The etiology and epidemiology of barley yellow dwarf virus in Montana : its importance and impact on small grain production
by Douglas James Yount

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Plant Pathology
Montana State University
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Abstract:
Barley yellow dwarf virus (BYDV) infects oats, barley, and wheat, causing serious losses in these crops worldwide. This virus also infects over 100 species of grasses and is transmitted only by aphids in a persistent manner.

During four years of field survey in central Montana, the virus induced disease, barley yellow dwarf (BYD), was observed in winter wheat and in spring wheat, barley, and oats. On the basis of symptom incidence and severity, winter wheat planted in August and early September appeared to be damaged more severely than late planted winter wheat or the spring grains. Two epiphytotics of BYD were diagnosed in winter wheat in 1980 and 1981. Early seeding and moderate temperatures during September and October were determined to be the conditions favorable for the development of large viruliferous aphid populations attacking the 1980 and 1981 winter wheat crops in the epiphytotic areas. To date, planting winter wheat after September 10, appears to be an effective control measure for avoiding serious losses from BYD.

Four strains of the virus i.e. RPV, RMV, MAV, and PAV, were identified among isolates of BYDV recovered from diseased plant samples or native aphid populations collected in central Montana. The PAV-like isolates were found to be the most prevalent and also the most virulent types among the strains identified. The four principal cereal grain aphids and vectors of BYDV, the English grain aphid, the corn leaf aphid, the oat, bird cherry aphid, and the green-bug, were all found to be present in Montana. As both the common aphid vectors and strains of BYDV occur in central Montana, the disease may threaten small grain production to some extent each cropping season.

In three years of field plot testing, 23 cultivars and lines of spring barley, spring wheat and winter wheat were evaluated for their response to infection by BYDV, using a virulent PAV isolate as the inoculum source. None of the cultivars commonly grown in Montana were tolerant to BYDV. Averaged over cultivars and years, the yield reduction for the spring barleys, spring wheats, and winter wheats was 65.0%, 65.4%, and 67.3%, respectively.

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by

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A thesis submitted in partial fulfillment
of the requirements for the degree

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in

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TABLE OF CONTENTS

	Page
VITA	ii
ACKNOWLEDGMENTS	iii
TABLE OF CONTENTS	iv
LIST OF TABLES	vii
LIST OF FIGURES	xiii
ABSTRACT	xiv
INTRODUCTION	1
LITERATURE REVIEW	4
History and Importance of the Disease	4
Host Range of the Virus	6
Classification and Physical Characters of the Virus	7
Biology of Virus Acquisition and Transmission by Aphids	8
Virus - Vector Relationships	10
Factors Affecting Vector Specificity	13
Diagnosis and Characterization of BYDV by Serology	16
Separation of BYDV Variants Based on the Cytological Alterations They Cause in Plants	18
Characterization of BYDV Variants Based on Virulence and Host Range	19
Further Evidence for Taxonomic Division of BYDV Variants	21
Symptoms of BYDV in Small Grains	22
BYDV Effects on Yield Parameters and Correlation to Symptom Expression	24
Control of BYDV and Sources of Host Plant Resistance	29

TABLE OF CONTENTS (Con't)

CHAPTER | Page

I. FIELD DISEASE SURVEY AND IDENTIFICATION OF BARLEY YELLOW DWARF VIRUS 35

Materials and Methods 35

Aphid Rearing 37
Vector Acquisition of BYDV From Diseased Field Plants 38
Vector Transmission of BYDV to Indicator Test Plants 40
Transmission of BYDV by Field Collected Aphids 43
Virus Strain Identification 43

Results and Discussion 45

II. THE EFFECT OF BYDV ON GROWTH AND YIELD OF WINTER AND SPRING GRAINS UNDER FIELD CONDITIONS 70

Materials and Methods 70

Rearing of Viruliferous Aphids and Methods of Inoculation 71
1979 Field Evaluation of Spring Barley to Late Infection by Barley Yellow Dwarf Virus 72
1980 and 1981 Field Evaluation of Spring Barley Cultivars to Early Infection by BYDV 74
1980 and 1981 Field Evaluation of Spring Wheat Cultivars to Early Infection by BYDV 76
1980 and 1981 Field Evaluation of Winter Wheat Cultivars to Fall Infection by BYDV 77

Results and Discussion 79

1979 Barley Experiment 79
1980 and 1981 Spring Barley Experiments 84
1980 and 1981 Spring Wheat Experiments . 96

TABLE OF CONTENTS (Con't)

CHAPTER Page

1980 and 1981 Winter Wheat Experiments 107
Comparisons Between Spring Barleys, Spring Wheats and Winter Wheats Infected With BYDV 116
Discussion 119

APPENDIX 126

BIBLIOGRAPHY 135

LIST OF TABLES

Table		Page
1.1	Summary results for the recovery of BYDV isolates from field sources	46
1.2	Isolates of barley yellow dwarf virus recovered from various survey sites in Central Montana 1978-81	48
1.3	Aphid transmission results for the most prevalent vector-specific and vector non-specific strains of BYDV collected in Montana	51
1.4	Transmission of BYDV by four <u>Rhopalosiphum maidis</u> vector specific isolates	52
1.5	Enzyme Immunosorbent Assay results for BYDV isolates tested at Cornell University, Ithaca, N.Y.	54
1.6	Aphid populations in Central Montana found to be carrying BYDV	60
1.7	Diagnosis of pathological disorders in winter wheat collected May 13, 1981 in Pondera County, MT	67
1.8	1980 estimated yield loss to barley yellow dwarf virus in winter wheat	69
2.1	Disease score and 500 kernel weight (g) response of six spring barley cultivars and four spring barley lines inoculated with BYDV-PAV isolate MT 792 at Bozeman, MT 1979	80
2.2	Effect of barley yellow dwarf virus on 500 kernel weight for 10 spring barley cultivars and lines inoculated with PAV isolate MT 792 at Bozeman, MT 1979 . . .	81

LIST OF TABLES (Con't)

Table		Page
2.3	Correlation of disease symptom responses with 500 kernel weight for ten barley cultivars and lines inoculated with PAV isolate MT 792 at Bozeman, MT 1979	81
2.4	Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets per head for seven spring barley cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980	86
2.5	Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and yield per plant for seven spring barley cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980	87
2.6	Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets per head for seven spring barley cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1981	88
2.7	Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and plant yield for seven spring barley cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1981	89
2.8	Performance ranking among two rowed and six rowed spring barley cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980	92

LIST OF TABLES (Con't)

Table | Page

2.9 Performance ranking among two rowed and six rowed spring barley cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1981 93

2.10 Effect of barley yellow dwarf virus on yield for six spring barley cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 94

2.11 Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets per head for six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980 99

2.12 Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and yield per plant for six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980 100

2.13 Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets/head for six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1981 101

2.14 Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and yield per plant for six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1981 102

LIST OF TABLES (Con't)

Table		Page
2.15	Performance ranking among six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980 . .	104
2.16	Performance ranking among six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1981 . .	104
2.17	Effect of barley yellow dwarf virus on yield for six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT	106
2.18	Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets per head for five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1979	110
2.19	Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and plant yield for five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1979	111
2.20	Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets per head for five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980	112
2.21	Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and yield per plant for five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980	113

LIST OF TABLES (Con't)

Table | Page

2.22 Performance ranking among five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1979 . . 115

2.23 Performance ranking among five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980 . . 115

2.24 Comparisons of the percent reduction in growth and yield parameters between winter wheat, spring wheats, and spring barleys infected with PAV isolate MT 792, averaged over cultivars and environments 117

Appendix Tables

1 Small grain cultivars used in the 1979-81 field experiments 126

2 BYDV yellows index used for determining disease severity ratings among ten spring barley cultivars and lines inoculated with PAV isolate MT 792 at Bozeman, MT 1979 128

3 Effects of barley yellow dwarf virus on growth and yield components for seven spring barley cultivars inoculated in 1980 129

4 Effects of barley yellow dwarf virus on growth and yield components for seven spring barley cultivars inoculated in 1981 130

5 Effects of barley yellow dwarf virus on growth and yield components for six spring wheat cultivars inoculated in 1980 131

LIST OF TABLES (Con't)

Appendix Table Page

6 Effects of barley yellow dwarf virus on growth and yield components for six spring wheat cultivars inoculated in 1981 132

7 Effects of barley yellow dwarf virus on growth and yield components for five winter wheat cultivars inoculated in 1979 133

8 Effects of barley yellow dwarf virus on growth and yield components for five winter wheat cultivars inoculated in 1980 134

LIST OF FIGURES

Figure | Page

1.1 Barley yellow dwarf virus survey area . . . 36

1.2 Distribution of BYDV strains found in Central Montana 47

1.3 BYDV epiphytotic on winter wheat in Judith Basin and Fergus Counties, 1980 62

1.4 BYDV epiphytotic on winter wheat in Pondera and surrounding counties, 1981 65

ABSTRACT

Barley yellow dwarf virus (BYDV) infects oats, barley, and wheat, causing serious losses in these crops worldwide. This virus also infects over 100 species of grasses and is transmitted only by aphids in a persistent manner.

During four years of field survey in central Montana, the virus induced disease, barley yellow dwarf (BYD), was observed in winter wheat and in spring wheat, barley, and oats. On the basis of symptom incidence and severity, winter wheat planted in August and early September appeared to be damaged more severely than late planted winter wheat or the spring grains. Two epiphytotics of BYD were diagnosed in winter wheat in 1980 and 1981. Early seeding and moderate temperatures during September and October were determined to be the conditions favorable for the development of large viruliferous aphid populations attacking the 1980 and 1981 winter wheat crops in the epiphytotic areas. To date, planting winter wheat after September 10, appears to be an effective control measure for avoiding serious losses from BYD.

Four strains of the virus i.e. RPV, RMV, MAV, and PAV, were identified among isolates of BYDV recovered from diseased plant samples or native aphid populations collected in central Montana. The PAV-like isolates were found to be the most prevalent and also the most virulent types among the strains identified. The four principal cereal grain aphids and vectors of BYDV, the English grain aphid, the corn leaf aphid, the oat, bird cherry aphid, and the greenbug, were all found to be present in Montana. As both the common aphid vectors and strains of BYDV occur in central Montana, the disease may threaten small grain production to some extent each cropping season.

In three years of field plot testing, 23 cultivars and lines of spring barley, spring wheat and winter wheat were evaluated for their response to infection by BYDV, using a virulent PAV isolate as the inoculum source. None of the cultivars commonly grown in Montana were tolerant to BYDV. Averaged over cultivars and years, the yield reduction for the spring barleys, spring wheats, and winter wheats was 65.0%, 65.4%, and 67.3%, respectively.

INTRODUCTION

Barley yellow dwarf (BYD) is an aphid-borne virus disease that occurs on a wide range of Graminaceous hosts. It is economically important in oats, barley, wheat, and rye, and therefore of potential concern wherever these crops are grown. The disease is known to be present in North and South America, Europe, North Africa, Australia, and Asia.

Historically, barley yellow dwarf was described as early as the 1890's, before the true causal agent was known. After 1951, the year it was determined that barley yellow dwarf virus (BYDV) was the cause of barley yellow dwarf (BYD), several known epiphytotics of the disease have occurred in North America and Europe. The epiphytotic on oats in 1959, which developed in the North Central Region of the United States was most notable. This epidemic brought to light the full realization for economic losses attributable to the virus. Although the impact of BYD was most seriously felt in the North Central Region, the disease was reported to be significant in many outlying states, including Montana. As reported by E. L. Sharp (108), Montana State University, Bozeman, MT., the disease was diagnosed primarily in spring barley and to a lesser extent in oats. In some late planted barley fields, yield losses were estimated at 50 percent. The diagnosis of BYD at that

time was based on visual plant symptoms in association with the presence of aphid infestations. No attempts were made to confirm the diagnosis by aphid transmission tests. However, four years earlier, in August of 1955, barley and oat samples were obtained from Montana by C.A. Suneson (3), University of California, Davis, California, and attempts made to recover BYDV by aphid transmission. In those transmission tests, non-viruliferous apple-grain aphids, _Rhopalosiphum prunifoliae_ (Fitch), were used as the vector species. No virus was recovered from those samples. As stated by the investigators, "the somewhat desiccated condition of the plants received from Montana may have made it impossible to recover the virus."

Another explanation for lack of transmission, although speculative, is that the plant samples were infected by a strain of BYDV that could not be transmitted by the apple-grain aphid.

Since the time of those earlier reported occurrences and attempts to recover BYDV from plant samples, no effort has been made to confirm the presence of BYD in small grains grown in Montana.

The objectives considered in this investigation were:

1) To determine the incidence and severity of BYDV in winter wheat, spring wheat, spring barley, and to a lesser extent spring oats grown in central Montana.
2) To develop facilities and useful techniques for diagnosis of BYD by aphid transmission.
3) To identify the variant or variants of BYDV recovered from field samples and native cereal aphid populations in the area surveyed.
4) To determine the effects of BYDV on plant development and seed yield of spring barley, spring wheat, and winter wheat cultivars grown in Montana.
5) To define more accurately the etiology and epidemiology of BYD in small grains in the central region of Montana.

Fulfillment of these objectives should lead to a more thorough understanding of BYD and its impact on small grain production in Montana. Once the disease has been diagnosed precisely, and its development observed, an effective control procedure could be recommended. In addition, a disease response evaluation of the important small grain cultivars grown in Montana to infection by BYDV may identify those which are least affected by the virus. Thus, if tolerant cultivars are identified they could be recommended for planting in the state.

LITERATURE REVIEW

History and Importance of the Disease

Barley yellow dwarf was first recognized as a virus disease of barley in 1951, when it was discovered by Oswald and Houston (59) in California. They described a severe yellows disease of barley occurring throughout the state, and characterized the causal agent as a virus transmitted by aphids. Further investigations by these two researchers extended the virus host range to oats and wheat, causing a 'red leaf' and 'chlorosis' disease respectively (60,62). Although Oswald and Houston (60) first suggested the similarity between BYD in oats and the oat disease referred to as 'red leaf', it was Takeshita (115) who verified that in fact, the red leaf disease of oats was caused by BYDV.

Possibly the first record of BYD in the United States was reported in 1890 by Galloway and Southworth (30), as a "mysterious oat disease" in the Eastern and Central States. Other epiphytotics on oats as well as on barley and wheat have likely occurred and been discussed in the literature prior to characterization of the causal agent in 1951 (10,79). Murphy (57) suggested that outbreaks of BYD on oats in 1907 and 1949 resulted in greater losses to the national (U.S.A.) oat crop than the epiphytotic of 1959.

Estimated losses for oats in 1959 were comparable to those suffered from epiphytotics of Victoria blight and crown rust occurring in 1947 and 1953,respectively (57). In Iowa alone, 1959 losses to the oat crop were estimated at more than 26 million bushels (8). More recently, participants in a BYDV workshop held at Urbana, Illinois in 1977, estimated average annual losses at 1-3% of the total wheat, barley, and oat production in the United States and Canada, with losses of 20-30% in some areas (unpublished).

In Great Britain, Saunders and Doodson (104) have estimated yield losses in cereals to be 3-10% during most years. However, in yield trials conducted at the National Institute of Agricultural Botany, Cambridge, England, yield losses of up to 90% were reported for certain cultivars of oats and barley and a 43% yield loss for most wheat cultivars (25).

The most thorough evaluation of actual yield losses resulting from BYD epiphytotics occurring over the years has been conducted by Canadian researchers. In 1959, the epiphytotic on oats in Eastern Ontario caused as high as 42% loss in plant yield (109). Intensive surveys begun in 1964, indicate that BYDV infects cereals each year and periodic epiphytotics cause severe damage to the cereal

crops (39,40). In 1965, oat losses in Manitoba were estimated at 2.25 million bushels (36). In 1969, barley losses in one cultivar 'Herta' alone, were estimated at 1.4 million bushels (39). In Manitoba and Saskatchewan, the 1974 BYD epiphytotic resulted in oat losses of 2.3 million bushels and a loss of 2.1 million bushels in two barley cultivars, 'Conquest' and 'Herta' (40). A 1976 outbreak of BYD in eastern Canada was reported to be the most important epiphytotic of the disease occurring in the last 20 years (19). Yield losses of 20-50% were reported in many areas were oats, barley, and spring wheat were affected. Gill (45) reported that a 1978 epiphytotic resulted in a 5.85 million bushel loss in bread wheat production, representing about a 7% loss in the total potential yield.

Host Range of the Virus

Barley yellow dwarf virus infects a wide diversity of hosts among the Gramineae, which is of great importance in considering the etiology and epidemiology of the disease. The early work of Oswald and Houston (61), Bruehl and Toko (19), and Watson and Mulligan (117), established a host range of 84 species within the Gramineae, many of which were symptomless carriers. The virus is now known to infect

over 100 species of grasses, including many which are common range, turf, and forage species (87).

The importance of grasses as inoculum sources of the virus and as hosts for aphid vectors has been well documented (10,14,74,79,109,110). Certain species of grasses are better hosts for the virus, vectors, or both, than are other species. The spatial relationship of such grass hosts to cultivated crops is certainly an important consideration in the epidemiology. For instance, in England, Wales, Australia, and New Zealand, perennial ryegrass pastures were found to have a high percentage of plants infected with BYDV (14,23,53). Such pastures have been implicated as the overwintering sources of BYDV and as the host for early build-up of aphid vectors, which subsequently move to small grains (14,53). It is interesting to note however, that little emphasis has been given to the direct effect of BYD on the production of pasture or forage grass species such as perennial ryegrass.

Classification and Physical Characters of the Virus

BYDV is the type member of the luteovirus group, which includes other aphid-vectored, 'yellows' type viruses

(56). Members of this group are characterized as being non-seed and non-mechanically transmissible, single stranded RNA viruses, which are transmitted in a persistent, circulative manner by aphids (56,87). BYDV and the other members of this group have not been shown to propagate in the vector, as is the case for some Rhabdoviruses (63,85).

The virion's of BYDV are isometric, spherical particles, approximately 23-25 nm in diameter, with an RNA content of about 28.0%. The RNA has a molecular weight of about 2.0×10^6 daltons (6,65). The virion capsid is composed of a single protein with a molecular weight of 23,500 to 24,450, depending on the particular strain of the virus (105).

Biology of Virus Acquisition and Transmission by Aphids

In infected plants, BYDV is found primarily in the sieve tubes of the phloem and to a lesser extent in phloem parenchyma cells (27,41,48). As aphids feed almost exclusively on phloem sieve tube elements, the capacity for acquisition of the virus is dependent on feeding within an infected cell.

The concentration of virus within a diseased plant

is very low, as yields of purified virus have been reported to range from 6 to 136 ug per 100g of infected plant tissue (29,65). Thus, within a single phloem cell the amount of virus present would be extremely small. The ability of aphids to selectively acquire the virus from phloem sap has been related to the physiology of the insect in receiving adequate nutrients during the feeding process (10,22). The aphid when feeding, exudes excess sap solutions through the rectum as nitrogenous materials are selectively absorbed through the gut wall (10,22). Virus particles also accumulate in the aphid by this differential absorption process, supposedly to a concentration sufficient to transmit the virus for long periods of time after a single acquisition feeding period (10,22). After ingestion, virus particles pass through the gut wall into the hemolymph and eventually into the salivary system, which is the basis for the circulative nature of the virus in the vector (22). The subsequent infection of phloem cells by the probing or feeding of the viruliferous aphid results from the egestion of salivary fluids containing virus particles into these cells (22).

Studies by Paliwal and Sinha (63) have shown that virus particles accumulate in the gut and hemolymph of the

aphid. However, it has been suggested that virus transmission specificity and the persistent nature of transmission are regulated by the salivary system (31,32,33). Gildow and Rochow (31) in studies using the ferritin-antibody technique for electron microscopy, observed the presence of virus particles in accessary salivary glands and in intracellular canals and cytoplasmic vesicles that drain the salivary glands. They hypothesized that cells of the salivary glands have receptor sites which recognize virus protein coat components of transmissible strains of the virus. These cells supposedly would possess only a limited number of specific receptor sites. This limitation would serve to restrict the flow of virus through the salivary system and concentrate virus particles in the hemocoel. Thus, the persistence of the virus in the aphid may be a function of this restrictive flow phenomenon, and further explain how a non-propagative virus is transmitted by a vector throughout its lifetime after a relatively short acquisition feeding period.

Virus - Vector Relationships

Within the luteovirus group the relationships and interactions between the virus and aphid vectors are best

understood for BYDV. Actually, BYDV is considered to be a group of viruses sharing the commonality of host specificity, physiological and anatomical effects on the host, and basic biological relationships with the aphid vectors (101). However, considerable variability exists among the BYD viruses with respect to vector specificity, serological homologies, cytological effects in plants, and virulence.

