were 20 blocks, each containing one row of each of Conquest barley, Harmon oats and Manitou wheat. The rows, allotted at random within blocks, were made up of 10 hills each. Different randomizations were used for different rows. Hills, seeded with 20 seeds, were planted on 1.5 m centres on May 15. The treatments were as follows: 1) malathion, 50% emulsifiable concentrate applied at 1.40 litres per hectare, twice a week for 5 weeks beginning 26 days after seeding; 2) untreated to allow natural infestation with

aphids; 3) 10 viruliferous aphids per hill when the plants were in the 2-3 leaf growth stage 22 days after seeding; 4) 100 viruliferous aphids per hill 22 days after seeding; 5) 10 nonviruliferous aphids per hill 22 days after seeding; 6) 100 nonviruliferous aphids per hill 22 days after seeding; 7) 10 viruliferous aphids per hill when the plants were just beginning to tiller 38 days after seeding; and 8) 10 nonviruliferous aphids per hill 38 days after seeding. Treatments 3 and 7 were applied to two hills in each row; the others to one hill per row. The wheat and oats were infested with the English grain aphid and the barley with the corn leaf aphid.

Malathion was used to control aphids in 1973 because its mammalian toxicity is lower than that of Metasystox R. The LD 50 for rats for malathion is 2,800 mg/kg while that for Metasystox R is 65 mg/kg. However, Metasystox R has the advantage of being a systemic as well as a contact poison.

The wheat, barley and oats were harvested, respectively, on August 27, 28 and 29. For each hill, the seed yield, 1000 kernel weight, the number of plants and heads, and the plant heights, at harvest, were recorded.

The corn leaf aphid was used on barley because it is the main aphid found on barley in Manitoba. Robinson and Hsu (1963) stated that there were large losses due to this aphid in 1955, but they did not say whether the losses were due to aphid feeding or to virus spread by the aphid. Apablaza and Robinson (1967) found that barley was much more adversely affected by the corn leaf aphid than were wheat and oats. They also

showed that the corn leaf aphid exhibited a preference for barley over wheat over oats while the English grain aphid showed no such preference.

Greenhouse trials

Trials were conducted in greenhouses at the Canada Agriculture, Research Station, Winnipeg, Manitoba. The greenhouse compartments used were maintained at 20 $\pm$ 2°C and had supplemental cool-white fluorescent light for 16 hours a day. Vents in the greenhouses were screened to prevent entry of insects.

Plants to be tested for their response to BYDV were grown in a nonsterilized soil mixture of 3 parts Red River clay to 1 part peat, in disposable composition pots 12.7 cm in diameter. Three kernels were seeded to each pot, and after germination the plants were thinned to one per pot. The plants were used, for tests, at the 3-leaf stage, about 3 weeks after seeding.

For the inoculation feed, aphids were caged on the plants with plastic cylinders, 3.7 cm x 46 cm covered at the top with Parafilm "M"*. The duration of the feed was 2 days. After this period the aphids were killed by spraying with tetraethylpyrophosphate (TEPP). The aphids were sprayed while still in the cages. The cages were removed the next day. From then to maturity the plants were sprayed routinely twice a week with TEPP to limit the possibility of contamination.

The first six experiments were of basically the same design.

---

*Manufactured by American Can Company Marathon Products, Neenah, Wisconsin, U.S.A.

The treatments were:

(1) Plants completely free of aphids

(2) Plants infested with one nonviruliferous aphid

(3) Plants infested with 20 nonviruliferous aphids

(4) Plants infested with 100 nonviruliferous aphids

(5) Plants infested with one viruliferous aphid

(6) Plants infested with 20 viruliferous aphids

(7) Plants infested with 100 viruliferous aphids

Forty plants were used in each treatment except in treatment (5) where 100 plants were used. Additional plants were used in treatment (5) in an attempt to obtain 40 BYDV-infected plants since Gill (1967a) and Halstead and Gill (1971b) had shown transmission by the bird cherry oat aphid was about 50%.

The cereals used in this series of greenhouse experiments were Herta barley, Rodney oats and Selkirk wheat. These varieties were used because they were known to be susceptible to BYDV (Gill, unpublished). Each of the cereals was tested with the nonspecific BYDV isolate 6801, with the bird cherry oat aphid as vector (experiments 1 to 3). The experiments were repeated with the corn leaf aphid and virus isolate 7005 (experiments 4 to 6).

After inoculation, the main culm of each plant was labelled with a small tag so that it could be identified at harvest. The first appearance of symptoms was recorded to determine time from inoculation to symptom appearance. Just before plant senescence, infection of the plants was checked by the leaf-cut method, in each case using the

species of aphid used in the original transmission, with Coast black oats as the indicator plant. This back-check was carried out for experiments 2 to 6 but not for experiment 1. If the back-check was negative, the plant was considered not to be infected with BYDV. This technique also served as a check on the control plants, particularly if there was any suspicion of contamination. Originally, it was planned to back-check all the plants in an experiment, but this was found to be very time consuming. Thereafter, only the plants that had been infested with viruliferous aphids, and a random sample from those exposed to nonviruliferous aphids were regularly tested. Plants, not exposed to viruliferous aphids, that were discoloured or deformed, in any way, were also tested.

Measurements were taken on the main culm as follows: height at harvest, head length, number of seeds and weight of seed. The weight of 1000 kernels was calculated for all heads that produced 10 or more seeds. Measurements taken for the whole plant were number of fertile tillers, number of seeds and seed weight. The weight of 1000 kernels was calculated as before.

A seventh experiment was carried out to check on the variability of yield obtained with Selkirk wheat infected with BYDV. Some of the plants infected with isolate 6801 of BYDV gave extremely high yields and it was thought that these plants may have been tolerant to BYDV. Therefore, 10 plants were grown from seed of each of the 10 highest and lowest yielding plants from the controls, and from each of the 10 highest and lowest yielding plants from those treated with 100 viruliferous aphids. Five of these plants were infested with 20 viruliferous

bird cherry oat aphids (isolate 6801) for a 2-day inoculation feed and five were kept as uninfested controls. The plants were back-checked for infectivity as in the other experiments, and grown to maturity. Measurements were taken as before.

In all these experiments, the plants were completely randomized in the greenhouse compartments. All the plants were pre-caged before infestation and the cages on the control plants were sealed with parafilm before any infestations were carried out. Infestations with non-viruliferous aphids were always made prior to infestation with viruliferous aphids. All infestations were carried out in the headerhouse and never in the greenhouse compartment where the plants were to be grown.

Throughout these experiments the plants were watered as required. The plants were allowed to wilt slightly periodically to avoid adverse effects associated with overwatering, particularly in barley. The plants were fertilized every 3 weeks with "Plant Prod"*, a soluble fertilizer.

Analysis of variance and tests of significance were carried out as outlined by Steel and Torrie (1960).

---

*Plant-Prod super soluble 15-30-15 obtained from Plant Products Co. Ltd., 70 Wesley Avenue, Port Credit, Ontario, Canada.

CHAPTER IV

RESULTS AND DISCUSSION OF FIELD TRIALS

Field trials 1971

In 1971, there were no aphid colonies in the sprayed plots and only a few in the naturally infested plots in either the oats or barley. In the barley plots left for natural infestation there were more corn leaf aphids than English grain aphids, but as already noted, population levels were very low. The English grain aphids that were placed in the artificially infested plots survived, but did not produce large numbers of progeny. The corn leaf aphid was also present in these latter plots but the English grain aphid predominated.

As indicated by an analysis of variance (Appendix 1) there were no significant differences between any of the treatments, for either oats or barley, in the seed weight from the two middle rows, the whole plot, or the 1000 kernel weights (Table 1). This would be expected for the naturally infested plots, since aphid populations were very low. For the artifically infested plots, it appeared that by the time the aphids became established, the plants had reached a stage of maturity at which they were not affected either by the direct feeding of the aphids or by any BYDV that they may have transmitted. In fact, it was not possible to detect symptoms of BYD on plants in these plots as the leaves began to show evidence of natural senescence about 2 weeks after the aphids were added to the plots.

Some strains of BYDV apparently are adapted to late infection, as shown by Jones and Catherall (1970) who found an isolate of BYDV,

TABLE 1

MEAN WEIGHT OF SEED FROM FIELD PLOTS OF CONQUEST BARLEY AND HARMON OATS SPRAYED WITH METASYSTOX R OR EXPOSED TO DIFFERENT APHID AND VIRUS REGIMES, 1971

Treatment	Seed yield (g)				1000 kernel weight (g)	
	Middle two rows		Whole plots			
	Barley	Oats	Barley	Oats	Barley	Oats
Metasystox R	1493	1029	3054	1998	35.26	24.39
Untreated	1373	1066	2877	2020	35.48	25.28
Viruliferous aphids	1434	958	2883	2030	35.01	24.82
Nonviruliferous aphids	1407	1047	2915	2084	35.01	24.63

transmitted by the English grain aphid, that caused a greater loss in yield of barley when transmitted at a late stage of plant development than at an early stage of development. However, this occurred only with plants carrying a gene for resistance to BYDV. Smith and Wright (1964) and Smith (1967), in New Zealand, have reported that some cereal varieties, especially those with a moderate level of tolerance, are affected more by severe late infection of BYDV than by early infection.

In a further analysis of the data, a combined coefficient of variation for the barley and oats was calculated for the yield of the middle two rows, the whole plot and the 1000 kernel weight determined in this experiment. This was done by expressing the square root of the error mean square as a percent of the experimental mean. The coefficient of variation is the same as the standard error per unit expressed as a percent of the mean as used by Cochran and Cox (1957).

Burnett and Baker (1973) used the method of Cochran and Cox (1957) to estimate the number of replicates that would be required to have an 80% probability of detecting a specific difference between treatments if a particular coefficient of variation were to occur in an experiment. Their model was based on the assumption that there would be four treatments and replicates in the proposed experiment. There would, therefore, be 3 (r-1) error degrees of freedom. The method was based on the further assumption that the treatment differences would be tested by a one tailed t-test and judged significant if the t value exceeded the tabular value for the 5% level of probability.

In the current experiment, the combined coefficients of variation were, 11.7% for the weight of the middle two rows, 9.0% for the weight

of the whole plots and 3.5% for the 1000 kernel weights. According to the curves constructed by Burnett and Baker (1973), with a coefficient of variation of 12% it would be necessary to have 70 replicates to detect a difference of 5%. Conversely, as there were only six replicates in the experiment, and the coefficient of variation was 11.7% it would be possible only to detect differences of the order of 20%. The actual differences between treatments were small, the highest being approximately 8%. With the limitations imposed by the experiment these could not be detected as significant.

On the basis of this experiment it may be concluded that infestation of oats and barley at a late stage, with the English grain aphid, will likely have little effect on yield either due to direct feeding activity or to BYDV, and that if these differences are to be detected, the design of the experiment must include a large number of replicates.

Field trials 1972

In the field experiment in 1972, aphids survived and colonies developed on all plots except those sprayed with Metasystox R. However, the colonies were discontinuous, so that it was not possible to compare the treatments on the basis of the number of aphids per plot. Symptoms of BYDV infection were observed only in plots which had been infested with aphids at 28 days after seeding. These symptoms were rated on a presence or absence basis by two independent observers and were progressively more obvious in oats than in barley than in wheat.

An analysis of variance (Appendix 2) showed that there were no differences between treatments in seed yield or 1000 kernel weight for

barley. For wheat, there were no significant differences among treatments for seed yield of the two middle rows, but the 1000 kernel weights were significantly greater in the plots treated with Metasystox R than in plots of any other treatment (Table 2). The weights were significantly lower in plots treated with viruliferous aphids than in the other unsprayed plots. One thousand kernel weights were significantly lower in the plots treated with viruliferous aphids 28 days after seeding than at 41 days after seeding.

For oats there was no significant differences among treatments for grain weight of the middle two rows. Analysis of variance showed that 1000 kernel weights of oats were significantly lower on plots treated with viruliferous aphids at 28 days after seeding than in plots of any other treatment.

The fact that there was no loss in yield due to aphids and/or virus in the barley was possibly due to the fact that barley is not a preferred host of the English grain aphid, so the majority of the introduced aphids may not have survived. Even though colonies were seen, it is possible that there were proportionally fewer aphids on barley than on the other crops, but this is not known since it was not practical to take relative counts. In fact, the rating of abundance of aphids in the field plots was made mainly on a presence or absence basis and on whether colonies were formed or not. Apablaza and Robinson (1967) reported that the English grain aphid showed no preference for any of the cereals, in the laboratory, but it has been observed that wheat is a favoured host for this aphid in the field

TABLE 2

MEAN WEIGHT OF SEED FROM FIELD PLOTS OF CONQUEST BARLEY, HARMON OATS AND MANITOU WHEAT SPRAYED WITH METASYSTOX R OR EXPOSED TO DIFFERENT APHID AND VIRUS REGIMES, 1972

Treatment	Seed yield middle two rows (g)			1000 kernel weight (g)		
	Barley	Oats	Wheat	Barley	Oats	Wheat
Metasystox R	525[a]	494[a]	560[a]	35.75[a]	34.97[a]	29.39[b]
Untreated	501[a]	481[a]	539[a]	35.23[a]	34.40[a]	28.50[a]
Viruliferous aphids at 28 days after seeding	483[a]	442[a]	512[a]	34.92[a]	33.10[b]	27.03[d]
Nonviruliferous aphids at 28 days after seeding	559[a]	488[a]	546[a]	35.39[a]	34.48[a]	28.26[a]
Viruliferous aphids at 41 days after seeding	507[a]	477[a]	548[a]	35.13[a]	34.39[a]	28.10[c]
Nonviruliferous aphids at 41 days after seeding	518[a]	515[a]	544[a]	35.16[a]	34.29[a]	28.43[a]

Means followed by the same letter are not significantly different from one another at the 5% level (analysis of variance and t-test). Read vertically.

(Burnett, unpublished).

Coefficients of variation were calculated for the yield of the middle two rows and the weight of 1000 kernels for barley, oats and wheat (Table 3). As indicated by Burnett and Baker (1973), with 12 replicates and a coefficient of variation of 12-15% (Table 3), only differences of 12% or more would be detected. The actual percentage losses in yield, in this trial, were 8.0%, 10.5% and 8.6%, and 3.4%, 3.4% and 2.1% for barley, oats and wheat, respectively, when the plots were infested with viruliferous English grain aphids 28 and 41 days after seeding, respectively (Table4). Again, because of the limitations of the experiment, one would not expect any of these observed differences to be recognized as significant reductions in yield due to treatment. This was the case (Table 2).

From this discussion, it is apparent that in order to detect small losses in yield great care should be exercised in planning an experiment. For example, it has been demonstrated that inadequate replication may severely limit the sensitivity of an experiment. However, in some cases, achievement of a particular limit of confidence may be beyond the physical resources available and it may then be best to abandon the experiment.

The coefficients of variation obtained for the 1000 kernel weights, respectively, 3.6%, 4.0% and 3.4% for barley, oats and wheat, were much lower than those obtained for the seed yields (Table 3).

Accordingly, it would be expected that smaller differences could be detected as significant. Looking again at the curves derived by

TABLE 3

COEFFICIENTS OF VARIATION FOR SEED YIELD AND 1000 KERNEL WEIGHT. FIELD TRIAL, 1972

Crop	Measurement	Coefficient of variation (%)
Conquest barley	Seed yield	15.5
	1000 kernel weight	3.6
Harmon oats	Seed yield	11.6
	1000 kernel weight	4.0
Manitou wheat	Seed yield	11.9
	1000 kernel weight	3.4

TABLE 4

PERCENTAGE LOSS IN SEED YIELDS AND 1000 KERNEL WEIGHTS OF CONQUEST BARLEY, HARMON OATS AND MANITOU WHEAT IN PLOTS EXPOSED TO APHID AND VIRUS REGIMES AS COMPARED TO PLOTS TREATED WITH METASYSTOX R. FIELD TRIAL, 1972

Treatment	Seed yield			1000 kernel weight		
	Barley	Oats	Wheat	Barley	Oats	Wheat
Metasystox R	-	-	-	-	-	-
Untreated	4.6	2.6	3.8	1.5	1.6	3.0
Viruliferous aphids at 28 days after seeding	8.0	10.5	8.6	2.3	5.3	8.0
Nonviruliferous aphids at 28 days after seeding	-6.5*	1.2	2.5	1.0	1.4	3.8
Viruliferous aphids at 41 days after seeding	3.4	3.4	2.1	1.7	1.7	4.4
Nonviruliferous aphids at 41 days after seeding	1.3	-4.3*	2.9	1.6	1.9	3.3

*Values higher by this % than the plots sprayed with Metasystox R.

