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Title: Assessment of Resistance and Inheritance to Barley Yellow Dwarf Virus Disease in Five Wheat Cultivars (*Triticum aestivum* L.)

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Barley Yellow Dwarf Virus (BYDV) is a major disease of wheat. Unfortunately, unlike barley where the Yd2 gene provides adequate levels of resistance, the situation in wheat is more complex. This study was designed to provide information regarding: 1) evaluation of methods of measuring resistance among selected cultivars; 2) identification of sources of resistance; and 3) determination of the nature of inheritance controlling BYDV resistance.

Five wheat cultivars with possible different levels of resistance to BYDV and the resulting $F_1$, $F_2$, $F_3$, BC-1 and BC-2 populations provided the experimental material. An assessment of the damage inflicted by aphids feeding per se and aphid plus virus on the five cultivars was determined under greenhouse conditions. Cultivars and the resulting progeny were grown in the field to confirm the greenhouse findings and to determine nature of inheritance.

Aphid feeding per se did not influence most cultivars other than for plant height involving Yamhill and Anza. Despite the lack of visual symptoms, BYDV did significantly influence the six parameters measured with the cultivars Stephens and Riebesel exhibiting the greatest reduction. No immunity was observed for any of the cultivars tested.

Under field conditions Stephens, followed by Riebesel, were the most susceptible cultivars with Yamhill, Novi Sad and Anza being the most resistant based on the parameters measured.

The inheritance pattern appeared to be quantitative with both additive and nonadditive genetic variability involved in controlling resistance. This was verified by the transgressive segregation noted in $F_2$ and $F_3$ generations and the significant General and Specific Combining Ability estimates for the BYDV score.

Due to the quantitative nature of BYDV resistance and the different genetic factors observed for the cultivars in this study, a recurrent selection program should result in higher levels of resistance than exhibited by the cultivars employed in this study. Also, the use of a visual BYDV score appears to be an effective means of identifying resistant parents.

# Assessment of Resistance and Inheritance to Barley Yellow Dwarf Virus Disease (BYDV) in Five Wheat Cultivars (*Triticum aestivum* L.)

by

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Typed by Kathleen Miller for Jaime Tola

IN DEDICATION TO

Nacha, my wife, for her help and encouragement;

Patricio, Lucrecia and Cristina, my children, that this thesis serve as an example of perseverance;

Cielo and Estrella, my mother and my aunt, for their loneliness and suffering during my absence.

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## INTRODUCTION

Barley Yellow Dwarf Virus (BYDV) is a major disease of wheat. This disease complex involves the interaction of three biological systems: a host, a virus and a vector.

A wide array of plants, including wheat, barley, oats, rye and a wide range of grasses serve as host species. The virus damages the phloem tissue of susceptible plants. Resulting symptoms in cereals include: reduced root development and tillering, delayed heading, sterility, failure of kernels to fill and a reduction in kernel number and subsequent decrease in grain yield.

Symptom expression can vary due to the degree of virulence of different strains of BYDV, the age of the plant when infection occurs, the differential ability of vector species to transmit the virus and environmental conditions.

Basic knowledge of the complex relationships among pathogen, vector and host plant is of paramount importance to successful disease control. The most suitable method of control is the use of resistant cultivars. This has been successfully demonstrated in barley where the gene Yd2 is responsible for resistance to BYDV. However, little is known in wheat about the possible sources of genetic resistance.

Several cultivars showing differing reactions to BYDV throughout their life cycle have been identified. Unfortunately, poor correlation between visual symptoms and yield reduction frequently exist. Furthermore, symptoms of the disease are not as strongly expressed in wheat as in barley or oats, however, yield losses can be of the same magnitude.

The purpose of this investigation was to provide information regarding possible genetic resistance to BYDV in selected wheat cultivars by: (1) evaluation of methods of detecting and measuring resistance among cultivars, (2) identification of possible sources of resistance and (3) determination of the nature of inheritance controlling BYDV resistance.

# LITERATURE REVIEW

## The Disease

Barley Yellow Dwarf Virus disease was first reported by Oswald and Houston (1951) on barley in California. Infected plants were characterized by a brilliant yellowing of the leaves accompanied by moderate to severe stunting. Coincidental with the yellowing condition observed in barley, abnormal conditions in wheat and oats, including stunting and chlorosis, were also detected (Oswald and Houston, 1953).

Following this outbreak in 1951, numerous investigations of BYDV have been carried out and its destructive role has been clearly demonstrated (Bruehl, 1961; Rochow, 1970, 1979; Gill, 1970; Schaller, et al., 1963). The many different strains of the virus, the numerous aphid species which serve as vectors, and the fact that practically all grain and grasses are susceptible to the virus, make BYDV potentially one of the most economically important plant viruses (Harris and Maramorosch, 1977).

Symptoms, depending on the host, include reduced tillering, root reduction, suppressed heading, sterility and failure of kernels to fill (Agrios, 1978). Visual symptoms are usually less severe in barley than in oats, and even less pronounced in wheat. The reddening of leaves, characteristic of infection in oats can also be present in wheat (Rochow, 1970). The most important pathologic effect appears to be a degeneration of the phloem which results in the disruption of the translocation mechanism of the plant (Esau, 1957; Allen, 1957). External symptoms are indirect, secondary expressions of the collapse of the phloem.

## The Causal Agent

The viral nature of the disease has been assumed since 1951 (Oswald and Houston, 1951). Barley Yellow Dwarf Virus is a 22-30 nanometer diameter polyhedral virus containing a single component of single stranded RNA of molecular weight 2.0 x $10^6$ (Jensen, 1969; Paliwal, 1978; Brakke and Rochow, 1974). The virus protein has one major polypeptide subunit of about 24,000 daltons (Rochow and Israel, 1976). It is the most well-known of the Luteoviruses Group, sharing properties such as being small, isometric, low virus yield, vector-dependent transmission by aphids in the persistent circulative manner, lack of mechanical virus transmission and restriction to phloem tissue of infected plants (Shepherd, 1977; Rochow and Duffus, 1981; Rochow, 1979).

## The Vector

More than fourteen species of aphids that feed on cereals and grasses are known to transmit the virus (Rochow, 1970). Most common vectors are *Rhopalosiphum padi* (Linnaeus), *R. maidis* (Fitch), *Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker), *M. festucae* (Theobald) and *Schizaphis graminum* (Rondani). The virus is circulative in its vectors requiring a latent period (over days) before transmission occurs (Smith, 1965). It does not pass from adult vector to progeny (Oswald and Houston, 1953) and its does not multiply within the vector (Paliwal and Sinka, 1970).

There is a remarkable specialization among isolates of the virus (strains) and the aphid vectors (Foxe and Rochow, 1975). Slykhuis

(1976) distinguished five strains of BYDV which have been differentiated on the basis of vector specificity: *Rhopalosiphum maidis* (RMV), *R. padi* (RPV), *Macrosiphum avenae* (MAV), *Sitobion avenae* and *R. padi* (PAV) and *Schizaphis graminum* (SGV).

## The Host

The host range of BYDV appears to be limited to the Gramineae, nonetheless, the wide distribution of many susceptible perennial grass hosts has helped to spread the virus. Rochow and Duffus (1981) pointed out that it would be unusual to find a grass specie not susceptible to one or more isolates of BYDV. About 100 plant species are known to be susceptible (Oswald and Houston, 1953; Rochow, 1961, 1970). Genetic differences among strains with respect to host range have been reported (Rochow, 1959; Allen, 1957; Toko and Bruehl, 1959).

## The Environment

Three biological systems: plant, virus and aphid, plus the environment interact to create a great variability in symptom expression of the disease (Agrios, 1978; Gill, 1967; Schaller et al., 1963).

Oswald and Houston (1953) described environmental conditions relating to the epidemiology of the disease. Rochow (1961) and Bruehl (1961) reviewed the factors contributing to the development of the disease. Date of seeding and early mild weather conditions favoring the building up of aphid populations appeared to be particularly important. Yield losses associated with late planted wheat were first reported by Oswald and Houston (1953) and werereflected in an abundance of light-green stunted plants, many of which failed to head.

Endo (1957), Orlob and Arny (1961) and Rochow (1969) have presented results showing symptom severity affected by temperature, time of infection and time of feeding and transmission. Under cooler temperatures (65-75°F) symptom severity was greater than warmer temperatures (82-88°F). Temperature and daylength affected not only the activity of the virus, but also the vectors. Virus infection at early stages of plant growth resulted in greater yield losses, more stunting in addition to more intense discoloration than infection at later stages.

## Control

Elimination of virus source plants, adjustment of crop planting time, application of insecticides and use of resistant crop cultivars have been suggested as four major methods for BYDV control.

The adjustment of planting time and chemical control are designed to avoid maximum aphid populations and prevent early infection (Rochow and Duffus, 1981). Chemical control of vectors is not practical since applications are costly and require precise timing in terms of applications (Leonard, 1964). Aphids can also acquire and spread the virus with momentary feedings before the insecticides can take effect.

Though control of the disease might rest with any or a combination of the components of the vector-virus-host-environment complex, investigations have led to the consensus that the most reliable and effective means of control is the development of cultivars tolerant or resistant to the virus (Bruehl, 1961; Schaller et al., 1963; Hayes et al, 1971; Qualset et al. 1973, 1977; Topcu, 1975; Cisar et al. 1982b).

Sources of Resistance and Genetic Studies

Effective control of BYDV by genetic resistance means have been successfully demonstrated in barley (Arny and Jedlinski, 1966; Catherall and Hayes, 1967; Schaller, 1977).

Suneson and Ramage (1957) reported a single recessive gene conditioning resistance in the barley cultivar Rojo. This gene was designed as Yd1. Rasmusson and Schaller (1959) crossed four susceptible barley cultivars with resistant Ethiopian lines. The $F_1$ generation was intermediate in disease reaction showing incomplete dominance. Ratios of 1:2:1 resistant, segregating and susceptible, respectively were found in $F_3$ families; and test cross progeny gave a 1:1 ratio, indicating that the resistance was conditioned by a single gene. The gene was designated as Yd2. Damsteeg and Bruehl (1964) and Schaller et al. (1964) conducted similar studies on Ethiopian cultivars. Ten additional Ethiopian barley cultivars selected for high level of resistance to BYDV were also used. Their results indicated that resistance is controlled by a single, incompletely dominant gene, and that all Ethiopian cultivars possessed the same Yd2 gene. Some differences in the intensity of symptom expression were detected among those resistant lines, however. It was suggested that modifying genes might be involved and that they may vary in number and expression depending on a particular line.

Sieveking (1969) reported that the lines CI 3208-4, CI 9654 and CI 9795 also had the Yd2 gene. He found that when a resistant cultivar carrying the Yd2 gene was crossed with a cultivar with a gene conditioning a low level of resistance, the Yd2 gene was expressed as recessive rather than incomplete dominant. Catherall et al, (1970) suggested that there is more than one allele for resistance at the Yd2 locus, each with different levels of effectiveness. Gill and Buchannon (1972) transferred the gene for resistance in the Ethiopian barley CI 5791 to susceptible cultivars. Some hybrids were tolerant to either one or the other of the two isolates used, but not both, suggesting that the effect of the gene could be changed by different genetic backgrounds. Schaller (1977) indicated that in barley the Yd2 gene is effective against all strains of BYDV, however, the degree of yellowing in barley as a result of BYDV infection is apparently controlled by other genes.

The degree of protection in the presence of Yd2 gene is still a matter of controversy. A number of cultivars listed as resistant have been found to be susceptible when grown in different locations (Schaller et al., 1963). Frequencies of resistant genotypes have been correlated, in part, with elevation. The higher the elevation, the greater the frequency of the resistant genotypes (Harlan, 1977). Hayes et al. (1971) indicated that the Yd2 gene may not provide as much protection in cooler areas where the growing period is longer, such as Northern Europe. It was found also that the effectiveness of the Yd2 gene was dependent upon the rate of plant growth and development (Jones and Catherall, 1970).

Brown and Poehlman (1962) studied the heritability of BYDV resistance in oats. Heritability estimates range from 23.3% for the susceptible x susceptible cross to 50.8% for the susceptible x resistant cross. Parent, $F_2$ and $F_3$ showed distinct symptoms of the disease. Mean leaf damage ranged from 87.7% for the susceptible cultivar to 38.1% for the most tolerant. Mean leaf damage of $F_2$

populations varied from 81.9% in a susceptible x susceptible cross to 54.5% in a susceptible x tolerant cross. None of the $F_2$ means differed significantly from the mean of their respective parent. Means of the $F_3$ populations varied from 62.1% leaf damage for a susceptible x susceptible cross to 36.8% for a susceptible x tolerant cross. The authors indicate that resistance to BYDV appears to be quantitatively inherited.

Comeau and Dubuc (1978) stressed that transgressive segregation has produced oat lines possessing higher levels of BYDV resistance than were previously available and that some oat lines displayed a level of resistance approaching that of Ethiopian barleys possessing the Yd2 gene. These finds are similar to that reported by Weerapat et al. (1974) who reported increased grain yield in $F_1$ and $F_2$ populations from resistant x resistant, and resistant x susceptible oat crosses. There were cultivar differences in resistance to BYDV and the nature of the inheritance appeared to be quantitative rather than controlled by major genes.

Reports on the inheritance of resistance to BYDV in wheat are very limited. Immunity is not known, and no major gene conditioning resistance has been identified (Qualset et al., 1973; Gill, 1967; Dowler and Briggle, 1977; Topcu, 1975). However, some sources of resistance have been reported (Qualset et al., 1973; Doodson and Saunders, 1970; Smith, 1967; Bruehl, 1961; Cisar et al., 1982b).

Topcu (1975) studied the inheritance of resistance to BYDV in populations from crosses of Anza (resistant) x Bluebird (susceptible) and Anza (resistant) x CA 63121 (resistant) spring wheat cultivars. The $F_2$ data of both crosses showed continuous variation.

Transgressive segregation was observed with resistance being greater in resistant x resistant than resistant x susceptible crosses, suggesting that parents in the former have different genes for resistance or a favorable gene interaction was involved. The $F_3$ data showed genetic variability among lines within crosses for resistance, suggesting resistance was controlled by several genes.

Qualset et al, (1973) reported significant genetic variability for resistance to BYDV in wheat. Heritability estimates of BYDV reaction in $F_3$ lines of crosses where a BYDV resistant cultivar, Anza, was crossed to four cultivars with varying degrees of resistance, ranged from 24 to 37%. They suggested that recurrent selection may be an effective method of breeding for resistance to BYDV in wheat.

The inheritance of resistance to BYDV under field conditions was studied by Cisar et al, (1982a) in twelve winter wheat cultivars. General combining ability effects for resistance and mean parental response to BYDV infection were good indicators of parental value, particularly if the parent was very tolerant or very susceptible. Additive effects of genes were most important in determining resistance of the progeny to BYDV, with nonadditive genetic effects and reciprocal effects being less important.

## Assessment of Resistance

The mechanism of resistance to BYDV seems to be under genetic control leading to the consensus that an effective means of control is the development of resistant cultivars. In barley it has been demonstrated that one major gene conditions the resistance to the virus and it is expressed with different levels of effectiveness. No such gene has been discovered in wheat. Rather, resistance appears to be under the control of genes inherited in a quantitative manner.

For some virus disease an explanation for resistance is based on supression of virus replication. Most such studies have involved viruses that are relatively easy to assay because they are mechanically transmissible and reach high titers in infected plants.

Barley Yellow Dwarf resistance seems to arise from species differences with respect to the degree of phloem degeneration (Esau, 1957), with lower BYDV extracts (Jedlinsky et al., 1977) and with differences in the rate of systemic movement of the virus (Jensen, 1973). All three factors are related to the process of virus replication.

Yield components and visual reaction have been commonly used to assess the effects of BYDV on plants. Endo and Brown (1962) showed that it was not possible to predict grain loss in individual oat cultivars on the basis of disease severity reading for leaves or from the number of leaves with symptoms. Catherall and Hayes (1967) reported that barley cultivars with higher values for leaf yellowing, generally denoted susceptibility and low values a greater or lesser degree of resistance.

The standardization of estimating the disease based on a visual score has always been a challenged topic (Dowler and Briggle, 1977). Comeau and Dubuc (1978) found a provide poor correlation between visual plant scores and grain yield.

Harvest index and grain yield evaluation per se have been reported as the most effective means to measure the effects of BYDV (Dowler and Briggle, 1977; Cisar et al., 1982b). However, Carrigan et al. (1981) reported that Barley Yellow Dwarf significantly reduced the grain yield, number of heads, plant height, kernel weight, kernel number and above ground plant weight. It did not affect the harvest index and protein percentage, however.

Cisar et al. (1982b) measured resistance reaction in winter wheat by means of visual disease severity ratings and grain yield of infected plants, expressed as a percent of an entry control mean. They concluded that yield and certain yield components are valuable criteria to discriminate a broad range in BYDV symptom expression.

# MATERIALS AND METHODS

## Experimental Material

Five wheat cultivars (*Triticum aestivum* L.) were selected for this study. These included four winter wheats ('Stephens', 'Riebesel', 'Yamhill' and 'Novi Sad 874-4') and one spring wheat ('Anza'). A description of the cultivars is given in Appendix Table 1.

Yamhill and Stephens were developed at Oregon State University and were selected for this study representing resistant and susceptible cultivars, respectively, based on their reaction to Barley Yellow Dwarf Virus (BYDV) when grown in the Willamette Valley of Oregon in 1978 and 1979. Riebesel, Novi Sad 874-4 and Anza were introduced cultivars and have been reported to have some resistance to BYDV by other research workers (Qualset et al., 1973).

In the spring of 1980, ten possible single crosses were made between the five cultivars. To develop $F_2$ populations, a portion of the resulting $F_1$ seed was vernalized in the growth chamber for 6 weeks at $6^{o}C$ and under a daylength of 10 hours and transplanted to the greenhouse during the winter of 1981.

A random sample of the resulting $F_2$ seed from each cross was taken and the same vernalization procedure was followed to obtain a minimum of 120 plants for a $F_3$ generation per cross prior to Fall, 1981. The remaining $F_2$ seed was saved for the field experiments. Also, in the Spring of 1981, all twenty possible reciprocal backcrosses to each parent were made with the ten $F_1$s. In addition to the parents, the following populations representing the five crosses were available: $F_1$, $F_2$, $F_3$, BC to each parent.

Two studies were conducted. The first was to assess the damage caused by the aphid alone and the aphid plus BYDV. A second study was designed to determine the possible nature of inheritance for resistance to BYDV.

Study 1: Evaluation of damage to wheat caused by the aphids per se and aphids plus BYDV

The five cultivars were tested for their reaction to BYDV with aphids collected at the Hyslop Agronomy Farm and transferred on barley and oat plants (cultivars 'Julia' and 'Cayuse', respectively) to check for infectivity. To obtain virus-free insects, aphids were collected from barley and oats which did not exhibit the symptoms. Such aphids were killed after they laid their eggs. The resulting progeny were retested to susceptible barley and oat plants, multiplied and used as a source of aphid-free virus from plants not showing symptoms.

Seed of the winter wheat cultivars was vernalized in the growth chamber for six weeks, as previously described. The cultivars were transplanted to three-quart pots and grown in the greenhouse. Anza, the spring cultivar, was planted without a vernalization period. The soil was a silt loam to which a complete fertilizer (15-15-15) 2 g/pot had been added. Each pot contained two plants and the experimental unit consisted of two pots. Fifteen treatments were developed as follows:

T-1 to T-5: cultivars protected from aphid and BYDV

T-6 to T-10: cultivars plus aphids

T-11 to T-15: cultivars plus aphids plus virus.

Viruliferous aphids (Sitobion avenae, Fabricius) were identified using a key developed for field identification of apterous and alate cereal aphids (Cohen, 1974). Five adult aphids were transferred to each plant with a camel's hair brush. Virus-free S. avenae were transferred in the same manner. Dates of transferring are provided in Appendix Table 2.

Cages of fine cheesecloth and nylon screen were used to confine the aphids during rearing and subsequently inoculation feedings on the plants. A 72-hour inoculation feeding period was allowed after which the experiment was kept free of aphids with 25% Malathion.

Greenhouse temperatures were approximately 20°C during the day and 15°C at night. It was not always possible to keep the temperature within this range because of sunny and unexpected warm days in April and May of 1982. The daily photoperiod was 16 hours until the first aphid transfer and then it was reduced to 12 hours.

A complete randomized block design with four replications involving the five cultivars and three treatments, which included protected cultivars, cultivars plus non-viruliferous aphids and aphids plus BYDV. Data were collected on the four plants for each experimental unit. A visual score for BYDV was taken when the plants were at boot stage. Traits measured were plant height, number of tillers, plant weight, grain yield, kernel weight and harvest index.

Analysis of variance using mean values per treatment were calculated for each measurement. The F test was utilized to determine the differences between measurements. Multiple comparisons between cultivars and treatments were estimated using Tukey test at the 1 percent probability level. Contrast comparisons were also run for all combinations involving cultivars and treatments.

Study 2: <u>Nature of inheritance controlling BYDV resistance</u>

In 1980 the aphid trap technique (Schaller et al., 1963) consisting of an early planting of a mixture of barley and oat plants, and different planting dates for the five cultivars used in this investigation were tested to obtain maximum BYDV infection under field conditions.

The genetic materials, which were comprised of the five cultivars, 10 $F_1$'s, 10 $F_2$'s, 10 $F_3$'s and 20 backcrosses for a total of 55 entries were planted at Hyslop Agronomy Farm in the Fall of 1981 (Appendix Table 3).

Two rows for the parents, $F_1$'s, $F_3$'s and BC's and four rows for the $F_2$ generation were planted in 1981. Each row consisted of 20 plants spaced 15 cm apart. The distance between rows was 30 cm with a row length of 1.8 m.

The experimental design was a randomized complete block with three replications. Aphid traps, as previously described, were planted in-between the blocks and around the experimental area (Appendix Figure 1). Plants within the aphid trap were cut and carried to the test plants during February and March. These aphid-bearing plants were shaken and spread between the plots in an attempt to get a uniform infection.

To ensure adequate levels of infection the experiment was planted on the 18th of September, 1981. Data obtained in 1980 suggested that this was the optimum date to obtain maximum infection. This is one and one-half months ahead of the recommended planting date for wheat at this location. The two procedures, aphid traps and the early planting data, were employed to enhance the build-up of the aphid population.

Four treatments were established involving the five parents. These included: (1) parents were caged from emergence to harvest, (2) parents were caged in fall only, (3) parents were protected with 6 kg/ha (Thimet 15-G), systemic insecticide (the insecticide was applied at planting time and again in early March prior to the aphid flights) and (4) a nonprotected plot. Cages were built with a fine mesh cloth and placed individually over the cultivars.

To avoid other disease problems, Benomyl (50% a.i.) at the rate 1.12 kg/ha was applied on March 5, at the middle of the tillering stage. Chlorothalanil (40.4% a.i.) at the rate 0.7 l/ha plus Triadimefon (50% a.i.) 0.3 kg/ha were applied on April 21 or at the end of stem elongation. Propiconazol (41.8% a.i.) at the rate of 1.0 kg/ha was applied on May 5 at the heading stage.

Diuron (80% a.i.) at 1.2 kg/ha of active material, was applied as a post-emergence spray for weed control on October 10 at three leaf stage of growth. An additional post-emergence spray was done with a mixture of Buctril at 0.85 kg/ha of active ingredient plus Dicamba (47% a.i.) at 0.15 kg/ha of active ingredient on February 25, at the mid-tillering stage. Fertilizer application included 30 kg/ha of nitrogen prior to seeding and a single application of 50 kg/ha of nitrogen (urea 46%) applied as a top dressing on March 4, at the late tillering stage. The phosphorus level in the soil was adequate for satisfactory plant growth. One irrigation (30 mm) on May 25 after heading stage was applied due to the lack of measurable rain during the two previous months.

The plant population for each replication was 40 plants for parents, $F_1$'s, $F_3$'s and BC's and 80 plants for $F_2$ populations. Data were collected on an individual plant basis. Sample size for each replication was 10 plants for parents and $F_1$'s; 15 plants for $F_3$'s and BC's and 20 plants for $F_2$'s. Plants were selected at random and tagged before the first visual disease reaction was scored.

Visual BYDV symptoms were scored on a 1 to 10 scale used by Qualset et al. (1973). The assessment of the disease is based on disease severity symptoms in infected plants as is described in Appendix Table 4.

Two readings were taken on individual plants; the first scoring was done the second week of April (boot stage) and the second was completed the third week of May about two weeks after heading. Since a close correlation was observed between the two dates, coupled with the fact that the second date was closer to the actual yield determination, it was used for all analyses.

Plant height and yield components data were collected on the same plants in which BYDV reaction was scored.

Plant height was obtained at maturity by measuring from the base of the crown to the tip of the spike of the tallest tiller, excluding awns. Number of tillers per plant was recorded as the number of culms bearing fertile spikes. Fresh plant weight, excluding roots, and grain weight per plant were recorded in grams. Harvest index values were scored as the ratio of grain yield per plant to the weight of the whole plant excluding roots. One hundred kernel weight in grams was also obtained. These characters were examined to study the relationship between disease symptoms and yield related characters.

Mean BYDV scores, mid-parent values, frequency distribution and deviations of $F_1$'s from mid-parent values for parents, crosses and generations were obtained.

An analysis of variance including all generations was conducted for each character to determine whether differences existed among generations. The F test was utilized to determine if significant differences were present. Plot means were used for the analysis. Mean values for each treatment were compared using Tukey test at the 5 percent probability level.

Separate analyses for each population were also performed for each trait to determine within-plot variances. Heritability in the narrow sense was estimated following Warner's method (Ketata et al., 1976) as:

$$h^2_{ns} = \frac{2V_{F2} - (V_{BC1} + V_{BC2})}{V_{F2}}$$

where $V_{F2}$, $V_{BC1}$, and $V_{BC2}$ are the variances of the $F_2$, Backcross 1, and Backcross 2 generation. The standard error for $h_{ns}$ is derived as:

$$Vh^2_{ns} = 2\left\{\left[(V_{BC1}+V_{BC2})^2/df_{F2}\right] + (V^2_{BC1}/df_{BC1}) + (V^2_{BC2}/df_{BC2})\right\}/V_{F2}$$

To determine relationships between the degree of BYDV infection and the yield components, simple regressions were carried out using BYDV score as the independent variable and the agronomic traits were the dependent variable. Correlation and coefficient of determination were also computed for each parental cross.