In regard to vector specificity, it has been well established that some variants or strains of BYDV are transmitted efficiently by only a single species of aphid, whereas other variants are transmitted efficiently by two or more species (35,76,86,116,118). Jedlinski (47) recently listed 18 species of aphids which are capable of transmitting the virus. However, due to the complexity of aphid taxonomy, some of the different species reported in the early literature as BYDV vectors may, in fact, be only a single species (47,112). Rochow (76,80,86,89) has identified five variants of BYDV having distinct differences in the efficiency by which four species of grain aphids transmit each variant. Each of the five variants has been symbolically named by Rochow, reflecting the relative efficiency of transmission by these four cereal grain aphid species.

PAV (padi - avenae - virus) is a strain transmitted efficiently by <u>Rhopalosiphum</u> <u>padi</u> (Linnaeus), the oat, bird-cherry aphid, and <u>Macrosiphum</u> <u>avenae</u> = <u>Sitobian</u> <u>avenae</u> (Fabricus), the English grain aphid, occasionally by <u>Schizaphis</u> <u>graminum</u> (Rondani), the greenbug, and seldom by <u>R</u>. <u>maidis</u> (Fitch), the corn leaf aphid. PAV is commonly referred to as a vector non-specific variant. RPV (<u>R</u>. <u>padi</u>-virus), MAV (<u>M</u>. <u>avenae</u>-virus), RMV (<u>R</u>. <u>maidis</u>-virus) and SGV (<u>S</u>. <u>graminum</u>-virus) strains are transmitted efficiently only by <u>R</u>. <u>padi</u>, <u>M</u>. <u>avenae</u>, <u>R</u>. <u>maidis</u>, and <u>S</u>. <u>graminum</u> respectively. The RPV, MAV, RMV, and SGV variants are commonly referred to as vector-specific strains. Although the transmission of these vector-specific strains is most often by the designated efficient aphid species, one or more of the non-efficient vectors may occasionally effect a transmission (80, 86,89). Thus, the transmission of vector-specific strains is not always absolute and more often than not, it is relative to the efficiency of transmission among the different vector species.

The four aphid species discussed are considered to be the most important vectors of BYDV in small grains (10). One other species, <u>Metapolophium</u> <u>dirhodum</u> (Walker), the rose grass aphid, is occasionally an important small grain

pest and a vector of BYDV in England and Canada (35,67). Gill (35) found the transmission of various strains of BYDV by *M. dirhodum* to be very similar to the transmission patterns by *M. avenae*. However, Plumb (67) reported that *M. dirhodum* specific strains occur in England and the pattern of transmission of different virus isolates by *M. dirhodum* and *M. avenae* is not necessarily the same.

Factors Affecting Vector Specificity

Studies by Rochow (81) indicate that aphids can acquire strains of the virus which they cannot transmit. As such, failure to acquire the virus is not the basis for vector specificity. It is fairly well established that vector specificity is a function of the virus-vector relationship (93,97). The unique intrinsic properties of the virus particle and special biological characteristics of the vector combine to produce strain specificity (82). Genetic plant host factors, plant-virus interactions, or vector characteristics alone, do not give rise to the virus-vector specificity (82). Gildow and Rochow (31,32,33) have recently provided strong evidence for the role of salivary glands in the vector specificity of BYDV variants. The different aphid species apparently have evolved specialized

salivary cell receptor sites which only recognize transmissible strains of the virus. As such it is this compatibility between the virus coat protein and salivary cell receptor sites, that governs the efficient transmission of only certain strains of the virus by selected aphid species.

Since vector specificity is a relatively stable phenomenon, BYDV isolates are frequently characterized by differential aphid transmission tests. However, the result of influences by the many factors involved in the host, virus, vector, and environment interaction do significantly affect the pattern of strain transmission by different aphid species (93).

Studies by Rochow (76) have illustrated the importance of the environment as it influences the virus-vector relationship. In testing the transmission of RMV at 15-20°C, *R. padi* and *M. avenae* rarely transmitted the virus. But the incidence of transmission by these two less efficient vectors was increased when both acquisition and inoculation test feedings were at 30°C. The virus source plant is also a source of variation. Foxe and Rochow (29) showed that the age of virus source leaves affected the transmission efficiency of PAV by *M. avenae* but not by *R. padi*. Gill (37) found that a similar situation occurred in the

transmission of a SGV isolate by three vector species, where the relative transmission efficiency was dependent on the age of source leaves. The developmental stage of the aphid vector is another source of variation. Investigations by Johnson and Rochow (49) showed that first or second instar nymphs of S. graminum transmit the SGV strain more efficiently than do adults. A similar situation has been reported for R. maidis in transmitting the RMV strain (38). Clones of single aphid species have been shown to differ in their ability to transmit various strains of the virus. Such differences have been found among clones of R. maidis, R. padi, S. graminum, and R. fitchii (58,77,83,103). The genetic diversity of the virus itself is evident by the wide distribution of vector-specific and vector non-specific isolates in nature (35,37,84,101). Variations in transmission efficiency by the different aphid species is especially evident among vector non-specific isolates (37,84,93). For example, Gill (37) has reported the occurrence of non-specific isolates in Canada which are transmitted most efficiently by S. graminum, whereas PAV-like isolates are transmitted best by R. padi.

Characterization of an isolate as a vector non-specific strain and the assignment of the vector species in

order of transmission efficiency may sometimes be erroneously determined. This is an evident problem where mixed infections (more than one strain infecting a single plant) occurs. R. padi transmits both the RPV vector-specific strain and also vector non-specific strains. The separate identity of RPV and a vector non-specific isolate in mixed infections cannot be determined by vector transmission studies (100). As such, R. padi may not be the most efficient vector of the vector non-specific isolate alone.

Diagnosis and Characterization of BYDV by Serology

To aid in the diagnosis and characterization of BYDV isolates, the application of serological techniques has greatly augmented vector transmission tests, especially where mixed infections are encountered (100). Specific antisera prepared against the PAV, MAV, RPV and RMV variants have been used to identify strains of the virus from field collected plants, for serological grouping of the virus variants, and to investigate basic biological relationships in the virus-vector interaction (1,31,54,64,90,96,100,101, 102). Most recently, the use of specific antisera in the enzyme immunosorbent assay (EIA) technique has enhanced the

detection and identification of virus strains, especially in doubly infected plants (100).

Rochow and co-workers (1,90,102) have established that two serological groups exist among the variants of BYDV. The MAV and PAV variants are serologically related and are grouped accordingly. The RPV variant is serologically unrelated to MAV and PAV, and is considered as the other distinct group. The RMV variant appears to be related to the RPV variant.

Although serologically unrelated, the RPV and MAV strains exhibit a unique relationship when both occur in the same infected plant. A phenomenon of phenotypic mixing or transencapsidation occurs in such doubly infected plants. During virus assembly in doubly infected plants, the MAV genomic integrity is maintained but the MAV-RNA is encapsidated with RPV coat protein (70,88,92,99). In serial transfer from doubly infected plants, _R. padi_ regularly transmits RPV and MAV together, as evident by recovery of MAV by _M. avenae_ (70). Studies by Rochow (70), and Rochow and Gill (99) showed that _R. padi_ would transmit RPV and MAV even after specific antiserum against MAV was injected into the viruliferous aphids. Additionally, when _R. padi_ aphids were allowed to feed through membranes on virus

preparations made from doubly infected plants, after serologically blocking the preparation with MAV specific antiserum, *R. padi* continued to transmit MAV.

A similar situation of transencapsidation occurs between the RMV and MAV variants. However, the ability of *R. maidis* to transmit MAV from doubly infected plants is lost after a maximum of eight serial transfers (95). In the RPV-MAV complex, the ability of *R. padi* to transmit MAV is not lost through serial transfer (95). The phenotypic mixing of vector specific strains may play an important role in the maintenance of such strains in nature (91).

Separation of BYDV Variants Based on the Cytological Alterations They Cause in Plants

The division of BYDV variants into two distinct groups has further been substantiated by cytological effects they cause in host plant tissues. Gill and co-workers (41, 43,44) investigated the cytological manifestations in plants infected with the vector specific MAV, RPV, RMV, and SGV variants, and two vector non-specific variants. One of the vector non-specific strains is transmitted most readily by *R. padi* and the other is transmitted best by *S. graminum*. Based on the cytological evidence, subgroup one contains

the MAV, SGV, PAV, and *S. graminum* non-specific variants and subgroup two contains the RMV and RPV variants. The division of BYDV variants based on cytological evidence (43) is in agreement with their classification by serology (1,90,102).

Characterization of BYDV Variants Based on Virulence and Host Range

Differences in virulence among BYDV variants have been used to identify and group virus isolates, in conjunction with aphid transmission tests (35,76,86,116). Generally, vector non-specific isolates cause more severe symptoms in host plants than do vector specific isolates (35, 76,86). However, numerous factors affect the expression and degree of symptom severity produced by different strains and by different isolates of any one particular strain.

Environmental conditions such as shading and temperature affects the relative severity of symptoms quite significantly. As reviewed by Bruehl (10), numerous researchers have shown that low light intensities and high temperatures tend to mask symptoms and can cause symptom remission. The relative severity of symptoms caused by different virus strains is also quite variable when compari-

sons are made among different small grain cultivars (4,86). For example, Rochow (86) showed that RPV and RMV strains caused more severe symptoms in 'California Red' oats than in 'Coast Black' oats, whereas MAV and PAV were more severe in Coast Black oats.

The variations in symptom severity as a result of infection by different isolates with differing virulence ratings was shown by Jones and Catherall (51). They found that both mild and severe virulence types occurred among virus isolates transmitted specifically by _M. avenae_ and also among isolates transmitted most efficiently by _R. padi_. Plant stunting in a susceptible barley cultivar infected at an early growth stage was more severe when caused by _R. padi_ isolates than by _M. avenae_ isolates, regardless of the virulence classification. However, in the same barley cultivar infected at a later growth stage, _M. avenae_ isolates caused more severe symptoms than _R. padi_ isolates. They postulated that with _R. padi_ transmitted isolates, the virus concentration was the important factor in retarding plant growth. However, they suggested that for _M. avenae_ transmitted isolates, virulence was more important than concentration. Studies by Burnett and Gill (11) indicate that symptoms are more severe in small grain cultivars with in-

creased dosage of the virus. Research findings by many investigators have shown that symptom expression and severity in the host is quite variable with respect to dosage, developmental stage of the host at the time of infection, the crop or cultivar affected, and virulence of the isolate (4, 26,34,51,111,113).

The use of a host range among species of Gramineae alone has not proved to be adequate in differentiating isolates of BYDV (10,79). Rochow (79) has suggested that much of the variability in symptom expression is a result of the genetic diversity among plants of any one grass species, the variability among virus isolates, and the readiness with which aphids feed on different grass species. Considering all of the factors that affect the variability in symptom expression and disease severity, symptoms alone have not been a reliable means for differentiation of the virus variants.

Further Evidence for Taxonomic Division of BYDV Variants

The unique characteristics of the *R. padi* vector-specific group of BYDV variants has merited distinction for special status as a separate luteovirus. Catherall (17)

has suggested that *R. padi* vector-specific isolates are distinct from other BYDV variants based on symptoms in ryegrass, and proposed the name ryegrass chlorotic streak virus for such isolates.

Further evidence for this distinction exists in the strong serological relatedness of *R. padi* specific strains to other luteoviruses, such as beet western yellows virus (98). Other BYDV variants, notably MAV show a more distant relationship (98). Additionally, the rice giallume disease, which is caused by a virus transmitted by *R. padi*, shows marked similarities to the *R. padi* vector-specific strains of BYDV (43). This evidence further supports the division of *R. padi* vector specific isolates from other BYDV variants. Future investigations may provide strong support to classify and group the *R. padi* specific variants as a separate luteovirus of Gramineae hosts.

Symptoms of BYDV in Small Grains

Even though there is considerable variation in the degree of symptom expression produced by different strains of BYDV, the visual symptoms, regardless of the infecting strain type, are diagnostic and characteristic of the disease. Symptoms caused by BYDV in small grains have been

well documented (10,61,79).

In barley, yellowing of the leaves and plant stunting are the most apparent symptoms. The color is a brilliant golden yellow and the chlorosis usually starts at the left tip and progressively developes down along the leaf margin. However, the chlorosis may begin as irregular blotches midway in the leaf blade and eventually coalesce, turning the leaf totally yellow. Extreme stunting occurs in some cultivars, and a stimulation of the tillering process is sometimes observed.

In oats, color changes in leaves range from a yellow-red to a brilliant scarlet, and is dependent on the cultivar as well as environmental conditions. Symptom development in oat leaves is similar to that in barley. In highly susceptible cultivars, plants become severely stunted and blasting of florets is common. When susceptible oat and barley cultivars are artifically inoculated and grown in greenhouse environments, deep leaf margin serrations may develop in newly emerging leaves.

Symptoms in spring and winter wheats are less dramatic than in oats or barley, although wheat yields may be dramatically reduced. Color changes in infected plants range from a gradual chlorosis to a bright yellowing. Ex-

pression of red to scarlet anthocyanin pigmentation often occurs, which is dependent on the cultivar and environment. In some cultivars, interveinal chlorosis is apparent, starting at the leaf tip and extending down the leaf blade, mostly along the margins. Tillering is suppressed in wheat and plants are dwarfed, although not to the extent that susceptible oat and barley cultivars are affected.

The effect of BYDV on growth and development of all small grains can be quite variable and highly dependent on the stage of plant growth when infection occurs, prevailing environmental conditions, and the virulence of the infecting virus isolate.

BYDV Effects on Yield Parameters and Correlation to Symptom Expression

The effect of the virus on yield parameters is as variable as the other interactions in the complex biological relationships between the virus, vectors, the host, and the environment. Generally, losses in yield resulting from BYDV are due to reductions in the number and fertility of headed tillers, reduced inflorescence size, and reductions in kernel number and kernel weight (10,13,24,25,26,28,39, 45,61). A great deal of the variability in the yield re-

sponse of small grains to virus infection is related to the susceptibility of individual cultivars (10,15,24,25,36,61).

Doodson and Saunders (24,25) in assessing varietal reactions of spring and winter grown cereals to BYDV infection, found that yield was reduced for all cultivars when compared to healthy controls. However, not all cultivars of a particular crop (oats, barley, or wheat) responded in the same manner to infection. For example, in glasshouse trials Doodson and Saunders (24) found that most spring and winter wheat cultivars produce fewer fertile shoots than their respective controls, whereas two cultivars produced more but smaller fertile shoots. Furthermore, the reduction in tiller number for all the crops, except oats, contributed significantly to decreases in grain yield. However, in field trials they found that reduction in tiller number was not significantly correlated to yield loss (25). In general, tiller reduction was greater in wheat than barley, and spring wheat cultivars were less affected than winter wheat cultivars. In comparing the yield losses of oat, barley, and wheat cultivars, barley and oats were more significantly affected than the wheats, and spring wheats were more tolerant than winter wheats. Contrary to the finding of Doodson and Saunders (24,25) Oswald and Houston (61) found that

wheat was more severely damaged by BYDV than oats or barley.

Correlations between symptoms and yield have not necessarily proved to be stable parameters for predicting yield response or for differentiating cultivars into tolerant versus susceptible classes relative to expected yields (5,7,15,20,28,119). Doodson and Saunders (24,25) reported that leaf symptoms were correlated with seedling height and both symptoms positively correlated to decreases in yield. However, Catherall and Hayes (15) reported that no significant correlation existed between leaf yellowing and stunting for the 13 barley cultivars tested. They found that leaf yellowing was a better measure for predicting yield losses than plant stunting. But, because of environmental variability and differences in the virulence of virus isolates, leaf yellowing was not a very stable parameter by which grain losses could be predicted. Doodson and Saunders (24,25) indicated that the number of grains per head and kernel weight were significantly correlated to yield. However, the number of grains per head proved to be a better estimate of yield response to infection than kernel weight.

Although the extent of yield reduction due to virus infection is highly dependent on the relative degree of tolerance or susceptibility of the particular crop or cul-

tivar in question, other factors also influence the extent of yield reduction significantly. Such factors include the developmental stage of plant growth at the time of infection, the virulence of the infecting strain, virus dosage, and influences of the environment.

Studies by Panayotou (66) indicate that the stage of plant growth at the time of inoculation affects vegetative growth of oereals significantly. He found that yield was reduced more notably in early than late infected oats, but that late infection reduced yields in barley and wheat more dramatically than early infection. In the case of late infection among certain cultivars, the virus stimulated growth and the greater the stimulatory effect, the more severe were the yield losses obtained. Conversely, studies by Doodson and Saunders (25) indicate that yield differences between control and infected plots for small grain cultivars were frequently insignificant when inoculation was at late growth stages.

The effect of the virus virulence and virus dosage on yield is similar to the influence both have on symptom expression discussed in the previous section. Generally, the more virulent strains of BYDV reduce yield in the crop more severely than less virulent strains (26,51). Increased

dosage of the virus has a similar effect on yield (11,113).

The environment has a substantial influence on the yield potential of BYDV infected cultivars. Conditions that favor disease development in the plant quite obviously increase the likelihood for drastic yield reductions, as opposed to conditions which favor rapid plant growth and coincidentally, do not favor development of the disease. Classical studies of the influence of the environment as it relates to the development of the host and of the virus within the host were conducted by Jones and Catherall (50), and Catherall, Jones, and Hayes (16). In investigating the genetics of tolerance to BYDV in barley, these investigators noted that some cultivars which seemed to be highly tolerant to BYDV under glasshouse conditions were susceptible in the field (50). They concluded that tolerance was most fully expressed in those genotypes and environments which resulted in rapid plant growth. Also involved was the level of tolerance conferred by different alleles of the gene that govern tolerance in barley (16), the implications of which will be discussed in the following section.

Control of BYDV and Sources of Host Plant Resistance

Bruehl (10), in reviewing the first decade of research on BYDV, discusses the methods for control of the disease, many aspects of which are still true today. Control measures such as the use of insecticides to kill the vectors, host resistance to aphids, and cultural practices, such as seeding dates to avoid times of high aphid populations, have not proved to be totally dependable control strategies (10).

Control of BYDV by the application of systemic insecticides to kill the aphid vectors has only occasionally been effective. Caldwell and co-workers (12) were successful in protecting oats with a single application of Dimethoate. Schaller and Qualset (unpublished) reported that the effects of BYDV can be minimized in experimental plots by the application of Thimet at seeding time. Studies by Close (18) indicate that systemic insecticide application can reduce the amount of damage by preventing secondary spread of the virus from initial foci of infection. Unfortunately, in most situations the use of insecticides in commercial fields has failed to limit the incidence and spread of BYDV (10). Failure of vector control to reduce losses

from BYDV has usually been a result of heavy and repeated infestations of viruliferous aphids (10). Also of significance is the necessity for the momentary feeding of the aphid vectors to acquire lethal levels of insecticide, which is probably of sufficient duration to transmit the virus.

Host resistance to aphids has also not been a successful approach to minimize losses from BYDV. Aphid resistance in the host is generally conditioned by antibiosis, tolerance, non-preference, or a combination of these factors (122). Such host resistance affects the duration of feeding, fecundity, viability, and movement of the aphids, but again does not prevent momentary feeding and subsequent transmission of the virus (123). Furthermore, cultivars resistant to one specific aphid species or biotype within a species are not necessarily resistant to another biotype or different aphid species (21,42,55,114,120,121). For example, Gill and Metcalfe (42), in studies on resistance in barley to the corn leaf aphid, found that a barley cultivar and its hybrid derivative were resistant but not immune to _R. maidis_. However, the resistance did not affect four other aphid species tested. A majority of the work done in developing host resistance to aphids has centered on green-

bug because of the toxic effect this species has on plants. A number of biotypes of this species exists and the cultivars resistant to one particular biotype are not necessarily resistant to the other biotypes (21,114,121). Here again, the host resistance mechanism generally does not completely inhibit aphid feeding and thus the level of resistance does not prevent virus infection from occurring. From an epidemiological standpoint, host resistance to aphids could perhaps limit the rapid build-up of viruliferous aphid populations if the use of resistant cultivars was widespread. It is not however, a practical solution considering the limitations aforementioned.