Burnett and Baker (1973), it was noted that differences of the order of 4-5% should be detectable with 12 replicates when the coefficient of variation is in the range of 3.4-4%. This was borne out in the field trial where a loss of 5.3% in the 1000 kernel weight of oats (Table 4), on plots exposed to viruliferous aphids 28 days after seeding, as compared with sprayed plots, was detected as significantly different from the other treatments (Table 2). Similarly, losses of 8.0 and 4.4% in 1000 kernel weights of wheat (Table 4), in plots exposed to viruliferous aphids 28 and 41 days, respectively, after seeding were shown to be significantly different from the other treatments (Table 2).

An easily-measured component of yield with an inherently low coefficient of variation could be useful as an indicator of yield loss. In this field trial, the 1000 kernel weights would appear to meet these requirements. However, the response of plants to virus infection may vary markedly depending on a number of factors, such as, the kind of virus, the dosage, and the stage of plant development at the time of infection. For example, if the plant responds to the infection by producing few seeds, the weight of individual seeds--the 1000 kernel weight--may be abnormally high. Conversely, if the response is the production of additional tillers and a large number of seeds, the weight of individual seeds may be abnormally low. These variations in response must be known and understood before a particular component of yield can be taken as a reliable indicator.

Field trials 1973

In 1973, aphid colonies developed in most hill plots that were not sprayed with malathion. Occasionally aphids were present in some of the sprayed hills. Symptoms of BYDV were observed mainly in hills that had been artificially infested with viruliferous aphids, especially in those that had been infested with 100 viruliferous aphids 22 days after seeding.

The mean number of seedlings per hill was 15.8 for barley, 14.9 for wheat and 14.2 for oats. Thus, 10 aphids per hill was approximately the same density as that used in the plots (two per three plants) in the experiments in 1971 and 1972.

An analysis of variance (Appendix 3) showed that there was no significant difference, due to treatment, for any of the measurements made for barley (Table 5). However, it should be noted that reaction of barley to isolate 7005 of BYDV, used in this study, may be mild. Investigations have shown that this isolate causes very little loss in yield in Herta barley in the greenhouse.

For oats, there were significant differences between treatments for the heights of the plants, the number of heads per hill, the 1000 kernel weight per hill and the seed yield per hill (Table 5). The hills treated with malathion gave the highest yield. The greatest decrease, in the measurements made, occurred in hills infested with 100 viruliferous English grain aphids 22 days after seeding. There were no significant differences in yield between hills sprayed with malathion and those infested with nonviruliferous English grain aphids

TABLE 5

MEAN VALUES FOR MEASUREMENTS PER HILL FROM FIELD HILLS OF CONQUEST BARLEY, HARMON OATS AND MANITOU WHEAT SPRAYED WITH MALATHION OR EXPOSED TO DIFFERENT APHID AND VIRUS REGIMES, 1973

Treatment	Plant height (cm)			Number of heads per hill		
	Barley	Oats	Wheat	Barley	Oats	Wheat
Malathion	83.9[a]	85.8[a]	73.6[a]	64.1[a]	56.3[a]	75.0[a]
10 Nonviruliferous aphids/hill 22 days after seeding	81.8[a]	87.3[a]	75.4[a]	60.0[a]	54.5[a]	74.5[a]
100 Nonviruliferous aphids/hill 22 days after seeding	83.5[a]	85.8[a]	73.4[a]	62.2[a]	53.5[ab]	70.3[ab]
10 Nonviruliferous aphids/hill 38 days after seeding	79.9[a]	84.3[a]	74.9[a]	60.3[a]	47.1[bc]	75.1[a]
Untreated	81.8[a]	85.4[a]	72.4[a]	62.3[a]	46.0[cd]	73.0[a]
10 Viruliferous aphids/hill 38 days after seeding	83.6[a]	83.5[a]	74.5[a]	66.6[a]	45.2[cd]	68.5[ab]
10 Viruliferous aphids/hill 22 days after seeding	81.6[a]	85.3[a]	72.9[a]	63.3[a]	43.1[cd]	62.6[b]
100 Viruliferous aphids/hill 22 days after seeding	81.0[a]	77.8[b]	70.1[a]	58.5[a]	39.4[d]	65.6[ab]

Means followed by the same letter are not significantly different from one another at the 5% level (analysis of variance and t-tests). Read vertically.

TABLE 5 (cont'd.)

Treatment	1000 kernel weight (g)			Seed yield per hill		
	Barley	Oats	Wheat	Barley	Oats	Wheat
Malathion	38.2[a]	32.7[a]	23.2[a]	111.9[a]	70.3[a]	47.3[a]
10 Nonviruliferous aphids/hill 22 days after seeding	40.6[a]	33.0[a]	23.5[a]	106.8[a]	67.3[a]	44.6[ab]
100 Nonviruliferous aphids/hill 22 days after seeding	38.1[a]	32.8[a]	23.4[a]	107.3[a]	65.0[a]	40.0[abc]
10 Nonviruliferous aphids/hill 38 days after seeding	37.9[a]	31.2[a]	22.6[a]	98.1[a]	52.5[b]	37.9[bc]
Untreated	37.8[a]	31.7[a]	23.5[a]	107.0[a]	50.3[b]	43.0[ab]
10 Viruliferous aphids/hill 38 days after seeding	37.0[a]	31.9[a]	24.5[a]	107.3[a]	47.1[b]	40.2[abc]
10 Viruliferous aphids/hill 22 days after seeding	37.4[a]	31.1[ab]	23.5[a]	107.1[a]	42.8[b]	37.5[bc]
100 Viruliferous aphids/hill 22 days after seeding	38.8[a]	28.5[b]	22.6[a]	103.4[a]	23.7[c]	34.1[c]

whether at 10 or 100 per hill at 22 days after seeding, but these three treatments were significantly different from all other treatments. When compared to hills treated with malathion, there was a 66.3% reduction in yield in hills infested with 100 viruliferous English grain aphids 22 days after seeding, a 39.0% reduction in yield for hills infested with 10 viruliferous English grain aphids 22 days after seeding and a 28.4% reduction in yield for untreated hills (Table 6). The reason why oat hills infested with nonviruliferous English grain aphids yielded more than untreated hills is unknown. Perhaps the presence of aphids, in the hills infested with nonviruliferous aphids, was a deterrent to invasion by naturally occurring aphids.

For wheat, the analysis showed that significant differences occurred between treatments in the number of heads per hill and the seed yield per hill (Table 5). As with oats, hills treated with malathion gave the highest yield. Hills infested with 10 viruliferous English grain aphids 22 days after seeding gave a significantly lower yield than hills treated with malathion; hills infested with 100 viruliferous English grain aphids, 22 days after seeding, gave the lowest yield. When compared to hills treated with malathion there was a 27.9% reduction in yield in hills infested with 100 viruliferous English grain aphids 22 days after seeding, a 20.7% reduction in yield for hills infested with 10 viruliferous English grain aphids 22 days after seeding and 9.1% reduction in yield for untreated hills (Table 6).

Coefficients of variation were calculated for the seed yield and the 1000 kernel weights for the 3 crops grown in 1973 (Table 7). It

TABLE 6

PERCENTAGE LOSS IN SEED YIELD AND 1000 KERNEL WEIGHT OF CONQUEST BARLEY, HARMON OATS AND MANITOU WHEAT IN HILLS EXPOSED TO APHID AND VIRUS REGIMES AS COMPARED TO PLOTS TREATED WITH MALATHION. FIELD TRIAL, 1973

Treatment	Seed yield			1000 kernel weight		
	Barley	Oats	Wheat	Barley	Oats	Wheat
Malathion	-	-	-	-	-	-
10 Nonviruliferous aphids/hill 22 days after seeding	4.6	4.3	5.7	-6.3*	-0.9*	-1.3*
100 Nonviruliferous aphids/hill 22 days after seeding	4.1	7.5	15.4	0.3	-0.3*	-0.9*
10 Nonviruliferous aphids/hill 38 days after seeding	12.3	25.3	19.9	0.8	4.6	2.8
Untreated	4.4	28.4	9.1	1.0	3.0	-1.3*
10 Viruliferous aphids/hill 38 days after seeding	4.1	33.0	15.0	3.4	2.4	-5.7*
10 Viruliferous aphids/hill 22 days after seeding	4.3	39.0	20.7	2.1	4.9	-1.3*
100 Viruliferous aphids/hill 22 days after seeding	7.6	66.3	27.9	-1.8*	12.8	3.0

*Values higher by this % than the plots sprayed with malathion.

TABLE 7

COEFFICIENTS OF VARIATION FOR SEED YIELD AND 1000 KERNEL WEIGHT. FIELD TRIAL, 1973

Crop	Measurement	Coefficient of variation (%)
Conquest barley	Seed yield	32.3
	1000 kernel weight	13.6
Harmon oats	Seed yield	36.0
	1000 kernel weight	8.3
Manitou wheat	Seed yield	28.4
	1000 kernel weight	17.8

is of interest to note that the coefficients of variation obtained for hill plots were 3-4 times higher than those obtained for the rod-row plots in 1971 for both yield and 1000 kernel weight. This would suggest that 3 to 4 times as many hills as plots would be required to achieve the same degree of sensitivity.

For barley, with 20 replicates and a coefficient of variation of 32.3% for seed yield, differences of less than about 25% would not be detected (Burnett and Baker 1973). Similarly with a coefficient of variation of 13.6% for the 1000 kernel weights, differences of less than 10-15% would not be detected. The reductions in seed yield and 1000 kernel weight, compared to hills sprayed with malathion, although as high as 12.3% and 3.4%, respectively, were below the range of sensitivity of the experiment and were thus not detected as significant.

For oats, where the coefficients of variation were 36.0% for seed yield and 8.3% for 1000 kernel weight, detection of differences of less than 30% for seed yield and 8% for 1000 kernel weights would not be expected (Burnett and Baker, 1973). For wheat, the coefficients of variation were 28.4% for the seed weight and 17.8% for the kernel weight, so again, differences less than 20-25% for the seed yield and about 15% for 1000 kernel weight would not be detected.

From the results of the 1972 field trial it was suggested that 1000 kernel weights might serve as an easily measured component of yield on which to base yield loss estimates because of an inherently low coefficient of variation in this component. This may not appear to be borne out by the results of the 1973 trials where the coefficient

of variation ranged from 8.3-17.8%. However, the difference in the value of the coefficient of variation for 1000 kernel weight and that for seed yield in the 1973 trials, is of about the same order--about a factor of 3--as that in the 1972 trials.

In the 1971 field experiment there were no differences between any of the treatments. This was primarily because natural populations of aphids were low and artificial infestations did not become established until the crops were nearing maturity and were not affected either by aphid feeding or virus. In the 1972 experiment, because only a small number of viruliferous aphids were used to infest plots, the associated yield losses were small being significant only for oats. However, there was a trend toward a decrease in yield and kernel weight for barley and wheat infested with viruliferous aphids. The results of the field experiment in 1973, where a low and high level of viruliferous aphids was established, definitely show that there were more detrimental effects on plants exposed to a large number of viruliferous aphids than on plants exposed to a small number of viruliferous aphids. For example, symptoms were always more apparent in hills that had received 100 viruliferous aphids than in hills that received only 10 viruliferous aphids. Hills of oats that received 100 viruliferous aphids were significantly shorter in plant height than those that received only 10 viruliferous aphids. There was not a statistically significant reduction in height per plant for wheat and barley, but the plants that received 100 viruliferous aphids were shorter than those that received 10 viruliferous aphids.

Again, although the differences were not statistically significant there were fewer heads per hill on barley and oats infested with 100 viruliferous aphids than those infested with 10 viruliferous aphids.

These results agree, in general, with those of numerous other workers who have reported that, with BYDV, as the number of viruliferous aphids was increased, yield was decreased. Smith (1967) reported that with barley and wheat, symptoms were more pronounced or apparent, and that yield loss was greater with large numbers of aphids than with small numbers of aphids. The differences in yield were greater than those in the current studies. However, Smith (1967) used five and 150 aphids per plant, respectively, for his low and high levels of infestations, whereas in the current studies the two levels of aphids were, respectively, 10 and 100 per hill. Since there were approximately 15 plants per hill, the lower level of 10 aphids per hill was roughly equivalent to the level of two aphids per three plants used in the 1971 and 1972 field trials, while the higher level of 100 aphids per hill was approximately seven aphids per plant. Catherall (1966), in a field trial with barley, in Wales, used a larger number of viruliferous aphids per plant, in both the low and high levels of infestation, than in the present study. He found that with an increase in the number of viruliferous aphids there was an increase in the percentage of tillers showing yellowing symptoms, a reduction in the total number of tillers and percent fertile tillers, and a decrease in yield of 43.6% at the low level and 77.0% at the high level.

The dosage hypothesis, for BYDV, originally proposed by Smith and Richards (1964), was used to explain differences in the response of plants to a single isolate of BYDV when infected by different species of aphids. Symptoms of the disease were less severe with one species than the other and it was hypothesized that one species was injecting a smaller dose of the virus than the other. Smith (1967) extended the hypothesis to cover the situation of differences in response of plants to different numbers of viruliferous aphids. According to this concept of dosage, the results of Catherall (1966) would also be considered a dosage effect.

The current trials, although following the same trend as that of Smith (1967) and Catherall (1966), were different in that there was a possibility that at the low level of aphids not all the plants in a hill were infected, whereas with 100 viruliferous aphids per hill all plants would be expected to be infected. Differences in yield could thus be a reflection of the differences in numbers of plants infected. According to the hypothesis, this would not be a dosage effect in terms of plants, but only in terms of hills.

In each of these experiments, a nonviruliferous aphid check was provided to determine the effect on plants of direct aphid feeding as opposed to that of the BYDV. At the level of aphid populations used there was no indication that aphid feeding alone was detrimental to the plants (Tables 1, 2, 5 and 6).

The yield losses, due to BYDV, recorded in these trials were much smaller than those generally reported. This was probably a reflection

of the differences in numbers of aphids used. In the present experiments an attempt was made to approximate low levels of aphid populations that may be encountered with natural infestations in the field rather than to use abnormally large populations which produce maximum plant response or reaction. In many instances, such as in the current study, small or moderate losses are not detected because of limitations--mainly insufficient replication--in experimental design. It is therefore of vital importance to establish, in advance, the magnitude of loss to be detected and then to design the experiment accordingly.

CHAPTER V

RESULTS AND DISCUSSION OF THE GREENHOUSE TRIALS

To further examine the dosage hypothesis, greenhouse trials were conducted to determine whether BYDV infections were more severe when initiated by a large number of viruliferous aphids than by one or a small number of viruliferous aphids. Yield and the parameters of yield were considered to be the most useful criteria for judging the effect, on the plant, of infection by different numbers of viruliferous aphids. Other measurements, such as, time from initiation of infection to symptom expression, plant height, and head length were also considered as possible plant responses of value in determining the effect of dosage.

Environmental variability in a greenhouse is usually high, so in order to detect small differences, with confidence, large numbers of replicates are required (Burnett and Baker, 1973). For this reason, 40 or more replicates of each treatment were used in these trials.

In the course of the experiments conducted during this study it was found that not all aphids from "viruliferous" colonies transmitted BYDV. Thus, in tests with one aphid per plant, usually 100 plants were used in an attempt to obtain sufficient replicates. However, in most of the experiments the percentage transmission was low with single aphids and many plants escaped infection even when exposed to 20 or 100 viruliferous aphids (Tables 8 and 9). With a low percentage transmission, occasional escapes would be expected with 20 aphids per plant,

TABLE 8

PERCENTAGE OF CEREAL PLANTS INFECTED WITH BYDV[1] WHEN INFESTED WITH DIFFERENT NUMBERS OF VIRULIFEROUS APHIDS[2]

Cereal	Number of viruliferous aphids		
	1	20	100
Herta barley	16	45	92
Rodney oats	73	100	100
Selkirk wheat	19	87	92

[1] isolate 6801
[2] *Rhopalosiphum padi* (L.)

TABLE 9

PERCENTAGE OF CEREAL PLANTS INFECTED WITH BYDV[1] WHEN[2] INFESTED WITH DIFFERENT NUMBERS OF VIRULIFEROUS APHIDS

Cereal	Number of viruliferous aphids		
	1	20	100
Herta barley-1	7	70	83
Rodney oats	19	90	83
Selkirk wheat	5	78	93
Herta barley-2	9	33	58

[1] isolate 7005
[2] *Rhopalosiphum maidis* (F.)

but not with 100 aphids per plant since according to the theorem on the expansion of the binomial the probability of escapes should be extremely low.