Genetic correlations were calculated based in $F_1$ and $F_2$ correlations assumed to be environmental and phenotypic correlations (Falconer, 1981) as:

$$r_{Ph} = H_x \; H_y \; r_g + E_x \; E_y \; r_e$$

Combining ability analysis for the BYDV score for the $F_1$ generation was computed using Model I Method 4 as proposed by Griffing (1956) to estimate general (GCA) and specific combining ability (SCA). The fixed model, Model I, was used because the parents constituted a select group of cultivars. Contributions of the parents due to GCA and SCA effects were computed for the BYDV score by this method.

To confirm the presence of the virus and to determine the nature of strain of virus in the plants, leaf and stem samples were sent to Dr. Richard Lister, Department of Plant Pathology, Purdue University for Laboratory analysis. Aphid specimens were also sent to Dr. Tokuwo Kono, California Department of Agriculture for identification as well.

# RESULTS

## Study 1

Significant observed mean square values for six traits were obtained involving three treatments despite a very low visual symptom expression (BYDV score) (Table 1). Unusual high temperatures during April and May increased the temperatures of the greenhouse and/or optimum plant development may have modified the visual symptoms. This might have also contributed to the high C.V. value (35.49). The highest mean BYDV score was denoted by Stephens (3.75) followed by Riebesel (2.25) when infected with the virus.

Based on Tukey test for BYDV score, only the treatment Stephens + aphid + virus was significantly different (Table 2). However, when the infected cultivars (Variety + Aphid + Virus) were compared using an orthogonal comparison, significant differences were observed for all comparisons except Yamhill vs Novi Sad, Yamhill vs Anza and Novi Sad vs Anza (Table 3).

In Table 4 an orthogonal comparison is provided for three groupings. These include cultivars, cultivars plus aphids and cultivars plus aphids plus virus. A difference was found between cultivars and cultivars + aphids for only plant weight. By contrast, significant differences are shown between cultivars and cultivars + aphids + virus for BYDV score, plant weight, grain yield and kernel weight. Similar results were found for the cultivars + aphids vs cultivars + aphids + virus comparison except that a significant difference was not noted for kernel weight.

Table 1. Observed mean values for BYDV score and six agronomic characters involving five wheat cultivars alone, with non-viruliferous, and BYDV viruliferous aphids conducted in the Greenhouse, 1982.

| Cultivars | BYDV Score | Plant Height (cm) | Tiller Number | Plant Weight (gm) | Grain Yield (gm) | Kernel Weight (gm) | Harvest Index |
|---|---|---|---|---|---|---|---|
| Stephens | 1.00 | 80.3 | 22.0 | 188.5 | 40.00 | 4.62 | .212 |
| Riebesel | 1.00 | 107.3 | 21.3 | 119.0 | 34.62 | 4.26 | .291 |
| Yamhill | 1.00 | 93.3 | 16.3 | 175.5 | 44.42 | 4.88 | .253 |
| Novi Sad | 1.00 | 71.5 | 22.8 | 140.3 | 29.22 | 4.42 | .209 |
| Anza | 1.00 | 63.8 | 25.3 | 164.5 | 30.90 | 3.88 | .188 |
| Spn + A[1] | 1.00 | 78.3 | 23.8 | 182.0 | 39.02 | 4.68 | .214 |
| Rb + A | 1.25 | 105.0 | 20.5 | 123.3 | 35.80 | 4.25 | .291 |
| Ymh + A | 1.00 | 89.0 | 17.3 | 154.5 | 42.70 | 4.89 | .277 |
| NS + A | 1.25 | 72.5 | 21.0 | 147.3 | 29.50 | 4.34 | .200 |
| Anz + A | 1.25 | 63.8 | 25.3 | 147.0 | 29.30 | 3.95 | .199 |
| Spn + A + V[2] | 3.75 | 74.5 | 27.0 | 142.5 | 27.20 | 4.41 | .189 |
| Rb + A + V | 2.25 | 102.0 | 22.3 | 113.3 | 30.82 | 4.18 | .272 |
| Ymh + A + V | 1.25 | 91.0 | 16.3 | 144.3 | 42.12 | 4.82 | .292 |
| NS + A + V | 1.50 | 74.3 | 20.0 | 140.0 | 27.15 | 4.41 | .194 |
| Anz + A + V | 1.50 | 66.5 | 24.5 | 166.8 | 30.82 | 3.73 | .185 |
| Mean Squares | 2.136** | 875.1** | 43.16** | 1998.71** | 143.56** | .5134** | .0072** |
| C.V. | 35.49 | 3.16 | 6.30 | 5.95 | 8.13 | 1.53 | 7.10 |

**,*: significant at the one and five percent probability levels, respectively.

[1]Aphid [2]Aphid + Virus

Table 2. Tukey test for BYDV score in five wheat cultivars alone, carrying non-viruliferous and BYDV viruliferous aphids. Conducted in Greenhouse, 1982.

| Cultivar | Mean | Range |
|---|---|---|
| Stephens + A + V[1] | 3.75 | a |
| Riebesel + A + V | 2.25 | b |
| Anza + A + V | 1.50 | b |
| Novi Sad + A + V | 1.50 | b |
| Yamhill + A + V | 1.25 | b |
| Anza + A[2] | 1.25 | b |
| Novi Sad + A | 1.25 | b |
| Riebesel + A | 1.25 | b |
| Yamhill + A | 1.00 | b |
| Stephens + A | 1.00 | b |
| Anza | 1.00 | b |
| Novi Sad | 1.00 | b |
| Yamhill | 1.00 | b |
| Riebesel | 1.00 | b |
| Stephens | 1.00 | b |

[1]Aphid + Virus [2]Aphid HSD: 1.25

Table 3. Comparison of observed mean squares and F values for BYDV score among five wheat cultivars carrying BYDV viruliferous aphids. Conducted in Greenhouse, 1982.

| Comparison | BYDV Score | |
|---|---|---|
| | M.S. | F |
| Spn + A + V vs Rb + A + V[1] | 4.50 | 18.22** |
| Spn + A + V vs Ymh + A + V | 12.50 | 50.61** |
| Spn + A + V vs NS + A + V | 10.125 | 40.99** |
| Spn + A + V vs Anz + A + V | 10.125 | 40.99** |
| Rb + A + V vs Ymh + A + V | 2.00 | 8.10** |
| Rb + A + V vs NS + A + V | 1.125 | 4.55* |
| Rb + A + V vs Anz + A + V | 1.125 | 4.55* |
| Ymh + A + V vs NS + A + V | 0.125 | <1 |
| Ymh + A + V vs Anz + A + V | 0.125 | <1 |
| NS + A + V vs Anz + A + V | 0.001 | <1 |

[1]A + V = Aphid + Virus

**,* = significant at the one and five percent probability levels, respectively.

Table 4. Comparison of observed mean square and F values for BYDV score and six agronomic characters among cultivars carrying non-viruliferous and cultivars with viruliferous aphids. Conducted in Greenhouse, 1982.

| Comparison | BYDV Score | | Plant Height | | Tiller Number | | Plant Weight | |
|---|---|---|---|---|---|---|---|---|
| | MS | F | MS | F | MS | F | MS | F |
| Cultivars vs Cvs + A | 0.23 | 1.00 | 22.5 | 3.34 | 0.025 | 1.00 | 455.62 | 5.72* |
| Cultivars vs Cvs + A + V | 11.03 | 44.63** | 24.03 | 3.56 | 2.50 | 1.34 | 2624.4 | 32.94** |
| Cvs + A vs Cvs + A + V | 8.10 | 32.79** | 0.03 | 1.00 | 2.03 | 1.08 | 893.03 | 11.21** |

| Comparison | Grain Yield | | Kernel Weight | | Harvest Index | |
|---|---|---|---|---|---|---|
| | MS | F | MS | F | MS | F |
| Cultivars vs Cvs + A | 3.25 | 1.00 | 0.0008 | 1.00 | 0.00033 | 1.23 |
| Cultivars vs Cvs + A + V | 177.24 | 22.86** | 0.0235 | 5.23* | 0.00016 | 1.00 |
| Cvs + A vs Cvs + A + V | 132.50 | 17.08** | 0.0156 | 3.47 | 0.00075 | 3.53 |

[1]Cvs + A = Cultivars + Aphids [2]Cvs + A + V = Cultivars + Aphids + Virus

**,*: significant at the one and five percent probability levels, respectively.

Mean square values for individual cultivars when compared with aphids and aphids + virus for the seven measurements can be found in Table 5. No differences were observed when a comparison is made between Stephens and Stephens plus aphids. In contrast, with the exception of harvest index, differences were noted for all measurements when Stephens is compared with the treatment Stephens + Aphids + Virus. Differences were observed for all measurements involving Stephens + Aphid and Stephens + Aphid + Virus.

When the treatments involving Yamhill are noted, differences for plant height, plant weight and harvest index are found when the aphids were present. Differences for plant weight and harvest index were observed when Yamhill alone is compared with the aphid plus the virus. No differences were detected when the aphid alone was compared with the aphid plus virus treatment.

For Riebesel, differences were observed for the treatments when both the aphid and virus were present for BYDV score and plant height when compared to Riebesel alone. A comparison between aphid and aphid + virus resulted in only grain yield exhibiting a difference.

In the treatments involving Novi Sad only the treatment of Novi Sad compared to Novi Sad + Aphid + Virus showed significance and that was for tiller number.

Differences for the treatments involving Anza were found for plant weight when the aphids were present, and for kernel weight when both aphids and virus were present. The comparison between aphid and aphid + virus resulted in differences being detected for plant height and kernel weight.

When all measurements are considered, fewer differences in

Table 5. Comparison of observed mean square values for BYDV score and six agronomic characters among cultivars, cultivars carrying non-viruliferous and cultivars with viruliferous aphids. Conducted in Greenhouse, 1982.

| Comparisoin | BYDV Score | Plant Height | Tiller Number | Plant Weight | Grain Yield | Kernel Weight | Harvest Index |
|---|---|---|---|---|---|---|---|
| Spn vs Spn + A[1] | 0.01 | 8.00 | 6.13 | 84.5 | 1.90 | 0.007 | 0.001 |
| Spn vs Spn + A + V[2] | 15.12** | 66.12** | 50.00** | 4232.0** | 327.00** | 0.090** | 0.001 |
| Spn + A vs Spn + A + V | 15.12** | 28.12* | 21.13** | 3120.0** | 279.00** | 0.148** | 0.0012* |
| Ymh vs Ymh + A | 0.001 | 36.13* | 2.00 | 882.0** | 5.95 | 0.0002 | 0.0011* |
| Ymh vs Ymh + A + V | 0.125 | 10.13 | 0.01 | 1953.0** | 10.58 | 0.006 | 0.0030** |
| Ymh + A vs Ymh + A + V | 0.125 | 8.00 | 2.00 | 210.0 | 0.66 | 0.0084 | 0.00046 |
| Rb vs Rb + A | 0.12 | 10.13 | 1.12 | 36.12 | 2.76 | 0.0002 | 0.00001 |
| Rb vs Rb + A + V | 3.12** | 55.13* | 2.00 | 66.12 | 28.88 | 0.0144 | 0.0007 |
| Rb + A vs Rb + A + V | 2.00* | 18.0 | 6.13 | 200.00 | 49.50* | 0.011 | 0.0007 |
| NS vs NS + A | 0.125 | 2.0 | 6.13 | 98.0 | 0.15 | 0.0144 | 0.0001 |
| NS vs NS + A + V | 0.500 | 15.13 | 15.13* | 0.12 | 8.61 | 0.00011 | 0.0004 |
| NS + A vs NS + A + V | 0.125 | 6.13 | 2.00 | 105.0 | 11.05 | 0.012 | 0.00007 |
| Anz vs Anz + A | 0.125 | 0.01 | 0.01 | 612.5** | 5.12 | 0.0098 | 0.00026 |
| Anz vs Anz + A + V | 0.500 | 15.12 | 1.13 | 10.12 | 0.10 | 0.0435** | 0.000015 |
| Anz + A vs Anz + A + V | 0.125 | 15.12 | 1.13 | 780.0** | 4.65 | 0.0946** | 0.0004 |

[1]A = Aphid     [2]A + V = Aphid + Virus

**,*: significant at the one and five percent probability levels, respectively. (1.41 d.f.)

agronomic traits were found for treatments involving Yamhill, Novi Sad and Anza. It can be noted that these same cultivars had the lower BYDV scores. The exception to this observation was with Riebesel where, despite a moderately high BYDV score, few differences were noted for other traits measured. Aphid damage per se was not detected for Stephens, Riebesel and Novi Sad in most of the seven parameters measured. However, Anza and Yamhill showed a significant reduction in plant weight with Yamhill also exhibiting a reduction in plant height and harvest index.

In general, significant differences between cultivars with non-viruliferous aphids and cultivars with aphids carrying the virus were detected. These results are in close agreement with differences between the cultivars and cultivars with viruliferous aphids. Therefore, the differences observed appear to be the result of the virus and not from the feeding of the aphids per se. There were some exceptions to this situation. For example, there was a significant difference for grain yield between Riebesel plus aphids and Riebesel plus viruliferous aphids. Furthermore, plants of Anza carrying aphids responded differently in plant weight compared to plants carrying viruliferous aphids. This was found even though no differences between Anza and Anza + Aphids was noted.

Of the traits measured, plant weight was the most sensitive to the attack of the virus and to the feeding of the aphids, while tiller number and harvest index appeared to be the least affected. All six traits studied were influenced by the virus with Stephens appearing to be the most sensitive.

Study 2

Mean BYDV Scores for Parents

To determine the most meaningful stage for the most reliable BYDV score, data were collected at the booting and heading stage of development (Appendix Table 5). The correlation coefficient between the first and second reading p was r = 0.87. The mean BYDV scores for all treatments for the first and the second reading were 3.27 and 4.31, respectively. A higher BYDV score was obtained for all treatments at the second or heading stage. Since there was a high correlation between the two dates and with heading being closer to final grain yield determination it was selected for the analysis.

In order to assess the response of the five cultivars to Yellow Dwarf Virus infection, three methods of protection were established and compared to the nonprotected check plots. The data for this study are provided in Table 6.

The average BYDV score (4.6) for the parents shows that with no protection the score was twice that of the plants which were completely caged (2.5). Insecticide and fall protection gave almost the same mean scores (4.3 and 4.1, respectively). Nonprotected cultivar Stephens exhibited the highest score (7.6) followed by Riebesel (4.8). The lowest BYDV score was found for Yamhill (3.1) followed by Novi Sad (3.7) and Anza (3.9)

The mean grain yield for the five cultivars under different levels of protection are presented in Table 7. An average yield reduction of 23.4% was observed when the completely caged treatment (19.6) is compared with the nonprotected (15.0). Also, the insecticide treatment did give some protection (16.2) with the largest

Table 6. Observed mean values for BYDV scores for five wheat cultivars grown under different levels of BYDV field protection at the Hyslop Agronomy Farm in 1982-83.

| | Nonprotected | | Fall Caged | | Insecticide | | Completely Caged | |
|---|---|---|---|---|---|---|---|---|
| Cultivar | Mean | Sx | Mean | Sx | Mean | Sx | Mean | Sx |
| Stephens | 7.6 | 1.72 | 7.7 | 1.16 | 6.0 | 2.36 | 4.20 | 1.48 |
| Riebesel | 4.8 | 2.13 | 5.1 | 1.73 | 2.2 | 1.23 | 3.10 | 1.52 |
| Yamhill | 3.1 | 1.06 | 2.2 | 0.79 | 3.8 | 2.20 | 1.50 | 0.53 |
| Novi Sad | 3.7 | 1.61 | 2.2 | 1.14 | 5.3 | 2.11 | 1.90 | 0.99 |
| Anza | 4.0 | 1.59 | 4.1 | 1.37 | 3.3 | 1.64 | 1.60 | 0.84 |
| Mean | 4.6 | | 4.3 | | 4.1 | | 2.5 | |

Table 7. Comparison of the mean grain yield per plant in grams for five wheat cultivars grown under different levels of BYDV field protection at the Hyslop Agronomy Farm in 1982-83.

| | Nonprotected | | Fall Caged | | Insecticide | | Completely Caged | |
|---|---|---|---|---|---|---|---|---|
| Cultivar | Mean | Sx | Mean | Sx | Mean | Sx | Mean | Sx |
| Stephens | 13.6 | 7.22 | 14.6 | 4.99 | 19.6 | 9.41 | 17.2 | 7.80 |
| Riebesel | 9.6 | 6.61 | 8.3 | 4.83 | 15.4 | 8.11 | 16.0 | 6.07 |
| Yamhill | 18.3 | 7.00 | 10.1 | 3.87 | 17.9 | 10.78 | 23.8 | 5.18 |
| Novi Sad | 17.2 | 7.53 | 13.7 | 4.83 | 10.1 | 9.12 | 20.3 | 6.29 |
| Anza | 16.2 | 9.24 | 14.8 | 7.38 | 17.8 | 6.27 | 20.5 | 12.20 |
| Mean | 15.0 | | 12.3 | | 16.2 | | 19.6 | |

loss being observed with the fall-caged (12.3). In Table 8, the average yield reduction by cultivars is presented. Riebesel had the largest reduction (40%) with Novi Sad being least affected (15.4%). The yield reduction for Stephens was low (20.8%) even though it had the highest BYDV score (7.6) under nonprotected conditions (Table 6); however, the completely caged plants for this cultivar score was also the highest (4.2). Yamhill which showed the lowest BYDV score for nonprotected and completely caged plants of 3.1 and 1.5, respectively, resulted in a yield decrease of 23.2%.

In Figures 1 and 2, a graphic presentation can be observed for the four treatments and five cultivars in terms of BYDV score and grain yield, respectively. From these comparisons, both BYDV score and grain yield, it is apparent that the cultivars responded differently to the treatments as previously noted.

## Mean BYDV Scores for Progeny

Mean BYDV scores, mid-parent values and deviation from mid-parent values for the $F_1$, $F_2$ and $F_3$ generations are reported in Table 9. When the overall means of the populations are considered by generation, a lower score was recorded for the $F_1$ generation (3.51). With the subsequent segregation in the $F_2$ and $F_3$, higher values were realized of 4.96 and 4.68, respectively. In crosses between susceptible and moderately resistant parents, the mean BYDV scores for the $F_1$ generation of Spn/Rb, Spn/Ymh, Spn/NS and Spn/Anz were 5.1, 3.2, 3.5, and 2.5, respectively. The midparent values in the same order were 6.2, 5.1, 5.7 and 5.8, respectively. Deviations of $F_1$'s from midparent values are -1.1 for Spn/Rb, -1.85 for Spn/Ymh, -2.15 for Spn/NS and -3.30 for Spn/Anz. When the scores for the parents

Table 8. Comparison of percentages of yield reduction for five wheat cultivars under different levels of BYDV protection grown at Hyslop Agronomy Farm, 1982-83.

| Cultivar | Completely Caged | Nonprotected |
|---|---|---|
| Stephens | 100 | 20.2 |
| Riebesel | 100 | 40.0 |
| Yamhill | 100 | 23.2 |
| Novi Sad | 100 | 15.4 |
| Anza | 100 | 20.9 |

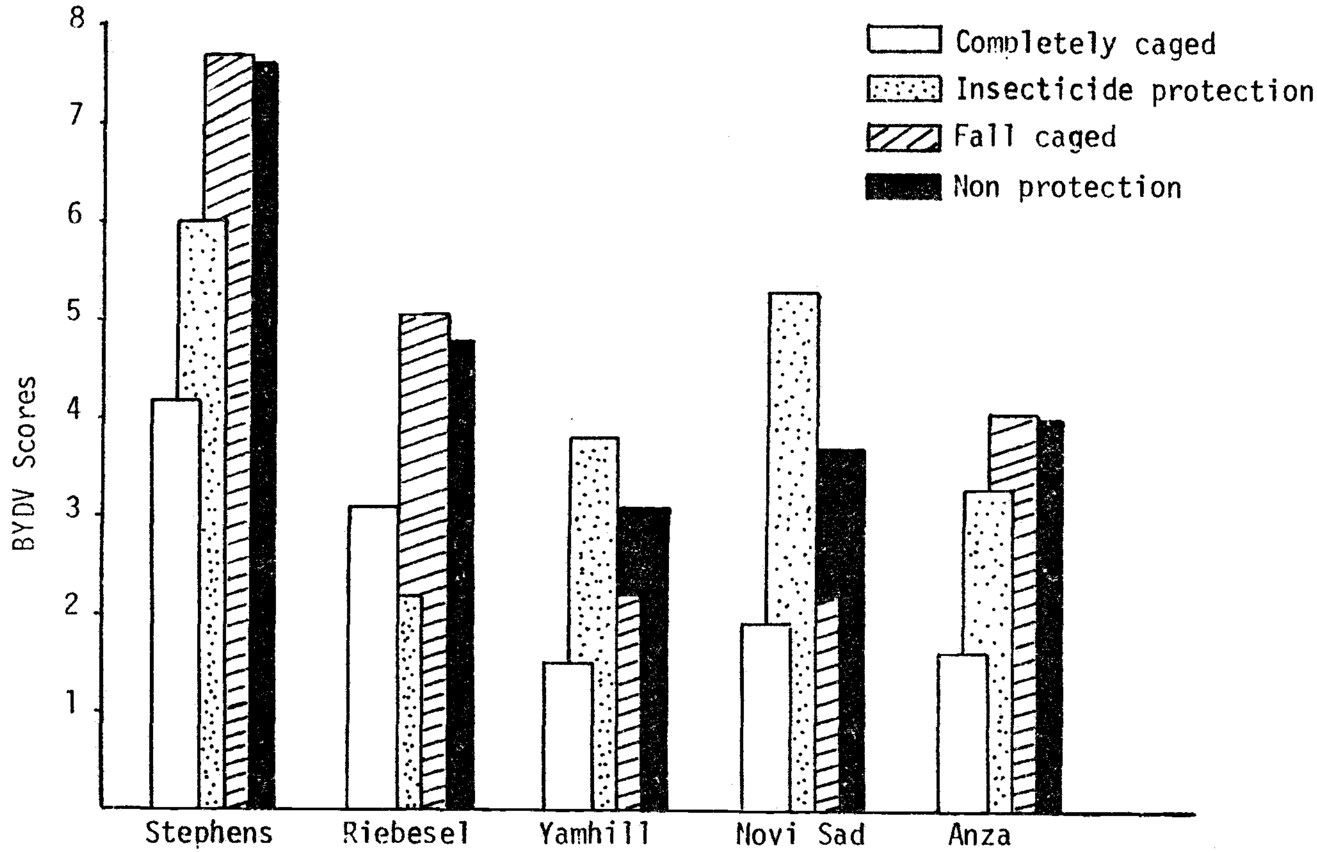


**Figure 1.** BYDV mean scores for five wheat cultivars with different levels of protection when grown on the Hyslop Agronomy Farm, 1982.

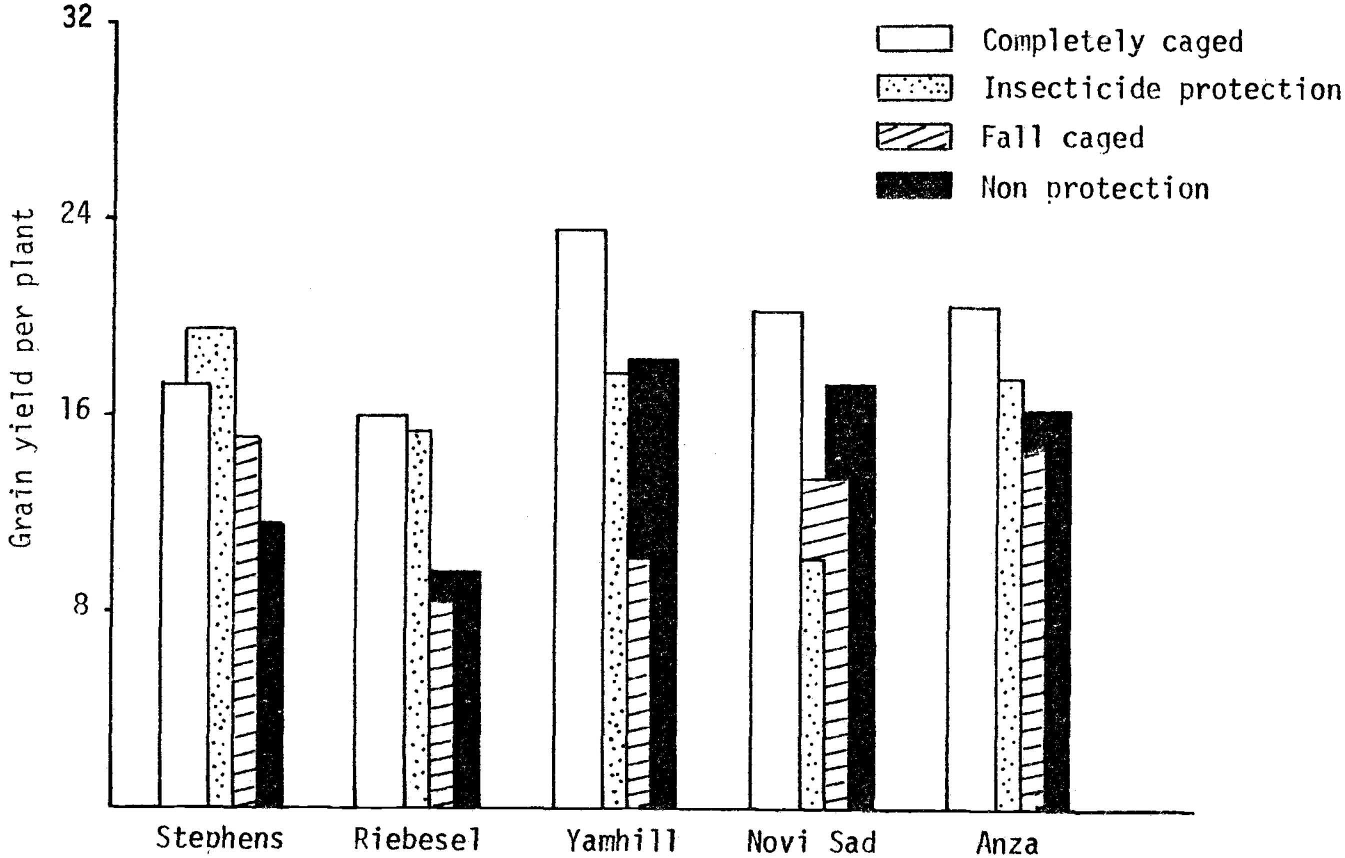


Figure 2. Grain yield means for five wheat cultivars with different levels of protection when grown on the Hyslop Agronomy Farm, 1982.