With regard to cultural practices, only planting date for small grains has been useful in preventing heavy losses from BYDV, and only in certain geographic areas (10). Success with disease avoidance by proper planting date is solely dependent on the biology of aphid population maintenance and movement within or migration into a particular agricultural region. Therefore, some knowledge of cereal grain aphid, population dynamics, including time of migration, overwintering potential, and potential infestation periods, are necessary to determine planting dates which will provide some level of disease avoidance in any partic-

ular area. As a general recommendation, early fall seeding of winter habit cereals and late spring planting of spring habit grains are to be avoided, as these times often coincide with periods of rapid and extensive aphid population build-up and migration (10,69).

Currently the most successful and actively pursued method for control of BYDV is in the development of tolerant resistant small grain cultivars. To date, release of agrinomically acceptable, BYDV tolerant barley cultivars has made the most progress. Some success in providing tolerant oat varieties has been realized, whereas an acceptable level of tolerance in wheats for the most part, has yet to be found.

The source and genetics for resistance to BYDV is most well established for barley. Schaller and co-workers (106), in testing 6,689 barley cultivars for their reaction to BYDV at Davis, California, found 117 cultivars which showed a high level of tolerance. Of these 117 cultivars, 116 were of Ethiopian origin and one was from China. When some or all of these tolerant cultivars were tested by researchers in other geographic areas, a few of the entries were classified as being susceptible (5,46). The apparent reasons for differences in the reaction of such barley

cultivars have been attributed to the pathogenicity of virus isolates, the environment, and the growth rate of the particular cultivar in those environments (5,46).

Genetic analyses of resistance to BYDV have shown that one gene (<u>Yd_2</u>), conditions resistance in all cultivars that have been tested (15,20,46,73). According to the work of Schaller and co-investigators (107), this gene is located on the left arm of chromosome 3. Although only a single gene appears to govern BYDV resistance in barley, the possibility of closely linked genes or a series of alleles cannot be excluded. Hayes and co-workers (46) found that the tolerant parent source affected the genetic ratio of F_2 generation progeny from tolerant x susceptible crosses. The nature of inheritance in these studies ranged from complete dominance to recessive, depending on the source of tolerance. They also found that there was a positive correlation between levels of tolerance expressed by the parents and progeny with their growth rate. Jones and Catherall (50) have suggested that virus replication is retarded more so in fast growing genotypes than in slow growing genotypes, all of which were homozygous for the tolerance gene. Thus, the genetic background as well as the parental source of tolerance seem to be important in the level of tolerance

expressed. Schaller and Qualset (unpublished) have stated that the varying levels of tolerance could be a result of closely linked genes, multiple alleles and genetic background, or modifier genes, which may influence growth rate or other biological aspects of the virus-host interaction.

In wheat, a number of resistant sources have been identified but only moderate success has been realized in release of agronomically acceptable, tolerant cultivars (10,71,72). The origin of tolerant sources for wheat, as is the case for barley, seems to be limited to Ethiopia. Currently, only two tolerant spring wheat cultivars, Anza and Shasta, are grown on a commercial basis (Schaller and Qualset, unpublished).

The limited genetic analyses on tolerance in spring wheat suggests that inheritance is dominant, but not simply inherited, and that a recurrent selection would be the most effective method to breed for resistance in wheats (71). Commercially available winter wheat cultivars tolerant to BYDV have yet to be released, although considerable emphasis is being placed on discovering and exploiting sources of tolerance in winter wheat.

CHAPTER I

FIELD DISEASE SURVEY AND IDENTIFICATION OF BARLEY YELLOW DWARF VIRUS

Materials and Methods

To ascertain the occurrence and prevalence of barley yellow dwarf in Montana, grain fields in a 10 county area were monitored four consecutive years, beginning in 1978. Cascade, Chouteau, Pondera, Toole, Teton, Judith Basin, Fergus, Gallatin, Glacier, and Yellowstone Counties constituted the survey area (Figure 1.1). These 10 counties are located in the north- to southcentral portion of the state, where the majority of small grains are grown.

During the surveys, fields of winter wheat, spring wheat, spring barley, and spring oats were examined for plants exhibiting symptoms of the disease. Individual plants showing symptoms typical of BYDV infection were collected from the field survey sites. Such plants were subsequently used as source material for vector transmission of BYDV to indicator test seedlings. Live aphids were also collected from naturally occurring infestations found in small grain fields. Aphid samples provided a means by which BYDV could be isolated directly from the vector population.

Strain identification of BYDV isolates originally

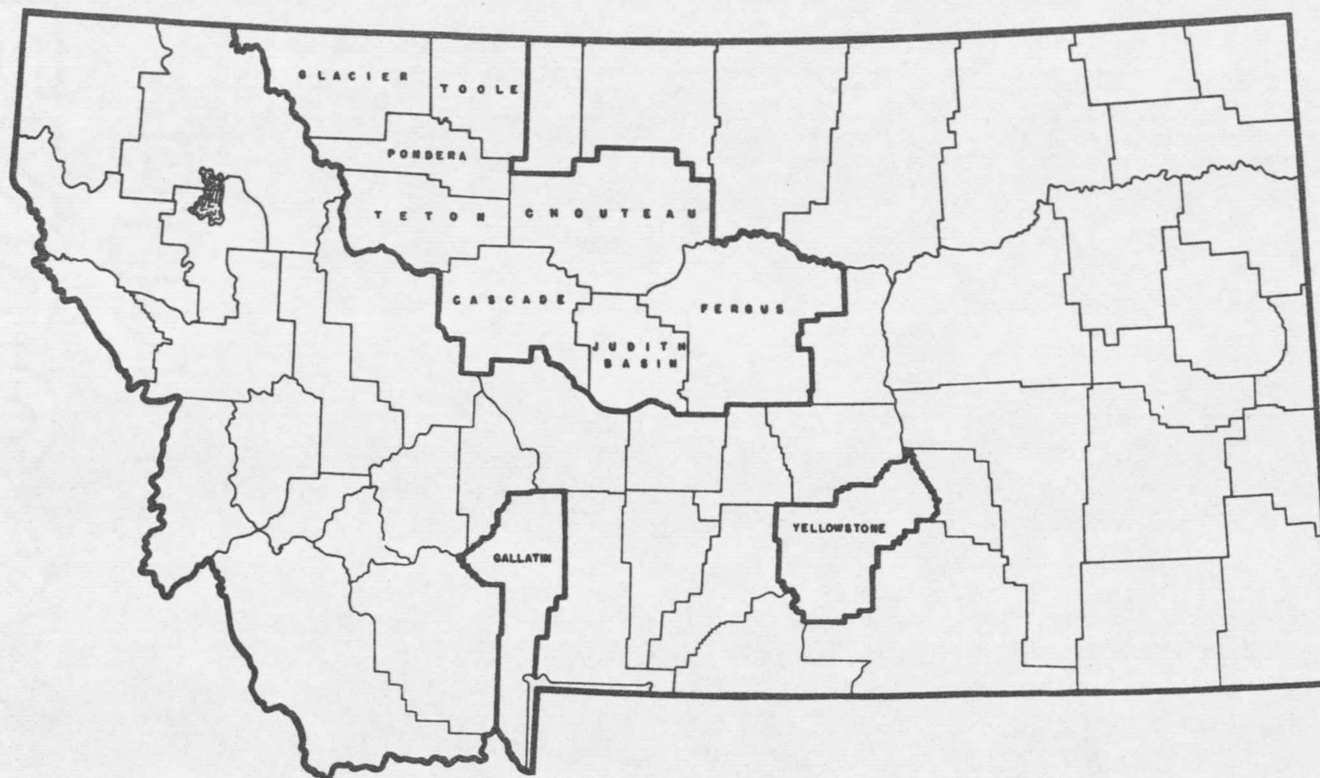

Figure 1.1. Barley yellow dwarf virus survey area.

transmitted from field plants or by aphids from native populations was accomplished by vector-strain specificity studies and enzyme immunosorbent assay.

Four aphid species were used to transmit barley yellow dwarf virus from diseased field plants to indicator test plants. The four species were *Rhopalosiphum padi* (Linnaeus), the oat bird-cherry aphid; *Macrosiphum avenae* (Fabricus), the English grain aphid; *Rhopalosiphum maidis* (Fitch), the corn leaf aphid; and *Schizaphis graminum* (Rondani) the greenbug. Biotypes of these aphid species were kindly provided by W. F. Rochow, Cornell University, Ithaca, New York. These New York biotypes of proven vector efficiency were used for most of the transmission studies in preference to Montana biotypes of unproven vector efficiency.

Aphid Rearing

Colonies of the four aphid species were reared and maintained in the insectary facilities at Montana State University, Bozeman, Montana. Colonies were raised on 'Klages' barley, grown in greenhouse soil in 15.0 cm diameter clay pots. Approximately 30 seeds were sown per pot and the 5-7

day-old seedlings were subsequently infested with 10-15 aphids. Colonies were started with first instar nymphs less than 24 hours old. This practice was done to insure that the resulting aphid populations would be non-viruliferous, as newly borne nymphs fail to acquire BYDV (18). The individual colonies were confined with a nylon mesh cage. Cages were constructed using a 7.5 cm long x 15.0 cm diameter piece of acrylic resin tube (Almac plastics, N.Y.) as a base, to which a 297/6.5 cm^3 mesh Nitex fabric (Tetko Inc., N.Y.) cage, 25.0 cm high x 15.0 cm in diameter, was attached to one end.

Colonies were reared for 21-25 days before the aphids were used for a transmission experiment. After the necessary aphids were removed from colony support plants, the plants were placed in an oven operating at 270°C for a period of 5-10 minutes. This procedure was used to limit the escape of any remaining aphids into the rearing area.

Vector Acquisition of BYDV From Diseased Field Plants

Two methods were used for recovery of BYDV from diseased field plants by the aphid vectors. The first method was the 'detached leaf technique', as described by W. F. Rochow (75,76). Leaves from field collected plants exhibiting BYDV symptoms were detached at the base

of the leaf blade. Leaf pieces, 12-15 cm long, taken from the base to middle portion of the detached leaves, were placed in plastic dishes along with non-viruliferous aphids. Aphids of each of the four species were caged separately on pieces of leaves detached from the field collected sample, and allowed a 48 hour acquisition access feeding period in the dark at 15°C.

The second recovery method used was the 'membrane feeding technique', also developed by W. F. Rochow (78). This procedure allows aphids to acquire the virus by feeding on the liquid preparations of plant tissue extracts when they probe through parafilm membranes.

Feeding cages were made from sponge rubber sheets, 15.0 cm x 15.0 cm x 1.3 cm. Six 1.0 cm diameter holes were made in each cage with a cork borer and a seventh hole made in the center. To one surface of the cage was attached a piece of Nitex nylon mesh, forming the bottom of the feeding well. About 10-20 non-viruliferous aphids were transferred to each well with a camel hair brush, except to the center one, which was left open for air circulation. After the aphids had been deposited into each well, the hole was closed using a glass tube, 12 mm in diameter x 5 cm long, one end of which was covered with a tightly stretched para-

film membrane. The membrane covered end faced down into the feeding well. The feeding cage containing aphids and membranes was then placed over an open petri dish filled with water. Approximately 0.5 ml of the liquid plant tissue extract to be tested was placed in each tube.

The liquid extract was prepared by homogenizing the plant sample tissue in distilled water (1.0g/2.0 ml water) in a Waring blender. Usually, 50 g of tissue and 100 ml of water were used per sample. The homogenate was centrifuged at 3550 g for 15 minutes in a GSA Sorvall Rotor at 4°C. The supernatant liquid was adjusted to 10% sucrose (wt/vol.) and allowed to warm to room temperature before being placed in each feeding tube. The aphids were given a 16-18 hour acquisition access feeding period at 4°C and then transferred from the membranes to indicator test seedlings.

Vector Transmission of BYDV to Indicator Test Plants

In the virus transmission studies, the indicator test plant for all experiments was oats (*Avena byzantina* K. Koch 'Coast Black'), unless otherwise stated. Seeds of 'Coast Black' oats were planted 4-5 per pot in greenhouse soil in 8.0 cm clay pots. Each of the 5-7 day-old seedlings were infested with 10-15 aphids previously allowed to acquire BYDV from detached leaves or plant tissue extracts.

After the seedlings had been infested with the vector aphids, the seedlings were caged for the transmission access feeding period of 5 days. Cages were made from clear acrylic resin tubing, 25 cm long x 8 cm diameter, with one end covered by a piece of Nitex nylon mesh. During the transmission access feeding period the indicator test seedlings were placed under cool white fluorescent lights for a 24 hour per day photoperiod, at approximately 10,000 lux illumination and at 21°C. At the end of the transmission feeding period the aphids were killed by fumigating the test plants in a closed chamber, using Vapona (dichlorovos) insecticide (Pratt Chemical, N.J.). Test seedlings were then placed in the greenhouse for a 21 day post-inoculation period. The greenhouse facilities were fumigated with Vapona insecticide every 7-10 days to maintain an aphid-free environment. During the symptom development period the indicator test plants were grown under metal-halide, incandescent lights for a 16 hour per day photoperiod, at approximately 40,000 lux illumination. During the summer, daily temperatures in the greenhouse ranged from 20°C to 40°C, which is less than ideal for BYDV symptom expression (10). Therefore, whenever possible, test seedlings were placed in an Conviron growth chamber (Controlled Environments, Winnepeg, Canada) after

the 5 day transmission access feeding period. Growth conditions in the chamber were maintained at 21°C with a 16 hour per day photoperiod, at approximately 40,000 lux illumination and at 30% relative humidity. BYDV symptom development in the indicator test plants was monitored weekly and final evaluations were made at the end of the 21 day symptom expression period.

In all of the virus transmission studies where plant material was the virus source, test aphids of each species were transferred from the leaf samples after the virus acquisition feeding period to separate groups of indicator test plants. By this procedure, some indication of the vector-strain specificity could be determined from the initial transmission of BYDV. Additionally, in all experiments where reared aphids were used to vector BYDV, a portion of the aphid population from each colony was used as a control. Aphids from each colony were transferred directly to indicator test seedlings for a 5 day transmission access feeding period. This control procedure assured that the colonies of aphids were non-viruliferous prior to their use in each virus transmission study.

Transmission of BYDV by Field Collected Aphids

Test aphids collected from field populations were transferred directly onto 5-7 day-old oat or barley (*Hordeum vulgare* L. emend Bowden 'California mariout') seedlings for a 5 day transmission access feeding period. In most transmission tests, single aphids of a particular species from a field population sample were transferred to single test seedlings. However, in some experiments, groups of 2-5 aphids were placed on single test seedlings. Infested seedlings were caged individually with a 2.54 cm diameter x 25.4 cm long clear butyrate tube, one end of which was sealed with a sponge rubber stopper. The identity of aphids collected in the field was determined by Dr. V. Eastop, British Museum of Natural History, London, England.

Virus Strain Identification

Two procedures were followed to differentiate and identify variants (strains) of the virus isolated from field collected plants and native aphid populations. The initial procedure required the use of the four aphid species to determine the vector-strain specificity of each field isolate. This procedure is referred to as the "4 bug" method by W. F. Rochow. After one cycle with the "4 bug" method, in which BYDV is transmitted from field material to indica-

tor test plants, a second "4 bug" cycle is used to transfer the virus from originally infected test plants to a second set of indicator test plants. For example, if from the original source, R. padi and M. avenae transmitted BYDV to individual test seedlings, aphids of the four vector species were separately placed on detached leaf pieces from both the R. padi and M. avenae vectored sources independently. At least three "4 bug" cycles of serial transmission were completed before a determination was made as to the vector-strain specificity of a particular isolate. Once the BYDV isolate had been characterized by such vector specificity studies, a confirmation of the strain identity was obtained by serology. Leaf samples of oat test plants, 4-6 weeks old, infected by a particular isolate were sent to Dr. W. F. Rochow for testing by Enzyme Immunosorbent Assay (54). This test relies on a specific precipitation reaction between the virus antigen and one or more of the immunoglobulins produced specifically against known strains of BYDV. Thus, isolates recovered from diseased field plants or aphids from native populations were characterized as to their vector specificity and serological grouping.

Results and Discussion

Over the four year disease survey period a total of 179 sources including both plant and aphid samples, were tested for the presence of BYDV. From these 179 sources, 27 isolates of the virus were recovered (Table 1.1). Among these 27 isolates, four variants of BYDV were identified by aphid transmission tests and/or EIA and were found to be widely distributed in central Montana (Figure 1.2). The strain type, source of recovery, and location of recovery for each isolate are listed in Table 1.2.

In 1978, one isolate, MT 781, a MAV vector-specific strain, was recovered by the 'membrane feeding technique'. This isolate was acquired from diseased oat tissue extract and transmitted to indicator test seedlings by *M. avenae*. In 1978 and 1979, an additional 16 plant samples were tested using the 'membrane feeding technique'. None of the test aphids transmitted virus from these samples. Rochow (78) has reported that among the four species of test aphids used, only *M. avenae* efficiently and consistently acquires virus from plant tissue extracts. It is quite possible, that these 16 samples expressing 'typical' BYDV symptoms may have been infected with vector-specific strains not readily transmitted by *M. avenae*. Because of this inherent problem in using the 'membrane feeding technique' for recovery of BYDV

Table 1.1. Summary results for the recovery of BYDV isolates from field sources.

Source	No. Tested	No. of Isolates Recovered
Oats	6	2
Barley	20	6
Spring Wheat	12	2
Winter Wheat	38	8
Native Grasses	5	1
Aphid Colonies	98	8
Total	179	Total 27

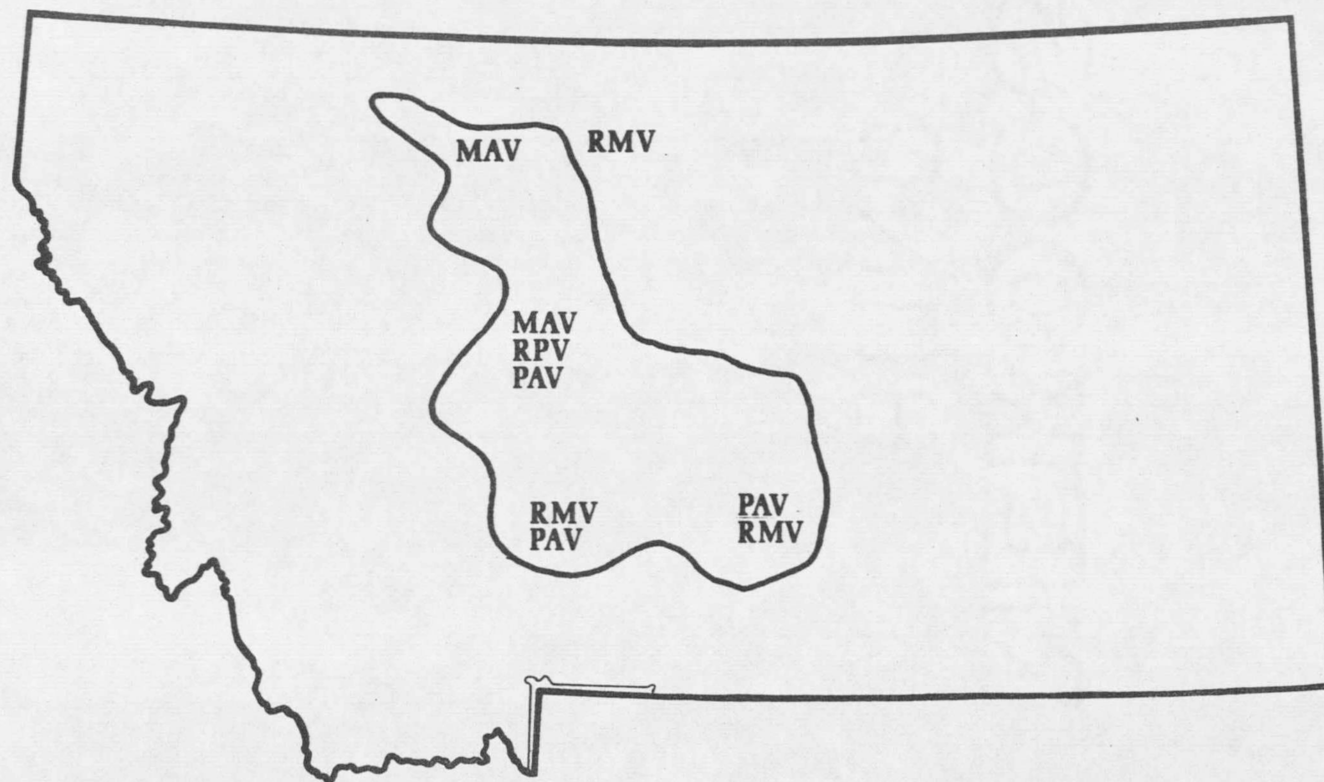

Figure 1.2. Distribution of BYDV strains found in central Montana.