The procedure for obtaining viruliferous aphids is considered to have been faulty. In the procedure, virus-free barley plants about 4 weeks from seeding, were infested with viruliferous aphids about 1 week before aphids, in large numbers, were required for experiments. Plants of this age were used in order to sustain the large numbers of aphids required, but because of the stage of maturity of the plant the virus may not have spread through the plant tissue sufficiently to provide an adequate source of virus for the aphids. Had the plants been used at an earlier stage of development it is possible that a larger percentage of aphids would have become viruliferous.

In order to obtain a sufficient number of aphids to set up an experiment, viruliferous aphids from several plants or colonies were required. The aphids from the various colonies were not bulked, but taken in succession from individual colonies. Thus, if transmission by aphids in a colony was particularly low the effect on the experiment would be more detrimental than if the aphids had been bulked. This is considered a further flaw in the procedure used in the trials.

The experiments were analysed as if there had been 10 treatments, control, three levels of nonviruliferous aphids (NV), three levels of viruliferous aphids (V-) where plants did not develop symptoms and were negative for a BYDV back-check, and three levels of viruliferous aphids (V+) where plants developed definite symptoms and were positive for a BYDV back-check.

The back-check for virus was carried out some time after the plants had headed, but while leaf tissue was still green. At this stage, virus recovery is not always certain so that some infected plants may have been missed. In this case, although gross symptoms were mild or lacking, the presence of the virus may have elicited some responses in the plant which could account for the observed differences in values between controls and plants designated as V-.

In recording the data, plants were first categorized as sterile or fertile on the basis of whether or not they produced seed. No further data were taken for the sterile plants, but several measurements were made separately for each of the main culm and the whole plant for those that were fertile. The height, head length, number of seeds, seed yield and 1000 kernel weight were taken for the main culm, and the number of seeds, seed yield and 1000 kernel weight for the whole plant. The number of fertile heads was the only other measurement taken.

For the first six experiments the values obtained for all the measurements taken, in the different aphid treatments, were compared to those for the control group by the use of a two-tailed t-test.

The mean values for all the measurements, together with their standard errors, are listed in Appendices 4 to 9.

Effect of different dosages of inoculum on the responses of barley, oats and wheat, using BYDV isolate 6801 and the bird cherry oat aphid as vector

Herta barley

In the experiments with Herta barley a high percentage of the plants

that were infected with BYDV were sterile (Table 10). The percentage of sterile plants increased as the number of viruliferous aphids (V+), used to initiate the infection, was increased. Of 16 plants that were infected with BYDV, when one viruliferous aphid was used to initiate the infection, three or approximately 19% were sterile; of 18 plants that were positive for BYDV when 20 aphids were used, nine or 50% were sterile; and of 37 plants that were positive for BYDV when 100 aphids were used, 23 or 62% were sterile (Table 10).

Similarly, the period from inoculation to symptom expression was shorter as the number of viruliferous aphids used to initiate the infection was increased. That is, the symptoms appeared sooner when 20 aphids were used than when one aphid was used and also when 100 aphids were used than when 20 aphids were used.

The main culm was shorter for plants exposed to viruliferous (V+) aphids than for the controls, and there was a trend to progressively shorter plants as the number of viruliferous aphids was increased (Table 11). However, the differences in height of plants, between the three treatments, were not significant so there was no detectable dosage effect. The head length of the main culm was significantly reduced from that of the controls for plants infected by 20 or 100 viruliferous aphids (Table 11). As before, a trend indicative of dosage effect was apparent, but the differences in head length between the three groups were not significant (Table 12). Nevertheless, since the head length of plants exposed to one viruliferous aphid was not significantly different from the controls and that of plants exposed

TABLE 10

NUMBER AND PERCENT STERILE PLANTS FOR HERTA BARLEY, RODNEY OATS AND SELKIRK WHEAT EXPOSED TO DIFFERENT NUMBERS OF NONVIRULIFEROUS AND VIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

	Treatment									
					1V		20V		100V	
Symptoms	Control -	1NV -	20NV -	100NV -	+	-	+	-	+	-
Herta barley										
Number of plants	40	40	40	40	16	84	18	22	37	3
Number of sterile plants	0	0	0	0	3	2	9	0	23	0
% sterile	0	0	0	0	18.8	2.4	50.0	0	62.0	0
Rodney oats										
Number of plants	32	40	37	38	73	27	40	0	39	0
Number of sterile plants	0	0	0	0	2	0	0	0	0	0
% sterile	0	0	0	0	2.8	0	0	0	0	0
Selkirk wheat										
Number of plants	40	40	40	40	19	81	35	5	38	2
Number of sterile plants	0	0	0	1	0	1	0	0	1	0
% sterile	0	0	0	2.5	0	1.2	0	0	2.6	0

NV plants infested with nonviruliferous Rhopalosiphum padi (L.)
V plants infested with viruliferous (BYDV isolate 6801) R. padi
\- not infected
\+ infected

TABLE 11

MEAN RESPONSES OF HERTA BARLEY TO INFESTATION WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

Treatment	Plant reaction	Main culm					Number fertile heads per plant	Whole plant		
		Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)		Number of seeds	Yield (g)	1000 kernel weight (g)
Control		62.80	8.16	20.68	0.80	38.42	5.60	88.20	3.28	37.12
1NV		63.07	8.26	21.38	0.82	38.43	5.07	84.47	3.14	37.34
20NV		65.02	8.39	22.10	0.81	36.64	5.13	87.75	3.14	35.71
100NV		63.50	7.92	20.20	0.77	38.43	5.30	81.20	2.96	36.70
1V	-	62.81	8.55	21.56	0.84	38.80	5.05*	86.48	3.19	37.07
20V	-	60.86	7.99	20.68	0.76	36.05	5.41	81.55	2.91	35.02
100V	-	61.33	8.30	22.00	0.79	35.99	6.67	111.67	3.77	33.94
1V	+	53.31**	6.85	13.00**	0.46**	35.11	3.00**	34.36**	1.26**	33.31
20V	+	49.44**	5.93**	10.89**	0.37**	37.12	3.78*	28.33**	0.88**	31.95
100V	+	48.97**	4.69**	5.93**	0.11**	14.92**	1.43**	7.57**	0.16**	16.17**

*,** significantly different from control at 0.05 and 0.01 levels of probability, respectively
NV plants infested with nonviruliferous Rhopalosiphum padi (L.)
V plants infested with viruliferous (BYDV isolate 6801) R. padi
- not infected
+ infected

TABLE 12

DIFFERENCES IN RESPONSES OF HERTA BARLEY TO INFESTATION BY INCREASING NUMBERS OF VIRULIFEROUS APHIDS

Comparison	Main culm					Number fertile heads per plant	Whole plant		
	Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)		Number of seeds	Yield (g)	1000 kernel weight (g)
1V+ vs 20V+	NS	NS	NS	NS	NS	NS	NS	NS	NS
20V+ vs 100V+	NS	NS	**	**	**	*	**	**	*
1V+ vs 100V	NS	NS	**	**	**	*	*	*	*
Dosage effects	No	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes

NS,*,** not significantly different, significantly different at 0.05 and 0.01 levels of probability, respectively

V+ plants infected by BYDV isolate 6801 transmitted by Rhopalosiphum padi (L.)

to 20 or 100 viruliferous aphids was different ($P \leq 0.01$) a dosage effect was established.

Infected plants produced significantly fewer seeds than the controls both on the main culm and the whole plant. Although there was a difference in the number of seeds produced by plants infested with one aphid and those infested with 20 aphids, it was not significant. However, there was a significant difference between number of seeds produced by plants infested with 20 and 100 aphids, thus continuing the trend of effect of dosage. This relationship also held for the yield of the main culm, the yield of the whole plant and the number of fertile tillers. However, for kernel weights for both the main culm and the whole plants the only significant difference was for plants in which virus infection was initiated by 100 viruliferous aphids.

In the data for the number of fertile heads per plant, the value for plants that were not infected, although exposed to one viruliferous aphid (1V-), was significantly different from the control. The only explanation that can be offered is that with a large number of replicates (82 plants), in the group, small differences can be expected to be detected as significant.

In general, all the measurements taken for Herta barley in this experiment show the effect of dosage and strongly support the dosage hypothesis proposed by Smith and Richards (1963) and confirmed in the work of Smith (1967) and Smith et al., (1968).

It should be noted that in the preceding discussion only plants that produced seed were considered. As indicated previously, many of

the infected plants were sterile, the number of sterile plants increasing with increased numbers of viruliferous aphids (Table 10). Had these been included in establishing the mean values of the measurements, dosage effects would have been more pronounced.

Rodney oats

In this experiment, 73 of the 100 plants exposed to individual viruliferous aphids became infected and all of the plants exposed to 20 and 100 viruliferous aphids became infected (Table 10). There were, therefore, no plants in the treatments designated as 20V- and 100V- (Table 13). Only two plants in this experiment were sterile; both were in the group in which plants were infested with one viruliferous aphid.

As with the barley, symptoms of infection appeared sooner in the oats as the number of viruliferous aphids used to initiate the infection was increased. The main culm was significantly shorter ($P \leq 0.01$) for infected plants than for the controls, but there were no significant differences in the height of the main culm among plants infested with the three levels, 1V+, 20V+ and 100V+, of viruliferous aphids (Table 13). The mean length of the heads on the main culms was reduced significantly ($P \leq 0.01$), compared to the controls, on all the plants infected with BYDV. Among the infected groups, there was no difference in head length due to dosage between plants exposed to one and 20 viruliferous aphids, but there was a difference due to dosage between those exposed to one and 100, and 20 and 100 viruliferous aphids (Table 14). Curiously, the head length for the main culms of plants

TABLE 13

MEAN RESPONSES OF RODNEY OATS TO INFESTATION WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

Treatment	Plant reaction	Main culm					Number fertile heads per plant	Whole plant		
		Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)		Number of seeds	Yield (g)	1000 kernel weight (g)
Control		96.91	18.31	49.16	1.77	36.85	3.47	124.53	4.19	33.87
1NV		96.50	20.07*	44.72	1.23**	27.78**	3.22	121.60	3.82	31.40*
20NV		94.95	20.39*	46.62	1.29**	28.06**	3.43	119.30	3.69	30.93**
100NV		98.08	19.74	49.11	1.68	34.06	3.21	114.71	3.83	33.26
1V	-	92.19	18.54	45.33	1.42*	31.82	2.52**	97.19*	3.21*	32.02
20V	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
100V	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1V	+	74.93**	13.60**	9.96**	0.35**	34.68	2.11**	16.10**	0.58**	36.48*
20V	+	79.17**	13.29**	5.42**	0.20**	39.51	2.62**	13.92**	0.46**	33.65
100V	+	75.90**	12.01**	4.47**	0.18**	37.62	2.28**	11.05**	0.39**	35.29

*,** significantly different from control at 0.05 and 0.01 levels of probability, respectively
NV plants infested with nonviruliferous Rhopalosiphum padi (L.)
V plants infested with viruliferous (BYDV isolate 6801) R. padi
- not infected
+ infected

TABLE 14

DIFFERENCES IN RESPONSES OF RODNEY OATS TO INFESTATION BY INCREASING NUMBERS OF VIRULIFEROUS APHIDS

Comparison	Main culm					Number fertile heads per plant	Whole plant		
	Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)		Number of seeds	Yield (g)	1000 kernel weight (g)
1V+ vs 20V+	**	NS	**	**	*	**	NS	NS	*
20V+ vs 100V+	NS	*	NS	NS	NS	NS	NS	NS	NS
1V+ vs 100V+	NS	**	**	**	NS	NS	**	**	NS
Dosage effect	No	Yes	Yes	Yes	No	No	Yes	Yes	No

NS,*,** not significantly different, significantly different at 0.05 and 0.01 levels of probability, respectively

V+ plants infected by BYDV isolate 6801 transmitted by Rhopalosiphum padi (L.)

exposed to one and 20 nonviruliferous aphids were significantly lower ($P \leq 0.05$) than those for the controls. No explanation can be offered to account for this occurrence.

The number of seeds and the seed yield, for the main culm and the whole plant, were severely reduced from that of the controls (Table 13), the reductions being of the order of 80 to 90% for both seed number and yield. For the main culm, there was a significant dosage effect for the number of seeds and yield between plants exposed to one and 20 or 100 viruliferous aphids, but not between those exposed to 20 and 100 viruliferous aphids (Table 14). For the whole plant, the dosage effect for number of seeds and yield was only detected between plants exposed to one viruliferous aphid and those exposed to 100 viruliferous aphids (Table 14). No significance was detected in the differences between 1V+ and 20V+ or between 20V+ and 100V+ (Table 14).

There were significantly fewer seeds ($P \leq 0.05$) for the whole plant and there was a significantly lower yield for both the main culm and the whole plant, as compared to the controls, for plants in treatment 1V-. This suggests that some of the plants in this group were infected. If so, the infection must have been mild and/or late since it was not detected by symptoms or the back-check, and the reduction in numbers of seeds and yield were relatively small (Table 13).

No satisfactory explanation can be offered for the reduction in yield for the main culm of plants exposed to one and 20 nonviruliferous aphids since plants exposed to 100 nonviruliferous aphids were not affected. It is likely that this was associated with some early

influence, on these two groups of plants, which also had an effect on the head lengths, the kernel weights, and to a lesser extent on some of the other plant responses that were measured. The effect was carried through to the kernel weights of the whole plant (Table 13). Although the yields on the main culm of plants exposed to one and 20 nonviruliferous aphids were significantly lower than those for the controls, the yields for the whole plant in these treatments were not similarly reduced. The loss in yield of the main culm was, therefore, compensated by an increased yield from the tillers.

In general, although there were some significant differences in the kernel weights, due to treatments, the effects were not consistent. Seeds produced by infected plants tended to be as heavy or heavier than seeds from healthy plants. It should be noted that infected plants produced very few seeds and for this reason, the seeds may have been heavier. There was no dosage effect in this plant response.

The number of fertile heads per plant was significantly fewer for plants in treatments 1V+, 20V+ and 100V+ than for the controls, the reduction being of the order of 25 to 30%. The number of fertile heads for plants in treatment 1V- was reduced to about the same extent. This supports the earlier suggestion that there may have been infected plants in this group.

The results from this experiment indicate that loss in yield due to BYDV, in oats, was mainly due to two factors, a moderate reduction in number of fertile heads, and a severe reduction in the number of seeds per head. In other words, the main loss in yield was due to

the marked reduction in the number of seeds produced. This contrasts with the situation in barley where both the number of seeds and seed weight were reduced.

As in the experiment with Herta barley, dosage effect in a number of plant responses, to BYDV infection, was apparent in this experiment with Rodney oats.

Selkirk wheat

With Selkirk wheat, only 19 of the 100 plants exposed to individual viruliferous aphids became infected and not all the plants exposed to 20 and 100 viruliferous aphids became infected (Table 10). This is similar to the experience with barley, but not that with oats where a high percentage of all the plants exposed to viruliferous aphids became infected (Table 8). However, in general, there was a trend toward a higher percentage infection with an increased number of viruliferous aphids. Only three plants in the test did not produce seed.

As observed with barley and oats, the period from inoculation to symptom expression in Selkirk was progressively shorter as the number of aphids used to initiate the BYDV infection was increased from one to 20 to 100 viruliferous aphids. The severity of the symptoms appeared to follow the same trend.