Table 9. Observed mean BYDV scores for F1, F2, and F3 generations; midparent values and deviations of F1's from the midparent value when the materials were grown on the Hyslop Agronomy Farm in 1982.

| | Generations | | | | |
|---|---|---|---|---|---|
| | $F_1$ | $F_2$ | $F_3$ | | Deviation |
| Crosses | Mean | Mean | Mean | Midparent Value | From MP Value |
| Spn x Rb | 5.1 | 5.2 | 5.4 | 6.2 | -1.1 |
| Spn x Ymh | 3.2 | 4.5 | 4.4 | 5.1 | -1.9 |
| Spn x NS | 3.5 | 5.3 | 4.5 | 5.7 | -2.2 |
| Spn x Anz | 2.5 | 4.9 | 4.3 | 5.8 | -3.3 |
| Rb x Ymh | 3.3 | 4.3 | 4.8 | 4.0 | -0.7 |
| Rb x NS | 4.3 | 6.0 | 6.7 | 4.3 | 0.0 |
| Rb x Anz | 2.5 | 4.2 | 3.6 | 4.4 | -1.9 |
| Ymh x NS | 3.3 | 4.3 | 4.2 | 3.4 | -0.1 |
| Ymh x Anz | 3.9 | 4.7 | 4.6 | 3.6 | 0.3 |
| NS x Anz | 3.5 | 6.2 | 4.3 | 3.9 | -0.4 |
| Overall Mean | 3.51 | 4.96 | 4.68 | | |
| Sx | 1.42 | 1.78 | 1.64 | | |

(Table 7) are compared with the $F_1$'s (Table 9) the $F_1$ progeny tended to favor the more resistant parent in every cross where a susceptible parent was involved (Figure 3). This trend is further illustrated in the $F_3$ when the parents and $F_1$'s are compared. Also, the negative values of midparent deviations are closer to the scores of more resistant cultivars Yamhill, Novi Sad and Anza. For susceptible x susceptible (Spn/Rb) the resulting $F_1$'s were intermediate in reaction. In crosses with Rb, which had been reported previously as being resistant, the $F_1$'s displayed deviations from midparent values toward the resistant parent, i.e. Rb/Ymh (-0.7), Rb/Anz (-1.9). However, Rb/NS did not show such a trend being similar to the MP value.

It is interesting to note that $F_1$'s from crosses between cultivars with low BYDV scores were equal or very close to the midparent values (Table 9). For example, NS/Ymh (3.3), Ymh/Anz (3.9) and NS/Anz (3.5) were similar to the midparents of the respective parents (3.4, 3.6 and 3.9, respectively). Similar results were obtained with other cross combinations where both parents had low BYDV score.

For the $F_2$ and $F_3$ mean BYDV scores observed (Table 9) a similar trend can be seen as described for the $F_1$ generation. The crosses involving Stephens tended to have higher BYDV scores in contrast to crosses involving moderately resistant parents. The one exception is found in the $F_2$ generation of the cross NS/Anz where a value of 6.2 was found.

Figure 4 shows the frequency distribution for BYDV scores of $F_2$ plants of the crosses Spn/Rb and Spn/Ymh. It is apparent that in both $F_2$ crosses there is a skewness in the distribution. Of particular

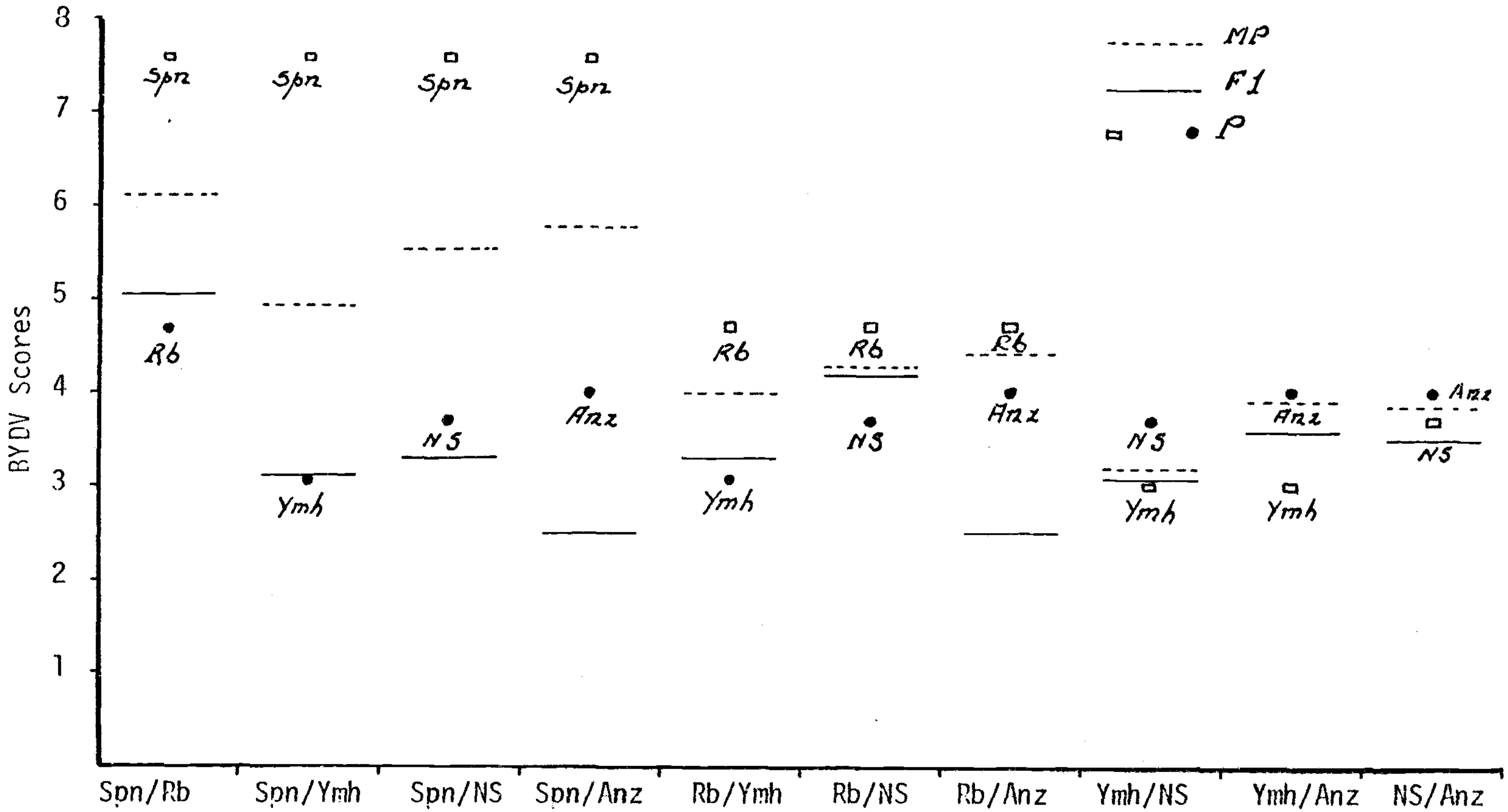


Figure 3. Observed BYDV score parental (P) values, $F_1$'s ($F_1$) values and mid-parent (MP) values for five wheat cultivars and ten derived crosses when grown on the Hyslop Agronomy Farm, 1982.

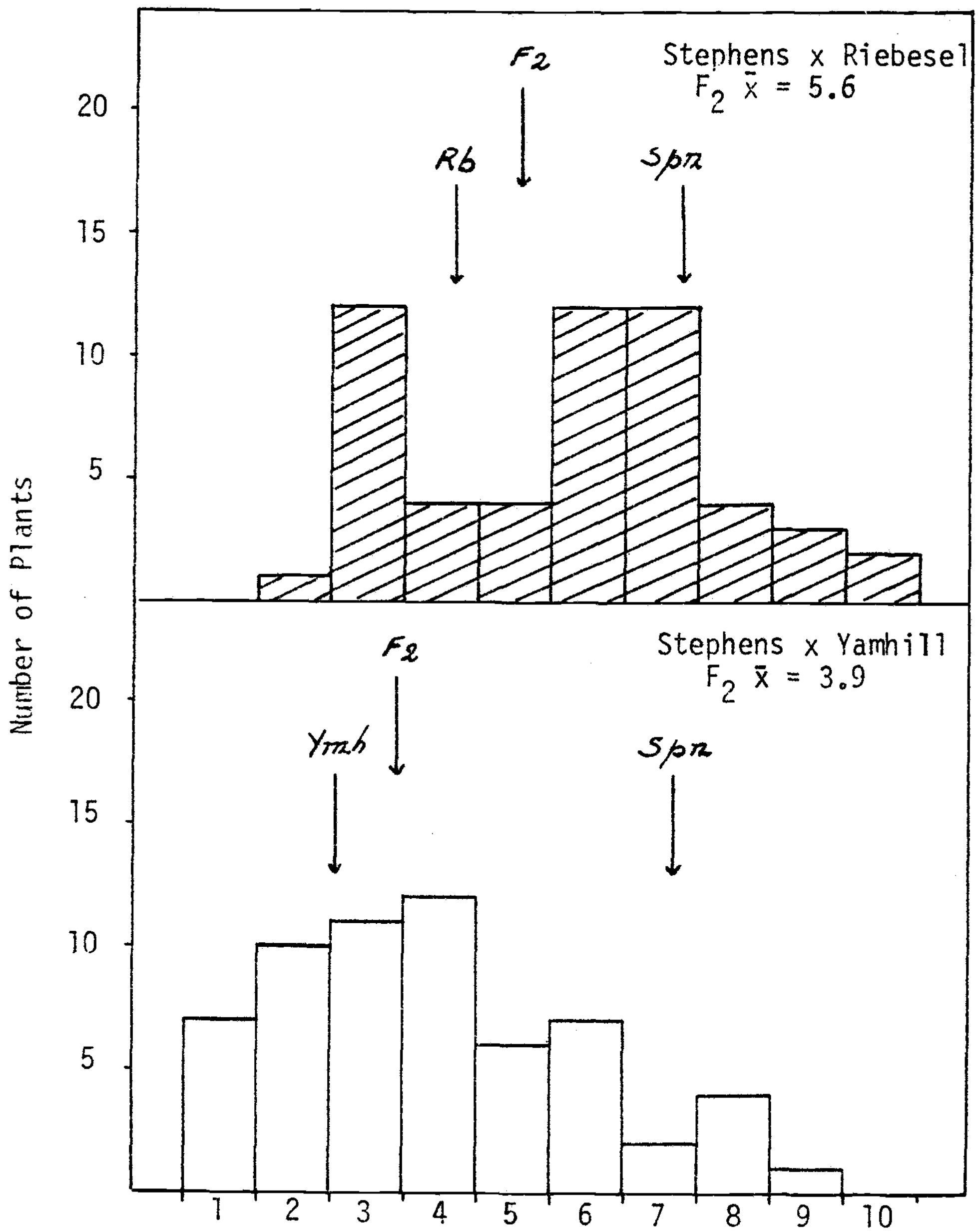


Figure 4. Frequency distributions for BYDV score from $F_2$ populations of crosses Stephens x Riebesel and Stephens x Yamhill. Arrows indicate mean values ($F_2$, N = 60; parents, N = 30)

interest is that in the Rb/Spn cross, the distribution is toward the susceptible parent, in contrast to the Spn/Ymh cross where the skewness is toward Yamhill or the resistant parent. The same trend is observed for the $F_3$ populations of the same crosses (Figure 5).

Figure 6 and Figure 7 show the frequency distribution for BYDV scores of $F_2$ and $F_3$ plants of the crosses Spn/NS and Spn/Anz, respectively. Since the parents have different disease reactions, the $F_2$ mean scores tend to be intermediate. Skewness toward resistance can be noted particularly with the Spn/NS cross. $F_3$ mean scores are similar to those for $F_2$, however, an increase of resistant types are noticed for both crosses.

The frequency distribution for the $F_2$ of the crosses Rb/Ymh and Rb/NS are found in Figure 8. It is apparent from the $F_2$ distribution of the Rb/Ymh that there is a definite skewness toward a lower BYDV score. This is in contrast to the $F_2$ distribution for the Rb/NS cross where more plants appeared to be susceptible. A similar trend can be noted in Figure 9 for the $F_3$ distribution of both crosses. Again, when Yamhill is involved, there is a tendency for more plants to exhibit a lower BYDV score or more resistant response.

The frequency distribution for $F_2$ and $F_3$ of the crosses Anz/Rb and Anz/NS can be found in Figures 10 and 11. Skewness toward resistant BYDV score for the Anz/Rb cross is apparent in both the $F_2$ and $F_3$ distribution. However, for Anz/NS segregates tend to deviate toward susceptibility. The $F_3$ plants of Anz/Rb cross shows a distribution reflecting an accumulation of intermediate BYDV score levels.

For the $F_2$ and $F_3$, frequency distribution of the crosses Ymh/NS

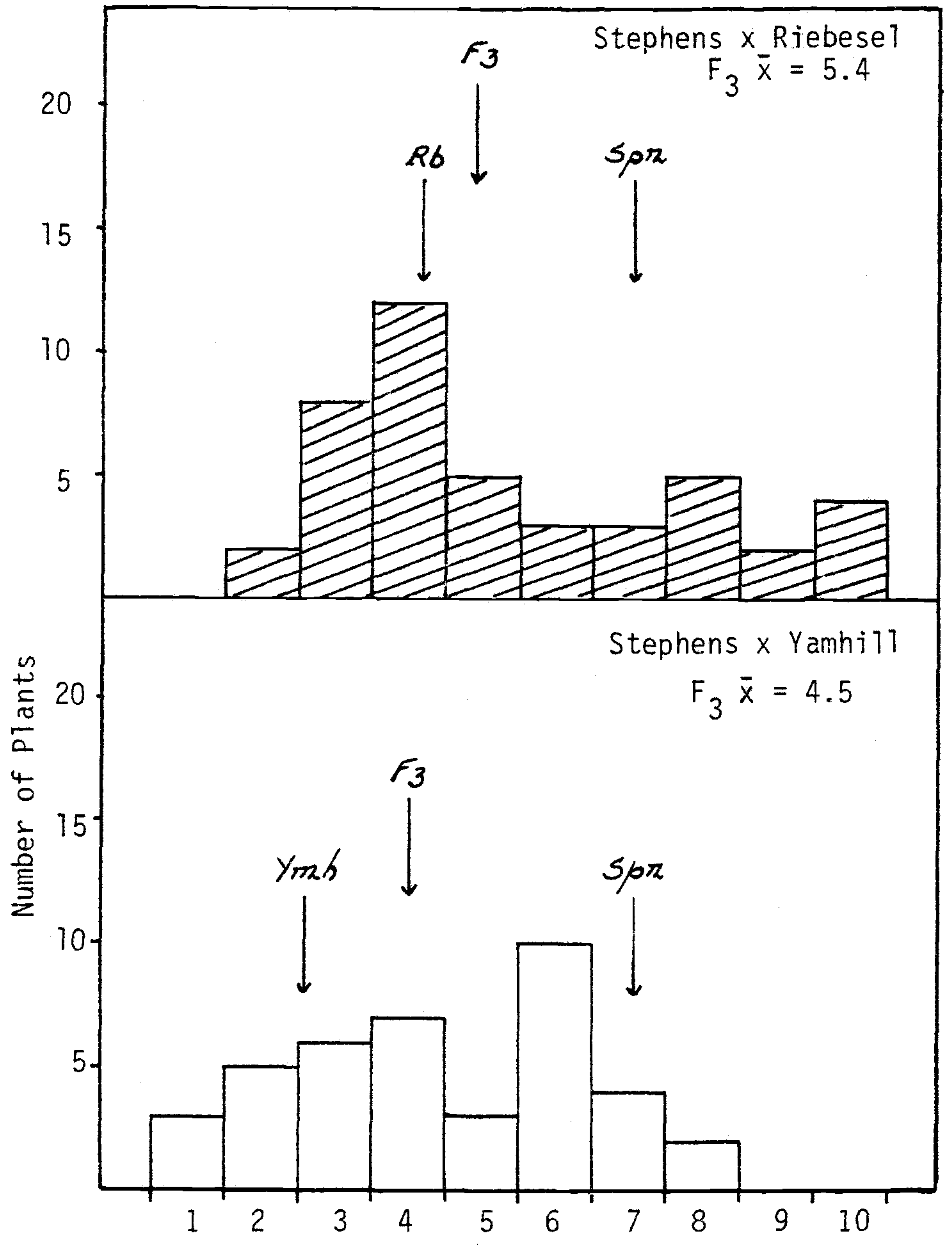


Figure 5. Frequency distributions for BYDV score from $F_3$ populations of crosses Stephens x Riebesel and Stephens x Yamhill. Arrows indicate mean values ($F_2$, N = 45; parents, N = 30)

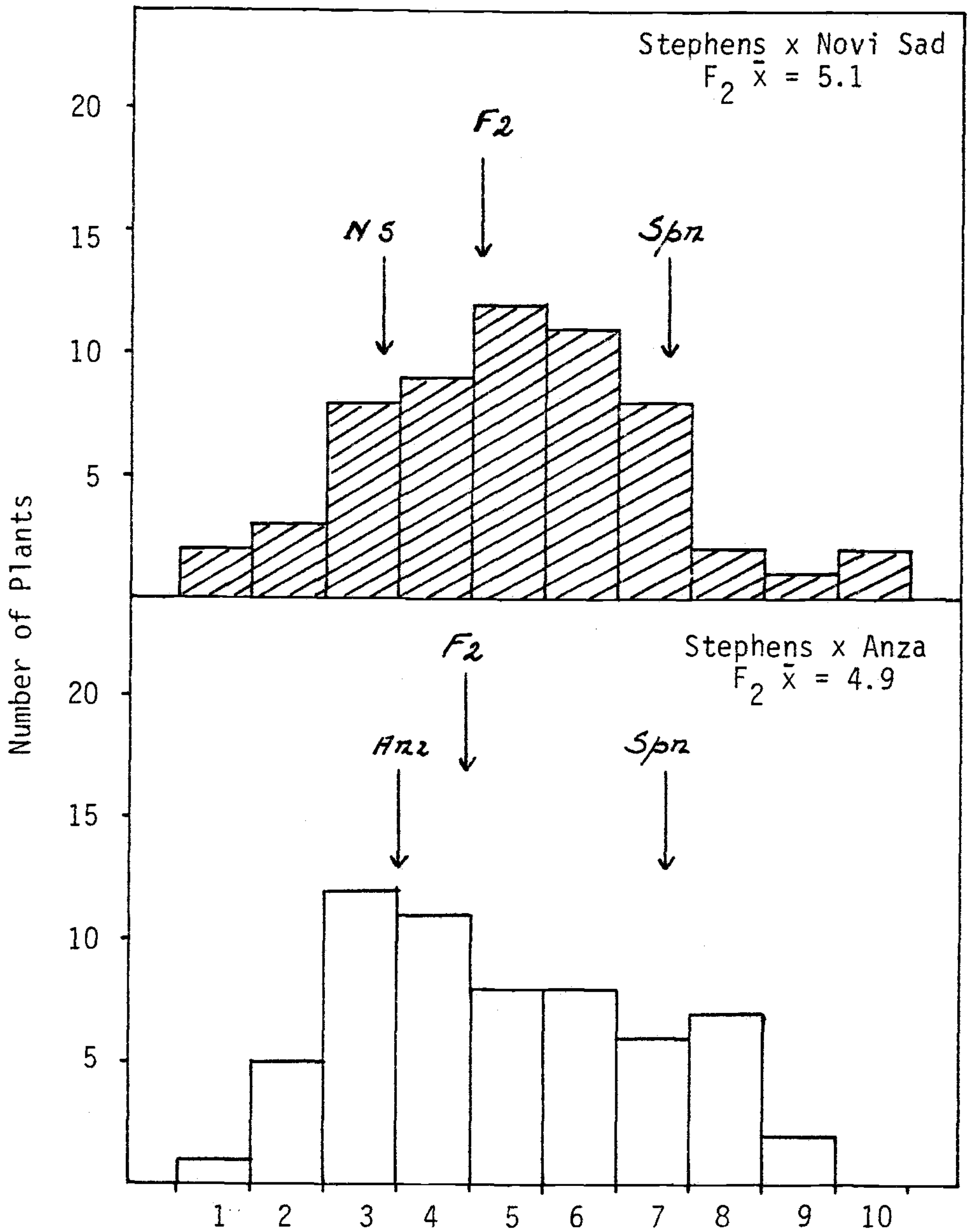


Figure 6. Frequency distributions for BYDV score from $F_2$ populations of crosses Stephens x Novi Sad and Stephens x Anza. Arrows indicate mean values ($F_2$, N = 60; parents, N = 30)

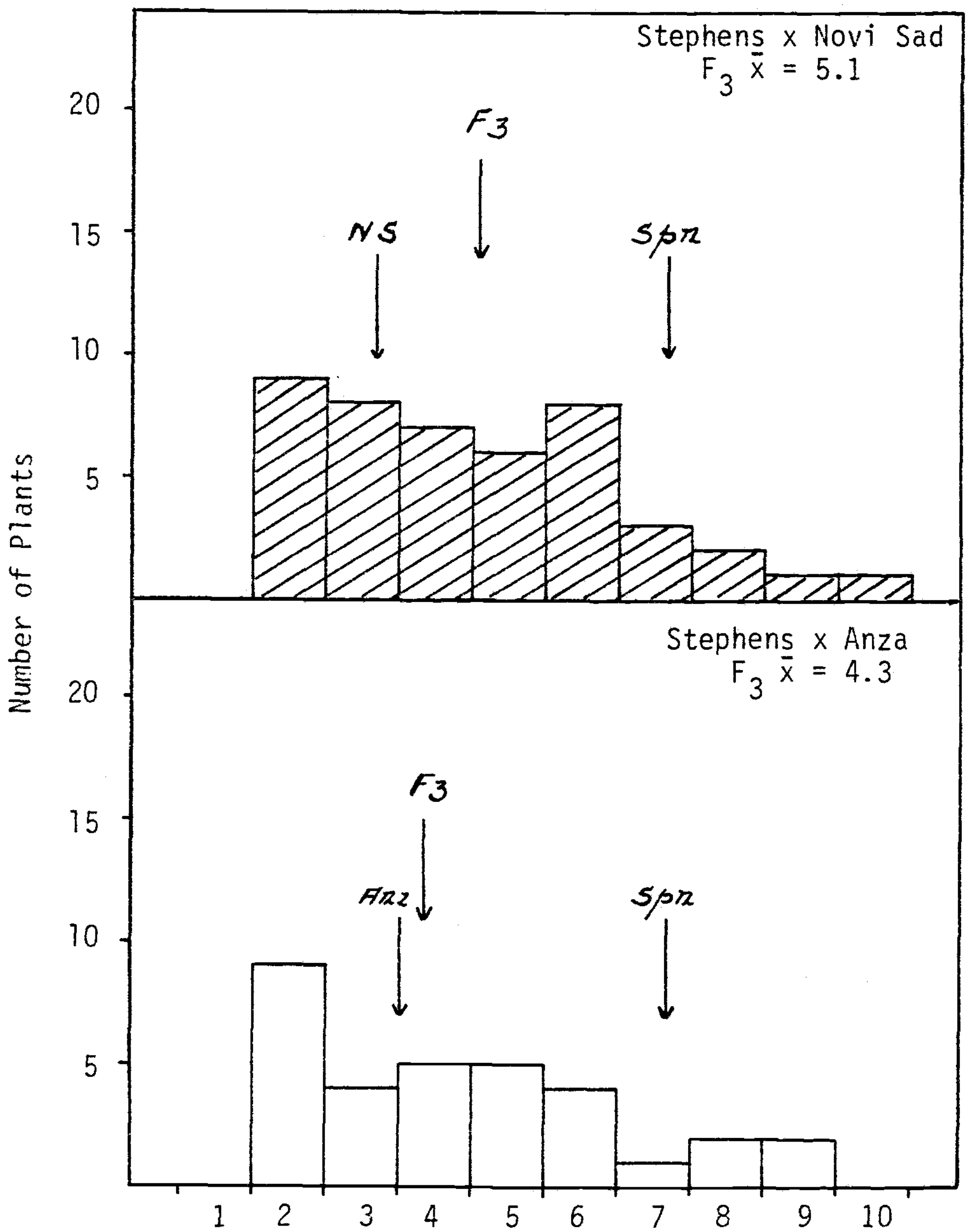


Figure 7. Frequency distributions for BYDV score from $F_3$ populations of crosses Stephens x Novi Sad and Stephens x Anza. Arrows indicate mean values ($F_3$, N = 40; parents, N = 30)

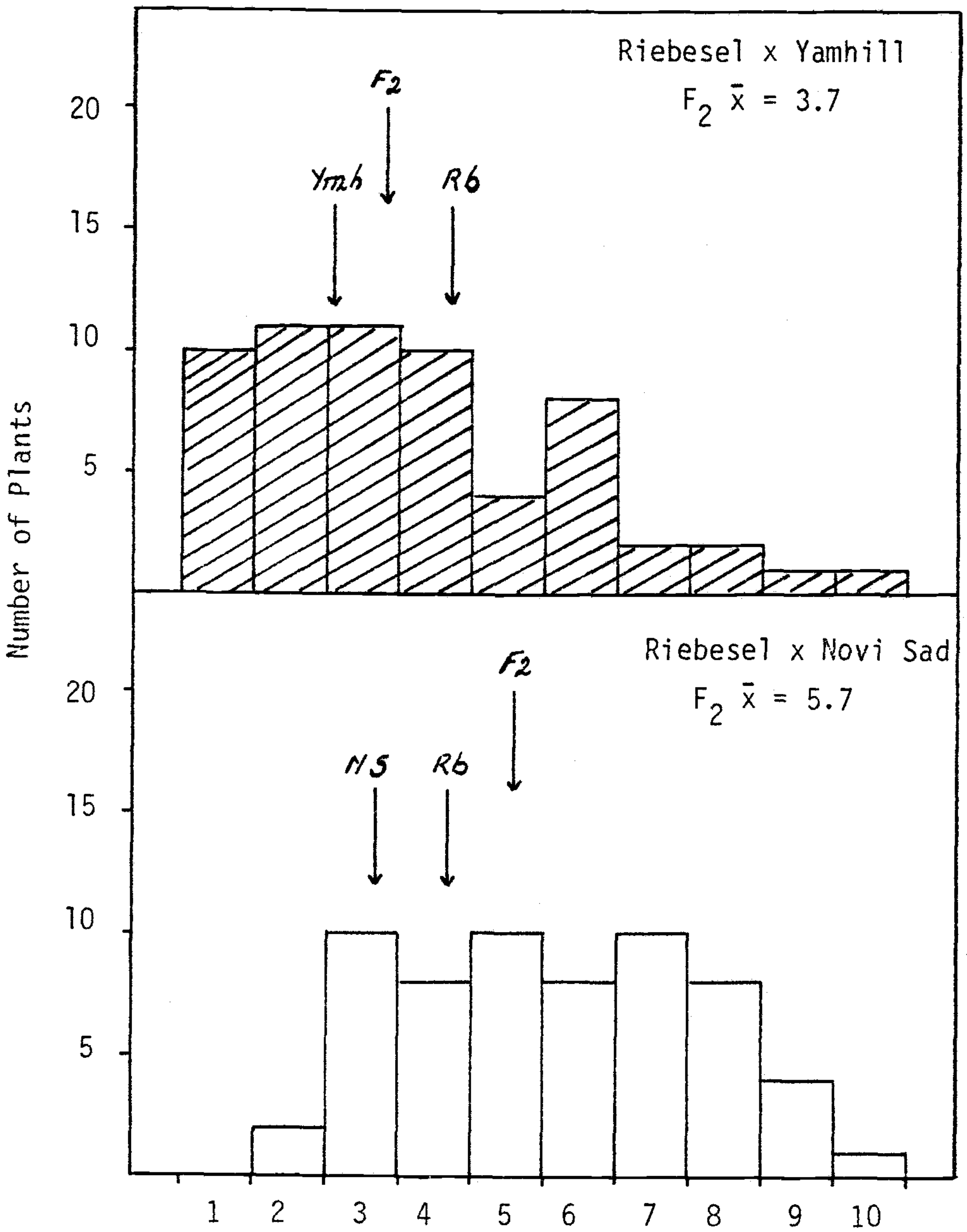


Figure 8. Frequency distributions for BYDV score from $F_2$ populations of crosses Riebesel x Yamhill and Riebesel x Novi Sad. Arrows indicate mean values ($F_2$, N = 60; parents, N = 30)