Table 1.2. Isolates of barley yellow dwarf virus recovered from various survey sites in Central Montana 1978-81.

Isolate[1/]	Strain Type[2/]	Source[3/]	County
MT 781	MAV c	Oats	Toole
MT 782	PAV c	Oats	Gallatin
MT 791a	RMV a	*R. maidis*	Yellowstone
MT 791b	RMV a	Barnyard Grass	Yellowstone
MT 792	PAV c	Barley	Gallatin
MT 793	RMV a	Barley	Gallatin
MT 801	PAV a	Winter Wheat	Pondera
MT 802	PAV c, RPV b	Spring Wheat	Pondera
MT 803	PAV c, RPV b	Barley	Teton
MT 804	PAV c	*M. avenae*	Pondera
MT 805	PAV c	*R. padiformis*	Judith Basin
MT 806	PAV c	*M. avenae*	Pondera
MT 807	PAV a	*R. padi*	Chouteau
MT 808	RMV a	*R. maidis*	Gallatin
MT 809	RMV a	*R. maidis*	Gallatin
MT 8010	RMV a	*R. maidis*	Gallatin
MT 8011	RMV a	Barley	Judith Basin
MT 8012	RMV a	Winter Wheat	Judith Basin
MT 8013	RMV a	Barley	Judith Basin
MT 811	PAV c, MAV c	Winter Wheat	Pondera
MT 812	MAV c	Winter Wheat	Pondera
MT 813	MAV c	Winter Wheat	Pondera
MT 814	PAV c	Winter Wheat	Pondera
MT 815	PAV a	Winter Wheat	Pondera
MT 816	PAV c	Spring Wheat	Yellowstone

Table 1.2 (Continued)

Isolate[1/]	Strain Type[2/]	Source [3/]	County
MT 817	RMV a	Barley	Hill
MT 818	RMV a, PAV c	Winter Wheat	Pondera

[1/]The first two numbers in the isolate code denote the year of collection.

[2/]The letter a, b, or c following the strain classification indicate if the strain was characterized by aphid transmission only, EIA only, or aphid transmission and EIA, respectively. Where two strain types are recorded, both were recovered from the same plant sample.

[3/]Isolates were recovered from plant sources by aphid transmission tests, and/or identified by EIA. Some isolates were recovered from aphid sources directly after transmission of the virus sample by the field collected aphids of each indicated species.

from plant samples, its use was discontinued in favor of the 'detached leaf technique'. Thus, the remainder of isolates recovered from plant sources were obtained by aphid transmission from detached leaves.

Three variants of BYDV were recovered by aphid transmission experiments and their identity determined by vector specificity studies. Four isolates were of the MAV strain type, fourteen isolates were of the PAV strain type and eleven isolates were of the RMV strain type (Table 1.2). The transmission results for the MAV-, PAV-, and RMV-like isolates are consistent with those reported in the literature for each of these BYDV variants. MAV-like isolates were consistently transmitted only by _M. avenae_, PAV-like isolates were transmitted by _R. padi_, _M. avenae_, and _S. graminum_, and RMV-like isolates were transmitted most efficiently by _R. maidis_ and occasionally by _R. padi_ and _S. graminum_ (Table 1.3).

Although the RMV-like isolates recovered were characterized as _R. maidis_ vector-specific strains, considerable variability in the transmission pattern by the less efficient vectors _R. padi_ and _S. graminum_ was observed (Table 1.4). Isolate 791b was transmitted by _R. maidis_ only, whereas the transmission patterns for isolates MT 809, MT 8010,

Table 1.3. Aphid transmission results for the most prevalent vector-specific and vector non-specific strains of BYDV collected in Montana. Transmission data is consolidated over all '4 bug' tests and over all isolates for the specific strain type indicated.

Vector Species	Strain Type[1]			
	PAV	MAV	RMV	Control[3]
R. padi	379/417[2]	22/148	32/254	0/301
M. avenae	360/434	171/226	0/249	0/315
R. maidis	0/381	0/140	178/264	0/298
S. graminum	120/374	3/131	30/271	0/298

[1] For each strain type, the transmission data is a consolidation for several isolates, each being transferred through at least three cycles of serial transfer using the four species of aphids ('4 bug' test).

[2] The denominator is the total number of plants infested with test aphids and the numerator is the total number of test plants that became infected.

[3] The control results are consolidated over all transmission tests for all of the strain types. In each separate '4 bug' experiment, 40-60 aphids were taken directly from each of the aphid colonies used in the experiment and placed on indicator test seedlings. This was done to assure that the aphids were non-viruliferous prior to their use in an experiment.

Table 1.4. Transmission of BYDV by four *Rhopalosiphum maidis* vector specific isolates.

Isolate	Transmission Results[1/]			
	MT 791b	MT 809	MT 8010	MT 808
Vector				
R. maidis	34/60[2/]	26/33	48/57	57/63
R. padi	0/60	0/28	8/50	24/64
S. graminum	0/60	5/33	7/50	21/67
M. avenae	0/60	0/33	0/52	0/60

[1/] The transmission results for each strain are consolidated over at least three cycles of serial transfer using the four species of aphids ('4 bug' test).

[2/] Numerator is the number of coast black oat indicator test seedlings that became infected and denominator is the number of seedlings infested with test aphids. None of 319 test plants used as controls became infected.

and even more so for isolate MT 808, were relative among the aphid vectors, *R. maidis* being the most efficient vector whereas *R. padi* and *S. graminum* transmitted these isolates but less frequently. In several experiments all four of the isolates were transmitted to test plants during the same period, such that any environmental influences can be discounted as possibly affecting the pattern of vector transmission. More likely an explanation is that RMV-like isolates represent a heterogeneous group within the barley yellow dwarf viruses. Variation in transmission patterns are probably a result of differences in the intrinsic biological properties among such RMV isolates, a hypothesis supported by Rochow (personal communication).

A fourth BYDV variant, RPV, which is transmitted specifically by *R. padi*, was identified by EIA but not recovered in aphid transmission studies (Table 1.5). The reason for this non-recovery by aphids is a result of confounding by the presence of another, yet different strain of the virus present in the particular plant samples tested. Isolates MT 802 and MT 803 were transmitted from infected spring wheat and barley plants respectively (Table 1.2). In aphid transmission studies, both isolates were transmitted in order of efficiency by *R. padi*, *M. avenae*, and *S. grami-*

Table 1.5. Enzyme Immunosorbent Assay results for BYDV isolates tested at Cornell University, Ithaca, N.Y.

		A405 With Immuoglobulin Shown[1/]				
Isolate	Date	RPV	MAV	PAV	RMV	Strain Type[2/]
MT 781	6/7/79	.009	1.40	.123	.004	MAV
MT 792		.007	.115	1.25	.006	PAV
NY PAV		.003	.099	.860	.001	PAV
NY MAV		.013	1.50	.063	.008	MAV
Healthy Ck.		.005	.007	.010	.007	
MT 782	4/3/80	.030	.060	.209	.008	PAV
MT 791b		.039	.018	.011	.011	RMV
MT 791b		.055	.039	.016	.018	RMV
NY PAV		.020	.170	.730	.011	PAV
NY RMV		.054	.015	.021	.150	RMV
NY MAV		.018	1.10	.095	.010	MAV
NY RPV		.750	0.24	.011	.020	RPV
Healthy Ck.		.031	.023	.025	.015	
MT 791b	7/9/80	.015	.007	.010	.009	RMV
NY RMV		--	--	--	.135	RMV
Healthy Ck.		.008	.007	.005	.011	
MT 811a	8/7/81	.003	.096	.865	.012	PAV
MT 811b		.005	>1.50	.055	.002	MAV
MT 812		.001	1.12	.043	.022	MAV
MT 813		.049	.202	.017	.035	MAV
MT 815		.000	.076	.784	.002	PAV
MT 814	10/29/81	.016	.062	.324	.009	PAV
MT 818a		.005	.100	.624	.010	PAV
MT 818b		.012	.010	.025	.011	RMV
MT 817		.002	.002	.010	.005	RMV
MT 808		.002	.007	.014	.011	RMV
MT 803		.308	.034	.294	.007	RPV, PAV
MT 816		.011	.095	.475	.007	PAV
MT 802		.982	.054	.283	.005	RPV, PAV
MT 806		.009	.088	.668	.010	PAV
MT 804		.011	.036	.288	.007	PAV
MT 805		.009	.062	.489	.007	PAV
NY RPV		.925	--	--	--	RPV
NY MAV		--	1.439	--	--	MAV

Table 1.5. (Continued)

		A405 With Immunoglobulin Shown 1/				
Isolate	Date	RPV	MAV	PAV	RMV	Strain Type 2/
NY PAV		--	--	.897	--	PAV
NY RMV		--	--	--	.978	RMV
Healthy Ck.		--	.015	.010	.011	

1/ Spectrophotometric absorbence reading through a 1 mm light path.

2/ The RMV strains from Montana did not react strongly with any of the four immunoglobulins, such that, identification by EIA results was not possible. Strain identification therefore was based only on comparative aphid transmission tests.

num, suggesting that PAV, the vector non-specific variant was the strain type involved. However, 'Coast Black' oat plants infected with either of the MT 802 or MT 803 isolates were severely stunted with respect to un-inoculated control plants, as well as plants inoculated with other known PAV-like isolates. Subsequent analysis by EIA determined that isolates MT 802 and MT 803 were mixed infections of PAV and RPV variants, the identity of each being inseparable by aphid transmission patterns (Table 1.5).

Among the 27 BYDV isolates, the strain identity for 18 was determined or confirmed by EIA results (Table 1.5). In comparison to New York MAV and PAV variants, the Montana MAV and PAV types were remarkably similar in homologous and heterologous reactions with immunoglobulins prepared against New York MAV and PAV antigens respectively (Table 1.5). However, the RMV-like isolates found in Montana failed to react with the immunoglobulin prepared against the New York RMV variant, or against any of the other variants. All Montana RMV-like isolates, i.e. MT 791b, MT 818, MT 817, and MT 808, were similar in that regard, even though the patterns of aphid transmission by the less efficient vectors were not always the same, i.e. MT 791b vs. MT 808 (Table 1.4). The EIA data for Montana RMV variants supports the

hypothesis that these variants are very similar, yet somewhat genetically different with respect to their variability of transmission by the less efficient vectors.

Among the plant samples tested by EIA, four were found to be infected by a mixture of BYDV strains (Table 1.5). Isolates MT 818a and 818b were recovered from winter wheat and transmitted to test plants by *R. padi* and *R. maidis*, respectively. The two strains involved were PAV and RMV types, as characterized by both aphid transmission and EIA. In New York transmission tests, isolates MT 811a and MT 811b were recovered from a winter wheat sample where MT 811a was selectively transmitted by *R. padi* and *S. graminum* and MT 811b was selectively transmitted by *M. avenae*. As determined by aphid transmission tests and EIA, isolates MT 811a and MT 811b were PAV and MAV variants, respectively. In Montana transmission tests using detached leaves from the same winter wheat sample, only a MAV variant was recovered by *M. avenae*. Apparently *R. padi* occasionally fails to acquire virus from field plant materials, a phenomenon occasionally observed by Rochow (personal communication). Isolates MT 802 and MT 803 were found to be a mixture of PAV and RPV strains (Table 1.5) by EIA but not separable by aphid transmission studies.

Rochow (94) has reported that mixed infections are most often found to occur in winter wheat or winter barley samples and seldom in spring oats. Both MT 802 and MT 803 isolates were recovered from spring grains, which may have important epidemiological significance considering the mixture of strains found to be present. As is the case for winter wheat doubly infected with different strains, perhaps doubly infected spring grains may provide an inoculum reservoir for aphid species that are not yet present in the crop producing area (91). In the case of the MT 802 and MT 803 isolates, RPV and PAV are available for acquisition by *R. padi*, *M. avenae*, and *S. graminum*, the latter two species able to transmit only the PAV variant. However, *R. padi* being capable of transmitting both strains, provides the potential to incite further double infections and thus, an expanded virus reservoir for the other two vector species.

Among the native grasses sampled for the presence of BYDV, from only one, Barnyard-grass, *Echinochloa* sp., was virus recovered. Isolate 791b a RMV-like variant was found to be the infecting strain, as was the case for isolate 791a recovered from barley in the same field. Barnyard-grass being a perennial, may provide an overwintering reservoir for the virus, although its actual importance in the epidem-

iology of BYDV in Montana is unknown.

A total of eight isolates were recovered from aphid populations sampled in 1979 and 1980 (Table 1.2). Five species of aphids among those populations sampled were identified by V. E. Eastop, Entomologist, British Museum of Natural History, four of which were the common cereal grain aphids _R_. _padi_, _M_. _avenae_, _S_. _graminum_ and _R_. _maidis_. The fifth species was identified as _R_. _padiformis_ (Richards), previously known only from British Columbia. Only two strain types, PAV and RMV were recovered directly from transmission by the sampled aphid populations. In most vector transmission experiments, the percentage of aphid populations shown to be viruliferous was very low or non-existent (Table 1.6). However, in two situations, the percentage of viruliferous aphids in the population sampled was very high (Table 1.6).

Plumb (68) found that over a period of four years, the percentage of viruliferous aphids of any one species caught in suction traps was never more than 11.5%. A'Brook and Dewar (2) found that the percent viruliferous alatae aphid vectors caught in suction traps was as high as 38.9% for any one particular species. They also observed that over a ten year period, the species with the greatest proportion of in-

Table 1.6. Aphid populations sampled in Central Montana found to be carrying BYDV.

Location	Aphid Species Collected	No. of Colonies Tested	% of Sampled Aphid Populations Infective
Huntley, MT	*R. maidis*	12	12
	S. graminum	11	0
	M. avenae	2	0
Buffalo, MT	*R. maidis*	12	85
	R. padi	6	0
Bozeman, MT	*R. maidis*	13	71
Central MT [1/]	*R. padi* *M. avenae* *S. graminum* *R. padiformis*	38	10

[1/] During field surveys aphid populations were sampled randomly from both 'healthy' and 'diseased' plants. Individual aphids were selected and placed directly onto indicator test seedlings of 'Coast Black' oats or 'California Mariout' barley.

fective alatae was *R. maidis*. Furthermore, the greatest proportion of infective aphid vectors were often caught in August through early October.

The *R. maidis* colonies from Huntley, Bozeman, and Buffalo, Montana were collected August 8, 1979, September 15, 1980, and September 23,1980 respectively. The highest percentage of infective aphids was found at the latter two locations sampled in September. Although the vector populations were not monitored on a monthly basis, this evidence and the supportive findings of A'Brook and Dewar (2) suggest that for *R. maidis* acting as a BYDV vector, late summer to early fall infection of winter wheat may perhaps be an important epidemiological factor in Montana.

In 1978 and 1979, the prevalence of BYDV symptoms in fields surveyed in the ten county area was very low to negligible. Only occasionally were fields found that showed any level of BYDV infection, and then only as scattered diseased plants along field margins.

In 1980 however, a severe BYDV epiphytotic on winter wheat was diagnosed in Judith Basin and Fergus Counties, based on observable symptoms (Figure 1.3). In the epiphytotic area, it was noted that fields of winter wheat planted prior to about September 10, 1979 were severely affected,

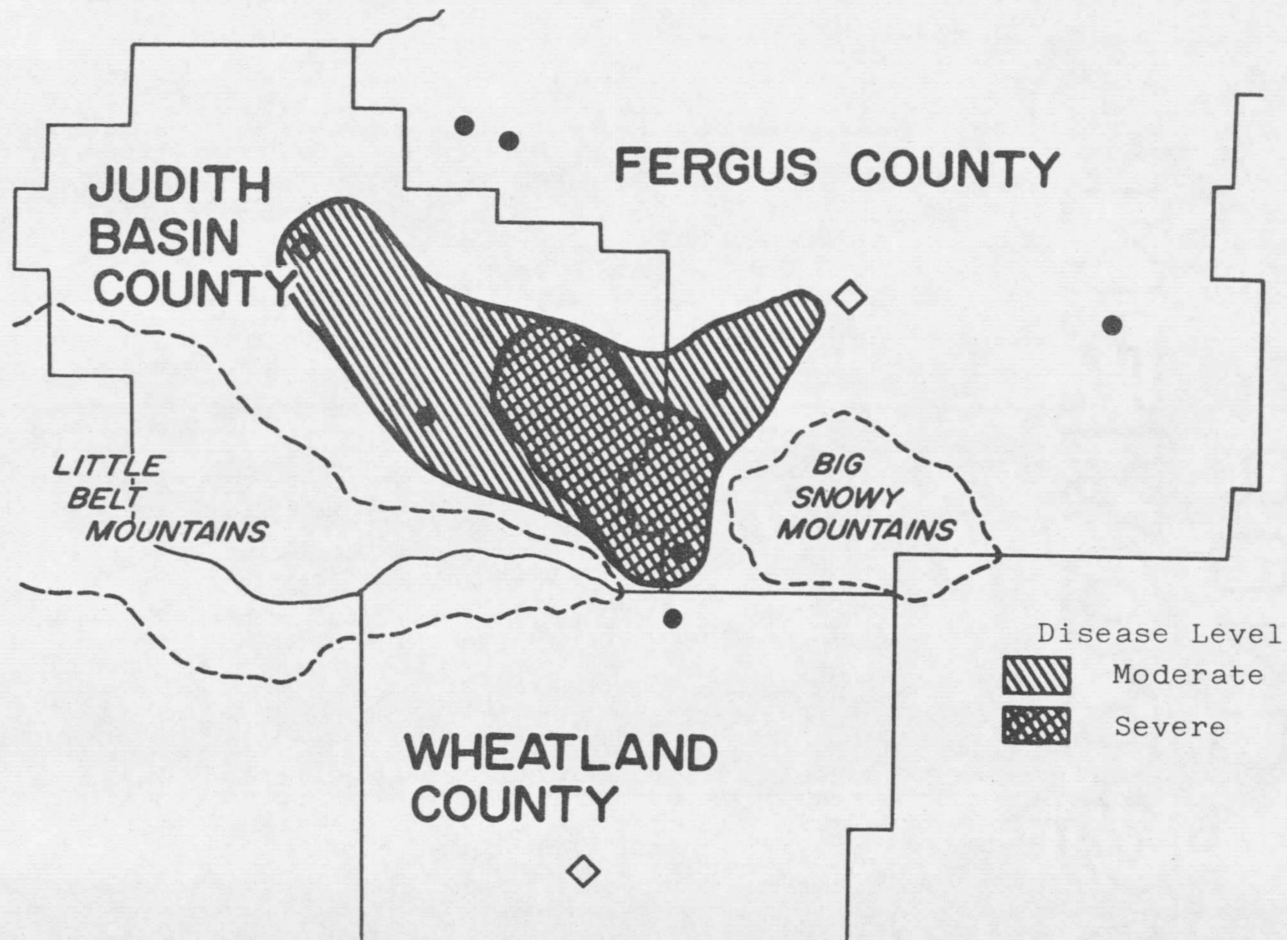

Figure 1.3. BYDV ephiphytotic on winter wheat in Judith Basin and Fergus Counties, 1980.

whereas those planted after that date were only slightly affected or free of the disease. The major foci of infection appeared to be located just north of Judith Gap, Montana. The epiphytotic extended from that point in a northwesterly direction, coincidentally with the direction of prevailing fall winds in the area. Additionally, heavy aphid populations were present in late August through mid-September in 1979 (A. Dubbs, Superintendent, Central Montana Agricultural Experiment Station, personal communication). The evidence indicates that fall infection of winter wheat was by a major infestation of viruliferous aphids in the area.

Numerous samples of winter wheat were collected and tested for BYDV by aphid transmission. However, these studies failed to detect the virus. This failure may have been a result of high greenhouse temperatures during these particular transmission experiments, which were obviously non-ideal for symptom expression. Additionally, the indicator test plants used were 'California Mariout' barley which is more sensitive to environmental masking of symptoms at high temperatures than are 'Coast Black' oats.

Although virus was not recovered by aphid transmission from field plant samples, a PAV-like variant was trans-

mitted by _R. padiformis_ colonies, collected at the Moccasin Agricultural Experiment Station (Table 1.2). Furthermore, in September 1980 both _R. maidis_ and _R. padi_ populations were in abundance in several fields of volunteer winter wheat and spring barley, and the _R. maidis_ but not the _R. padi_ populations proved to be infective (Table 1.6). Therefore, the potential for a second epiphytotic in winter wheat was present for the following year. Although evidence for BYDV infection by aphid transmission of the virus from plant materials was lacking, the supportive evidence strongly implicated BYDV as the infectious agent.