In general, of the plant responses measured, there were no consistent differences due to treatments except for plants exposed to 20 and 100 viruliferous aphids (Table 15). In these groups, height, head length, yield and kernel weight for the main culm, and yield and kernel weight for the whole plant were significantly reduced from that of the

TABLE 15

MEAN RESPONSES OF SELKIRK WHEAT TO INFESTATION WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

		Main culm						Whole plant		
Treatment	Plant reaction	Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)	Number fertile heads per plant	Number of seeds	Yield (g)	1000 kernel weight (g)
Control		70.45	7.27	18.15	0.69	38.35	4.17	77.82	2.74	35.07
1NV		69.45	7.56	19.38	0.75	39.42	4.13	79.65	2.88	36.16
20NV		70.50	7.46	19.80	0.76	39.40	4.30	81.00	2.87	35.56
100NV		69.36	7.89*	21.67**	0.80	36.96	4.23	78.64	2.76	35.50
1V	-	69.06	7.77**	20.79*	0.78*	38.32	4.41	84.17	2.90	34.68
20V	-	64.40*	6.58	16.20	0.55	34.12	5.00	64.60	1.76*	27.56**
100V	-	59.00*	6.20	13.00	0.46	35.64	5.50	78.50	1.87	26.44
1V	+	66.47	7.02	17.63	0.62	35.82	4.58	75.79	2.30	30.73*
20V	+	64.40**	6.71**	16.91	0.57**	33.68**	5.23*	76.71	2.19**	28.82**
100V	+	63.71**	6.39**	15.95	0.56**	35.28*	5.73**	76.68	2.28*	30.06**

*,** significantly different from control at 0.05 and 0.01 levels of probability, respectively
NV plants infested with nonviruliferous Rhopalosiphum padi(L.)
V plants infested with viruliferous (BYDV isolate 6801) R. padi
- not infected
+ infected

controls. The number of seeds was not affected for either the main culm or the whole plant, but the number of fertile tillers was significantly increased. Although statistically significant, the differences, ranging mainly from 10 to 15%, were small relative to those experienced with barley and oats.

As with barley and oats there was generally no effect on wheat due to exposure to nonviruliferous aphids. However, some inconsistencies occurred. Most cannot be explained satisfactorily. For example, in treatments 100NV and 1V-, the increases in head length and number of seeds in the main culm are probably related, but the cause is unknown.

Some apparent inconsistencies in the results are a reflection of small sample size in some treatments. For example, there were only five and two plants, respectively, in treatments 20V- and 100V-. The small number of replicates appears, firstly, to have led to a bias in the results for these treatments and, secondly, to difficulties in analysis of the data. Due to the small sample size, differences were not detected with the same sensitivity as with a large sample size and in some cases were not detected at all. For example, values for height of main culm in these treatments were detected only at the 5% level of significance, whereas, in treatments with a larger number of replicates values with lesser differences were detected at the 1% level. Similarly, because of a small number of replicates yields of 0.55 g and 0.46 g were not detected as significantly lower than that of the control, whereas, with a larger number of replicates, yields

of 0.57 g and 0.56 g were detected as such at the 1% level of significance. Similar circumstances accounted for other apparent inconsistencies.

There was evidence of effect of dosage of BYDV in four of the plant responses measured. For the main culm, height and yield were not significantly different from the control for plants exposed to one viruliferous aphid, but they were different for plants exposed to 20 and 100 viruliferous aphids. This is not a dosage effect in the same sense as has been demonstrated for oats and barley where differences due to increased numbers of aphids occurred among infected plants. Nevertheless, these can be considered as true dosage effects. There was a dosage effect demonstrated for head length of the main culm where there was a significant difference in length between plants exposed to one viruliferous aphid and plants exposed to 100 viruliferous aphids (Table 16). A similar example of dosage was noted in the number of fertile heads per plant.

Each of the three cereals responded differently to inoculation with the three levels of viruliferous aphids. In Herta barley, the number of fertile tillers, number of seeds and kernel weight were all reduced. These effects were reflected in a reduced yield from the whole plant. These effects became more pronounced as the number of viruliferous aphids used to initiate the virus infection was increased. In Rodney oats, the number of fertile tillers and the number of seeds were reduced, but the kernel weight was not. In fact, in treatment 1V+, the kernel weight was significantly higher

TABLE 16

DIFFERENCES IN RESPONSES OF SELKIRK WHEAT TO INFESTATION BY INCREASING NUMBERS OF VIRULIFEROUS APHIDS

Comparison	Main culm					Number fertile heads per plant	Whole plant		
	Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)		Number of seeds	Yield (g)	1000 kernel weight (g)
1V+ vs 20V+	NS	NS	NS	NS	NS	NS	NS	NS	NS
20V+ vs 100V+	NS	NS	NS	NS	NS	NS	NS	NS	NS
1V+ vs 100V+	NS	*	NS	NS	NS	*	NS	NS	NS
Dosage effect	No	Yes	No	No	No	Yes	No	No	No

NS,* not significantly different and significantly different at 0.05 level of probability
V+ plants infected by BYDV isolate 6801 transmitted by Rhopalosiphum padi (L.)

than that for the controls. The reason for this lies in the fact that infected plants produce few seeds which tend to be heavier than normal due to limited interseed competition. Further, this response would be expected to be greatest in treatment 1V+ since BYDV infection initiated by one viruliferous aphid is generally less severe than that initiated by 20 or 100 viruliferous aphids. The reduction in the number of seeds, and also the yield, became more pronounced as the number of viruliferous aphids used to initiate the infection was increased. In Selkirk wheat the kernel weight was reduced, the number of fertile tillers was increased, but the seed number remained constant. The yield of the whole plant was reduced to approximately the same extent regardless of the number of viruliferous aphids used to initiate the infection.

Effect of different dosages of inoculum on the responses of barley, oats and wheat using BYDV isolate 7005 and the corn leaf aphid as vector

In the preceding experiments some responses of cereals to different doses of inoculum of BYDV isolate 6801, transmitted by the bird cherry oat aphid, were examined. The bird cherry oat aphid was used as the vector as it is considered to be the most efficient vector among the species of aphids occurring in Manitoba. Isolate 6801 of BYDV is a nonspecific isolate which is considered to be severe on oats.

In the experiments to follow, isolate 7005 of BYDV, specific for the corn leaf aphid, was used. It was selected, firstly, because it is an isolate about which little is known, and secondly, because, in some years, the corn leaf aphid is very abundant on cereals, especially

barley, in Manitoba.

Herta barley

With BYDV isolate 7005 and the corn leaf aphid as vector, the pattern of plant responses was essentially the same as that with isolate 6801 and the bird cherry oat aphid. However, the responses were of a lower magnitude and, in most cases, although the trend was obvious, the observed differences were not statistically significant (Table 17). For example, for the main culm, head length, number of seeds, yield and to a lesser extent kernel weight of infected plants were reduced from that of the controls and plants exposed to nonviruliferous aphids. The number of seeds, yield and kernel weight were similarly reduced for the whole plant. The actual yield of the infected plants was reduced by about 20% from that of the controls, and although this was not detected as statistically significant, the reduction was substantial. This follows the same trend as that established in the previous experiment with barley where seed yield was reduced due to a reduction in both number of seeds and weight per seed.

There were no significant differences, for any of the responses measured, due to differences in numbers of viruliferous aphids used to initiate infections. That is, although trends were apparent, there were no detectable dosage effects (Table 18).

It is apparent, from these results, that isolate 7005 was less virulent than isolate 6801 on Herta barley since in all the plant responses measured the effect was more severe with the latter isolate. In addition, many plants failed to produce seed when infected with

TABLE 17

MEAN RESPONSES OF HERTA BARLEY TO INFESTATION WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

Treatment	Plant reaction	Main culm					Number fertile heads per plant	Whole plant		
		Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)		Number of seeds	Yield (g)	1000 kernel weight (g)
Control		59.25	6.16	16.16	0.63	38.74	6.26	78.46	3.02	37.87
1NV		59.30	6.50	16.23	0.67	41.46	5.80	71.67	2.73	37.73
20NV		57.87	6.07	16.11	0.65	40.32	5.50	71.03	2.72	36.79
100NV		59.45	6.40	17.26	0.69	39.89	6.45	87.00	3.30	37.17
1V	-	58.10	6.01	15.97	0.63	39.78	6.21	83.57	3.02	36.85
20V	-	56.55	5.56	14.44	0.59	41.77	4.60	59.20	2.25	38.03
100V	-	61.57	6.60	17.14	0.65	38.10	6.14	79.00	2.83	34.19
1V	+	58.14	5.87	14.29	0.57	40.08	5.00*	57.14*	2.23	38.44
20V	+	59.54	5.78	14.48	0.55	38.40	6.33	72.13	2.60	35.81
100V	+	58.73	5.89	15.00	0.54	36.44	6.03	68.37	2.40	35.25*

* significantly different from control at 0.05 level of probability
NV plants infested with nonviruliferous Rhopalosiphum maidis (F.)
V plants infested with viruliferous (BYDV isolate 7005) R. maidis
\- not infected
\+ infected

TABLE 18

DIFFERENCES IN RESPONSES OF HERTA BARLEY TO INFESTATION BY INCREASING NUMBERS OF VIRULIFEROUS APHIDS

Comparison	Main culm					Number fertile heads per plant	Whole plant		
	Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)		Number of seeds	Yield (g)	1000 kernel weight (g)
1V+ vs 20V+	NS	NS	NS	NS	NS	NS	NS	NS	NS
20V+ vs 100V+	NS	NS	NS	NS	NS	NS	NS	NS	NS
1V+ vs 100V+	NS	NS	NS	NS	NS	NS	NS	NS	NS
Dosage effect	No	No	No	No	No	No	No	No	No

NS not significantly different
V+ plants infected by BYDV isolate 7005 transmitted by Rhopalosiphum maidis (F.)

isolate 6801 but not so with isolate 7005. Isolate 7005 thus appears to have a more favourable relationship with this host than does isolate 6801, and is better adapted as a parasite since it did not cause sterility.

Rodney oats

In this experiment, the responses of oats to infection with BYDV isolate 7005 were similar to those with isolate 6801. Symptoms of BYDV appeared progressively earlier, on infected plants, as the number of viruliferous aphids used to initiate the infection was increased. As in the previous trial with oats, height, head length, number of seeds and yield of the main culm, and number of fertile heads, number of seeds and yield of the whole plant were reduced significantly in comparison to the controls (Table 19). Also, as in the previous trial, kernel weight was not reduced on infected plants.

There were some inconsistencies in the results. For example, the number of seeds on the main culm was significantly greater on plants exposed to one nonviruliferous aphid than on the controls. Since kernel weight remained constant, the yield of plantsin this treatment was also significantly greater than that for the control. As before, no explanation can be offered for this result, particularly since plants with 20 and 100 nonviruliferous aphids were not affected. There were also some anomalies such as occurred with the number of seeds for the main culm. A value of 57.20, for treatment 1NV, was detected as significantly different from that of the controls, whereas, a value of 57.86, for treatment 100V-, was not. Again, this was probably

TABLE 19

MEAN RESPONSES OF RODNEY OATS TO INFESTATION WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

Treatment	Plant reaction	Main culm					Number fertile heads per plant	Whole plant		
		Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)		Number of seeds	Yield (g)	1000 kernel weight (g)
Control		97.00	19.32	49.29	1.74	35.51	2.71	77.87	2.75	35.54
1NV		98.95	19.52	57.20*	2.00*	34.89	2.80	87.02	3.06	35.13
20NV		97.72	19.67	53.35	1.83	34.32	2.72	81.55	2.81	34.32
100NV		96.60	19.35	49.20	1.77	35.00	2.90	81.97	2.79	34.28
1V	-	97.09	19.25	54.21	1.88	34.64	2.81	84.09	2.92	34.73
20V	-	92.50	17.75	45.50	1.44	31.18	3.25	67.00	2.08	29.77
100V	-	102.00	20.00	57.86	2.07	35.66	1.86*	79.71	2.78	34.85
1V	+	93.89	18.79	31.89**	1.25**	37.37	1.47**	35.26**	1.37**	41.78
20V	+	92.28*	18.19**	25.44**	1.02**	40.14**	1.39**	27.86**	1.10**	39.71**
100V	+	91.48**	16.88**	22.19**	0.78**	34.82	1.39**	23.19**	0.80**	34.04

*,** significantly different from control at 0.05 and 0.01 levels of probability, respectively
NV plants infested with nonviruliferous Rhopalosiphum maidis (F.)
V plants infested with viruliferous (BYDV isolate 7005) R. maidis
- not infected
+ infected

due to inadequate replication.

Dosage effects were noted in all but two of the responses measured (Tables 19 and 20). For height of the main culm, the dosage effect was apparent only in the sense that plants infected with 20 or 100 viruliferous aphids were significantly shorter than the controls, whereas, plants infected with one viruliferous aphid were not shorter. For head length, the situation was similar except that in addition there were dosage effects between the groups of plants, 1V+, 20V+ and 100V+, infected by the different levels of aphids (Table 20). In the other cases, the effect of dosage was apparent only between plants infected with the different levels of viruliferous aphids. This was most pronounced for yield where there was a progressively greater loss with 20 viruliferous aphids than with one viruliferous aphids, and similarly with 100 viruliferous aphids than with 20 viruliferous aphids.

As observed before, there was no dosage effect for kernel weight since this value remained relatively constant whether or not the plants were infected. Although there was a trend toward dosage effect in the number of fertile tillers between plants infected by one and 20 or 100 viruliferous aphids, the difference was not detected as significant. The low value for plants exposed to 100 nonviruliferous aphids per plant appears to be due to inadequate sample size. However, there is a possibility that some plants in this group were infected, thus accounting for the reduced number of fertile heads.

Isolate 7005 was less virulent than isolate 6801, in that plant responses were of a lesser magnitude with isolate 7005 than with isolate 6801. For example, there was a greater yield loss with

TABLE 20

DIFFERENCES IN RESPONSES OF RODNEY OATS TO INFESTATION BY INCREASING NUMBERS OF VIRULIFEROUS APHIDS

Comparison	Main culm					Number fertile heads per plant	Whole plant		
	Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)		Number of seeds	Yield (g)	1000 kernel weight (g)
1V+ vs 20V+	NS	NS	*	*	NS	NS	*	*	NS
20V+ vs 100V+	NS	*	NS	*	*	NS	NS	*	*
1V+ vs 100V+	NS	**	**	**	NS	NS	**	**	NS
Dosage effect	No	Yes	Yes	Yes	No	No	Yes	Yes	No

NS,*,** not significantly different, significantly different at 0.05 and 0.01 levels of probability, respectively

V+ plants infected by BYDV isolate 7005 transmitted by Rhopalosiphum maidis (F.)

isolate 6801 initiated by one viruliferous aphid than with isolate 7005 initiated by 100 viruliferous aphids. The responses of Herta barley to infection by the two isolates also indicated that isolate 6801 was more virulent than isolate 7005.

Selkirk wheat

Symptoms of BYDV appeared earlier and were more pronounced when 100 viruliferous aphids were used to initiate the infection than when 20 viruliferous aphids or one viruliferous aphid were used. Nevertheless, symptoms of BYDV in wheat with isolate 7005 were generally mild and difficult to detect.

In the preceding experiments there have been no indications, apart from isolated and inconsistent responses, that plants were adversely affected by direct feeding by nonviruliferous aphids. This appears to be the case in this experiment also except for the mean head lengths of plants exposed to 100 nonviruliferous aphids and 20 and 100 viruliferous aphids that apparently did not transmit virus. The response for height and number of seeds, for these groups, was less consistent and, as shown, there was no effect on yield (Table 21). These responses, although statistically significant, are thus considered to have been spurious. However, there were consistent and significant differences, compared to the controls, in almost all the other responses measured, for plants exposed to 20 and 100 viruliferous aphids. This is in general agreement with the results of the previous experiment with Selkirk wheat using isolate 6801 (Table 15).

TABLE 21

MEAN RESPONSES OF SELKIRK WHEAT TO INFESTATION WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

Treatment	Plant reaction	Main culm					Number fertile heads per plant	Whole plant		
		Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)		Number of seeds	Yield (g)	1000 kernel weight (g)
Control		68.23	8.04	24.05	0.94	39.36	2.85	53.41	1.85	35.02
1NV		67.15	7.83	22.54	0.92	41.30	2.90	55.03	1.89	34.78
20NV		68.18	7.71	22.34	0.85*	38.26	2.72	52.79	1.75	33.73
100NV		67.67	7.69*	21.90*	0.86	39.24	2.50*	50.90	1.80	35.76
1V	-	65.84	7.94	23.14	0.87	37.89	2.65	50.59	1.69	33.22
20V	-	64.38	7.36*	17.75*	0.73	40.63	3.63	58.63	2.00	34.01
100V	-	54.67*	7.47**	23.00	0.73	31.74	3.00	52.67	1.52	27.41
1V	+	63.60	7.40	19.80	0.78	39.29	2.80	49.60	1.80	36.16
20V	+	58.40**	7.33**	18.37**	0.67**	36.45	3.55**	52.74	1.64	30.70**
100V	+	55.81**	7.16**	16.86**	0.63**	37.89	3.39*	47.69	1.51**	32.01*

*,** significantly different from control at 0.05 and 0.01 levels of probability, respectively
NV plants infested with nonviruliferous Rhopalosiphum maidis (F.)
V plants infested with viruliferous (BYDV isolate 7005) R. maidis
- not infected
+ infected

There was no dosage effect detected among plants exposed to the three levels of viruliferous aphids although a trend was evident in several of the plant responses measured (Table 22). However, as in the previous greenhouse experiment with wheat, a dosage effect was apparent in that values for responses of plants exposed to 20 and 100 viruliferous aphids were, in most cases, significantly different from the controls, whereas, those for plants exposed to one aphid per plant were not significantly different.