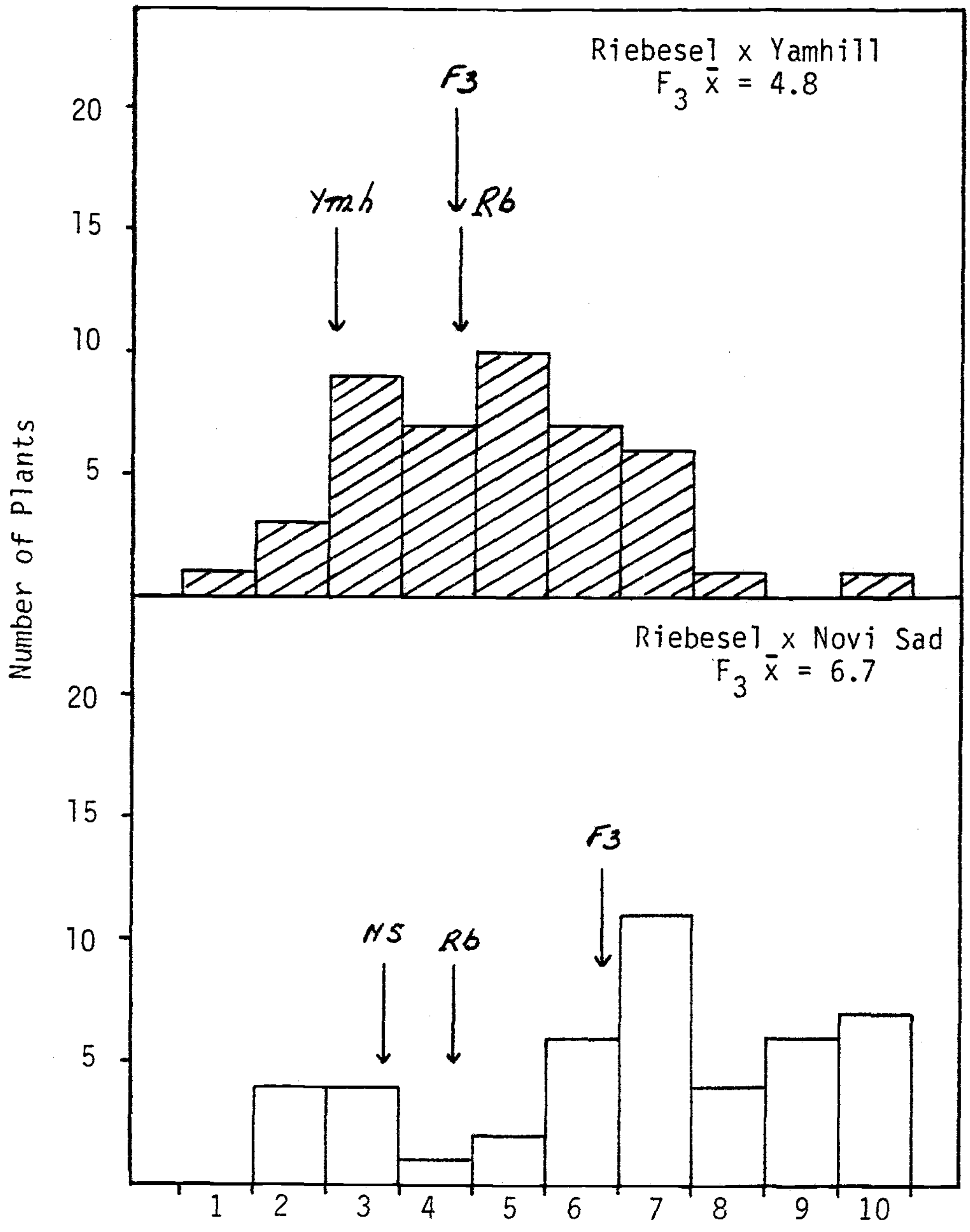


Figure 9. Frequency distributions for BYDV score from $F_3$ populations of crosses Riebesel x Yamhill and Riebesel x Novi Sad. Arrows indicate mean values ($F_3$, N = 45; parents, N = 30)

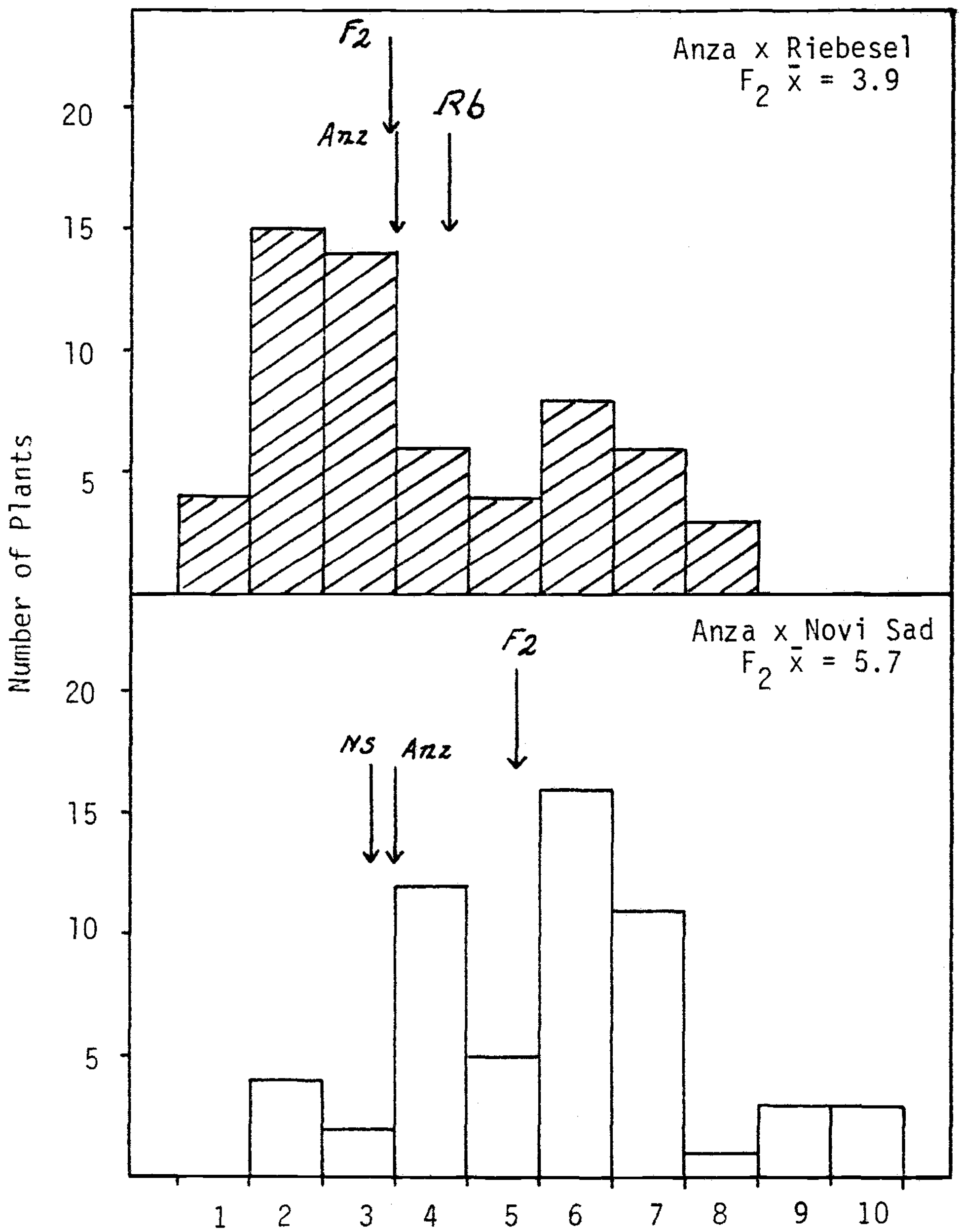


Figure 10. Frequency distributions for BYDV score from $F_2$ populations of crosses Anza x Riebesel and Anza x Novi Sad. Arrows indicate mean values ($F_2$, N = 60; parents, N = 30)

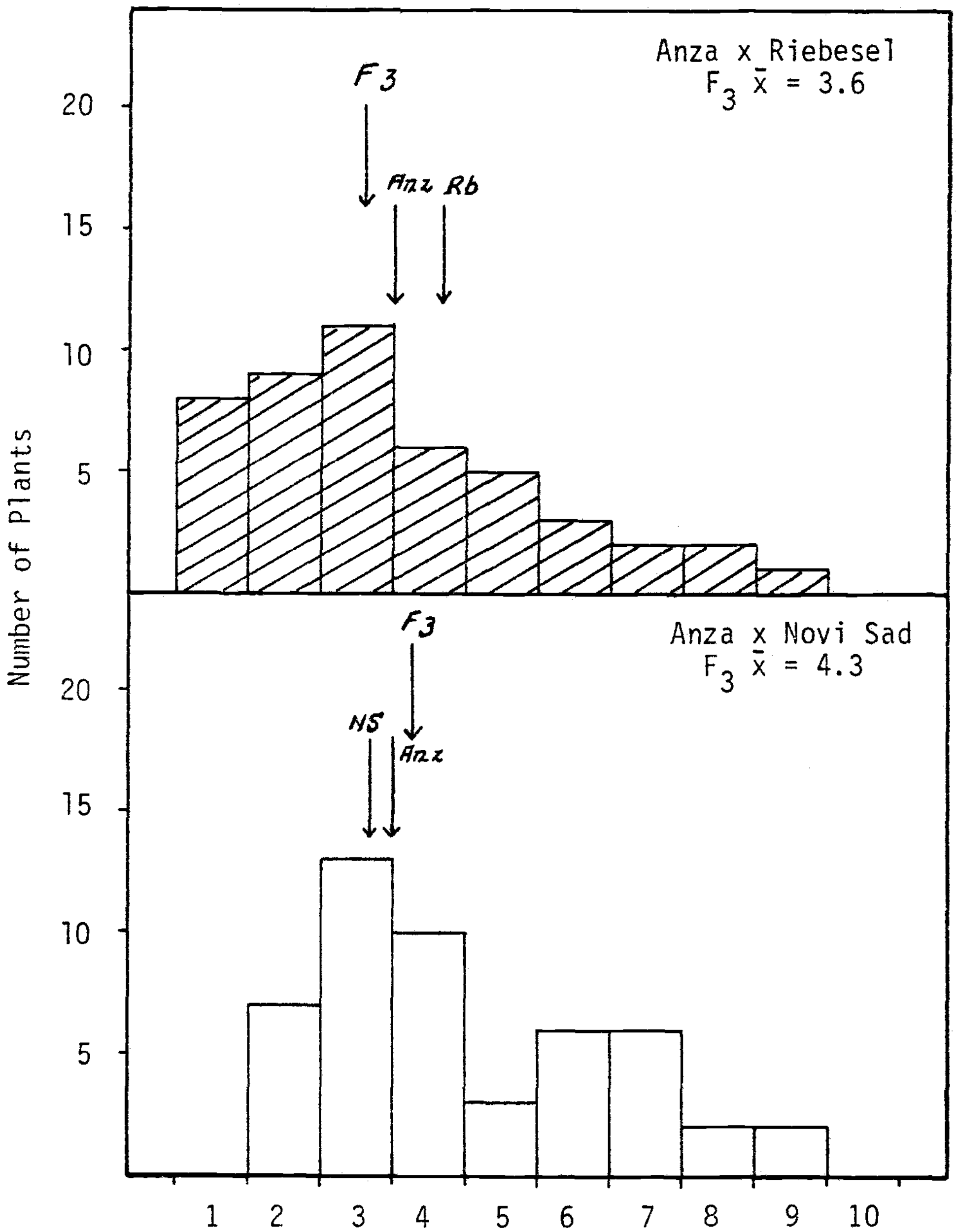


Figure 11. Frequency distributions for BYDV score from $F_3$ populations of crosses Anza x Riebesel and Anza x Novi Sad. Arrows indicate mean values ($F_3$, N = 45; parents, N = 30)

and Ymh/Anz are provided in Figures 12 and 13. It can be noted that the populations are strongly skewed toward the resistant side showing scores very close to the parents involved. This is particularly true for the cross Ymh/Anz. The $F_3$ distributions showed a wider segregation pattern than the $F_2$ and resemble a normal distribution curve.

The frequency distribution values for BYDV scores for parents, $F_1$, $F_2$, $F_3$ and reciprocal backcrosses are shown in Appendix Table 6. To determine if the nature of inheritance was qualitatively inherited, an arbitrary classification with 1-3 being considered as resistant and 4-10 as susceptible was established. In the $F_2$ generation, only two crosses (Spn/Rb and Spn/NS) had a chi square value and level of probability supporting the hypothesis that one major dominant gene for resistance was involved. Unfortunately, backcross data did not support this conclusion, thus the nature of resistance observed for the cultivars involved in this investigation was regarded as being quantitatively inherited and analyzed as such (Appendix Table 7).

## BYDV and Five Agronomic Traits

Observed mean squares from the analysis of variance for BYDV score, plant height, tiller number, plant weight, grain yield, kernel weight and harvest index are presented in Table 10. Significant differences for all traits measured were obtained for genotypes, between generations and within generations. For parents, differences were detected for all traits except grain yield. Differences in the $F_1$ and $F_2$ populations were observed for all traits other than grain yield and kernel weight. With the $F_3$, BYDV scores and kernel weight were the only traits where differences were not noted. For the two

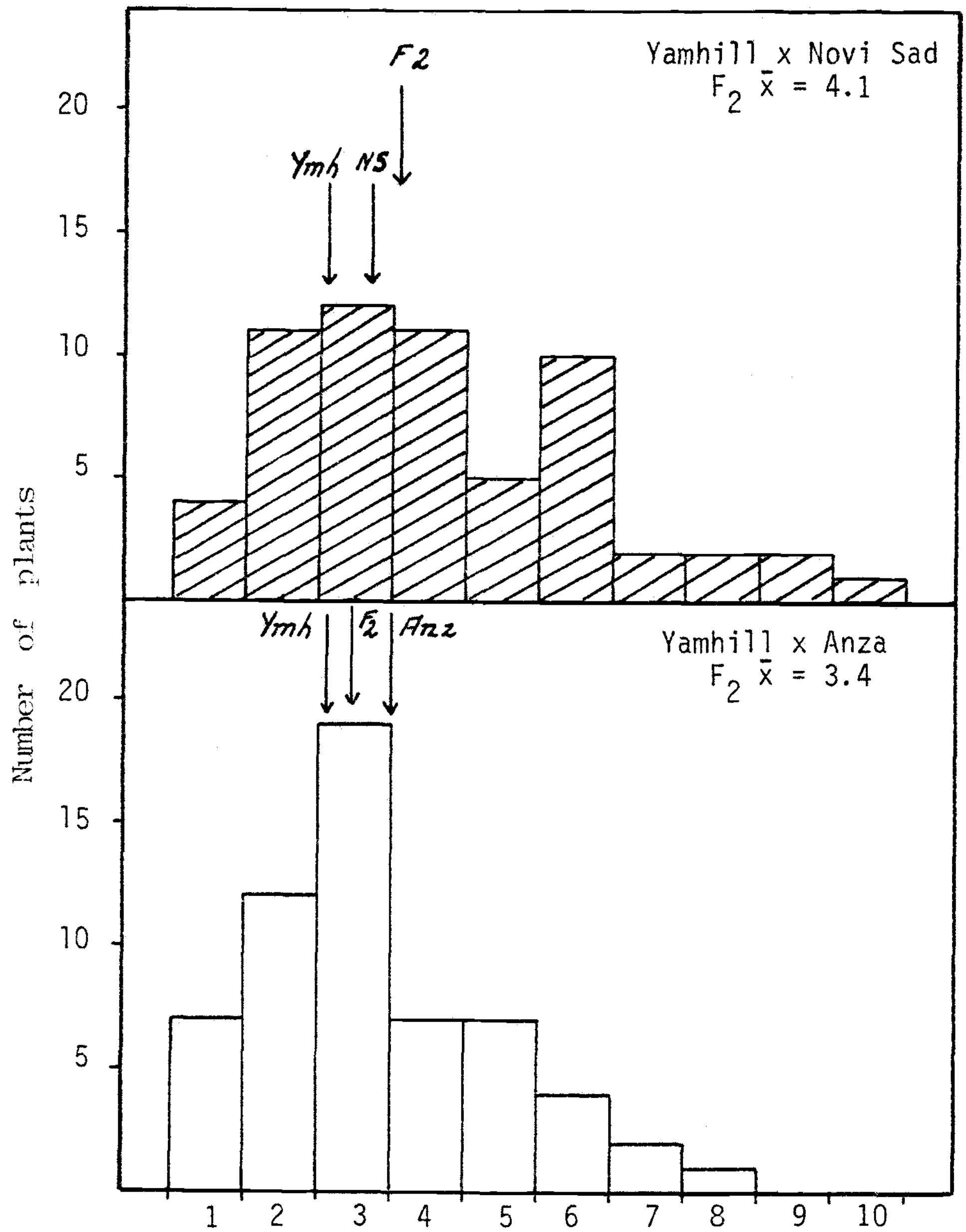


Figure 12. Frequency distributions for BYDV score from $F_2$ populations of crosses Yamhill x Novi Sad and Yamhill x Anza. Arrows indicate mean values ($F_2$, N = 60; parents, N = 30)

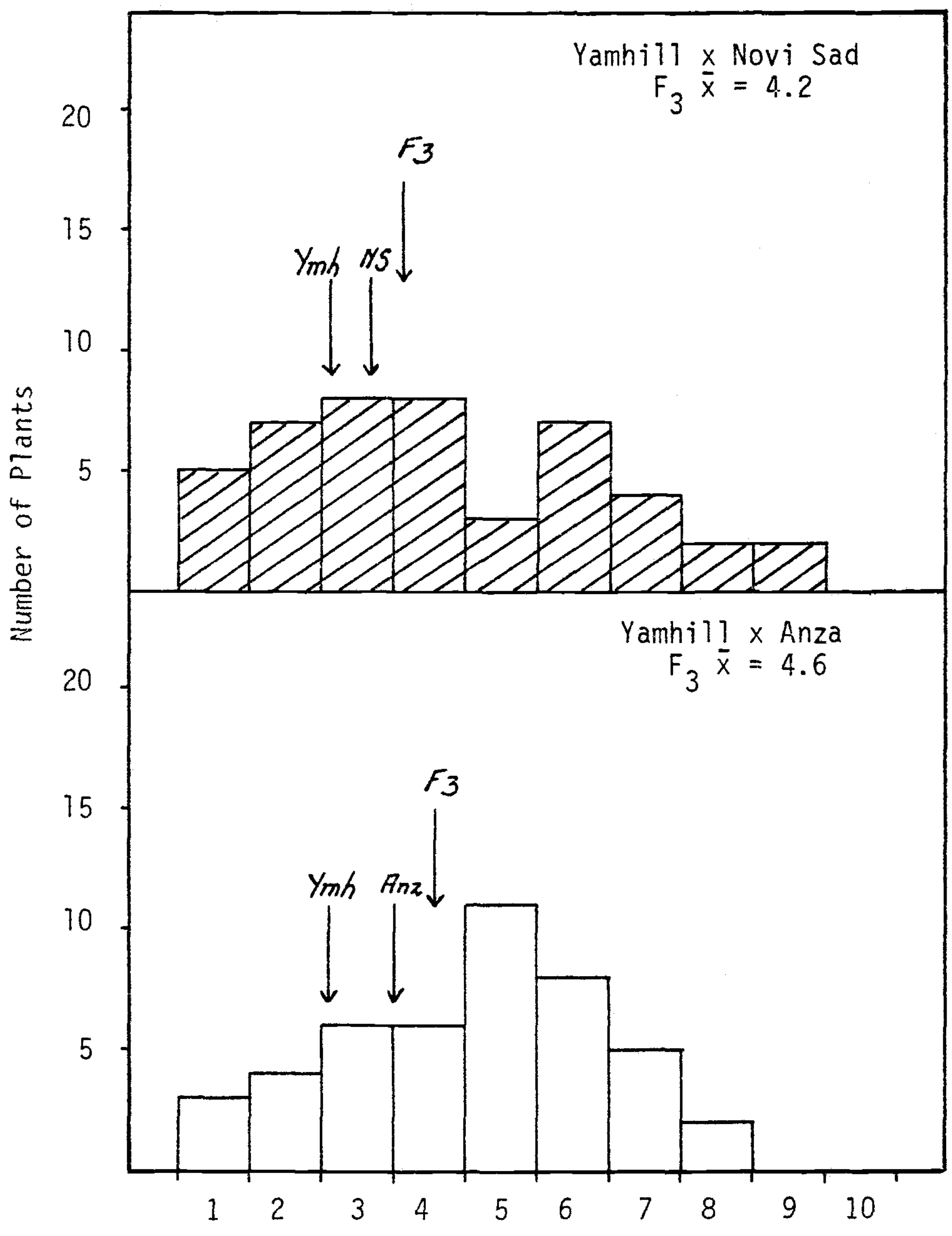


Figure 13. Frequency distributions for BYDV score from $F_3$ populations of crosses Yamhill x Novi Sad and Yamhill x Anza. Arrows indicate mean values ($F_3$, N = 45; parents, N = 30)

Table 10. Observed mean square values for BYDV score, plant height, tiller number, plant weight, grain yield, kernel weight and harvest index for parents, F1's, F2's, F3's and BC generations. Field Experiment.

| Source | DF | BYDV Score | Plant Height | Tiller Number | Plant Weight | Grain Yield | Kernel Weight | Harvest Index |
|---|---|---|---|---|---|---|---|---|
| Genotypes | 59 | 3.51** | 231** | 3.08** | 279** | 32.5** | 0.58** | 0.008** |
| Between Generations | 5 | 7.96** | 701** | 7.74** | 627** | 91.5** | 1.33** | 0.014** |
| Within Generations | 54 | 3.10** | 187** | 2.65* | 247** | 27.0** | 0.51** | 0.007** |
| Parents | 9 | 7.61** | 502** | 14.80** | 763** | 21.8 | 0.76** | 0.011** |
| $F_1$'s | 9 | 1.86* | 280** | 9.38** | 918** | 48.3 | 0.57 | 0.007** |
| $F_2$'s | 9 | 1.52** | 276** | 4.19** | 422** | 21.0** | 0.19* | 0.005** |
| $F_3$'s | 9 | 2.22 | 341** | 7.36** | 538** | 33.8** | 0.50 | 0.006** |
| BC-1 | 9 | 3.02** | 388** | 2.67** | 657** | 13.3** | 0.49** | 0.006** |
| BC-2 | 9 | 2.35** | 194** | 6.46** | 424** | 23.8** | 0.54** | 0.006** |

*,**: significant at the 0.10 and 0.01 levels of probability, respectively.

backcross populations, differences were found for all traits.

Multiple comparison using Tukey's test were conducted for each of the generations where significant differences at the .05 level of probability or above were found for the traits measured.

In Table 11, similar comparisons for the nonprotected and protected are made for the BYDV score. Nonprotected Stephens and Riebesel parents shared a common range; however, Riebesel was not significantly different from the remaining protected and nonprotected parents. For the $F_1$'s there was a difference between Spn/Rb and Rb/Anz. Three ranges can be observed for the $F_2$ populations with NS/Anz having the highest score and Rb/Ymh, Ymh/NS and Rb/Anz being in a separate group having the lowest BYDV score. Riebesel/Novi Sad was different from Ymh/NS and Rb/Anz for the $F_3$ generation. When the BC group 1 generation are noted, Rb/Ymh//Rb and Rb/Ymh//Ymh were significantly different from the other populations. No differences were found between BC group 2 comparisons for BYDV score.

For plant height (Table 12) differences were observed with the protected Riebesel and Yamhill being the tallest and the nonprotected semidwarf Anza being the shortest. In general, it can be observed that those parents which were protected were taller than the height level found in the unprotected treatment. In the $F_1$ generation, Rb/Anz was significantly different from the remaining crosses. Only one cross, NS/Anz, was significantly different in the $F_2$ generation as well. Riebesel/Anza was significantly taller than Rb/NS and Spn/Anz in the $F_3$. When the backcross group 1 (BC-1) generation is observed, the population falls into three ranges with Rb/Ymh//Rb being the tallest and Spn/Anz//Anz being the shortest. No differences were

Table 11. Observed BYDV Score Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment. (P = protected)

| Parents | Mean | Range |
|---|---|---|
| Stephens | 7.63 | a |
| Riebesel | 4.79 | ab |
| Stephens (P) | 4.20 | b |
| Anza | 3.97 | b |
| Novi Sad | 3.67 | b |
| Riebesel (P) | 3.10 | b |
| Yamhill | 3.07 | b |
| Novi Sad (P) | 1.90 | b |
| Anza (P) | 1.60 | b |
| Yamhill (P) | 1.50 | b |

HSD: 3.3

| $F_1$ | Mean | Range |
|---|---|---|
| Spn/Rb | 5.07 | a |
| Rb/N.S. | 4.33 | ab |
| Ymh/Anz | 3.93 | ab |
| Spn/N.S. | 3.50 | ab |
| N.S./Anz | 3.47 | ab |
| Rb/Ymh | 3.27 | ab |
| Ymh/N.S. | 3.26 | ab |
| Spn/Ymh | 3.17 | ab |
| Spn/Anz | 2.53 | ab |
| Rb/Anz | 2.46 | b |

HSD: 2.57

[1]0.05 probability level.

