Barley Yellow Dwarf

A Proceedings of the Workshop

December 6-8, 1983 CIMMYT Mexico

Sponsored by: The United Nations Development Programme and CIMMYT

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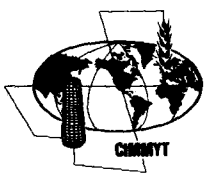

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P.A. Burnett
Workshop Organizer

Participants of the Barley Yellow Dwarf workshop. See Appendix II for a complete listing.

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Preface

P.A. Burnett, Wheat Program, CIMMYT, Mexico

"It does not do to leave a live dragon out of your calculations if you live near him" (J.R.R. Tolkien, 1978). Barley yellow dwarf virus (BYDV) is just such a dragon and all of us who are working with cereals are living very near him. His fire and smoke may vary in intensity from season to season, but he is alive and well and capable of causing damage in most cereal growing areas of the world.

Barley yellow dwarf (BYD), an aphid transmitted disease, attacks all of the small grain cereals, including bread wheat, durum wheat, barley, oats and triticale; it is ubiquitous in the world's cereal crop. The virus also infects at least 100 other grass species, including maize and rice, and these hosts can act as reservoirs of the virus and aphid hosts.

BYDV has only recently been recognized in the developing world as a serious constraint to the production of wheat, barley, oats and triticale. The insidious nature of the disease makes it difficult to diagnose, particularly in wheat. This has resulted in a lack of recognition of the magnitude of the losses it causes on a global scale.

In the USA, losses due to BYD are estimated to be between one and three percent annually. However, it is known that, under conditions favorable to the development and spread of the virus, losses up to 40% are not uncommon. Recent reports of losses due to BYD in developing countries throughout the world have led to the conclusion that it probably has one of the most extensive but least known distribution patterns of any disease affecting cereal crops. BYD unquestionably results in the loss of substantial amounts of important food grains.

Advances in technology in the developed countries are making possible more accurate diagnosis of BYDV; many problems associated with the disease are still ill-defined in the developing countries.

The Workshop

The technical expertise for BYDV research is currently located in only a few institutions, mainly in the developed world. In order to share this technology with researchers from developing countries, the United Nations Development Programme sponsored a BYD workshop at CIMMYT on December 6 to 8, 1983. The workshop was attended by selected professionals from developing countries and from research institutions in the developed world. A list of the participants is included in these proceedings (Appendix II).

The workshop program—The workshop began with reports by the participants on the importance of BYD in their various countries. These short situation reports reviewed the incidence of BYD, the yield losses it causes and the current state of knowledge on BYD in the countries or regions represented. CIMMYT outreach staff gave further information whenever possible.

Papers were then presented by selected contributors in the following areas:

- Biology of the virus, the plant and the aphid;
- Resistance to BYD and resistance screening techniques for all of the small grains;
- Control of BYD by chemical and/or cultural methods;
- Methods for surveying for the incidence of BYD;

- Purification of BYDV;
- Specific BYD research programs, and
- *Diuraphis noxia*, an aphid recently recognized as creating problems in cereals; it may also be a vector of BYDV.

The workshop objectives—The benefits of holding such a BYD workshop are several. The major benefit was that a global forum was established, permitting the exchange of information and views among researchers from developing countries and their counterparts from the developed countries. The workshop provided an opportunity for the representatives from the developing countries to acquire much of the BYDV knowledge which exists in developed country institutions. Similarly, it enabled the representatives from the developed countries to gain an understanding of the extent of the disease in the developing world. It has led to cooperative liaisons between a number of developing and developed country scientists.

The publication of the workshop proceedings provides a comprehensive benchmark as to the present status of BYD. It is hoped that this document will stimulate an awareness of the importance of BYD, as well as provide a concise review of the work being carried out in the field.

Barley Yellow Dwarf

In this introduction to the workshop proceedings, the following aspects of BYD will be touched upon:

- History
- Classification
- Symptoms
- Host Range
- World Distribution
- Vectors
- Virus Isolates
- Yield Losses

Some of these areas are more thoroughly covered in papers by other authors in this publication.

Historical Background of BYD

The disease of cereals and grasses now known as BYD was recognized as an aphid transmitted virus disease by Oswald and Houston in 1951. Much earlier, however, workers had noted disorders of plants that are now considered to have been BYD. Possibly the earliest record of the disease in the USA was in 1890 when Galloway and Southwood published a paper entitled "Preliminary Notes on a New and Destructive Oat Disease."

In 1909, Manns, in his review of red leaf of oats, said that he believed that red leaf was due to a simultaneous infection of the plant by two bacteria in a symbiotic relationship, and that this infection was aided by cool, damp weather (Bruehl, 1961). In 1907, in Ohio, Thorne and Gossard had noted that a large number of aphids and thrips were associated with oat crops that had these symptoms, but whether or not the insects had anything to do with the disease was not known (Bruehl, 1961). These observations led Manns to take English grain aphids, *Sitobion avenae*, from diseased plants and cage them on healthy seedlings. He found that, after 10 to 12 days, the plants inside the cage showed symptoms of the disease while those outside did not. He wrongly concluded that the aphids were vectors for a bacteria.

Barrus (1937) described a red leaf disease of oats that was prevalent and had long been known in New York State. Reports of similar types of symptoms in cereals were made by McKinney (1950) and Johnston (1951). Moore (1952) reported aphid transmission of red leaf of oats; much earlier, he had recognized the disease

as being one of virus etiology and aphid transmission, but failed to make a formal report. In many other countries there were reports of physiological reddening of oats, which was most likely a symptom of barley yellow dwarf.

It was, perhaps, a mistake to name the virus barley yellow dwarf virus instead of cereal yellow dwarf virus as some of the early researchers had suggested. The name barley yellow dwarf virus can lead to confusion, especially among administrators and funding agencies, giving the impression that the virus is only a problem of barley and not of other cereal crops. However, the name is too well established to contemplate changing it.

Classification of BYDV

BYDV belongs to the luteovirus group, members of which cause the yellows diseases; other economically important members of the group are beet western yellows and potato leaf roll. The term BYDV includes several related viruses (Rochow and Duffus, 1981). Properties of these virions include:

- Isometric particles of approximately 25 nm in diameter;
- A single-stranded RNA genome, molecular weight 2.0 x 10^6d;
- A protein coat of molecular weight 24 x 10^3 d;
- A sedimentation coefficient of 115 to 118 S;
- Strongly immunogenic reactions;
- Replication confined to the phloem, and
- Persistant transmission by aphids (Mathews, 1979).

Plumb (1983) states in his review, "BYD is probably best considered as a convenient all-embracing name for diseases with similar symptoms and effects that are caused by persistently aphid transmitted viruses, only some of which are serologically related."

Symptoms of BYD

The symptoms of BYD vary with the crop cultivar, the age of the plant at time of infection, the strain of virus, the number of aphids present and environmental conditions.

It appears that the virus interferes with translocation by partially plugging the phloem. It can cause severe stunting of plants, inhibition of root formation, delaying or prevention of heading and reduction in yield. BYDV often causes the following color changes in cereal plants:

- Barley: A bright yellow discoloration begins at the leaf tip and margins and moves rapidly down the whole leaf. This symptom may sometimes be confused with nitrogen deficiency; BYDV-infected plants, however, may be found scattered throughout the crop, while nitrogen deficiency generally appears more uniform.
- Oats: Leaves turn reddish or purple, sometimes with yellowing and stiffening of the whole plant. Seed heads are often badly blasted.
- Wheat, rye and triticale: Leaves yellow and sometimes show a little reddening; occasionally the edges of wheat leaves may be serrated.In infected areas of wheat crops, the ears stay erect and may become black and discolored during ripening due to infestations by fungal pathogens. Rye expresses few symptoms.
- Maize: The lower leaves show purpling and yellowing.
- Rice: Leaves turn yellow to orange; the discoloration begins at the tips and edges and progresses down the leaf.

Cultivars vary in their susceptibility or resistance to the virus. In general, wheat is more resistant to BYDV than oats and barley; some primitive barleys are immune. Typically, discoloration begins 7 to 20 days after infection. Among the cereals, the incubation time of the virus is usually longer in barley than in oats and is still longer in wheat.

Until quite recently, the only practical method for diagnosing BYDV was by transmission with aphids to indicator plants with the resulting development of typical disease symptoms. Recently, the enzyme-linked immunosorbent assay (ELISA) has been developed. However, in a great many parts of the world, diagnosis of BYDV still has to be carried out on the basis of symptoms alone, as workers do not have the facilities to carry out the aphid transfers that have served researchers in the developed countries so well.

Host Range of BYDV

Oswald and Houston (1951) reported that wheat, oats and barley were susceptible to BYDV. Bruehl (1961) summarized many studies and produced a list of 97 susceptible species from 34 genera within the family Gramineae. His list included rye, corn, sorghum, rice and most of the common grass species, e.g., Kentucky bluegrass, cocksfoot, timothy, perennial ryegrass and bromegrass. Slykhuis (1967) reported that about 100 species of grasses were susceptible to BYDV and warned that some were symptomless. He also stated that no dicotyledonous plants were known to be susceptible.

Bruehl (1961) pointed out that, because of the extremely wide host range of this virus among long-lived grass species, there was little chance of its being eradicated as a result of the elimination of the host. He cautioned, however, that most host-range studies have been carried out in the greenhouse where the viruliferous aphids are forced to feed on the plant species being tested, and that the recorded range may not therefore represent a true host range in the field. Nevertheless, in most areas where BYD occurs in cereals, noncereal grasses play a role in the epidemiology of the disease. Between 50 and 80% BYDV infection has been reported in pasture grasses in countries where surveys have been taken (Latch, 1977; Fargette *et al.*, 1982).

World Distribution of BYD

The BYD disease is ubiquitous. A search of the literature will show that it has been recorded from most areas of the world (Bruehl, 1961; Slykhuis, 1962; 1967). The absence of reports of BYD occurring in certain areas is probably due to a lack of recognition of the disease or a lack of work having been done on it. The situation reports in these proceedings offer a comprehensive report on the distribution of BYD, especially in the developing countries. As Plumb (1983) states, BYD is truly a global problem.

Vectors of BYDV and their Biology

The principal vectors of BYDV are the aphids, *Rhopalosiphum padi*, *R. maidis*, *Sitobion avenae*, *Shizaphis graminum* and *Metopolophium dirhodum*. Comprehensive lists of the aphid vectors have recently been published by A'Brook (1981), 23 species, and Jedlinski (1981), 18 species.

The relative importance of the different aphid species as vectors of BYDV varies from country to country or from region to region. The vectors have never been found to occur all together, and they have never been tested simultaneously for comparative transmission efficiency with a single virus isolate. The importance of transient aphids as vectors of BYDV has also not been studied.

BYDV is not transovarially transmitted to the progeny of vectors; however, nymphs may be just as effective as adults in transmitting the virus. Whether or not aphids involved in vectoring BYDV have an alternative host that is not a source of BYDV can be important in the epidemiology of the disease. For example, in Britain, gynoparae and males can transmit BYDV and so act as a source of infection even though they cannot supply progeny to spread the infection. Spring migrants from the alternative host are virus free (Plumb, 1983), a fact further complicated by some aphid species having alternative hosts in some countries and not in others; *R. padi*, for example, alternates hosts in Britain but not in New Zealand.

Long distance migrations of viruliferous aphids may be important in some continents or countries and not in others. In North America, long distance migrations of *S. graminum* and *S. avenae* and subsequent BYDV infection are associated with low-level jet winds (Wallin and Loonan, 1971). In Canada, large numbers of winged aphids have been observed to appear on cereal crops within the period of a day.

It is important that researchers study aphid biology and the epidemiology of BYD in the countries or areas where they are working; conclusions cannot be drawn from results obtained by workers in other areas.

In these proceedings, F.E. Gildow discusses the biology of the aphid vectors of BYDV and the effects of BYDV on those vectors.

Isolates of BYDV

Isolates of BYDV have been grouped according to their vector specificity. The groups are designated by the initial letters of their principal vector or vectors (Rochow 1970; 1979):

- RPV - transmitted specifically by *Rhopalosiphum padi*;
- RMV - transmitted specifically by *R. maidis*;
- MAV - transmitted specifically by *Macrosiphum avenae*, now called *Sitobion avenae*;
- SGV - transmitted specifically by *S. graminum*, and
- PAV - transmitted nonspecifically by *R. padi* and *S. avenae*.

Sometimes an additional variant is included:

- SGV - transmitted nonspecifically, but transmitted most efficiently by *S. graminum* (Gill, 1969).

Recent work has shown that these five BYDV isolates can be divided into two groups by serological comparisons. It seems that the RPV and RMV types are related and distinct from the MAV and PAV types which also are related. The SGV isolate appears to have some antigens in common with PAV (Rochow and Carmichael, 1979). This grouping agrees with that produced by the comparison of ultrastructural changes found in the tissue of oat plants infected by the different isolates of BYDV (Gill and Chong, 1976; 1979).

Identifying BYDV isolates by vector specificity can be complicated by a phenomenon termed "dependent transmission." The suggestion is that, during simultaneous synthesis of the two virus isolates, MAV and RPV, the protein of RPV sometimes encapsulates the nucleic acid of MAV, allowing it to be acquired and transmitted by *R. padi* (Rochow, 1977).

Relationships between isolates from different parts of the world are unknown. However, a British PAV-like isolate reacts in serologically specific electron microscopy (SSEM) tests with a broad spectrum of antisera (PAV + RPV) from Kentucky, USA, as well as with the homologous antiserum. The British antiserum also has been used to detect a virus from Chile (Plumb, 1983). It must be stressed that typing a virus isolate still tells nothing about its virulence or pathogenicity.

Again, a quote from Plumb (1983) seems appropriate: "Recent evidence of relationships among BYDV, beet western yellows virus and potato leaf roll virus . . . suggests that BYD is caused by only some of a continuous, overlapping range of viruses." The paper contributed by Lister et al. in these proceedings deals with this subject in greater detail.

A letter has been received from W.F. Rochow, Research Plant Pathologist for the USDA stationed at Cornell University, Ithaca, New York, USA; it discusses nomenclature for the BYDV isolates. The letter was circulated among the participants in this workshop and is included in these proceedings in an attempt to solicit constructive comments that may lead to a standard naming system (Appendix I).

Yield Losses Due to BYD

Many workers have attempted to estimate the losses in yield caused by BYD. Bruehl (1961) and Rochow (1961) both summarized the losses found in the USA. The occurrence and extent of the disease throughout the USA, area by area, can be found in The Epidemic of Barley Yellow Dwarf on Oats in 1959, Supplement 262, Plant Disease Reporter. At the 1977 meeting of cereal virologists at Urbana, Illinois, a 1 to 3 percent annual yield loss was suggested, but it was stressed that losses may reach 20 to 30 percent.

It is extremely difficult to quantify accurately the losses due to BYD as the epiphytotics of the disease are irregular in both time and space, i.e., BYD can occur in one year in one area and not in another immediately adjacent; then it may not occur again for several years.

Many techniques have been used for measuring losses due to BYD. One recommended method is that used in California, a comparison of the yield of isogenic barley lines with and without the *Yd2* gene (CM 67, tolerant, and California Mariout, susceptible). These cultivars are compared in the field under prevailing conditions. In 19 location x yield comparisons, the tolerant cultivar had a mean yield superiority of 19% over its susceptible counterpart (California situation report, these proceedings). This shows the value of breeding for resistance to BYD and gives a measure of the potential loss due to BYD.

In Australia, average losses historically have been thought to be around two percent; when an epiphytotic occurs (every 5 to 7 years), losses in afflicted areas are much higher (Australia situation report, these proceedings). In Britian, it is difficult to give an estimate because of regional and seasonal differences but, because of the value of the cereal crop, a yield loss of even one to two percent is worth eliminating (Britain situation report, these proceedings).

Gill (1980) reported a seven percent loss due to BYD in spring wheat in Manitoba, Canada. His was a realistic figure as it was based on an estimate of the percentage of infected plants; yields were then measured on plants expressing various symptoms.

Although it is difficult to measure or estimate losses due to BYD, readers are referred to the situation reports contained in these proceedings for recent estimates of yield losses in different parts of the world. It must be stressed again that BYD does have epiphytotics, causing much higher losses some years. Therefore, the losses expressed in the reports are often only potential losses; they do, however, highlight the necessity of breeding for resistance to BYD and the urgency with which well-adapted sources of resistance are required.

In closing, let me say that organizing this workshop has been a pleasure, as was the presence here at CIMMYT of all of the workshop participants. It is hoped that these proceedings will be useful both to them and to others with an interest in the BYD problem.

References

A'Brook, J. 1981. Vectors of barley yellow dwarf virus. Euraphid: Rothamsted 1980, L.R. Taylor, ed. Rothamsted Experimental Station, Harpenden, UK. P. 21.

Barrus, M.F. 1937. Red leaf and blast of oats. Plant Disease Reporter 21:359-361.

Bruehl, G.W. 1961. Barley yellow dwarf, a virus disease of cereals and grasses. Monograph no. 1. American Phytopathological Society.

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

Fargett, D., R.M. Lister and E.L. Hood. 1982. Grasses as a reservoir of barley yellow dwarf virus in Indiana. Plant Disease 66:1041-1045.

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

Gill, C.C. 1969. Annual variation in strains of barley yellow dwarf virus in Manitoba, and the occurrence of greenbug-specific strain isolates. Canadian Journal of Botany 47:1277-1283.

Gill, C.C. 1980. Assessment of losses on spring wheat naturally infected with barley yellow dwarf virus. Plant Disease 64:197-203.

Gill, C.C., and J. Chong. 1976. Differences in cellular ultrastructural alterations between variants of barley yellow dwarf virus. Virology 75:33-47.

Gill, C.C., and J. Chong. 1979. Cytopathological evidence for the division of barley yellow dwarf virus isolates into two subgroups. Virology 95:59-69.

Jedlinski, H. 1981. Rice root aphid, *Rhopalosiphum rufiabdominalis*, a vector of barley yellow dwarf virus in Illinois, and the disease complex. Plant Disease 65:975-978.

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

Latch, G.C.M. 1977. Incidence of barley yellow dwarf virus in ryegrass pastures in New Zealand. New Zealand Journal of Agricultural Research 20:87-89.

Mathews, R.E.F. 1979. Classification and nomenclature of viruses: third report of the International Committee on Taxonomy of Viruses. Intervirology 12:129-296.

McKinney, H.H. 1950. Infectious and noninfectious pigment disorders in the small grains, with particular reference to the southeastern areas. Plant Disease Reporter 34:151-154.

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

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

Plumb, R.T. 1983. Barley yellow dwarf virus - a global problem. *In* Plant Virus Epidemiology, R.T. Plumb and J.M. Thresh, eds. Backwell Scientific Publications, Oxford. Pp. 185-198.

Rochow, W.F. 1961. The barley yellow dwarf virus disease of small grains. Advances in Agronomy 13:217-248.

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

Rochow, W.F. 1977. Dependent virus transmission from mixed infections. *In* Aphids as Virus Vectors, K.F. Harris and K. Marmorosch, eds. Academic Press, New York. Pp. 253-273.

Rochow, W.F. 1979. Field Variants of barley yellow dwarf virus: detection and fluctuation during 20 years. Phytopathology 69:655-660.

Rochow, W.F., and L.E. Carmichael. 1979. Specificity among barley yellow dwarf viruses in enzyme immunosorbent assays. Virology 95:415-420.

Rochow, W.F., and J.E. Duffus. 1981. Luteoviruses and yellows diseases. *In* Handbook of Plant Virus Infections and Comparative Diagnosis, E. Kurstak, ed. Elseveir/North Holland Biomedical Press, Amsterdam. Pp. 147-170.

Slykhuis, J.T. 1962. An international survey for virus diseases of grasses. FAO Plant Protection Bulletin no. 10.

Slykhuis, J.T. 1967. Virus disease of cereals. Review of Applied Mycology 46:401-429.

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

2

Welcome to the Barley Yellow Dwarf Workshop

R.D. Havener, Director General, CIMMYT, Mexico

On behalf of the wheat group and the entire CIMMYT staff, it is indeed my pleasure to welcome you to CIMMYT for our second Barley Yellow Dwarf Workshop. The first was in December 1980, with perhaps a dozen participants from some half-dozen countries; a few of you were present then. If I read the program correctly, there are some forty or fifty participants from 25 or 26 countries here for this second workshop, a three-year expansion that is phenomenal. If we project this rate of growth over the next fifteen years, CIMMYT will not have the facilities necessary to host the workshop in 1998.

Just prior to the time of that first workshop, the late Dr. Glenn Anderson was in a European country and asked whether the scientists meeting with him were doing research on the barley yellow dwarf virus (BYDV) disease. The answer they gave him was, "No, we have never seen it in our country, and our producers have no problem with it." That conversation took place while they were standing in a half-acre patch that Glenn believed showed symptoms of being seriously infected with BYDV. The recognition level has gone up substantially in the three years since that time.

Last year, Dr. Curtis and I had the pleasure of being in Australia for the 1983 Australian Plant Genetics Symposium. On that occasion, Dr. Albert Pugsley, widely recognized as the dean of wheat specialists in Australia, said that barley yellow dwarf was the single most important disease causing economic losses of small grains in the world today. That may be a slight overstatement, but at least one wheat expert is convinced that your work here this week is very serious and economically important.

The result of the first BYD workshop was a proposal for a coordinated global network of scientists working on the barley yellow dwarf virus disease, and the hope was that the network would be funded by one or more international donors. CIMMYT was given the challenge of mobilizing the external resources to fund the project. This, it turned out, has not been an easy task; the aid climate in the world generally is not favorable at the present time and, perhaps more importantly, most of the major work on BYDV today is being conducted in the developed countries. It is relatively easy to get the government of a developed country to sponsor research in a developing country, but it is not easy, for example, to obtain US AID money to sponsor research in Australia or Australian money to sponsor research in Canada. Therefore, sustained funding has been difficult to mobilize for a global BYDV network.

Available resources, however, have increased. The United Nations Development Programme is now supporting Peter Burnett's salary at CIMMYT, where he is spending the bulk of his time on coordination activities related to BYDV. In addition, UNDP is funding a major portion of the cost of this workshop. CIMMYT is also committing its own resources to an expanded effort on the BYDV program. In some of the countries you represent we have been marginally successful in assisting in the mobilization of government resources to support your own research on BYDV.

The most serious limiting factor is that of funding for networking across national boundaries to adequately support a truly international program. We are, however, not pessimistic and, later this week, we will be reporting on steps we have taken. It looks as though, in the near future, we will have some increase in funds available for networking. In the meantime, I can assure you that, within CIMMYT's available resources, we will continue to allocate funds to help the global scientific community attack this important problem.

I wish you every success in this workshop.

3

Contributed Papers

Biological Differences Between Barley Yellow Dwarf Viruses in Relation to their Epidemiology and Host Reactions

R.M. Lister, D. Clement and M. Skaria, Purdue University, and J.E. Foster, United States Department of Agriculture, Purdue University, USA

The term barley yellow dwarf virus (BYDV) includes at least five variously interrelated viruses or types (Gill, 1967; Rochow, 1969; Rochow and Muller, 1971). Their symptomatology may differ, but the fundamental distinguishing criterion is vector relationship, as suggested by the acronyms of Rochow for his isolates of each type, which were derived from the names of their vectors. For example, the MAV isolate of Rochow (loc. cit.) is specifically transmitted by *Macrosiphum* (= *Sitobion) avenae*, the RPV isolate by *Rhopalosiphum padi*, the SGV isolate by *Schizaphis graminum* and the RMV isolate by *R. maidis*; Rochow's PAV isolate is nonspecifically transmitted by both *R. padi* and *M. avenae*. Each of these isolates probably exemplifies a group that may include a continuum of variants differing from each other with respect to some feature (e.g., Allen, 1957). Overall, however, serotype grouping (Aapola and Rochow, 1971; Rochow and Carmichael, 1979), ultrastructural effects (Gill and Chong, 1976; 1979) and other major features appear to follow separation by vector relationship. These features indicate some general affinities between isolates of the PAV, MAV and SGV types, RPV and RMV types, and also between isolates of the RPV type and beet western yellows virus (Rochow and Duffus, 1981).

From the practical point of view, the important properties distinguishing the cereal-yellowing luteoviruses are the biological ones influencing disease causation and spread. Of these, specificity of transmission and host reaction to infection are crucial.

Virus-vector specificity appears to depend on the specificity of receptor sites in the aphid with respect to the viral capsid protein (Gildow and Rochow, 1980; Gildow, 1982). It is not absolute, and one factor potentially influencing the frequency of nonspecific transmission in the field is the frequency of mixed infections, from which heterologously coated viral genomes can be transmitted because of the transcapsidation phenomenon (Rochow, 1965; 1982). However, vector specificity underlines the epidemiology of BYDV, and a knowledge of the occurrence and dymanics of specific virus types and vectors is basic for understanding virus ecology and spread. In turn, this knowledge is a basis for designing strategies for management and control, including the choice of appropriate cereal cultivars known to resist the effects of the locally significant types of BYDV.

Host reactions to BYDV have been categorized by plant breeders as susceptible or resistant, terms describing the relative severity of the diseases caused by BYDV types in different cultivars and selections, especially in relation to yield. These criteria clearly govern whether or not BYDV is important in a given situation. However, another component of host reaction is the extent to which virus accumulates in a given host. For some viruses, symptomatic resistance has been correlated with reduced virus replication (Bancroft and Pound, 1954; Bjorling, 1966; Gidding, 1964). There is evidence that this is also true of BYDV in some virus/host combinations (Jedlinski *et al.*, 1977). Thus, the possibility exists that virus content could provide a genetic marker for some types of resistance to BYDV. Moreover, it has also been suggested that cultivars symptomatically resistant to BYDV may be relatively poor sources of virus for transmission by vectors because of reduced virus content (Jedlinski *et al.*, 1977). If so, regardless of any relationship with symptoms, reduced virus content could have profound epidemiological effects, making it in itself an attribute worth selecting for in breeding programs and for virus management.

Because of difficulties in detection, differential diagnosis and virus assay, detailed information on the ecology, epidemiology and host relationships of BYDV has been hard to acquire. Now, however, with the advent of enzyme-linked immunosorbent assay (ELISA) applications (Lister and Rochow, 1979), this situation should change rapidly. This contribution reviews recent Purdue studies of differences in the epidemiology of BYDV types and their capacity to accumulate in specific cereals, as assessed by ELISA.

Occurrence and Epidemiology of BYDV in Indiana

Soft red winter wheat is the third most important arable crop in Indiana, accounting for about 450,000 hectares annually. Wheat is sown from mid-September to late October, overwinters as young tillered plants and is harvested in July. Although most is grown in the southern half of the state, wheat is cultivated throughout the arable crop areas, alongside corn and soybeans (the major crops) and in farm areas contiguous with cultivated and wild perennial grasses.

Occurrence in grasses and cereals—In 1980 and 1981, surveys were conducted to investigate BYDV occurrence in those potential reservoir hosts, the perennial grasses, mainly *Poa pratensis* L. and *Festuca arundinacea* (Fargette *et al.*, 1982). Samples were tested against antisera to PAV, RPV and MAV types of BYDV, and the results indicated that BYDV was common and widespread in perennial grasses throughout the state; around 50% of the samples were infected. The predominant virus type detected, both at the Purdue Farm, close to Lafayette, and elsewhere, was the RPV type. During the same period, however, surveys of cereals at the Purdue Farm suggested that isolates of the PAV type predominated among infections in winter wheat and spring oats, even when they were surrounded by perennial grasses infected with isolates of the RPV type.

Other, more intensive tests of cereal samples conducted in 1981, 1982 and 1983, using PAV and RPV antisera (D. Clement *et al.*, unpublished), confirmed the prevalence of isolates of the PAV type. Similarly, tests made in 1982 on cereal samples collected more widely in Indiana, as well as in ten other states, indicated that cereal infections were predominantly of the PAV type. In this wide-range sampling, 73% of 66 oat samples contained PAV types and 3% contained RPV types; 91% of 23 wheat samples contained PAV types and 22%, RPV types.