Isolate 7005 appeared to be less virulent than isolate 6801 on Selkirk wheat, although considering the number of aphids used, Selkirk was not severely affected by either of the isolates.

In general, the results of the greenhouse study reported in the preceding experiments confirm the dosage hypothesis of Smith and Richards (1963) and Smith (1967) that "strains of BYD virus . . . may have the severity of their effect modified by varying the number of aphids used for inoculation." Smith and Richards proposed their dosage hypothesis largely on the basis of severity of symptoms, but Smith (1967) later provided additional evidence in support of the hypothesis on the basis of yield. He showed that, with wheat, oats and barley, plants in which infection was initiated with a large number of aphids yielded less than plants in which infection was initiated by a small number of aphids. This was supported in the present study and information was also provided on a number of other responses, some of which indicated how the yield losses were brought about. For example, for Herta barley the number of seeds and kernel weight were both reduced, for Rodney oats the number of seeds was

TABLE 22

DIFFERENCES IN RESPONSES OF SELKIRK WHEAT TO INFESTATION BY INCREASING NUMBERS OF VIRULIFEROUS APHIDS

Comparison	Main culm					Number fertile heads per plant	Whole plant		
	Height (cm)	Head length (cm)	Number of seeds	Yield (g)	1000 kernel weight (g)		Number of seeds	Yield (g)	1000 kernel weight (g)
1V+ vs 20V+	NS	NS	NS	NS	NS	NS	NS	NS	NS
20V+ vs 100V+	NS	NS	NS	NS	NS	NS	NS	NS	NS
1V+ vs 100V+	NS	NS	NS	NS	NS	NS	NS	NS	NS
Dosage effect	No	No	No	No	No	No	No	No	No

NS not significantly different
V+ plants infected by BYDV isolate 7005 transmitted by Rhopalosiphum maidis (F.)

reduced, but kernel weight remained the same while for Selkirk wheat, the number of seeds remained the same and kernel weight was reduced.

The mode of action in infection of plants with different numbers of viruliferous aphids is unknown. However, it may be theorized that with a large number of viruliferous aphids the initial dosage or concentration of virus in a plant is higher than with a small number of viruliferous aphids. If it is assumed that virus multiplication follows a pattern, which may be represented by a sigmoid curve as shown by Verhoyen (1966), then the higher the initial concentration the more rapidly the curve will rise towards its maximum. Verhoyen (1966) showed this to be the case with alfalfa mosaic virus. As BYDV is a phloem blocking virus, the higher the initial concentration the more rapid and serious will be the blockage. This interferes with seed development and in turn with yield.

Variability among plants of Selkirk wheat grown in a greenhouse

In the greenhouse experiment in which Selkirk wheat was infected with BYDV isolate 6801 transmitted by the bird cherry oat aphid, it was observed that there was a large variation in yield among both infected and control plants (Table 23). It was decided to conduct a further greenhouse study to determine whether or not the variation in yield had a genetic or an environmental basis. To this end, seed from the 10 highest and 10 lowest yielding plants among those in which infection had been initiated with 100 viruliferous aphids was selected. Similarly seed was selected from the 10 highest and lowest yielding plants among the controls. Ten progeny of each of the plants

TABLE 23

YIELDS OF THE TEN HIGHEST AND TEN LOWEST YIELDING SELKIRK WHEAT PLANTS FROM EACH OF BYDV[1] INFECTED AND CONTROL GROUPS OF PLANTS IN GREENHOUSE EXPERIMENTS

Ten highest yielding plants			Ten lowest yielding plants		
Plant No.	Seed No.	Weight (g)	Plant No.	Seed No.	Weight (g)
		Virus infected plants			
1	123	3.91	1	49	1.08
2	126	3.80	2	43	1.28
3	113	3.64	3	53	1.36
4	105	3.48	4	46	1.41
5	71	3.46	5	42	1.42
6	108	3.23	6	47	1.44
7	109	3.23	7	51	1.53
8	121	3.14	8	46	1.55
9	115	3.11	9	53	1.55
10	101	2.93	10	51	1.56
		Control plants			
1	105	4.28	1	47	1.21
2	120	4.05	2	62	1.63
3	105	3.82	3	58	1.67
4	100	3.75	4	57	1.81
5	99	3.75	5	74	1.87
6	94	3.69	6	76	1.89
7	62	3.57	7	57	1.98
8	58	3.55	8	69	2.03
9	115	3.43	9	61	2.04
10	80	3.32	10	78	2.05

[1] virus isolate 6801 transmitted by Rhopalosiphum padi (L.)

were grown, five were infected with BYDV while five were kept as controls. The height and head length for the main culm at harvest, and the number of heads, number of seeds, 1000 kernel weight and yield, for the whole plant, were recorded (Table 24). Only those plants that were positively back-checked were considered to be infected with BYDV.

An analysis of variance (Appendix 10) showed that there was no significant difference, in any of the responses, whether the seed source was a high or a low yielding plant (Table 24). However, there was a significant difference for all responses between the control and infected plants from all the seed sources. The responses of the plants to BYDV infection followed much the same pattern as observed in the preceding experiments. The height, head length, number of seeds, yield and kernel weight were significantly reduced from that of the controls while the number of fertile heads was significantly increased. The reason for significant differences occurring between plants within groups (Appendix 10) is unknown.

This study has shown that the observed variability in yield of individual plants of Selkirk wheat in the greenhouse did not have a genetic basis, but was due solely to the environment. This is probably true for most cereals grown in greenhouse trials and thus points out the need for a large number of replicates to allow for environmental variation.

TABLE 24

SOME RESPONSES OF PROGENY FROM HIGH AND LOW YIELDING SELKIRK WHEAT PLANTS FROM EACH OF BYDV[1] INFECTED AND CONTROL GROUPS OF PLANTS IN GREENHOUSE EXPERIMENTS

	Progeny responses											
	Height of main culm (cm)		Head length main culm (cm)		Number of seeds per plant		Yield		Number of heads		1000 kernel weight (g)	
Seed source	Control	Infected	Control	Infected	Control	Infected	Control	Infected	Control	Infected	Control	Infected
Controls												
High yield	69.22	64.18**	8.70	7.87**	67.06	59.94**	2.29	1.92**	3.10	3.60**	34.05	31.89**
Low yield	69.44	64.00**	8.86	7.63**	74.56	54.30**	2.46	1.74**	3.39	3.62**	33.17	32.24**
Infected plants												
High yield	67.66	62.60**	8.95	7.87**	66.44	55.96**	2.33	1.75**	2.90	3.66**	35.19	31.43**
Low yield	68.06	62.26**	8.81	7.87**	69.00	56.98**	2.32	1.80**	3.10	3.52**	33.91	31.79**

[1]virus isolate 6801 transmitted by *Rhopalosiphum padi* (L.)
**infected significantly different from control at .01 level of probability

CHAPTER VI

SUMMARY AND CONCLUSIONS

Field trials were carried out in 1971, 1972 and 1973 to determine the effect of aphid feeding and barley yellow dwarf on the yield of barley, oats and wheat. In 1971, the English grain aphid was used as the vector of BYDV isolate 6801 with Conquest barley and Harmon oats in an experiment with six replicates of rod-row plots. In 1972, Manitou wheat was added and there were 12 replicates. In 1973, two levels of population of aphids with 20 replicates of hill plots were used to determine whether or not a dosage effect existed.

In 1971, there were no differences in yield or kernel weight for either barley or oats infested 50 days after seeding with nonviruliferous or viruliferous aphids at the rate of two aphids per three plants when compared to naturally infested plots or plots sprayed with Metasystox R.

In 1972, there were no significant differences in yield for barley when plants were infested 28 and 41 days after seeding. Yields from plots of oats infested with viruliferous aphids 28 days after seeding were significantly less than those of plots treated with Metasystox R, and kernel weight was lower than in any other treatment. No significant differences were observed for yield of wheat, but kernel weight was significantly lower in plots infested with viruliferous aphids than in the controls or plots sprayed with Metasystox R. No differences due to infestation with nonviruliferous aphids were observed for any of the cereals tested.

In 1973, barley was not significantly affected, for any of the responses measured, when plants were infested with nonviruliferous or viruliferous aphids at either 10 or 100 aphids per hill. Plant height, number of heads, kernel weight and seed yield per hill, for oats, were significantly reduced, from that of the controls, in hills infested with 100 viruliferous aphids 22 days after seeding. Hills treated with malathion gave the highest yields. For wheat, the number of heads and yield for hills infested with viruliferous aphids 22 days after seeding were significantly lower than those for hills treated with malathion. A dosage effect was apparent, particularly in oats, where all the plant responses observed were affected to a greater degree when hills were infested with 100 viruliferous aphids than with 10 viruliferous aphids.

In these experiments, only gross differences in plant response were detected because of limitations in experimental design, namely, the limited number of replicates. In experiments with small field plots where the coefficient of variation may be high, a large number of replicates are required. It is, therefore, essential to establish in advance the size of treatment differences to be detected so that the experiment may be designed accordingly.

In greenhouse trials, barley, oats and wheat were exposed to three levels (one, 20 and 100) of nonviruliferous and viruliferous aphids to examine more closely the dosage hypothesis. In three experiments, the bird cherry oat aphid was used as the vector of BYDV isolate 6801 and in a further three experiments, the corn leaf aphid was used as the vector of BYDV isolate 7005.

With Herta barley, the number of fertile tillers, the number of seeds and kernel weight were all reduced. These effects were reflected in a reduced yield from the whole plant. These effects were more pronounced and the number of sterile plants increased as the number of viruliferous aphids used to initiate the virus infection was increased.

With Rodney oats the number of fertile tillers and the number of seeds was reduced but the kernel weight was not. The reduction in the number of seeds, and also the yield became more pronounced as the number of viruliferous aphids used to initiate the infection was increased.

With Selkirk wheat the kernel weight was reduced, the number of fertile tillers was increased but the seed number remained constant. The yield of the whole plant was reduced to approximately the same extent regardless of the number of viruliferous aphids used to initiate the infection. The dosage effect demonstrated in wheat was not as pronounced as that in barley and oats.

When the corn leaf aphid was used as a vector of BYDV isolate 7005 the responses of Herta barley were essentially the same as those obtained with 6801 except that they were of much lower magnitude. There were no significant differences for any of the responses measured due to differences in number of viruliferous aphids used to initiate infections. A dosage trend was observed but no dosage effect could be measured.

With Rodney oats, with BYDV isolate 7005, dosage effects were

noted in all but two of the responses measured. This effect was most pronounced with yield where there was a progressively greater loss with 20 viruliferous aphids than with one viruliferous aphid, and similarly with 100 viruliferous aphids than with 20 viruliferous aphids.

With Selkirk wheat there was no dosage effect detected among plants exposed to the three levels of viruliferous aphids although a trend was evident in several of the plant responses measured. As in the previous experiment with wheat, there was a dosage effect apparent in the values of the responses measured for plants exposed to 20 or 100 viruliferous aphids but not those exposed to one viruliferous aphid.

In general, isolate 6801 of BYDV was more virulent than isolate 7005 for the varieties of cereals tested.

Throughout all the greenhouse trials there was no consistent indication that plants were adversely affected by direct feeding of nonviruliferous aphids.

A seventh greenhouse trial was conducted to determine the cause of the variability observed in individual plant yields in the greenhouse experiment in which Selkirk wheat was infected with BYDV isolate 6801 by the bird cherry oat aphid. This study showed that the observed variability in yield did not have a genetic basis, but was solely due to environment.

The following conclusions, subject to the limitations of the species and varieties used, were drawn from this study:

1. Feeding by nonviruliferous aphids even at densities of 100 aphids per plant for 2 days, is not detrimental to barley, oats or wheat.

2. Feeding by viruliferous aphids, even at low densities, causes adverse plant responses, such as, loss in yield in barley, oats and wheat, due to virus infection.
3. The magnitude of the response increases with increased numbers of viruliferous aphids.
4. Some isolates of BYDV are more virulent than others.
5. Significant increases in yield of oats and wheat may be obtained with the application of insecticides for control of aphids which are viruliferous.
6. Large numbers of replicates are required in experiments (small field plot or greenhouse) where the coefficient of variation is large.

BIBLIOGRAPHY

Aapola, A. I. E. 1968. Serological relationships and *in vivo* interactions among isolates of barley yellow dwarf virus. Ph.D. Thesis Cornell University, Ithaca, N.Y.

Adams, J. B. and M. E. Drew. 1965. Grain aphids in New Brunswick. III. Aphid populations in herbicide-treated oat fields. Can. J. Zool. 43: 789-794.

Adams, J. B. and M. E. Drew. 1969. Grain aphids in New Brunswick. IV. Effect of malathion and 2,4-D amine on aphid populations and on yield of oats and barley. Can. J. Zool. 47: 423-426.

Allen, T. C. 1957. Strains of the barley yellow-dwarf virus. Phytopathology 47: 481-490.

Apablaza, J. U. and A. G. Robinson. 1967. Effects of three species of aphids on barley, wheat or oats at various stages of plant growth. Can. J. Plant Sci. 47: 367-373.

Barrus, M. F. 1937. Red leaf and blast of oats. Pl. Dis. Reptr 21: 359-361.

Bindra, O. S. and E. S. Sylvester. 1961. Effect of insect numbers on aphid transmission of potato leafroll virus. Hilgardia 31: 279-325.

Bremer, K. 1965. Characteristics of the barley yellow dwarf in Finland. (Abstr.) Annls. agric. Fenn. 4: 105-120.

Browning, J. Artie, J. G. Wheat and K. J. Frey. Yellow dwarf of oats in Iowa in 1959. Pl. Dis. Reptr Suppl. 262: 336-341.

Bruehl, G. W. 1958. Comparison of eastern and western aphids in the transmission of barley yellow dwarf virus. Pl. Dis. Reptr 42: 909-911.

Bruehl, G. W. 1961. Barley yellow dwarf, a virus disease of cereals and grasses. Monograph No. 1, American Phytopath. Soc., 52 pp.

Bruehl, G. W. and V. D. Damsteegt. 1959. Observations on cereal yellow dwarf of oats in Washington in 1959. Pl. Dis. Reptr Suppl. 262: 369-370.

Bruehl, G. W., H. H. McKinney and H. V. Toko. Cereal yellow dwarf as an economic factor in small grain production in Washington, 1955-1958. Pl. Dis. Reptr 43: 471-474.

Bruehl, G. W. and H. V. Toko. 1957. Host range of two strains of the cereal yellow-dwarf virus. Pl. Dis. Reptr 41: 730-734.

Burnett, P. A. and R. J. Baker. 1973. Number of replicates required in experiments designed to determine yield loss on small plots. Man. Ent. 6 (1972): 27-31.

Burnett, P. A. and A. G. Robinson. 1973. Effect of barley yellow dwarf virus on yield of cereals in field plots in Manitoba, 1971-1972. Man. Ent. 6 (1972): 32-34.

Butler, F. C., N. E. Grylls and D. J. Goodchild. 1959. The occurrence of barley yellow dwarf virus in New South Wales. J. Aust. Inst. Agric. Sci. 26: 57-59.

Caldwell, R. M., M. C. Wilson and J. F. Schafer. 1959. Protection of oats against transmission of barley yellow dwarf virus through control of aphids with dimethoate. Pl. Dis. Reptr Suppl. 262: 334-335.

Carsner, E. and C. F. Lackey. 1929. Mass action in relation to infection with special reference to curly top of sugar beet. (Abstr) Phytopathology 19: 1137.

Carter, W. and C. T. Schmidt. 1935. Mass action phenomena in mealybug wilt. Ann. Ent. Soc. Am. 28: 296-403.

Catherall, P. L. 1965. Barley yellow-dwarf virus. In Rept. Welsh Pl. Breed. Stn., 1964, p. 101.

Catherall, P. L. 1966a. Effects of barley yellow dwarf virus on the growth and yield of single plants and simulated swards of perennial ryegrass. Ann. appl. Biol. 57: 155-162.

Catherall, P. L. 1966b. Field-inoculating barley with the yellow-dwarf virus. Pl. Path. 15: 41-43.