Table 11. (continued) Observed BYDV Score Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment. (P = protected)

| $F_2$ | Mean | Range |
|---|---|---|
| N.S./Anz | 6.24 | a |
| Rb/N.S. | 5.95 | ab |
| Spn/N.S. | 5.30 | abc |
| Spn/Rb | 5.15 | abc |
| Spn/Anz | 4.90 | abc |
| Ymh/Anz | 4.72 | abc |
| Spn/Ymh | 4.47 | bc |
| Rb/Ymh | 4.32 | c |
| Ymh/N.S. | 4.30 | c |
| Rb/Anz | 4.17 | c |

HSD: 1.61

| $F_3$ | Mean | Range |
|---|---|---|
| Rb/N.S. | 6.73 | a |
| Spn/Rb | 5.44 | ab |
| Rb/Ymh | 4.76 | ab |
| Ymh/Anz | 4.60 | ab |
| Spn/N.S. | 4.53 | ab |
| Spn/Ymh | 4.36 | ab |
| N.S./Anz | 4.31 | ab |
| Spn/Anz | 4.29 | ab |
| Ymh/N.S. | 4.16 | b |
| Rb/Anz | 3.60 | b |

[1]0.05 probability level.

HSD: 3.04

Table 11. (continued) Observed BYDV Score Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment. (P = protected)

| BC-1 | Mean | Range |
|---|---|---|
| Spn/Anz//Anz | 6.34 | a |
| Spn/Rb//Spn | 5.64 | ab |
| Spn/Rb//Spn | 5.11 | ab |
| Spn/N.S.//Spn | 4.73 | ab |
| Spn/N.S.//N.S. | 4.36 | ab |
| Spn/Ymh//Spn | 4.29 | ab |
| Spn/Anz//SPn | 4.24 | ab |
| Spn/Ymh//Ymh | 4.22 | ab |
| Rb/Ymh//Rb | 3.15 | b |
| Rb/Ymh//Ymh | 3.11 | b |

[1]0.05 probability level. HSD: 3.13

Table 12. Observed plant height in cm using Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment. (P = protected)

| Parents | Mean | Range |
|---|---|---|
| Riebesel (P) | 117 | a |
| Yamhill (P) | 110 | ab |
| Novi Sad (P) | 102 | abc |
| Yamhill | 100 | abc |
| Riebesel | 98 | abcd |
| Stephens (P) | 97 | bcd |
| Novi Sad | 95 | bcd |
| Anza (P) | 92 | bcd |
| Stephens | 81 | cd |
| Anza | 80 | d |

HSD: 19.6

| $F_1$ | Mean | Range |
|---|---|---|
| Rb/Anz | 125 | a |
| Rb/Ymh | 110 | b |
| Ymh/N.S. | 109 | b |
| Ymh/Anz | 107 | b |
| Rb/N.S. | 106 | b |
| Spn/Rb | 105 | b |
| Spn/Ymh | 104 | b |
| Spn/N.S. | 102 | b |
| Spn/Anz | 102 | b |
| N.S./Anz | 101 | b |

[1]0.05 probability level. HSD: 12.8

Table 12. (continued) Observed plant height Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment. (P = protected)

| $F_2$ | Mean | Range |
|---|---|---|
| Rb/Anz | 108 | a |
| Rb/Ymh | 100 | a |
| Ymh/N.S. | 98 | a |
| Spn/Ymh | 97 | a |
| Ymh/Anz | 96 | ab |
| Spn/Rb | 95 | ab |
| Spn/N.S. | 95 | ab |
| Rb/N.S. | 93 | ab |
| Spn/Anz | 90 | ab |
| N.S./Anz | 80 | b |

HSD: 16.3

| $F_3$ | Mean | Range |
|---|---|---|
| Rb/Anz | 110 | a |
| Rb/Ymh | 106 | ab |
| Spn/Rb | 103 | abc |
| Ymh/N.S. | 97 | abc |
| Spn/N.S. | 97 | abc |
| Ymh/Anz | 96 | abc |
| N.S./Anz | 92 | abc |
| Spn/Ymh | 92 | abc |
| Rb/N.S. | 88 | bc |
| Spn/Anz | 85 | c |

[1]0.05 probability level.

HSD: 20.7

Table 12. (continued) Observed plant height Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment. (P = protected)

| BC-1 | Mean | Range |
|---|---|---|
| Rb/Ymh//Rb | 115 | a |
| Rb/Ymh//Ymh | 106 | ab |
| Spn/Ymh//Ymh | 101 | abc |
| Spn/Rb//Spn | 96 | bcd |
| Spn/Rb//Rb | 96 | bcd |
| Spn/Anz//Spn | 96 | bcd |
| Spn/Ymh//Spn | 96 | bcd |
| Spn/N.S.//Spn | 95 | bcd |
| Spn/N.S.//N.S. | 88 | cd |
| Spn/Anz//Anz | 83 | d |

[1]0.05 probability level. HSD: 17.9

detected in the BC-2 generation for plant height.

In Table 13, a comparison is provided for tiller number. Two ranges were found with nonprotected Novi Sad and Riebesel being significantly different from the other treatments. No differences were observed in the $F_1$, $F_2$, $F_3$ and BC group populations.

Since significant differences for plant weight were observed only in the $F_2$ and $F_3$ generations, Table 14 provides only this information. Rb/Anz and Spn/NS were found to be different from NS/Anz for the $F_2$ generation. Only Spn/Rb was significantly lower in plant weight in the $F_3$.

Table 15 includes comparisons for grain yield for the parents, $F_3$ and BC-2, as these were the only generations where significant differences were observed. Only nonprotected Riebesel was found to have a significantly lower yield when compared to the other parents. In the $F_3$ generation, Spn/Rb and Rb/NS yielded significantly less than the other crosses. The backcross Rb/Anz//Rb was found to be significantly lower in yield than the other BC-2 crosses.

When kernel weight is considered, three groups emerge (Table 16). Protected Stephens had the highest value of 5.66 while nonprotected Riebesel was the lowest at 3.73. Again, in all comparisons, the protected parent had a higher kernel weight than did the nonprotected parents. For the $F_2$, Spn/Anz had the higher weight with Rb/Ymh being significantly lower. Spn/Ymh had a significantly higher kernel weight than did Rb/Ymh and Ymh/NS in the $F_3$ generation. Two groups based on levels of significance were noted in the BC-1 and BC-2 groups, with BC-1 Spn/Rb//Spn being the highest with two ranges being identified with some overlapping. In the BC-2 group, Rb/Anz//Rb was

Table 13. Observed tiller number Tukey[1] ranges for parents. Field experiment. (P = protected)

| Parents | Mean | Range |
|---|---|---|
| Anza (P) | 13.2 | a |
| Anz | 11.0 | ab |
| Novi Sad (P) | 9.9 | ab |
| Riebesel (P) | 9.8 | ab |
| Yamhill (P) | 9.4 | ab |
| Stephens (P) | 9.3 | ab |
| Stephens | 9.0 | ab |
| Yamhill | 8.1 | ab |
| Novi Sad | 7.8 | b |
| Riebesel | 7.5 | b |

HSD: 4.69

[1]0.05 probability level

Table 14. Observed plant weight Tukey[1] ranges for $F_2$ and $F_3$ generations. Field experiment. (P = protected)[3]

| $F_2$ | Mean | Range |
|---|---|---|
| Rb/Anz | 65.6 | a |
| Spn/N.S. | 60.3 | a |
| Ymh/Anz | 56.2 | ab |
| Rb/Ymh | 55.8 | ab |
| Ymh/N.S. | 55.5 | ab |
| Spn/Ymh | 53.9 | ab |
| Spn/Rb | 53.0 | ab |
| Rb/N.S. | 51.9 | ab |
| Spn/Anz | 48.9 | ab |
| N.S./Anz | 33.4 | b |

HSD: 26.4

| $F_3$ | Mean | Range |
|---|---|---|
| Rb/Anz | 65.3 | a |
| Rb/Ymh | 61.5 | ab |
| Spn/Ymh | 59.8 | ab |
| spn/N.S. | 56.5 | ab |
| Ymh/N.S. | 52.6 | ab |
| N.S./Anz | 45.7 | ab |
| Ymh/Anz | 44.4 | ab |
| Spn/Anz | 43.0 | ab |
| Rb/N.S. | 39.7 | ab |
| Spn/Rb | 37.4 | b |

HSD: 27.4

[1]0.05 probability level.

Table 15. Observed grain yield Tukey[1] ranges for parents, $F_3$'s and backcross generations. Field experiment. (P = protected)

| Parents | Mean | Range |
|---|---|---|
| Yamhill (P) | 23.8 | a |
| Anza (P) | 20.5 | ab |
| Novi Sad (P) | 20.3 | ab |
| Yamhill | 18.3 | ab |
| Stephens (P) | 17.2 | ab |
| Novi Sad | 17.1 | ab |
| Riebesel (P) | 16.0 | ab |
| Stephens | 13.6 | ab |
| Anza | 12.2 | ab |
| Riebesel | 9.6 | b |

HSD: 11.9

| $F_3$ | Mean | Range |
|---|---|---|
| Spn/Ymh | 19.7 | a |
| Rb/Anz | 16.1 | asb |
| Ymh/N.S. | 14.4 | ab |
| Spn/Anz | 14.2 | ab |
| Spn/N.S. | 14.0 | ab |
| Ymh/Anz | 13.9 | ab |
| Rb/Ymh | 13.6 | ab |
| N.S./Anz | 13.1 | ab |
| Spn/Rb | 8.4 | b |
| Rb/N.S. | 8.2 | b |

[1]0.05 probability level. HSD: 9.9

Table 15. (continued) Observed grain yield Tukey[1] ranges for parents, $F_3$'s and backcross generations. Field experiment. (P = protected)

| BC-2 | Mean | Range |
|---|---|---|
| N.S./Anz//N.S. | 18.9 | a |
| N.S./Anz//Anz | 17.5 | a |
| Ymh/N.S.//N.S. | 14.5 | ab |
| Ymh/Anz//Anz | 14.1 | ab |
| Rb/N.S.//N.S. | 14.1 | ab |
| Rb/Anz//Anz | 13.6 | ab |
| Ymh/N.S.//Ymh | 13.6 | ab |
| Rb/N.S.//N.S. | 11.8 | ab |
| Ymh/Anz//Ymh | 11.4 | ab |
| Rb/Anz//Rb | 9.2 | b |

[1]0.05 probability level. HSD: 8.2

Table 16. Observed kernel weight Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment. (P = protected)

| Parents | Mean | Range |
|---|---|---|
| Stephens (P) | 5.66 | a |
| Yamhill (P) | 4.77 | b |
| Stephens | 4.62 | bc |
| Novi Sad (P) | 4.57 | bc |
| Riebesel (P) | 4.55 | bc |
| Anza (P) | 4.54 | bc |
| Yamhill | 4.45 | bc |
| Novi Sad | 4.31 | bcd |
| Anza | 4.02 | cd |
| Riebesel | 3.73 | d |

HSD: 0.70

| $F_2$ | Mean | Range |
|---|---|---|
| Spn/Anza | 4.67 | a |
| Spn/Ymh | 4.50 | ab |
| N.S./Anz | 4.34 | ab |
| Ymh/N.S. | 4.29 | ab |
| Spn/N.S. | 4.27 | ab |
| Rb/Anz | 4.25 | ab |
| Rb/N.S. | 4.24 | ab |
| Spn/Rb | 4.24 | ab |
| Ymh/Anz | 3.89 | ab |
| Rb/Ymh | 3.80 | b |

[1]0.05 probability level.

HSD: 0.83

Table 16. (continued) Observed kernel weight Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment. (P = protected)

| $F_3$ | Mean | Range |
|---|---|---|
| Spn/Ymh | 5.33 | a |
| Spn/N.S. | 4.53 | ab |
| Spn/Anz | 4.35 | ab |
| Ymh/Anz | 4.33 | ab |
| Rb/Anz | 4.23 | a |
| N.S./Anz | 4.14 | ab |
| Rb/N.S. | 4.11 | ab |
| Spn/Rb | 4.08 | ab |
| Rb/Ymh | 4.03 | b |
| Ymh/N.S. | 3.85 | b |

HSD: 1.29

| BC-1 | Mean | Range |
|---|---|---|
| Spn/Rb//Spn | 4.99 | a |
| Spn/Rb//Rb | 4.96 | a |
| Spn/Anz//Spn | 4.95 | a |
| Spn/N.S.//Spn | 4.58 | ab |
| Spn/Ymh//Ymh | 4.30 | ab |
| Rb/Ymh//Ymh | 4.27 | ab |
| Spn/N.S.//N.S. | 4.16 | b |
| Spn/Rb//Rb | 4.12 | b |
| Spn/Anz//Anz | 4.00 | b |
| Rb/Ymh//Ymh | 3.99 | b |

[1]0.05 probability level.

HSD: 0.79

Table 16. (continued) Observed kernel weight Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment. (P = protected)

| BC-2 | Mean | Range |
|---|---|---|
| Rb/N.S.//N.S. | 5.11 | a |
| N.S.//Anz//Anz | 4.77 | ab |
| N.S./Anz//N.S. | 4.59 | ab |
| Ymh/N.S.//Ymh | 4.26 | ab |
| Rb/Anz//Anz | 4.21 | ab |
| Rb/N.S.//Rb | 4.10 | ab |
| Ymh/Anz//Anz | 4.04 | ab |
| Ymh/N.S.//N.S. | 4.01 | ab |
| Ymh/Anz//Ymh | 3.92 | ab |
| Rb/Anz//Rb | 3.73 | b |

[1]0.05 probability level. HSD: 1.35

significantly lower than the other backcrosses.

Significant differences were found for all generations when harvest index is considered (Table 17). For the parents, protected and nonprotected Riebesel were separated into one range in contrast with the other treatments and parents. Three groups were noted in the $F_1$ generation, Rb/Ymh, Ymh/NS and Spn/Rb being the lowest. In the $F_2$, six groups were observed with Spn/Anz being the highest and three crosses involving Riebesel (Rb/Anz, Rb/NS and Rb/Ymh) having the lowest harvest index values. Riebesel was also one of the parents in the four lowest $F_3$ crosses. In this generation, Spn/Ymh had the highest harvest index. For the BC-1 the highest harvest indexes were observed where Stephens was involved and those involving Riebesel were the lowest. In BC-2, the highest harvest indexes were found for crosses where Anza was used. Again, where Riebesel was the recurrent parent, the lowest harvest indexes were noted.

## Relationship between Barley Yellow Dwarf Virus Score and Selected Agronomic Traits

To determine the possible relationships between the BYDV score and selected agronomic traits correlations and regression values were obtained. For the regression analysis, BYDV score was considered as the independent variable and the agronomic traits as the dependent variables. The means, correlations, coefficient of differentiation, regression equation and t values are provided in Table 18 for the five nonprotected parents involving the six attributes measured.

In looking at plant height, significant negative correlations were observed with all cultivars with the exception of Yamhill where the correlation was also negative ($r = -0.25$) but not significant.

Table 17. Observed harvest index Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment. (P = protected)

| Parents | Mean | Range |
|---|---|---|
| Anza (P) | 0.344 | a |
| Novi Sad | 0.342 | a |
| Anza | 0.339 | a |
| Novi Sad (P) | 0.331 | a |
| Yamhill (P) | 0.303 | a |
| Yamhill | 0.295 | a |
| Stephens (P) | 0.283 | ab |
| Stephens | 0.277 | ab |
| Riebesel | 0.195 | b |
| Riebesel (P) | 0.194 | b |

HSD: 0.091

| $F_1$ | Mean | Range |
|---|---|---|
| Spn/Anz | 0.335 | a |
| N.S./Anz | 0.319 | ab |
| Ymh/Anz | 0.308 | ab |
| Spn/N.S. | 0.282 | abc |
| Spn/Ymh | 0.273 | abc |
| Rb/Anz | 0.253 | abc |
| Rb/N.S. | 0.251 | abc |
| Rb/Ymh | 0.217 | bc |
| Ymh/N.S. | 0.207 | bc |
| Spn/Rb | 0.190 | c |

HSD: 0.117

[1]0.05 probability level.

Table 17. (continued) Observed harvest index Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment.[1] (P = protected)

| $F_2$ | Mean | Range |
|---|---|---|
| Spn/Anz | 0.286 | a |
| Ymh/Anz | 0.272 | b |
| Spn/Ymh | 0.262 | c |
| Ymh/N.S. | 0.257 | cd |
| N.S./Anz | 0.249 | d |
| Spn/N.S. | 0.229 | e |
| Spn/Rb | 0.202 | f |
| Rb/Anz | 0.201 | f |
| Rb/Anz | 0.201 | fg |
| Rb/N.S. | 0.192 | g |
| Rb/Ymh | 0.156 | g |

HSD: 0.093

| $F_3$ | Mean | Range |
|---|---|---|
| Spn/Ymh | 0.317 | a |
| Ymh/Anz | 0.298 | ab |
| Spn/Anz | 0.297 | ab |
| N.S./Anz | 0.282 | abc |
| Ymh/N.S. | 0.244 | abcd |
| Spn/N.S. | 0.242 | abcd |
| Rb/Anz | 0.225 | bcd |
| Spn/Rb | 0.211 | cd |
| Rb/Ymh | 0.208 | cd |
| Rb/N.S. | 0.178 | d |

[1]0.05 probability level.

HSD: 0.84

Table 17. (continued) Observed harvest index Tukey[1] ranges for parents, $F_1$'s, $F_2$'s, $F_3$'s and backcross generations. Field experiment. (P = protected)

| BC-1 | Mean | Range |
|---|---|---|
| Spn/Ymh//Spn | 0.293 | a |
| Spn/Anz//Spn | 0.290 | a |
| Spn/Ymh//Ymh | 0.277 | b |
| Spn/Anz//Anz | 0.258 | c |
| Spn/N.S.//Spn | 0.238 | d |
| Rb/Ymh//Ymh | 0.227 | e |
| Spn/N.S.//N.S. | 0.225 | ef |
| Spn/Rb//Spn | 0.222 | f |
| Spn/Rb//Rb | 0.200 | g |
| Rb/Ymh//Rb | 0.141 | h |

HSD: 0.070

| BC-2 | Mean | Range |
|---|---|---|
| N.S./Anz//Anz | 0.311 | a |
| Ymh/Anz//Anz | 0.294 | ab |
| N.S./Anz//N.S. | 0.259 | ab |
| Rb/N.S.//N.S. | 0.253 | ab |
| Ymh/Anz//Ymh | 0.246 | b |
| Ymh/N.S.//N.S. | 0.240 | bc |
| Ymh/N.S.//Ymh | 0.239 | bc |
| Rb/Anz//Anz | 0.238 | bc |
| Rb/N.S.//Rb | 0.178 | cd |
| Rb/Anz//Rb | 0.158 | d |

[1]0.05 probability level.

HSD: 0.064

Table 18. Correlation coefficients between BYDV score and plant height, tiller number, plant weight, grain yield, kernel weight and harvest index for the parental cultivars.

| Parents | Traits | Trait Means | r | Regression Equation |
|---|---|---|---|---|
| Stephens | Plant Height | 81.2 | -0.90** | y = 123.63 - 5.55x |
| Riebesel | | 97.8 | -0.51** | y = 110.21 - 2.41x |
| Yamhill | | 100.0 | -0.25 | y = 103.38 - 1.10x |
| Novi Sad | | 95.3 | -0.78** | y = 109.75 - 5.70x |
| Anza | | 80.1 | -0.58** | y = 91.37 - 2.53x |
| Stephens | Tiller Number | 8.97 | -0.53** | y = 15.47 - 0.85x |
| Riebesel | | 7.47 | -0.37* | y = 9.74 - 0.51x |
| Yamhill | | 8.10 | 0.14 | y = 7.04 + 0.35x |
| Novi Sad | | 7.83 | -0.49** | y = 11.11 - 1.29x |
| Anza | | 10.98 | -0.58** | y = 15.85 - 1.35x |
| Stephens | Plant Weight | 46.3 | -0.77** | y = 137.68 - 11.97x |
| Riebesel | | 48.2 | -0.49** | y = 75.48 - 5.68x |
| Yamhill | | 61.7 | -0.06 | y = 65.31 - 1.16x |
| Novi Sad | | 48.2 | -0.64** | y = 73.67 - 10.05x |
| Anza | | 50.4 | -0.59** | y = 79.44 - 7.98x |

**,*: significant at the one and five percent probability levels, respectively.

Table 18. (continued)

| Parents | Traits | Trait Means | r | Regression Equation |
|---|---|---|---|---|
| Stephens | Grain | 13.63 | -0.77** | y = 45.04 - 4.11x |
| Riebesel | Yield | 9.61 | -0.53** | y = 17.41 - 1.52x |
| Yamhill | | 18.27 | -0.08 | y = 19.77 - 0.49x |
| Novi Sad | | 17.17 | -0.68** | y = 28.67 - 4.49x |
| Anza | | 12.22 | -0.53** | y = 25.25 - 2.54x |
| Stephens | Kernel | 4.62 | -0.72** | y = 6.867 - 0.296x |
| Riebesel | Weight | 3.73 | -0.36* | y = 4.309 - 0.365x |
| Yamhill | | 4.45 | -.46* | y = 4.812 - 0.123x |
| Novi Sad | | 4.31 | -0.70** | y = 5.101 - 0.314x |
| Anza | | 4.02 | -0.61** | y = 4.73 - 0.195x |
| Stephens | Harvest | 0.277 | -0.40* | y = 0.3743 - 0.0127x |
| Riebesel | Index | 0.195 | -0.10 | y = 0.2136 - 0.0039x |
| Yamhill | | 0.295 | -0.17 | y = 0.3115 - 0.005x |
| Novi Sad | | 0.342 | -0.70** | y = 0.428 - 0.034x |
| Anza | | 0.339 | -0.22 | y = 0.473 - 0.195x |

**,*: significant at the one and five percent probability levels, respectively.

With regards to the regression values, the greatest response with BYDV score was found for Novi Sad (b = -5.70) followed by Stephens (b = -5.55).

For tiller number, significant negative correlations were detected for four of the cultivars with again Yamhill being the exception where a positive correlation of r = 0.14 was noted. Anza and Novi Sad were found to have the largest reductions (b = -1.35 and b = -1.29 respectively) when the regression values are considered. Yamhill responded in a positive manner (b = 0.35).

With regards to plant weight, again Yamhill was the only parent where a significantly negative correlation was not found (r = -0.06). The regression equation suggests that the largest negative response was noted for Stephens (b = -11.97) followed by Novi Sad (b = -10.05).

The correlation values obtained between BYDV score and grain yield showed a similar pattern as with the previous traits. Significantly negative r values were noted for all parents except Yamhill (r = -0.08). Regression values showed a negative response with the highest values being detected for Novi Sad (b = -4.49) and Stephens (b = -4.11).

When kernel weight is considered, significant and negative correlations can be observed for all parents. The largest negative response as indicated by the regression analysis was with Riebesel (b = -0.365) followed by Novi Sad (b = -0.314).

For harvest index only Novi Sad (r = -0.70) and Stephens (r = -0.40) reflect significantly negative correlation values. The largest changes as reflected by the regression equation was with Anza (b = -0.195).

Similar information regarding the relationship between BYDV score and the six attributes evaluated for the 10 $F_1$ crosses can be found in Table 19.

All correlation values with plant height were negative with significant differences being noted for all crosses except Spn/NS and Rb/Ymh. The regression equation also featured all negative responses with the largest decreases noted for Rb/Anz (b = -4.86) and Rb/NS (b = -3.96).

Negative correlations were also observed for tiller number and BYDV score with Spn/Ymh, Rb/NS and Rb/Anz resulting in values which were significant (r = -0.61, r = -0.47 and r = -0.42, respectively). For the regression values the $F_1$ Spn/NS was positive (b = 0.30) the remaining $F_1$ populations were negative.

Plant weight and BYDV score correlations were negative for all $F_1$ crosses with Spn/Rb, Spn/Ymh, Rb/Ymh, Rb/NS, Rb/Anz and Ymh/Anz being significantly different. Spn/Ymh (b = -13.21) and Rb/Anz (b = -12.96) represented the largest negative change with regard to regression equation.

The correlation values noted for grain yield were also negative for all $F_1$ populations. Spn/Ymh (r = -0.73) and Ymh/NS (r = -0.71) exhibited the largest negative associations. A similar result can be noted from the regression values with the largest negative relationships again being noted for Spn/Ymh (b = -4.15) and Ymh/NS (b = -4.09).