During 1981, 1982 and 1983, intensive surveys of sets of 12 wheat plots, distributed through a rotation experiment at the Purdue Farm, gave more information on the relative prevalence of PAV and RPV types and also indicated when virus spread occurred (Table 1). Thus, in June 1981, 78% of wheat plants sampled near maturity were infected; 76% of them contained PAV-type viruses and 10%, RPV-type viruses. Most of the latter were mixed infections of RPV and PAV types. In March 1982, 20% were infected, 13% containing PAV types and 10% containing RPV types; most of the latter contained RPV types alone. By June of 1982, 83% of samples were infected, 82% containing PAV types and 21% containing RPV types, all but one of which were mixed infections with PAV types. In March 1983, 27% of samples were infected and, again, most of those that contained RPV types were infected with those alone. March samplings, collected before resumption of plant growth and before aphid arrival, provide an index of infection from sowing to the onset of severe winter conditions, whereas June samplings summarize infections for the entire growing season. Interestingly, the percentage of infections in samples in June 1983 was close to that of those of March 1983, indicating there had been essentially no further infections in wheat during the spring of 1983. The absence of new infections in wheat that spring was associated with

Table 1. Incidence of BYDV in Samples from Wheat Plots in the Integrated Pest Management Experiment at the Purdue Agronomy Farm, 1981-1983[a/]

Date of sample collection	Number of samples	Virus infections (%)			
		ELISA – positive for:			
		PAV	RPV	PAV & RPV	Total
June, 1981[b/]	370	76	10	8	78
March, 1982[c/]	216	13	10	3	20
June, 1982	504	82	21	20	83
March, 1983	216	24	3	0.5	27
June, 1983	360	22	9	3	28

a/ Clement *et al.*, unpublished
b/ June sample results indicate infections that occurred the previous fall or during the spring
c/ March sample results indicate infections that occurred the previous fall

exceptionally low aphid populations in April and May. However, BYDV did spread into oats at the Purdue Farm in 1983; 42 of 100 oat samples collected from a field in June were infected, 36 with PAV types and 100 with RPV types. Presumably this spread occurred too late in the season to be detectable in wheat.

Besides indicating very high rates of infection in wheat in 1981 and 1982, and that PAV types were overall more prevalent than RPV types, these data suggest that RPV types occurred together with PAV types in infections occurring in wheat in spring and summer of 1981 and 1982, whereas during the fall of 1981 and 1982 this was not the case. A survey of an oat field at the Purdue Farm in June 1982 also indicated that RPV was always found together with PAV in infections that occurred in the 1982 growing season. Of 300 symptomatic and nonsymptomatic plants collected from the field, 74% yielded PAV types and 12% yielded RPV plus PAV types. No samples contained RPV types alone.

Taken together, these results suggest that spread from local grass reservoir hosts may contribute significantly to total infections in the fall, but is overshadowed by spread from other sources in the spring and summer in typical seasons. Evidence of a large influx of PAV-type viruses into wheat and oat crops during spring and summer, coupled with relatively low prevalence of this type of virus in grass reservoir hosts, argues a distant origin for the virus infecting cereals during that time. Also, as perennial grass reservoirs could presumably accumulate various BYDV types over time, the fact that they predominantly contain RPV types suggests that they may be more susceptible to them. As RPV and PAV types have a common vector, aphid preference does not seem to be a factor. Similar disparities between the BYDV types found in local grasses and those occurring in cereals have also been reported elsewhere (Rochow and Muller, 1974; 1976; Plumb, 1977). These indications of biological differences between RPV and PAV types, capable of influencing virus epidemiology, merit further study.

Time of spread—To investigate when BYDV spread occurs, pots containing five to ten oat bait plants were placed alongside wheat plots in an arable area, in grass, and alongside oats or wheat in a plot surrounded by a grass area (Clement *et al.*, 1983; and unpublished). A total of 116 pots were thus exposed at approximately weekly intervals in each of the growing seasons of 1981, 1982 and 1983, 72 alongside wheat, 22 in grass and 22 by oat/wheat plots. After exposure, the bait plants were examined for aphids, sprayed with insecticide and grown for a further two weeks in the greenhouse. The grouped plants in each pot were then tested by ELISA for the presence of RPV and PAV virus types. Data for 1983 is not yet complete, but those for 1981 and 1982 showed similar patterns of virus spread and aphid activity (Figure 1). In both years, aphid occurrence on bait plants peaked abruptly in April and then fell in late May to June; another major peak of activity occurred in the fall and a minor one in August between wheat crops. Virus infections in bait plants roughly coincided with those peaks of aphid activity. Infections occurred in 50% of the pots exposed during a particular period and, overall, 70 to 85% of the infections detected were of the PAV type. Infections with RPV occurred sporadically throughout the exposure periods, but about one-half of those occurring in 1981 were in October. Patterns of infection were similar, regardless of plot location.

In each year, aphid activity appeared suddenly in late April and subsided in late May to June. A second peak of activity occurred August to October,

with a summer peak in July and August, between wheat crops, and perhaps associated with population build-up on volunteer wheat and oats. Rapid onset of a high degree of aphid activity in spring, together with disparity between the virus types found in local grasses and the cereals themselves, again suggests that BYDV is spread into the crop at that time from a distance. A mechanism for this influx exists in the low-level jet winds which have been suggested as explaining movement of *S. graminum* northwards from southern states (Hodson and Cook, 1960), the spread of maize dwarf mosaic virus to sweet corn crops in Minnesota, far from reservoir hosts (Zeyen and Stromberg, 1977), and the spread of BYDV itself (Wallin and Loonan, 1971). Indications from the data for 1983 so far seem to indicate that virus spread has been far less than that of 1981 and 1982. The spring peak of aphid activity was delayed, and this may be associated with anomalous weather conditions, including a more northerly than usual location of the interface between major cold and warm air masses; this may have affected the pattern of the low-level jet winds. Meteorological data for the three years have yet to be compared in detail.

In late fall, there is also the possibility of spread back to local wheat crops from corn infected by viruliferous aphids from volunteer wheat and oats, for an *R. padi* build-up to high populations was noted on corn in September and October in both 1981 and 1982. Sampling of apterous aphids from corn ears both years indicated 2 to 5% infections, again of the PAV type. Populations did not build up prior to corn senescence in 1983.

In summary, a major source of BYDV for Indiana wheat is likely to be in those aphid populations moving from distant crops in wind currents, especially in the spring. Transmission from grasses seems likely to occur sporadically throughout the season, but may contribute most significantly to infections in the fall. Aphid populations in the fall probably include components from both distant crops and local sources, especially corn crops, whenever appropriate population build-up has occurred on them. The epidemiology of BYDV in the Midwest is clearly very complex, and detailed understanding will require much more extensive investigation. One feature requiring explanation is why the epidemiologies of the RPV and PAV types appear to differ, even though they have a common vector.

BYDV Symptomatology and Virus Content

The complexity of the epidemiology of BYDV in the Midwest, and the fact that its epidemics seem typically to be open rather than closed, i.e., to have significant input from distant sources of virus, support the use of virus resistance rather than crop or vector management as the primary basis for disease control. Therefore, in a second series of experiments, the question was asked as to whether symptom severity reflected virus content in cereals infected with BYDV. If so, the virus content assay could be a basis for breeding for reduced virus production and could provide a tool for plant breeders to follow resistance more precisely. The results have shown that whether or not this is the case depends on the BYDV type involved as well as on the cultivar.

Seedlings of selected cultivars were inoculated with the PAV, MAV or RPV isolates by aphid infestations and placed in a growth chamber at 20°C with 14 hours of illumination. Subsequently, three samples of five random plants each were collected at four to six day intervals for about one month. Roots and shoots (all above-ground portions) of those plants were separated, weighed, and extracted for ELISA comparisons of virus content.

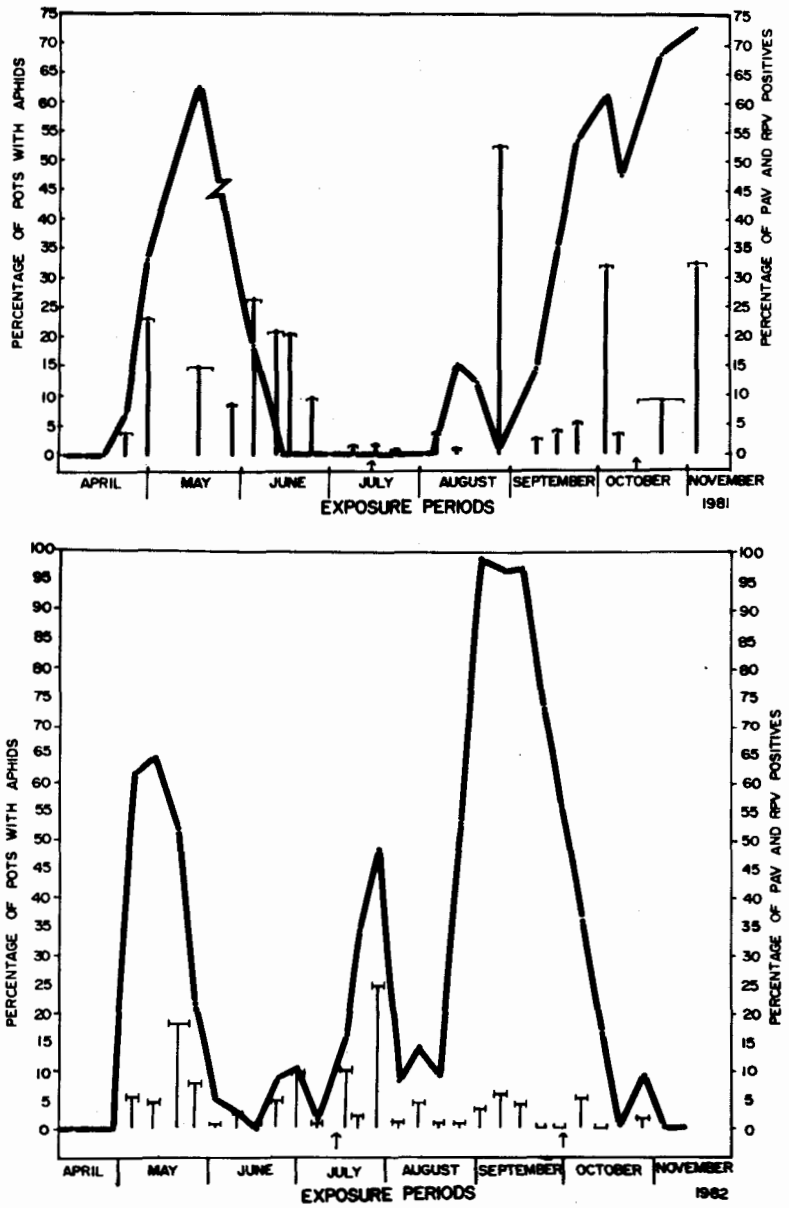

Figure 1. Aphid activity and seasonal spread of BYDV as indicated by its incidence in oat bait plants exposed at the Purdue Agronomy Farm, 1981 and 1982

Some of the results (Skaria *et al.*, 1983; and unpublished) are illustrated in Figure 2. Initially, pairs of barley, oats and wheat were compared, one member of each having been previously assessed by plant breeders as resistant (R) and one as susceptible (S) on the basis of symptoms, especially yield reduction. The barleys were California Mariout (S) (Weibe and Reid, 1961) and CM 67 (R)

(Schaller and Chim, 1969); the oats were Clintland 64 (S) (Patterson and Schaffer, 1978) and Porter (R) (Ohm *et al.*, 1982) and the wheats were Abe (S) (Patterson *et al.*, 1975) and Elmo (R) (Ohm *et al.*, 1981).

Of the barley pair, the California Mariout (S) samples contained more virus in both shoots and roots after inoculation with PAV than did those of CM 67 (R). Similarly, shoots of Clintland 64 (S) yielded more PAV than Porter (R), although their roots contained similar amounts of virus. No difference in PAV content was noted between the wheats; this remained true in experiments in which the wheats were vernalized after inoculation to simulate overwintering.

Of these pairs, the barleys were selected because they were near-isogenic; however, CM 67 (R) contains the Yd_2 gene, a factor identified in some Ethiopian barleys that confers symptomatic resistance to BYDV (Rasmusson and Schaller, 1959). Further experiments examined two other near-isogenic pairs distinguished by the presence or absence of the Yd_2 gene. These were selections from Atlas crosses, A 68 (+ Yd_2) and A 57 (-Yd_2) and Prato (+ Yd_2) and Briggs (-Yd_2) (all kindly supplied by C.W. Schaller). In each case, the selections containing Yd_2 yielded significantly less virus when inoculated with the PAV isolate.

Since the PAV and MAV isolates are more closely related to each other in several respects than either is to RPV, there was interest in comparing their effects. When the original barley pair, California Mariout (S) and CM 67 (R), were infected with MAV, no significant differences were noted in virus content; the result was the same when they were infected with RPV. With the oat pair, however, Clintland 64 (S) infected with MAV yielded more virus than Porter (R), although there was no such difference with RPV. With the wheat pair, small but statistically significant differences in virus contents occurred between Abe (S) and Elmo (R) when infected with MAV, but not when infected with RPV.

Some of the studies with barleys and oats have been checked over two seasons in field trials with plants inoculated with PAV or RPV. Results have been similar, thus validating the short-term growth chamber experiment as a substitute for field experiments taking much longer. In summary, the results confirm that for some virus/host combinations, symptomatic resistance as determined in plant breeding work is associated with reduced virus productivity. However, the effect is both cultivar and virus-type specific. The virus type specificity of the effect could be an important consideration in breeding for resistance. It also extends the range of biological differences between the various disparate viruses presently covered by the term BYDV.

Acknowledgements

This contribution reviews recent work conducted as part of the general cooperative program in cereal breeding at Purdue, involving several other colleagues. Their cooperation is acknowledged as well as that of Dr. C.W. Schaller, in discussions, supplying seed, etc. Expert technical assistance by Jo Anne McFatridge is also acknowledged. Various aspects of the work have received support from Special Grant No. 9011542 from the United States Department of Agriculture Science and Education Administration, from the USDA Agricultural Research Service Integrated Pest Management Project at Purdue and from the Indiana Crop Improvement Association.

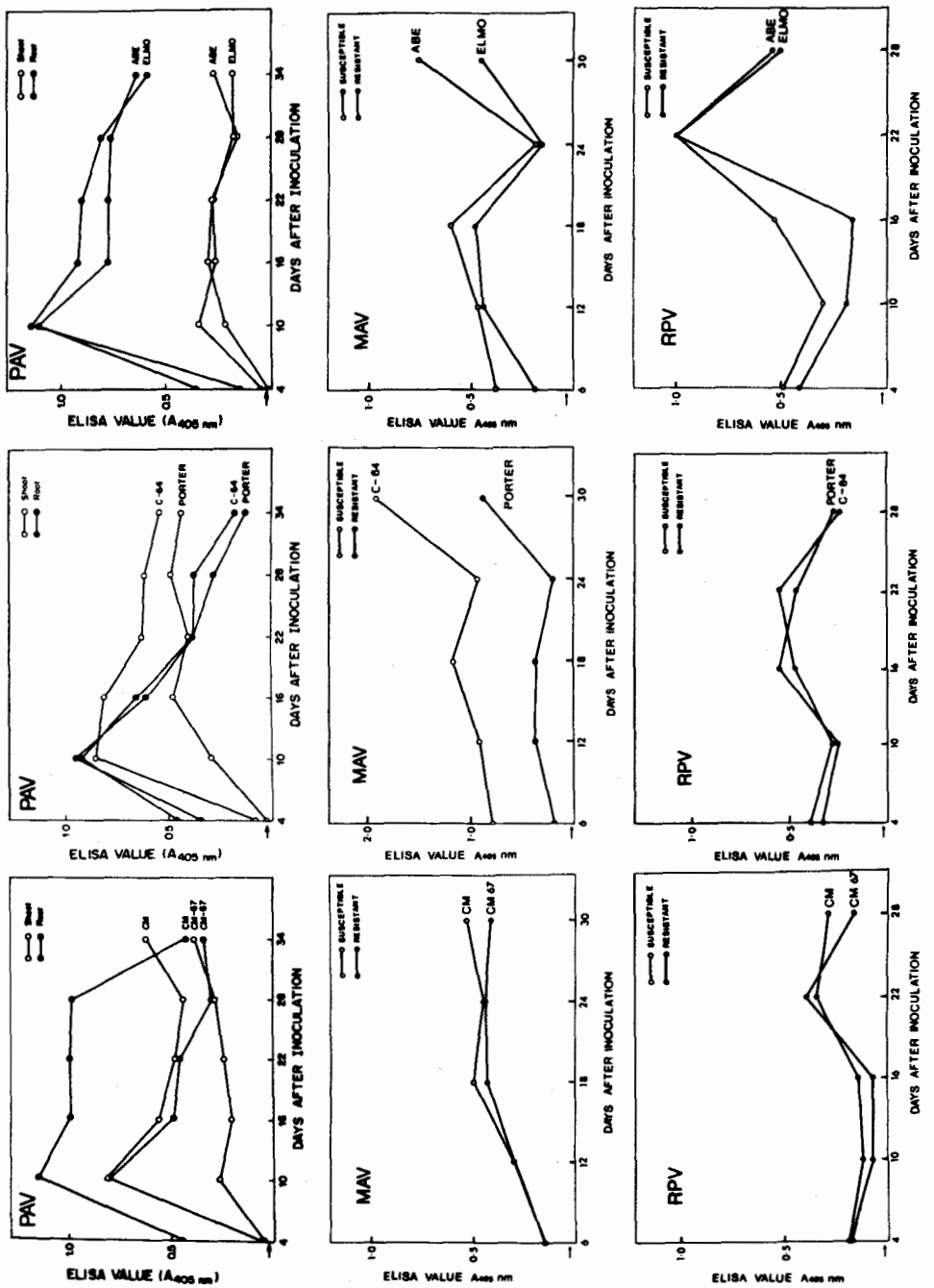

Figure 2. Comparisons of virus contents of samples of paired resistant or susceptible cereal cultivars infected with PAV isolate of BYDV (Skaria *et al.*, 1983; and unpublished)

References

Aapola, A.I.E., and W.F. Rochow. 1971. Relationships among three isolates of barley yellow dwarf virus. Virology 46:127-141.

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

Bancroft, J.B., and G.S. Pound. 1954. Effects of air temperature on multiplication of tobacco mosaic virus in tobacco. Abstract. Phytopathology 44:481-482.

Bjorling, K. 1966. Virus resistance problems in plant breeding. Acta Agriculturae Scandinavica Supplement 16:119-136.

Clement, D., R.M. Lister and J.E. Foster. 1983. Occurrence and spread of barley yellow dwarf virus in Indiana. Abstract. Phytophatology 73:790.

Fargette, D., R.M. Lister and E.L. Hood. 1982. Grasses as a reservoir of barley yellow dwarf virus in Indiana. Plant Disease 66:1041-1045.

Gidding, N.J. 1964. Some factors in fluencing curley top virus concentration in sugar beets. Phytopathology 36:38-52.

Gildow, F.E. 1982. Coat-vesicle transport of luteoviruses through salivary glands of Myzus persicae. Phytopathology 72:1289-1296.

Gildow, F.E., and W.F. Rochow. 1980. Role of accessory salivary glands in aphid transmission of barley yellow dwarf virus. Virology 104:97-108.

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

Gill, C.C., and J. Chong. 1976. Differences in cellular ultrastructural alterations between variants of barley yellow dwarf virus. Virology 75:33-47.

Gill, C.C., and J. Chong. 1979. Cytopathological evidence for the division of barley yellow dwarf virus isolates into two subgroups. Virology 95:59-69.

Hodson, A.C., and E.F. Cook. 1960. Long-range aerial transport of the harlequin bug and the greenbug into Minnesota. Journal of Economic Entomology 53:604-608.

Jedlinski, H., W.F. Rochow and C.M. Brown. 1977. Tolerance to barley yellow dwarf virus in oats. Phytopathology 67:1408-1411.

Lister, R.M., and W.F. Rochow. 1979. Detection of barley yellow dwarf virus by enzyme-linked immunosorbent assay. Phytopathology 69:649-654.

Ohm, H.W., F.L. Patterson, L.L. Carrigan, G.E. Shaner, J.E. Foster, R.E. Finney and J.J. Roberts. 1981. Registration of Elmo common wheat germplasm. Crop Science 21:803.

Ohm, H.W., F.L. Patterson, G.E. Shaner, J.E. Foster, R.E. Finney and J.J. Roberts. 1982. Registration of Porter spring oat. Crop Science 22:447-448.

Patterson, F.L., R.L. Gallun, J.J. Roberts, R.E. Finney and G.E. Shaner. 1975. Registration of Arthur 71 and Abe wheat. Crop Science 15:736.

Patterson, F.L., and J.F. Schafer. 1978. Registration of Clintland 60 and Clintland 64 oats. Crop Science 18:354-355.

Plumb, R.T. 1977. Grass as a reservoir of cereal viruses. Annals of Phytopathology 9:361-364.

Rasmusson, D.C., and C.W. Schaller. 1959. The inheritance of resistance in barley to the yellow-dwarf virus. Agronomy Journal 51:661-664.

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

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

Rochow, W.F. 1982. Dependent transmission by aphids of barley yellow dwarf luteoviruses from mixed infections. Phytopathology 72:302-305.

Rochow, W.F., and L.E. Carmichael. 1979. Specificity among barley yellow dwarf viruses in enzyme immunosorbent assays. Virology 95:415-420.

Rochow, W.F., and I. Duffus. 1981. Luteoviruses and yellows diseases. *In* Handbook of Plant Virus Infections and Comparative Diagnosis, E. Kurstak, ed. Elsevier/North Holland Biomedical Press, Amsterdam.

Rochow, W.F., and I. Muller. 1971. A fifth variant of barley yellow dwarf virus in New York. Plant Disease Reporter 55:874-877.

Rochow, W.F., and I. Muller. 1974. Mixed infections of barley yellow dwarf isolates in winter grains. Plant Disease Reporter 58:472-475.

Rochow, W.F., and I. Muller. 1976. Gradual change in predominating isolates of barley yellow dwarf virus in New York. Plant Disease Reporter 60:387-390.

Schaller, C.W., and C.I. Chim. 1969. Registration of CM 67 barley. Crop Science 9:521.

Skaria, M., R.M. Lister, J.E. Foster and G.E. Shaner. 1983. Barley yellow dwarf virus content as an index of symptomatic resistance in cereals Abstract. Phytopathology 73:793.

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

Weibe, G.A., and D.A. Reid. 1961. *In* Classification of Barley Varieties Grown in the United States and Canada in 1958. USDA-ARS Technical Bulletin no. 1224.

Zeyen, R.J. and E.L. Stromberg. 1977. The 1977 MDMV epidemic: long distance aphid flight hypothesis. *In* Sweet Corn Disease Report. Food Processors' Association, Minnesota. Pp. 4-15.

Comments

G. Herrera and C. Quiroz, Chile

The distribution of BYDV and some epidemiological factors have been studied in Chile in research based on the collection of samples from affected areas and the counting of vector populations on experimental plots and on commercial wheat fields.

It has been concluded that BYDV is present from Vallenar in the north to Valdivia in the south, with a higher frequency of PAV-like isolates in the northern part of the country and a mixture of PAV and MAV-like isolates in the south. The counting of vector populations from 1976 to 1980 indicated that the aphids decreased in population during those years. Also, variations were observed in time of arrival to the fields and relative abundance of the different BYDV transmitting species, *R. padi*, *S. avenae*, *M. dirhodum* and *S. graminum*.

R.T. Plumb, UK

It is important to be able to distinguish between strains of BYDV both biologically and serologically, as the interaction between strains and their vectors is the underlying cause of crop loss. The initial step in any investigation of BYDV should be to determine, as far as possible, which vectors and virus strains are present and which are prevalent. This will indicate the extent of the existing problem as well as future problems that may result, especially from changes in crop husbandry.

While much is known about the relative efficiencies of vectors and the effects of different strains on cereal crop growth, information on the role of sources of viruses is often scanty. BYDV rarely survives perennially on cereals, although in some regions (e.g., France) there seems to be at least a partial alternation between maize and small grain cereals. In most regions, grasses, either wild or cultivated, provide the principal perennial source. It is, therefore, interaction between vectors and virus strains on those hosts which probably determine which strains of BYDV are introduced into crops. Once cereals are infected, the factor determining virus spread is probably the size of the population of the most efficient vector(s) on the crop.

While there is no doubt as to the need for distinguishing between strains of BYDV both biologically and serologically, there is concern among pathologists that the concept of the disease BYD may be lost as knowledge of the viruses that cause it increases.

For serological diagnosis, it has been found to be quite satisfactory to work with two serologically distinct strains which seem to have a broad spectrum of relationships to isolates from Britain, Australia and Chile. Conversely, isolates of BYDV in Britain have been effectively detected by antisera prepared in the USA and Switzerland.

For practical purposes, there is a question of how specific antisera need to be for BYDV diagnosis. Once the range of virus isolates and their vectors have been determined, the principal need is for a reliable method of diagnosis, not necessarily one that unequivocally identifies the strain. The achieving of such detailed identification may be of more trouble that it is worth, especially in relatively poorly equipped field laboratories. However, if differential resistance (tolerance) to strains of BYDV should be shown, the need to distinguish isolates accurately becomes obvious.

H. Jedlinski, Illinois, USA

Different isolates of BYDV vary greatly in the level and spectrum of virulence, vector specificity and the rapidity with which they produce symptoms. With better understanding of the inter-relationships of luteoviruses, the group to which BYDV belongs, different BYDV isolates could be used more effectively in screening for tolerance in the identification of divergent sources of resistance in small grains. It is important from the standpoint of epidemiology and control to know which member and type of the luteovirus group is prevalent, which plant host species represent the virus reservoir, which vectors are most important and their relationships.

A shift in prevalence from a vector nonspecific PAV-type to a specific RPV strain, both transmitted by *R. padi*, as well as a mixture of the two, has been noted in Illinois in recent years. The isolates exhibit different levels of virulence and synergism in oats. Their identification by transmission tests at Urbana and enzyme-linked immuno-sorbent assays by W.R. Rochow at Ithaca, New York, have been in full agreement. Research is in progress to assess the effect of synergism of virus-host interactions in different oat and winter wheat genotypes.

Biology of Aphid Vectors of Barley Yellow Dwarf Virus and the Effect of BYDV on Aphids

F.E. Gildow, Pennsylvania State University, USA

Of the 3,742 identified aphid species (Eastop, 1977), only 18 species have been reported to transmit barley yellow dwarf virus (BYDV) to cereals (Jedlinski, 1981). The best known vectors of BYDV include *Metopolophium dirhodum*, *Rhopalosiphum maidis*, *R. padi*, *Schizaphis graminum* and *Sitobion avenae*. Other closely related species are important BYDV vectors in various geographical locations (Jedlinski, 1981; Vickerman and Wratten, 1979).

The biology, relating to survival, of any vector aphid population may be relatively simple or complex. Some aphid species are monoecius, feeding and completing their sexual life cycle on only one type of plant, e.g., *S. avenae* and *R. maidis* on Gramineae. Other aphids are heteroecious and require more than one host to complete the sexual cycle. The best known of the BYDV vectors with a dioecious cycle is *R. padi*. This aphid responds to decreasing photoperiod and temperature in the fall by producing males and oviparous females which feed, mate and deposit eggs on bird cherry trees (*Prunus padus* L.); the following spring the eggs hatch as females (fundatrix) which are capable of asexual pathenogenetic viviparous reproduction. Progeny produced by these females are all parthenogenetic females (emigrants) which eventually disperse to feed and reproduce on cereals and grasses (Dixon, 1973). This type of holocyclic life cycle, one which involves a sexually produced egg, is necessary for aphid survival in harsh climates. In mild temperate and tropical climates, however, most BYDV vector species are probably able to survive as anholocyclic asexually reproducing females.

Effects of Host Plants on Cereal Aphids

The parthenogenetic females found on cereals during the growing season may mature as either winged (alatae) or nonwinged (apterae) adults; all aphid nymphs are believed to possess primordial wingbuds (Johnson and Birk, 1960). Whether or not wings develop depends on both intrinsic and extrinsic factors influencing aphid physiology. The concentration of juvenile hormone, produced by the corpus allatum endocrine gland, plays a key role in regulating wing development (Dixon, 1973). External factors also influencing aphid morphology include tactile stimulation resulting from crowding, temperature and photoperiod (Lees, 1966) and nutrition (Schaefers, 1972).

Age or growth stage of cereal grains has been reported to influence aphid development in several ways. Studies by Walters and Dixon (1982) indicate increased attraction for and increased reproduction of *S. avenae* on wheat plants at flowering and at water-ripe stages as compared to wheat at other growth stages. Reproductive rates and generation times were also shown to differ among *S. avenae* reared on oats of different ages (Watt, 1979). Wheat plants in the late stages of growth have also been shown to favor induction of

winged alatae of *S. avenae* as compared to young plants (Watt and Dixon, 1981). This substantiates an earlier report by Dean (1978) that only nonwinged apterae of *S. avenae* were observed in grain fields early in the season; alatae appeared only in midseason when plants were beginning to mature and senesce. The above reports indicate important effects of host plant physiology on aphid development and suggest that senescing cereals favor alatae production in some aphid species.