In other areas of central Montana surveyed during 1980, several isolates were recovered (Table 1.2). However, plants exhibiting symptoms of virus infection were found scattered along field margins and no fields surveyed outside of the Judith Basin epiphytotic area were observed to be severely affected.

In 1981, a second BYDV epiphytotic on winter wheat was encountered in Pondera County and surrounding areas (Figure 1.4). Again, fields planted prior to about September 10 were severely affected whereas those planted past that date showed considerably less incidence of disease. Two virus strains, PAV and MAV were identified as the pre-

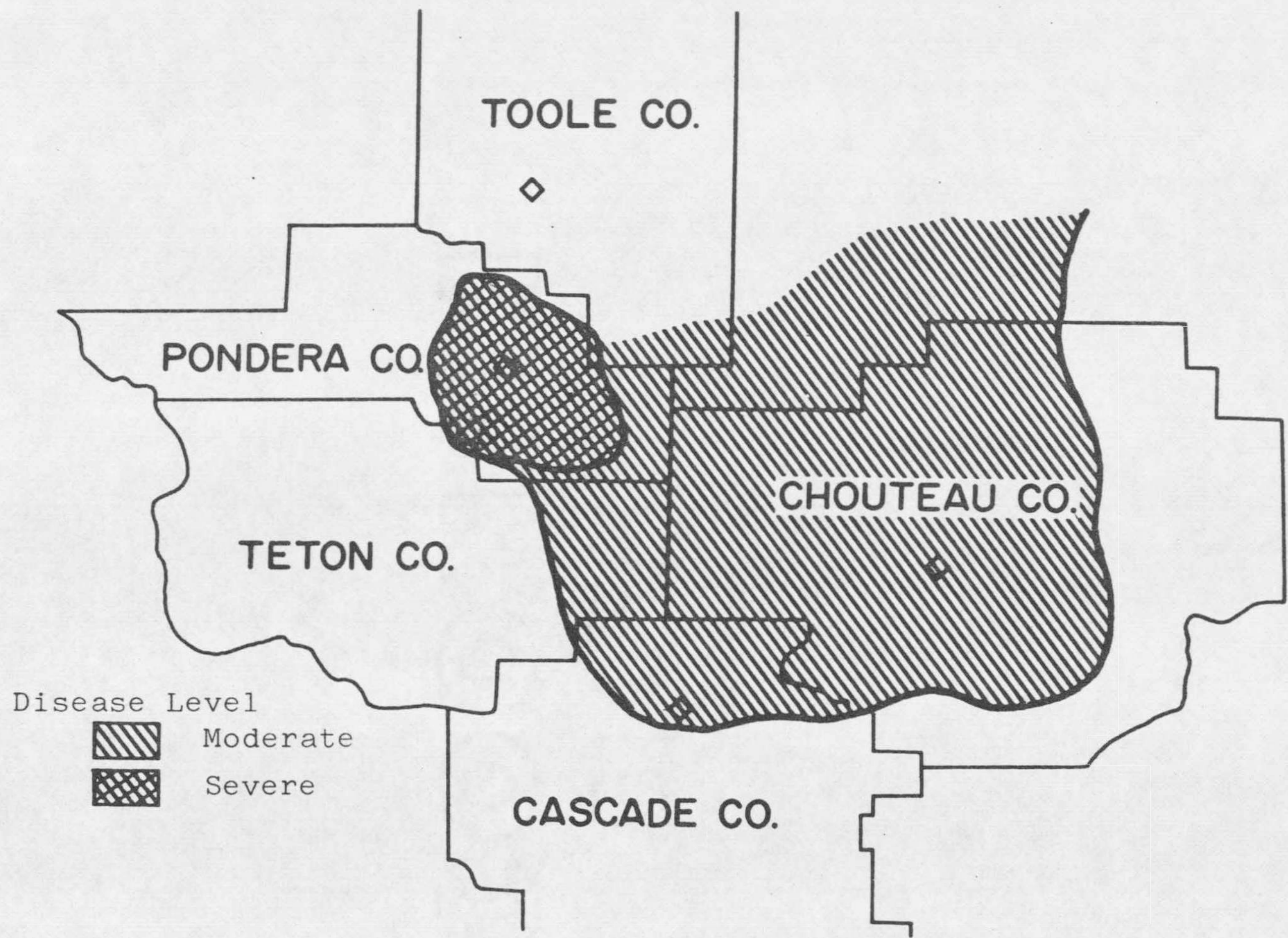

Figure 1.4. BYDV epiphytotic on winter wheat in Pondera and surrounding counties, 1981.

dominant variants by aphid transmission studies (Table 1.2) and EIA results (Table 1.5). A third strain RMV, was identified in a winter wheat sample also infected with a PAV variant (Isolate MT 818, Table 1.2). Winter wheat samples collected May 13, 1981, exhibited typical symptoms of BYDV infection, which was confirmed by EIA results (Table 1.5). However, as the growing season progressed, remission of BYDV symptoms was observed in many of the fields for which BYDV infection had been positively identified. No doubt, the abundant spring precipitation followed by the warm summer allowed infected plants to "grow away" from the virus. Furthermore, diagnosis of BYDV later in the season was confounded by a coincidental epiphytotic of wheat streak mosaic virus (WSMV) in central Montana. In fact, some winter wheat samples were doubly infected with both BYDV and WSMV (Table 1.7). Rochow (94) has noted that BYDV can be recovered from winter wheat plants which appear to be healthy. Under environmental conditions which favor rapid plant growth and BYDV symptom remission, i.e. adequate soil moisture and high temperatures, the virus may perhaps become latent in the host. This may be especially true for less virulent isolates of the virus. A situation such as this was observed in certain fields within the Pondera County epiphytotic

Table 1.7. Diagnosis of pathological disorders in winter wheat collected May 13, 1981 in Pondera County, MT.

Location[1]	Diagnostic Test Used		
	Aphid Transmission	EIA	SSEM-WSMV[2]
1 mi. N. Brady	MAV	MAV/PAV	-
Forstman	---	---	+
Bartch	RMV		
Kellogg	---	---	
O'Brien	---	MAV	+
Wipperman	---		+
Matheson	---	MAV	+
Huggie	---		+
Ratsburg	---		+
E. Community	---	RMV	+
Sprague	PAV	PAV	+
Jermansen	---	---	+

[1] Locations are named for towns or growers' fields from which the samples were taken.

[2] The presence of WSMV was confirmed by serologically specific electron microscopy (SSEM).

area. At the O'Brien location (Table 1.7), MAV (Isolate MT 812, Table 1.2) was the infecting strain. By mid-June BYDV symptoms were not apparent. However, in another field 3 miles north of the O'Brien location, BYDV symptoms were evident throughout the growing season. In this field, the infecting strain was PAV (Isolate MT 815, Table 1.2), a more virulent strain than MAV. Thus, the virulence and prevalence of the infecting strains along with climatic conditions may have facilitated the early remission of BYDV symptoms in the Pondera County epiphytotic.

Yield losses due to the 1981 BYDV epidemic were not determined, in part because of the coincidental occurrence of the WSMV epidemic in the same area. Losses were estimated for the 1980 Judith Basin epidemic by A. Dubbs, Superintendent, Central Montana Agricultural Experiment Station (Table 1.8). The 550,000 bushel loss is a conservative estimate based on the 10 year average yield for winter wheat in the Judith Basin area. However, if the yield loss is calculated on the estimated potential yield of winter wheat in 1980, the loss would be about 1,100,000 bushels. The potential for considerable yield reduction in winter wheat due to fall infection is quite evident from this yield loss assessment.

Table 1.8. 1980 estimated yield loss to barley yellow dwarf virus in winter wheat in central Montana.

Potential yield of winter wheat in Judith Basin (relative to the 1980 spring wheat and barley yields)	50 bu/Ac
Average yield of winter wheat in Judith Basin in 1980	30 bu/Ac
10 year average yield for winter wheat in Judith Basin	40 bu/Ac
Total number of acres affected	55,000
Estimated loss due to BYDV	10 bu/Ac
Total bushel loss	550,000
Monetary loss at $3.25/bu	$1,787,000

CHAPTER II

THE EFFECT OF BYDV ON GROWTH AND YIELD OF WINTER AND SPRING GRAINS UNDER FIELD CONDITIONS

Materials and Methods

The effects of BYDV on growth and yield parameters of spring wheat, spring barley, and winter wheat cultivars were evaluated over a three cropping-year period. Experimental plots were located at the Field Experimental Laboratory of the Bozeman Agricultural Experiment Station, Bozeman, MT., hereafter referred to as Bozeman, MT. The field experiments consisted of separate healthy and diseased plots, where the diseased plots were artificially inoculated with a vector non-specific strain (PAV), isolate MT 792, of BYDV, hereafter referred to as MT-PAV. This isolate was selected because it was one of the most virulent strains of the virus identified in Montana. For each experiment conducted, direct comparisons of the growth and yield parameters measured were made between healthy and diseased plants for each cultivar entry. Cultivars were also evaluated based on symptom expression in response to BYDV infection.

Rearing of Viruliferous Aphids and Methods of Inoculation

Virus infected plants for rearing viruliferous aphids were either 'Coast Black' oats or 'Klages' barley. The virus source plants were inoculated as 5-7 day-old seedlings with the MT-PAV strain, using *R. padi* as the vector. After inoculation, the virus source plants were allowed to grow aphid-free for three to four weeks prior to re-infestation. After that period, a population of *R. padi* from a non-viruliferous colony was transferred to the virus source plants and allowed to build up and acquire the MT-PAV strain.

Rearing of the aphid population for field dissemination was done in a Conviron growth chamber, maintained at 21°C under continuous light and about 40% relative humidity. Enough viruliferous aphids were available for field plot inoculation four to five weeks after the time of infesting the virus source plants with the non-viruliferous *R. padi* colony. At the end of the rearing period, aphids were removed from the virus source plants and placed in plastic dishes for transport to the field. Prior to spreading the aphids along rows in the disease nursery plots, talc powder was sprinkled over the aphids. This practice aided in disseminating the aphids evenly along the rows and also to some extent, prevented the alatae (winged-forms) from flying.

1979 Field Evaluation of Spring Barley to Late Infection by Barley Yellow Dwarf Virus

In the 1979 field experiment, 6 barley cultivars and 4 barley breeding lines were evaluated for their response to a late infection by BYDV. The 6 cultivars were 'Piroline', 'Steptoe', 'Klages', 'Unitan', 'Hector', and 'Compana' (Appendix Table 1). The 4 breeding lines were Hiproly-Steptoe selections 657357, 657358, 657361, and 657370 (Appendix Table 1), the seed of which was obtained from E. A. Hockett, USDA-ARS, Bozeman, MT. Plots were arranged in a split plot design, with each barley entry represented once within each of four blocks. Plot rows were 1.5 m long and spaced 35 cm apart, with each plot separated by a 1.2 m alley. Inoculative aphids were spread on two of the four plots June 17, at which time the barley plants were heading and at a growth stage of 10.1-10.5 according to Feekes scale (52). The two uninoculated plots served as the healthy control. Both the healthy and inoculated plots were sprayed with the systemic insecticide dimethoate, 7 days after the inoculative aphids were disseminated.

Disease ratings for each of the barley entries were made 14 days after the first symptoms of infection appeared. A disease severity score for each barley entry was deter-

mined based on the number of infected tillers per row and yellows index rating (Appendix Table 2). The disease severity score was then calculated by the formula: number of infected tillers per row x average yellows score per row ÷ total number of tillers per row. At maturity, the center 1.0m of row for each barley entry in the diseased and healthy plots was harvested and 500 kernel weights determined.

Statistical analysis to evaluate differences in 500 kernel weight between healthy and diseased plants was by analysis of variance for a randomized block design. Although the field plot design was a split plot, the randomized block method of analysis was chosen to increase precision in evaluating differences between diseased and healthy plant response among cultivars. Treatments and cultivars were therefore treated as factors within the randomized block design analysis, rather than main plot and subplot affects of a split plot design. Differences in 500 kernel weight between healthy and diseased plants for each cultivar were determined by the 'Least Significant Difference' (LSD) method. Correlations between disease symptoms and percent reduction in 500 kernel weight were conducted.

1980 and 1981 Field Evaluation of Spring Barley Cultivars to Early Infection by BYDV

In 1980 and 1981, seven cultivars of spring barley were planted in a split plot design with two replications. Main plots were healthy versus virus inoculated treatments, with cultivars randomized within main plots as subplots. Each cultivar was replicated twice in each of the four blocks. Rows were 3.0 m and spaced 35 cm apart, with 1.2 m alleys between blocks. In the 1980 field experiment, the cultivar entries were 'Klages', 'Hector', 'Compana', 'Piroline', 'Steptoe', 'Unitan', and 'Sutter' (Appendix Table 1). In the 1981 field experiment, the cultivar entries were the same except that 'Piroline' was replaced by the cultivar 'Coracle' (Appendix Table 1). In the 1980 field experiment, cultivars were planted May 12, and inoculated when the seedlings were in the five leaf to first tiller formation stage of development. In the 1981 field experiment, cultivars were planted May 21, and inoculated when seedlings were in the second tiller formation stage of development. Both healthy and diseased plots were sprayed with Malation 5-7 days after the inoculation aphids were disseminated, to prevent further spread of the virus.

For both experimental years the growth and yield parameters evaluated included plant height, spike length,

number of tillers per plant, number of florets per head, number of seeds per head, total weight of grain harvested, and 1000 kernel weight. Measurements were made on single plants harvested at maturity from the center 2.0 m of row.

Statistical evaluation, conducted on the 1980 spring barley experimental data, was by analysis of variance for a randomized block design. This analysis method was used for the reasons mentioned previously. All of the growth and yield parameters measured were subjected to analysis of variance and significant differences between healthy and diseased plant response determined by the LSD method (Appendix Table 3). The performance ranking of cultivars in response to BYDV infection was calculated on a percent of control basis and significant differences again determined by the LSD test. Similarly, the data tabulated for the 1981 barley trial was evaluated by analysis of variance and LSD tests (Appendix Table 4). However, only one barley plot was inoculated because of a shortage of viruliferous aphids. Therefore, the analysis of variance method used was for a completely randomized design, as only one inoculated and one uninoculated plot were available for comparison. Year to year variation in cultivar response to virus infection was evaluated for yield, using percent of control data, and tested by analysis

of variance for both year's data combined.

1980 and 1981 Field Evaluation of Spring Wheat Cultivars to Early Infection by BYDV

In 1980 and 1981, six cultivars of spring wheat were planted in a split plot design with two replications. Main plot effects were healthy versus virus inoculated treatments with cultivars randomized within main plots as subplots. Each cultivar was replicated twice in each of the four blocks. Rows were 3.0 m and spaced 35 cm, with 1.2 m alleys between blocks. In both the 1980 and 1981 field experiments, the cultivar entries were 'Fortuna,' 'Lew', 'Tioga', 'Prodax', 'Olaf', and 'Anza' (Appendix Table 1). In 1980, cultivars were planted May 2, and inoculated when the seedlings were in the five leaf stage of development. In 1981, cultivars were planted April 22, and inoculated when the seedlings were in the 3-5 leaf stage of development. Both healthy and diseased plots were sprayed with Malathion 5-7 days after the inoculative aphids were disseminated, to prevent further spread of the virus. Statistical analysis was by analysis of variance for a randomized block design conducted on each year's data separately (Appendix Table 5 and Table 6). Differences between healthy and diseased plant response were determined by the LSD method. Year to

year variation in cultivar response was evaluated for yield, based on percent of control data, and tested by analysis of variance for the combined data.

1980 and 1981 Field Evaluation of Winter Wheat Cultivars to Fall Infection by BYDV

In 1979 and 1980, five cultivars of winter wheat were planted in a randomized design in two blocks, one of which was inoculated and the other remaining block the healthy control. In 1979, cultivars were replicated three times in each block, each cultivar row being randomly assigned in both blocks. In 1980, cultivars were planted as four row plots with cultivars randomized in each block. Rows were 3.0 m and spaced 35 cm, with 1.2 m alleys. In 1979, no border rows were planted, whereas in 1980 a four-row border of winter wheat was planted around the perimeter of the two blocks, to limit the spread of BYDV outside of the experimental unit. The cultivar entries for both years were 'Centurk', 'Cheyenne', 'Winalta', 'Winoka', and 'Warrior' (Appendix Table 1).

Statistical evaluation was by analysis of variance for a completely randomized design, conducted for each year's data separately (Appendix Table 7 and Table 8). Data for all growth and yield parameters measured were subjected to

analysis of variance and differences between healthy and diseased plant response for each cultivar determined by the LSD method. Year to year variation in cultivar response to infection was not determined for the winter wheat yield data, as difficulties were encountered in the analysis where replication was not equal for each year of testing.

Results and Discussion

1979 Barley Experiment

In the 1979 spring barley experiment, symptoms of virus infection appeared in the diseased plots about 13 days after inoculation. Symptom development began as leaf tip chlorosis of the lower leaves and was evident in all barley entries. However, at 27 days after inoculation when symptom readings were taken, not all entries exhibited similar levels of disease prevalence or disease severity (Table 2.1). Un-inoculated plots appeared to remain healthy throughout the growth season as no symptoms typical of BYDV were observed.

Seed yield based on 500 kernel weight was less for seed harvested from diseased rows than healthy rows. The differences were statistically significant for all barley entries but three, 'Steptoe', 'Compana', and MT 657370' (Table 2.1). By analysis of variance (Table 2.2) treatments and cultivars were significant, indicating that PAV decreased 500 kernel weight over all entries and that some entries were less affected than others (Table 2.1). In regression analysis, only the symptom index of disease severity rating was significantly ($P = 0.1$) correlated with kernel weight reduction (Table 2.3). Neither disease prevalence nor the

Table 2.1. Disease score and 500 kernel weight (g) response of six spring barley cultivars and four spring barley lines inoculated with BYDV-PAV isolate MT 792 at Bozeman, MT 1979.

Barley Entry	Disease Prevalence[1]	Disease Severity Rating[2]	Disease Score[3]	500 kernel Wt.(g)[4] Inoc.	Cont.	% Red.
Klages	.06	2.2	0.13	16.9*	20.9	19.1
Piroline	.12	1.6	0.30	17.8*	20.2	11.9
Steptoe	.24	3.1	0.74	20.8	22.6	8.0
Unitan	.43	2.6	1.12	19.1*	22.0	13.2
Compana	.39	3.0	1.17	26.6	28.2	5.7
Hector	.36	1.8	0.65	18.2*	21.6	15.7
Hiproly x Steptoe lines						
MT 657357	.24	1.2	0.29	14.8*	17.0	12.9
MT 657358	.30	1.6	0.48	16.6*	20.0	17.0
MT 657361	.45	2.5	1.12	15.5*	18.0	13.9
MT 657370	.26	2.4	0.62	17.7	19.5	9.2

*Significant at P = 0.05 by LSD test. See Table 2.2 for analysis of variance and LSD value.

[1] Expressed as ratio of no. of infected tillers per row/total no. of tillers per row.

[2] Average disease rating = sum of rating scores for all infected tillers per row/total no. of infected tillers.

[3] Product of disease prevalence x disease rating.

[4] Values in Inoc. and Cont. columns are mean 500 kernel weights averaged over two replications.

Table 2.2. Effect of barley yellow dwarf virus on 500 kernel weight for 10 spring barley cultivars and lines inoculated with PAV isolate MT 792 at Bozeman, MT, 1979. Analysis of variance (ANOV) was computed as a two factorial randomized block design.

ANOV			
Source	df	M.S.	F-value
Blks	1	1.257	1.25
Treatments	1	69.30	69.09*
Cultivars	9	40.50	40.38*
Trt x Cult.	9	0.6457	.6438
Error	19	1.003	

LSD @ 0.05, df 19 = 2.10

*P = 0.05

Table 2.3. Correlation of disease symptom responses with 500 kernel weight for ten barley cultivars and lines inoculated with PAV isolate MT 792 at Bozeman, MT. 1979. Correlation coefficients are for the regression analysis of the independent variables, disease prevalence, disease severity rating, and disease score against the dependent variable 500 kernel weight..

Variable	Correlation Coefficient
Disease Prevalence	-.2771
Disease Severity Rating	-.5555*
Disease Score	-.5126

*P = 0.1

disease score variable were significantly correlated to kernel weight reduction (Table 2.3). However, all three independent variables did show negative correlation coefficients, which is evidence that an increase in either disease prevalence or disease severity corresponds to a decrease in kernel weight (Table 2.3).