For kernel weight the only positive correlation was for Ymh/NS (r = 0.22) all other associations were negative with Spn/Ymh (r = -0.79) and Ymh/Anz (r = -0.76) showing the largest values. A similar trend

Table 19. Correlation coefficents between BYDV score and plant height, tiller number, plant weight, grain yield, kernel weight and harvest index for $F_1$ crosses.

| Crosses | Traits | Trait Means | r | Regression Equation |
|---|---|---|---|---|
| Spn/Rb | Plant Height | 105.4 | -0.68** | y = 119.50 - 2.78x |
| Spn/Ymh | | 104.2 | -0.70** | y = 116.49 - 3.87x |
| Spn/NS | | 102.5 | -0.72** | y = 110.48 - 2.29x |
| Spn/Anz | | 102.1 | -0.33 | y = 105.36 - 1.27x |
| Rb/Ymh | | 110.4 | -0.22 | y = 114.61 - 1.28x |
| Rb/NS | | 105.6 | -0.66** | y = 122.43 - 3.96x |
| Rb/Anz | | 125.3 | -0.64** | y = 137.61 - 4.86x |
| Ymh/NS | | 109.3 | -0.42* | y = 119.36 - 3.01x |
| Ymh/Anz | | 107.5 | -0.70** | y = 119.28 - 2.99x |
| NS/Anz | | 100.9 | -0.72** | y = 113.07 - 3.52x |
| Spn/Rb | Tiller Number | 8.2 | -0.06 | y = 8.62 - 0.076x |
| Spn/Ymh | | 9.5 | -0.61** | y = 13.19 - 1.166x |
| Spn/NS | | 8.0 | 0.24 | y = 6.96 + 0.30x |
| Spn/Anz | | 7.9 | -0.13 | y = 8.35 - 0.17x |
| Rb/Ymh | | 8.9 | -0.27 | y = 11.01 - 0.63x |
| Rb/NS | | 7.3 | -.47** | y - 9.77 - 0.56x |
| Rb/Anz | | 10.3 | -0.42* | y = 12.14 - 0.73x |
| Ymh/NS | | 8.2 | -0.10 | y = 9.00 - 0.25x |
| Ymh/Anz | | 9.4 | -0.32 | y = 12.39 - 0.77x |
| NS/Anz | | 9.0 | -0.06 | y = 9.45 - 0.12x |
| Spn/Rb | Plant Weight | 54.6 | -0.50** | y = 83.64 - 5.726x |
| Spn/Ymh | | 68.3 | -0.67** | y = 110.15 - 13.21x |
| Spn/NS | | 54.0 | -0.08 | y = 55.59 - 0.73x |
| Spn/Anz | | 56.7 | -0.30 | y = 64.43 - 3.02x |
| Rb/Ymh | | 64.6 | -0.42* | y = 91.87 - 8.32x |
| Rb/NS | | 56.0 | -0.57** | y = 85.84 - 6.89x |
| Rb/Anz | | 88.4 | -0.55** | y = 121.19 - 12.96x |
| Ymh/NS | | 62.4 | -0.30 | y = 81.87 - 5.85x |
| Ymh/Anz | | 68.5 | -0.65** | y = 111.05 - 10.83x |
| NS/Anz | | 63.3 | -0.33 | y = 78.59 - 4.41x |

Table 19. continued.

| Crosses | Traits | Trait Means | r | Regression Equation |
|---|---|---|---|---|
| Spn/Rb | Grain Yield | 10.2 | -0.36* | y = 14.46 - 0.835x |
| Spn/Ymh | | 19.2 | -0.73** | y = 32.34 - 4.151x |
| Spn/NS | | 16.1 | -0.06 | y = 13.69 - 0.12x |
| Spn/Anz | | 19.0 | -0.43* | y = 23.12 - 1.59x |
| Rb/Ymh | | 14.3 | -0.27 | y = 20.17 - 1.80x |
| Rb/NS | | 14.6 | -0.57** | y = 23.01 - 1.95x |
| Rb/Anz | | 22.4 | -0.57** | y = 31.69 - 3.68x |
| Ymh/NS | | 13.1 | -0.07 | y = 14.21 - 0.34x |
| Ymh/Anz | | 21.3 | -0.71** | y = 37.38 - 4.09x |
| NS/Anz | | 20.7 | -0.43 | y = 28.12 - 2.15x |
| Spn/Rb | Kernel Weight | 4.42 | -0.35 | y = 4.890 - 0.083x |
| Spn/Ymh | | 5.15 | -0.79** | y = 6.044 - 0.288x |
| Spn/NS | | 4.85 | -0.66** | y = 5.360 - 0.144x |
| Spn/Anz | | 5.80 | -0.46** | y = 6.411 - 0.237x |
| Rb/Ymh | | 4.68 | -0.22 | y = 5.321 - 0.196x |
| Rb/NS | | 4.65 | -0.53** | y = 5.205 - 0.128x |
| Rb/Anz | | 4.84 | -0.60** | y = 5.175 - 0.133x |
| Ymh/NS | | 4.41 | 0.22 | y = 4.195 + 0.064x |
| Ymh/Anz | | 4.34 | -0.76** | y = 5.038 - 0.177x |
| NS/Anz | | 5.02 | -0.53** | y = 5.81 - 0.228x |
| Spn/Rb | Harvest Index | 0.190 | 0.11 | y = 0.1761 + 0.003x |
| Spn/Ymh | | 0.273 | -0.54** | y = 0.3194 - 0.015x |
| Spn/NS | | 0.282 | -0.14 | y = 0.3284 - 0.013x |
| Spn/Anz | | 0.335 | -0.62** | y = 0.3787 - 0.017x |
| Rb/Ymh | | 0.217 | -0.02 | y = 0.2219 - 0.001x |
| Rb/NS | | 0.251 | -0.38* | y = 0.2964 - 0.010x |
| Rb/Anz | | 0.253 | -0.21 | y = 0.2698 - 0.007x |
| Ymh/NS | | 0.207 | 0.39* | y = 0.1530 + 0.016x |
| Ymh/Anz | | 0.308 | -0.54** | y = 0.3516 - 0.012x |
| NS/Anz | | 0.319 | -0.52** | y = 0.3851 - 0.019x |

can be observed for the regression values with only the Ymh/NS showing a positive association (b = .064).

Positive associations can be noted for harvest index for the $F_1$'s, Spn/Rb (r = 0.11) and Ymh/NS (r = 0.39). The remaining correlations were negative. Very little response was detected with the regression values as noted for this trait and BYDV score for the 10 $F_1$ crosses.

In Tables 20 and 21, similar data are presented for the $F_2$ and $F_3$ generations. It can be observed that a similar trend as found in the $F_1$ becomes apparent with most correlations and regression values being negative. However, when comparing the various crosses, differences in magnitude of the values can be seen.

For plant height, NS/Anz did not exhibit a significant association in the $F_2$ (r = -0.26) whereas in the $F_3$ this was true for Spn/NS (r = -0.21). In terms of the regression value involving plant height the largest negative response in the $F_2$ was with Rb/N.S. (b = -3.90) closely followed by Ymh/Anz (b = -3.86). Rb/NS also had the largest regression value (b = -5.03) for the $F_3$ generation with Ymh/NS (b = -4.21) being next.

When tiller number is considered, similarities between the $F_2$ and $F_3$ generations emerge for both the correlation and regression values. For example, Rb/NS had the largest negative correlation value both in the $F_2$ (r = -0.46) and $F_3$ (r = -0.63). This was also true for the regression values ($F_2$ = -0.784) and ($F_3$ = -0.915). Stephens/NS had the smallest negative correlation and regression values in both the $F_2$ (r = -0.05, b = -0.108) and $F_3$ (r = -.003, b = -.005) generations.

Negative correlation and regression values for BYDV score and

Table 20. Correlation Coefficients between BYDV score and plant height, tiller number, plant weight, grain yield, kernel weight and harvest index for the $F_2$ crosses.

| Crosses | Traits | Trait Means | r | Regression Equation |
|---|---|---|---|---|
| Spn/Rb | Plant Height | 95.4 | -0.46** | y = 120.76 - 3.58x |
| Spn/Ymh | | 96.8 | -0.48** | y = 107.35 - 2.69x |
| Spn/NS | | 95.1 | -0.33** | y = 104.09 - 1.77x |
| Spn/Anz | | 89.9 | -0.65** | y = 107.53 - 3.62x |
| Rb/Ymh | | 100.1 | -0.51** | y = 112.92 - 3.45x |
| Rb/NS | | 92.7 | -0.52** | y = 114.75 - 3.90x |
| Rb/Anz | | 107.9 | -0.39** | y = 118.23 - 2.65x |
| Ymh/NS | | 98.4 | -0.58** | y = 111.44 - 3.13x |
| Ymh/Anz | | 96.2 | -0.54** | y = 109.22 - 3.86x |
| NS/Anz | | 80.1 | -0.26 | y = 91.33 - 1.88x |
| Spn/Rb | Tiller Number | 8.5 | -0.34* | y = 11.68 - 0.565x |
| Spn/Ymh | | 8.6 | -0.29* | y = 10.43 - 0.467x |
| Spn/NS | | 9.1 | 0.05 | y = 9.63 - 0.108x |
| Spn/Anz | | 7.5 | -0.25 | y = 9.02 - 0.315x |
| Rb/Ymh | | 7.6 | -0.23 | y = 8.76 - 0.313x |
| Rb/NS | | 7.8 | -0.46** | y = 12.20 - 0.784x |
| Rb/Anz | | 8.9 | -0.20 | y = 10.04 - 0.298x |
| Ymh/NS | | 8.7 | -0.27* | y = 10.28 - 0.390x |
| Ymh/Anz | | 8.5 | -0.24 | y = 10.36 - 0.546x |
| NS/Anz | | 7.6 | -0.19 | y = 9.80 - 0.361x |
| Spn/Rb | Plant Weight | 53.0 | -0.49** | y = 90.57 - 6.72x |
| Spn/Ymh | | 53.9 | -0.42** | y = 76.77 - 5.75x |
| Spn/NS | | 60.3 | -0.20 | y = 81.08 - 4.07x |
| Spn/Anz | | 48.9 | -0.57** | y = 75.94 - 5.84x |
| Rb/Ymh | | 55.8 | -0.40** | y = 75.11 - 5.20x |
| Rb/NS | | 51.9 | -0.51** | y = 94.66 - 7.50x |
| Rb/Anz | | 65.6 | -0.40** | y = 88.32 - 5.81x |
| Ymh/NS | | 55.5 | -0.44** | y = 77.06 - 5.17x |
| Ymh/Anz | | 56.2 | -0.31* | y = 75.57 - 5.72x |
| NS/Anz | | 33.4 | -0.30* | y = 48.01 - 2.48x |

**,*: significant at the one and five percent probability levels, respectively.

Table 20. (continued)

| Crosses | Traits | Trait Means | r | Regression Equation |
|---|---|---|---|---|
| Spn/Rb | Grain Yield | 11.05 | -0.47** | y = 20.14 - 1.62x |
| Spn/Ymh | | 15.34 | -0.43** | y = 23.98 - 2.18x |
| Spn/NS | | 14.47 | -0.17 | y = 19.15 - 0.92x |
| Spn/Anz | | 14.17 | -0.59** | y = 25.28 - 2.26x |
| Rb/Ymh | | 9.26 | -0.23 | y = 11.79 - 0.68x |
| Rb/NS | | 10.53 | -0.62** | y = 24.05 - 2.31x |
| Rb/Anz | | 13.72 | -0.41** | y = 19.68 - 1.53x |
| Ymh/NS | | 14.99 | -0.37** | y = 21.81 - 1.60x |
| Ymh/Anz | | 15.76 | -0.44** | y = 23.88 - 2.40x |
| NS/Anz | | 8.71 | -0.26* | y = 13.16 - 0.76x |
| Spn/Rb | Kernel Weight | 4.24 | -0.26* | y = 4.777 - 0.095x |
| Spn/Ymh | | 4.50 | -0.26* | y = 4.852 - 0.090x |
| Spn/NS | | 4.27 | -0.35** | y = 4.823 - 0.118x |
| Spn/Anz | | 4.67 | -0.40** | y = 5.497 - 0.168x |
| Rb/Ymh | | 3.80 | -0.26* | y = 4.049 - 0.066x |
| Rb/NS | | 4.24 | -0.14 | y = 4.630 - 0.070x |
| Rb/Anz | | 4.25 | -0.46** | y = 4.780 - 0.137x |
| Ymh/NS | | 4.29 | -0.39** | y = 4.946 - 0.157x |
| Ymh/Anz | | 3.89 | -0.49** | y = 4.525 - 0.183x |
| NS/Anz | | 4.34 | -0.19 | y = 3.880 - 0.082x |
| Spn/Rb | Harvest Index | 0.202 | -0.18 | y = 0.2335 - 0.006x |
| Spn/Ymh | | 0.262 | -0.17 | y = 0.2904 - 0.007x |
| Spn/NS | | 0.229 | -0.06 | y = 0.2396 - 0.002x |
| Spn/Anz | | 0.286 | -0.38** | y = 0.3628 - 0.016x |
| Rb/Ymh | | 0.156 | 0.08 | y = 0.1457 + 0.003x |
| Rb/NS | | 0.192 | -0.46** | y = 0.3001 - 0.019x |
| Rb/Anz | | 0.201 | -0.34** | y = 0.2418 - 0.010x |
| Ymh/NS | | 0.257 | -0.19 | y = 0.2896 - 0.008x |
| Ymh/Anz | | 0.272 | -0.34** | y = 0.3278 - 0.017x |
| NS/Anz | | 0.249 | -0.06 | y = 0.2654 - 0.003x |

**,*: significant at the one and five percent probability levels, respectively.

Table 21. Correlation Coefficients between BYDV score and plant height, tiller number, plant weight, grain yield, kernel weight and harvest index for the $F_3$ crosses.

| Crosses | Traits | Trait Means | r | Regression Equation |
|---|---|---|---|---|
| Spn/Rb | Plant Height | 92.3 | -0.53** | y = 109.66 - 3.24x |
| Spn/Ymh | | 91.9 | -0.38* | y = 102.50 - 2.17x |
| Spn/NS | | 96.7 | -0.21 | y = 104.21 - 1.65x |
| Spn/Anz | | 84.7 | -0.44** | y = 95.09 - 1.87x |
| Rb/Ymh | | 106.1 | -0.55** | y = 121.37 - 3.21x |
| Rb/NS | | 88.1 | -0.71** | y = 121.92 - 5.03x |
| Rb/Anz | | 110.3 | -0.37* | y = 121.33 - 3.07x |
| Ymh/NS | | 97.3 | -0.56** | y = 114.64 - 4.21x |
| Ymh/Anz | | 96.4 | -0.32* | y = 105.35 - 1.94x |
| NS/Anz | | 103.1 | -0.30* | y = 112.46 - 2.16x |
| Spn/Rb | Tiller Number | 6.6 | -0.12 | y = 7.37 - 0.15x |
| Spn/Ymh | | 9.0 | -0.12 | y = 9.82 - 0.21x |
| Spn/NS | | 9.1 | 0.003 | y = 9.07 + 0.005x |
| Spn/Anz | | 9.0 | -0.40* | y = 12.06 - 0.673x |
| Rb/Ymh | | 8.8 | -0.33* | y = 11.55 - 0.573x |
| Rb/NS | | 6.6 | -0.63** | y = 12.78 - 0.915x |
| Rb/Anz | | 9.3 | -0.26 | y = 11.33 - 0.556x |
| Ymh/NS | | 7.4 | -0.40** | y = 9.94 - 0.607x |
| Ymh/Anz | | 7.2 | -0.42** | y = 10.27 - 0.66x |
| NS/Anz | | 7.4 | -0.18 | y = 8.49 - 0.25x |
| Spn/Rb | Plant Weight | 37.4 | -0.25 | y = 47.64 - 1.92x |
| Spn/Ymh | | 59.8 | -0.41** | y = 87.70 - 6.45x |
| Spn/NS | | 56.4 | -0.14 | y = 65.13 - 1.92x |
| Spn/Anz | | 43.0 | -0.33 | y = 56.77 - 2.90x |
| Rb/Ymh | | 61.5 | -0.44** | y = 94.58 - 6.96x |
| Rb/NS | | 39.7 | -0.77** | y = 97.96 - 8.65x |
| Rb/Anz | | 65.3 | -0.42** | y = 93.01 - 7.69x |
| Ymh/NS | | 52.6 | -0.57** | y = 83.97 - 7.55x |
| Ymh/Anz | | 44.3 | -0.59** | y = 73.28 - 6.31x |
| NS/Anz | | 45.7 | -0.36* | y = 62.00 - 3.78x |

**,*: significant at the one and five percent probability levels, respectively.

Table 21. (continued)

| Crosses | Traits | Trait Means | r | Regression Equation |
|---|---|---|---|---|
| Spn/Rb | Grain Yield | 8.4 | -0.25 | y = 11.50 - 0.58x |
| Spn/Ymh | | 19.7 | -0.36* | y = 27.92 - 2.00x |
| Spn/NS | | 14.0 | -0.04 | y = 14.66 - 0.14x |
| Spn/Anz | | 14.2 | -0.46** | y = 20.61 - 1.54x |
| Rb/Ymh | | 13.6 | -0.41** | y = 21.26 - 1.71x |
| Rb/NS | | 8.2 | -0.72** | y = 24.04 - 2.31x |
| Rb/Anz | | 16.1 | -0.44** | y = 25.31 - 2.62x |
| Ymh/NS | | 14.4 | -0.56** | y = 26.92 - 2.99x |
| Ymh/Anz | | 13.9 | -0.64** | y = 25.97 - 2.62x |
| NS/Anz | | 13.1 | -0.45** | y - 20.94 - 1.82x |
| Spn/Rb | Kernel Weight | 4.08 | -0.40** | y = 4.711 - 0.118x |
| Spn/Ymh | | 5.33 | -0.43** | y = 6.159 - 0.230x |
| Spn/NS | | 4.53 | -0.16 | y = 4.738 - 0.046x |
| Spn/Anz | | 4.35 | -0.66** | y = 5.705 - 0.266x |
| Rb/Ymh | | 4.03 | -0.27 | y = 4.327 - 0.063x |
| Rb/NS | | 4.11 | -0.46** | y = 5.471 - 0.202x |
| Rb/Anz | | 4.23 | -0.39** | y = 4.749 - 0.143x |
| Ymh/NS | | 3.85 | -0.64** | y = 4.864 - 0.246x |
| Ymh/Anz | | 4.33 | -0.29* | y = 4.814 - 0.105x |
| NS/Anz | | 4.14 | -0.55** | y = 5.183 - 0.243x |
| Spn/Rb | Harvest Index | 0.211 | -0.37** | y = 0.2673 - 0.011x |
| Spn/Ymh | | 0.317 | -0.21 | y = 0.3423 - 0.007x |
| Spn/NS | | 0.242 | -0.25 | y = 0.2042 - 0.009x |
| Spn/Anz | | 0.297 | -0.62** | y = 0.3920 - 0.0209x |
| Rb/Ymh | | 0.208 | -0.14 | y = 0.2268 - 0.004x |
| Rb/NS | | 0.178 | -0.49** | y = 0.3010 - 0.018x |
| Rb/Anz | | 0.225 | -0.40** | y = 0.2746 - 0.0136x |
| Ymh/NS | | 0.244 | -0.55 | y = 0.3473 - 0.0249x |
| Ymh/Anz | | 0.298 | -0.48** | y = 0.3857 - 0.0189x |
| NS/Anz | | 0.282 | -0.33* | y - 0.3397 - 0.0134x |

**,*: significant at the one and five percent probability levels, respectively.

plant weight can also be observed. In fact, only one correlation value in the $F_2$ (Spn/NS, r = -0.20) and three correlations in the $F_3$ (Spn/Rb, r= -0.25; Spn/NS, r = -0.14; and Spn/Anz, r = -0.33) were not significant. In considering the regression values, the largest decrease in the $F_2$ and $F_3$ was with Rb/NS cross,b = -7.50 and b = -8.65, respectively.

In evaluating the relationship between BYDV score and grain yield again the cross Rb/NS in both the $F_2$ and $F_3$ had the largest negative association r = -.063, r = -0.72, respectively. Whereas for the regression values Ymh/Anz and Ymh/NS exhibited the greatest negative effect in the $F_2$ and $F_3$ (b = -2.40 and b = -2.99) respectively.

The cross Ymh/Anz had the largest negative values for both correlation and regression in the $F_2$ (r = -0.49, b = -.183) for kernel weight. In the $F_3$, Spn/Anz was observed to have the largest negative correlation and regression values (r = -0.66 and b = -.266, respectively). However, Ymh/NS reflects negative values of nearly the same magnitude (r = -0.64 and b = -.246).

Harvest index and BYDV scores again reflect mostly a negative relationship for both the correlation and regression values in the $F_2$ and $F_3$ generations. In the $F_2$, Rb/NS (-0.46) and for the $F_3$, Spn/Anz (-0.62) had the largest negative correlation values. As can be noted from Tables 20 and 21, BYDV scores have little effect on harvest index.

In Table 22, the correlation and regression values are provided for the 20 backcross populations.

For plant height, significant negative correlation values can be noted for all backcross populations. For certain traits, consistent

Table 22. Correlation Coefficients between BYDV score and plant height, tiller number, plant weight, grain yield, kernel weight and harvest index for the backcross populations.

| Traits | Backcrosses | Trait Means | r | Regression Equation |
|---|---|---|---|---|
| Plant Height | Spn/Rb//Spn | 96.1 | -0.40** | y = 111.84 - 2.79x |
| | Spn/Rb//Rb | 96.0 | -0.33* | y = 103.11 - 1.39x |
| | Spn/Ymh//Spn | 95.6 | -0.60** | y = 108.95 - 3.12x |
| | Spn/Ymh//Ymh | 101.5 | -0.61** | y = 115.36 - 3.24x |
| | Spn/NS//Spn | 95.1 | -0.66** | y = 111.74 - 3.48x |
| | Spn/NS//NS | 87.9 | -0.60** | y = 100.45 - 2.88x |
| | Spn/Anz//Spn | 95.7 | -0.41** | y = 103.45 - 1.83x |
| | Spn/Anz//Anz | 83.1 | -0.61** | y = 103.04 - 3.14x |
| Tiller Number | Spn/Rb//Spn | 8.27 | -0.32* | y = 10.26 - 0.35x |
| | Spn/Rb//Rb | 7.53 | -0.07 | y = 8.03 - 0.10x |
| | Spn/Ymh//Spn | 7.20 | -0.47** | y = 9.55 - 0.49x |
| | Spn/Ymh//Ymh | 7.31 | -0.35* | y = 9.21 - 0.44x |
| | Spn/NS//Spn | 7.18 | -0.39** | y = 9.87 - 0.55x |
| | Spn/NS//NS | 6.80 | -0.33* | y = 8.33 - 0.43x |
| | Spn/Anz//Spn | 7.93 | -0.26 | y = 9.54 - 0.35x |
| | Spn/Anz//Anz | 8.10 | -0.40* | y = 12.65 - 0.69x |
| Plant Weight | Spn/Rb//Spn | 53.8 | -0.64** | y = 90.26 - 6.45x |
| | Spn/Rb//Rb | 66.2 | -0.12 | y = 76.03 - 1.92x |
| | Spn/Ymh//Spn | 47.4 | -0.58** | y = 71.72 - 5.65x |
| | Spn/Ymh//Ymh | 51.4 | -0.54** | y = 76.25 - 5.83x |
| | Spn/NS//Spn | 48.7 | -0.59** | y = 81.19 - 6.87x |
| | Spn/NS//NS | 37.3 | -0.48** | y = 56.88 - 4.49x |
| | Spn/Anz//Spn | 51.0 | -0.38 | y = 69.63 - 4.40x |
| | Spn/Anz//Anz | 41.3 | -0.63** | y = 78.37 - 6.04x |

**,*: significant at the one and five percent probability levels, respectively.

Table 22. (continued)

| Traits | Backcrosses | Trait Means | r | Regression Equation |
|---|---|---|---|---|
| Grain Yield | Spn/Rb//Spn | 12.54 | -0.48** | y = 20.10 - 1.32x |
| | Spn/Rb//Rb | 13.53 | -0.13 | y = 15.95 - 0.47x |
| | Spn/Ymh//Spn | 14.18 | -0.57** | y = 22.19 - 1.87x |
| | Spn/Ymh//Ymh | 14.47 | -0.47** | y = 21.88 - 1.74x |
| | Spn/NS//Spn | 11.55 | -0.54** | y = 20.85 - 1.93x |
| | Spn/NS//NS | 8.76 | -0.38** | y = 13.47 - 1.06x |
| | Spn/Anz//Spn | 15.02 | -0.49** | y = 22.96 - 1.87x |
| | Spn/Anz//Anz | 11.03 | -0.59** | y = 22.15 - 1.81x |
| Kernel Weight | Spn/Rb//Spn | 4.99 | -0.44** | y = 5.50 - 0.091x |
| | Spn/Rb//Rb | 4.12 | -0.30* | y = 4.46 - 0.066x |
| | Spn/Ymh//Spn | 4.96 | -0.72** | y = 5.98 - 0.236x |
| | Spn/Ymh//Ymh | 4.30 | -0.37* | y = 4.82 - 0.121x |
| | Spn/NS//Spn | 4.58 | -0.27 | y = 5.06 - 0.101x |
| | Spn/NS//NS | 4.16 | -0.31* | y = 4.59 - 0.098x |
| | Spn/Anz//Spn | 4.95 | -0.64** | y = 5.93 - 0.229x |
| | Spn/Anz//Anz | 4.00 | -0.54** | y = 5.29 - 0.206x |
| Harvest Index | Spn/Rb//Spn | 0.222 | -0.08 | y = 0.234 - 0.002x |
| | Spn/Rb//Rb | 0.200 | -0.14 | y = 0.2154 - 0.003x |
| | Spn/Ymh//Spn | 0.293 | -0.17 | y = 0.3103 - 0.004x |
| | Spn/Ymh//Ymh | 0.277 | -0.16 | y = 0.3011 - 0.006x |
| | Spn/NS//Spn | 0.238 | -0.021 | y = 0.2609 - 0.008x |
| | Spn/NS//NS | 0.225 | -0.12 | y = 0.2474 - 0.005x |
| | Spn/Anz//Spn | 0.290 | -0.45** | y = 0.3467 - 0.013x |
| | Spn/Anz//Anz | 0.258 | -0.29 | y = 0.3166 - 0.009x |

**,*: significant at the one and five percent probability levels, respectively.

Table 22. (continued)

| Traits | Backcrosses | Trait Mean | r | Regression Equations |
|---|---|---|---|---|
| Plant Height | Rb/Ymh//Rb | 115.4 | -0.61** | y = 128.94 - 4.30x |
| | Rb/Ymh//Ymh | 106.4 | -0.50** | y = 117.16 - 3.45x |
| | Rb/NS//Rb | 100.0 | -0.70** | y = 122.21 - 4.32x |
| | Rb/NS//NS | 98.3 | -0.54** | y = 112.08 - 3.20x |
| | Rb/Anz//Rb | 105.0 | -0.68** | y = 124.43 - 3.97x |
| | Rb/Anz//Anz | 98.4 | -0.56** | y = 115.41 - 3.78x |
| Tiller Number | Rb/Ymh//Rb | 7.22 | -0.21 | y = 8.33 - 0.274x |
| | Rb/Ymh//Ymh | 7.40 | -0.26 | y = 9.16 - 0.451x |
| | Rb/NS//Rb | 7.42 | -0.40** | y = 10.70 - 0.612x |
| | Rb/NS//NS | 6.78 | -0.37* | y = 9.70 - 0.731x |
| | Rb/Anz//Rb | 8.20 | -0.47 | y = 10.91 - 0.600x |
| | Rb/Anz//Anz | 7.96 | -0.09 | y = 8.78 - 0.153x |
| Plant Weight | Rb/Ymh//Rb | 67.0 | -0.53** | y = 92.57 - 8.09x |
| | Rb/Ymh//Ymh | 61.6 | -0.42** | y = 85.84 - 7.79x |
| | Rb/NS//Rb | 58.5 | -0.55** | y = 98.56 - 7.80x |
| | Rb/NS//NS | 50.0 | -0.50** | y = 80.94 - 7.24x |
| | Rb/Anz//Rb | 54.6 | -0.69** | y = 86.26 - 6.47x |
| | Rb/Anz//Anz | 55.2 | -0.44** | y = 83.99 - 6.39x |