Effect of BYDV-Infected Plants on Aphid Vectors

Cereals infected with BYDV have also been shown to influence aphid vectors. Both *S. avenae* (Miller and Coon, 1964) and *R. padi* (Markkula and Laurema, 1964) have been reported to have higher reproductive capacity on BYDV-infected plants than on healthy controls. In addition, evidence suggests that alatae emigrants show a preference for BYDV-infected plants during dispersal (Ajayi and Dewar, 1983).

While rearing English grain aphids (*S. avenae*) on healthy or BYDV-infected oats for electron microscope studies of virus transmission, more aphids were observed to mature as winged alatae on infected plants than on healthy plants. Several futile attempts to rear nonwinged apterae on BYDV-infected oats suggested that this phenomenon was not coincidental, and that BYDV-infected plants infuence aphid wing development. To test this hypothesis, a series of experiments were conducted under controlled conditions on New York clones of *S. avenae* and *R. padi* (Gildow, 1980). Virus-free adults were allowed to produce nymphs for 24 or 48 hours on healthy oats (*Avena byzantina* Koch, Coast Black) or on oats previously infected with BYDV. The adults were then removed and the progeny allowed to mature on the plants in a growth chamber at 21°C with a 16-hour photoperiod. Winged and nonwinged forms were then counted on healthy and BYDV-infected plants.

The results of ten separate experiments indicated a consistent difference in the alatae production of *S. avenae* when reared on healthy as opposed to BYDV-infected oats. Of 1,254 nymphs reared on BYDV-infected oats, 69% matured as alatae, compared to only 32% of 1,204 nymphs reared on healthy oats. Similar experiments showed that the ability of the aphid to transmit BYDV was not related to the increase in alatae progeny. In one experiment, the percentage of aproximately 150 *S. avenae* nymphs which matured as alatae on healthy oats, oats infected with the PAV isolate (transmitted) and oats infected with the RPV isolate (nontransmitted) of BYDV was 40%, 83% and 70%, respectively.

Differences in the ratio of alatae to apterae produced on healthy or BYDV-infected plants were observed only if parent aphids were reared on healthy colony plants and control aphids reared on healthy oats free of physiological abnormalities. When aphids were reared on BYDV-free oats showing poor growth, chlorosis or leaf tip necrosis, most nymphs (90%) matured as alatae, similar to aphids reared on BYDV-infected plants; likewise, approximately 95% of the nymphs born and fed 24 hours on detached oat leaves from healthy plants matured as alatae. These results suggest that detached leaves, senescing plants and BYDV-infected plants share some common factors for influencing aphid wing development.

Recent studies (Gildow, 1983) have shown that increased alatae maturation on BYDV-infected cereals occurs in other clones of *S. avenae* and *R. padi*. Similar responses were observed on

different cultivars of oats and barley. A greater percentage of alate *R. padi* matured on BYDV-infected California Red oats and Briggs barley, which developed severe symptoms of BYD, as well as on Kanatoa oats and Prato barley which were almost symptomless, relative to healthy controls. Results of three field collections made in April of 1980 and 1981 at Davis, California, showed the potential significance of this phenomenon to aphid populations in the field. Of 907 *R. padi* nymphs born on BYDV-infected barley in the field, 87% matured as alatae but, of 400 nymphs born on healthy barley, only 25% matured as alatae. Other factors affecting host plant physiology, such as brome mosaic virus infection of barley and pesticide treatment of healthy plants, favored alate production relative to untreated controls.

These results cannot be extrapolated to other aphid species or host plants as indicated by results of similar experiments with *Myzus persicae* which failed to detect increased alatae production on various luteovirus hosts (Gildow, 1983). In addition, recent experiments (unpublished) with *S. graminum* reared on healthy and BYDV-infected oats showed little difference between the two groups in alatae production.

BYDV/Aphid Vector Interactions

Aphids transmit BYDV and other viruses of the luteovirus group in a persistent or circulative manner. They acquire the virus with the ingestion of phloem sap from BYDV-infected plants. In order to be transmitted, the virus must be drawn up the aphid food canal in the stylets and passed into the alimentary canal. The virus is then transported through the epithelial cells of the gut and deposited in the body cavity (hemocoel) of the aphid. Virus particles circulate throughout the hemocoel suspended in the blood (hemolymph). To be transmitted, virus isolates pass into the accessory salivary gland and are excreted, along with accessory gland secretory cell products, into the salivary duct (Gildow, 1982; Gildow and Rochow, 1980). While making feeding probes into plant hosts, aphids excrete a variety of substances through the salivary duct of the stylet to aid feeding (Miles, 1972). Presumably, infectious virions are inoculated into viable phloem cells of host plants in this manner. Apparently luteoviruses must be inoculated directly into phloem cells with little damage to the cell, thus allowing the virus to disperse and infect adjacent cells. Attempts to artificially inoculate BYDV into plants have been unsuccessful; only feeding aphids can transmit BYDV in nature.

Although the relationship between luteoviruses and their vectors is very specific, there is no evidence that luteoviruses infect and replicate in their vectors. On the contrary, recent attempts to serially transmit luteoviruses from aphid to aphid have been unsuccessful (Eskandari *et al.*, 1979), and enzyme-linked immunosorbent assays have failed to detect increases of virus in viruliferous aphids reared on immune plants (Tamada and Harrison, 1981) or on membranes (W.F. Rochow, personal communication).

Results of ultrastructural studies in the Buckhout Laboratory on *S. avenae, R. padi* and *M. persicae* over the past several years have failed to detect convincing evidence of luteovirus replication in aphid tissues. For the above reasons, it is currently believed that luteoviruses do not replicate in their vectors. The possibility that luteoviruses could be replicating at a very low level in some cells, however, has not been entirely disproven. If luteoviruses do not replicate in the vectors, then the effect of BYDV on the vector must be indirectly mediated through effects of the virus on the infected plant, which also acts as a host to the vector.

Effect of BYDV on Host Plants

The cytopathological and physiological alteration of cereal grains resulting from BYDV infection are well-documented. Replication of BYDV occurs primarily in phloem tissues and induces phloem necrosis (Jensen, 1969). Xylem tissue has also been reported to support replication when plants are doubly infected with different BYDV isolates (Gill and Chong, 1981). Following inoculation of cereal grains with BYDV, several physiological effects have been noted. In barley and wheat, photosynthesis and transpiration rates decrease and the respiration rate increases (Jensen, 1972; Orlob and Arny, 1961). Accompanying these physiological abnormalities is an accumulation of soluble carbohydrates (sugars) and starch in the infected leaves (Goodman *et al.*, 1965; Jensen, 1972). This is presumed to be a result of phloem degeneration leading to a blockage of the translocation pathway in the plant, an idea that is supported by the fact that carbohydrate concentration decreases in root tissue following infection (Orlob and Arny, 1961).

An increase in nitrogenous compounds, including free amino acids, has been reported in leaf tissue of BYDV-infected oats (Markkula and Laurema, 1964) and barley (Jensen, 1969). In general, these physiological changes which occur as a result of infection are similar to those observed in senescing tissue. During sequential senescence of cereal grain leaves, a combination of protein degradation and decreased protein synthesis results in the accumulation of amino acids which are translocated out of the leaf (Beevers, 1976). Symptoms of BYDV infection are reminiscent of senescence, and the observed accumulation of amino acids in infected leaves could result from retarded protein synthesis due to pathological alteration of metabolic membrane systems. Premature senescence might also be induced by failure of the translocation of root synthesized hormones (cytokinins and auxins) into the leaf tissue. In BYDV-infected cereals, amino acids are not transported out of the leaves due to resistance to translocation, and the amino acids, therefore, accumulate in a manner similar to that observed in senescing detached leaves (Beevers, 1976).

Conclusions

Physiological changes in host plants due to normal senescence or aging, as well as abnormal physiology in response to injury or infection, have been shown to influence vector biology and behavior, reproductive potential and morphology. The information presented here provides circumstantial evidence that nutritional similarities in nitrogen metabolism between senescing and BYDV-infected plant tissues may influence aphid morphology. Further research is required on these aphid developmental mechanisms and on nutritional or hormonal factors in BYDV-infected plants which induce wing development.

References

Ajayi, O., and A.M. Dewar. 1983. The effect of barley yellow dwarf virus on field populations of the cereal aphids, *Sitobion avenae* and *Metopolophium dirhodum*. Annals of Applied Biology 103:1-11.

Beevers, L. 1976. Senescence. *In* Biochemistry, J. Bonner and J.E. Varner, eds. Academic Press, New York. Pp.771-794.

Dean, G.J. 1978. Observations on the morphs of *Macrosiphium avenae* and *Metopolophium dirhodum* on cereals during the summer and autumn. Annals of Applied Biology 89:1-7.

Dixon, A.F.G. 1973. Biology of Aphids. Edward Arnold Ltd., London.

Eastop, V.F. 1977. Aphid vectors. *In* Aphids as Virus Vectors, K.F. Harris and K. Maramorosch, eds. Academic Press, New York. Pp. 3-47.

Eskandari, F., E.S. Sylvester and J. Richardson. 1979. Evidence for lack of propagation of potato leafroll virus in its aphid vector, *Myzus persicae*. Phytopathology 69:45-47.

Gildow, F.E. 1980. Increased production of alatae by aphids reared on oats infected with barley yellow dwarf virus. Annals of the Entomological Society of America 73:343-347.

Gildow, F.E. 1982. Coated-vesicle transport of luteoviruses through salivary glands of *Myzus persicae*. Phytopathology 72:1289-1296.

Gildow, F.E. 1983. Influence of barley yellow dwarf virus-infected oats and barley on morphology of aphid vectors. Phytopathology 73:1196-119.

Gildow, F.E., and W.F. Rochow. 1980. Role of accessory salivary glands in aphid transmission of barley yellow dwarf virus. Virology 104:97-108.

Gill, C.C., and J. Chong. 1981. Vascular cell alterations and predisposed xylem infection in oats by inoculation with paired barley yellow dwarf viruses. Virology 114:405-413.

Goodman, P.J., M.A. Watson and A.R.C. Hill. 1965. Sugar and fructosan accumulation in virus-infected plants: rapid testing by circular-paper chromatography. Annals of Applied Biology 56:65-72.

Jedlinski, H. 1981. Rice root aphid, *Rhopalosiphum ruflabdominalis*, a vector of barley yellow dwarf virus in Illinois, and the disease complex. Plant Disease 65:975-978.

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

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

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

Johnson, B., and P.R. Birk. 1960. Studies on wing polymorphism in aphids. 1. The developmental process involved in the production of the different forms. Entomologia Experimentalis et Applicata 3:327-339.

Lees, A.D. 1966. The control of polymorphism in aphids. Advances in Insect Physiology 3:207-277.

Markkula, M., and S. Laurema. 1964. Changes in the concentration of free amino acids in plants induced by virus disease and the reproduction of aphids. Annales Agriculturae Fenniae 3:265-271.

Miles, P.W. 1972. The saliva of hemiptera. Advances in Insect Physiology 9:183-256.

Miller, J.W., and B.F. Coon. 1964. The effect of barley yellow dwarf virus on the biology of its vector, the English grain aphid, *Macrosiphum granarium*. Journal of Economic Entomology 57:970-974.

Orlob, G.B., and D.C. Arny. 1961. Some metabolic changes accompanying infection by barley yellow dwarf virus. Phytopathology 51:768-775.

Schaefers, G.A. 1972. The role of nutrition in alary polymorphism among the *Aphididae*—an overview. Search Agriculture 2:1-8.

Tamada, T., and B.D. Harrison. 1981. Quantitative studies on the uptake and retention of potato leafroll virus by aphids in laboratory and field conditions. Annals of Applied Biology 98:261-276.

Vickerman, G.P., and S.D. Wratten. 1979. The biology and pest status of cereal aphids (*Hemiptera: Aphididae*) in Europe: a review. Bulletin of Entomological Research 69:1-32.

Walters, K.F.A., and A.F.G. Dixon. 1982. The effect of host quality and crowding on the settling and take-off of cereal aphids. Annals of Applied Biology 101:211-218.

Watt, A.D. 1979. The effect of cereal growth stages on the reproductive activity of *Sitobion avenae* and *Metopolophium dirhodum*. Annals of Applied Biology 91:147-157.

Watt, A.D., and A.F.G. Dixon. 1981. The role of cereal growth stages and crowding in the induction of alatae in *Sitobion avenae* and its consequences for population growth. Ecological Entomology 6:441-448.

Comments

R.T. Plumb, UK

All aspects of vector biology may affect their ability to transmit BYDV. Of most epidemiological significance are whether or not a species alternates between hosts susceptible to BYDV and the timing and size of its migratory flights; almost equally important is how it perennates. In temperate regions this means survival over the winter when hosts are normally abundant but temperatures may be lethally cold whereas, in Mediterranean-type regions, survival depends on the ability to find the relatively sparse hosts present in cool microclimates.

Another difference between the two regimes is that, in temperate conditions, there is often a sexual generation of vectors; in Mediterranean conditions, sexual generations are rare or absent. In temperate, maritime regions such as the British Isles, aphids can survive parthenogenetically as well as by eggs. The relative success of parthenogenetic overwintering determines, to a large extent, how early and numerous infective vectors will be the following spring. Survival as eggs may be more successful but, for those genera that lay eggs on rosaceae (*Rhopalosiphum* and *Metopolophium*), migration into crops is slowed as well as the transmission of virus within them. Such alternative survival strategies add to the difficulty of predicting when aphids will occur, whether they will carry virus and how widespread the infection will be.

An essential requirement for epidemiological studies is a knowledge of vector migration. This is rarely known in detail and even more rarely for a period of several years. Britain and Europe are fortunate in having had an efficient aphid-monitoring scheme for some 15 years. This monitoring service is based on nonselective sampling by suction traps and, for any epidemiological study, such sampling accompanied by crop monitoring is essential.

As well as considering the possible direct effects of BYDV on aphids, the indirect effects resulting from virus modification of the aphids' host plant should not be ignored. Plants infected by BYDV support larger aphid populations than virus-free plants and are predisposed to infection of the ears by the sooty moulds, *Cladosporium* spp. and *Verticillium* spp. Aphids and honeydew increase the incidence of *Cladosporium* spp. on wheat ears but not on barley. As the effect of BYDV is to increase the carbohydrate concentration of leaves, this influences the presence of fungal infection, root rots, mildew and *Septoria*.

H. Jedlinski, USA

Severe outbreaks of BYD were observed in Illinois in midsummer 1982, at which time the vector, *R. padi*, was confined primarily to crowns and roots of spring oats. Since roots contain higher virus concentrations than tops, they may represent an important although not readily recognized virus reservoir in nature. The biology and dynamics of root feeding by other vectors, *R. rufiabdominalis*, *R. insertum* and *Rhopalomyzus poae*, should be further explored in relation to the transmission and epidemiology of BYDV in nature.

G. Herrera and C. Quiroz, Chile

In 1977 and 1978, trials were conducted in Chile at La Platina Experimental Station (INIA) to determine the effect of BYDV and the aphid *M. dirhodum* on the wheat cultivar Toquifén. The trials were carried out in cages covered with muslin. Results were similar for the two seasons, with significant reductions being detected when the wheat was inoculated with BYDV between stages 5 and 7 on the Feekes scale (30 to 32 on the decimal growth scale). It was also shown that BYDV causes a reduction in kernel weight, number of kernels per spike and plant height, and an increase in percentage of shriveled kernels. An increase in numbers of viruliferous aphids did not lead to further yield reductions. Large populations of nonviruliferous aphids, present during the same growth stages as the viruliferous, did not reduce yield significantly.

Purification of Barley Yellow Dwarf Luteoviruses

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The Past

The first purification of virus particles from plants infected with barley yellow dwarf virus (BYDV) was reported in 1964 (Rochow and Brakke, 1964). Frozen oat leaf tissue (*Avena bizantina* C. Koch Coast Black) was ground in a fruit juice extractor and the sap clarified with chloroform and n-amyl alcohol, followed by differential and density gradient centrifugation. Less than 50 µg of the *Sitobion* (= *Macrosiphum*) *avenae*-specific (MAV) isolate was obtained from every liter of clarified juice. The authors predicted that "low virus concentration in infected plants will no doubt continue to be a major limitation in studies of BYDV." However, they also discovered one of the strong points of most barley yellow dwarf (BYD) luteoviruses, their stability. The MAV isolate was stable to freezing, organic solvents and enzymes, all of which characteristics would be exploited in future purification studies.

Two other BYD luteoviruses were first purified by a similar procedure in 1971 (Rochow *et al.*, 1971). Both a *Rhopalosiphum padi*-specific isolate (RPV) and a vector-nonspecific isolate (PAV) were successfully purified from Coast Black oats although, even after two extractions, yields were even lower than for MAV (Table 1). The authors also examined the use of polyethylene glycol (PEG) as a clarification agent; the procedure was quick and the virus clean. Yields, however, were cut in half. It was first noted here that better yields of a more severe isolate, PAV, were obtained from tissue harvested soon after inoculation. The importance of cool temperatures (15 to 20°C) for production of tissue for purification was reported. Using 200 to 350 µg of the three BYD luteovirus isolates, purified over a two-year period, the first antisera to those viruses were produced.

In 1974, Brakke and Rochow once again undertook the solving of the central problem of the extraction of BYD luteoviruses. Stating that "grinding the fibers is much like griding an old felt hat," they tried freezing tissue with liquid nitrogen in a mortar and pulverizing it with a pestle. Triton X-100 was used for clarification. Both of these methods would be criticized in later work.

The highest yields of MAV, RPV and PAV isolates were reported by Foxe and Rochow in 1975 (Table 1). By selecting young tissue, MAV yields from Coast Black oats could be increased ten-fold and PAV, three-fold; no difference in RPV yields from leaves of different ages was noted. Purification methods were essentially those reported earlier, with the addition of a 20% sucrose pad in the final high speed centrifugation. However, no positive effect from the use of liquid nitrogen was noted; in fact, yields of MAV decreased with that extraction procedure.

The first report of purification of BYD luteoviruses from outside the USA was in 1978 (Paliwal, 1978) when Canadian isolates with vector specificities like those of Rochow's MAV, RPV and PAV were purified from frozen Coast Black oat tissue. A Wiley mill and minute glass beads were used to maximize

extraction and, for the first time, the one mg per kg yield barrier was broken (Table 1). Paliwal also tried an enzyme extraction with cellulase; 20% more virus was obtained, but the final preparation was dirtier. He stated that "the results obtained with the enzyme digestion method suggest that there is potential for future improvement in virus yields."

In 1983, D'Arcy *et al.* reported an average yield of 4.4 mg per kg for an Illinois vector-nonspecific isolate purified from winter-grown Coast Black oats. Highest yields were obtained with extraction of root tissue with liquid nitrogen, rather than with enzymes or the Wiley mill. Triton X-100 and chloroform clarification gave higher yields than PEG precipitation; much virus was always lost in the PEG pellet.

In contrast, Hammond *et al.* (1983) found enzyme extraction (cellulase plus pectinase) with prolonged blending and PEG clarification to be the optimal method for purification of an Indiana vector-nonspecific BYD luteovirus. The use of Triton X-100 or n-butanol for clarification reduced yields. Clintland 64, Lang and Illinois 732664 (Ogle) oats were equally good or better sources of tissue for purification than Coast Black oats.

Table 1. Average Yields of Some Purified Barley Yellow Dwarf Luteoviruses

Isolate	Average yield (ug/kg)	Reference
MAV	106	Rochow *et al.*, 1971
RPV	79	Rochow *et al.*, 1971
PAV	20	Rochow *et al.*, 1971
MAV	830	Foxe and Rochow, 1975
RPV	290	Foxe and Rochow, 1975
PAV	200	Foxe and Rochow, 1975
MAV-like	1360	Paliwal, 1978
RPV-like	630	Paliwal, 1978
PAV-like	520	Paliwal, 1978
PAV-like	4400	D'Arcy *et al.*, 1983

The Present

In 20 years, many improvements in purification methodology have made possible a more than 100-fold increase in yields of BYD luteovirus isolates. Even with this success, however, caution should be observed; it seems clear that there is no single purification procedure which will give optimal yields of all isolates of BYD luteoviruses. The disease is incited by a group of viruses which vary in biological properties, such as vector specificity and cytopathology. It is to be expected that their physiochemical properties, upon which purification is based, also vary. Therefore, it seems logical that no single purification scheme can be expected to result in optimal yields of all BYD luteoviruses, although the methods developed to date do provide sound starting points for the development of the most useful method for a particular BYD luteovirus isolate. This was the reason for the attempt to summarize the history of BYD luteovirus purification in the preceding section.

It is not necessary to achieve the "optimal" purification for every BYD luteovirus isolate. The great stability of most isolates, and their corresponding ability to elicit excellent antibody response, make possible the production of antiserum, the goal of many purification efforts, with only a few hundred micrograms of purified virus.

For those interested in purification *per se*, there remain many unanswered questions about the purification of BYD luteoviruses, for example, whether yield of all MAV-like isolates is reduced when liquid nitrogen is used for extraction, whether Triton X-100 clarification reduces yields of all BYD isolates and whether there are universally useful hosts other than Coast Black oats. Given these, and many other unanswered questions, it is necessary to decide what the priorities should be.

The Future

Probably the major goal of future purifications of BYD luteovirus isolates should be to expand the relatively narrow range of isolates on which current knowledge is based. Reports of purification of only three types of isolates (*S. avenae*-specific, *R. padi*-specific and vector-nonspecific) exist in current literature. More importantly, all of those isolates are from North America. In order to more fully understand the complex group of viruses which incite BYD, isolates with other vector specificities and from other regions of the world need to be purified. Only then, can the physiochemical and serological properties of the isolates be used to help clarify the taxomomy of the viruses called BYDV.

References

Brakke, M.K., and W.F. Rochow. 1974. Ribonucleic acid of barley yellow dwarf virus. Virology 61:240-248.

D'Arcy, C.J., A.D. Hewings, P.A. Burnett and H. Jedlinski. 1983. Comparative purification of two luteoviruses. Phytopathology 73:755-759.

Foxe, M.J., and W.F. Rochow. 1975. Importance of virus source leaves in vector specificity of barley yellow dwarf virus. Phytopathology 65:1124-1129.

Hammond, J., R.M. Lister and J.E. Foster. 1983. Purification, identity and some properties of an isolate of barley yellow dwarf virus from Indiana. Journal of General Virology 64:667-676.

Paliwal, R.C. 1978. Purification and some properties of barley yellow dwarf virus. Phytopathologische Zeitschrift 92:240-246.

Rochow, W.F., A.I.E. Aapola, M.K. Brakke and L.E. Carmichael. 1971. Purification and antigenicity of three isolates of barley yellow dwarf virus. Virology 46:117-126.

Rochow, W.F., and M.K. Brakke. 1964. Purification of barley yellow dwarf virus. Virology 24:310-322.

Surveying for Barley Yellow Dwarf

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The Past

The earliest survey method for barley yellow dwarf (BYD) was, as for most other plant diseases, visual assessment of symptoms. This method proved inadequate for several reasons. Symptoms of BYD can be confused with those caused by other biotic and abiotic factors and symptomless infections can occur in many hosts, including barley, corn and wheat. Also, symptoms are often masked in warm weather. However, one way in which symptomatology is still used for BYD surveys is to place highly susceptible trap or bait plants in a field. Symptom development on those plants can give useful information on the incidence of BYD luteoviruses.

In the late 1950s, the vector specificities of the luteoviruses which caused BYD were described. From that time to the present, the most widely used survey method for BYD has been on parallel transmission tests by various aphid species on highly susceptible indicator plants. Gill routinely uses five aphid species for his tests, *Metopolophium dirhodum, Rhopalosiphum maidis, R. padi, Schizaphis graminum and Sitobion* (= *Macrosiphum*) *avenae* (Gill, 1967); Rochow uses only the last four (Rochow, 1979).

There are several disadvantages to the aphid transmission survey method, the principal of which is time. Results are obtained, at best, after four weeks, and may require several months if the first series of tests is inconclusive. The necessity of maintaining colonies of several aphid species, free of contamination, is another drawback. However, this method has been the basis for categorization of BYD luteoviruses into vector-specific and vector-nonspecific groups. Such grouping has been supported by cytopathological, serological and biochemical data.

Serological methods have been developed to survey for many plant viruses. Unfortunately, the very low concentration of BYD luteoviruses in infected tissue prohibits the formation of visible immunoprecipitates or electron microscopic detection in leaf dips. Therefore, serological methods only became applicable to BYD surveys upon the development of more sensitive tests. Two sensitive serological tests which have been examined for usefulness in BYD surveys are the enzyme-linked immunosorbent assay (ELISA) and serologically specific electron microscopy (SSEM).

SSEM has been used by Paliwal to detect BYD luteoviruses in plant tissue (Paliwal, 1977) and in aphid vectors (Paliwal, 1982). The technique is very sensitive; a high percentage of samples that are positive by aphid transmission tests are also positive by SSEM. Other advantages over earlier methods include speed (one to two days) and detection of symptomless infections. Although the method is conservative of antiserum, the serological specificity of BYD luteoviruses requires that several different BYD antisera be used for optimal detection. Also disadvantages are the time necessary for the preparation and examination of each sample and the need for an electron microscope.

In 1979, ELISA was adapted for the detection of BYD luteoviruses in plant tissue (Lister and Rochow, 1979) and in aphid vectors (Denéchère *et al.*, 1979). Lister and Rochow ran parallel aphid transmission and ELISA experiments and concluded that ELISA "appears to have vast potential for simplifying . . . surveys." The advantages of ELISA include sensitivity, rapidity (two to three days) and the ability to assay 96 samples on a single microtiter plate. As with SSEM, however, the serological specificity of BYD luteoviruses becomes important. The disadvantage of this specificity is the necessity for using several antisera in the ELISA; the advantage is the ability to recognize many strains from their homologous and heterologous reactions.

In 1982, Rochow reported an extensive comparison of ELISA and aphid transmission tests. For 80% of 216 field samples, the two tests agreed; for another 18%, ELISA gave more complete information than did aphid transmission tests. Major advantages of ELISA are quick detection of mixed infections and the ability to analyze samples whose condition is too poor for aphid feedings. However, in certain instances, especially with RMV-like isolates, ELISA may give anomalous results. Rochow concluded that he would continue to maintain aphid colonies.

The Present

At this time, ELISA constitutes the best survey method for BYD in plants in terms of speed, reliability and economy. The major disadvantage is the requirement of antiserum to nearly as many BYD luteoviruses as are likely to be found in the survey. For identification of the relatively few BYD luteovirus isolates which give unclear results with ELISA, aphid transmission tests must be used.

Currently, ELISA is not sensitive enough to reliably detect BYD luteoviruses in individual aphid vectors. In the University of Illinois ELISA system, only about 2/3 of adult *R. padi* reared on plants infected with an Illinois vector-nonspecific BYD luteovirus give positive results. While 80% transmission of BYDV has been obtained with individual aphid inoculation tests, SSEM is more reliable; it is, however, also much more time-consuming. At present, group assays of trapped aphid vectors of BYD luteoviruses seem to be the simplest survey method. It is necessary to identify and assay only known vectors; other species may ingest BYD luteoviruses but not transmit them.

The Future

Increases in sensitivity of methods have allowed the adaptation of serological techniques to BYD surveys. It is feasible that further increases in sensitivity will allow for easy detection of BYD luteoviruses in individual trapped aphids, thus making possible the rapid and accurate testing of trapped aphids necessary for epidemiological studies and recommendations for BYD control. Variations on ELISA, such as a fluorogenic substrate, have been shown to increase sensitivity to a limited degree. For greater increases, other methods, such as the use of nucleic acid hybridization, may become increasingly common.

References

Denéchère, M., F. Cante and H. LaPierre. 1979. Detection immunoenzymatique du virus de la jaunisse nanisante de l'orge dans son vecteur *Rhopalosiphum padi* (L.). Annals of Phytopathology 11:507-514.

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

Lister, R.M., and W.F. Rochow. 1979. Detection of barley yellow dwarf virus by enzyme-linked immunosorbent assay. Phytopathology 69:649-654.

Paliwal, Y.C. 1977. Rapid diagnosis of barley yellow dwarf virus in plants using serologically specific electron microscopy. Phytopathologische Zeitschrift 89:25-36.

Paliwal, Y.C. 1982. Detection of barley yellow dwarf virus in aphids by serologically specific electron microscopy. Canadian Journal of Botany 60:179-185.

Rochow, W.F. 1979. Field variants of barley yellow dwarf virus: detection and fluctuation during twenty years. Phytopathology 69:655-660.

Rochow, W.F. 1982. Identification of barley yellow dwarf viruses: comparison of biological and serological methods. Plant Disease 66:381-384.