That these symptom indices used in attempting to predict differential response in kernel weight among cultivars as a measure of tolerance were unsuccessful, can be illustrated by comparing the response of 'Klages' and 'Compana' (Table 2.1). Both disease prevalence and disease severity were less in 'Klages' than in 'Compana', yet kernel weight reduction in 'Klages' was considerably greater than that in 'Compana'.

A number of factors may be responsible for the poor correlation between symptom indices and reduction in kernel weight. The barley entries selected are all susceptible to BYDV, although 'Hiproly', one of the parents in the Montana lines has been reported to perhaps have a low level of tolerance to the virus (R. Sears, personal communication). In this experiment at least, there was no apparent level of tolerance in these lines when compared to the other susceptible cultivars (Table 2.1). As such, the correlation analysis

was evaluated on susceptible entries which essentially responded to virus infection to about the same degree. With little or no differential response, it is difficult in this case to ascertain whether or not these disease symptom indices could potentially be applicable to predict tolerance against kernel weight loss based on the regression analysis. Secondly, the barley entries were inoculated at a late growth stage and the full effect of the virus on each barley entry not realized. Had infection occurred in the early seedling stage, symptom differences among the barley entries may have expressed a wider range of prevalence and severity readings, corresponding to greater differences in yield response. However, even when barley cultivars that differ in susceptibility to virus infection are scored for leaf discoloration, such ranking has not necessarily provided a good predictive measure of tolerance against yield loss (15,20, 73). Rasmusson and Schaller (73) have successfully used a rating scale combining symptoms of leaf discoloration and stunting to identify tolerant barley cultivars. But, even a disease scale such as this may not provide a reliable means of identifying a low level of tolerance among susceptible cultivars, especially when infection occurs at a late growth stage.

1980 and 1981 Spring Barley Experiments

In both 1980 and 1981, symptoms of virus infection appeared in the inoculated plates about 17 days after the viruliferous aphids were applied. Infection was uniform throughout the inoculated plots for both years, with essentially 100% of the plants becoming infected. The un-inoculated plots, except for the occurrence of a few scattered infected plants along row borders, remained healthy throughout the growing seasons. Symptom development in the susceptible cultivars began as leaf tip chlorosis and eventually, as the growing seasons progressed, early emerged leaves became completely yellow. The pattern of chlorosis development started at the leaf tip, extended down the leaf margin, with the intra-marginal area of the leaf blade becoming progressively mottled. Newly emerged leaves including the flag leaves followed the same pattern of leaf symptom development. All of the barley entries, including the tolerant cultivars 'Sutter' (1980 and 1981) and 'Coracle' (1981), were stunted in comparison to the un-inoculated controls (Table 2.4 and (Table 2.6). Growth of the cultivars Piroline (1980) and Klages (1980 and 1981) was affected to the extent that heads seldom emerged from the boot and some plants of each cultivar were observed to not grow past a rosette stage of devel-

opment. The tolerant cultivars 'Sutter' and 'Coracle', although exhibiting a slight stunting in diseased plants, showed no appreciable expression of any other symptoms of virus infection when compared to healthy plants.

All of the growth and yield parameters measured i.e. plant height, rachis length, tillers per plant, spikelets per head, seeds per head, seeds per spikelet, 1000 kernel weight and yield per plant were reduced for diseased susceptible cultivars in comparison to un-inoculated controls, in both 1980 and 1981 experiments (Tables 2.4, 2.5, 2.6 and 2.7). For the cultivars 'Sutter' and 'Coracle' some of the parameters measured such as plant yield (Table 2.5 and Table 2.7) were increased in diseased plants when compared to healthy plants. Catherall and Hayes (15) have stated that such a positive increase in inoculated plants indicates tolerance. Such increases are not likely due to stimulatory effects of the virus as has been observed by Panayotou (66), but probably a function of competition effects. Tolerant cultivars planted adjacent to inoculated susceptible cultivars have a better competitive advantage for light, nutrients, and water, than when grown adjacent to the same susceptible cultivars which are healthy.

Among the parameters measured, seeds per spikelet

Table 2.4. Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets per head for seven spring barley cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980.

	Plant Height (cm)			Rachis Length (cm)			Tillers/Plant (no.)			Spikelets/Head (no.)		
Cultivar	Inoc.[1/]	Cont.	% Red.[2/]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Hector	78.0	90.6	14.0	7.0	8.0	11.6	6.5[NS]	7.2	10.3	20.5[NS]	22.2	7.9
Compana	70.4	87.7	19.8	5.8	7.4	21.6	5.8	7.2	20.7	15.0[NS]	19.5	23.1
Klages	61.6	83.3	26.0	7.7[NS]	8.2	5.5	6.0	7.0	14.3	21.5[NS]	23.8	9.5
Piroline	63.2	85.8	26.3	7.1	8.6	17.0	5.0[NS]	5.5	9.1	20.5[NS]	23.2	11.8
Unitan	76.5	96.2	20.4	5.1	7.4	30.7	4.0[NS]	4.2	5.9	34.8	45.0	22.8
Steptoe	75.0	92.8	19.3	5.0	5.8	13.7	3.8[NS]	4.5	16.7	40.8	48.2	15.5
Sutter	81.8	88.9	8.1	6.4[NS]	6.3	+ 4.0	5.0[NS]	4.2	+17.6	49.8[NS]	49.5	+ 0.5

1/ Data in Inoc. and Cont. columns are treatment means. Fifteen plants were harvested from each of two rows/cultivar/plot/treatment. Treatments were replicated twice in a split plot design with cultivars as subplots. The difference between inoculated and control treatment means are all significant at $P = 0.05$, except where indicated by NS = nonsignificant. See Appendix Table 3 for mean square error and least significant difference values.

2/ Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal. A + indicates a percent increase over control.

Table 2.5. Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and yield per plant for seven spring barley cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980.

	Seeds/Head (no.)			Seeds/Spikelet (no.)			1000 Kernel Wt. (g)			Yield/Plant (g)		
Cultivar	Inoc.[1/]	Cont.	% Red.[2/]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Hector	19.2[NS]	21.2	9.4	.94[NS]	.96	1.6	30.4	41.4	26.7	2.4	4.5	47.6
Compana	14.0	18.8	25.3	.93[NS]	.96	3.1	31.2	50.5	38.1	1.6	5.2	69.1
Klages	18.8[NS]	21.8	13.8	.88[NS]	.92	4.4	18.0	40.6	55.5	0.7	4.5	84.9
Piroline	18.0	23.2	22.6	.88	1.0	12.5	14.2	37.2	61.9	0.3	3.5	91.5
Unitan	33.0	42.0	21.4	.96[NS]	.94	+ 1.6	31.0	39.4	21.4	2.5	5.2	51.1
Steptoe	39.0	48.5	19.6	.96[NS]	1.0	5.0	29.7	41.2	27.9	2.9	5.6	48.8
Sutter	47.2[NS]	46.5	+ 1.6	.96[NS]	.94	+ 1.6	37.4	34.6	+ 8.4	7.2	4.8	+49.0

1/ Data in Inoc. and Cont. columns are treatment means. Fifteen plants were harvested from each of two rows/cultivar/plot/treatment. Treatments were replicated twice in a split plot design with cultivars as subplots. The difference between inoculated and control treatment means are all significant at P = 0.05, except where indicated by NS = nonsignificant. See Appendix Table 3 for mean square error and least significant difference values.

2/ Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal. A + indicates a percent increase over the control.

Table 2.6. Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets per head for seven spring barley cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1981.

	Plant Height (cm)			Rachis Length (cm)			Tillers/Plant (no.)			Spikelets/Head (no.)		
Cultivar	Inoc.[1/]	Cont.	% Red.[2/]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Hector	48.2	66.3	27.2	8.2	10.0	18.9	2.5	5.4	53.7	21.2	26.3	19.4
Compana	50.3	58.2	13.6	8.2^{NS}	8.6	4.1	3.2	5.6	41.4	19.9^{NS}	20.6	3.2
Klages	47.6	66.6	28.5	9.3^{NS}	10.2	9.3	2.8	5.3	48.1	23.9	27.5	13.1
Coracle	66.8^{NS}	68.4	2.3	11.2^{NS}	10.6	+ 6.6	3.6^{NS}	3.9	9.0	26.4^{NS}	24.7	+ 6.7
Unitan	51.9	61.8	16.1	6.9^{NS}	7.6	8.6	2.2^{NS}	3.4	32.8	44.7^{NS}	47.1	5.3
Steptoe	47.2	58.3	19.0	6.2^{NS}	6.4	3.1	2.4^{NS}	2.7	11.1	45.3	51.6	12.2
Sutter	62.0^{NS}	64.1	3.2	6.9^{NS}	6.6	+ 5.3	4.2^{NS}	4.2	+ 1.2	49.2^{NS}	45.3	+ 8.6

1/ Data in Inoc. and Cont. columns are treatment means. Ten plants were harvested from each of two rows/ cultivar/treatment. Treatments in 1981 were not replicated. The difference between inoculated and control treatment means are all significant at P = 0.05, except where indicated by NS = nonsignificant. See Appendix Table 4 for mean square error and least significant values.

2/ Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal. A + indicates a percent increase over control.

Table 2.7. Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and plant yield for seven spring barley cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1981.

Cultivar	Seeds/Head (no.)			Seeds/Spikelet (no.)			1000 Kernel Wt. (g)			Yield/Plant (g)		
	Inoc.[1/]	Cont.	% Red.[2/]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Hector	19.1	25.6	25.2	0.9NS	1.0	7.2	28.8	42.7	32.4	1.1	4.2	74.9
Compana	18.1NS	20.4	11.3	0.9	1.0	8.5	35.5	57.1	37.8	1.5	4.6	66.7
Klages	21.6	26.1	17.2	0.9NS	1.0	5.3	31.6	44.0	28.1	1.3	4.8	72.7
Coracle	25.6NS	24.1	+ 6.4	1.0NS	1.0	0.5	46.6NS	45.6	+ 2.2	3.8NS	4.0	+ 7.3
Unitan	34.6	45.2	23.5	0.8	1.0	19.3	30.0	43.8	31.6	1.6	5.8	72.1
Steptoe	35.2	49.0	28.1	0.8	1.0	18.4	33.6	47.0	28.5	2.0	4.9	58.7
Sutter	46.8NS	43.7	+ 7.0	0.9NS	1.0	1.6	36.6NS	35.9	+ 2.1	5.0NS	4.6	+ 8.4

[1/] Data in Inoc. and Cont. columns are treatment means. Ten plants were harvested from each of two rows/cultivar/treatment. Treatments in 1981 were not replicated. The difference between inoculated and control treatment means are all significant at P = 0.05, except where indicated by NS = nonsignificant. See Appendix Table 4. for mean square error and least significant difference values.

[2/] Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal. A + indicates a percent increase over control.

was calculated to evaluate whether or not floral sterility was a significant contributing factor in reducing yield for any of the barley cultivars. For barley, anatomically only one seed can be produced per spikelet (= floret). Therefore, an absolute value of less than one for the number of seeds per spikelet, is actually an indication that some spikelets on the rachis failed to set seed. This may be due to sterility of a particular floret, or that the seed did not develop beyond the embryonic stage. In 1980, 'Piroline' (Table 2.5) was the only cultivar which showed a significant reduction in the number of seeds produced per spikelet parameter. In 1981, the cultivars 'Compana', 'Unitan', and 'Steptoe' (Table 2.7) showed significant reductions in this parameter. In highly susceptible barley cultivars, but perhaps more so for oats, sterility has been reported to be an important yield loss response to BYDV infection (61,66). The observation that some plants of the cultivar 'Piroline' never progressed past the rosette stage of development, and that plant yield (Table 2.5) was dramatically reduced, shows the extreme case of susceptibility in barleys to virus infection.

In ranking the cultivars for their response in tiller production, seed set, kernel weight, and plant yield to

virus infection, it was apparent that 'Steptoe' showed the highest degree of tolerance among the susceptible cultivars (Table 2.8 and Table 2.9). However, in comparison to the cultivars 'Sutter' and 'Coracle', 'Steptoe' could not be classed as a highly tolerant cultivar. In comparing the two year's data (Table 2.8 and Table 2.9), the cultivars did not respond the same in each year's performance ranking although 'Steptoe' was fairly consistent in both years. For example, 'Hector' in 1980 (Table 2.8) was the highest yielding two-rowed cultivar whereas in 1981 (Table 2.9) it was the lowest. Overall, yields for all inoculated susceptible cultivars were less in 1981 than in 1980, partially due to a considerable reduction in tiller production (Table 2.8 and Table 2.9). By analysis of variance (Table 2.10) for yield over environments, using percent of control as the response variable, year to year variation was not significant for the six cultivars included in the test. This indicates that the combined cultivar response to virus infection was about the same in both experimental years. The mean response in yield for the cultivars averaged over the two years was highly significant (Table 2.10), indicating the obvious differences in cultivar response to virus infection (Table 2.8 and Table 2.9). Significant interactions between treatment and culti-

Table 2.8 Performance ranking among two rowed and six rowed spring barley cultivars inoculated with PAV isolate MT. 792 at Bozeman, MT. 1980. Values for yield per plant, 1000 kernel weight, seeds per head, and tillers per plant are expressed as percent of control.

Cultivar[1/]	Yield/ Plant	1000 Kernel Wt.	Seeds/ Head	Tillers/ Plant
	%	%	%	%
Two Rowed				
Piroline	9.0a[2/]	38.5a	77.0ab	91.0a
Klages	15.0a	44.5a	86.5 bc	86.0a
Compana	31.0	62.0 b	75.0a	79.5a
Hector	53.0	73.0 b	90.5 c	90.0a
Six Rowed				
Unitan	51.0a	78.5a	79.0a	94.0a
Steptoe	53.0a	72.0a	80.5ab	83.5a
Sutter	150.0	108.0	102.0	122.0

1/ The analysis for two rowed and six rowed cultivars was computed separately.

2/ Values followed by the same letter are not significantly different at $P = 0.05$ by LSD method.

Table 2.9 Performance ranking among two rowed and six rowed spring barley cultivars inoculated with PAV isolate MT. 792 at Bozeman, MT. 1981. Values for yield per plant, 1000 kernel weight, seeds per head, and tillers per plant are expressed as percent of control.

Cultivar[1/]	Yield/ Plant	1000 Kernel Wt.	Seeds/ Head	Tillers/ Plant
	%	%	%	%
Two Rowed				
Hector	25.0a[2/]	67.5a	75.0a	46.5a
Klages	28.0a	72.0a	83.0a	51.5a
Compana	33.0a	62.0a	88.5ab	59.0a
Coracle	94.0	102.5	106.5 b	90.5
Six Rowed				
Unitan	28.0a	68.5a	77.5a	67.5a
Steptoe	41.5 c	71.5a	72.0a	89.0a
Sutter	111.0	102.5	107.0	105.0

1/ The analysis for two rowed and six rowed cultivars was computed separately.

2/ Values followed by the same letter are not significantly different at P = 0.05 by LSD method.

Table 2.10 Effect of barley yellow dwarf virus on yield for six spring barley cultivars inoculated with PAV isolate Mt. 792 at Bozeman, MT. Analysis of variance (ANOV) for 1980 and 1981 combined environments using percent of control as the indicator for disease response.

ANOV			
Source	df	M.S.	F-Value
Blks/Years	2	.0407	1.548
Environments	1	.1262	3.101
Cultivars[1/]	5	.6303	23.966*
Error	15	.0263	

*P = 0.05

1/ Cultivars included in the analysis were 'Sutter', 'Steptoe', 'Unitan', 'Hector', 'Klages', and 'Compana'.

vars were indicated for a number of the response variables (Appendix Table 3 and Table 4). Such treatment by cultivar interactions would be expected when tolerant cultivars, which respond differently to virus infection than susceptible cultivars, are included in the analyses.

In addition to climate differences during the two experimental years, virus dosage and the plant growth stage at the time of inoculation may have also influenced the cultivar response to virus infection. Virus dosage has been shown to dramatically affect the growth and yield response of both tolerant and susceptible barley cultivars. Even though the level of infection in the inoculated plots was essentially 100%, and dissemination of viruliferous aphids appeared uniform during both years, there was no assurance that the virus dosage on a plant to plant or row to row basis was the same during 1980 and 1981 experiments. Also, the 1981 plots were inoculated at a later plant growth stage than that of the 1980 plots. This does not in itself, suggest that the inoculated cultivars in 1981 would yield higher than the same cultivars inoculated in 1980. Panayotou (66) has in fact, shown that late infection can have either a stimulatory or suppressive effect on growth depending on the particular cultivar. Undoubtedly, both virus dosage

and growth stage at the time of inoculation contributed to some of the variability in growth and yield parameters measured among the different cultivars between the 1980 and 1981 experiments. However, the influence of the environment is quite obvious in comparing the data for un-inoculated plants for both years, where the number of tillers per plant for most cultivars was less in 1981 than in 1980 (Table 2.4 and Table 2.6). Certainly, the virus dosage, plant growth stage at time of inoculation, and the environment interact and contribute to the variable response of a particular cultivar or between cultivars to virus infection.

1980 and 1981 Spring Wheat Experiments

In the 1980 and 1981 spring wheat experiments the diseased plots appeared to be uniformly inoculated, as essentially 100% of the plants became infected. In both years the uninoculated plots remained healthy except for some movement of inoculative viruliferous aphids into border rows in the 1980 plots. However, enough healthy plants were noted and tagged in these rows for valid comparisons to be made. Symptom development in susceptible cultivars during both years was typical for BYDV in spring wheat. Symptoms were first observed about 15 days after inoculation in 1980

and 1981 as leaf tip chlorosis. Leaves that first showed symptoms eventually became totally yellow and prematurely senesced in comparison to healthy plants. Newly emerged leaves including flag leaves first developed leaf tip chlorosis followed by marginal and interveinal yellowing extending about half way to two thirds down the leaf blade, giving a chevron pattern appearance. In comparison to symptoms in barley, leaf mottling in spring wheat was not as apparent but did occur. Later in the growing season anthocyanin pigmentation developed in leaf tips and along the leaf margins. There appeared to be no differential response in symptom development between the susceptible cultivars. In 'Anza', the tolerant cultivar included in both test years, symptom development lagged about 4-5 days behind that in susceptible cultivars, although evidence of virus infection was obvious. Symptoms were not as severe in 'Anza', being limited to leaf tip and leaf margin chlorosis, and anthocyanin pigmentation was not observed as in the other cultivars. Plant stunting was significant in all the cultivars for both test years, although 'Anza' was least affected in this regard (Table 2.11 and Table 2.13).

All of the growth and yield parameters measured in 1980 and 1981 were reduced for diseased plants in comparison

to healthy plants for all cultivars, except for one case (Tables 2.11, 2.12, 2.13 and 2.14). The cultivars 'Fortuna' and 'Tioga' showed a positive but nonsignificant increase in the number of spikelets produced per head for diseased plants, relative to healthy plants in both years tested (Table 2.11 and Table 2.13). This response may in fact be a stimulatory effect of virus infection, as it was a consistent observation between years and only for these two cultivars. It is not likely due to a competitive advantage, as both 'Fortuna' and 'Tioga' are very susceptible to BYDV. However, component compensation in diseased plants of 'Fortuna' and 'Tioga' cannot be discounted, as these two cultivars may respond and compensate differently to virus infection, or any other stress phenomenon for that matter, in relation to the other susceptible cultivars.

Seeds per spikelet was measured to determine if BYDV caused either sterility or a decrease in the number of floral embryos which subsequently develop into mature seeds among the cultivars tested. For wheats, anatomically there are multiple florets produced per each spikelet, where the average is often 2-3 fertile florets per spikelet in healthy plants. In both test years, all the cultivars showed significant decreases in the number of seeds produced per spike-

Table 2.11. Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets per head for six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980.