Chiykowski, L. N. and R. K. Chapman. 1965. Migration of the six-spotted leafhopper in central North America. Part 2 of Migration of the six-spotted leafhopper Macrosteles fascifrons (Stål). Research Bulletin 261, University of Wisconsin, August 1965. p. 23-45.

Close, R. C. 1969. Summary of trials for the control of barley yellow dwarf virus. Proc. 22nd N. Z. Weed and Pest Control Conf. p. 214-226.

Cochran, W. G. and G. M. Cox. 1957. Experimental designs. John Wiley and Sons, New York. Second Edition 611 pp.

Doodson, J. K. 1967. A survey of barley yellow dwarf virus in perennial ryegrass in England and Wales 1966. Pl. Path. 16: 42-45.

Doodson, J. K. and P. J. W. Saunders. 1970. Some effects of barley yellow dwarf virus on spring and winter cereals in glass-house trials. Ann. appl. Biol. 65: 317-325.

Endo, R. M. 1957. The effect of shading and of temperature upon the expression of symptoms in cereals infected with barley yellow dwarf virus. (Abstr.) Phytopathology 47: 520.

Endo, R. M. and C. M. Brown. 1957. Effect of yellow-dwarf on the yield of oats. Agron. J. 49: 503-505.

Endo, R. M. and C. M. Brown. 1963. Effects of barley yellow dwarf virus on yield of oats as influenced by variety, virus strain, and development stage of plant at inoculation. Phytopathology 53: 965-968.

Esau, K. 1957a. Phloem degeneration in Graminae affected by the barley yellow-dwarf virus. Am. J. Bot. 44: 245-251.

Esau, K. 1957b. Anatomic effects of barley yellow dwarf virus and maleic hydrazide on certain Graminae. Hilgardia 27: 15-69.

Fehn, L. M. 1970. Estudos da acao de insecticidas granulados sistemicos e de profundidade, no controle de pulgoes, em trigo. [Studies on the action of granular systemic insecticides for soil application for control of aphids on wheat.] (Abstr.) Pesqui. Agropecu. Bras. 5: 259-264.

Forbes, A. R. 1962. Aphid populations and their damage to oats in British Columbia. Can. J. Plant Sci. 42: 660-666.

Galloway, B. T. and E. A. Southwood. 1890. Preliminary notes on a new and destructive oat disease. J. Mycol. 6: 72-73.

Gibbs, A. J. and J. C. Gower. 1960. The use of a multiple-transfer method in plant virus transmission studies--some statistical points arising in the analysis of results. Ann. appl. Biol. 48: 75-83.

Giddings, N. J. 1946. Mass action as a factor in curly-top virus infection of sugar beet. Phytopathology 36: 53-56.

Gill, C. C. 1967a. Transmission of barley yellow dwarf virus isolates from Manitoba by five species of aphids. Phytopathology 57: 713-718.

Gill, C. C. 1967b. Susceptibility of common and durum spring wheats to barley yellow dwarf virus. Can. J. Plant Sci. 47: 571-576.

Gill, C. C. 1969a. Cyclical transmissibility of barley yellow dwarf virus from oats with increasing age of infection.

Gill, C. C. 1969b. Annual variation in strains of barley yellow dwarf virus in Manitoba, and the occurrence of greenbug-specific strain isolates. Can. J. Bot. 47: 1277-1283.

Gill, C. C. 1970a. Aphid nymphs transmit an isolate of barley yellow dwarf virus more efficiently than do adults. Phytopathology 60: 1747-1752.

Gill, C. C. 1970b. Epidemiology of barley yellow dwarf in Manitoba and effect of the virus on yield of cereals. Phytopathology 60: 1826-1830.

Gill, C. C. 1972. Further studies on the transmission of certain isolates of barley yellow dwarf virus by nymphs and adults of Rhopalosiphum maidis. Can. J. Plant Sci. 52: 107-109.

Gill, C. C., K. W. Buchannon and P. H. Westdal. 1969. Susceptibility to the yellow dwarf virus of barley varieties grown in Manitoba and assessment of African varieties for tolerance. Can. J. Plant Sci. 49: 287-292.

Gill, C. C. and P. H. Westdal. 1966. Effect of temperature on symptom expression of barley infected with aster yellows or barley yellow dwarf virus. Phytopathology 56: 369-370.

Gill, C. C., P. H. Westdal and H. P. Richardson. 1969. Comparison of aster yellows and barley yellow dwarf of wheat and oats. Phytopathology 59: 527-531.

Halstead, B. E. and C. C. Gill. 1971a. Transmission of barley yellow dwarf virus by different stages of the greenbug. Phytopathology 61: 749-750.

Halstead, B. E. and C. C. Gill. 1971b. Effect of inoculation of oats with paired combinations of barley yellow dwarf isolates. Can. J. Bot. 49: 577-581.

Harpaz, I. and M. Klein. 1969. Occurrence of barley yellow dwarf virus (BYDV) in Israel. Pl. Dis. Reptr 49: 34-35.

Harper, A. M. 1973. English grain aphid: Effect on yield of wheat in Alberta. J. econ. Ent. 66: 1326.

Harwood, R. F. and G. W. Bruehl. 1961. Seed systemics for control of aphids on oats and barley. J. econ. Ent. 54: 883-885.

Holmes, Francis O. 1929. Local lesions in tobacco mosaic. Bot. Gaz. 87: 39-55.

Hooker, W. J., and A. P. Benson. 1960. Time of response in Datura tatula L. to potato virus X as a function of virus concentration. Virology 10: 245-256.

Jacob-Haupt, R. 1969. Zur Bekampfung von Blattlausen an Getreide. [On the control of aphids on cereals.] (Abstr.) Anz Schaedlingskd Pflanzenschutz 42: 150-153.

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.

Jenkins, G. 1966. Comparison of tolerance to barley yellow dwarf virus in barley and oats. Ann. appl. Biol. 57: 163-168.

Jensen, D. D., N. W. Frazier and H. E. Thomas. 1952. Insect transmission of yellow leaf roll of peach. J. econ. Ent. 45: 335-337.

Jensen, R. E. and J. R. Wallin. 1965. Weather and aphids: a review. U. S. Dept. of Commerce. Technical note 5 - Agmet-1: 19 pp.

Jensen, S. G. 1968. Photosynthesis, respiration, and other physiological relationships in barley infected with barley yellow dwarf virus. Phytopathology 58: 204-208.

Jensen, S. G. 1969a. Occurrence of virus particles in the phloem tissues of BYDV-infected barley. Virology 38: 83-91.

Jensen, S. G. 1969b. Composition and metabolism of barley leaves infected with barley yellow dwarf virus. Phytopathology 59: 1694-1698.

Jensen, S. G. 1972. Metabolism and carbohydrate composition in barley yellow dwarf virus-infected wheat. Phytopathology 62: 587-592.

Johnston, C. O. 1951. The "red leaf" disease of oats still a mystery in Kansas. 1950 Oat National Newsletter 1: 20-21.

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.

Kemeny, L. J., L. O. Mott and J. E. Pearson. 1971. Titration of equine infectious anemia virus. Effect of dosage on incubation time and clinical signs. Cornell Vet. 61: 687-695.

Kennedy, J. S., M. F. Day and V. F. Eastop. 1962. A conspectus of aphids as vectors of plant viruses. Commonw. Inst. Ent. London 114 pp.

Kirkpatrick, H. C. and A. F. Ross. 1952. Aphid-transmission of potato leafroll virus on solanaceous species. Phytopathology 42: 540-546.

Kolbe, W. 1969. Studies on the occurrence of different aphid species as the cause of cereal yield and quality losses. Pflanzenschutz-Nachr. 22: 171-204.

Kolbe, W. 1970. Further studies on the reduction of cereal yields by aphid infestation. Pflanzenschutz-Nachr. 23: 144-162.

Kristensen, H. R. and B. Engsbro. 1966. Havre-rodsof [Barley yellow dwarf] (Abstr.) Tidsskr. Planteaul 70: 209-223.

Lopez, G. M. and G. E. Galvez. 1969. Identification del virus del enanismo amarillo de la cebada on Columbia [Identification of barley yellows-dwarf virus in Columbia]. (Abstr.) Rev. Inst. Colomb. Agropec 4: 45-52.

Lowe, A. D. 1968. Alate aphids trapped over 8 years at two sites in Canterbury, New Zealand. N. Z. Jl. agric. Res. 11: 829-847.

Martens, J. W. and W. C. McDonald. 1970. Assessment of yield losses from barley yellow dwarf in oats. Can. Plant Dis. Surv. 50: 88-89.

McKinney, H. H. 1950. Infectious and non-infectious pigment disorders in the small grains, with particular reference to the southeastern areas. Pl. Dis. Reptr 34: 151-154.

Moore, M. B. 1952. The cause and transmission of blue dwarf and red leaf of oats. (Abstr.) Phytopathology 42: 471.

Nagaich, B. B. and K. S. Vashisth. 1963. Barley yellow dwarf: a new viral disease for India. Indian Phytopath. 16: 318-319.

Oppitz, K. 1970. Einfub von getreidevirosen auf ertag und korneigenschaften von gersten-, weizen- und hafersorten bei vershiedenen infektionszeitpunkten. [Effect of cereal virus diseases on yield and grain characteristics of barley, wheat and oat varieties as influenced by the date of infection]. Z. Acker-Pflanzenbau 131: 302-324.

Orlob, G. B. 1959. Studies on the barley yellow dwarf virus disease. Ph.D. Thesis of the Univ. of Wisconsin.

Orlob, G. B. 1962. Further studies on the transmission of plant viruses by different forms of aphid. Virology 16: 301-304.

Orlob, G. B. and D. C. Arny. 1959. Observations on vectors of barley yellow dwarf virus in Wisconsin. Pl. Dis. Reptr Suppl. 262: 375.

Orlob, G. B. and D. C. Arny. 1960. Transmission of barley yellow dwarf virus by different forms of the apple grain aphid, Rhopalosiphum fitchii (Sand.). Virology 10: 273-274.

Orlob, G. B. and D. C. Arny. 1961. Influence of some environmental factors and growth substances on the development of barley yellow dwarf. Pl. Dis. Reptr 45: 192-195.

Oswald, J. W. and B. R. Houston. 1951. A new virus disease of cereals, transmissible by aphids. Pl. Dis. Reptr 35: 471-475.

Oswald, J. W. and B. R. Houston. 1953a. The yellow-dwarf virus disease of cereal crops. Phytopathology 43: 128-136.

Oswald, J. W. and B. R. Houston. 1953b. Host range and epiphytology of the cereal yellow dwarf disease. Phytopathology 43: 309-313.

Oswald, J. W. and T. H. Thung. 1955. The barley yellow dwarf virus disease on cereal crops in the Netherlands. (Abstr.) Phytopathology 45: 695.

Paliwal, Y. C. and R. C. Sinha. 1970. On the mechanism of persistence and distribution of barley yellow dwarf virus in an aphid vector. Virology 42: 668-680.

Palmer, L. T. and W. H. Sill, Jr. 1966. Effect of barley yellow dwarf virus on wheat in Kansas. Pl. Dis. Reptr 50: 234-238.

Price, R. D. and W. E. Birkenhead. 1971. Barley yellow dwarf virus (BYDV). In Victorian Plant Research Institute Report No. 6 Jan. 1970-Dec. 1971 p. 44-45.

Raatikainen, M. and A. Tinnita. 1961. Occurrence and control of aphids causing damage to cereals in Finland in 1959. Publ. Finn. State Agric. Res. Board 183: 5-27.

Rautapää, J. 1966. The effect of the English grain aphid Macrosiphum avenae (F.) (Hom., Aphididae) on the yield and quality of wheat. Annls. agric. Fenn. 5: 334-341.

Rautapää, J. 1968. Reduction in yield and changes in brewing quality of barley caused by Macrosiphum avenae (F.) (Hom: Aphididae). Acta. Agric. Scand. 18: 233-241.

Robinson, A. G. and Sze-Jih Hsu. 1963. Host plant records and biology of aphids on cereal grains and grasses in Manitoba (Homoptera: Aphididae). Can. Ent. 95: 134-137.

Rochow, W. F. 1958a. Barley yellow dwarf virus disease of oats in New York. Pl. Dis. Reptr 42: 36-41.

Rochow, W. F. 1958b. The role of aphids in vector specificity of barley yellow dwarf virus. Pl. Dis. Reptr 42: 905-908.

Rochow, W. F. 1959a. Transmission of strains of barley yellow dwarf virus by two aphid species. Phytopathology 49: 744-748.

Rochow, W. F. 1959b. Differential transmission of barley yellow dwarf virus from field samples by four aphid species. Pl. Dis. Reptr Suppl. 262: 356-359.

Rochow, W. F. 1960. Specialization among greenbugs in the transmission of barley yellow dwarf virus. Phytopathology 50: 881-884.

Rochow, W. F. 1961a. Vector specificity of three strains of barley yellow dwarf virus. (Abstr.) Phytopathology 51: 578-579.

Rochow, W. F. 1961b. A strain of barley yellow dwarf virus transmitted specifically by the corn leaf aphid. Phytopathology 51: 809-810.

Rochow, W. F. 1961c. The barley yellow dwarf virus disease of small grains. Adv. Agron. 13: 217-248.

Rochow, W. F. 1965. Apparent loss of vector specificity following double infection by two strains of barley yellow dwarf virus. Phytopathology 55: 62-68.

Rochow, W. F. 1969a. Biological properties of four isolates of barley yellow dwarf virus. Phytopathology 59: 1580-1589.

Rochow, W. F. 1969b. Specificity in aphid transmission of a circulative plant virus. In Viruses, Vectors and Vegetation. Maramorosch Ed. Interscience Publishers New York p. 175-198.

Rochow, W. F. 1970. Barley yellow dwarf virus: Phenotypic mixing and vector specificity. Science 167: 875-878.

Rochow, W. F. 1972. The role of mixed infections in the transmission of plant viruses by aphids. Ann. Rev. Phytopath. 10: 101-124.

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.

Rochow, W. F. and V. F. Eastop. 1966. Variation within Rhopalosiphum padi and transmission of barley yellow dwarf virus by clones of four aphid species. Virology 30: 286-296.

Rochow, W. F. and Irmgard Muller. 1971. A fifth variant of barley yellow dwarf virus in New York. Pl. Dis. Reptr 55: 874-877.

Roland, G. 1960. Note preliminaire sur une virose des cereales. (Abstr.) Parasitica 16: 62-65.

Roland, G. 1962. Recherches effectuees sur le virus de la jaunisse de l'orge (barley yellow dwarf virus) (Research carried out on the barley yellow-dwarf virus). (Abstr.) Viertiende Internationaal Symposium over Fytofarmacie en Fytiatrie, 8 mei 1962 - Meded Landb Hogesch. Gent. 27 No. 3 3pp [5+] 671-1370. Ghent 1962.

Rothman, P. G. 1966. Summer hosts of barley yellow dwarf virus in the Mississippi delta. Pl. Dis. Reptr 50: 692-693.

Rothman, P. G., D. H. Bowman and S. S. Ivanoff. 1959. Occurrence of barley yellow dwarf on oats in Mississippi, 1959. Pl. Dis. Reptr Suppl. 262: 348-350.

Saksena, K. N., S. R. Singh and W. J. Sill, Jr. 1964. Transmission of barley yellow-dwarf virus by four biotypes of the corn leaf aphid, Rhopalosiphum maidis. J. econ. Ent. 57: 569-570.

Sanderson, F. R. and R. I. Mulholland. 1969. Effect of the grain aphid on yield and quality of wheat. Proc. 22nd. N. Z. Weed and Pest Control Conf. 227-235.

Sanderson, F. R. and R. I. Mulholland. 1970. The grain aphid and its control. N. Z. Wheat Rev. 11: 44-47.

Sechler, D. T., J. M. Pehlman, M. D. Whitehead and O. H. Calvert. 1959. The barley yellow dwarf virus-bacterial blight complex on oats in Missouri 1959. Pl. Dis. Reptr Suppl. 262: 351-353.

Severin, H. H. P. 1931. Modes of curly-top transmission by the leafhopper, Eutettix tennellus (Baker). Hilgardia 6: 254-276.

Sheffield, F. M. L. 1957. Virus disease of sweet potato in east Africa. I. Identification of the viruses and their insect vectors. Phytopathology 47: 582-590.

Sill, W. H. Jr., Claude L. King and Elmer G. Heyne. 1959. Barley yellow dwarf in Kansas oats and barley in 1959. Pl. Dis. Reptr Suppl. 262: 342-345.