Screening Survey Samples for the Presence of Barley Yellow Dwarf Viruses

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Serological methods offer the most useful means currently available for routine surveys of the occurrence of barley yellow dwarf virus (BYDV) in cereals and grasses. Of the procedures successfully used, that of enzyme-linked immunosorbent assay (ELISA) (Lister and Rochow, 1979) is most used in the Purdue laboratory for its simplicity, convenience, specificity and economy of time and materials. So far, the polyclonal antisera used is that produced in rabbits by various protocols, of which intradermal injection appears to be advantageous (Lister *et al.*, 1983). However, as is well-known, polyclonal antisera vary in their serological reactivity and specificity. Therefore, there is considerable interest in the potential of monoclonal antibodies with defined narrow or broad reactivity for detecting BYDV, although this technology has not yet produced antisera for routine use (Diaco *et al.*, 1983; Hsu *et al.*, 1983; S. Wyatt, personal communication).

Test tissue or extracts thereof have been stored frozen indefinitely (-20 or -80°C), and have still reacted in ELISA (Lister and Rochow, 1979; Rochow, 1979). Extracts can be made by grinding at 1:2-5, w,v in 0:1 M phosphate buffer at pH 7.0, either in liquid nitrogen or in a Polytron, followed by further grinding in two to eight volumes of the widely used ELISA extraction buffer which consists of phosphate-buffered saline, 0.05% Tween 20 and 2% polyvinyl pyrrolidone (PBS-Tween-PVP) (Clark and Adams, 1977). Various other buffers can also be used; extensive tests in the laboratory comparing buffers for extraction of a PAV isolate of BYDV showed that high molarity phosphate at pH 6.0 gave higher ELISA values than any other buffer tested (Table 1).

Since BYDV tends to remain in the fibrous residue left after extraction (Brakke and Rochow, 1974; Hammond *et al.*, 1983), it may be helpful to pulverize leaf tissue in liquid nitrogen rather than extract by homogenization in a buffer. Intermittent homogenization, over an extended period, has also been shown to improve extraction, but the use of cellulase and pectinase enzymes to improve virus yields by macerating fiber was deleterious to ELISA (Hammond *et al.*, 1983). Some improvement in ELISA values was obtained in tests of leaf extracts infected with the RPV isolate of Rochow (although not with the MAV isolate) when homogenates were clarified by further grinding with chloroform (Lister and Rochow, 1979); this also may reduce "background," healthy control reactions.

Among host variables are 1) different hosts of BYDV differ considerably in virus content, 2) some resistant cereal cultivars contain much smaller amounts of virus than susceptible ones, 3) virus content varies with age at infection and with incubation time and 4) roots usually contain more virus than leaves (Hammond *et al.*, 1983; Skaria *et al.*, 1983; unpublished data). Virus yields also depend on sample condition and storage, and virus content can vary among different leaves of the same plant. There seems to be little information on these factors, although leaves are known to differ as sources of virus for aphids (Foxe and Rochow, 1975).

In screening samples for BYDV, it is usually necessary to accept what tissue is available. Special efforts to improve virus extraction for ELISA may be worthwhile, especially in doubtful cases and those with poorly productive hosts such as grasses (Fargette *et al.*, 1982).

Table 1. Efficiency of Extraction Buffers for Barley Yellow Dwarf Virus[a/]

Buffer	Efficiency[b/] ranking	ELISA value[c/] (A405 nm)
0.5 M citrate, pH 7.0	10	1.856
0.1 M citrate, pH 7.0	3	2.024
0.5 M glycine/NaOH, pH 7.5	6	1.955
0.1 M glycine/NaOH, pH 7.5	12	1.850
0.5 M tris-borate, pH 8.3	15	1.491
0.1 M tris-borate, pH 8.3	4	1.988
0.5 M phosphate, pH 6.0	1	2.319
0.2 M phosphate, pH 6.0	2	2.212
0.1 M phosphate, pH 6.0	11	1.853
0.5 M phosphate, pH 7.0	13	1.848
0.2 M phosphate, pH 7.0	14	1.845
0.1 M phosphate, pH 7.0	8	1.925
0.5 M phosphate, pH 7.0[d/]	9	1.916
0.2 M phosphate, pH 7.0[d/]	5	1.974
0.1 M phosphate, pH 7.0[d/]	7	1.934

a/ Data developed by Hammond *et al.* (1983) with a PAV-like isolate; extracts (1:4, w,v) of infected Clintland 64 tissue were made, cell debris removed by filtration and the solution tested by ELISA

b/ Efficiency ranked by relative yield of virus as indicated by ELISA

c/ Average for triplicate experiments; diluting antigen two-fold reduced ELISA values about 40%; values for control tissue about 0.05

d/ Soaked 24 hours before clarification

In some hosts, such as corn, virus may be distributed so erratically among leaves that ELISA is unsuitable for direct tests of leaf tissue extracts (Hammond *et al.*, 1983; Wyatt, personal communication).

In surveys, it is of considerable importance that ELISA activity seems to survive well in leaf tissue. In Purdue tests, infection has remained readily detectable in leaf that has been either frozen or dried in various ways, even in an incubator at 37°C (Table 2). The survival of ELISA activity in leaves over time makes it feasible to transport samples over long distances, for example, by mail, for testing at appropriately equipped centers. In recent years, some practical assessment of this possibility has developed through tests of leaf samples mailed to this laboratory from various parts of the USA and elsewhere; the same is true for work done by Rochow (1982). For the tests, US samples were simply collected

Table 2. ELISA Values for Extracts from Clintland 64 Oat Leaves Infected with Barley Yellow Dwarf Viruses and Stored under Conditions Specified [a/]

Storage conditions [b/]	ELISA value [c/] Virus type: PAV	MAV	RPV
Dried over $CaCl_2$ in cold room (4-5°C)	1.169	1.082	0.636
Dried over $CaCl_2$ at room temperature (25°C)	1.280	1.342	1.280
Fresh leaf stored at -20°C	1.412	1.640	1.189
Fresh leaf stored at -80°C	1.600	1.720	1.048
Air dried at room temperature (25°C)	1.351	1.242	0.598
Air dried at 37°C	1.021	1.037	0.665
Air dried at 60°C	0.218	0.189	0.490
Fresh leaf stored in cold room (4-5°C)	1.574	1.880	0.764
Fresh healthy leaf	0.040	0.064	0.070

[a/] 2-gram samples of leaf stored as indicated, extracted in a Polytron homogenizor in 4 ml 0.1 M phosphate buffer at pH 7.0 and 5 ml PBS-Tween-PVP added (BYDV isolates from cultures supplied by W.F. Rochow)

[b/] All extracts stored for four days

[c/] All values means of duplicate ELISA values for three separate samples; diluting antigen two-fold reduced ELISA values about one-third

fresh (i.e., ranging from actively growing to senescent), placed in sealed polyethylene envelopes and mailed. Results suggested that successful detection was possible, even when samples had deteriorated considerably in transit, and BYDV infections were confirmed for many US locations (Table 3).

Samples from Ecuador, sent by H.J. Dubin in several consignments, became air dried in transit, since they were packed in paper envelopes. Results for one such consignment are listed in Table 4, again suggesting that virus detectability survives transit well.

However, as such data is not comparative, it gives no information on the reduction of virus reactivity or cross-reactivity to BYDV antisera during transit. In tests currently in progress, dried and fresh leaf samples from the same batches of infected leaf tissue are being compared as sources of ELISA-detectable virus after transportation through mailings to various locations worldwide. In this way, it is hoped not only to define simple procedures for handling survey samples, but also to predict their chances of success in detecting BYDV infections in ELISA tests with appropriate antisera.

Table 3. ELISA-Positive Reactions in Symptomatic Cereal Samples Received at Purdue, 1982-1983

Origin	Crop	Number of samples	Antiserum source of immunoglobulin used for ELISA[a/]		
			PAV	RPV	PAV & RPV
Indiana	Wheat	169	67	14	5
	Oats	13	13	1	0
	Barley	6	6	3	3
Illinois	Oats	6	4	0	0
Iowa	Oats	10	3	0	0
Minnesota	Oats	5	3	0	0
Wisconsin	Wheat	15	15	3	3
	Oats	10	8	0	0
Michigan	Oats	8	5	0	0
Ohio	Wheat	12	9	2	1
	Oats	10	5	1	0
New York	Oats	3	2	0	0
North Dakota	Oats	8	3	1	0
South Dakota	Oats	7	3	0	0
	Wheat	20	7	3	0
Oregon	Wheat	8	7	0	0

a/ Sample extracts giving ELISA values of at least two or more times those for healthy control extracts were rated as positive. Most gave much higher values and an obvious yellow color. Positive values ranged between 0.111 and 2.010 with means of 0.794 and 0.265 for PAV and RPV, respectively. Healthy control values ranged between 0.01 and 0.048 (antisera made at Purdue from viruses isolated from sources supplied by W.F. Rochow).

As BYDV is spread naturally only by aphid vectors feeding on fresh tissue, transfer of dry leaf tissue presents no quarantine hazard and so would be an especially valuable procedure. Results so far indicate that, in fact, virus detectability persists well in air-dried leaf when samples are subjected to the environmental variations encountered in transit by mail (Table 5).

Acknowledgements

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Table 4. ELISA Values for Extracts from Wheat Leaf Samples from Ecuador as Tested with Two Immunoglobulins[a/]

	Immunoglobulin[b/]			Immunoglobulin[b/]	
Sample	**PAV**	**RPV**	**Sample**	**PAV**	**RPV**
1	1.088 (+)	0.050	19	0.641 (+)	0.055
2	1.115 (+)	0.038	20	1.163 (+)	0.046
3	1.568 (+)	0.046	21	0.532 (+)	0.069
4	0.081	0.032	22	0.111	0.053
5	0.040	1.436 (+)	23	0.197 (+)	0.054
6	2.750 (+)	0.069	24	0.088	0.055
7	0.269 (+)	0.045	25	1.794 (+)	0.039
8	0.140 (+)	0.044	26	0.088	0.141
9	1.124 (+)	0.038	27	0.247 (+)	0.197 (+)
10	0.220 (+)	0.042	28	0.090	0.505 (+)
11	0.394 (+)	0.048	29	1.466 (+)	0.056
12	1.002 (+)	1.253 (+)	30	0.068	0.877(+)
13	0.167 (+)	0.865 (+)	31	0.104	0.045
14	0.416 (+)	0.290 (+)	32	0.064	0.587 (+)
15	0.734 (+)	0.043	33	0.157 (+)	0.069
16	0.117	0.052	34	0.043	0.029
17	0.149 (+)	0.085	Healthy	0.041	0.056
18	0.068	0.436 (+)	PAV[c/]	2.064	0.060
			RPV[c/]	0.086	1.679 (+)

a/ Coating immunoglobulins and conjugates used at 2.5 ug/ml
b/ Values regarded as positive are three or more times the values for healthy control tissue and with obvious yellow color (borderline values require rechecking for confirmation)
c/ Samples from standard cultures maintained at Purdue

Table 5. ELISA Values for PAV-Infected Leaf Samples Sent by Airmail between Purdue and Locations in Selected Geographical Areas, November, 1983

Sample description[a]	ELISA values[b] Air-dried leaf means (ranges)	Untreated leaf means	Days in transit (or storage)
Geographical provenance of mailings (no. of locations)[c]			
Canada (2)	.459 (.394-.523)	.075	9-19
Europe (3)	.372 (.346-.428)	.150	19-26
Australia (2)	.361 (.298-.424)	.078	14-19
Asia (3)	.333 (.321-.351)	.114	12-20
USA (7)	.323 (.251-.397)	.070	6-19
UK (4)	.280 (.214-.402)	.123	12-23
Latin America (4)	.255 (.120-.427)	.094	14-27
Controls			
Infected leaf stored at 2°C	.391 --	.160	(28)
Infected leaf stored at 5°C	.362 --	.188	(28)
Infected leaf stored at -20°C	.652 --	.803	(28)
Infected leaf stored at -80°C	.701 --	.961	(28)
Infected leaf extract stored at -20°C	.398 --	.842	(28)
Healthy leaf stored at -20°C	.019 --	.033	(28)

a/ Duplicate 1-g samples were sealed in polyethylene and either mailed to correspondents or kept at Purdue as controls under the conditions specified. When returned, the samples were extracted (1:10, w,v in 0.1 M pH 7.0 phosphate) and extracts stored at -20°C until tested along with controls 28 days after the original mailing.

b/ Means for duplicate samples tested in duplicate wells. Diluting antigen concentration to one-quarter reduced ELISA value by one-half.

c/ Europe samples from France, Portugal and Spain; Asia samples from Japan, Pakistan and Taiwan; Latin America samples from Argentina, Brazil, Chile and Mexico; USA samples included one from Hawaii.

Note: further tests indicate that MAV and RPV-infected samples behaved similarly

References

Brakke, M.L., and W.F. Rochow. 1974. Ribonucleic acid of barley yellow dwarf virus. Virology 61:240-248.

Clark, M.F., and A.N. Adams. 1977. Characteristics of the microplate method of enzyme-linked immunosorbent assay for the detection of plant viruses. Journal of General Virology 34:475-483.

Diaco, R., R.M. Lister, D.P. Durand and J.H. Hill. 1983. Production of monoclonal antibodies against three isolates of barley yellow dwarf virus. Abstract. Phytopathology 73:788.

Fargette, D.F., R.M. Lister and E.L. Hood. 1982. Grasses as a reservoir of barley yellow dwarf virus in Indiana. Plant Disease 66:1041-1045.

Foxe, M.J., and W.F. Rochow. 1975. Importance of virus source leaves in vector specificity of barley yellow dwarf virus. Phytopathology 65:1124-1129.

Hammond, J., R.M. Lister and J.E. Foster. 1983. Purification, identity and some properties of an isolate of barley yellow dwarf virus from Indiana. Journal of General Virology 64:667-676.

Hsu, H.T., J. Aebig, W.F. Rochow and R.H. Lawson. 1983. Isolations of hybridomas secreting antibodies reactive to RPV and MAV isolates of barley yellow dwarf virus and carnation etched ring virus. Abstract. Phytopathology 73:790.

Lister, R.M., J. Hammond and D.L. Clement. 1983. Comparison of intradermal and intramuscular injection for raising plant virus antisera for use in ELISA. Journal of Virological Methods 6:179-182.

Lister, R.M., and W.F. Rochow. 1979. Detection of barley yellow dwarf virus by enzyme-linked immunosorbent assay. Phytopathology 69:649-654.

Rochow, W.F. 1979. Field variants of barley yellow dwarf virus: detection and fluctuation during twenty years. Phytopathology 69:655-660.

Rochow, W.F. 1982. Identification of barley yellow dwarf viruses: comparison of biological and serological methods. Plant Disease 66:381-384.

Skaria, M., R.M. Lister, J.E. Foster and G.E. Shaner. 1983. Barley yellow dwarf virus content as an index of symptomatic resistance in cereals. Abstract. Phytopathology 73:793.

Comments

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The method chosen for surveys of BYDV depends, to some extent, on the host and the purpose of the survey. Most of the experience in Britain in surveying for BYDV has been with vectors, but work has also been done with test plants on which aphids have fed and on samples sent from overseas. The methods that have been most used are immunospecific electron microscopy (ISEM) and fluorogenic ELISA.

ISEM has been found to be a reliable and easy method of detecting BYDV in vectors and plants. Antiserum diluted to one part per 1000 is used and decorating antiserum at one part per 100. The clarification of plant and, more especially, aphid extracts in 50/50 chloroform/butanol has been found to be valuable; it gives a reliable sample and allows unequivocal identification of virus particles. From 0.05 to 0.1 gram of leaf is diluted ten times in 0.06 M phosphate buffer, and each aphid extracted in 40 µl of buffer.

Tests in cooperation with colleagues in Britain and Australia have shown that electron microscope grids activated by BYDV antiserum retain their sensitivity for two to three weeks if kept in a cool humid atmosphere; after a month they still attract 50% as many particles as when used immediately. This ability can be exploited to overcome one of the disadvantages of ISEM as compared with ELISA. Activated grids prepared at Rothamsted were sent to Australia where Dr. Sward treated them with various samples. The washed and stained but unlabeled grids were returned to Rothamsted for examination where there was almost 100% agreement between the results and the treatments applied, even to the point of demonstrating the presence of an unusual isolate. This method, therefore, has the advantage that little equipment is required (a bench centrifuge would be desirable) and the chemicals are readily available or can be provided as a kit. With this method, tests can be carried out in remote areas and dispatched to a center for diagnosis. It also eliminates the need for sending infected material through the mail with the associated difficulties of survival and phytosanitary regulations.

The fluorogenic ELISA system developed by Torrance and Jones (1982) has been used in conjunction with the aphid trapping scheme. Two suction traps are operated, with potential BYDV vectors caught in one being tested directly by letting them feed on plants. Potential vectors caught in the second trap are identified and then frozen for extraction and testing by fluorogenic ELISA.

There have been some difficulties in methods and in the criteria to use for positive tests but, in 1982, the results from the two methods were similar. The principal difficulty when testing aphids is the interpretation of the results. Viruliferous aphids can be detected which do not, or are biologically unlikely to, transmit disease; the distinction between viruliferous and infective is not always sufficiently stressed. These tests will be repeated and the direct methods continued to be used until the indirect serological method is equally reliable. Should that become possible, there will be great opportunities for testing aphids from many sites and for many viruses.

Reference

Torrance, L., and R.A.C. Jones. 1982. Increased sensitivity of detection of plant viruses obtained by using a fluorogenic substrate in enzyme-linked immunosorbent assay. Annals of Applied Biology 101:501-509.

R.J. Sward, Australia

The nature of the source tissue in the plant is one of the single most important factors in achieving high BYDV yields. The concentration of virus in wheat, barley and oats was monitored in Australia over an eight-week period using ELISA. An important finding was that concentrations of virus were far higher in the root tissues than in the tops for much of this time period in each of the three cereals. The virus concentration reached a definite peak in barley and wheat roots around 10 to 14 days after inoculation and subsequently decreased; in oats, however, a high concentration in the roots appeared to be maintained over a long period.

The temperature and light intensity at which the plants were grown and the productivity of the specific cereal cultivar were also considered. Under greenhouse conditions with natural light and temperatures between 15 and 25°C, the barley cultivar Lara had high productivity as well as high virus concentration. In root tissue harvested 12 days after inoculation, an RPV-like isolate yielded around one mg per kg of source tissue. The purification procedure was similar to that of Rochow and Brakke (1964). Liquid nitrogen was used prior to pulverization of plant materal to aid virus extraction.

A further important point is that, when alternate cycles of high and low speed centrifugation were used, significant amounts of virus were absorbed in plant host material and then pelleted during the low speed run. After removing the supernatant, the pellet was resuspended in buffer and a second low speed spin carried out. For purifying virus for antiserum production, sucrose density gradients were used. The preparation that resulted had a sufficiently low background level of host material, with the antiserum being highly active against BYDV and quite adequate for ELISA. In some preparations, it may be necessary to cross-absorb the antiserum with purified host protein from healthy plants to produce a suitable antiserum for ELISA.

Reference

Rochow, W.F., and M.K. Brakke. 1964. Purification of barley yellow dwarf virus. Virology 34:310-322.

G. Herrera, Chile

An isolate of BYDV affecting oat crops in the north central region of Chile has been purified and compared with other luteoviruses. The partially purified virus had a yield of 0.72 mg per kg fresh tissue, an absorbance spectrum with an average A 260/280 and a ratio of 0.89 with a maximum 274 nm and minimum 254 nm according to the enzyme-linked immunosorbent assay (ELISA). This isolate is PAV-like and is similar to PAV isolates found in Indiana and Washington.

Chemical and Cultural Control of Barley Yellow Dwarf

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The most appropriate method for the control of barley yellow dwarf (BYD) will depend upon the conditions under which a crop is grown and the epidemiology of the barley yellow dwarf virus (BYDV) under those conditions. Losses caused by BYD can be minimized as a result of breeding for resistance to BYDV, avoiding infection or killing vector aphids with pesticides.

Cultural Control

Sowing date—Avoidance of infection seems the best method of virus control as it often requires nothing more than sowing at a particular time. However, it may be difficult to sow at the best time and the potential yield of a crop thus avoiding infection may be less than that of one that is exposed to infection. At Rothamsted from 1979 to 1981, winter wheat sown in the middle of September yielded, on average, 0.45 tons per hectare more than crops sown a month later. The September-sown crop was exposed to BYDV infection when young, whereas the later sown crop was not; the farmer, had he made his sowing decision entirely on the grounds of avoiding infection, would have sacrificed the difference in yield of the two crops. In one of those three years, he could have increased the yield advantage of the early sown crop even more by spraying it with insecticide to control aphid vectors of BYDV. In addition, by sowing late, he would have risked not being able to sow all the crops he wished to sow in the autumn because of deteriorating weather conditions. For autumn-sown cereals in Britain and Western Europe, generally, it seems unlikely that sowing date will be decided upon entirely to avoid BYDV.

In Britain, there is a great contrast between autumn and spring-sown cereals. Spring-sown barley at Rothamsted from 1976 to 1983 had at least twice as much infection when sown in the second half of April as when sown in early March. Fortunately, avoiding BYDV by sowing in early spring agrees with the recommendations of agronomists as to the sowing date leading to maximum yield (Forbes, 1966).

Previous crop—When cereals follow fallow or a crop not susceptible to BYDV, there is no within-crop source of inoculum present when the crop is sown; the virus must be brought in by aphid vectors. However, when the cereal follows a grass sward or other cereal, BYDV sources may be present within the newly sown crop. Especially dangerous is the possibility of aphids moving from dying grass to emerging cereals. It is then probable that the aphids carry BYDV and can infect the plants as soon as, and sometimes before, they emerge. While complete crop failure as a result of such infection is fortunately uncommon, several autumn-sown crops in Britain have to be plowed up in the spring of most years because of BYDV infection. Such damage is normally associated with a short interval between cultivating grass and sowing a cereal.

How long the interval between cultivation and sowing should be depends on the methods used to destroy the grass. Conventional plowing is a slow way of destroying the virus source, as the inverted grass dies slowly. Aphids can live for some time on the dying leaves and roots, and an interval of at least four to six weeks

between plowing and sowing seems desirable. Killing grass with a chemical before plowing destroys the virus source rapidly, and quick-acting herbicides such as paraquat and diquat seem more effective than the slower acting glyphosate. Some farmers have even sprayed grass with an aphicide before cultivating, but the effectiveness of that method has not been proved.

Volunteers or grassy stubble must be infected by aphids between the harvesting of one crop and the sowing of the next before they can act as a source of infection. In Britain, most of this problem results from winter barley which now covers 50% of the entire barley area. Winter barley is usually sown in September and harvested the following July, almost a month before spring-sown barley and winter wheat. Grain that is shed when the autumn-sown barley is harvested germinates quickly and thick stands of volunteers can appear within 10 to 14 days, at a time when aphids are still migrating from other cereals. In September, 1982, tests on volunteers from a previous winter barley crop showed that 60% of the plants were infected.

Efficiency of sources—Measurements of BYDV concentration using the enzyme-linked immunosorbent assay (ELISA) showed that, in *Lolium* spp. and maize, virus concentration was much less than in cereals, especially oats (Lennon *et al.*, 1979). There is also some evidence that the proportion of vectors acquiring virus from various hosts is positively correlated with the concentration of virus in the source plant. After 24 and 48-hour acquisition feeds on *Lolium* spp., 42% and 70%, respectively, of single *Rhopalosiphum padi* bred on the grass transmitted the disease; when oats were the source of aphids and virus, the corresponding figures were 92% and 100%.

Conclusion—There are various alternative strategies for the control of BYDV by the modification of husbandry practices; whether or not they are practical depends upon individual circumstances. A clear conclusion from experience in Britain is that crops will be sown at a time which is a compromise between that which offers the greatest potential yield and that which is possible for the farmer. Especially important is the need for the removal of cereal stubbles and the timely destruction of grass swards when they are to be followed by a cereal.

Vector Populations

With the exception of crops following grass swards or volunteers, the information which is needed on which to base sound advice for BYDV control, either by avoidance or by pesticide use, is which aphids occur when and in what numbers and whether they transmit virus. There has been an attempt to do this in Britain for some years using information from the Rothamsted Insect Survey (RIS) (Taylor, 1973). The RIS provides data on all aphids caught in 22 suction traps throughout the British Isles; a weekly bulletin lists the number of each species caught. The network of traps has recently been extended into Europe, increasing it to a total of 35 sites (Taylor, 1983). As a result, the time of flights of most migrant species is now known.

There are three distinct migrations of cereal aphids. In the spring (May to June), they move into crops from their overwintering hosts and, in the summer (June to August), disperse within crops and later migrate to perennial hosts as the crops ripen. In the autumn (September to November), there is mainly a return migration to primary hosts.

Vector Infectivity

Infection by BYDV cannot be predicted from aphid numbers alone and, in Britain, the RIS data is supplemented by the catching of aphids in suction traps. The traps are 1.7 meters above the ground, and the aphids are collected live from them in dry jars; they can stay alive for at least 12 hours after trapping. The traps are emptied twice a day, the catch sorted, the aphids identified and potential vectors of BYDV placed singly on susceptible oat test seedlings. Infective vectors are identified by plants which show symptoms or are serologically diagnosed as infected. This method copies the behaviour of aphids in crops but, by confining them on plants on which they might not otherwise feed, the proportion of aphids that will transmit is probably over-estimated. However, this direct system has the advantage that it provides other information of epidemiological value, including whether the aphids survive and reproduce.

An indirect method for detecting infectivity is being investigated, using the fluorogenic modification of the ELISA system as developed by Torrance and Jones (1983). Immuno-specific electron microscopy has also been used to detect BYDV in single aphids. The principal advantage of the serological detection method is its speed, 24 hours as compared to two to four weeks for the direct method. However, its disadvantage is the difficulty of interpreting results. Serological methods will detect viruliferous vectors, i.e., aphids which contain virus, but may not identify infective vectors, i.e., aphids capable of transmitting the virus they contain to plants.

The method being investigated at present involves a combination of the two methods. Aphids are caught live, identified and allowed access to test seedlings for a minimum of 48 hours. The plants on which they have fed are then serologically tested for BYDV seven days after the beginning of the infection feed. Tests have shown that more than 95% of infections are detected by this method. Determination of infectivity and its integration with aphid numbers has provided much useful information, but the most valuable result has been the development of a scheme for predicting which crops are likely to benefit from an insecticidal spray to prevent virus spread.

In spring crops—In the spring, there is a fairly consistent relationship between the first capture of each species in the RIS traps and the first infective capture. The different intervals between these two events reflect the influence of the biology of the species on the likelihood of its acquiring BYDV. For *R. padi*, which is nearly always the first infective species caught, the interval is 11 days (May 19, first capture, to May 30, first infective). For *Sitobion avenae*, the interval is 27 days (May 23 to June 19) and, for *Metopolophium dirhodum*, it is 33 days (June 3 to July 6). By the end of May, as most autumn-sown cereals are close to ear emergence, they are difficult to infect and unlikely to suffer much yield loss from virus infection; therefore, spring spraying of autumn-sown cereals is not recommended for controlling BYDV. Similarly, early spring-sown cereals (February to March) are much less likely to be infected than those sown in late April or May; in the latter, crop infection can be widespread and damaging. Although at present there is no detailed scheme for predicting which spring-sown crops should be sprayed, advice is given on the basis of crop-sowing date and the time of probable occurrence of infective vectors.

In autumn crops—In September, October and November, cereal aphid migrants caught in suction traps are almost exclusively *Rhopalosiphum* spp., either *R. padi* or *R. insertum*. They are a mixture of both parthenogenetic and sexual forms, with the proportion of males usually increasing to 60 to 70% during the migration. At present, the infective proportion of *Rhopalosiphum* spp. is determined, although all aphids are identified as to species. The proportion of infective *S. avenae* are determined separately, although rarely more than two or three are caught in a week.

Using the proportion of infective aphids and the number caught by RIS each week, an infectivity index is calculated by multiplying one by the other. Although the infective proportion for all *Rhopalosiphum* spp. is calculated, only the number of *R. padi* caught is used to calculate the index at present. Fewer *R. insertum* have been found to be infective than *R. padi*, and most of them migrate to apple, their primary host. However, they can infect cereals even if they do not colonize, and the virus can then be spread by the colonizing *R. padi*.

The infectivity index is calculated weekly and each crop can therefore be assigned an index number. Obviously, crops are not exposed to infection until they emerge, except perhaps when they follow grass, so, logically, the index should relate to the date of emergence. However, although few farmers know the dates for crop emergence, they all know when they are sown; therefore, the index is usually based on date of sowing.

Data necessary for index calculation has been obtained at Rothamsted since 1969, but it is only in the last four years that it has been widely used for forecasting. Since 1969, a total of 36 field experiments have been carried out on autumn-sown crops there and at Woburn (40 kilometers north of Rothamsted), including a comparison of sowing dates and autumn pesticide treatment. Regressions of the change in yield from the autumn pesticide treatment against the infectivity index at sowing show a significant correlation for September-sown crops (correlation coefficient r = 0.68); every 50 increments in the index gives an extra 0.15 tons of yield. The correlation of yield response and all sowing dates was less good (r = 0.51). This makes biological sense, as September-sown crops are exposed the longest to potential virus vectors. If it is assumed that crops take ten days to emerge, and the index is calculated for emergence dates, significant correlations are again found. For each 50 increments in the index and emergence, the expected yield increase is 0.4 tons.