	Plant Height (cm)			Rachis Length (cm)			Tillers/Plant (no.)			Spikelets/Head (no.)		
Cultivar	Inoc.[1]	Cont.	% Red.[2]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Fortuna	77.0	103.8	25.8	7.7^{NS}	8.2	6.1	7.5	9.0	16.7	14.0^{NS}	13.2	+6.1
Tioga	79.8	103.5	22.9	8.8^{NS}	9.0	2.2	7.8^{NS}	8.8	11.4	14.2^{NS}	14.0	+1.4
Lew	74.1	103.4	28.3	8.8	9.6	8.3	7.5	9.2	18.9	14.2^{NS}	15.0	5.0
Olaf	67.6	81.7	17.3	7.0^{NS}	7.2	3.5	6.2^{NS}	7.2	13.9	14.0^{NS}	14.0	0.0
Prodax	62.0	80.4	22.9	9.3	10.5	11.4	5.5	7.0	21.4	15.5^{NS}	16.0	3.1
Anza	64.0	74.7	14.3	7.1^{NS}	7.5	5.3	7.3^{NS}	7.8	6.4	14.5^{NS}	15.0	3.3

1/ Data in Inoc. and Cont. columns are treatment means. Fifteen plants were harvested from each of two rows/cultivar/plot/treatment. Treatments were replicated twice in a split plot design with cultivars as subplots. The difference between inoculated and control treatment means for each cultivar are all significant at P = 0.05, except where indicated by NS = nonsignificant. See Appendix Table 5 for mean square error and least significant difference values.

2/ Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal. A + indicates a percent increase over control.

Table 2.12. Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and yield per plant for six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT. 1980.

	Seeds/Head (no.)			Seeds/Spikelet (no.)			1000 Kernel Wt. (g)			Yield/Plant (g)		
Cultivar	Inoc.[1/]	Cont.	% Red.[2/]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Fortuna	20.2	28.2	28.4	1.4	2.1	30.9	25.8	42.8	39.7	2.5	7.8	67.3
Tioga	20.8	28.5	27.0	1.4	2.0	27.5	23.5	37.9	38.1	2.4	7.1	65.8
Lew	20.8	31.0	32.9	1.4	2.0	30.0	21.8	31.8	33.3	2.0	6.5	69.3
Olaf	26.8	32.8	18.3	1.9	2.4	18.8	26.8	33.6	20.2	2.9	6.8	57.5
Prodax	36.2	51.8	30.1	2.4	3.2	26.6	19.9	34.4	42.4	2.3	6.5	75.7
Anza	37.0	41.8	11.5	2.6	2.8	8.9	23.4	32.3	27.3	4.0	7.2	44.5

1/ Data in Inoc. and Cont. columns are treatment means. Fifteen plants were harvested from each of two rows/cultivar/plot/treatment. Treatments were replicated twice in a split plot design with cultivars as subplots. The difference between inoculated and control treatment means for each cultivar are all significant at P = 0.05, except where indicated by NS = nonsignificant. See Appendix Table 5 for mean square error and least significant difference values.

2/ Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal.

Table 2.13. Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets/head for six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1981.

	Plant Height (cm)			Rachis Length (cm)			Tillers/Plant (no.)			Spikelets/Head (no.)		
Cultivar	Inoc.[1/]	Cont.	% Red.[2/]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Fortuna	85.0	102.4	16.9	8.2[NS]	8.4	2.4	2.0	2.8	26.8	15.0[NS]	14.9	+ 6.7
Tioga	80.8	101.9	20.7	8.6	9.2	6.5	2.0	2.5	20.4	15.0[NS]	14.8	+ 1.4
Lew	78.4	99.7	21.4	8.3	9.6	13.5	1.4	2.4	42.9	14.8	16.2	8.6
Olaf	68.7	83.8	18.1	6.8	7.4	6.8	2.1[NS]	2.2	4.5	14.4[NS]	14.8	3.0
Prodax	64.8	80.7	19.7	10.0[NS]	10.2	0.9	1.6	2.3	32.6	16.0[NS]	16.5	2.7
Anza	62.6	71.4	12.3	7.6	8.2	6.7	1.8[NS]	1.8	0.0	15.1[NS]	15.2	0.6

1/ Data in Inoc. and Cont. columns are treatment means. Ten plants were harvested from each of two rows/cultivar/plot/treatment. Treatments were replicated twice in a split plot design with cultivars as subplots. The difference between inoculated and control treatment means for each cultivar are all significant at P = 0.05, except where indicated by NS = nonsignificant. See Appendix Table 6 for mean square error and least significant difference values.

2/ Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal. A + indicates a percent increase over control.

Table 2.14. Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and yield per plant for six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1981.

	Seeds/Head (no.)			Seeds/Spikelet (no.)			1000 Kernel Wt. (g)			Yield/Plant (g)		
Cultivar	Inoc.[1/]	Cont.	% Red.[2/]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Fortuna	23.0	31.9	27.7	1.6	2.2	27.9	23.4	43.2	45.7	0.95	3.2	70.2
Tioga	24.5	30.3	19.1	1.6	2.1	19.5	23.6	36.4	35.2	0.97	2.0	51.7
Lew	22.1	35.3	37.4	1.5	2.0	31.8	20.8	37.4	44.2	0.60	2.5	76.4
Olaf	24.4	35.9	32.0	1.7	2.4	29.2	20.0	34.6	42.0	0.89	2.2	60.2
Prodax	30.2	49.0	38.4	1.9	3.0	35.6	14.5	39.0	62.8	0.60	3.2	81.5
Anza	33.0	42.4	22.0	2.2	2.8	20.0	23.4	33.4	29.8	1.1	2.1	46.2

1/ Data in Inoc. and Cont. columns are treatment means. Ten plants were harvested from each of two rows/cultivar/plot/treatment. Treatments were replicated twice in a split plot design with cultivars as subplots. The difference between inoculated and control treatment means for each cultivar are all significantly different at $P = 0.05$. See Appendix Table 6 for mean square error and least significant difference values.

2/ Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal.

let in diseased plants (Table 2.12 and Table 2.14). However, the number of seeds per head was also significantly decreased in diseased plants for all cultivars (Table 2.12 and Table 2.14), yet the number of spikelets per head was not significantly reduced (Table 2.11 and Table 2.13). In this case the decrease in viable florets per spikelet reasonably accounts for a portion of the reduced seed yield in virus infected plants.

The tolerant cultivar 'Anza' showed the least yield reduction due to BYDV among the cultivars tested, although the decrease was significant, 44.5 percent in 1980 and 46.2 percent in 1981 (Table 2.12 and Table 2.14). Among the Montana grown cultivars 'Tioga' and 'Olaf' showed the least yield reduction in both years tested (Table 2.12 and Table 2.14). In comparing the performance ranking among the cultivars, in terms of percent of control for diseased plants (Table 2.15 and Table 2.16), only 'Tioga' and 'Olaf' were ranked differently in 1980 and 1981 experiments. In 1980, the number of seeds produced per head and kernel weight for diseased plants were significantly different in comparing 'Tioga' to 'Olaf', the latter being the least reduced (Table 2.15). However, in 1981, only seeds per head was significant, where for 'Tioga' this yield component was consider-

Table 2.15 Performance ranking among six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980. Values for yield per plant, 1000 kernel weight, seeds per head, and tillers per plant are expressed as percent of control.

Cultivar	Yield/ Plant	1000 Kernel Wt.	Seeds/ Head	Tillers/ Head
	%	%	%	%
Prodax	24.5a[1/]	58.0a	70.0a	78.5a
Lew	31.0ab	69.0ab	67.0a	81.0a
Fortuna	32.5 b	60.5a	71.5a	83.5a
Tioga	34.0 b	62.0a	72.5a	89.5a
Olaf	42.5 c	80.0 b	81.5 b	86.5a
Anza	50.0 c	72.5ab	89.0 b	93.5a

1/ Values followed by the same letter are not significantly different at P = 0.05 by LSD method.

Table 2.16 Performance ranking among six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1981. Values for yield per plant, 1000 kernel weight, seeds per head, and tillers per plant are expressed as percent of control.

Cultivar	Yield/ Plant	1000 Kernel Wt.	Seeds/ Head	Tillers/ Head
	%	%	%	%
Prodax	19.0a[1/]	37.0a	61.5a	68.0ab
Lew	24.0ab	56.0ab	63.0a	57.0a
Fortuna	30.0abc	54.0ab	72.5abc	73.0abc
Olaf	41.0abc	58.0ab	68.0ab	95.5 bc
Tioga	48.0 bc	65.0ab	81.0 c	79.5abc
Anza	54.0 c	71.5 b	78.0 bc	97.5 c

1/ Values followed by the same letter are not significantly different at P = 0.05 by LSD method.

ably less reduced than for 'Olaf' (Table 2.16). It is difficult in this case to determine if the change from year to year in these two cultivars is a function of virus infection or environment. In 1981, (Table 2.16) tiller production was considerably more variable among the cultivars than in 1980 (Table 2.15). In 1981, (Table 2.16) tiller production in 'Olaf' was not significantly affected by virus infection. However, the greater reduction in kernel weight and seed production for 'Olaf' in 1981 may have been influenced by a compensation effect of the tillering process, in addition to the direct effects of the virus. In 'Tioga' perhaps the opposite was true, where low tiller production was offset by increasing seed production and kernel weight in diseased plants. However, the compensating effects may not have been equal between the two cultivars and as such the yield per plant for 'Tioga' was slightly better than that of 'Olaf' (Table 2.16).

In analyzing the yield response for all cultivars over the two years tested, year to year variation in the response of those cultivars to virus infection was nonsignificant (Table 2.17). Thus, virus infection reduced the yield for all the cultivars to about the same degree in 1980 as in 1981. That the mean response in yield for the cultivars

Table 2.17 Effect on barley yellow dwarf virus on yield for six spring wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT. Analysis of variance (ANOV) for 1980 and 1981 combined environments using percent of control as the indicator for disease response.

ANOV			
Source	df	M.S.	F-value
Blks/Years	2	.01767	3.31
Environment	1	.000038	.00215
Cultivars	5	.04895	9.2306*
Error	15	.005303	

*P = 0.05.

averaged over the two years was significant (Table 2.17) indicates the obvious differences in cultivar response to virus infection in both years tested (Table 2.15 and Table 2.16).

1980 and 1981 Winter Wheat Experiments

Symptoms in the inoculated winter wheat plots for both 1980 and 1981 experiments did not appear until growth in the spring resumed. The first indications of virus infection were the dwarfing and general light green appearance of the plants in the inoculated plots in comparison to the healthy plots. Later, leaf tip chlorosis and mild chlorotic mottle symptoms became visible in leaves that had emerged the previous fall and in the first leaves developed in the spring. These leaves eventually became totally yellow and senesced prematurely in comparison to healthy plants. As the season progressed, newly emerged leaves, including the flag leaves, developed leaf tip chlorosis, marginal chlorosis, and a chlorotic mottle, much more so than in spring wheats. Anthocyanin pigmentation was extensive, where some leaves were completely changed to a red-scarlet color. Very little interveinal chlorosis was observed in the winter wheats in comparison to the spring wheats. An obvious difference be-

tween diseased and healthy plants was the stature of infected leaves. Leaves of inoculated plants were short and narrow, slightly cupped abaxially, and spike-like, whereas leaves of healthy plants were long, wide, and tended to bend downward from the culm. Symptoms in winter wheat have been reported to be mild and considerably less diagnostic of the disease than in barley, oats, and even spring wheat (61). Winter wheat can in fact, be infected yet symptomless (94). In both the 1980 and 1981 inoculated field plots, winter wheat symptoms of BYDV infection were quite diagnostic, which in part, may be the result of using a highly virulent strain of the virus as the inoculum. However, early symptoms of the disease could easily be mistaken for nitrogen deficiency or 'wet-feet', a condition often observed in Montana as a result of cool soil temperatures and saturated soil conditions in early spring, which retards nitrogen uptake.

In comparing plant height for diseased versus healthy plants, the virus caused significant stunting in all cultivars in both years (Table 2.18 and Table 2.20) For all parameters evaluated in the two years of testing, diseased plants consistently showed reductions in comparison to healthy plants for all the cultivars evaluated (Tables 2.18,

2.19, 2.20, and 2.21). Among the yield components, tiller production and seed production were most significantly affected by virus infection, whereas kernel weight was the least reduced yield component in diseased plants. Similar results for winter wheat response to BYDV infection have been reported (13,25,28). As was indicated for spring wheats, the number of seeds per spikelet was significantly reduced in inoculated winter wheat cultivars in comparison to the controls (Table 2.19 and Table 2.21). Thus, a reduction in the number of fertile or viable florets in diseased plants partially accounts for the reduction in seed yield. However, the number of spikelets per head was also significantly reduced for most cultivars (Table 2.18 and Table 2.20), which also contributed to the decreased seed yield of infected plants.

In ranking the winter wheat cultivars for both years tested, 'Centurk' consistently yielded higher than the other cultivars, when comparing the yield of diseased plants to healthy plants on a percent of control basis (Table 2.22 and Table 2.23). In 1981, (Table 2.23) tiller production was less for all inoculated cultivars than in 1980 (Table 2.22), although some cultivars i.e. 'Centurk' and 'Warrior' show more or less dramatic changes in tiller production between

Table 2.18. Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets per head for five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1979.

Cultivar	Plant Height (cm)			Rachis Length (cm)			Tillers/Plant (no.)			Spikelets/Head (no.)		
	Inoc.[1/]	Cont.	% Red.[2/]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Centurk	88.3	114.9	23.1	6.1 NS	7.7	20.8	8.0	12.0	33.3	14.0	16.3	14.1
Warrior	91.1	124.0	26.5	6.2 NS	7.8	20.5	8.3	11.7	29.1	12.3	15.0	18.0
Winoka	91.7	128.8	28.8	6.6	8.6	23.3	6.3	12.3	48.8	12.3	14.7	16.3
Winalta	91.3	130.2	29.9	6.6 NS	8.3	20.5	7.3 NS	9.0	18.9	12.3	14.7	16.3
Cheyenne	86.2	119.5	27.9	6.0	8.0	25.0	7.3	12.3	40.7	11.3	15.0	24.7

[1/] Data in Inoc. and Cont. columns are treatment means. Fifteen plants were harvested from each of three rows/cultivar/treatment. The difference between inoculated and control treatment means for each cultivar are all significant at P =0.05, except where indicated by NS = nonsignificant. See Appendix Table 7 for mean square error and least significant difference values.

[2/] Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal.

Table 2.19. Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and plant yield for five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1979.

	Seeds/Head (no.)			Seeds/Spikelet (no.)			1000 Kernel Wt. (g)			Yield/Plant (g)		
Cultivar	Inoc.[1/]	Cont.	% Red.[2/]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Centurk	28.3	41.7	32.0	2.0	2.6	20.8	30.1	32.4	7.3	4.9	10.5	53.1
Warrior	21.7	35.3	38.7	1.8	2.4	26.4	31.4	34.6	9.4	3.7	9.8	62.0
Winoka	20.7	36.7	43.6	1.7	2.5	33.3	29.3	35.2	16.7	2.6	11.8	78.4
Winalta	20.0	35.7	43.9	1.6	2.4	32.9	29.4	35.0	16.1	2.8	8.2	65.0
Cheyenne	19.3	38.7	50.0	1.7	2.6	33.8	31.2	36.7	15.0	3.3	12.0	72.8

1/ Data in Inoc. and Cont. columns are treatment means. Fifteen plants were harvested from each of three rows/cultivar/treatment. The difference between inoculated and control treatment means for each cultivar are all significant at P = 0.05, except where indicated by NS = nonsignificant. See Appendix Table 7 for mean square error and least significant difference values.

2/ Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal.

Table 2.20. Effects of barley yellow dwarf virus on plant height, rachis length, tillers per plant, and spikelets per head for five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980.

Cultivar	Plant Height (cm)			Rachis Length (cm)			Tillers/Plant (no.)			Spikelets/Head (no.)		
	Inoc.[1/]	Cont.	% Red.[2/]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Centurk	98.0	132.6	26.1	7.2	8.2	13.3	7.2	11.8	39.7	16.4[NS]	17.3	5.2
Warrior	108.4	140.5	22.8	6.0	8.3	28.3	4.9	10.6	53.1	13.1	17.4	24.7
Winoka	99.1	147.3	32.7	6.6	7.9	17.1	5.0	10.0	50.0	12.5	13.7	8.8
Winalta	102.9	144.6	28.8	6.4	8.2	21.8	5.8	10.4	44.2	13.7	15.2	9.9
Cheyenne	107.0	134.9	20.7	6.2	7.4	16.3	5.4	11.1	50.9	14.8[NS]	15.6	5.1

1/ Data in Inoc. and Cont. columns are treatment means. Ten plants were harvested from each of the two center rows in four row plots/cultivar/treatment. The difference between inoculated and control treatment means are all significant at $P = 0.05$, except where indicated by NS = nonsignificant. See Appendix Table 8 for mean square error and least significant difference values.

2/ Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal.

Table 2.21. Effects of barley yellow dwarf virus on seeds per head, seeds per spikelet, 1000 kernel weight, and yield per plant for five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980.

Cultivar	Seeds/Head (no.)			Seeds/Spikelet (no.)			1000 Kernel Wt. (g)			Yield/Plant (g)		
	Inoc.[1/]	Cont.	% Red.[2/]	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.	Inoc.	Cont.	% Red.
Centurk	30.1	45.9	34.4	1.8	2.6	30.2	32.7 NS	31.8	+ 2.8	4.6	11.6	60.9
Warrior	13.1	35.5	63.7	1.0	2.0	50.0	29.2 NS	31.8	8.5	1.5	5.7	74.6
Winoka	14.4	28.1	48.9	1.2	2.0	42.5	28.0	31.8	11.9	1.6	5.3	70.1
Winalta	16.6	29.4	43.7	1.2	2.0	38.5	30.3 NS	32.6	7.0	1.6	5.4	71.3
Cheyenne	14.4	26.0	44.7	1.0	1.7	44.1	29.6 NS	31.8	6.9	1.4	3.8	64.5

[1/] Data in Inoc. and Cont. columns are treatment means. Ten plants were harvested from each of two center rows in four row plots/cultivar/treatment. The difference between inoculated and control treatment means are all significantly different at P= 0.05, except where indicated by NS = nonsignificant. See Appendix Table 8 for mean square error and least significant difference values.

[2/] Percent reductions were calculated using treatment mean values before rounding to one digit right of decimal. A + indicates a percent increase over control.

years. The minor differences in yield reduction between 1980 and 1981 results for each of the cultivars are most probably a result of different climatological influences and a response of the individual cultivars to those changes. Involved also may be the component compensation phenomenon, where one yield component may show a decrease and another show an increase in diseased plants, but the individual cultivars may not all be affected or respond in a similar manner. An analysis of year to year yield response averaged over all inoculated cultivars was not conducted. However, in comparing the percent of control data for 1980 and 1981 (Table 2.22 and Table 2.23) and in considering that the spring barley and spring wheat experiments showed no significant year to year variation in the yield response to virus infection, a similar statement can be made for the winter wheat response. Averaged over all cultivars, the yield reduction as a percent of control was 34.4% and 31.9% for 1980 and 1981 respectively. Thus, the virus isolate MT 792 caused consistently similar reductions in the yield of infected winter wheat cultivars for both years.

Table 2.22 Performance ranking among five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1979. Values for yield per plant, 1000 kernel weight, seeds per head, and tillers per plant are expressed as percent of control

Cultivar	Yield/ Plant	1000 Kernel Wt.	Seeds/ Head	Tillers/ Plant
	%	%	%	%
Winoka	23.0a[1/]	83.3a	56.7ab	52.3a
Winalta	35.3ab	83.7a	56.0ab	83.0 b
Cheyenne	27.7a	85.3ab	50.0a	59.7ab
Warrior	38.0ab	90.3 bc	61.3 bc	72.7ab
Centurk	48.0 b	92.7 c	67.7 c	67.0ab

1/ Values followed by the same letter are not significantly different at P =0.05 by LSD method.

Table 2.23 Performance ranking among five winter wheat cultivars inoculated with PAV isolate MT 792 at Bozeman, MT 1980. Values for yield per plant, 1000 kernel weight, seeds per head, and tillers per plant are expressed as percent of control.

Cultivar	Yield/ Plant	1000 Kernel Wt.	Seeds/ Head	Tillers/ Plant
	%	%	%	%
Warrior	25.5a[1/]	92.0a	37.0a	46.5a
Winoka	29.5ab	88.0a	51.0ab	49.5a
Winalta	29.0ab	93.0a	57.0 b	55.5ab
Cheyenne	36.5ab	93.0a	55.5 b	49.0a
Centurk	39.0 b	102.0a	65.0 b	60.5 b

1/ Values followed by the same letter are not significantly different at P= 0.05 by LSD method.