**,*: significant at the one and five percent probability levels, respectively.

Table 22. (continued)

| Traits | Backcrosses | Trait Means | r | Regression Equations |
|---|---|---|---|---|
| Grain Yield | Rb/Ymh//Rb | 10.08 | -0.44** | y = 14.96 - 1.51x |
| | Rb/Ymh//Ymh | 14.16 | -0.50** | y = 20.65 - 2.09x |
| | Rb/NS//Rb | 11.76 | -0.56** | y = 22.54 - 2.10x |
| | Rb/NS//NS | 14.08 | -0.51** | y = 24.43 - 2.70x |
| | Rb/Anz//Rb | 9.19 | -0.52** | y = 14.55 - 1.10x |
| | Rb/Anz//Anz | 13.60 | -0.53 ** | y - 22.86 - 2.05x |
| Kernel Weight | Rb/Ymh//Rb | 3.99 | -0.54** | y = 4.65 - 0.209x |
| | Rb/Ymh//Ymh | 4.27 | -0.56** | y = 4.80 - 0.171x |
| | Rb/NS//Rb | 4.10 | -0.67** | y = 5.48 - 0.304x |
| | Rb/NS//NS | 5.11 | 0.04 | y = 5.08 + 0.028x |
| | Rb/Anz//Rb | 3.73 | -0.33* | y = 4.21 - 0.117x |
| | Rb/Anz//Anz | 4.21 | -0.50** | y = 4.99 - 0.172x |
| Harvest Index | Rb/Ymh//Rb | 0.141 | -0.27 | y = 0.1679 - 0.009x |
| | Rb/Ymh//Ymh | 0.227 | -0.25 | y = 0.2503 - 0.007x |
| | Rb/NS//Rb | 0.178 | -0.55** | y = 0.2640 - 0.017x |
| | Rb/NS//NS | 0.253 | -0.24 | y = 0.3039 - 0.010x |
| | Rb/Anz//Rb | 0.158 | -0.009 | y = 0.1594 - 0.0002x |
| | Rb/Anz//Anz | 0.238 | -0.560** | y = 0.3196 - 0.018x |

**,*: significant at the one and five percent probability levels, respectively.

Table 22. (continued)

| Traits | Backcrosses | Trait Means | r | Regression Equations |
|---|---|---|---|---|
| Plant Height | Ymh/NS//Ymh | 104.9 | -0.52** | y = 115.38 - 3.02x |
| | Ymh/NS//NS | 101.5 | -0.31* | y = 108.58 - 2.08x |
| | Ymh/Anz//Ymh | 95.0 | -0.69** | y = 108.29 - 2.79x |
| | Ymh/Anz//Anz | 90.4 | -0.59** | y = 109.24 - 3.35x |
| | NS/Anz//NS | 101.9 | -0.39** | y = 110.82 - 3.09x |
| | NS/Anz//Anz | 94.6 | -0.42** | y = 102.87 - 2.70x |
| Tiller Number | Ymh/NS//Ymh | 7.47 | -0.08 | y = 8.19 - 0.14x |
| | Ymh/NS//NS | 8.13 | -0.04 | y = 8.31 - 0.097x |
| | Ymh/Anz//Ymh | 7.16 | -0.34* | y = 8.74 - 0.0400x |
| | Ymh/Anz//Anz | 8.31 | -0.03 | y = 8.37 = 0.062x |
| | NS/Anz//NS | 9.17 | -0.09 | y = 10.25 - 0.302x |
| | NS/Anz//Anz | 9.13 | -0.22 | y = 10.42 - 0.481x |
| Plant Weight | Ymh/NS//Ymh | 55.7 | -0.36* | y = 73.36 - 5.13x |
| | Ymh/NS//NS | 56.2 | -0.35* | y = 77.73 - 6.30x |
| | Ymh/Anz//Ymh | 43.5 | -0.58** | y = 67.66 - 5.07x |
| | Ymh/Anz//Anz | 47.0 | -0.49** | y = 70.18 - 4.76x |
| | NS/Anz//NS | 65.6 | -0.29 | y = 85.07 - 6.90x |
| | NS/Anz//Anz | 57.5 | -0.35* | y = 72.37 - 4.89x |

**,*: significant at the one and five percent probability levels, respectively.

Table 22. (continued)

| Traits | Backcrosses | Trait Means | r | Regression Equations |
|---|---|---|---|---|
| Grain Yield | Ymh/NS//Ymh | 13.56 | -0.34* | y = 18.47 - 1.41x |
| | Ymh/NS//NS | 14.48 | -0.41** | y = 23.81 - 2.70x |
| | Ymh/Anz//Ymh | 11.41 | -0.65** | y = 21.77 - 2.18x |
| | Ymh/Anz//Anz | 14.11 | -0.53** | y = 22.63 - 1.80x |
| | NS/Anz//NS | 17.52 | -0.18 | y = 21.47 -1.38x |
| | NS/Anz//Anz | 18.88 | -0.41** | y = 25.75 - 2.26x |
| Kernel Weight | Ymh/NS//Ymh | 4.26 | -0.35* | y = 4.64 - 0.107x |
| | Ymh/NS//NS | 4.10 | -0.33* | y - 4.48 - 0.135x |
| | Ymh/Anz//Ymh | 4.92 | -0.60** | y = 4.85 - 0.196x |
| | Ymh/Anz//Anz | 4.40 | -0.55** | y = 4.76 - 0.135x |
| | NS/Anz//NS | 4.59 | -0.36* | y = 4.91 - 0.116x |
| | NS/Anz//Anz | 4.77 | -0.51** | y = 5.27 - 0.164x |
| Harvest Index | Ymh/NS//Ymh | 0.239 | -0.19 | y = 0.2576 - 0.005x |
| | Ymh/NS//NS | 0.240 | -0.35* | y = 0.3077 - 0.020x |
| | Ymh/Anz//Ymh | 0.246 | -0.57** | y = 0.3587 - 0.024x |
| | Ymh/Anz//Anz | 0.294 | -0.16 | y = 0.3144 - 0.005x |
| | NS/Anz//NS | 0.259 | 0.13 | y = 0.2473 + 0.007x |
| | NS/Anz//Anz | 0.311 | -0.65** | y = 0.3821 - 0.0232x |

**,*: significant at the one and five percent probability levels, respectively.

differences are noted when specific parents were used as the recurrent parent. A similar observation can also be made for the regression values involving this trait; however, there are differences between backcross populations. The largest negative correlation and regression values were noted for the backcross Spn/NS//Spn ($r = -0.66$, $b = -3.48$).

When tiller number is considered, the same negative trend in both the correlation and regression values are noted; however, there appear to be fewer significant differences in the correlation values. As with plant height, Stephens figures prominently where the greatest negative values are observed (Spn/Ymh//Spn: $r = -0.47$, Spn/NS//Spn: $b = -0.55$).

Plant weight and BYDV score appears to be again represented by high negative correlations and regression values. However, as with tiller number, Stephens and, in this instance, Anza appear in those crosses which are associated with the largest negative value.

In only two backcross population (Spn/Rb//Rb and NS/Anz//NS) was the correlation value not significant when grain yield and BYDV score are considered. For the regression values, all backcross populations resulted in negative relationships. No consistent trends were observed for any of the populations with regards to specific cultivars being involved.

Kernel weight and BYDV score again provided negative values for both correlation and regression values. For correlations the smallest values were noted for the backcrosses Spn/NS//Spn and Rb/NS//NS where significant differences were not noted.

Of particular interest are the correlation and regression values observed when harvest index is considered. There are no consistent trends with specific recurrent parents; however, harvest index appears less affected by BYDV than any of the other traits with the exception of tiller number.

In summary, even though there was a general lack of consistency among the relationship between BYDV score and the six measured agronomic traits, some interesting factors surfaced. There were no significant correlations between BYDV score and plant height, tiller number, plant weight, grain yield and harvest index observed with the cultivar Yamhill. One exception was the significant negative correlation noted with kernel weight.

In contrast, when looking at similar correlations involving Stephens, higher significantly different negative correlations were noted for all agronomic traits except harvest index where the correlation was significant at the .05 level of probability. For Riebesel, Novi Sad and Anza correlations were again significant except for harvest index.

## Genetic Correlations

To provide additional information regarding the relationship between BYDV score and four of the agronomic traits measured, genetic correlations were determined for the $F_1$ and $F_2$ generations. The values for these associations are presented in Table 23. Information for tiller number and harvest index were omitted from the analysis as little or no variability was detected using narrow sense heritability analysis (Table 24).

As with phenotypic correlations, the genetic associations were negative for all comparisons involving the 10 crosses. There were

Table 23. Genetic correlations among BYDV scores and four agronomic characters using F1 and F2 generations on ten wheat crosses at Hyslop Agronomy Farm, 1981-82.

| Crosses | Plant Height | Plant Weight | Grain Yield | Kernel Weight |
|---|---|---|---|---|
| Stephens/Riebesel | -0.54 | -0.52 | >-1.00 | -0.34 |
| Stephens/Yamhill | -0.48 | -0.48 | -0.23 | -0.13 |
| Stephens/Novi Sad | -0.12 | >-1.00 | -0.47 | -0.30 |
| Stephens/Anza | >-1.00 | >-1.00 | >-1.00 | -0.74 |
| Riebesel/Yamhill | -1.0 | -0.26 | -0.04 | -- |
| Riebesel/Novi Sad | -0.58 | -0.46 | -0.40 | -0.13 |
| Riebesel/Anza | -0.46 | -0.27 | -0.22 | -0.10 |
| Yamhill/Novi Sad | -0.43 | >-1.00 | >-1.00 | >-1.00 |
| Yamhill/Anza | >-1.00 | >-1.00 | -0.47 | -0.15 |
| Novi Sad/Anza | -0.19 | -0.11 | -0.49 | >-1.00 |

some differences in the magnitude with some values exceeding a r value of -1. The lowest association between BYDV score and plant height was observed with the crosses Spn/NS (-0.12) and NS/Anz (-0.19). The latter cross was also found to have the lowest negative value for BYDV score and plant weight (-0.11) followed by Rb/Ymh (-0.26) and Rb/Anz (-0.27). When the association between BYDV score and grain yield are examined, Rb/Ymh had the lowest negative value (-0.04) For kernel weight, Rb/Anz (r = -0.10), Rb/NS (r = -0.13) and Spn/Ymh (r = -0.13) were lowest for this association.

## Heritability values

Since the data in this investigation suggested that Barley Yellow Dwarf Virus resistance was under the influence of many genetic factors, narrow sense heritability estimates ($h^2$) were determined for the BYDV scores for the 10 $F_2$ and BC populations (Table 24). The $h^2$ estimates were low with the Ymh/NS populations being the highest at 16% with Spn/Anz having the lowest value of 9%.

## Combining Ability Analysis

To better understand the nature of gene action influencing BYDV resistance a combining ability analysis was also conducted. Mean squares for General and Specific Combining Ability estimates are provided in Table 25. Differences were observed for General Combining Ability for BYDV score. Specific Combining Ability, differences were also noted for BYDV score.

Of particular interest is the individual combining ability effects contributed by the individual parents. The estimates of general combining ability effect by the parents for BYDV score is

Table 24. Magnitudes of narrow sense heritability generated in the F2 and backcross population for BYDV resistance.

| Crosses | Heritability Values | Sx |
|---|---|---|
| Spn/Rb | 0.114 | 0.126 |
| Spn/Ymh | 0.156 | 0.110 |
| Spn/NS | 0.143 | 1.125 |
| Spn/Anz | 0.092 | 0.149 |
| Rb/Ymh | 0.136 | 0.055 |
| Rb/NS | 0.123 | 0.084 |
| Rb/Anz | 0.134 | 0.128 |
| Ymh/NS | 0.164 | 0.081 |
| Ymh/Anz | 0.108 | 0.164 |
| NS/Anz | 0.090 | 0.176 |

Table 25. Observed mean squares for general and specific combining ability in the F1 generation of a parent diallel for BYDV score in five wheat cultivars.[1]

| Character | M.S. Crosses | GCA | SCA | Error |
|---|---|---|---|---|
| BYDV Score | 2.20164 | 1.89098** | 2.45016** | 0.3575 |

[1]Degrees of freedom were 9, 4, 5 and 18 for crosses, GCA, SCA and Error, respectively.

*,**: Significant at the five and one percent level of probability, respectively.

Table 26. Estimates of general combining ability effects for all traits measured from all possible single crosses involving five wheat cultivars.

| Character | Stephens | Riebesel | Yamhill | Novi Sad | Anza |
|---|---|---|---|---|---|
| BYDV Score | 0.09 | 0.38 | -0.12 | 0.19 | -0.54 |

presented in Table 26. For BYDV score, Yamhill and Anza (-0.12 and -0.54, respectively) contributed the greatest effect to reducing the visual expression of the disease.

In Table 27, information regarding specific combining ability effect for BYDV score is provided for each of the parents. The largest effects for BYDV score can be observed for crosses involving Rb/Anz (-0.88), Spn/Anz (-0.53) and Ymh/Rb (-0.49). It can be noted that those single crosses where Yamhill, Anza and Novi Sad are involved, a reduction in the expression of the symptoms can be noted. A major exception is the cross Ymh/Anz where a large positive effect is noted (1.09). Of special interest is that the Specific Combining Ability effects for specific parents are in agreement with some $F_1$ and segregating populations being similar to the more resistant parent suggesting nonadditive gene action.

Table 27. Estimates of effects for specific combining ability for BYDV score for all single crosses involving five wheat cultivars.

| Parent | Character | Riebesel | Yamhill | Novi Sad | Anza |
|---|---|---|---|---|---|
| Stephens | BYDV | 1.10 | -0.30 | -0.28 | -0.53 |
| Riebesel | BYDV | | -0.49 | 0.27 | -0.88 |
| Yamhill | BYDV | | | -0.31 | 1.09 |
| Novi Sad | BYDV | | | | 0.32 |

# DISCUSSION

Barley Yellow Dwarf Virus is rapidly becoming a major disease of wheat throughout the world. Unlike barley where the Yd2 gene has provided adequate levels of resistance, no such qualitatively inherited pattern for resistance has been reported in wheat. A further complication in wheat is that the interaction of the host, vector, virus and environment does not result in a clearly defined visual symptom of the disease. As a result, it has been difficult to identify and use sources of genetic resistance as a means of control. However, numerous studies have suggested that the most effective and economic control of BYDV is through the development of resistant cultivars.

If resistant cultivars are to be developed, it is apparent that: (1) more reliable methods of detecting and measuring resistance must be identified, (2) additional genetic sources of resistance must be found and (3) the nature of inheritance controlling BYDV must be determined. It was the overall objective of this investigation to provide information regarding these factors so that the most effective approach to breeding resistant cultivars can be undertaken.

The experimental materials used in this study represented four cultivars which have been reported to have some resistance to BYDV. These included Yamhill, Anza, Riebesel and Novi Sad. The latter cultivar was of particular interest as it was reported to be resistant to BYDV in India and that resistance was due to a single major gene. The fifth cultivar was Stephens which has been found to be susceptible to BYDV in the Willamette Valley. All possible crosses were made between these five parents and the parents, $F_1$'s, $F_2$'s, $F_3$'s, BC-1 and

BC-2 generations were grown under a number of different environments and treatments in this investigation.

Study I: Greenhouse Experiment

The greenhouse was employed to control as many variables as possible so that the response of the five cultivars to aphid feeding alone and to the aphid plus virus could be determined. A BYDV score and six agronomic traits were measured.

Cultivar differences did appear due to aphid feeding alone. A significant reduction in plant weight was noted for Anza and for plant weight, plant height and harvest index for Yamhill.

Perhaps due to ideal growing conditions observed in the greenhouse and higher temperatures than desired in April and May, the visual BYDV symptoms in infected plants were difficult to detect in the greenhouse. Stephens did show some yellowing of the leaves, but no visual reduction in plant vigor was observed. However, the cultivars did show a differential response to the six agronomic traits measured. Stephens was adversely affected particularly for grain yield, plant weight, plant height, kernel weight and tiller number. This is in agreement with other investigators' reports. Stephens, along with Riebesel, had a significant BYDV score. Riebesel also exhibited a significant difference for plant height.

Other cultivars showed different responses depending on the agronomic trait. Yamhill exhibited a decrease in plant weight and harvest index while Novi Sad had a reduction in tiller number. Anza expressed a significant decrease in kernel weight. These findings suggest that perhaps cultivars achieve their resistance in different ways and that the genetic background plays a role which should be considered in making crosses between specific cultivars for resistance.

Another factor which must be considered with regard to the response of various traits is the dosage hypothesis put forth by Smith (1967). In the greenhouse study fewer aphids per plant were used than larger populations which may often be found under field conditions. This may also explain the lack of effect by aphids between the controls and plants where non-viruliferous aphids were transferred. Progressive effects of the disease with increasing aphid number were confirmed for barley by Boulton and Catherall (1980). Burnett and Gill (1976) reported that seed yield decreased progressively with an increase of viruliferous aphids. Also, when the plants are infected might well influence which of the components of yield would be influenced most.

In this study, the aphids were transferred during the tiller stage, thus perhaps this component would have been less affected. Under natural field conditions, where infection may take place at the two or three leaf stage, a different response in plant development may result. Therefore, to examine this possibility and to evaluate the performance of the progeny when these different cultivars were hybridized, a field experiment was conducted.

## Study II: Field Experiment

### BYDV Symptom Expression

In contrast to the lack of visual symptoms in the greenhouse, a strong expression of the disease was noted in the field. It was also apparent than when levels of fall-spring infection are compared with spring infection, that symptom development becomes more conspicuous and severe the earlier infection takes place.

Under field conditions it was not difficult to classify plants based on their visual BYDV score. A wide spectrum of reaction types among plants within segregating populations was found varying from very susceptible to those which appeared to be uninfected. However, when all the parameters were measured, no immunity nor high level of genetic resistance was found.

When the five cultivars are considered, Yamhill appeared to have the highest overall potential for resistance. It showed the lowest BYDV score under a strong field infection which corroborates the findings for Yamhill noted in the greenhouse. For Anza and Novi Sad, it appears that moderate levels of resistance may be present even when intermediate BYDV scores are noted; however, in selecting resistant reactions, it would appear that BYDV scores of 1 or 2 should be considered. Stephens was unquestionably the most susceptible cultivar based on BYDV score with Riebesel showing an intermediate score. When yield reductions were considered, it was found that Riebesel had a greater reduction than Stephens (40% vs 28%, respectively). This suggests that one must know the material they are working with or be careful to verify the BYDV scores with actual yield data as BYDV scores alone, in some circumstances, may be very misleading.

A factor which did add to the complexity of interpreting the resistant mechanism was the presence of a few very diseased plants within the otherwise moderately resistant cultivars, Yamhill, Novi Sad and Anza. Likewise, a limited number of resistant plants were observed within the otherwise susceptible cultivar, Stephens. Assuming that the cultivars are homozygous and homogeneous, the most logical explanation is that these offtype plants were escapes or the cultivars were in fact not genetically uniform. An important factor is that despite a high level of infection, the average yield loss (23.4%) suggests that with the cultivars used in this study a complete breakdown of the defense mechanism did not occur. It is apparent that even the most susceptible cultivar in this study (Stephens) must have some genes for resistance. This is also reflected in that for Stephens there was no difference in kernel weight as the result of BYDV infection. If these cultivars do have different genes for resistance, then accumulation of such genes through breeding would be worthwhile.

As noted earlier, losses due to BYDV attack in wheat seem to be related to the stage of growth when infection occurs. Cisar et al. (1982b) reported 63% and 41% yield decreases for fall vs spring infection, respectively. Carrigan et al. (1981) found 58% reduction in yield under fall infection and 38% for spring infection in 1978 and 33 and 27% reduction for the same comparison the following year.

In the present study there was an early fall infection as the result of the early planting date. This fact was verified by the aphid trap plants. Thus, the cultivars in this study were exposed to the infection for an extended period and may well account for the fact that the moderately resistant cultivars, Yamhill and Novi Sad, sustained a 23 and 15.4% yield reduction, respectively. Had they been planted at the recommended date for commercial production, the yield reduction would not be expected to be as great. Also, other field treatments where the time of infection was delayed through exclusion using cages or the greenhouse data would support that these cultivars do have some mechanism for resistance.

Barley Yellow Dwarf Virus Score and Selected Agronomic Traits

The subjectivity of any visual rating involving BYDV symptoms has been a matter of extensive arguments (Endo and Brown, 1962; Catherall and Hayes, 1967; Dowler and Briggle, 1977; Comeau and Dubuc, 1978). Questions have surfaced as to how effective can a subjective scale of disease judgement be in evaluating and selecting genetic materials when breeding for resistance. Up to what point can disturbing the plant's metabolism be correlated with some visual parameters when coupled with an environmental influence? Most reports confirm that a close relationship between BYDV infection and yield components does exist. Gill (1970) reported a correlation of -0.97 between yield and intensity of BYDV in wheat. For Cisar et al. (1982b), r = -0.65 between disease severity rating and yield was strong enough to ensure the genetic advance toward reduced yield loss by selection based on visual assessment of disease severity. However, Carrigan et al. (1981) and Comeau and Dubuc (1978) note that severe yield reduction can occur without distinct yellowing or dwarfing.

Findings in this study observed that BYDV visual symptoms were strongly negatively correlated with most if not all of the agronomic traits measured under field conditions. When all possible correlations between BYDV score and six agronomic traits are considered, 74% were negative and significant. When tiller number and harvest index are omitted, this percentage increases to 84%. This trend did not change over generations. Thus, the effectiveness of the visual rating system was amply demonstrated for cultivars, $F_1$, $F_2$, $F_3$ crosses and for backcross populations in identifying BYDV resistance.

One exception, Yamhill, deserves special discussion. No significant correlation between disease score and traits except kernel weight was found. This can be attributed either to plant resistance per se or to a poor correlation between virus damage and phenotypic reaction of the cultivar. Stephens and Riebesel with the highest negative phenotypic correlations confirmed their susceptibility to BYDV. Therefore, the variation accounted for by regression was mostly due to linearity of the relation between disease rating and the trait in question. This is in agreement with the high $r^2$ values (0.24 - 0.81) reported for the parental cultivars.

The variation in the magnitude of the correlation values observed for segregating populations suggests that different genetic backgrounds are involved in controlling the BYDV defense mechanism. The correlation between BYDV score and the agronomic traits for $F_1$ crosses involving Yamhill, Novi Sad and Anza are higher than other susceptible x susceptible crosses (i.e.: Stephens/Riebesel). In other words, genetic differences among cultivars are projected at different levels of disease severity within resulting progeny such that the more negative the correlation value the higher degrees of resistance. The question based on the association between visual symptoms and agronomic trait is which of the latter are more affected.

Based on the results of this study, there is no consistent answer as it depended on the specific cultivar. Thus, kernel weight was the only yield component significantly reduced for Yamhill. However, for most cultivars, kernel weight, grain yield, plant height and plant weight, in that order, were the most affected characters by the disease. These traits also showed the highest negative correlation values with BYDV score. Carrigan et al. (1981) and Topcu (1975) reported yield, plant height, kernel weight, kernel number and plant weight, in that order, as being the most affected traits. These traits could be used in assessing plant responses to BYDV infection and may be useful in a selection index in breeding for BYDV resistance.

Harvest index and tiller number were the least affected parameters in measuring the effect of BYDV in this study. Carrigan et al. (1981) obtained similar results for harvest index. Cisar et al. (1982a) point out that fall infection was more damaging than spring infection with traits like kernel weight and harvest index showing reduction for BYDV spring infection only.

## Genetic Control of Resistance

When evaluation the $F_1$ and segregating populations in terms of their frequency distribution, it is apparent that resistance to BYDV is quantitatively inherited and that, unlike barley, no major genes are present for resistance. This is also true for Novi Sad, which had been previously reported to carry a major gene for resistance to BYDV in India. Apparently differences in vectors or perhaps the environment did not support this hypothesis in the Willamette Valley.

The fact that frequency distributions did not fall into distinct classes would suggest that major genes were not involved. They gave a distribution which was generally skewed toward the more resistant parent. This was true for the $F_1$ population which genetically would be expected to represent heterozygous plants but a homogeneous population. Since there was variability within the $F_1$ populations, it is assumed that it was due to the environment. In the cross between the two most susceptible parents, Stephens/Riebesel, the $F_1$ population had an intermediate response with a mean value close to the midparent value. This would suggest that the gene action was predominantly additive in nature. In contrast, the $F_1$ populations from susceptible x resistant crosses tended to be distributed more toward the most resistant parent. This would indicate that at least a portion of the total genetic variability for resistance was controlled by genes behaving in a nonadditive manner. Where resistant x resistant parents were involved, the $F_1$ BYDV score again appeared to be close to the midparent value.

If there were genetic factors contributing to additive genetic variability for resistance, it would be possible to find transgressive segregation in the $F_2$ and $F_3$ generations should the parents have different alleles. Despite the small population sizes, segregates which exceeded one or both parents in reaction to BYDV was apparent, especially when either Stephens or Riebesel were involved in the crosses. When Riebesel was crossed with either Yamhill or Anza, the segregating populations exhibited more transgressive segregates toward the resistant reaction types.

In the $F_3$ generation, it appeared that the variation in symptom expression was under genetic control. For the susceptible x susceptible cross (Stephens/Riebesel) a higher number of progeny favored a susceptible reaction pattern. Where resistant x susceptible cultivars were used (Stephens/Yamhill), a majority of the progeny were classified as resistant. For resistant x resistant crosses (Anza/Novi Sad, Yamhill/Novi Sad or Yamhill/Anza) there was an increase in resistant progeny; however, transgressive segregation for both resistance and susceptibility were noted. The importance of these observations is that it provides further evidence that the cultivars in this study carry different genes for resistance. This suggests that a breeding system where crosses are made to a number of different cultivars, such as used in this study, followed by intermating would offer considerable promise in establishing higher levels of BYDV resistance. Such an approach supports the conclusions reached by Qualset et al. (1973) and Topcu (1975).