The economic threshold for Rothamsted, based on these calculations, is an index of about 50 based on sowing date and 20 based on emergence. This assumes a cost for pesticide and its application of £ 15 ($22 US) per hectare (slightly more than current prices) and a crop value of £ 100 ($147 US) per ton (less than current prices). Advice is based on this information, but farmers and advisers are encouraged to compare between years and make their decisions based on their own experience as well as on the index. Ultimately, it is the farmer who makes the decision of whether to spray; the function of the researcher is to provide the best information possible for his use in making that decision.

Equally good data is not available for other sites, but it seems certain that thresholds will differ between regions and that local forecasts will be necessary. Testing for aphid infectivity is now being carried out at nine sites.

Sprays and Timing of Spraying

Pesticides, either applied as granules or sprays, have been widely used to control the vectors of BYDV. If experience suggests that infection seems certain, then the use of granules at sowing may be justified; however, when the likelihood of infection fluctuates from year to year, insecticidal sprays applied when and if they become necessary are more acceptable ecologically and economically. There is, at present, no difficulty in killing aphid vectors of BYDV as no insensitivity to pesticides has been detected (Stribley *et al.*, 1983). Only those aphids that occur in the whorls of leaves or in leaves rolled as a result of aphid feeding are sometimes difficult to kill with contact insecticides.

The essential prerequisite for effective control of BYDV by spraying is to know when to spray. In Britain, spraying trials have shown that the optimum spraying time in autumn-sown cereals is just before, or just after, the end of the autumn aphid migration. In most years, this is at the end of October and the beginning of November.

Several chemicals have been approved for use on autumn-sown cereals to control aphids and BYDV (anonymous, 1983). The evidence from spraying trials suggests that the synthetic pyrethroids (cypermethrin, deltamethrin, permethrin and fenvalerate) and the more persistent organophosphorous chemicals (demeton-S-methyl and thiometon) are the most effective. Less effective is the more aphid-specific, but less persistent, pirimicarb (Barrett *et al.*, 1981). Recently, concern has been expressed that, if BYDV is introduced by aphids early in the autumn migration, it may spread before sprays are applied; this would suggest that two sprayings may be needed. This may be justified economically in Britain but the environmental hazards are great; such frequent use of pesticides seems likely to increase the risk of the development of insensitive aphid populations.

Conclusions

It seems probable that, in most temperate regions, pesticides will remain the preferred method for control of BYD as, at present, breeding for resistance to BYD has a very low priority. Under these circumstances, it is essential that the use of chemicals be based on a sound knowledge of virus epidemiology.

References

Anonymous, 1983. Use of fungicides and insecticides on cereals in 1983. Booklet no. 2257, Ministry of Agriculture, Fisheries and Food, UK.

Barrett, D.W.A., P.J. Northwood and A. Horellou. 1981. The influence of rate and timing of autumn applied pyrethroid and carbamate insecticide sprays on the control of barley yellow dwarf virus in English and French winter cereals. *In* Proceedings, 1981 British Crop Protection Conference: Pests and Diseases 2:405-412.

Forbes, N. 1966. Varieties, seed rates and nitrogen for late sowing of spring cereals. Experimental Husbandry 13:11-19.

Lennon, E.A., R.T. Plumb and M.F. Clarke. 1979. BYDV and enzyme-linked immunosorbent assay (ELISA). Report of Rothamsted Experimental Station for 1978, Part 1, p. 211.

Stribley, M.F., G.D. Moores, A.L. Devonshire and R.M. Sawicki. 1983. Application of the FAO-recommended method for detecting insecticide resistance in *Aphis fabae* Scopoli, *Sitobion avenae* (F.), *Metopolophium dirhodum* (Walker) and *Rhopalosiphum padi* (L.) (Hemiptera:Aphididae). Bulletin of Entomological Research 73:107-115.

Taylor, L.R. 1973. Monitor surveying for migrant insect pests. Outlook on Agriculture 7:109-116.

Taylor, L.R. 1983. EURAPHID: Synoptic monitoring for migrant vector aphids. *In* Plant Virus Epidemiology: the Spread and Control of Insect-Borne Viruses, R.T. Plumb and J.M. Thresh, eds. Pp. 133-146.

Torrance, L., and R.A.C. Jones. 1982. Increased sensitivity of detection of plant viruses obtained by using a fluorogenic substrate in enzyme-linked immunosorbent assay. Annals of Applied Biology 101:501-509.

Comments

J.M. McEwan, New Zealand

Delayed sowing is recommended in New Zealand for the reduction of BYDV infection in autumm-sown wheat. Aphid trapping in the South Island from 1959 to 1966 had shown a marked periodicity of autumm flights of *R. padi*. Those flights were generally over by the first of June, which was then suggested as the earliest safe sowing date. Crops sown in May were likely to have some aphid infestation, while crops sown before the first of May would definitely have aphids. The recommendation was that sowing be delayed until June 1 if practicable; crops sown prior to that date should be inspected for aphids during July. With the finding of aphids, treatment with an aphicide spray at recommended rates prior to September 1 was advised.

Delaying sowing to reduce BYDV damage has led to a demand for earlier maturing cultivars, a demand that has been partially satisfied by the release of the cultivar Rongotea.

P.A. Burnett, Mexico

In New Zealand, four aphid species are commonly found infesting cereals, *R. padi, R. maidis, S. miscanthi* and *M. dirhodum*. All of them may be involved as vectors in the transmission of BYDV. *R. padi* is the major vector; *R. maidis* and *S. miscanthi* may act as vectors but are thought of as being of little relative importance. The significance of *M. dirhodum* is not yet known as it only became established in the country late in 1982.

It is almost impossible to avoid aphid infestations, especially of *R. padi*, in spring cereals. In a heavy infestation, chemical control will reduce the numbers of aphids and the incidence of BYDV; however, the economic feasibility of the practice is not yet known. J.M. McEwan has already commented on the recommendations for autumn-sown cereals. During the last decades, the number of cereal aphids and the incidence of BYDV has been low in the main cropping areas. However, it has been found that earlier autumn sowing results in increased yields and, with the adoption of the practice, the severity of BYDV may increase.

Not all of this decline in aphid numbers and BYD incidence can be due to late sowing of cereal crops; it has been postulated that the banning of DDT as a chemical for pasture pest control may also be a factor. DDT may have killed a higher proportion of aphid predators and parasites than of the aphids themselves, although those insects were not the target. Resistance to DDT may have developed more rapidly in aphids, thus putting them at an advantage over their predators and parasites and leading to the high populations recorded historically.

In summary, the two general methods for controlling *R. padi* are sowing late in the autumn to avoid aphid flights and treating to kill the aphids. In addition, it is advisable to use cultivars resistant to BYDV. Karamu is the most resistant wheat cultivar available in New Zealand, while Rongotea and Oroua also have good levels of resistance. The oat cultivars Omihi and Ohau are also resistant.

R.J. Sward, Australia

Trials were conducted in Victoria, Australia, to determine the effectiveness of demeton-S-methol and Aldicarb in controlling autumn and spring aphids and the subsequent effect on the levels of BYDV in wheat. Aldicarb granules were incorporated at sowing and demeton-S-methol was applied at selectively timed intervals. The Aldicarb-treated plots yielded 32% more grain than the untreated control plots, whereas demeton-S-methol had no significant effect. It was unlikely, however, that the 32% yield increase was solely due to a lowering of the incidence of BYDV. Aphid trapping data and incidence of symptoms in oat indicator plots showed a 5% BYDV level introduced with autumn aphid flights and 22% with spring flights. Previous experiments in the same area indicated that crop losses of 5 to 10% could be expected, so there must have been other contributing factors. Sampling for nematodes and other soil-borne pathogens, as well as further experiments with soil and seed treatments, did not provide any extra information and the reasons for the 32% yield increase have not yet been determined.

In other experiments, the synthetic pyrethrins, permethrin and cypermethrin, have been used. Fortnightly spray applications from emergence to heading have resulted in grain yield increases of up to 200% in many wheat cultivars and breeders' lines. However, this level of insecticide application is uneconomic, and trials are continuing to determine the effect of one or two applications at the critical seedling stage.

Aphid Rearing and Screening Methods for Resistance to Barley Yellow Dwarf Virus in Cereals

A. Comeau, Agriculture Canada, Quebec, Canada

The development of cereal cultivars resistant to barley yellow dwarf virus (BYDV) necessitates routine virus inoculation techniques that can be used successfully to test thousands of lines of cereals every year. As this virus is only aphid transmitted, detailed knowledge of the biology of aphids is as essential as that of virus isolates.

In order to assess BYDV resistance, some workers in key locations can rely on a high level of natural BYDV infection, which can be increased by various management methods (Rasmusson and Schaller, 1959). However, rearing viruliferous aphids is apparently the most common practice to test for reaction to BYDV among cereal lines.

From 1971 to 1973, the methods of Endo (1963), Catherall and Hayes (1966) and Damsteegt and Bruehl (1964) were used in Quebec. It was discovered in 1973 that aphids mixed with talcum powder could be handled in bulk and deposited near the plants with an aphid spreader. Without talcum powder, the aphids stuck together, glued to death by waxy secretions from their cornicles (Comeau, 1976).

By 1983, gradual improvement in methodology had led to the ability to test more than 40,000 individual cereal plots. This was due in part to better aphid rearing and handling methods, and in part to the use of microplots instead of large plots. The following methodology is therefore based on 12 years of empirical observations and experience in screening for BYDV resistance. Described here are necessary equipment and facilities, the care of virus strains, rearing techniques for large numbers of aphids and techniques for harvesting aphids, carrying them to the field and applying them to the plants. Field work methods and the criteria for assessing resistance are also discussed.

Equipment and Facilities

A growth cabinet is necessary to keep colonies of virus-free and viruliferous aphids year round. The calendar schedule used in the Quebec laboratory requires seeding new plants and starting new aphid colonies approximately every three weeks. Colonies are kept at 12 to 14°C under 250 to 350 uE light intensity with a 16:8 light:darkness cycle. More growth cabinet space is needed during the first 39 days of aphid rearing (Figure 1).

The standard aphid cage is a 10-cm diameter translucent acrylic cylinder, with 3-mm walls, which fits on top of a 15-cm flower pot. Ventilation is insured through six 6-cm side holes and a top ring, each of which is covered by nylon screens inside and out. This double screen, with a 3-mm air space, prevents any accidental probing by viruliferous aphids through the screen. The bottom of the pot also has a double screen to prevent the possibility of virus inoculation through the roots.

The principal aphid production for field inoculation is carried out in a large greenhouse, many types of which have been used successfully. Artificial heating and cooling are useful but not absolutely necessary under most climatic conditions if good ventilation is available. Aphid rearing is generally done in the spring or in the fall, when outdoor temperatures are not above 30°C. Some aphid species such as *Metopolophium dirhodum* are very sensitive to heat (Dean, 1974) and require a good cooling system. The species most frequently reared for BYDV transmission, *Rhopalosiphum padi*, suffers damage above 32°C and death at 37°C (Belvett *et al.*, 1965). The aphids can be reared on plants in pots, in flats or in rows seeded in soil-filled benches. Rows seeded directly into the native soil at ground level in commercial-type greenhouses are also acceptable, provided a one-meter space is left between rows.

To produce the *R. padi* needed to inoculate one hectare of BYDV experiments in the field, an area of 50 square meters of bench space is necessary in research-type greenhouses equipped with heating and cooling systems. The same aphid production from plants seeded in native soil in greenhouses, equipped with ventilation only, requires 100 square meters of land area. The greenhouse must be insect-tight so that no predator or parasite can enter, and must also be free of volunteer grass or weeds before the start of operations. Preparing the greenhouse involves checking for gaps and spraying both the inside and the immediate perimeter outside with glyphosate, tetrachlorvinphos and mevinphos insecticides to kill any plants or insects; these steps are essential for success. Residual effects of the pesticides have not been found to interfere with research results.

Virus Isolates

There are a number of vector-specific BYDV isolates, those which are transmitted by only one aphid species. Among them are *R. padi*, *R. maidis*, *Macrosiphum avenae* and *Schizaphis graminum*; other isolates are nonspecifically transmitted. Stock virus isolates must frequently be transferred to new plants with the corresponding aphid species. Experimentation is under way on the storage of BYDV isolates in vitro at 0°C under aseptic conditions in wheat plantlets derived from embryo culture; this could be useful for long-term isolate preservation.

One isolate or a mixture of isolates can be chosen for large-scale multiplication. Certain mixtures give rise to the cross-protection phenomena (Jedlinski and Brown, 1965), which is not desirable in trials for BYDV resistance; however, preliminary tests of many isolate combinations in growth cabinets can give adequate information for avoiding such problems. Using less virulent isolates or mixtures necessitates increasing the number of repetitions per trial, leading to increased cost per line tested. The Quebec laboratory generally uses mixtures of two to four isolates for their trials; the isolates are kept separately until the aphids are liberated on the 56th day (Figure 1).

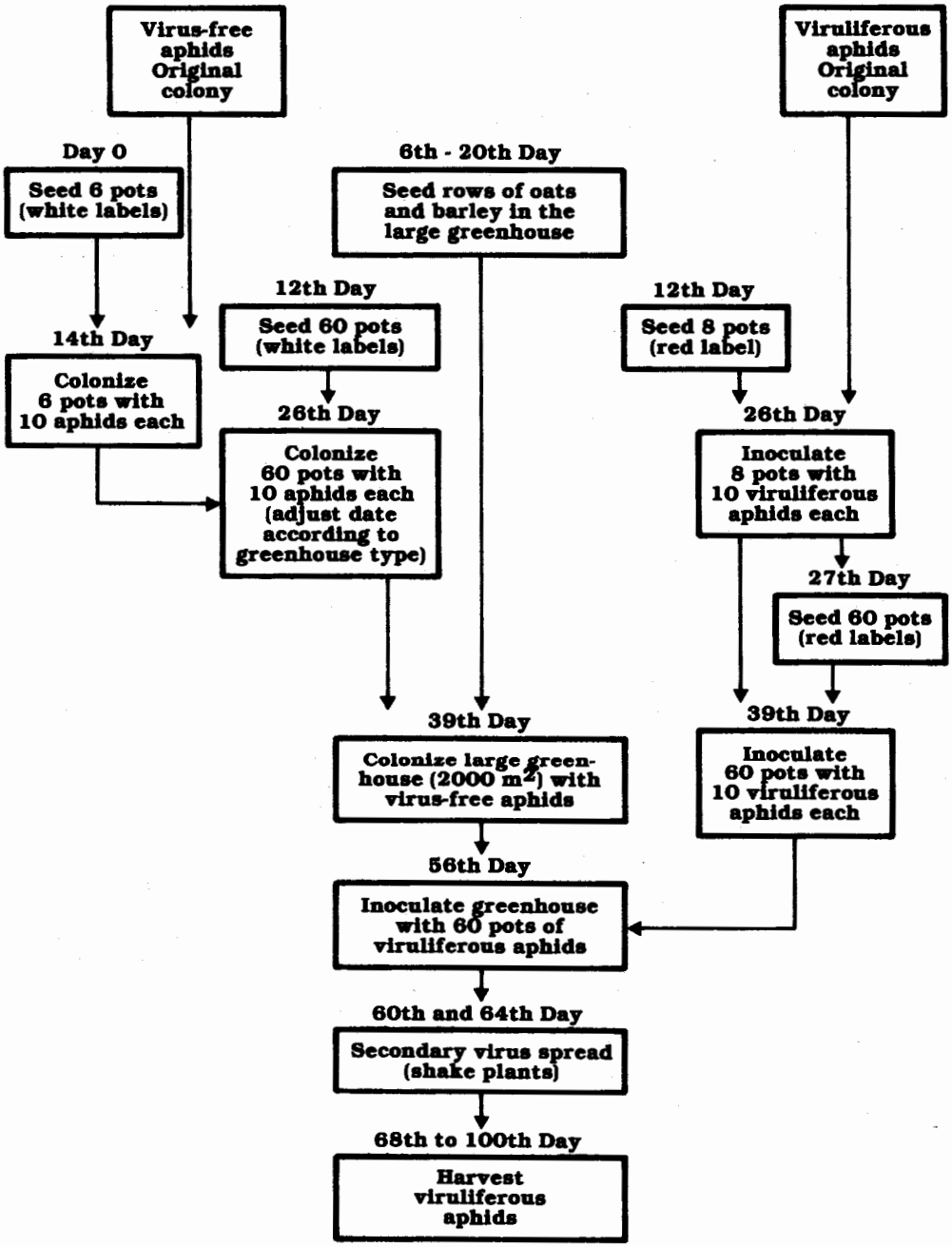


Figure 1. Schematic summary of the calendar of operations for mass rearing viruliferous aphids (*Rhopalosiphum padi*)

Aphid Rearing

The technique for aphid rearing is a three-step process: 1) growing virus-free aphids and viruliferous aphids (separately) in cages (Figure 1) and growing aphid-free rows of plants in a large greenhouse; 2) the infestation of the greenhouse with virus-free aphids on the 39th day and 3) the infestation of viruliferous aphids in the greenhouse on the 56th day. This method gives maximal plant biomass to obtain high aphid populations.

Over the years, many cereal species and cultivars have been used in the large greenhouse, and experimentation is still under way to find late, strong-strawed plant types with short, erect leaves to serve as rearing substrate for *R. padi*. Presently, the best results come from oats or a 75%oat/25%winter barley mixture. Reproduction of *R. padi* is very good on barley seedlings but, by flowering time, barley is an undesirable species as aphid reproduction is low (Leather and Dixon, 1981); the awns of barley may also cause problems when aphids are collected. *R. maidis* does poorly on ripening barley (Kieckhefer, 1983), while ripening oats, barley or wheat are a good substrate for *M. avenae*. Oat cultivars good for rearing *R. padi* and *M. avenae* include the spring-type cultivars Omihi and Mapua from New Zealand and the winter-type cultivars 74C 80889 and 72C 3034 from Texas. Early spring oats such as Clintland and Ogle should be added when rearing *M. avenae*; they provide a long period of flowering plants, ideal for that aphid. For *R. maidis*, it is necessary to use only winter barley, as other hosts are not well accepted by this species.

Diverse problems may develop inside a large greenhouse during the rearing process. Accidental entry of parasities and predators often cannot be avoided, as doors are opened periodically to water plants and to verify growth conditions. If the aphid predators *Coccinellidae* or *Syrphidae* appear in the greenhouse, they can be controlled with minimal aphid kill by spraying with tetrachlorvinphos at approximately 0.30 kg per ha active ingredient (a.i.). The spray should be applied through a herbicide nozzle to avoid the forming of a mist; it should be sprayed mostly on the ground and on those parts of the plants less colonized by the aphids. Mobile predators and parasites are also killed quite efficiently with the same dosage of carbaryl applied in a similar manner.

Aphid parasitoids are more resistant to such treatment and, when abundant, jeopardize the aphid rearing process. The percentage of parasitized aphids should be closely monitored following the technique used in South America (C. Quiroz, Chile, and D. Gassen, Brazil, personal communication). A sample of aphids is dropped in one ml diethyl ether in a petri dish and, when the ether evaporates, the aphids are covered with hydrogen peroxide (40-volume) freshly brought to the boiling point. The aphids explode and aphidiid larvae float to the surface.

When aphidiid parasitism, evaluated by this method, reaches 5%, the aphids should be harvested and taken to field plots within ten days or less; the aphid population will be at its peak and can collapse quickly. The parasitoid larvae may transform into pupae and adults in less than a week, and each adult may parasitize about 100 aphids in a week. The parasitized aphids will retain their ability to transmit virus for only a few days.

Excessive humidity in the greenhouse may cause the build-up of *Entomophthora* spp., fungus species that attack aphids; it will not develop in a well-ventilated greenhouse. If the problem occurs, incandescent light bulbs may radiate enough energy to create a microclimate that is unfavorable to *Entomophthora* build-up (V. Caetano, personal communication). Fungicides have been tried against *Entomophthora*, but without much success.

Powdery mildew, *Erysiphe graminis*, is the only plant disease that may be a problem in aphid rearing. To avoid it, seeds should be coated before seeding with ethirimol, a systemic fungicide specific for powdery mildew; it does not effect aphids at normal doses (L. Couture, personal communication). For 100 grams of seed, the rate used is 0.67 grams a.i. for barley, 0.92 grams a.i. for oats and 0.53 grams a.i. for wheat. If, despite this coating, the fungus still appears, it can be repressed by foliar sprays with the same chemical at 0.62 grams a.i. per liter. The use of benomyl against powdery mildew will kill the aphids (Partis and Bailiss, 1980).

Satisfactory aphid reproduction depends on plant health and good watering and fertilization, which will give abundant sap, rich in nitrogen, an essential for good aphid reproduction (Coon, 1959). The plants should be fed with a complete fertilizer formula every week until the 56th day. At about that time, plant care becomes more complex, necessitating great attention to keep the plants alive. The principal problem then is not the virus but, rather, aphid honeydew, which acts as an osmotic agent, extracting water from the leaves and resulting in severe leaf burns that can cause irreversible damage to the plant. When honeydew begins to show on leaves, a daily schedule of leaf washing must be followed; a fine mist drowns very few aphids. To prevent lodging, plants can be attached to a network made of wire and baler twine, although clipping the heads is sometimes sufficient. Repeated leaf washing causes serious mineral leaching problems, and a leaf fertilizer of dilute Hoagland solution (10% of normal strength) should be sprayed on twice a week to compensate for leaching. Anhydrous ammonia can also be used (30 grams evaporated per 100 cubic meters) if leaves are not sufficiently green.

Although the schedule predicts aphid harvest on the 68th day (Figure 1), there is some variation every year and, by the 56th day, the aphid population may already be too large (or too small). Something must be done quickly if the population is too large, i.e., 500 aphids per tiller, because then aphid damage will occur despite efforts to wash off honeydew. In Quebec, a pressurized spray formulation of synergized natural pyrethrins such as Raid House and Garden Insecticide (registered trademark) is used to reduce aphid populations. A very light mist (three to six seconds in 50 cubic meters) will kill

some of the aphids without residual effect the next day. This treatment can be used as often as three times a week and ensures subsequent production of wingless, healthy aphids instead of the small alates which result from overcrowding.

Plants should never have an unnecessarily large population of aphids, unless the aphids are to be harvested within 48 hours. While properly cared-for plants should show some BYDV symptoms, appropriate leaf washing and foliar fertilization may delay symptom expression. Symptoms, however, have no relationship to the virus content of the plants.

Aphid Harvest, Transportation and Field Spreading

The day before harvest, honeydew should be washed off the plants early in the morning. On the day of harvest, the aphids must be collected when the leaves are dry. Trays lightly dusted with talcum powder are inserted between rows and the plants tipped slightly toward the tray and tapped so that they vibrate for a few seconds; this causes the aphids to extract their proboscises and fall from the plant. Injured aphids emit an alarm pheromone that may assist in the process. The aphids are then transferred from the trays to plastic boxes which can be filled with layers of aphids five to eight mm thick. Just enough talcum powder is dusted on the top to whiten the surface.

When excessive leaf moisture is present, the trays should be covered with paper towels or cotton cloth and dusted heavily with talcum powder before harvesting the aphids; the material will absorb the water and clean aphids will be obtained. If the aphids are mixed with plant debris or larger insects, they should be sieved or cleaned by hand and transferred to the plastic storage boxes. The lids of the boxes should be lined with damp paper or cotton cloth and must not be left in the sun. For transporting, the boxes are placed in a stryrofoam ice chest; aphids may be thus kept for three hours. For longer storage, it is sometimes necessary to put a large plastic bag of ice cubes on top of the ice chest. It should not be put inside the chest as it will create condensation problems. With a bag of ice on top of the ice chest, aphids will keep for 12 hours and can be carried long distances by car. It is not easy to estimate the number of aphids harvested, because aphid size varies a great deal according to their health and the presence of alates. For *R. padi*, for instance, one million aphids weigh 300 to 450 grams and occupy a volume of 1.1 to 1.5 liters.

(continued)

Aphid spreading in the field is done with a new apparatus (Figure 2), similar to a previously illustrated prototype (Comeau, 1976). Aphids in small numbers are dropped from a triangular box into a funnel connected to a flexible tube which deposits them on the ground. The box measures 22 x 27 x 27 cm and has a triangular lid; it is made of 3-cm thick acrylic plastic and glued with methylene chloride. The tube is made of heavy gauge rubber hose with a blade of flexible metal inside. The jointed tube is very useful as it is necessary to fold the apparatus frequently to be able to kneel down to check the number of aphids per plant and the behavior of aphids deposited on the ground.

Figure 2. Aphid spreader, showing triangular container, funnel, tube and flexible articulation; tube for depositing aphids on the ground is about one meter in length.

Tapping the sides of the box gently, about two to four taps per second, causes the aphids to fall through a corner opening into the tube. About five to ten aphids per plant can be deposited by a person walking at normal speed; aphid flow is regulated by changing the angle of the triangular box. The aphids can be deposited either close to the plants or between rows if the soil surface is cool. It is necessary to agitate the aphids in the box every minute or two to avoid the formation of a plug of aphids and debris at the opening. In case of high winds, the apparatus can be protected with a polyethelene sleeve. In most cases, protection against the sun is also necessary; aluminium foil or wet towels can be used.

Careful attention to aphid behavior is necessary if the soil surface feels hot; if surface temperature exceeds 40°C, the aphids will move for only 10 to 60 seconds and then comatose. If a cloud covers the sun, the aphids may recover and move to shelter; otherwise they die. Paralysis of *R. padi* is much more rapid than the previously recorded paralysis of the pea aphid (Roitberg and Myers, 1979). Under very hot conditions, large water drums are carried to the field and a little water sprinkled over the plots before spreading aphids; this is enough to cool the soil for a few minutes and give good aphid survival. Cold conditions present no real obstacle unless the temperature is lower than 4°C at ground level. A forecast of rain should not delay aphid spreading; aphids can resist rain unless it is heavy and with very large drops. Rain may wash the aphids into low areas, and

those spots should be checked after the rain and extra aphids spread if necessary. In exceptional cases, where low numbers of aphids have to be distributed, a small paintbrush can be used to drop aphids one by one into the funnel.

Coccinellidae are fast-moving predators that may collect quickly, within one or two days, in areas where aphids have been deposited, and they can serve as a means of rapid biological control in parts of the field, causing uneven results. In some instances, tetrachlorvinphos has been used at 0.3 kg per hectare a.i. to destroy them.

Aphid populations may increase in the field, or they may be overcome as a result of biological control or heavy rains. If they multiply to more than 20 aphids per tiller, they should be killed with a nonphytotoxic insecticide such as pirimicarb or phosdrin if aphid damage is not desired.

Figure 3. This modified corn planter can be used to seed hill plots efficiently at low cost. The pointed beak digs a groove in the ground and, when the operator moves forward, the beak opens up and drops the seed as the apparatus is pulled out; the operator covers the seed with his foot. Using this apparatus, two workers can seed 5,000 plots per day.

Field Work Considerations

The initial work in Quebec involved large plots of some three square meters. Considering the high cost of aphids and the year-to-year reproducibility level of BYDV reaction, this was a great waste unless dealing with bulk F_2 or F_3 from which individual resistant plants had to be selected. H. Jedlinski obtained excellent results with hill plots, and they are now used in Quebec, hand seeded with a locally made planter (Figure 3). Short rows are also used and are sown with a Seedmatic from Wintersteiger, Austria. This seeder allows three workers to seed 20,000 85-cm rows in one day.

The cost-benefit ratio of BYDV research is very dependent on the type and size of plots used. Microplots can be seeded faster, and valid observations are obtained with minimum cost for aphids. With the microplots, one worker can easily inoculate up to 5,000 plots per day when aphid production has been abundant; two technicians can assess disease symptoms in about 1,500 plots per day. The research station in Quebec is now trying to develop photographic symptom scales to accelerate the scoring time. The total cost per plot is now about $9.50 US.

which includes salaries for one professial, two technicians, five summer helpers, all costs and depreciation due to laboratory and greenhouse operation, equipment and supplies, and salaries for support staff, such as computer help and secretaries. Increasing the size of the project would reduce the cost per plot.

Site selection is an important consideration. Soil should be selected that favors uniform germination; crusty or sandy soils must be avoided or improved with massive amounts of organic matter. Uneven germination gives a very large increase in variability of BYDV response. On good sites, one replicate may be adequate to evaluate BYDV reaction of barley and oats; two replicates are suggested for triticale and three for durum and bread wheat. This seems to apply to both spring and winter cereals. Large-scale screening of bread wheat can be done with one replicate, provided the best lines are tested with several replicates the following year.