Comparisons Between Spring Barleys, Spring Wheats and Winter Wheats Infected With BYDV

In comparing the response to BYDV infection of spring barleys, spring wheats and winter wheats averaged over cultivars and years (Table 2.24), the data appears to coincide well with the results of other investigators. For plant height the winter wheats were most reduced (26.8%), in comparison to spring wheats (20.4%) and spring barleys (20.2%). Oswald and Houston (61) reported that winter wheat plant height could be reduced by as much as one-third to one-half that of healthy plants, and often to a greater extent than in barley or oats. Tiller production in diseased winter wheats was considerably reduced (44.4%) with respect to spring wheats (21.2%) or spring barleys (20.2%), a response difference also observed by Doodson and Saunders (24). It is interesting to note that kernel weight was not an appreciably reduced yield component in diseased winter wheats (9.6%) but was for spring wheats (39.7%). However, Fitzgerald and Stoner (28) found that kernel weight was significantly reduced in the hard red winter wheats they tested, which included 'Winalta'. In comparing the response of winter and spring wheats to BYDV infection, it appears that the greater decrease in tiller production and seed pro-

Table 2.24 Comparisons of the percent reduction in growth and yield parameters between winter wheats, spring wheats, and spring barleys infected with PAV isolate MT 792, averaged over cultivars and environments.

Crop	Plant Height	Tillers/ Plant	Seeds/ Head	1000 Kernel Wt.	Yield/ Plant
	%	%	%	%	%
Winter Wheats[1/]	26.8	40.1	44.4	9.6	67.3
Spring Wheats[2/]	20.4	21.2	28.2	39.7	65.4
Spring Barleys[3/]	20.2	20.2	20.4	33.7	65.1
6 rowed	18.8	11.0	23.0	27.3	57.7
2 rowed	21.7	29.5	17.9	40.1	72.4

1/ Winter wheat cultivars: 'Winoka', 'Winalta', 'Centurk', 'Warrior', 'Cheyenne'.

2/ Spring wheat cultivars: 'Olaf', 'Prodax', 'Lew', 'Fortuna', 'Tioga'.

3/ Spring barley cultivars: 6 rowed -- 'Steptoe', 'Unitan'; 2 rowed -- 'Piroline', 'Hector', 'Klages', 'Compana'.

duction in winter wheats and the greater reduction in kernel weight for spring wheats tend to offset each other, as the yield reduction of winter wheats and spring wheats is not appreciably different (Table 2.24).

In comparing the response of two-rowed and six-rowed barley cultivars, tiller production is reduced more for the former than the latter, 29.5% and 11.0% respectively. This perhaps would be expected, as two-rowed barley cultivars tend to produce more tillers than 6-rowed cultivars. Tiller production in two-rowed types is the factor involved in offsetting the greater seed yield capacity of six-rowed types, making yields comparable between the two. As might be expected, the six-rowed cultivars showed a slightly greater reduction in seed production in diseased plants than the two-rowed cultivars (Table 2.24). However, kernel weight was reduced less for the six-rowed (27.3%) than the two-rowed (40.1%) cultivars and infected six-rowed types did in fact, yield better than two-rowed types (57.7% reduction versus 72.4% reduction). Thus, among the spring barleys, the two-rowed cultivars were more susceptible than the six-rowed cultivars to virus infection over two years of testing.

Discussion

Barley yellow dwarf virus is an economically important disease of small grains produced in the central region of Montana. Over the four years of field survey for the disease, two epidemics occurred and BYDV was recovered from diseased plants or aphid vectors each year from 1978 through 1981. Both BYDV epidemics occurred in winter wheat as a result of fall infestations of viruliferous aphids. A serious occurrence of BYDV was not observed in spring grains, although virus was recovered from spring oats, spring wheat, spring barley, or aphid samples collected in those crops.

The incidence of BYDV observed in spring grains was limited to scattered diseased plants or groups of plants along field margins. The major influencing factor for this low occurrence of BYDV in spring grains was the absence of aphid vectors during late spring and early summer periods. Although no monitoring of aphid populations was conducted, observations made during the field surveys suggest that cereal grain aphids do not become abundant until mid- to late-July. Perhaps a further contributing factor for the minimal incidence of BYDV in spring grains was the low percentage of the aphid populations sampled in mid-summer that proved to be infective (Table 1.6). Because of these two

factors, spring grains escape serious levels of virus infection early in the growing season, at which time the potential for drastic yield reduction is the highest. However, late infection may be prevalent, but diagnosis of the disease made difficult by the confusion of BYDV symptoms with natural maturation.

An important consideration in the epidemiology of BYDV, especially as it pertains to winter wheat, is the potential for late planted spring grains to provide an inoculum source of the virus and food host for aphid vectors. The resulting viruliferous aphid population could then move into the fall-sown grains. Perhaps of greater significance is the growth of volunteer spring and winter grains in the fall, which may act as a bridging host for large numbers of viruliferous aphids. The initial aphid populations, having previously acquired BYDV from other sources (potentially late planted spring grains) could then inoculate the volunteer plants and expand the virus reservoir available for acquisition by the developing aphid population. Such a situation was observed in Judith Basin, where viruliferous *R. maidis* populations were found in abundance on volunteer barley (Table 1.6).

That both epidemics of BYDV occurred on winter wheat

as a result of fall infection, is evidence that the greatest potential for a rapid buildup and migration of large populations of viruliferous aphids into this crop occurs in late summer and early fall. Winter wheat emerging at times corresponding to the presence of heavy aphid populations presents the greatest potential for economic losses, as evident by the Judith Basin epidemic. As aphid populations were not monitored, it is speculative to suggest that the BYDV epidemics of 1980 and 1981 resulted from a massive population migration of viruliferous aphids into the area. However, A'Brook and Dewar (2), have shown that the greatest proportion of infective alatae aphids appear in the fall. Under favorable weather conditions, these winged aphids reproduce prolifically, providing the large vector reservoir necessary for secondary spread of BYDV in winter-sown grains.

In both of the 1980 and 1981 epidemic areas, the temperatures were comparatively mild during the months of September and October. Thus, climatic conditions were favorable for aphid population increases and secondary spread. Whether or not the primary source of viruliferous aphid vectors arose locally or migrated in from a distant area is very difficult to ascertain. Even though the source of the infective aphid populations was undetermined, knowl-

edge that four strains of BYDV i.e. RPV, MAV, RMV, and PAV, are widely distributed in central Montana (Figure 1.2), provides an indication that some level of inoculum is always present. The movement of one or more of the four cereal grain aphids into an area can occur, and each can potentially acquire one or more of these virus strains locally. Nevertheless, aphid populations were abundant in the fall at both epidemic locations and secondary spread of viruliferous aphids undoubtedly occurred.

The observation that planting date was relevant to the incidence of BYDV in the two epidemic areas provided a potential means of control. Growers in the Judith Basin area were advised to plant winter wheat after September 10 as a general control recommendation. In a survey conducted September 23, 1980 only two fields of emerged winter wheat were found in the Judith Basin area. Yet, the potential for a second consecutive year of BYDV movement into the crop was evident by the presence of viruliferous R. maidis aphids in the area. Surveys conducted in the summer of 1981 found only a very low incidence of the disease indicating that adjusting planting dates was successful. Although planting date for the control of BYDV has not always been useful (10), it appears to be an effective control measure for Montana

growers.

From the 1980 and 1981 field experiment results, it is quite apparent that there is little or no tolerance in any of the Montana small grain cultivars tested. However among those evaluated, the winter wheat cultivar 'Centurk', the spring wheat cultivars 'Olaf' and 'Tioga', and the spring barley cultivar 'Steptoe', were least affected by the virus. With respect to the various yield components measured, the individual cultivars did not necessarily respond the same to virus infection from one year to another. Certainly the observed variability was a result of environmental influences, virus dosage, plant growth stage at the time of inoculation, and component compensation response, all of which varied to some extent from year to year. However, the diseased plant response of each cultivar, in terms of percent of control data for yield, was fairly consistent between years and indicates the potential for substantial yield reduction under the right circumstances.

In considering the low incidence of BYDV observed in spring grains, growing highly susceptible spring wheat or spring barley cultivars does not present a problem, unless perhaps they are planted late in the season. In Montana, the widespread use of BYDV tolerant cultivars such as

'Sutter', 'Coracle', or 'Anza' would have no particular advantage for increasing productivity. In the event that an epidemic of BYDV in spring grains occurred late in the growing season, the overall yield reduction would probably be minimal, as indicated by the 1979 spring barley experiment. As there was also no meaningful level of tolerance observed in the commonly grown winter wheat cultivars, adjustment of planting dates to avoid times of large viruliferous aphid populations is the most practical control measure at this time.

The yield reductions observed in the small grain cultivars tested were in response to the most virulent isolate of BYDV found thus far in Montana. The vector-specific strains found in Montana i.e. RPV, MAV, and RMV are less virulent than the MT-PAV strain. As such, the potential yield reduction in the commonly grown cultivars resulting from infection by one of these less virulent strains would likely be less than that observed for MT-PAV. Therefore, although some information is now available on the potential yield reduction in these cultivars, the actual losses attributable to BYDV for any given occurrence of the disease will be dependent on the virulence of the infecting strain(s), time of infection, prevalence of the disease, the cultivar

affected, and the influences of the environment.

In retrospect, the information gathered during the course of this study has provided a better understanding of the etiology and epidemiology of BYDV in central Montana. However, as there are substantial differences in climatic conditions between different geographic areas in Montana, the epidemiology of BYDV in other areas may not be the same as in central Montana. For instance, on the west side of the Rocky Mountains where the environment is moderated by pacific coast weather patterns, the ecology of aphids may be quite different than that in central Montana. Thus, the epidemiology of BYDV may also be quite variable, and the inferences and control methods which are valid for central Montana may not necessarily be applicable for western Montana.

There are still a great many factors involved in the etiology and epidemiology of BYDV in Montana which are unknown. Little is known about the life cycle and overwintering potential of cereal grain aphids in Montana. The source of the virus and the importance of native grasses as virus hosts are still undetermined parameters. Certainly these factors as well as others are areas that warrant further study and would enhance our knowledge of the etiology and epidemiology of BYDV in Montana.

APPENDIX

Appendix Table 1. Small grain cultivars used in the 1979-81 field experiments.

Name	C.I. or Identification No.	Background
Winter Wheats		
Warrior	C.I. 13190	Pawnee x Cheyenne
Winoka	C.I. 14000	Selection from Winalta
Winalta	C.I. 13670	Minter x Wichita
Cheyenne	C.I. 8885	Selection from Crimean C.I. 1435
Centurk	C.I. 15075	'Kenya 58'/2/'Newthatch'/3/'Hope'/2*'Turkey'/'Cheyenne'/5/'Parker'.
Spring Wheats		
Fortuna	C.I. 13596	'Rescue' x 'Chinook' x ('Frontana' x 'Kenya 58'-'Newthatch')
Lew	C.I. 17429	'Fortuna'/S6285
Olaf	C.I. 15930	'Waldron'/selection from 'Justin' x 'Conley' x 'Norin 10'
Tioga	C.I. 17286	'Fortuna'/S6285
Prodax	C.I. 17407	'Tezanos Pinto Precoz'/'Sonora 64'/3/'Lerma Rojo 64'/Tezanos Pinto Precoz'/'Andes Dwarf'/4/2*'Jaral'//'Mengavi'/8156
Anza	C.I. 15284	('Lerma Rojo' x Norin 10' - Brevon) x $Andes_e^3$'
Spring Barleys		
Hector	C.I. 15514	'Betzes' x 'Pallister'
Klages	C.I. 15478	'Betzes' x 'Domen'
Piroline	C.I. 9558	'Weihenstephaner Mehtaunesis-tente C.P.' x 'Morgenrot'
Compana	C.I. 5438	Selection from C.I. 4116
Coracle	British Cb 1029	C.I. 3906-1 x 'Deba $Abed^2$'

Appendix Table 1 (Con't).

Name	C.I. or Identification No.	Background
Steptoe	C.I. 15229	'Washington 3564' x 'Unitan'
Unitan	C.I. 10421	'Glacier' x 'Titan'
Sutter	C.I. 15475	Selection from C.I. 1237 x 'Winter Tennessee'
Montana Lines	MT. 657357	'Hiproly' x 'Steptoe'
	MT. 657358	'Hiproly' x 'Steptoe'
	MT. 657361	'Hiproly' x 'Steptoe'
	MT. 657370	'Hiproly' x 'Steptoe'

Appendix Table 2. BYDV yellows index used for determining disease severity ratings among ten spring barley cultivars and lines inoculated with PAV isolate MT 792 at Bozeman, MT 1979.

Leaf Symptoms Corresponding to Rating Scale[1/]			
Rating Scale	Flag Leaf	Penultimate Leaf	Third Leaf
1	Healthy	Healthy	Yellow
2	Healthy	Less than 1/2 yellow	More than 1/2 yellow
3	Healthy	More than 1/2 yellow	More than 1/2 yellow
4	Less than 1/2 yellow	More than 1/2 yellow	More than 1/2 yellow
5	More than 1/2	More than 1/2 yellow	More than 1/2 yellow

[1/] Disease severity rating was based on the amount of yellowing exhibited by the flag leaf, penultimate leaf and third leaf of each infected tiller. All infected tillers/3m row were scored and the average disease rating determined for each barley cultivar or line. (Average disease rating = sum of rating scores/row ÷ total number of infected tillers/row.)

Appendix Table 3. Effects of barley yellow dwarf virus on growth and yield components for seven spring barley cultivars inoculated in 1980. Values are presented for mean square errors and least significant differences between inoculated and control for plant height (S), rachis length (T), tillers per plant (U), spikelets per head (V), seeds per head (W), seeds per spikelet (X), 1000 kernel weight(Y), and yield per plant (Z).

Source	df	S	T	U	V	W	X	Y	Z
Treatments[1/]	1	2025.0*	7.98*	2.29*	122.2*	153.2*	0.007*	1232.0*	35.33*
Cultivar[2/]	6	123.5*	3.45*	5.64*	695.3*	660.7*	0.002*	99.87*	6.85*
Trt x Cult	6	29.38*	0.59*	0.49	12.51	13.62	0.002*	84.92*	4.48*
Error	13	5.24	0.089	0.22	6.40	4.87	0.0008	1.56	0.53
LSD @ 0.05[3/]	13	4.94	0.64	1.01	5.46	4.77	0.062	2.70	1.57

* P =0.05

[1/] Treatments: BYDV inoculated versus control plots.

[2/] Cultivars: Hector, Compana, Klages, Piroline, Unitan, Steptoe, Sutter.

[3/] LSD calculated from analysis of variance error mean square for a randomized block design with two factors, treatment and cultivars.

Appendix Table 4. Effects of barley yellow dwarf virus on growth and yield components for seven spring barley cultivars inoculated in 1981. Values are presented for mean square errors and least significant differences between inoculated and control for plant height (S), rachis length (T), tillers per plants (U), spikelets per head (V), seeds per head (W), seeds per spikelet (X), 1000 kernel weight (Y), and yield per plant (Z).

Source	df	S	T	U	V	W	X	Y	Z
Treatments[1/]		694.0*	1.37*	12.76*	22.32*	156.5*	0.049*	767.6*	39.77*
Cultivars[2/]		106.60*	11.30*	2.04*	640.9*	472.2*	0.008*	82.05*	2.08*
Trt x Cult		47.22*	0.70	1.48*	13.41*	37.7*	0.005*	69.38*	2.97*
Error		4.33	0.25	2.88	2.24	3.54	0.001	4.19	0.25
LSD @ 0.05[3/]		4.60	1.11	1.20	3.13	4.12	0.073	4.46	1.10

* P =0.05

[1/] Treatments: BYDV inoculated versus control plots.

[2/] Cultivars: Hector, Compana, Klages, Coracle, Unitan, Steptoe, Sutter.

[3/] LSD calculated from analysis of variance error mean square for a completely randomized design with two factors, treatments and cultivars.

Appendix Table 5. Effects of barley yellow dwarf virus on growth and yield components for six spring wheat cultivars inoculated in 1980. Values are presented for mean square errors and least significant differences between inoculated and control for plant height (S), rachis length (T), tillers per plant (U), spikelets per head (V), seeds per head (W), seeds per spikelet (X), 1000 kernel weight (Y), and yield per plant (Z).

Source	df	S	T	U	V	W	X	Y	Z
Treatments[1/]	1	2517.0*	1.84*	8.76*	.260	455.0*	1.87*	854.1*	135.8*
Cultivars[2/]	5	425.6*	5.06*	3.19*	2.24*	282.1*	.918*	32.28*	1.34
Trt x Cult	5	53.6*	.157	.210	.285	14.59*	.040*	15.76*	1.78*
Error	11	7.84	.054	.238	.147	1.37	.007	3.15	.447
LSD @ 0.05[3/]	11	6.16	.513	1.07	.843	2.57	.189	3.91	1.47

* P = 0.05

[1/] Treatments: BYDV inoculated versus control plots.

[2/] Cultivars: Fortuna, Tioga, Lew, Olaf, Prodax, Anza.

[3/] LSD calculated from analysis of variance error mean square for a randomized block design with two factors, treatments and cultivars.

Appendix Table 6. Effects of barley yellow dwarf virus on growth and yield components for six spring wheat cultivars inoculated in 1981. Values are presented for mean square errors and least significant differences between inoculated and control for plant height (S), rachis length (T), tillers per plant (U), spikelets per head (V), seeds per head (W), seeds per spikelet (X), 1000 kernel weight (Y), and yield per plant (Z).

Source	df	S	T	U	V	W	X	Y	Z
Treatments[1/]	1	1655.0*	1.76*	1.71*	0.74	758.3*	2.67*	1601.0*	17.24*
Cultivar[2/]	5	495.4*	4.24*	0.20*	1.32*	116.8*	0.35*	22.0*	0.22
Trt x Cult	5	21.53*	0.18*	0.16*	0.34	20.0*	0.047*	26.9*	0.47*
Error	11	3.90	0.050	0.046	0.28	1.98	0.005	5.98	0.089
LSD @ 0.05[3/]	11	4.35	0.49	0.47	1.17	3.10	0.15	5.38	0.66

* P = 0.05

[1/]Treatments: BYDV inoculated versus control plots.

[2/]Cultivars: Fortuna, Tioga, Lew, Olaf, Prodax, Anza.

[3/]LSD calculated from analysis of variance error mean square for a randomized block design with two factors, treatments and cultivars.

Appendix Table 7. Effects of barley yellow dwarf virus on growth and yield components for five winter wheat cultivars inoculated in 1979. Values are presented for mean square errors and least significant differences between inoculated and control for plant height (S), rachis length (T), tillers per plant (U), spikelets per head (V), seeds per head (W), seeds per spikelet (X), 1000 kernel weight (Y), and yield per plant (Z).

Source	df	S	T	U	V	W	X	Y	Z
Treatments[1/]	1	8550.0*	23.60*	120.0*	53.3*	1825.0*	4.03*	153.7*	366.0*
Cultivars[2/]	4	105.9*	0.60*	3.62	3.70*	51.78*	.064*	6.03*	4.82
Trt x Cult	4	33.5	.06	4.08	.50	8.62	.031*	3.85*	5.16
Error	20	19.9	.082	1.73	.534	4.20	.010	1.22	3.32
LSD @ 0.05[3/]	20	7.60	1.78	2.24	1.24	3.49	.173	1.88	3.80

* P = 0.05

[1/] Treatments: BYDV inoculated versus control plots.

[2/] Cultivars: Centurk, Warrior, Winoka, Winalta, Cheyenne.

[3/] LSD calculated from analysis of variance error mean square for a completely randomized design with two factors, treatments and cultivars.

Appendix Table 8. Effects of barley yellow dwarf virus on growth and yield components for five winter wheat cultivars inoculated in 1980. Values are presented for mean square errors and least significant differences between inoculated and control for plant height (S), rachis length (T), tillers per plant (U), spikelets per head (V), seeds per head (W), seeds per spikelet (X), 1000 kernel weight (Y), and yield per plant (Z).

Source	df	S	T	U	V	W	X	Y	Z
Treatments[1/]	1	6815.0*	12.17*	131.6*	15.14*	1167.0*	3.53*	20.40*	91.76*
Cultivars[2/]	4	54.97*	0.48*	2.46*	7.43*	210.8*	0.49*	3.20	19.26*
Trt x Cult	4	64.68*	0.27*	0.25	2.12*	18.19*	0.016	3.07	2.93*
Error	20	5.30	0.04	0.14	0.24	3.71	0.009	1.88	0.113
LSD @ 0.05	20	5.48	0.47	0.73	1.13	4.30	0.22	3.20	0.72

* P = 0.05

[1/] Treatments: BYDV inoculated versus control.

[2/] Cultivars: Centurk, Warrior, Winoka, Winalta, Cheyenne.

[3/] LSD calculated from analysis of variance error mean square for a completely randomized design with two factors, treatments and cultivars.

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