Based on the results of this study, it would appear that the nature of inheritance in wheat is similar to that reported in oats by Jedlinski et al. (1977). They reported segregation for marked resistance and susceptibility in progenies from crosses from partially resistant cultivars. On a positive note, the nature of resistance suggested in this study where many genes contribute to resistance in a quantitative manner, may result in more durable type of resistance to BYDV. Since minor genes are involved they would confer resistance to a wide spectrum of strains of the virus thereby preventing a sudden breakdown of resistance which is more likely with major gene or qualitative-type resistance.

## Genetic Correlations

The degree of genetic associations between symptom disease expression and the agronomic traits was also negative. The relationships between plant height, grain yield and plant disease expression had an obvious genetic basis. To a lesser extent was the genetic correlation with plant weight and kernel weight. This association varied depending on the cultivar. These findings indicate that improvement for resistance against BYDV may be feasible for the agronomic traits measured using the visual disease reaction of the individual plants.

The presence of some significant genetic correlation values may suggest a kind of pleiotropic action of the genes controlling certain traits and the activation of the defense mechanism, without discarding the possibility of certain linkage effects mainly because of populations derived from crosses between divergent cultivars (Falconer, 1981). Anza, the spring cultivar, and Riebesel, a European-derived cultivar are examples of such genetic diversity.

Heritability

Narrow sense heritability estimates ranged from 9 to 16% for Stephens/Anza and Stephens/Yamhill, respectively. These are lower than those reported by Brown and Poehlman (1962) (23.3 to 50.8%) and Qualset et al. (1977) (24 to 37%).This confirms the presence of large environmental variance as well as supporting the hypothesis of the quantitative nature of the BYDV resistance. Since narrow sense heritabilities measure that portion of the total genetic variation which is due to genes which behave in an additive manner, such low values might question the effectiveness of phenotypic selection. This is particularly true in the improvement of a self-pollinating species like wheat where the breeder is restricted to using only this form of gene action. Certainly the need to have a uniform infection of known severity will be extremely important if progress is to be made in selecting for resistance.

## Combining Ability

Additional opportunity to study the nature of gene action controlling BYDV resistance was provided by using the combining ability analysis. Combining ability effects can be partitioned into the relative contribution of an individual parent thereby allowing for the selection of parents for resistance to BYDV which may provide a high frequency of desireable segregates. This is particularly important if, as the results of this study suggest, that BYDV resistance in wheat is a quantitatively inherited trait.

General combining ability (GCA) mean squares was highly significant for BYDV score indicating that additive effects of genes are important in determining the resistance of the progeny to BYDV. Those effects can be fixed in the homozygous conditions. Yamhill and Anza produced observable degrees of resistance in their progeny. This was also noted in further generations ($F_2$'s and $F_3$'s) indicating that the additive gene effects for BYDV resistance remained unchanged. Also, transgressive segregation is further evidence that additive genetic variance is available in selected BYDV resistant cultivars.

Specific combining ability (SCA) mean squares was also significant for BYDV score. This finding suggests the presence of nonadditive gene action in the genetic variability was also responsible for BYDV resistance. This effect can not be fixed in successive generations of selfing, however, since some epistatic effects are additive in advanced generations such effects might also be fixed. This is particularly true in a allohexaploid species where intergenomic interactions may occur. Cisar, et al. (1982a) noted the importance of general combining effects in progeny resistant to BYDV.

He did not detect any important role for specific combining ability.

The active role of genes with additive and nonadditive effects governing the expression of resistance to BYDV were clearly noted for the experimental materials used in this study. It appears that GCA effects can help the breeder identify desirable parental combinations. Yamhill and Anza might provide promising combinations with the other parents. Progeny derived from the specific cross, Yamhill/Novi Sad, might also provide promising segregating population materials. It would appear that since the cultivars in this study did have different genetic sources for BYDV resistance, a recurrent selection program would be promising. This would include not only making crosses between the five cultivars, but also intermating among and between resistant plants in the $F_2$ and later generations. In this approach, it would be possible to accumulate those genetic factors for resistance. This could result in not only a high level of BYDV resistance, but also because of the nature of the resistance it would be expected to be more durable over time.

# SUMMARY AND CONCLUSIONS

The objectives of this investigations were: (1) to evaluate methods of detecting and measuring resistance among cultivars, (2) to identify sources of BYDV resistance and (3) to determine the nature of inheritance controlling BYDV resistance.

Experimental materials included four winter-type and one spring-type wheat and the resulting $F_1$, $F_2$, $F_3$, BC-a and BC-2 generations from crosses among the five cultivars.

Two studies were conducted. The first was conducted in the greenhouse where an assessment of the parental lines was made with regard to the injury of aphid feeding and aphids plus the virus. A field experiment was established to obtain information on the nature of inheritance.

The following observations were made based on the performance of the experimental material used in this investigation:

<u>Study 1</u>

1. Visual symptoms were difficult to detect with the most susceptible cultivar, Stephens, showing only moderate yellowing.
2. Aphid feeding, per se, appeared not to be a factor in terms of damage with only Anza and Yamhill showing a reduction in plant weight when exposed to non-viruliferous aphids.
3. Despite the low visual symptom expression, all cultivars were affected by the virus for most parameters measured. Stephens and Riebesel exhibited the greatest reduction for traits like grain yield, plant weight and plant height. Yamhill, Novi Sad and Anza showed the least damage.

4. No complete immunity was observed for any of the cultivars. In general, significant differences can be attributed to the virus rather than the feeding of aphids.

Study 2

1. PAV-BYDV strain and Sitophion avenae (Fabricius) vector were confirmed as being prevalent in this experiment.
2. No immunity nor high levels of resistance was found. However, there were different levels of resistance among cultivars.
3. Stephens appeared to be the most visibly susceptible cultivar by most parameters measured, however, Riebesel showed the highest yield reduction.
4. Yamhill showed the lowest BYDV score and appears to have the highest potential for resistance, followed by Novi Sad and Anza.
5. The BYDV visual scale was useful in assessing the BYDV effects in this study with significant negative correlations between BYDV score and agronomic traits measured. This was especially true for kernel weight, grain yield, plant height and plant weight. Harvest index and tiller number appeared to be the least affected.
6. The $F_1$ and $F_2$ segregating populations favored the resistant parent in susceptible x resistant crosses. For susceptible x susceptible and resistant x resistant crosses, the $F_1$ mean values were similar to the mid-parent values.
7. $F_2$ and $F_3$ frequency distributions suggested that resistance to BYDV was quantitative. Transgressive segregation was detected in all crosses.

8. Low Narrow Sense Heritability Estimates suggest that there is a large environmental component influencing the expression of BYDV resistance.
9. General combining ability values indicated that part of the genetic variability for BYDV resistance is controlled by genes which are additive in action. However, the specific combining ability also suggests the importance of nonadditive gene action.
10. A recurrent selection program using the cultivars in this study followed by intermating between and within $F_2$ generations would be a sound approach in increasing the levels of BYDV resistance.

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Appendix Table 1. Pedigree and Brief Description of Cultivars

**Yamhill:** Heines VII/Redmond (Alba)

A soft white common winter cultivar released by Oregon State University (OSU) in 1969. Late maturity, medium height, high yielding and awnless. Good milling and baking qualities, resistant to stripe rust and powdery mildew. Large fertile spikes and medium to large kernels. Susceptible to leaf rust. Tolerant to BYDV.

**Stephens:** Nord Desprez/Pullman Selection 101

A semidwarf winter cultivar, stiff straw and early maturity, released by OSU in 1975. It has soft white grain, awned, fusiform mid-dense spikes. High yielding, resistant to stripe and leaf rust. Susceptible to *Septoria tritici* and BYDV disease.

**Anza:** (Lerma Rojo $x_3$Norin 10-Brevor)x((Yaktana 54 x Norin 10-Brevor)xAndes$^3$)

Short stature, high yielding spring cultivar. Awned type semi-hard red grain. Susceptible to stripe rust, moderately to leaf rust and resistant to BYDV.

**Riebesel:** Criewener 104/Petkus Rye, D

A soft white winter cultivar. Late maturity, tall, short spike, medium yielding, awned type. Reported as having resistance to BYDV.

**Novi Sad 874-4:** Brkulja-4/NS-325

A hard red winter cultivar, short-medium height. Medium size-dense spike, early maturing, awned. Moderately resistant to stripe and leaf rust. Reported as tolerant to BYDV in India.

Appendix Table 2: Plant Stages for Aphid Transferring in the Greenhouse

| REPLICATION | VERNALIZATION | TRANSPLANTING | APHID TRANSFERRING | DATE |
|---|---|---|---|---|
| I | Jan. 24 | March 3 | Booting Stage | May 1 |
| II | Feb. 9 | April 3 | Tillering | May 21 |
| III | Feb. 25 | April 24 | Tillering | May 21 |
| IV | March 8 | May 2 | 4 leaf stage | May 21 |

Appendix Table 3: Parental Material, $F_2$, $F_3$ and Backcross Populations Originated from $F_1$ Crosses Tested Under Field Conditions

| Treatment Number | Genetic Material | Treatment Number | Genetic Material |
|---|---|---|---|
| 1 | Stephens (Spn) | 31 | Spn/Rb $F_3$ |
| 2 | Riebesel (Rb) | 32 | Spn/Ymh $F_3$ |
| 3 | Yamhill (Ymh) | 33 | Spn/N.S. F3 |
| 4 | Novi Sad 874-4 (N.S.) | 34 | Spn/Anza F3 |
| 5 | Anza (Anz) | 35 | Rb/Ymh F3 |
| 6 | Spn (protected) | 36 | Rb/N.S. F3 |
| 7 | Rb (protected) | 37 | Rb/Anz F3 |
| 8 | Ymh (protected) | 38 | Ymh/N.S. F3 |
| 9 | N.S. (protected) | 39 | Ymh/Anz F3 |
| 10 | Anz (protected) | 40 | N.S./Anz F3 |
| 11 | Spn/Rb F1 | 41 | Spn/Rb//Spn BC-1 |
| 12 | Spn/Ymh F1 | 42 | Spn/Rb//Rb BC-1 |
| 13 | Spn/N.S. F1 | 43 | Spn/Ymh//Spn BC-1 |
| 14 | Spn/Anz F1 | 44 | Spn/Ymh//Ymh BC-1 |
| 15 | Rb/Ymh F1 | 45 | Spn/N.S.//Spn BC-1 |
| 16 | Rb/N.S. F1 | 46 | Spn/N.S.//N.S. BC-1 |
| 17 | Rb/Anz F1 | 47 | Spn/Anz//Spn BC-1 |
| 18 | Ymh/N.S. F1 | 48 | Spn/Anz//Anz BC-1 |
| 19 | Ymh/Anz F1 | 49 | Rb/Ymh//Rb BC-1 |
| 20 | N.S./Anz F1 | 50 | Rb/Ymh//Ymh BC-1 |
| 21 | Spn/Rb F2 | 51 | Rb/N.S.//Rb BC-2 |
| 22 | Spn/Ymh F2 | 52 | Rb/N.S.//N.S. BC-2 |
| 23 | Spn/N.S. F2 | 53 | Rb/Anz//Rb BC-2 |
| 24 | Spn/Anz F2 | 54 | Rb/Anz//Anz BC-2 |
| 25 | Rb/Ymh F2 | 55 | Ymh/N.S.//Ymh BC-2 |
| 26 | Rb/N.S. F2 | 56 | Ymh/N.S.//N.S. BC-2 |
| 27 | Rb/Anz F2 | 57 | Ymh/Anz//Ymh BC-2 |
| 28 | Ymh/N.S. F2 | 58 | Ymh/Anz//Anz BC-2 |
| 29 | Ymh/Anz F2 | 59 | N.S./Anz/N.S. BC-2 |
| 30 | N.S./Anz F2 | 60 | N.S./Anz//Anz BC-2 |

Appendix Table 4. Barley Yellow Dwarf Virus Visual Rating Scale (Qualset et al., 1973)

| SCORE | SYMPTOM DESCRIPTION |
|---|---|
| 1 | Disease free; No visible yellowing of leaves. Plant may be immune or escaped infection. |
| 2 | Trace amounts of yellowing at the tips of a few leaves; vigorous plant appearance. |
| 3 | Restricted yellowing of leaves; larger proportion of yellowed areas; relative to class 2, more leaves were discolored. |
| 4 | Moderate to low amount of yellowing, no sign of dwarfing or reduction in tillering. |
| 5 | Moderate to somewhat extensive yellowing; no dwarfing, moderate to good plant vigor. |
| 6 | More extensive yellowing, moderate to poor plant vigor; some dwarfing. |
| 7 | High level of yellowing, poor plant vigor, apparent dwarfing. |
| 8 | Severe yellowing, small spikes, moderate dwarfing poor plant appearance. |
| 9 | Nearly complete yellowing of all leaves, dwarfing; tillering apparently reduced (rosette appearance), reduced spike size with some sterility. |
| 10 | Marked dwarfing; complete yellowing, few or no spikes with considerable sterility; forced maturity or drying of the plant before normal maturity is reached. |

Appendix Table 5. Observed mean values, mean squares, standard deviations and coefficient of variance for BYDV score obtained at booting and heading stages of plant growth from five wheat cultivars and derived segregating populations. Field Experiment.

| Date | DF | MS | x | Sx | CV |
|---|---|---|---|---|---|
| Booting Stage | 59 | 3.61** | 3.27 | 0.493 | 26.17 |
| Heading Stage | 59 | 3.51** | 4.31 | 0.583 | 23.43 |

**: Significant at the one percent probability level.

r = 0.87**

N = 60

Appendix Table 6. Frequency distribution for BYDV score for parents, F1, F2, F3 and backcross generations. Classifications based on disease visual score with 1-3 being considered resistant and 4-10 susceptible. Field Experiment.

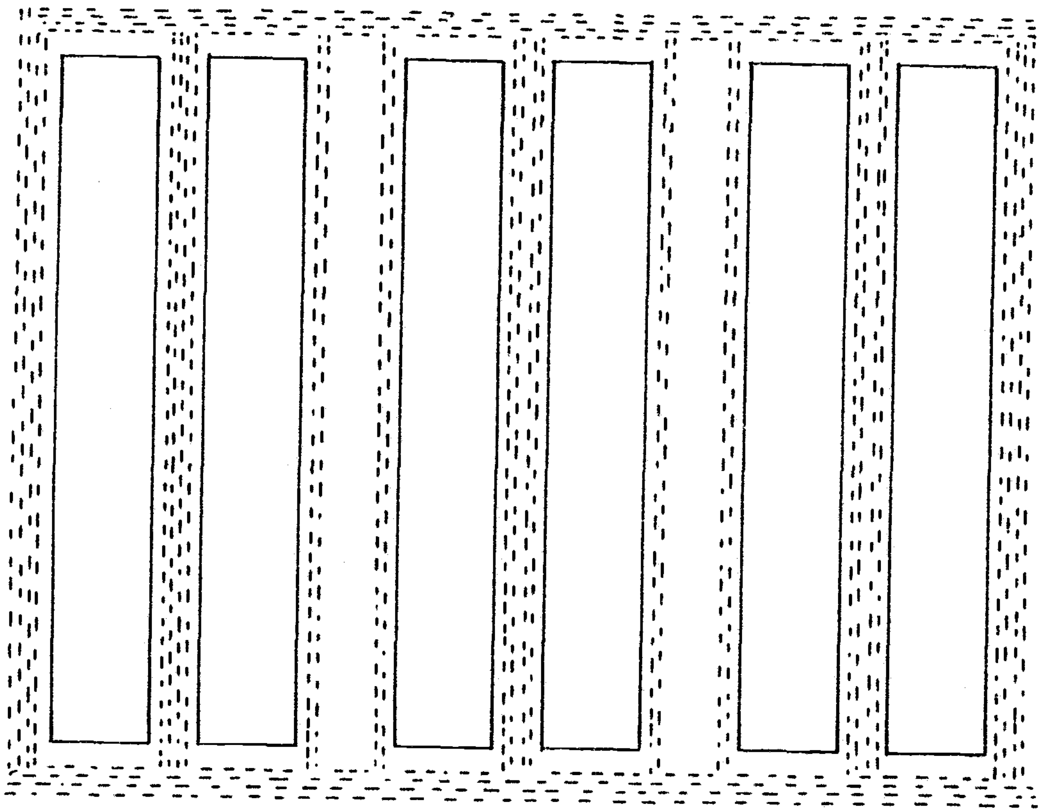
| Parent or Generation | Disease Score | | | | | | | | | | Model I | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | R(1-3) | S(4-10) |
| Spn | 0 | 1 | 2 | 0 | 1 | 3 | 3 | 8 | 7 | 5 | 3 | 27 |
| Rb | 1 | 2 | 5 | 3 | 2 | 7 | 4 | 2 | 1 | 0 | 8 | 19 |
| F1 | 1 | 3 | 3 | 8 | 0 | 7 | 5 | 2 | 1 | 0 | 7 | 23 |
| F2 | 1 | 6 | 10 | 12 | 3 | 9 | 10 | 4 | 3 | 2 | 17 | 43 |
| F3 | 0 | 2 | 9 | 12 | 4 | 3 | 3 | 5 | 3 | 4 | 11 | 34 |
| BC-1 | 2 | 7 | 4 | 1 | 3 | 8 | 10 | 5 | 1 | 4 | 13 | 32 |
| BC-2 | 4 | 3 | 8 | 8 | 1 | 8 | 3 | 3 | 4 | 3 | 15 | 30 |
| Spn | 0 | 1 | 2 | 0 | 1 | 3 | 3 | 8 | 7 | 5 | 3 | 27 |
| Ymh | 3 | 5 | 13 | 6 | 2 | 1 | 0 | 0 | 0 | 0 | 21 | 9 |
| F1 | 6 | 9 | 5 | 5 | 0 | 1 | 2 | 2 | 0 | 0 | 20 | 10 |
| F2 | 7 | 8 | 8 | 8 | 8 | 8 | 5 | 6 | 2 | 0 | 23 | 37 |
| F3 | 3 | 5 | 7 | 7 | 2 | 10 | 4 | 2 | 0 | 0 | 15 | 25 |
| BC-1 | 3 | 10 | 8 | 5 | 3 | 8 | 4 | 2 | 1 | 1 | 21 | 24 |
| BC-2 | 9 | 2 | 7 | 8 | 3 | 9 | 3 | 2 | 0 | 2 | 18 | 27 |
| Spn | 0 | 1 | 2 | 0 | 1 | 3 | 3 | 8 | 7 | 5 | 3 | 27 |
| NS | 4 | 8 | 7 | 4 | 1 | 2 | 0 | 1 | 2 | 1 | 19 | 11 |
| F1 | 4 | 8 | 5 | 3 | 6 | 0 | 4 | 0 | 0 | 0 | 17 | 13 |
| F2 | 2 | 4 | 4 | 9 | 13 | 13 | 8 | 4 | 1 | 2 | 10 | 50 |
| F3 | 0 | 9 | 8 | 7 | 6 | 8 | 3 | 2 | 1 | 1 | 17 | 28 |
| BC-1 | 1 | 10 | 5 | 7 | 6 | 4 | 4 | 6 | 1 | 1 | 16 | 29 |
| BC-2 | 4 | 6 | 7 | 8 | 9 | 5 | 3 | 1 | 1 | 2 | 17 | 29 |
| Spn | 0 | 1 | 2 | 0 | 1 | 3 | 3 | 8 | 7 | 5 | 3 | 27 |
| Anz | 3 | 5 | 6 | 1 | 3 | 4 | 1 | 1 | 0 | 0 | 14 | 10 |
| F1 | 13 | 7 | 4 | 1 | 0 | 3 | 1 | 0 | 1 | 0 | 24 | 6 |
| F2 | 4 | 4 | 9 | 15 | 4 | 8 | 4 | 9 | 3 | 0 | 17 | 43 |
| F3 | 1 | 9 | 4 | 5 | 5 | 4 | 1 | 2 | 2 | 0 | 14 | 19 |
| BC-1 | 1 | 9 | 10 | 8 | 4 | 6 | 3 | 3 | 1 | 0 | 20 | 25 |
| BC-2 | 0 | 2 | 3 | 1 | 3 | 4 | 9 | 3 | 3 | 2 | 5 | 25 |
| Rb | 1 | 2 | 5 | 3 | 2 | 7 | 4 | 2 | 1 | 0 | 3 | 27 |
| Ymh | 3 | 5 | 13 | 6 | 2 | 1 | 0 | 0 | 0 | 0 | 21 | 9 |
| F1 | 1 | 8 | 12 | 4 | 2 | 2 | 1 | 0 | 0 | 0 | 21 | 9 |
| F2 | 9 | 7 | 8 | 10 | 3 | 13 | 5 | 2 | 2 | 1 | 24 | 36 |
| F3 | 1 | 3 | 9 | 7 | 10 | 7 | 6 | 1 | 0 | 1 | 13 | 32 |
| BC-1 | 8 | 12 | 8 | 11 | 0 | 3 | 1 | 1 | 1 | 0 | 28 | 17 |
| BC-2 | 14 | 6 | 8 | 5 | 5 | 4 | 3 | 0 | 0 | 0 | 28 | 17 |

Appendix Table 6. (continued) Frequency distribution for BYDV score for parents, F1, F2, F3 and backcross generations. Classifications based on disease visual score with 1-3 being considered resistant and 4-10 susceptible. Field Experiment.

| Parent or Generation | Disease Score | | | | | | | | | | Model I | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | R(1-3) | S(4-10) |
| Rb | 1 | 2 | 5 | 3 | 2 | 7 | 4 | 2 | 1 | 0 | 3 | 27 |
| NS | 4 | 8 | 7 | 4 | 1 | 2 | 0 | 1 | 2 | 1 | 19 | 11 |
| F1 | 1 | 5 | 6 | 7 | 3 | 3 | 1 | 3 | 1 | 0 | 12 | 18 |
| F2 | 0 | 3 | 8 | 7 | 10 | 8 | 8 | 5 | 5 | 6 | 11 | 49 |
| F3 | 0 | 4 | 4 | 1 | 2 | 6 | 11 | 4 | 6 | 7 | 8 | 37 |
| BC-1 | 1 | 6 | 7 | 5 | 4 | 9 | 7 | 2 | 2 | 2 | 14 | 31 |
| BC-2 | 3 | 5 | 5 | 9 | 9 | 8 | 1 | 0 | 0 | 0 | 13 | 27 |
| Rb | 1 | 2 | 5 | 3 | 2 | 7 | 4 | 2 | 1 | 9 | 3 | 27 |
| Anz | 3 | 5 | 6 | 1 | 3 | 4 | 1 | 1 | 0 | 0 | 14 | 10 |
| F1 | 12 | 8 | 6 | 6 | 3 | 0 | 0 | 0 | 0 | 0 | 26 | 9 |
| F2 | 2 | 16 | 9 | 7 | 7 | 10 | 6 | 3 | 0 | 0 | 27 | 33 |
| F3 | 7 | 8 | 11 | 6 | 5 | 3 | 2 | 2 | 1 | 0 | 26 | 19 |
| BC-1 | 6 | 5 | 4 | 7 | 3 | 7 | 4 | 4 | 3 | 2 | 15 | 30 |
| BC-2 | 1 | 6 | 8 | 9 | 9 | 7 | 1 | 1 | 2 | 1 | 15 | 30 |
| Ymh | 3 | 5 | 13 | 6 | 2 | 1 | 0 | 0 | 0 | 0 | 21 | 9 |
| NS | 4 | 8 | 7 | 4 | 1 | 2 | 0 | 1 | 2 | 1 | 19 | 11 |
| F1 | 3 | 6 | 12 | 7 | 7 | 0 | 0 | 0 | 0 | 0 | 21 | 14 |
| F2 | 5 | 9 | 8 | 16 | 4 | 8 | 5 | 2 | 2 | 1 | 22 | 38 |
| F3 | 5 | 7 | 8 | 8 | 3 | 7 | 4 | 1 | 1 | 1 | 20 | 25 |
| BC-1 | 6 | 8 | 12 | 8 | 4 | 4 | 2 | 0 | 1 | 0 | 26 | 19 |
| BC-2 | 4 | 6 | 10 | 9 | 7 | 8 | 1 | 0 | 0 | 0 | 29 | 25 |
| Ymh | 3 | 5 | 13 | 6 | 2 | 1 | 0 | 0 | 0 | 0 | 21 | 9 |
| Anz | 3 | 5 | 6 | 1 | 3 | 4 | 1 | 1 | 0 | 0 | 14 | 10 |
| F1 | 5 | 3 | 4 | 6 | 7 | 1 | 3 | 0 | 1 | 0 | 12 | 18 |
| F2 | 2 | 8 | 11 | 5 | 10 | 11 | 9 | 3 | 1 | 0 | 21 | 39 |
| F3 | 3 | 4 | 6 | 6 | 11 | 8 | 5 | 2 | 0 | 0 | 13 | 32 |
| BC-1 | 3 | 7 | 6 | 5 | 6 | 6 | 6 | 3 | 3 | 0 | 16 | 29 |
| BC-2 | 3 | 5 | 2 | 4 | 3 | 6 | 9 | 2 | 2 | 0 | 10 | 26 |
| NS | 4 | 8 | 7 | 4 | 1 | 2 | 0 | 1 | 2 | 1 | 19 | 11 |
| Anz | 3 | 5 | 6 | 1 | 3 | 4 | 1 | 1 | 0 | 0 | 14 | 10 |
| F1 | 1 | 11 | 8 | 2 | 2 | 4 | 1 | 1 | 0 | 0 | 20 | 10 |
| F2 | 0 | 0 | 7 | 8 | 3 | 11 | 15 | 4 | 5 | 4 | 7 | 50 |
| F3 | 0 | 7 | 13 | 10 | 3 | 4 | 4 | 2 | 2 | 0 | 20 | 25 |
| BC-1 | 9 | 13 | 10 | 6 | 4 | 1 | 0 | 0 | 0 | 0 | 32 | 11 |
| BC-2 | 11 | 9 | 11 | 7 | 3 | 1 | 2 | 0 | 0 | 1 | 31 | 14 |

Appendix Table 7. Observed chi square results for BYDV score using backcross populations to test for either a 3:1 or 1:1 ratio depending on the specific cross.

| | $F_2$ | | BC | |
|---|---|---|---|---|
| | $x^2$ | P value | $x^2$ | P value |
| Stephens x Riebesel | 0.36 | 0.75-0.50 | 296.2** | <.001 |
| Stephens x Novi Sad | 0.36 | 0.75-0.50 | 4.29* | .05-0.025 |



Appendix Figure 1. Aphid trap (mixture of barley and oat plants) planted around the experimental area. (Field Experiment)