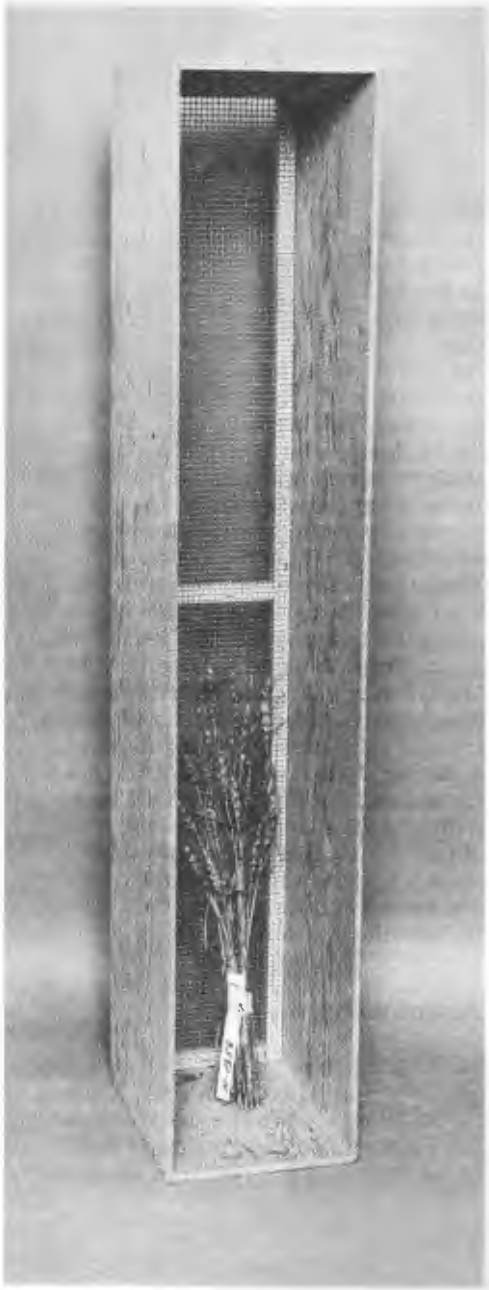
Minimum variability is obtained by inoculating barley with BYDV between the two-leaf stage and stage five of tillering; for oats, wheat, triticale and durum, there is a longer period when inoculation can be carried out, from the two-leaf stage to the appearance of the first three nodes in early stem elongation. Later inoculation can produce significant yield loss, but the statistical error term also becomes larger, necessitating more replications; this is not desirable in large-scale screening work. Winter cereals must be inoculated as soon as possible in the fall, from the one-leaf stage to early tillering.

Work has generally been carried out without uninoculated check plots in large-scale screening, as this would double the field work. Uninoculated plots are used in specific experiments only; they are then separated from the inoculated blocks by many buffer rows and sprayed a number of times with pirimicarb insecticide. Even then, some BYD contamination often occurs. Natural epidemics can also decrease the value of uninoculated plots.

Bread wheat, durum wheat and triticale are harvested for evaluation of BYD damage. The central 30 cm of the 85-cm row is harvested near ground level and the bundle tied together with masking tape, with a flexible plastic tag identifying the plot. The bundles are kept in harvest boxes with screen bottoms (Figure 4). The boxes fit into a solar-type dryer, actually a modified greenhouse with ventilation coming through the bottom of the harvest boxes. From the bundles, grain yield, biomass and harvest index data can be obtained.

Weed control in BYDV trials is surprisingly difficult and can become very costly since diseased plants offer no competition to weeds. The use of chlorsulfuron herbicide eliminated most of the hand weeding in 1983.

Bird damage can be more severe in microplots than in large plot trials. It is recommended that, if necessary, the whole field be covered with netting at sufficient height to allow workers to walk underneath.



Seeding plots in a greenhouse instead of in the field can give useful information if greenhouse conditions are adequately controlled. However, BYDV reaction may be strongly influenced by such an artificial environment, and caution is advised. A preliminary study should be made to see if greenhouse data correlate with field data under various artificial climatic conditions.

Criteria to Assess Resistance

Symptoms alone can be quite informative about the resistance level of oats and barley if inoculation is done properly. However, in the case of bread wheat, durum wheat and triticale, symptoms are not always reliable, because the effect of BYDV is mainly poor grain filling and dwarfing rather than the more visible yellowing. This means that visual symptoms often do not correlate highly with BYDV damage. Programs in South America have experienced similar problems (V. Caetano, personal communication).

Figure 4. Harvest boxes with screen bottoms are useful for keeping together bundles from the same trial. At harvest time, plants from the central 30 cm of the plot are harvested 1 to 2 cm from ground level and fastened with masking tape, with a flexible plastic plot tag in the bundle. Boxes can be stacked three meters high and ventilated from the bottom for drying. This system facilitates the measurement of harvest index, as the weight of the masking tape and tag is very small and can be compensate for when recording biomass.

Symptoms are a useful tool for eliminating the most BYD-susceptible lines but, to identify the best resistant lines, symptom scores alone are unreliable. It has been noted, however, that by observing a range of characters, namely symptoms, grain yield and harvest index (grain yield divided by biomass), the best BYDV-resistant wheats can be identified. They are the lines having low to moderate symptoms, high grain yield and high harvest index. Harvest index varies less than grain yield under different conditions of soil fertility, making it a useful indicator of BYDV resistance (Comeau and Barnett, 1979). In winter wheat, fall infection produces more severe yield loss than spring infection, but spring infection gives a more clear-cut reduction of harvest index (Cisar *et al.*, 1982). This confirms the use of a number of criterion for evaluation of resistance in wheat.

In large-scale tests without virus-free checks, three criteria are combined into a susceptibility index (SI) for deciding whether to keep or to reject a line. In 1982, different weights were given to grain yield in kg per hectare (y), harvest index (hi) and symptom score (s). The symptom scores depend on the species involved, with less importance placed on symptoms in those species where they are less useful. The formula used for durum and triticale was:

$$SI = 10-[.001\ y + 12\ hi + .3\ (10-s)]^{.77}$$

and that for bread wheat was:

$$SI = 10-[.001\ y + 12\ hi + .2\ (10-s)]^{.77}$$

(Comeau and St-Pierre, 1982). This approach can be used for selecting the best out of many thousands of lines; confirmation of resistance should be done on the few best lines, using a comparison of BYDV-inoculated versus uninoculated grain yield.

Conclusions

It has been shown in Quebec during the last ten years that appropriate aphid rearing techniques can yield from two to ten million BYDV-carrying aphids annually. The development of methods of bulk handling of aphids mixed with talcum powder has made possible the inoculation of 5,000 to 40,000 small plots with viruliferous aphids each year for evaluation for BYDV resistance. With minor modifications, many of these techniques could be used elsewhere in the world to help in breeding for BYDV or aphid resistance. Visual assessment of symptoms on microplots of barley and oats is adequate to assess BYDV resistance; such symptom scores, however, do not always give adequate information in the case of bread wheat, durum wheat and triticale. For those cereals, data on grain yield and harvest index must be considered, as well as yield comparison with uninoculated check plots. To obtain statistically valid information from a small number of replicated microplots, uniform germination and BYDV infection are required as well as severe BYDV damage.

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References

Belvett, V.B., R.Y. Sun and A.G. Robinson. 1965. Observations on laboratory rearing of grain aphids (Homoptera: Aphididae). Canadian Journal of Zoology 43: 619-622.

Catherall, P.L., and J.D. Hayes. 1966. Assessment of varietal reaction and breeding for resistance to the yellow-dwarf virus in barley. Euphytica 15:39-51.

Cisar, G., C.M. Brown and H. Jedlinski. 1982. Effect of fall or spring infection and sources of tolerance of barley yellow dwarf of winter wheat. Crop Science 22:474-478.

Comeau, A. 1976. Elevage en masse, cueillette et èpandage sur le terrain des pucerons (Aphidae) vecteurs du virus du nanisme jaune de l'orge (BYDV). Canadian Entomology 108:373-378.

Comeau, A., and C.-A. St-Pierre. 1982. Trials on the resistance of cereals to barley yellow dwarf virus (BYDV). Report no. 4. Research Station, Agriculture Canada, Sainte-Foy, Quebec, Canada.

Comeau, A., and G. Barnett. 1979. Effect of barley yellow dwarf virus on N, P, K fertilizer efficiency and on the harvest index of oats. Canadian Journal of Plant Science 59:43-54.

Coon, B.F. 1959. Aphid populations on oats grown in various nutrient solutions. Journal of Economic Entomology 52: 624-626.

Damsteegt, V.D., and G.W. Bruehl. 1964. Inheritance of resistance in barley to barley yellow dwarf. Phytopathology 54:219-224.

Dean, G.J. 1974. Effect of temperature on the cereal aphids *Metopolophium dirhodum* (Wlk.), *Rhopalosiphum padi* (L.) and *Macrosiphum avenae* (sic) (F.) (Hem., Aphididae). Bulletin of Entomological Research 63:401-409.

Endo, R.M. 1963. Hill technique for evaluating the resistance of cereals to barley yellow dwarf virus. Phytopathology 53:649-652.

Jedlinski, H., and C.M. Brown. 1965. Cross protection and mutual exclusion by three strains of barley yellow dwarf virus in *Avena sativa* L. Virology 26:613-621.

Kieckhefer, R.W. 1983. Host preferences and reproduction of four cereal aphids (Hemiptera: Aphididae) on certain wheatgrasses, *Agropyron* spp. Environmental Entomology 12:442-445.

Leather, S.R., and A.F.G. Dixon. 1981. The effect of cereal growth stage and feeding site on the reproductive activity of the bird-cherry aphid, *Rhopalosiphum padi*. Annals of Applied Biology 97:135-141.

Partis, G.A., and K.W. Bailiss. 1980. The toxicity of some benzimidazole fungicides to the pea aphid, *Acyrthosiphon pisum*. Annals of Applied Biology 96:137-142.

Rasmusson, D.C., and C.W. Schaller. 1959. The inheritance of resistance in barley to the yellow-dwarf virus. Agronomy Journal 51:661-664.

Roitberg, B.D., and J.H. Myers. 1979. Behavioural and physiological adaptations of pea aphids (Homoptera: Aphididae) to high ground temperatures and predator disturbance. Canadian Entomology 111:515-519.

Evaluation and Breeding Methods for Barley Yellow Dwarf Resistance

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Evaluation methods for detecting barley yellow dwarf virus (BYDV) resistance in breeding populations or germplasm collections should consider the nature of symptom expression and the complexity of inheritance of host plant resistance to the virus. There is now considerable information about the variation in symptom expression in barley, oats and wheat, but little information available on the potential sources of resistance in the wild and primitive relatives of these crops. Symptom expression in susceptible hosts varies from dramatic discoloration (yellowing or reddening) and dwarfing to very limited visual symptoms. This variation is due to genetic factors in the host and, probably, in the aphid vectors and in the virus itself. Environmental factors influence symptom expression, i.e., temperature can effect discoloration, and plant spacing can have an influence on dwarfing. Floret sterility is induced by BYDV and is usually, but not always, associated with yellowing or reddening of leaves. In addition, the growth stage of the plant at time of inoculation and the amount of virus actually received by the plant have a major influence on degree of symptom expression.

Genetics of Host Resistance

A few conclusions about the genetics of resistance will be mentioned here because of its importance in adopting a strategy and methodology for screening for resistance.

Barley was the first host plant in which barley yellow dwarf (BYD) was observed and studied. Fortuitously, sources of resistance were available in the breeding nurseries in California when the disease was first discovered. The very useful resistance in those sources was found to be controlled by one incompletely dominant gene, Yd_2 (Rasmusson and Schaller, 1959). Thus, resistance in breeding populations could be easily identified, and the development of resistant cultivars by backcrossing was highly successful (Schaller *et al.*, 1970). Several studies have failed to detect additional major genes, although barley no doubt also carries so-called minor genes for resistance, such as in the Manchurian types. The variety Rojo has some resistance, but at a far lower level than that conditioned by Yd_2. Suneson (1955) suggested that Rojo had an identifiable gene, Yd_1, but that gene or source of resistance has not been exploited.

The situation is quite different in oats and wheat. Resistance has been detected, but major genes are not evident. Studies which used quantitative genetic approaches have proven that there is heritable variation for symptom expression. In oats, a deliberate attempt to combine

resistance from several sources in Illinois was successful. Both the genetic and breeding studies in oats point to multiple gene systems in which individual genes have small effects on host resistance. However, H. Jedlinski has reported that there may be major gene segregation in some of the Illinois populations. In wheat, there is evidence that the resistance from different sources, although at rather low levels, is controlled by different genes, so that resistance levels higher than those presently existing may be achieved by selection (Qualset *et al.*, 1973b; Topcu, 1975).

Screening techniques must therefore be based on the fact that resistance may be due to major and/or minor genes. Methods that will detect major genes may not be adequate for selection for minor gene resistance. In the latter case, plants with rather substantial symptom expression should be selected in the initial phases to retain the minor genes in the population.

Resistance that may be present in wild species, such as the *Hordeum* species studied by Schooler in North Dakota (Schooler and Anderson, 1979; Schooler, 1980) or in polyploid relatives of wheat, should also be considered as having several genes conditioning resistance so that, in the gene transfer process, methods are used that ensure the recovery of that resistance in the cultivated species.

Factors to Be Considered in Designing Evaluation Methods

From the standpoint of the plant breeder who must handle germplasm source or breeding populations efficiently, the following points about BYD should be kept in mind:

- Both major and minor host resistance genes may be present;
- Variable symptom expression due to environmental effects, such as variation in time of infection, temperature and plant nutrition, will influence any technique for rating plants for BYD reaction;
- Symptom expression is influenced by the host genotype or such characters as maturity, plant height and tillering ability;
- Resistance and susceptibility are not fully expressed by visually scored discoloration, floret sterility and dwarfing;
- Immunity to BYD probably does not exist in cultivated species, so care should be taken to ensure that symptomless plants have been inoculated with the virus;
- Cross protection among virus strains is probably not important in selecting for resistance;
- Virus concentration in the plant may not be related to host resistance, and
- Vector specificity of virus strain transmission may be important. The population biology of aphid species needs special attention because of seasonal differences in the prevalence of aphid species.

Visual Scoring of BYD Symptoms

Severity of expression of BYD can be visually assessed. In the early work on barley (Schaller *et al.*, 1963), a 0 to 4 (resistant to susceptible) scale was used. Later, for wheat and oats, an expanded scale of 0 to 9 was developed (Schaller and Qualset, 1980, Table 1). The full range of this scale is most useful for scoring individual plants, but it can also be adopted for scoring the whole canopy of densely planted stands. Leaf discoloration scores alone do not seem to be adequate to describe response (as related to yield loss), so it is important to include floret sterility (very obvious as blasting of florets in oats) and dwarfing in the scale. Topcu (1975) found significant negative correlations with individual plant BYD scores and yield components.

Table 1. BYDV Visual Scoring System Used for Wheat

Rating	Description
0	No visible symptoms (immune, a symptomless carrier or has escaped infection)
1	Trace amounts of yellowing[a] at the tips of a few leaves; vigorous plant appearance
2	Restricted yellowing of leaves; larger proportion of yellowed areas; compared to class 1, more leaves discolored
3	Moderate to low amount of yellowing; no sign of dwarfing or reduction in tillering
4	Moderate to somewhat extensive yellowing; no dwarfing; moderate to good plant vigor
5	More extensive yellowing; moderate to poor plant vigor; some dwarfing
6	High level of yellowing; poor plant vigor; apparent dwarfing
7	Severe yellowing; small spikes; moderate dwarfing; poor plant appearance
8	Nearly complete yellowing of all leaves; dwarfing; tillering apparently reduced (rosette appearance); reduced spike size with some sterility
9	Marked dwarfing; complete yellowing; few or no spikes; considerable sterility; forced maturity or drying of the plant before normal maturity is reached

[a] In some wheats, red coloration is more prevalent than yellow

Methods of Evaluation

Natural infection—In areas where BYD is prevalent, there will often be natural occurrence of the disease in variety trials and breeding populations. When BYD is obvious by visual symptom expression, it is useful to make visual scores of all entries in all replications of the trials. Observations taken over several sites and over a period of years can give useful information. Mean scores over several environments will show trends in apparent resistance and susceptibility.

These observations are especially useful when the resistance level may be rather low but still useful. The Blount oat variety was shown to have some resistance from that type of data (Qualset, 1967). The first indication of BYD resistance in the wheat breeding line that was to become Anza was obtained from an ISWYN trial where the incidence of natural infection of BYD was sufficiently high for scoring (Qualset *et al.*, 1973a). This method does not give reliable information about yield losses due to BYD or the amount of protection provided by host resistance.

Managed natural infection—With general knowledge of the epidemiology of BYD, it is possible to manipulate the population of viruliferous aphids and the growth of the test plants to maximize symptom expression. This method has been used succesfully in California for more than 25 years (Schaller and Qualset, 1980). With this method, aphid trap plantings of a mixture of susceptible barley, oat and wheat varieties are made at monthly intervals beginning in September; fall flights of aphids will infest one or more of the plantings. No manual infestations are made, so no control over the aphid species or virus strain is maintained. The aphid traps are strips about ten meters in width with space left between the strips to plant the test materials.

There is usually an early spring aphid flight in California, so the materials to be tested for BYD are planted in February or March between the aphid traps. Thus, the spring flight of aphids may naturally infest the test plants, or there may be natural movement of aphids (apterous or alate forms) from the aphid traps to the test plants. For maximum symptom expression, the test plants should be inoculated at the two to three-leaf stage. If natural infestation is not heavy or uniform, the plants in aphid traps are cut and distributed over the test plants; this straw is removed after a few days. In three to four weeks the symptoms are generally adequate for visual scoring. Visual scores are taken before and after spike emergence.

This method is more effective in barley, where larger differences between resistant and susceptible plants are found because of the qualitative effects of *Yd2*, than it is in wheat or oats where quantitative effects come from minor genes. Also, with managed natural infections, quantitative estimates of yield losses can be obtained if control plots are protected from aphids by insecticides or by caging.

Neither of these two natural methods provides for the best estimate of yield loss. However, the last method is simple to apply, so that large numbers of entries can be tested. It tends to reduce some of the adverse environmental effects, but it does not account for all of the factors mentioned as important for designing evaluation methods. It has the advantage that naturally occurring vector species/virus isolate combinations are represented in the test plots. Thus, there is opportunity to select for "generalized" resistance.

Controlled inoculation—The above-mentioned methods may be adequate for initial screening of materials but, where quantitative estimates of BYD effects are needed or where symptoms are not well-expressed, it is desirable to apply additional controls to the testing method. Controlled inoculation can be carried out in the field or greenhouse, applying a precise number of viruliferous aphids having a specified virus strain at the specified plant growth stage; A. Comeau of Quebec and others have successfully used this method. Paired hill plots (infected and control) in the field provide a way to accommodate large numbers of entries with easy distribution of the required number of aphids.

This method has some difficulties, however, in that maintaining disease-free plants can be a confounding factor. The use of cages often has a direct effect on plant growth, as does the use of insecticides to keep aphids from feeding on control plants. This was illustrated in a study by Stanley and Qualset (1968); varietal differences in forage and grain yields in winter wheat and winter barley were found as a result of soil-applied disulfoton. On the other hand, no differences were found among three winter oat cultivars.

Further refinements in test procedures are needed. It appears that no single method will be fully adequate, and that a sequential procedure can be adopted. Future developments with detached leaf and ELISA techniques may become very useful in screening for resistance. In the meantime, the breeder can devise rather simple procedures that will maximize the retention of resistance in populations. Perhaps the two greatest concerns are that inadequate sources of resistance are available in all small grains and that test methods must be sensitive to detecting worthwhile germplasm even if the resistance level is rather low.

Breeding Methods and Strategies

Source materials having BYD resistance are obviously the starting point for a breeding program. The methods discussed here can be applied for evaluating potential sources of resistance, but it must be emphasized that genetic tests for heritable resistance are very important. This has been well-illustrated in this workshop by J.E. Tola, who has shown that the wheat introduction Novi Sad 874-4 might not be as good a resistance donor parent as may have been expected on the basis of initial observations of the line itself. Additional sources of resistance are urgently needed in wheat and barley. Even without new resistance sources, progress in breeding can be expected with existing materials. Conventional breeding methodologies may be used, although prebreeding resistance from one species to another may be necessary, as illustrated in this workshop by P.E. McGuire for the transfer of Yd_2 from barley to wheat. Following are some of the salient conditions for breeding BYD-resistant varieties.

Major gene resistance to BYD—If a major gene such as *Yd2* in barley is available, it can be rather easily handled by visual selection for low symptom expression. Transfer of resistance by backcrossing is effective and is the preferred method for incorporating resistance into a standard genotype. For multitrait selection programs, pedigree selection in segregating generations may be most efficient because BYD resistance and other characters may be selected. Bulk populations are also an efficient way to handle numerous biparental populations or populations created by intercrossing numerous parents. If BYD is present, the bulk populations may be subjected to selection on a plant basis for low BYD symptoms (by marking spikes of good plants shortly after anthesis), and the selected plants composited as selected bulks (Qualset and Vogt, 1980). With a single resistance gene segregating, the populations can be skewed to a high level of resistance rapidly; progeny rows can then be grown for selection for additional characters. Diverse populations have been created in barley having the *Yd2* gene (Composite Cross XXV, Qualset and Suneson, 1966; Composite Cross XXXIII, Montana workers), and they should be useful to breeders. These populations segregate for male sterility, accomodating increased recombination if desired by the breeder.

Minor gene resistance to BYD—If genetic analysis proves that heritable variation for BYD resistance can be generated by crossing a resistance source with susceptible materials, it will generally be rather difficult to transfer the full complement of resistance to BYD when numerous genes are involved. In this case, special attention must be given to 1) selection methods and 2) population development. Some form of recurrent selection should be adopted (Qualset *et al.*, 1973b).

First, a comment about selection methodology. It is more important to have uniform infection when selecting for minor gene resistance than for major gene resistance. This is because heritability is low, a factor that is compounded if noninfected, but susceptible, plants are selected. Direct comparisons of infected and healthy plants of the same genotype are desirable but obviously not possible in the early generations of a breeding program. In the experience with wheat at Davis, it has been found useful to space plants in a 30-cm grid in F_2 and later generations; in that way, visual scoring and measurement of yield components can be done on single plants (Topcu, 1975). Selection for low score (Table 1) and high yield component expression gives good assurance that the healthiest plants are selected. Progeny tests using the same selection method are necessary. Significant yield advances were realized using visual selection and single plant grain yields with spaced plants of F_3 lines as indicated above (Thakare and Qualset, 1978). Thus, this method provides for selection for several criteria simultaneously.

Populations developed as selected bulks, space or drill planted, can also be used effectively because many single progenies can be selected as single spikes. The spikes can be marked by tags or paint while BYD symptoms are evident, and the selected spikes threshed *en masse* to make the bulk population for the next generation. To increase the effectiveness of this method in selecting for minor gene resistance to BYD, the composited seed sample can be screened or air separated to eliminate small seeds that may result from BYD infection. It is recommended that selection in bulk populations be done for two or three successive generations, followed by progeny row plantings to examine individual advanced lines in detail for other characters and for hybridization.

Regarding population development, the choice of parents to be included is very important. Biparental crosses can be used, but a multiple parent crossing scheme increases the opportunity for combining minor genes for resistance from several sources. For wheat, where presently available sources of resistance give only partial protection against BYD, it is recommended that at least three or four resistant parents and only one or two susceptible parents (of good agronomic type) be included in the hybridization scheme; thus, segregating generations will tend to be dominated by plants with resistance genes.

Selection using either of the methods discussed above are effective. As soon as resistant plants can be identified, they should be intercrossed to initiate a second cycle of recurrent selection. Gametocides or male sterility can be used for the recombination cycle, but the number of crosses needed is not so large but what controlled hand pollinations can be made.

Combining major and minor gene resistance to BYD—This topic has recently become evident in two contexts. First, the Yd_2 gene in barley is not a fully effective gene in some genetic backgrounds; C.W. Schaller is reporting in these proceedings that this gene may not be universally effective. Second, in using the Yd_2 gene of barley in wheat, it should be considered that the susceptibility alleles of wheat may prevail and the Yd_2 gene be ineffective unless some minor genes for resistance are incorporated. The Yd_2 gene may then be a useful "enhancer" gene for BYD resistance in wheat.

To improve the resistance level in barley or to introduce new minor genes for resistance, it appears that selection for major gene and minor gene resistance should be done in parallel, but independent, programs using the methods discussed above. Intercrossing populations with major and minor gene resistance can be done in the late stages of the program to select for even higher levels of resistance with reasonable assurance that both gene systems will be included in the derived resistant types.

Conclusions

This paper highlights the major considerations for breeding for host resistance in a complex host-pathogen-vector system. Conclusions are given mainly without documentation. The methods described are not unique and are widely used, many with greater sophistication as can be seen in other contributions to this workshop, i.e., A. Comeau, J.E. Foster and D.T. Sechler.

The breeding and selection strategies discussed here have evolved through experience in selecting for other characters and from the need for systematic handling of large amounts of materials by a very limited staff. Recurrent selection in breeding for BYD resistance is obviously a method of choice and, after seeing the great success made in the oat program by C.M. Brown and H. Jedlinski in Illinois, it seemed certain that the same methods would work for wheat. Additional insight came from R. Caldwell, Purdue University, during a visit to his plots in July 1964; he emphasized the value of noting BYD symptoms on the flag leaf as an indicator of severity of infection.

Breeding for BYD resistance will be strongly influenced by local conditions, and methods will have to be developed to best take advantage of such factors as maximizing natural movements of aphids. It is hoped that this material will aid others in developing effective methodology.

References

Qualset, C.O. 1967. Tolerance to barley yellow dwarf in winter oats. Plant Disease Reporter 51:908-910.

Qualset, C.O., and C.A. Suneson. 1966. A barley gene-pool for use in breeding for resistance to the barley yellow dwarf virus disease. Crop Science 6:302.

Qualset, C.O., and H.E. Vogt. 1980. Efficient methods of population management and utilization in breeding wheat for Mediterranean-type climates. *In* Proceedings, Third International Wheat Conference, Madrid, Spain. University of Nebraska Agricultural Experiment Station publication MP41. Pp. 166-188.

Qualset, C.O., J.D. Prato, J.A. Rupert, H.E. Vogt, M.A. Khalifa, W.F. Lehman and W.H. Isom. 1973a. Anza - a new high-yielding, short-statured wheat variety. California Agriculture 27(2):14-15.

Qualset, C.O., J.C. Williams, M.A. Topcu and H.E. Vogt. 1973b. The barley yellow dwarf virus in wheat: importance, sources of resistance and heritability. *In* Proceedings, Fourth International Wheat Genetics Symposium, Columbia, Missouri. Pp. 465-470.

Rasmusson, D.C., and C.W. Schaller. 1959. The inheritance of resistance in barley yellow dwarf virus. Agronomy Journal 51:661-664.

Schaller, C.W., C.I. Chim, J.D. Prato and W.H. Isom. 1970. CM-67 and Atlas 67--two new yellow-dwarf-resistant barley varieties. California Agriculture 24(4):4-6.

Schaller, C.W., and C.O. Qualset. 1980. Breeding for resistance to the barley yellow dwarf virus. *In* Proceedings, Third International Wheat Conference, Madrid, Spain. University of Nebraska Agricultural Experiment Station publication MP41. Pp. 528-541.

Schaller, C.W., D.C. Rasmusson and C.O. Qualset. 1963. Sources of resistance to the yellow dwarf virus in barley. Crop Science 3:342-344.

Schooler, A.B. 1980. Intergeneric and interspecific barley hybrids show tolerance to barley yellow dwarf virus. North Dakota Farm Research 38(1):19-21.

Schooler, A.B., and M.K. Anderson. 1979. Interspecific hybrids between (*Hordeum brachyantherum* L. x *H. bogdanii* Wilensky) x *H. vulgare*. Journal of Heredity 70:70-72.

Stanley, W.W., and C.O. Qualset. 1968. Effect of a systemic insecticide of forage and grain production of wheat, barley, oat, and rye varieties. Agronomy Journal 60:306-308.

Suneson, C.A. 1955. Breeding for resistance to yellow-dwarf virus in barley. Agronomy Journal 47:283.

Thakare, R.B., and C.O. Qualset. 1978. Empirical evaluation of single-plant and family selection strategies in wheat. Crop Science 18:115-118.

Topcu, M.A. 1975. The inheritance of resistance to the barley yellow dwarf virus in wheat (*Triticum aestivum* L.). PhD Dissertation. University of California, Davis, California, USA.