Slykhuis, J. T. 1962. An international survey for virus diseases of grasses. F. A. O. Plant Prot. Bull. 10, 15 pp.

Slykhuis, J. T. 1967. Virus disease of cereals. Rev. appl. Mycol. 46: 401-429.

Slykhuis, J. T., F. J. Zillinsky, A. E. Hannah and W. R. Richards. 1959a. Barley yellow dwarf virus on cereals in Ontario. Pl. Dis. Reptr 43: 849-854.

Slykhuis, J. T., F. J. Zillinsky, M. Young and W. R. Richards. 1959b. Notes on the epidemiology of barley yellow dwarf virus in eastern Ontario in 1959. Pl. Dis. Reptr Suppl. 262: 317-322.

Smith, H. C. 1955. Report on yellow dwarf in wheat and oats in New Zealand. Commonw. Phytopath. News 1: 10-11.

Smith, H. C. 1959. Yellow-dwarf virus of wheat. N. Z. Wheat Rev. 7: 51-56.

Smith, H. C. 1963a. Aphid species in relation to the transmission of barley yellow dwarf virus in Canada. N. Z. Jl. agric. Res. 6: 1-12.

Smith, H. C. 1963b. Control of barley yellow dwarf virus in cereals. N. Z. Jl. agric. Res. 6: 229-244.

Smith, H. C. 1963c. Interactions between isolates of barley yellow dwarf virus. N. Z. Jl. agric. Res. 6: 343-353.

Smith, H. C. 1967. The effect of aphid numbers and stage of plant growth determining tolerance to barley yellow dwarf virus in cereals. N. Z. Jl. agric. Res. 10: 445-466.

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. Jl. agric. Res. 11: 500-505.

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. Ent. 95: 537-547.

Smith, H. C. and G. M. Wright. 1964. Barley yellow dwarf virus on wheat in New Zealand. N. Z. Wheat Rev. 9: 60-79.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Company, Inc., New York, Toronto, London, 481 pp.

Stern, V. M. 1967. Control of aphids attacking barley and analysis of yield increases in the Imperial Valley of California. J. econ. Ent. 60: 485-490.

Storey, H. H. 1938. Investigations of the mechanism of the transmission of plant viruses by insect vectors. II. Proc. Roy. Soc. Lond. Ser. B 125: 455-477.

Suneson, C. A. and R. T. Rammage. 1957. Studies on the importance of the yellow-dwarf virus. Agron. J. 49: 365-367.

Swenson, K. G. 1967. Plant virus transmission by insects. In Methods in Virology Vol. 1. Ed. K. Maramorosch and H. Koprowski, p. 267-307.

Swenson, K. G. 1969. Plant susceptibility to virus infection by insect transmission. In Viruses Vectors and Vegetation. Ed. K. Maramorosch, p. 143-157.

Sylvester, E. S. 1954. Aphid transmission of non-persistent plant viruses with special reference to the Brassica nigra virus. Hilgardia 23: 53-95.

Takeshita, R. M. 1956. Strains of the yellow-dwarf virus in cereals. (Abstr.) Phytopathology 46: 28.

Taylor, L. R. 1965. Flight behaviour and aphid migration. Proc. North Cent. Branch Ent. Soc. Am. 20: 9-19.

Tetrault, R. C., J. T. Schulz and R. G. Timian. 1963. Effect of population levels of three aphid species on barley yellow dwarf transmission. Pl. Dis. Reptr 47: 906-908.

Timian, R. G. 1964. Dodder transmission of barley yellow dwarf virus. Phytopathology 54: 910.

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.

Vacke, J. 1964. Zluta zakrslost jecmene v CSSR. [Barley yellow-dwarf virus disease in Czechoslovakia.] (Abstr.) Rosstl. Vyroba 10: 859-868.

Verhoyen, M. 1966. Effect of the concentration of inoculum on the multiplication and in vivo inactivation of alfalfa mosaic virus. In Viruses of Plants. Ed. A. B. R. Beemster and Jeanne Dykstra. North-Holland Publishing Company, Amsterdam, 342 pp.

Wallin, J. R. and D. O. Loonan. 1971. Low-level jet winds, aphid vectors, local weather and barley yellow dwarf virus outbreaks. Phytopathology 61: 1068-1070.

Watson, M. A. 1936. Factors affecting the amount of infection obtained by aphis transmission of the virus Hy. III. Roy. Soc. London, Phil. Trans., Ser. B. 226: 457-489.

Watson, M. A. 1946. The transmission of beet mosaic and beet yellows virus by aphids; a comparative study of a non-persistent and persistent virus having a host plant and a vector in common. Roy. Soc. Lond, Proc. Ser. B. 133: 200-219.

Watson, M. A. and T. Mulligan. 1957. Cereal yellow dwarf in Great Britain. Pl. Path. 6: 12-14.

Watson, M. A. and T. E. Mulligan. 1960a. Comparison of two barley yellow-dwarf viruses in glasshouse and field experiments. Ann. appl. Biol. 48: 559-574.

Watson, M. A. and T. Mulligan. 1960b. The manner of transmission of some barley yellow dwarf viruses by different aphid species. Ann. appl. Biol. 48: 711-720.

Watson, M. A. and F. M. Roberts. 1939. A comparative study of the transmission of Hyoscyamus virus 3, potato virus Y, and cucumber virus 4 by the vectors Myzus persicae (Sulz)., M. circumflexus (Buckton) and Macrosiphum gei (Koch). Roy. Soc. London, Proc., Ser. B 127: 543-576.

Wells, S. A. and S. McDonald. 1961. Note on the effect of stage of development and variety on damage to barley by the corn leaf aphid, Rhopalosiphum maidis Fitch. Can. J. Plant Sci. 41: 866-867.

Welsh, M. F. 1961. Terminology of plant virus disease. Can. J. Bot. 39: 1773-1780.

Williams, W. L. and A. F. Ross. 1957. Aphid transmission of potato leafroll virus as affected by feeding of nonviruliferous aphids on the test plants and by vector variability. (Abstr.) Phytopathology 47: 538.

Wilson, V. E. and H. C. Murphy. 1953. Red leaf of oats. Pl. Dis. Reptr 37: 21-23.

Wilson, M. C., H. F. Hodges, R. L. Gallun and R. E. Kirk. 1960. The use of phorate to control aphids and the Hessian fly on winter wheat. J. econ. Ent. 53: 197-200.

Wood, E. A. Jr. 1965. Effect of foliage infestation of the English grain aphid on yield of Triumph wheat. J. econ. Ent. 58: 778-779.

Wright, G. M. 1970. Effect of grain aphid on yield of wheat. N. Z. Wheat Rev. 11: 48.

APPENDIX 1

ANALYSIS OF VARIANCE OF CONQUEST BARLEY AND HARMON OATS - 1971 FIELD TRIALS

	d.f.	S.S.	M.S.	F
Weights of the middle two rows				
Oats vs barley	1	1,937,238.5208	1,937,238.5208	94.58**
Within oats	3	40,261.4584	13,420.4861	0.66^{NS}
Within barley	3	46,860.1667	15,620.0555	0.76^{NS}
Replication	5	25,200.6875	5,040.1375	0.25^{NS}
Error	33	675,943.4792	20,483.1357	
Total	45	2,725,504.3126		
Weights of the whole plot				
Oats vs barley	1	9,524,790.0833	9,524,790.0833	189.90**
Within oats	3	23,778.1250	7,926.0416	0.16^{NS}
Within barley	3	79,995.4584	26,665.1528	0.53^{NS}
Replication	5	178,913.6667	35,782.7333	0.71^{NS}
Error	33	1,655,136.3333	50,155.6464	
Total	45	11,462,613.6667		
Weights of 1000 kernels				
Oats vs barley	1	1,300.4172	1,300.4172	1160.98**
Within oats	3	2.5780	0.8593	0.77^{NS}
Within barley	3	0.9020	0.3007	0.27^{NS}
Replication	5	8.8690	1.7738	1.58^{NS}
Error	33	36.9638	1.1201	
Total	45	1,349.7300		

N.B. 2 missing plots
d.f. degrees of freedom
S.S. sum of squares
M.S. mean square
** significant at 1% level
NS not significant

APPENDIX 2

ANALYSIS OF VARIANCE OF CONQUEST BARLEY - 1972 FIELD TRIALS

	d.f.	S.S.	M.S.	F
		Weights of the middle two rows		
Treatment	5	43,492.0000	8,698.4000	1.40^{NS}
Replication	11	1,418,049.0000	128,913.5454	20.73**
Error	79	491,219.4999	6,217.9683	
Total	95	1,952,760.4999		
		Weights of 1000 kernels		
Treatment	5	7.1847	1.4369	NS
Replication	11	131.9955	11.9995	7.58**
Error	79	125.0805	1.5832	
Total	95	264.2607		

d.f. degrees of freedom
S.S. sum of squares
M.S. mean square
** significant at 1% level
NS not significant

APPENDIX 2 (cont'd.)

ANALYSIS OF VARIANCE OF HARMON OATS -
1972 FIELD TRIALS

	d.f.	S.S.	M.S.	F
		Weights of the middle two rows		
Treatment	5	371,489.9585	7,429.7917	2.10^{NS}
Replication	11	166,040.8334	15,094.6212	4.27**
Error	78	275,878.0415	3,536.8972	
Total	94	813,408.8334		
		Weights of 1000 kernels		
Treatment	5	27.9995	5.5999	2.95*
Replication	11	44.1108	4.0100	2.10**
Error	78	149.2166	1.9130	
Total	94	221.3269		

N. B. 1 missing plot
d.f. degrees of freedom
S.S. sum of squares
M.S. mean square
* significant at 5% level
** significant at 1% level
NS not significant

APPENDIX 2 (cont'd.)

ANALYSIS OF VARIANCE OF MANITOU WHEAT -
1972 FIELD TRIALS

	d.f.	S.S.	M.S.	F
		Weights of the middle two rows		
Treatment	5	16,331.7918	3,266.3583	NS
Replication	11	305,628.7084	27,784.4280	6.39**
Error	79	343,371.4582	4,346.4741	
Total	95	665,331.9584		
		Weights of 1000 kernels		
Treatment	5	47.1869	9.4373	10.01**
Replication	11	67.2766	6.1160	6.49**
Error	79	74.4804	0.9427	
Total	95	188.9439		

d.f. degrees of freedom
S.S. sum of squares
M.S. mean square
** significant at 1% level
NS not significant

APPENDIX 3

ANALYSIS OF VARIANCE FOR 1973 FIELD TRIAL

	d.f.	Mean square				
		Number of plants	Height of plants	Seed yield per hill	1000 kernel weights	Number heads/hill
Conquest barley						
Replication	19	47.73**	3986.93**	3551.86**	36.52^{NS}	1679.41**
Treatment	9	12.51^{NS}	662.05^{NS}	519.42^{NS}	25.66^{NS}	230.72^{NS}
Error	171	10.66	1263.88	1177.68	26.93	453.97
Harmon oats						
Replication	19	18.03**	345.92**	2699.42**	21.16**	959.77**
Treatment	9	13.16^{NS}	154.34**	3913.89**	37.67**	624.91**
Error	171	12.76	44.49	337.27	6.84	116.50
Manitou wheat						
Replication	19	41.93**	266.07**	435.42**	20.46^{NS}	929.42**
Treatment	9	6.58^{NS}	58.72^{NS}	320.04*	17.56^{NS}	490.95*
Error	171	7.96	43.12	132.14	17.41	222.30

d.f. degrees of freedom
* significant at 5% level
** significant at 1% level
NS not significant

APPENDIX 4

NUMBER OF PLANTS, MEANS AND STANDARD ERROR FOR RESPONSES OF HERTA BARLEY INFESTED WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

		Main culm													
		Height (cm)			Head length (cm)			Number of seeds			Yield (g)			1000 kernel weight (g)		
Treatment	Plant reaction	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		40	62.80	1.02	38	8.16	0.21	38	20.68	0.70	38	0.80	0.03	37	38.42	0.79
1NV		40	63.07	0.71	39	8.26	0.19	40	21.38	0.68	40	0.82	0.03	39	38.43	0.46
20NV		40	65.02	0.83	40	8.39	0.18	40	22.10	0.48	40	0.81	0.03	40	36.64	1.03
100NV		40	63.50	0.67	40	7.92	0.19	40	20.20	0.51	40	0.77	0.02	40	38.43	0.64
1V	-	84	62.81	0.71	82	8.55	0.14	82	21.56	0.48	82	0.84	0.02	81	38.80	0.42
20V	-	22	60.86	1.15	22	7.99	0.30	22	20.68	0.84	22	0.76	0.05	22	36.05	1.23
100V	-	3	61.33	0.88	3	8.30	0.40	3	22.00	0.58	3	0.79	0.02	3	35.99	1.71
1V	+	16	53.31	2.23	10	6.85	0.78	13	13.00	2.26	13	0.46	0.10	8	35.11	3.08
20V	+	18	49.44	2.09	9	5.93	0.54	9	10.89	1.05	9	0.37	0.06	6	37.12	3.27
100V	+	37	48.97	1.38	7	4.69	0.58	14	5.93	1.06	14	0.11	0.02	4	14.92	2.62

No. number of plants
S.E. standard error
NV plants infested with nonviruliferous Rhopalosiphum padi (L.)
V plants infested with viruliferous (BYDV isolate 6801) R. padi
- not infected
+ infected

APPENDIX 4 (cont'd.)

Treatment	Plant reaction	Number fertile heads per plant			Whole plant								
					Number of seeds			Yield (g)			1000 kernel weight (g)		
		No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		40	5.60	0.21	40	88.20	5.32	40	3.28	0.20	39	37.12	0.70
1NV		40	5.07	0.20	40	84.47	4.19	40	3.14	0.16	40	37.34	0.46
20NV		40	5.13	0.24	40	87.75	4.78	40	3.14	0.17	40	35.71	0.67
100NV		40	5.30	0.24	40	81.20	3.87	40	2.96	0.15	40	36.70	0.81
1V	-	82	5.05	0.15	82	86.48	3.50	82	3.19	0.13	82	37.07	0.42
20V	-	22	5.41	0.28	22	81.55	6.22	22	2.91	0.25	22	35.02	1.30
100V	-	3	6.67	0.88	3	111.67	8.25	3	3.77	0.31	3	33.94	2.58
1V	+	14	3.00	0.61	14	34.36	9.99	14	1.26	0.42	8	33.31	3.05
20V	+	9	3.78	0.72	9	28.33	5.82	9	0.88	0.20	6	31.95	2.48
100V	+	14	1.43	0.17	14	7.57	1.12	14	0.16	0.03	4	16.17	3.56

APPENDIX 5

NUMBER OF PLANTS, MEANS AND STANDARD ERROR FOR RESPONSES OF RODNEY OATS INFESTED WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

		Main culm													
		Height (cm)			Head length (cm)			Number of seeds			Yield (g)			1000 kernel weight (g)		
Treatment	Plant reaction	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		32	96.91	1.35	31	18.31	0.36	32	49.16	2.50	32	1.77	0.10	31	36.85	2.38
1NV		40	96.50	1.00	30	20.07	0.60	40	44.72	1.86	40	1.23	0.05	39	27.78	0.67
20NV		37	94.95	2.44	36	20.39	0.73	37	46.62	2.95	37	1.29	0.08	36	28.06	0.48
100NV		38	98.08	1.23	37	19.74	0.86	38	49.11	1.94	38	1.68	0.07	38	34.06	0.48
1V	-	27	92.19	2.06	26	18.54	0.63	27	45.33	3.83	27	1.42	0.12	26	31.82	1.14
20V	-	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
100V	-	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
1V	+	72	74.93	0.96	71	13.60	0.32	71	9.96	0.72	71	0.35	0.02	27	34.68	1.04
20V	+	40	79.17	1.29	40	13.29	0.28	38	5.42	0.55	38	0.20	0.02	5	39.51	1.20
100V	+	39	75.90	1.73	39	12.01	0.37	36	4.47	0.79	36	0.18	0.03	2	37.62	6.55

No. number of plants
S.E. standrd error
NV plants infested with nonviruliferous Rhopalosiphum padi (L.)
V plants infested with (BYDV isolate 6801) R. padi
- not infected
+ infected

APPENDIX 5 (cont'd.)