Comments

G. Herrera, Santiago, Chile

The lack of accurancy in the symptomatology of BYD on wheat for selection has been one of the factors explaining the lack of development of tolerant varieties worldwide. However, in field and greenhouse trials carried out in Chile at La Platina Experimental Station (INIA) during the 1980-81, 1981-82 and 1982-83 seasons, important relationships were observed as to the effects of artificial inoculations of the virus on the hectoliter weight.

Entries coming from regional nurseries, crossing blocks and yield trials were analyzed in a randomized block design after being inoculated artificially with aphids reared in greenhouse conditions and bearing the PAV and MAV-like isolates. The inoculations were made on plants at stages 5 and 9 on the Feekes scale.

Results show that, under severe BYDV infection, hectoliter weight is a reliable parameter to estimate BYDV tolerance.

P.A. Burnett, Mexico

In New Zealand, two different screening methods have been used. In the South Island at Christchurch, where the incidence of BYDV was low, varieties to be evaluated were sown in hill plots using 20 seeds per hill. A split plot design was used and each treatment bordered with a double row of susceptible oats. One treatment was sprayed with oxydemeton-methyl to control aphids, while the other was infested with aphids at a rate of approximately five aphids per plant.

The aphids were obtained by mass rearing on flats of barley and oats in a greenhouse or by collecting them from early autumn-sown plots of rye. The aphids from the greenhouse were shaken from the plants, using a technique similar to that reported by A. Comeau. The aphids collected from the field were harvested by cutting leaves bearing aphid colonies, and those leaves were stored overnight in vented plastic containers in the cold room. In that cool environment, the aphids tended to stop feeding and fall off the leaves. This aphid supply from the field was used only as a back-up supply. The hill plots were harvested for yield, so that a yield score, as well as one for symptoms, could be obtained.

At Palmerston North in the North Island, a site considered suitable for initial screening, short rows of 1.84 meters were sown with 35 seeds per row; these proved excellent for testing for resistance under the quite high natural infection that existed in the region. They were sown with a cone seeder, thus involving very little labor. It was not possible to measure plots for yield in the year that they were used. Twenty replicates were sown.

H. Jedlinski, Illinois, USA

The technique for resistance screening for BYDV in Illinois is based primarily on the use of inoculated and uninoculated replicated hills with 12 to 16 plants per hill. A visual scoring system for assessment of BYD disease severity on a scale of 0 (fully tolerant) to 9 (intolerant) is related to expression of symptoms after anthesis, the degree of dwarfing, tillering, discoloration and sterility. The disease severity scores for spring oats, using this technique, are highly correlated with depression in height, number of tillers and yield (see figures below) and, consequently, are sufficiently accurate to permit screening for tolerance.

Correlation Coefficients / Probability Levels

Height as % of control versus disease score	0.836 (0.0001)
Tillers as % of control versus disease score	0.741 (0.0001)
Yield as % of control versus disease score	0.814 (0.0001)

A similar technique is used in the screening of winter wheat and winter barley in which BYDV inoculations are made in fall and spring. The differences in symptom expression are less obvious by visual assessment than are those with spring oats and, therefore, disease severity ratings are supplemented with data on percent depression in various yield components. Tests are in progress on different sampling procedures to reduce the time and cost involved in the process with winter wheat.

John E. Foster and R.M. Lister, Indiana, USA

Since about 1976, a major effort has been devoted to BYD research in Indiana. It was started with the screening of a few selected entries and introductions in the greenhouse and in growth chambers. Later, testing was carried out in the field, using the greenhouse and growth chambers for rearing viruliferours aphids. Early seeding was relied on to optimize the probability of obtaining natural infestations, a method which did not work very well.

Currently, about 1,000 wheat entries are being tested to PAV and RPV-like isolates of BYD in hill plots. This is the backbone of the large selection and nursery operation. With this approach, it is possible to handle the segregating materials necessary to combine resistance to BYDV with all of the other essential characteristics for improved cultivar candidates. This modified, replicated hill plot technique is also used for testing about 300 spring oat lines to two isolates of BYDV. The procedure used is that of planting the oats in sets of three clumps per entry in styrofoam flats in the greenhouse. They are divided for three treatments, infestation by viruliferous aphids carrying the PAV isolate, infestation by viruliferous aphids carrying the RPV isolate, and the noninfested control. They are then transplanted side-by-side in the field to provide close comparison throughout the growing season. Visual symptoms, height, tillering and yield are measures taken to evaluate for tolerance to BYDV.

The Genetics of Resistance to Barley Yellow Dwarf Virus in Wheat

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Effective control of barley yellow dwarf virus (BYDV) by genetic resistance has been successfully demonstrated in barley (Arny and Jedlinski, 1966; Catherall and Hayes, 1967; Schaller, 1977). Reports on the inheritance of resistance to BYDV in wheat, however, are very limited. Immunity has not been found, and no major gene conditioning resistance has been identified (Qualset, *et al.*, 1973; Gill, 1967; Dowler and Briggle, 1977; Topcu, 1975), although some sources of resistance have been reported (Qualset, *et al.*, 1973; Doodson and Saunders, 1970; Smith, 1967; Bruehl, 1961; Cisar *et al.*, 1982b; Carrigan *et al.*, 1981).

Topcu (1975) studied the inheritance of resistance to BYDV in populations from crosses of spring wheat cultivars, Anza (resistant) x Bluebird (susceptible) and Anza (resistant) x CA 63121 (resistant). The F_2 data of both crosses showed continuous variation. Transgressive segregation was observed, with resistance being greater in resistant x resistant than in resistant x susceptible crosses, suggesting that parents in the former have different genes for resistance or that a favorable gene interaction was involved. The F_3 data showed genetic variability among lines within crosses for resistance, suggesting that resistance was controlled by several genes. Qualset *et al.* (1973) reported significant genetic variability for resistance to BYDV in wheat when Anza, the resistant cultivar, was crossed with four cultivars with varying degrees of resistance. Heritability estimates of BYDV reaction in F_3 crosses ranged from 24 to 37%.

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 very 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; nonadditive genetic effects and reciprocal effects were less important.

Yield components and visual reaction have commonly been used to assess the effects of BYDV on plants; however, estimation of the disease based on a visual score has always been challenged. Different researchers conclude that yield and certain yield components are valuable for discriminating a broad range in BYDV symptom expression.

Investigations on assessment of resistance and inheritance to BYDV in five wheat cultivars were carried out by Oregon State University in the Willamette Valley, USA. The objectives of the studies were 1) to evaluate methods for 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 wheat cultivars, Stephens (Spn), Riebesel (Rb), Yamhill (Ymh) and Novi Sad 874-4 (NS), one spring wheat, Anza (Anz) and the resulting F_1, F_2, F_3, backcross-1 and backcross-2 generations from crosses among the five cultivars. The cultivars, Yamhill and Stephens, developed at Oregon State University, represented resistant and susceptible cultivars, respectively, in their BYDV reaction there in 1978 and 1979. Anza, the spring wheat cultivar, had been reported as resistant in California, and Novi Sad and Riebesel had been reported as having degrees of resistance in Europe.

Two studies were made. The first was conducted in the greenhouse, where an assessment was made of the parental lines, with regard to the damage caused by the feeding of nonviruliferous aphids and aphids infected by BYDV. Aphids were collected from traps at the Hyslop Farm, Oregon State University, and transferred to barley and oat plants to check for BYDV infectivity. The following observations were made:

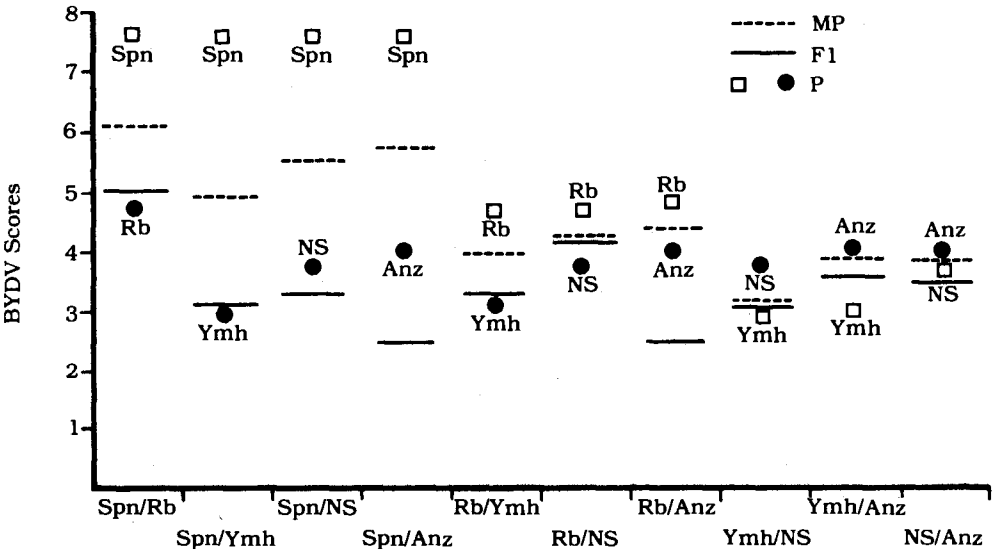
- Visual symptoms were difficult to detect, with the most susceptible cultivar, Stephens, showing only moderate yellowing;
- Aphid feeding, *per se*, did not appear to be a factor in terms of damage, as only Anza and Yamhill showed a significant reduction in plant weight when exposed to nonviruliferous aphids, and
- Despite the low visual symptom expression, all cultivars were affected by the virus for most parameters measured. Stephens and Riebesel exhibited the greatest reduction in grain yield, plant weight and plant height. Yamhill, Novi Sad and Anza showed the least damage, thus indicating a significant level of resistance.

Field Experiments

To ensure adequate levels of infection, two procedures, aphid trapping and early planting, were employed to enhance build-up of aphid population. In contrast to the lack of visual symptoms in the greenhouse, a strong expression of the disease was noted in the field. Stephens exhibited the highest score, followed by Riebesel (7.6 and 4.8, respectively). The lowest BYDV score was found for Yamhill (3.1), followed by Novi Sad (3.7) and Anza (3.9).

An average yield reduction of 23.4% was found when a completely caged treatment was compared with the nonprotected treatments. It was also apparent that, when levels of fall-spring infection were compared with spring infection, symptom development was more conspicuous and severe when infection took place earlier.

Mean BYDV scores for cultivars, midparent values for F_1's, deviations of F_1's from mid-parent values, and ten derived crosses can be observed in Figure 1. The F_1 progeny favored the more resistant parent in every cross where a susceptible cultivar was involved. F_1's from crosses between cultivars having low BYDV scores were equal or very close to mid-parent value (NS/Ymh, Anz/Ymh and Anz/NS). It was apparent that the resistance to BYDV had dominant effects when resistant x susceptible parents were involved. Progeny from parents with low BYDV reaction scored intermediate reaction. For example, the scores of NS/Ymh (3.3), Ymh/Anz (3.9) and NS/Anz (3.5) were similar to those of the mid-parents of the respective parents (3.4, 3.6 and 3.9, respectively).



Spn = Stephens; Rb = Riebesel; NS = Novi Sad 874-4; Anz = Anza, Ymh = Yamhill

Figure 1. Observed BYDV score: parental values (P), F_1 values (F_1) and mid-parent values (MP) for five wheat cultivars and ten derived crosses grown on the Hyslop Agronomy Farm, 1982

Figures 2 and 3 show the frequency distribution for BYDV scores of F_2 and F_3 plants of the crosses Spn/Rb and Spn/Ymh. It is apparent that in both crosses the distribution was skewed. In the Rb/Spn cross, the distribution was toward the susceptible parent; in contrast, in the Spn/Ymh cross, it was toward the resistant parent (Yamhill).

A factor which added 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.

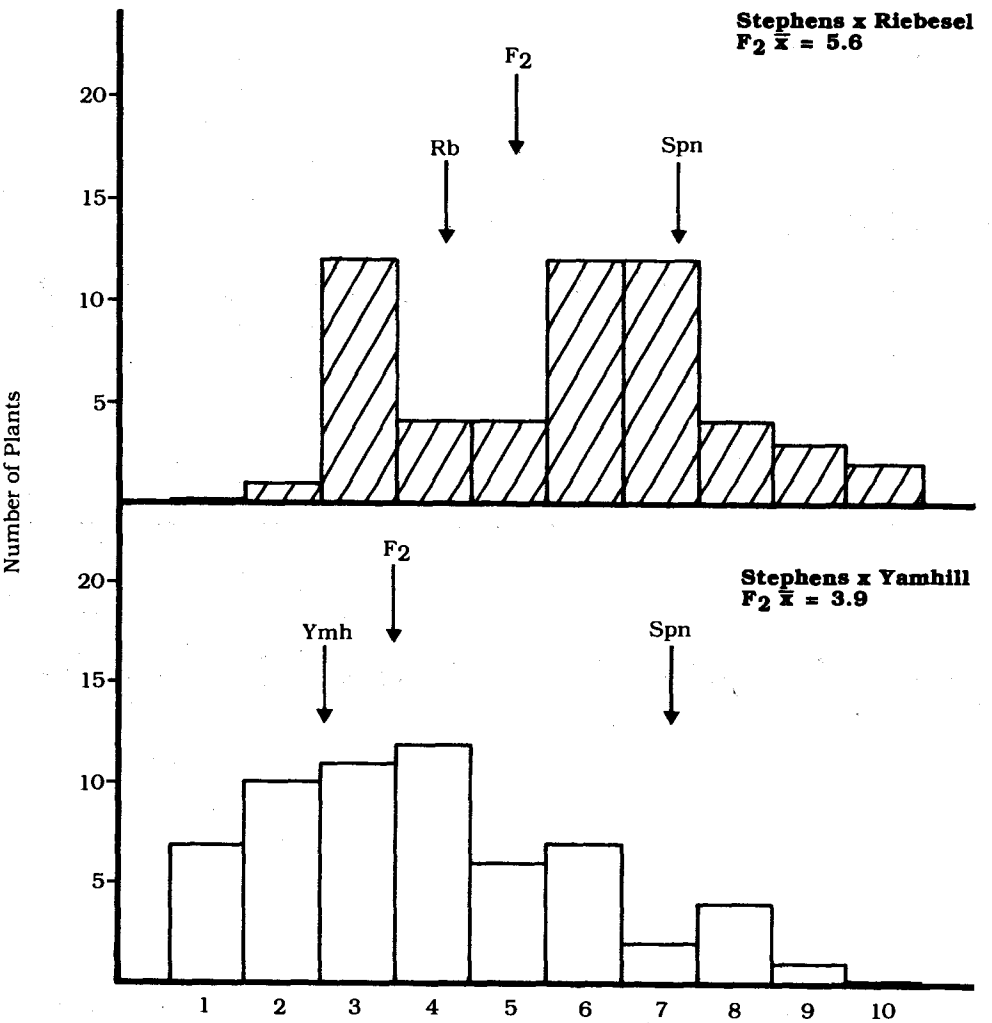


Figure 2. Frequency distributions for BYDV scores from F_2 populations of crosses Stephens x Riebesel and Stephens x Yamhill; arrows indicate mean values (F_2, N = 60; parents, N = 30)

Assuming that the cultivars are homozygous and homogeneous, the most logical explanation for this was that the off-type plants were escapes; otherwise, 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%) suggested that, in the cultivars used in the study, a complete breakdown of defense mechanisms did not occur. It was apparent that even the most susceptible cultivar in the study, Stephens, must have had some genes for resistance. This was also reflected in the fact that Stephens showed no difference in kernel weight as the result of BYDV infection.

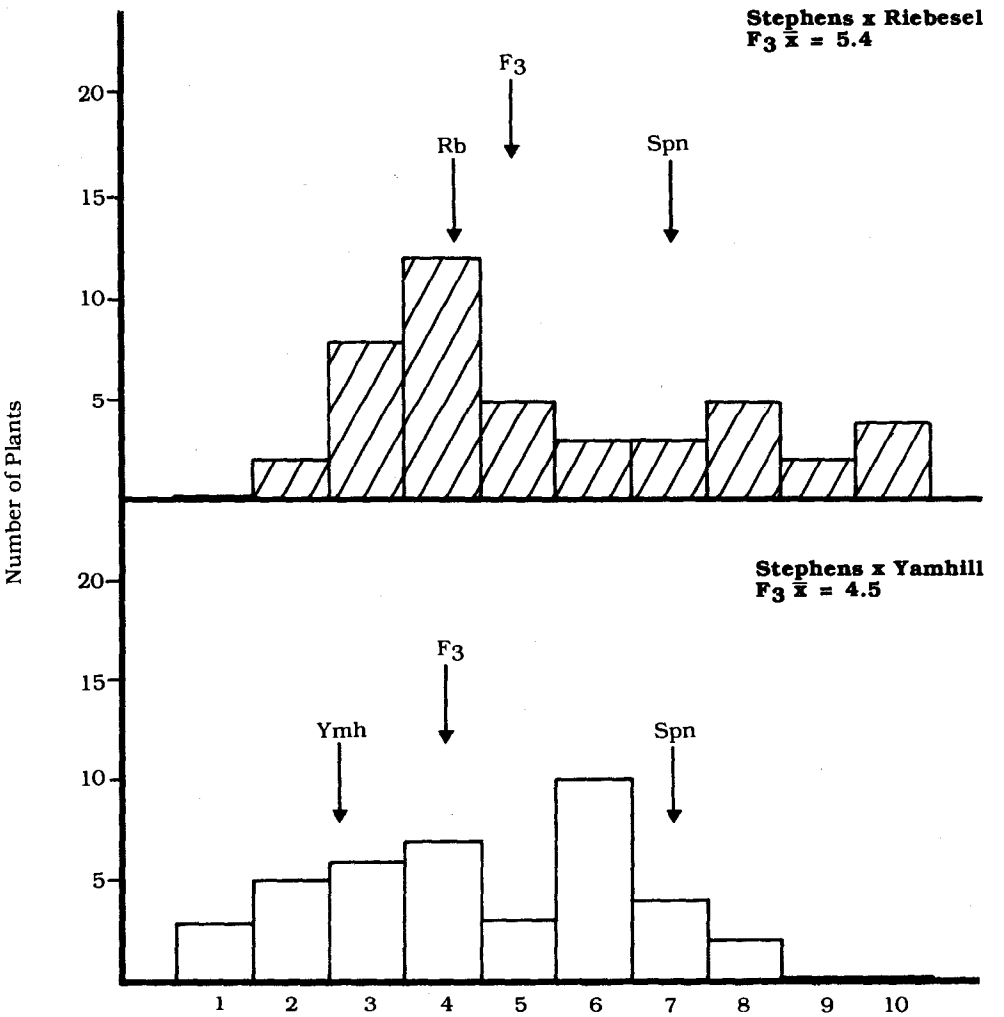


Figure 3. Frequency distributions for BYDV scores from F_3 populations of crosses Stephens x Riebesel and Stephens x Yamhill; arrows indicate mean values (F_3, N = 45; parents, N = 30)

Conclusions

Results of the research carried out on resistance to BYDV in wheat include:

- A PAV-like isolate and the *Sitobion avenae* vector were confirmed as being the most prevalent;
- No high levels of immunity or resistance were found, although there were different levels of resistance among cultivars;
- Stephens appeared to be the most visibly susceptible cultivar by most parameters measured, but Riebesel showed the highest yield reduction;
- Yamhill showed the lowest BYDV score and appeared to have the highest potential for resistance. It was followed by Novi Sad and Anza;
- The BYDV visual scale was useful in assessing BYDV effects, with significant negative correlations showing up between BYDV score and the 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. Genetic correlations were determined for the F_1 and F_2 generations (Table 1). As with phenotypic correlations, the genetic associations were negative for all comparisions involving the ten crosses;
- 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;
- F_2 and F_3 frequency distributions suggested that resistance to BYDV was quantitative. Transgressive segregation was detected in all crosses;
- Low narrow sense heritability estimates suggested that an environmental component influenced the expression of BYDV resistance. The estimates (Table 2) were low, with the Ymh/NS populations showing the highest value of 16% and Spn/Anz the lowest value of 9%, and
- General combining ability values (Table 3) indicated that part of the genetic variability for BYDV resistance was controlled by genes which are additive in action. For BYDV score, Yamhill and Anza (-0.12 and -0.54, respectively) contributed the greatest effect for reducing the visual expression of the disease.

Specific combining ability suggests the importance of non-additive gene action. Information regarding specific combining ability effect for BYDV is provided for each of the parents (Table 4).

Some effects for specific parents are in agreement, with some F_1 and segregating populations being similar to the more resistant parent; this would suggest non-additive generation.

Table 1. Genetic Correlations among BYDV Scores and Four Agronomic Characters, Using F_1 and F_2 Generations of 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	>-1.00	-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

Table 2. Magnitudes of Narrow Sense Heritability Generated in the F_2 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

Progeny derived from the specific cross, Ymh/NS, might also provide promising segregating population materials. It would appear that, since the cultivars in this study had different genetic sources for BYDV resistance, a recurrent selection program would be promising. Such an approach supports the conclusions reached by Qualset *et al.* (1973) and Topcu (1975). The program includes not only making crosses between the five cultivars, but also intermating among and between resistant plants in F_2 and later generations. By this approach, it would be possible to accumulate genetic factors for resistance. This could result in not only a high level of BYDV resistance but, because of the nature of that resistance, it would be expected to be more durable.

Table 3. Observed Mean Squares for General and Specific Combining Ability in the F_1 Generation of a Parent Diallel for BYDV Score in Five Wheat Cultivars[a/]

Character	M.S. crosses	M.S. GCA	M.S. SCA	M.S. Error
BYDV score	2.20164**	1.89098**	2.45016**	0.3575

a/ Degrees of freedom were 9, 4, 5 and 18 for crosses, GCA, SCA and error, respectively

** Significant at the 1% level of probability

Table 4. Estimates of General Combining Ability Effects for All Traits Measured from All Possible Single Crosses Involving Five Wheat Cultivars

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

References

Arny, D.C., and H. Jedlinski. 1966. Resistance to the yellow dwarf virus in selected barley varieties. Plant Disease Reporter 50:380-381.

Bruehl, G.W. 1961. Barley Yellow Dwarf, a Virus Disease of Cereals and Grasses. American Phytopathological Society, Monograph no. 1.

Carrigan, L.L., H.W. Ohm, J.E. Foster and F.L. Patterson. 1981. Response of winter wheat cultivars to BYDV infection. Crop Science 21:377-380.

Catherall, P.L., and J.D. Hayes. 1967. Assessment of varietal reaction and breeding for resistance to the yellow dwarf virus in barley. Euphytica 15:39-51.

Cisar, G., C.M. Brown and H. Jedlinski. 1982a. Diallel analysis for tolerance in winter wheat to the barley yellow dwarf virus. Crop Science 22:328-333.

Cisar, G., C.M. Brown and H. Jedlinski. 1982b. Effect of fall or spring infection and sources of tolerance of BYDV of winter wheat. Crop Science 22:474-477.

Doodson, J.K., and P.J.W. Saunders. 1970. Some effects of barley yellow dwarf virus on spring and winter cereals in yield trials. Annals of Applied Biology 66:361-364.

Dowler, W.M., and L.W. Briggle. 1977. Summary of BYDV workshop, University of Illinois, June 1-2, 1977. Urbana, Illinois, USA.

Gill, C.C. 1967. Susceptibility of common and durum spring wheats to BYDV. Canadian Journal of Plant Science 47:571-576.

Jedlinski, H., W.F. Rochow and C.M. Brown. 1977. Tolerance to BYDV in oats. Phytopathology 67:1408-1411.

Qualset, C.D., J.C. Williams, M.A. Topcu and H.E. Vogt. 1973. The BYDV in wheat: importance, sources of resistance and heritability. *In* Proceedings, Fourth International Wheat Genetics Symposium. Missouri Agricultural Experiment Station, Columbia, Missouri, USA. Pp. 465-470.

Schaller, C.W. 1977. Sources of BYDV resistance in cereals. *In* Summary of BYDV Workshop, University of Illinois, June 1-2, 1977. Urbana, Illinois, USA.

Smith, H.C. 1967. The effect of aphid numbers and stage of plant growth in determining tolerance to BYDV in cereals. New Zealand Journal of Agricultural Research 10:445-446.

Tola, J.E. 1982. Assessment of resistance and inheritance to barley yellow dwarf virus disease (BYDV) in five wheat cultivars (*Triticum aestivum* L). PhD Thesis. Oregon State University, Corvallis, Oregon, USA.

Topcu, M.A. 1975. The inheritance of resistance to the barley yellow dwarf virus in wheat. PhD Thesis. University of California, Davis, California, USA.

Comments

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The development of BYDV-resistant wheat depends upon the identification of usable sources of resistance, the key word here being *usable*. This can only be determined by the hybridization of the putative sources of resistance with susceptible types, followed by study of the segregating generations in the presence of BYD. Controlled inoculations with known aphid vectors and virus strains are desirable for genetic study of BYD resistance. The study by J.E. Tola in Ecuador provides an outstanding example of how putative sources of resistance can be evaluated; he has used both winter and spring habit types in his studies.

In the experience at Davis, California, the wide variation in growth habit in segregating populations confound the evaluation of BYD reaction. A word of caution should be added regarding this point; test environments must be devised to provide adequate BYD symptom expression. This may include vernalization or controlled photoperiod.

In the early studies at Davis, CI 13232 was used; under California conditions, it was late maturing. It was apparent that its resistance to BYD was quite good, and early maturing lines with low BYD scores were established from crosses with CI 13232. The Novi Sad selection used by Tola provides a similar example, although the value of that source under California conditions remains to be determined because of the wide segregation for growth habit and maturity in the spring-planted test environment.

Clearly, development of BYD-resistant wheats is hampered by the lack of good sources of genetic resistance. Additional screening of worldwide germplasm sources is necessary, including wild relatives of wheat. The various wheat-alien addition and substitution lines should be surveyed for BYDV resistance, and the best included in carefully controlled genetic studies.

G. Herrera and C. Quiroz, Chile

Over a period of five years, from 1976 to 1980, field trials and greenhouse tests were conducted for studying the effect of BYDV and aphid vectors on different wheat cultivars at La Platina Experiment Station (INIA), Santiago, Chile.

Results indicated a reduced effect of aphids and BYDV in 1979 and 1980 as compared to 1976, 1977 and 1978, when yield losses were over 15%. The cultivars V-19, Aurifén and Anza showed the best performance.

The Genetics of Resistance to Barley Yellow Dwarf Virus in Barley

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Barley yellow dwarf (BYD) is recognized as an important cereal disease in most of the major cereal producing areas of the world, with significant economic losses being reported from many areas. Recent renewed interest in the disease would suggest that it is becoming more widespread, that it has increased in severity or that it is being accurately identified by more workers. Although some success in reducing losses from BYD has been reported through the use of insecticides in preventing secondary spread of the virus from the initial foci of infection and by adjusting planting dates to avoid early and late aphid flights, resistant cultivars offer the only positive and economical method for reducing losses.

The development of cultivars of barley tolerant to BYD is generally considered to be more straightforward and the genetics of tolerance less complex than is the case for wheat or oats. This is predicated to a large extent on the apparent inherent higher levels of tolerance within barley germplasm, the identification of major genes conditioning tolerance, and more positive symptom expression, especially when contrasted with wheat. However, when all aspects are considered, including the total range of genetic variability within the species and the complex interactions involving the host, vector, virus and environment, the overall complexity approaches that of the other two species.

Despite worldwide interest and activity in the development of resistant cultivars, very little has been published regarding sources of resistance and the genetics thereof. The following discussion is an attempt to present a brief review of the information available, together with a few comments regarding some of the difficulties encountered.

More than 7,000 entries from the United States Department of Agriculture World Barley Collection have been screened at Davis, California, under field conditions (Qualset and Schaller, 1969; Schaller *et al.*, 1963). One hundred eighty-nine of the entries had mean values of 2.0 or less (0 to 4 scale), which is considered a tolerant reaction. However, there was a continuous range of symptom expression, from highly tolerant to extreme susceptibility, suggesting that total genetic diversity is extensive as well as complex. Of the tolerant types, all but six were introductions from Ethiopia; three of those were of hybrid origin from Ethiopian parentage, two were from Sudan (probably of Ethiopian origin) and one was from China.