Treatment	Plant reaction	Number fertile heads per plant			Whole plant								
					Number of seeds			Yield (g)			1000 kernel weight (g)		
		No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		32	3.47	0.19	32	124.53	7.01	32	4.19	0.23	31	33.87	0.88
1NV		40	3.22	0.12	40	121.60	5.18	40	3.82	0.17	40	31.40	0.65
20NV		37	3.43	0.17	37	119.30	6.98	37	3.69	0.23	37	30.93	0.51
100NV		38	3.21	0.13	38	114.71	5.76	38	3.83	0.20	38	33.26	0.56
1V	-	27	2.52	0.23	27	97.19	11.06	27	3.21	0.40	26	32.02	1.17
20V	-	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
100V	-	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
1V	+	71	2.11	0.08	71	16.10	1.00	71	0.58	0.04	56	36.48	0.76
20V	+	39	2.62	0.17	40	13.92	1.23	40	0.46	0.05	27	33.65	1.00
100V	+	39	2.28	0.17	39	11.05	1.20	39	0.39	0.04	20	35.29	1.03

APPENDIX 6

NUMBER OF PLANTS, MEANS AND STANDARD ERROR FOR RESPONSES OF SELKIRK WHEAT INFESTED WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

Treatment	Plant reaction	Main culm														
		Height (cm)			Head length (cm)			Number of seeds			Yield (g)			1000 kernel weight (g)		
		No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		40	70.45	1.36	40	7.27	0.14	40	18.15	0.74	40	0.69	0.03	39	38.35	0.94
1NV		40	69.45	1.66	40	7.56	0.17	40	19.38	0.92	40	0.75	0.03	40	39.42	0.77
20NV		40	70.50	1.29	40	7.46	0.16	40	19.80	0.95	40	0.76	0.03	40	39.40	0.86
100NV		39	69.36	1.77	39	7.89	0.20	39	21.67	1.03	39	0.80	0.04	39	36.96	0.89
1V	-	80	69.06	1.10	79	7.77	0.11	80	20.79	0.71	80	0.78	0.03	80	38.32	0.65
20V	-	5	64.40	1.83	5	6.58	0.50	5	16.20	1.93	5	0.55	0.07	5	34.12	1.67
100V	-	2	59.00	1.00	2	6.20	1.00	2	13.00	2.00	2	0.46	0.05	2	35.64	1.64
1V	+	19	66.47	1.65	19	7.02	0.24	19	17.63	1.11	19	0.62	0.04	19	35.82	1.45
20V	+	35	64.40	1.50	35	6.71	0.14	35	16.91	0.79	35	0.57	0.03	33	33.68	0.78
100V	+	38	63.71	1.25	38	6.39	0.17	37	15.95	0.81	37	0.56	0.03	35	35.28	0.70

No. number of plants
S.E. standard error
NV plants infested with nonviruliferous Rhopalosiphum padi (L.)
V plants infested with (BYDV isolate 6801) R. padi
- not infected
+ infected

APPENDIX 6 (cont'd.)

Treatment	Plant reaction	Number fertile heads per plant			Whole plant								
					Number of seeds			Yield (g)			1000 kernel weight (g)		
		No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		40	4.17	0.19	40	77.82	2.76	40	2.74	0.12	40	35.07	0.80
1NV		40	4.12	0.20	40	79.65	2.98	40	2.88	0.12	40	36.16	0.64
20NV		40	4.30	0.21	40	81.00	2.61	40	2.87	0.10	40	35.56	0.64
100NV		39	4.23	0.24	39	78.64	3.33	39	2.76	0.12	39	35.50	0.96
1V	-	80	4.41	0.16	80	84.17	2.64	80	2.90	0.09	80	34.68	0.54
20V	-	5	5.00	0.89	5	64.60	11.87	5	1.76	0.30	5	27.56	0.91
100V	-	2	5.50	2.50	2	78.50	32.50	2	1.87	0.38	2	26.44	6.17
1V	+	19	4.58	0.42	19	75.79	6.70	19	2.30	0.20	19	30.73	1.61
20V	+	35	5.23	0.35	35	76.71	5.29	35	2.19	0.15	35	28.82	0.61
100V	+	37	5.73	0.32	37	76.68	4.47	37	2.28	0.13	37	30.06	0.76

APPENDIX 7

NUMBER OF PLANTS, MEANS AND STANDARD ERROR FOR RESPONSES OF HERTA BARLEY INFESTED WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

		Main culm													
		Height (cm)			Head length (cm)			Number of seeds			Yield (g)			1000 kernel weight (g)		
Treatment	Plant reaction	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		40	59.25	1.20	39	6.16	0.23	38	16.16	0.79	38	0.63	0.04	34	38.74	1.18
1NV		40	59.30	1.04	39	6.50	0.19	39	16.23	0.64	39	0.67	0.03	36	41.46	0.76
20NV		39	57.87	1.05	38	6.07	0.24	38	16.11	0.87	38	0.65	0.04	32	40.32	0.78
100NV		40	59.45	0.87	38	6.40	0.19	38	17.26	0.74	38	0.69	0.04	37	39.89	1.61
1V	-	92	58.10	0.78	86	6.01	0.16	86	15.97	0.56	86	0.63	0.03	76	39.78	0.74
20V	-	11	56.55	3.08	9	5.56	0.67	9	14.44	2.01	9	0.59	0.09	8	41.77	2.00
100V	-	7	61.57	3.56	7	6.60	0.47	7	17.14	1.30	7	0.65	0.07	7	38.10	2.76
1V	+	7	58.14	1.47	7	5.87	0.40	7	14.29	1.86	7	0.57	0.07	6	40.08	1.80
20V	+	28	59.54	1.34	23	5.78	0.31	23	14.48	1.11	23	0.55	0.04	18	38.40	0.77
100V	+	33	58.73	1.48	28	5.89	0.33	28	15.00	1.09	28	0.54	0.04	23	36.44	1.13

No. number of plants
S.E. standard error
NV plants infested with nonviruliferous Rhopalosiphum maidis (F.)
V plants infested with (BYDV isolate 7005) R. maidis
- not infected
+ infected

APPENDIX 7 (cont'd.)

Treatment	Plant reaction	Number fertile heads per plant			Whole plant								
					Number of seeds			Yield (g)			1000 kernel weight (g)		
		No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		39	6.26	0.37	39	78.46	5.61	39	3.02	0.24	39	37.87	0.87
1NV		40	5.80	0.39	40	71.67	6.03	40	2.73	0.23	39	37.73	0.79
20NV		38	5.50	0.36	38	71.03	6.12	38	2.72	0.27	38	36.79	0.92
100NV		38	6.45	0.39	38	87.00	6.20	38	3.30	0.26	37	37.17	0.73
1V	-	86	6.21	0.26	86	83.57	5.87	86	3.02	0.18	82	36.85	1.02
20V	-	10	4.60	0.69	10	59.20	10.47	10	2.25	0.41	9	38.03	1.66
100V	-	7	6.14	1.10	7	79.00	15.42	7	2.83	0.60	7	34.19	1.76
1V	+	7	5.00	0.38	7	57.14	6.28	7	2.23	0.29	7	38.44	1.92
20V	+	24	6.33	0.50	24	72.13	6.79	24	2.60	0.25	23	35.81	0.63
100V	+	30	6.03	0.54	30	68.37	7.14	30	2.40	0.25	26	35.25	0.82

APPENDIX 8

NUMBER OF PLANTS, MEANS AND STANDARD ERROR FOR RESPONSES OF RODNEY OATS INFESTED WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

Treatment	Plant reaction	Main culm														
		Height (cm)			Head length (cm)			Number of seeds			Yield (g)			1000 kernel weight (g)		
		No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		38	97.00	1.10	38	19.32	0.26	38	49.29	2.63	38	1.74	0.09	38	35.51	0.63
1NV		40	98.95	0.95	40	19.52	0.19	40	57.20	1.63	40	2.00	0.06	40	34.89	0.28
20NV		40	97.72	1.05	40	19.67	0.24	40	53.35	1.66	40	1.83	0.06	40	34.32	0.46
100NV		40	96.60	1.46	40	19.35	0.30	40	49.20	2.03	39	1.77	0.06	39	35.00	0.37
1V	-	81	97.09	0.81	81	19.25	0.16	81	54.21	1.32	81	1.88	0.05	81	34.64	0.33
20V	-	4	92.50	4.11	4	17.75	0.95	4	45.50	5.98	4	1.44	0.26	4	31.18	2.78
100V	-	7	102.00	2.45	7	20.00	1.09	7	57.86	5.75	7	2.07	0.21	7	35.66	0.81
1V	+	19	93.89	2.02	19	18.79	0.31	19	31.89	2.21	19	1.25	0.08	18	37.37	1.75
20V	+	36	92.28	1.58	36	18.19	0.31	36	25.44	1.61	36	1.02	0.06	33	40.14	1.17
100V	+	33	91.48	1.63	32	16.88	0.48	31	22.19	2.54	31	0.78	0.10	23	34.82	2.17

No. number of plants
S.E. standard error
NV plants infested with nonviruliferous Rhopalosiphum maidis (F.)
V plants infested with viruliferous (BYDV isolate 7005) R. maidis
- not infected
+ infected

APPENDIX 8 (cont'd.)

Treatment	Plant reaction	Number fertile heads per plant			Whole plant								
					Number of seeds			Yield (g)			1000 kernel weight (g)		
		No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		38	2.71	0.16	38	77.87	5.25	38	2.75	0.18	38	35.54	0.72
1NV		40	2.80	0.14	40	87.02	3.60	40	3.06	0.13	40	35.13	0.30
20NV		40	2.72	0.13	40	81.55	3.18	40	2.81	0.12	40	34.32	0.44
100NV		40	2.90	0.16	40	81.97	4.60	40	2.79	0.15	39	34.28	0.52
1V	-	81	2.81	0.10	81	84.09	2.55	81	2.92	0.09	81	34.73	0.37
20V	-	4	3.25	0.48	4	67.00	11.17	4	2.08	0.47	4	29.77	2.58
100V	-	7	1.86	0.26	7	79.71	10.86	7	2.78	0.39	7	34.85	0.83
1V	+	19	1.47	0.16	19	35.26	2.61	19	1.37	0.10	19	41.78	4.65
20V	+	36	1.39	0.10	36	27.86	1.69	36	1.10	0.07	35	39.71	1.07
100V	+	31	1.39	0.10	31	23.19	2.55	31	0.80	0.10	23	34.04	2.12

APPENDIX 9

NUMBER OF PLANTS, MEANS AND STANDARD ERROR FOR RESPONSES OF SELKIRK WHEAT INFESTED WITH DIFFERENT NUMBERS OF VIRULIFEROUS AND NONVIRULIFEROUS APHIDS IN GREENHOUSE TRIALS

		Main culm													
		Height (cm)			Head length (cm)			Number of seeds			Yield (g)			1000 kernel weight (g)		
Treatment	Plant reaction	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		39	68.23	1.20	39	8.04	0.09	39	24.05	0.81	39	0.94	0.03	39	39.36	0.77
1NV		39	67.15	1.08	39	7.83	0.12	39	22.54	0.61	39	0.92	0.03	39	41.30	1.03
20NV		38	68.18	1.11	38	7.71	0.14	38	22.34	0.67	38	0.85	0.03	38	38.26	0.93
100NV		40	67.67	1.37	40	7.69	0.12	40	21.90	0.63	40	0.86	0.03	40	39.24	1.04
1V	-	94	65.84	0.91	94	7.94	0.08	94	23.14	0.58	94	0.87	0.03	91	37.89	0.80
20V	-	8	64.38	3.06	8	7.36	0.25	8	17.75	1.73	8	0.73	0.08	7	40.63	1.94
100V	-	3	54.67	1.76	3	7.47	0.03	3	23.00	2.65	3	0.73	0.17	3	31.74	6.82
1V	+	5	63.60	6.74	5	7.40	0.83	5	19.80	3.53	5	0.78	0.14	4	39.29	3.76
20V	+	30	58.40	1.09	30	7.33	0.10	30	18.37	0.92	30	0.67	0.03	28	36.45	1.22
100V	+	37	55.81	1.25	37	7.16	0.14	36	16.86	1.03	36	0.63	0.04	31	37.89	1.08

No. number of plants
S.E. standard error
NV plants infested with nonviruliferous Rhopalosiphum maidis (F.)
V plants infested with viruliferous (BYDV isolate 7005) R. maidis
- not infected
+ infected

APPENDIX 9 (cont'd.)

Treatment	Plant reaction	Number fertile heads per plant			Whole plant								
					Number of seeds			Yield (g)			1000 kernel weight (g)		
		No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.	No.	Mean	S.E.
Control		39	2.85	0.12	39	53.41	2.16	39	1.85	0.08	39	35.02	0.80
1NV		39	2.90	0.14	39	55.03	2.78	39	1.89	0.09	39	34.78	0.97
20NV		39	2.72	0.13	39	52.79	2.08	39	1.75	0.07	39	33.73	1.06
100NV		40	2.50	0.11	40	50.90	2.40	40	1.80	0.09	40	35.76	0.92
1V	-	94	2.65	0.09	94	50.59	1.56	94	1.69	0.06	92	33.22	0.75
20V	-	8	3.63	0.50	8	58.63	4.54	8	2.00	0.18	8	34.01	1.58
100V	-	3	3.00	0.58	3	52.67	7.42	3	1.52	0.44	3	27.41	5.16
1V	+	5	2.80	0.37	5	49.60	3.11	5	1.80	0.18	5	36.16	2.11
20V	+	31	3.55	0.16	31	52.74	2.61	31	1.64	0.10	31	30.70	0.93
100V	+	36	3.39	0.21	36	47.69	2.82	36	1.51	0.09	35	32.01	0.79

APPENDIX 10

ANALYSIS OF VARIANCE OF SOME RESPONSES OF PROGENY FROM HIGH AND LOW YIELDING SELKIRK WHEAT PLANTS FROM EACH OF BYDV INFECTED AND CONTROL GROUPS OF PLANTS IN GREENHOUSE EXPERIMENTS

	d.f.	S.S.	M.S.	F
		Height of the main stem		
Total	339	26,529.0000		
Groups	3	187.0000	62.3333	1.36^{NS}
Plants in groups	36	6,591.0000	183.0833	3.99**
Treatments	1	2,586.0000	2,586.0000	56.32**
Treatments x groups	3	4.0000	1.3333	NS
Treatments x plants in groups	36	2,469.0000	68.5833	1.49*
Error	320	14,692.0000	45.9125	
		Head length of the main head		
Total	399	405.2930		
Groups	3	1.6016	0.5339	NS
Plants in groups	36	70.1484	1.9486	3.04**
Treatments	1	104.2422	104.2422	162.73**
Treatments x groups	3	2.2344	0.7448	1.16^{NS}
Treatments x plants in groups	36	22.0625	0.6128	NS
Error	320	205.0039	0.6406	

APPENDIX 10 (cont'd.)

	d.f.	S.S.	M.S.	F
	Weight of seed per plant			
Total	339	158.2087		
Groups	3	0.4265	0.1422	NS
Plants in groups	36	21.8582	0.6071	2.08**
Treatments	1	30.3687	30.3687	104.18**
Treatments x groups	3	1.4709	0.4903	1.68^{NS}
Treatments x plants in groups	36	10.7966	0.2999	NS
Error	320	93.2878	0.2915	
	Number of seeds per plant			
Total	399	126,184.0000		
Groups	3	552.0000	184.0000	NS
Plants in groups	36	16,433.0000	456.4700	1.74*
Treatments	1	15,550.0000	15,550.0000	59.42**
Treatments x groups	3	2,337.0000	779.0000	2.98*
Treatments x plants in groups	36	7,563.0000	210.0833	NS
Error	320	83,749.0000	261.7156	

APPENDIX 10 (cont'd.)

	d.f.	S.S.	M.S.	F
	Number of heads per plant			
Total	339	307.0007		
Groups	3	1.8599	0.6200	NS
Plants in groups	36	28.1371	0.7816	1.13^{NS}
Treatments	1	25.0000	25.0000	36.16**
Treatments x groups	3	2.6592	0.8864	1.28^{NS}
Treatments x plants in groups	36	28.1372	0.7816	1.13^{NS}
Error	320	221.2073	0.6913	
	1000 kernel weight of whole plant			
Total	339	7,379.8750		
Groups	3	57.8750	19.2917	1.17^{NS}
Plants in groups	36	897.5000	24.9306	1.51*
Treatments	1	521.6875	521.6875	31.67**
Treatments x groups	3	82.8750	27.6250	1.68^{NS}
Treatments x plants in groups	36	548.9375	15.2483	NS
Error	320	5,471.0000	16.4719	

d.f. degrees of freedom
S.S. sum of squares
M.S. mean square
* significant at 5% level
** significant at 1% level
NS not significant