(continued)

Although reversals in reaction have been reported from tests in different areas, a number of the entries found to be tolerant at Davis have given tolerant reactions when tested over a wide area and exposed, undoubtedly, to different strains of the barley yellow dwarf virus (BYDV). P.L. Dyck (personal communication) tested 95 of the entries at Ottawa, Canada, and found good agreement with the Davis reactions. Smith (1967) tested 17 at Ottawa against two BYDV isolates, also finding good agreement. Smith also noted that two of the entries, CI 3926-3 and CI 9623, were highly tolerant in New Zealand. Arny and Jedlinski (1966), however, found significant reversals from the Davis reaction when tested at Madison, Wisconsin, and Urbana, Illinois. The majority were tolerant at both locations; 12 entries were susceptible and 16, intermediate susceptible. Eleven were susceptible only at Urbana and four only at Madison. It is of interest to note that three of the entries showing differential reactions at the two locations, CI 2376, resistant at both locations, CI 1237, intermediate susceptible at both locations and CI 1227, susceptible only at Urbana, exhibited a tolerant reaction at Davis, a fact shown to be conditioned by genes(s)/alleles at the same locus (Rasmusson and Schaller, 1959). All three have been used successfully as parents at Davis.

It is not clear whether the reversals noted above are due to genotype x virus interaction, genotype x envrionment interaction, genetic background effects, methods of evaluation, including inoculation techniques and scoring, or other factors. However, all of these must be considered when interpreting and comparing results obtained by different researchers.

Since all of the tolerant types show some degree of symptom expression and a continuous range of reaction responses from tolerance to extreme susceptibility, it is evident that, within the species, classification into reaction groups (tolerant, intermediate, susceptible) is arbitrary and will vary with individuals and methods of scoring. For example, in a genetic study with ten Ethiopian cultivars, Damsteegt and Bruehl (1964) found that resistance was controlled by one incompletely dominant gene and that the resistant segregates were as tall, green and thrifty as the resistant parents. Scoring was on a 1 to 4 scale, based on visual observations.

In a second experiment with the same cultivars, but measuring disease reaction on the differential response between inoculated and uninoculated plots (Bruehl and Damsteegt, 1964), the mean yield of the inoculated plots ranged from 25 to 60% of the uninoculated plots and, on the basis of their response, the cultivars would be classified as susceptible or moderately susceptible by most researchers. However, when compared with the response of locally grown cultivars, which ranged from 3 to 5% of the

control plots, it is evident that the experimental cultivars possessed considerable tolerance and would provide a fair degree of protection agains losses from the virus. Several of them have been successfully used as parental material in breeding programs thoughout the world.

Hayes *et al.* (1971), in testing some of the tolerant Ethiopian entries at Aberystwyth, Wales, found that the level of tolerance varied both within and between varieties depending on the envrionment and their rate of growth. In the greenhouse, only one of the six cultivars previously found to be tolerant at Davis was classed as susceptible; however, when tested simultaneously in the open using the same inoculation techniques, three were susceptible, one moderately susceptible and two tolerant. These individuals would be grouped into different reaction classes as a result of the different tests, and illustrate the strong genotype x environment interactions which may be encountered. In subsequent genetic experiments, the tolerance exhibited by the five cultivars in the greenhouse was found to be conditioned by gene(s)/ alleles at the same locus, suggesting either allele x environment or genetic background x environment interactions.

In a cooperative experiment with J.M. McEwan, Department of Scientific and Industrial Research, New Zealand, a number of introductions from Ethiopia are being screened both at Davis and at Palmerston North. Based on one-year observations, there appear to be significant reversals in reaction between the two locations. Additional tests are being grown in 1983-84 for confirmation of the preliminary observations.

Genetic analyses of resistance to BYDV in 20 Ethiopian barleys (Catherall and Hayes, 1966; Damsteegt and Bruehl, 1964; Hayes *et al.*, 1971; Munthe, 1975; Rasmusson and Schaller, 1959; Schaller *et al.*, 1964) have shown that the same gene, *Yd2*, conditioned resistance in all introductions tested, although the possibility of closely linked genes or a series of alleles cannot be excluded. This gene is located on chromosome 3 (Schaller *et al.*, 1964). Although apparently conditioned by the same gene (or locus), the level of tolerance between entries ranged from 0.83 to 1.60; these parental differences were observed among progenies of resistant x resistant crosses.

Hayes *et al.* (1971) found that the expression of tolerance in the F_2 generation of tolerant x susceptible crosses varied among tolerant parents and the conditions under which they were tested. Tolerance was expressed as complete dominance in crosses with CI 3906-1, which possessed the highest level of tolerance; it was incompletely dominant in crosses with parents of intermediate levels and, under some conditions, recessive in crosses with CI 1237, which had the lowest level. A significant positive correlation was also found between levels of tolerance expressed by the parents and progeny with growth rate, suggesting that

environmental or genetic factors which delay heading diminish the expression of BYDV tolerance.

Jones and Catherall (1970) experienced difficulty in recovering late maturing segregates and suggested that the Yd_2 gene operates by retarding virus multiplication, thus allowing the virus to reach higher concentrations in slower growing plants; this is not in complete agreement with experience at Davis. Sutter barley, three weeks later in maturity than CM 67, has tolerance levels as high or higher than CM 67 (Table 1); both possess the Yd_2 gene.

Suneson (1955) indentified a recessive gene, Yd_1, which was conditioning an intermediate reaction in the cultivar, Rojo. It has not been used in breeding programs at Davis, since the Yd_2 gene conditions a higher level of tolerance and is more readily followed in a breeding program. Its effectiveness in other areas has not been investigated. Melzer *et al.* (1980) evaluated two germplasm lines derived from inter-generic and interspecific crosses, ND 497 derived from *Hordeum vulgare* (4X)/*H. bulbosum* (4X)/*Elymus mollis* (4X), and ND 586 derived from *H. brachyantherum* (4X)/*H. bogdanii* (2X)/*H. vulgare* (4X)/3/*H. vulgare* (2X), for their reaction to BYDV. Compared with Atlas 68, Abate and CI 2376, all possessing the Yd_2 gene, they were less tolerant, but more tolerant than the susceptible cultivar, Black Hull-less (CI 666). Catherall (Aberystwyth, 1974) screened 53 winter barley introductions from the University College, Bangor, 1971 Nepal Expedition Collection; he found 12 to be highly tolerant, 18 moderately so and the remainder susceptible. No additional information on this collection is available in literature.

Grafton *et al.* (1982) reported striking differences in reaction in winter barley cultivars and experimental lines as measured by a number of criteria, including reduction in grain yield and winter survival. Grain yield of the two most susceptible cultivars, Harrison and Durra, was reduced 71.3 and 95.6%, respectively, when infected by BYDV. The yield of Perry was reduced 46.9% and that of the tolerant cultivar, Post, only 0.2%. The reaction of the four Missouri experimental lines were intermediate and similar in reaction to Perry. In the BYDV-free environment, the entries averaged 98.3% winter survival. Survival in the inoculated treatment for the susceptible cultivars, Harrison and Durra, were 49.4 and 16.9%, respectively, compared to 91.8% for Post and 86.7% for Perry. Overall, Post was identified as the most resistant cultivar, Perry and the four

Table 1. Effect of a Systemic Insecticide on BYDV Symptoms and Grain Yields (Three-Year Means)

	BYDV score		Yield (kg/ha)			Susc/Res(%)	
Variety	T	NT	T	NT	T/NT(%)	T	NT
Atlas 57	4.9	6.1	3390	2490	136	75	55
Atlas 68	1.8	1.6	4530	4500	101		
Cal. Mariout	4.7	6.0	3100	2330	133	80	66
CM 67	2.3	2.6	3880	3530	110		
Sutter	0.9	0.9	4660	4690	99		

T Soil treated at planting
NT No soil treatment

experimental lines as intermediate and Harrison and Durra, susceptible. None of the cultivars or experimental lines are related to the Ethiopian barleys which carry the *Yd2* gene, and the source of the genes for resistance is unknown.

Poehlman *et al.* (1981) suggested that the BYD resistance of the cultivars and experimental lines discussed in the above experiment is nonspecific and that the genes had been accumulated by selecting vigorous and high yielding lines over a period of several years in an environment where a moderate level of the disease had been present. Grafton (1982) crossed the cultivars Harrison and Pamina (both susceptible) and Perry (tolerant) with two Ethiopian lines which carried the *Yd2* gene. Resistance was intermediate between the parents for all F_2 populations.

Despite the difficulties encountered in the identification of tolerant germplasm and the complexity of the interactions involved, success in the development of tolerant cultivars of barley has been achieved. Five tolerant cultivars, all with the *Yd2* gene, have been released by the California Agriculture Experiment Station at Davis and are now grown on approximately 70% of the state barley acreage. Although leaf discoloration occurs under severe epiphytotic conditions, stunting and reduced productivity are minimal. This is evident from the data presented in Table 1, obtained by applying a systemic insecticide, phorate or difsulfoton, with the seed at planting time to reduce vector feeding and, thereby, minimize the effects of BYD (Schaller and Qualset, 1980). Yield reductions of 33 to 36% occurred with the susceptible cultivars, whereas corresponding reductions with the tolerant types ranged from 0 to 10% and showed a yield superiority of 34 to 45% over their susceptible isogenic counterparts. During the 16-year period that tolerant cultivars have been grown in California, there is no indication of reduced effectiveness of the *Yd2* gene.

Other released cultivars possessing the *Yd2* gene include Coracle (Wales), Shannon (Tasmania) and, possibly, Norbert (Canada) which has an Ethiopian introduction in its parentage. Recently registered winter barleys possessing tolerance include Perry (Missouri), Surry, Henry, Monroe and Muaury, all released by the Virgina Polytechnic Institute; none possess the *Yd2* gene. Undoubtedly, the listing for both spring and winter types is incomplete.

In summary, there appears to be sufficient tolerance within barley germplasm to provide suitable parental material for most areas. However, there is a lack of information as to the total genetic variability within the species, the presence and distribution of virus strains with differential pathogenicity and host x strain interactions. Since significant host x virus interactions have been established, emphasis in future research should be given to a systematic worldwide screening program to identify additional sources of tolerance; this would not only provide flexibility to plant breeders, but also help to minimize genetic vulnerability.

References

Arny, D.C., and H. Jedlinski, 1966. Resistance to the yellow dwarf virus in selected barley varieties. Plant Disease Reporter 50:380-381.

Bruehl, G.W., and V.D. Damsteegt. 1964. Degree of resistance to barley yellow dwarf in selected Ethiopian barleys. Plant Disease Reporter 48:470.

Carr, A.J.H., P.L. Catherall, J. A'Brook, P.W. Simmonds, L. Crossley and L.R. Potter. 1974. Report for 1973, UniversityCollege of Wales, Aberystwyth, UK.

Catherall, P.L., and J.D. Hayes. 1966. Assessment of varietal reaction and breeding for resistance to yellow dwarf virus in barley. Euphytica 15:39-51.

Damsteegt, V.D., and G.W. Bruehl. 1964. Inheritance of resistance in barley to barley yellow dwarf. Phytopathology 54:219-224.

Grafton, K.F. 1982. Studies on barley yellow dwarf in Missouri. Abstract. Dissertation Abstracts International 42:8.

Grafton, K.F., J.M. Poehlman, D.T. Sechler and O.P. Sehgal. 1982. Effect of barley yellow dwarf virus infection on winter survival and other agronomic traits in barley. Crop Science 22:596-600.

Hayes, J.D., P.L. Catherall and A.T. Jones. 1971. Problems encountered in developing BYDV tolerant European cultivars of barley. (Proceedings, Second International Barley Genetics Symposium. Washington State University Press.) Barley Genetics II:493-499.

Jones, A.T., and P.L. Catherall. 1970. The relationship between growth rate and the expression of the tolerance to barley yellow dwarf virus in barley. Annals of Applied Biology 65:137-145.

Melzer, J.M., J.D. Franchowiak and A.B. Schooler. 1982. Evaluation of two new sources of barley yellow dwarf virus resistance in spring barley. Abstract. Agronomy Abstracts. American Society of Agronomy, Madison, Wisconsin.

Munthe, T. 1975. Resistance to barley yellow dwarf virus in barley. Nordisk Jordbrugsforskning 57:1121-1122.

Poehlman, J.M., D.T. Sechler and K.F. Grafton. 1981. Barley yellow dwarf virus (BYDV): breeding for resistance in winter barley. (Proceedings, Fourth International Barley Genetics Symposium. Edinburgh University Press.) Barley Genetics IV:493-497.

Qualset, C.O., and C.W. Schaller. 1969. Additional sources of resistance to the barley yellow dwarf virus in barley. Crop Science 9:104-105.

Rasmusson, D.C., and C.W. Schaller. 1959. The inheritance of resistance in barley to the barley yellow dwarf virus. Agronomy Journal 51:661-664.

Schaller, C.W., and C.O. Qualset. 1980. Breeding for resistance to the barley yellow dwarf virus. *In* Proceedings, Third International Wheat Conference, Madrid, Spain. May 22-June 3, 1980. Pp. 528-541.

Schaller, C.W., C.O. Qualset and J.N. Rutger. 1964. Inheritance and linkage of the Yd_2 gene conditioning resistance to the barley yellow dwarf virus disease in barley. Crop Science 4:544-548.

Schaller, C.W., D.C. Rasmusson and C.O. Qualset. 1963. Sources of resistance to the yellow dwarf virus in barley. Crop Science 3:342-344.

Smith, H.C. 1967. The effect of aphid numbers and stage of plant growth in determining tolerance to barley yellow dwarf virus in cereals. New Zealand Journal of Agricultural Research 10:445-446.

Suneson, C.A. 1955. Breeding for resistance to barley yellow dwarf virus in barley. Agronomy Journal 47:283.

Comments

D.T. Sechler and J.M. Poehlman, Missouri, USA

Breeding for improved tolerance to BYDV in barley continues as the highest priority at the University of Missouri. If barley or oats are to serve as alternate crops for the Missouri farmer, BYDV tolerance is essential.

It is suggested that the BYDV resistance observed in winter barley cultivars at Missouri is nonspecific and that the genes have been accumulated over the years by selecting vigorous, high yielding lines in an environment where a moderate level of BYD has been present. The resistance to BYDV in Perry, released in 1979, is relatively good, and very respectable grain yields have been obtained, even in the northern part of the state.

In the Missouri breeding program, plant selections are made from segregating populations that are space planted under field conditions where BYDV is relatively prevalent. Concentrated aphid feeding on spaced plants results in more severe BYDV symptoms than observed in normal seedings, a situation in which BYDV-tolerant segregates can be identified. In the visual readings for selection, leaf discoloration, tiller uniformity and plant vigor serve as selection criteria. Plant selection screening for winter survival and grain yield and quality in replicated tests over several years identifies those lines with improved BYDV tolerance. The consistency of natural field infection makes this a relatively effective, low-cost approach.

A program was started during the winter of 1977-78 to transfer the specific resistance provided by the *Yd2* gene from a spring to a winter barley. Hopefully, this resistance can be added to the previously mentioned nonspecific resistance. The Ethiopian spring barley, CI 14088, is used as the donor of the *Yd2* gene. Observations at Columbia indicate that winter barley cultivars commercially grown in other parts of the United States have varying levels of resistance to BYDV. Efforts are underway to identify those segregates that carry the *Yd2* gene from crosses of CI 14088 to Perry, a relatively BYDV-tolerant winter cultivar, and Harrison, a relatively susceptible winter type.

P.A. Burnett, Mexico

One line from New Zealand, HW 202, has been found to be resistant to BYDV in field tests in New Zealand. This is an English line derived from a Maris Mink x Maris Cannon cross. Interestingly, this line was sent to H. Jedlinski in Illinois and to A. Comeau in Canada for testing; it appeared susceptible in both locations.

The Genetics of Resistance to Barley Yellow Dwarf Virus in Oats

H. Jedlinski, United States Department of Agriculture, University of Illinois, USA

Immunity to barley yellow dwarf virus (BYDV) infection has not been found in oats and other small grains (Rochow and Duffus, 1981), although reduced rates of BYDV replication in oats have been reported (Jedlinski *et al.*, 1977). Resistance to BYDV is very difficult to differentiate from tolerance because expression of both depends on a number of factors; for example, the disease is usually much less severe in greenhouse tests where reduced light and elevated temperatures promote rapid growth rates (Catherall *et al.*, 1977; Doodson and Saunders, 1970a; 1970b; Watson and Mulligan, 1960). High levels of tolerance are not always associated with low titer (Hammond *et al.*, 1983). Consequently, tolerance may represent an expression of many virus-host interactions that affect the metabolic state of the plant (Rochow and Duffus, 1981).

Barley yellow dwarf is a complex disease involving different luteoviruses and species of gramineaceous hosts, at least 18 different species of aphid vectors and all possible interactions of these factors with each other and the environment (Jedlinski, 1981; Rochow and Duffus, 1981). This complexity poses a major problem in the control of the disease in nature. Since the severe BYD epiphytotic in the USA in 1959 (Murphy, 1959), major efforts have been concentrated on the development of resistant oat cultivars as the most feasible method of controlling the disease.

The program at Urbana, Illinois, began in 1955 with the screening of oat collections under controlled field conditions by R.M. Endo of the United States Department of Agriculture (Endo and Brown, 1963; 1964), and it is still continuing. Since that time, more has been learned about the disease (Brown and Poehlman, 1962; Burnett and Gill, 1976; Doodson and Saunders, 1970a; 1970b; Gill and Comeau, 1977; Gill and Chong, 1979; Hammond *et al.*, 1983; Halstead and Gill, 1971; Jedlinski, 1972; 1981; Jedlinski *et al.*, 1977; Jenkins, 1966; Kieckhefer *et al.*, 1980; Lindsten, 1977; Qualset, 1967; Rochow and Duffus, 1981; Smith, 1961; 1967; Watson and Mulligan, 1960; Weerapat *et al.*, 1974), and progress has been made toward standardizing screening methods and identifying and improving sources of tolerance and incorporating them into agronomically acceptable cultivars (Brown and Jedlinski, 1978; Catherall *et al.*, 1977; Comeau, 1982; Comeau and Dubuc, 1976; 1978; Comeau and St-Pierre, 1982; Endo and Brown, 1963; 1964; Gill and McKenzie, 1977; Jedlinski *et al.*, 1977; Jenkins, 1976; Qualset, 1967; Rines *et al.*, 1979; Smith, 1963). Cultivars such as Brave, Jaycee, Lang, Larry, Ogle and Otee have been released in Illinois, Noble and Porter in Indiana, Preston in Minnesota and Bates and Pettis in Missouri. These cultivars have demonstrated considerable protection against BYDV under a wide range of field conditions.

No correlation has been found between the levels of tolerance to BYDV in oats and the levels of attractiveness and support of the four common aphid vectors (Kieckhefer *et al.*, 1980). This suggests that the development of cultivars tolerant to the virus, and not to the vector, is the best approach to the control of the disease in the field. In general, however, only one aphid species, *Rhopalosiphum padi*, has been used in experimental BYDV tolerance screening programs. Stability of tolerance over wide geographic areas appears quite common. Sources of tolerance in hexaploid oats, e.g., Albion and CI 7488, and diploid oats, such as Saia, identified in Illinois, were also tolerant in Canada (Comeau and Dubuc, 1978; Comeau and St-Pierre, 1982), England (Jenkins, 1966), New Zealand (H.C. Smith, personal communication) and Sweden (Lindsten, 1977). However, more coordinated research is needed in this area.

BYDV tolerance is heritable and can be used in breeding programs. The trait is relatively simply inherited, usually in a quantitative manner, with the nature of inheritance depending on the genotypes of the parents and the characters measured. For example, it seems that more genes are involved in the parental combination of CI 7448/(Victoria x Hajira-Banner) X (Victory x Hajira-Ajax) x MO 0-2052 (Brown and Poehlman, 1962) and in a cross with Pettis oats (Weerapat *et al.*, 1974) than in crosses of Albion x Minhafer or Albion x CI 7451 tested in Illinois.

Inheritance of tolerance to BYDV has also been studied by R.I.H. McKenzie and P.D. Brown, Agriculture Canada, Winnipeg, and P.A. Burnett, CIMMYT, Mexico (personal communication; technical report, American Oat Workers' Conference and First International Oat Research Workshop, University Park, Pennsylvania, 1982). From studies of crosses of *Avena sativa* Otee, M 921, FF 64/74 and CI 4492 with BYDV-intolerant Clintland 64 under a BYD epidemic in the field in New Zealand, it was concluded that simple inheritance was not involved in any of the crosses and that two or more genes conferred the tolerant reaction.

In the 13 oat germplasm lines recently released by the Illinois Agricultural Experiment Station and the USDA lines with the highest known level of tolerance currently available, tolerance resulted from transgressive segregation where diverse genes from several parents were combined (Brown and Jedlinski, 1978; Jedlinski *et al.*, 1977). The identification of divergent sources of tolerance was facilitated by the use of different BYDV isolates with differing spectrums of virulence (Jedlinski, 1972); this would indicate that several gene interactions are involved in expression of tolerance.

Good sources of tolerance have also been identified in other species of the genus, including *A. sterilis*, *A. strigosa* and *A. fatua* (Comeau, 1982; Comeau and St-Pierre, 1982; Endo and Brown, 1964; Jedlinski, 1972; Rines *et al.*, 1979). Inheritance studies with some *A. sterilis* crosses have indicated additive inheritance involving relatively few genes (Comeau and St-Pierre, 1982). Several *A. sterilis* derived lines have been successfully utilized in the Illinois oat improvement program. Some selections derived from *A. sterilis* hybridizations combined resistance to crown rust, tolerance to BYDV and good agronomic type. The promising advanced selections were derived from crosses with two Coker lines (C 227 and C 234) with *A. sterilis* background and excellent crown rust resistance and a moderate level of tolerance to BYDV. The selection IL 75-1056 (parents Coker 227 2 x Clintford x Portal), for example, shows considerable promise, although it is susceptible to oat smut. In other advanced spring oat lines, it has been possible to combine BYDV tolerance with resistance to most of the prevalent races of crown rust and covered and loose smut.

Oat selections found to be tolerant in more recent Illinois tests were reported at both the National Oat Conferences and at the Barley Yellow Dwarf Virus Workshop held at Urbana, Illinois, in 1977. Copies of those reports are available from the author upon request.

Sources of tolerance to BYDV in oats of different genetic backgrounds are available. The germplasm is maintained and distributed by the Plant Genetics and Germplasm Institute, United States Department of Agriculture, Beltsville, Maryland, USA. Unfortunately, most of the programs on the improvement of BYDV tolerance in oats have involved spring oats. There is an urgent need to improve the level of tolerance in winter oats, since very severe effects result from fall infections. More research is also needed for better understanding the host/pathogen/vector relationship, for combining BYDV tolerance with resistance to other major pathogens and for improving agronomic types. Further improvements would be facilitated by the development of a coordinated international BYD nursery program.

References

Brown, C.M., and H. Jedlinski. 1978. Registration of 13 germplasm lines of oats. Crop Science 18:1098.

Brown, G.E., and J.M. Poehlman. 1962. Heritability of resistance to barley yellow dwarf virus in oats. Crop Science 2:259-262.

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

Catherall, P.L., J.D. Hayes and R.E. Boulton. 1977. Breeding cereals resistant to virus diseases in Britain. Annals of Phytopathology 9:241-244.

Comeau, A. 1982. Geographic distribution of resistance to barley yellow dwarf virus in *Avena sterilis*. Canadian Journal of Plant Pathology 4:147-151.

Comeau, A., and J.P. Dubuc. 1976. Niveau de resistance de quelques cultivars d'avoine au virus du nanisme jaune de l' orge (BYDV). Canadian Journal of Plant Science 56:397-398.

Comeau, A., and J.P. Dubuc. 1978. Evaluation of new and old sources of tolerance to early-season barley yellow dwarf virus in oats. Canadian Journal of Plant Science 58:875-878.

Comeau, A., and C.-A. St-Pierre. 1982. Trials on the resistance of cereals to barley yellow dwarf virus (BYDV). Report no. 4. Agriculture Canada, Station de Recherches, and Department de Phytologie, Universite Laval, Sainte-Foy, Quebec, Canada.

Doodson, J.K., and P.J.W. Saunders. 1970a. Some effects of barley yellow dwarf virus on spring and winter cereals in glasshouse trials. Annals of Applied Biology 65:317-325.

Doodson, J.K., and P.J.W. Saunders. 1970b. Some aspects of barley yellow dwarf virus on spring and winter cereals in field trials. Annals of Applied Biology 66:361-374.

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

Endo, R.M., and C.M. Brown. 1964. Barley yellow dwarf resistance in oats. Crop Science 4:279-283.

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

Gill, C.C., and R.I.H. McKenzie. 1977. Susceptibility of oat cultivars to barley yellow dwarf virus in Manitoba. Canadian Journal of Plant Science 57:1021-1027.

Gill, C.C., and J. Chong. 1979. Cytopathological evidence for the division of barley yellow dwarf virus isolates into two subgroups. Virology 96:59-69.

Hammond, J., R.M. Lister and J.E. Foster. 1983. Purification, identity and some properties of an isolate of barley yellow dwarf virus from Indiana. Journal of General Virology 64:667-676.

Halstead, B.E., and C.C. Gill. 1971. Effects of inoculation of oats with paired combinations of barley yellow dwarf virus isolates. Canadian Journal of Botany 49:577-581.

Jedlinski, H. 1972. Tolerance to two strains of barley yellow dwarf virus in oats. Plant Disease Reporter 56:230-234.

Jedlinski, H. 1981. The rice root aphid, *Rhopalosiphum ruflabdominalis*, a vector of barley yellow dwarf virus in Illinois and the disease complex. Plant Disease 65:975-978.

Jedlinski, H., W.F. Rochow and C.M. Brown. 1977. Tolerance to barley yellow dwarf virus in oats. Phytopathology 67:1408-1411.

Jenkins, G. 1966. Comparison of tolerance to barley yellow dwarf virus in barley and oats. Annals of Applied Biology 57:163-168.

Kieckhefer, R.W., H. Jedlinski and C.M. Brown. 1980. Host preferences and reproduction of four cereal aphids on 20 Avena selections. Crop Science 20:400-402.

Lindsten, K. 1977. Aspects of the variation of yellow dwarf. Annals of Phytopathology 9:301-305.

Murphy, H.C. 1959. The epidemic of barley yellow dwarf on oats in 1959. Plant Disease Reporter Supplement 262.

Qualset, C.O. 1967. Tolerance to barley yellow dwarf in winter oats. Plant Disease Reporter 51:908-910.

Rines, H.W., D.D. Stuthman, L.W. Briggle, V.L. Youngs, H. Jedlinski, D.H. Smith, J.A. Webster and P.G. Rothman. 1979. Collection and evaluation of *Avena fatua* for use in oat improvement. Crop Science 20:63-68.

Rochow, W.F., and J.E. Duffus. 1981. Luteoviruses and yellows diseases. *In* Handbook of Plant Virus Infections and Comparative Diagnosis, Kurstak, ed. Elsevier/ North Holland, Amsterdam. Pp. 147-170.

Smith, H.C. 1961. Susceptibility of Saia and Fulghum oat varieties to some strains of barley yellow dwarf virus. Canadian Plant Disease Survey 41:178-181.

Smith, H.C. 1963. Control of barley yellow dwarf virus in cereals. New Zealand Journal of Agricultural Research 6:229-244.

Smith, H.C. 1967. The effect of aphid numbers and stage of plant growth in determining tolerance to barley yellow dwarf virus in cereals. New Zealand Journal of Agricultural Research 10:445-446.

Watson, M.A., and T.E. Mulligan. 1960. Comparison of two barley yellow-dwarf viruses in glasshouse and field experiments. Annals of Applied Biology 48:559-574.

Weerapat, P., D.T. Sechler and J.M. Poehlman. 1974. Barley yellow dwarf virus resistance in crosses with Pettis oats. Crop Science 14:218-220.

Comments

P.A. Burnett, Mexico

As stated by H. Jedlinski in his paper, R.I.H. McKenzie and P.D. Brown of Agriculture Canada, Winnipeg, A. Comeau and this author have been involved in a study on the inheritance of resistance to BYDV in *Avena sativa* L. Four unrelated oat accessions with tolerance to BYDV, Otee, M 921, FF 64/74 and CI 4492 have been crossed to the susceptible cultivar, Clintland 64. Up to 200 random F_5 lines per cross obtained by single seed descent have been tested in replicated trials in New Zealand and in two sites in Canada.

There was no evidence of simply inherited BYD resistance in any of the crosses. Resistance to the New Zealand isolate seems to be conferred by two or more genes.

There is concern about the variation among BYDV isolates from region to region; thus, it would seem that international testing nurseries are necessary for the development of BYDV resistance in oats.

J.M. McEwan, New Zealand

R.I.H. McKenzie's experiment was somewhat confounded in New Zealand when Clintland 60 showed some degree of resistance to natural BYDV infection.

This reinforces P.A. Burnett's comments on the necessity for testing for BYDV resistance over a number of environments.

The Genetics of Resistance to Barley Yellow Dwarf Virus in Triticale

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The presence of barley yellow dwarf virus (BYDV) in triticale had received very little attention from scientists before the CIMMYT report on wheat improvement stated that it was the major disease of triticale (CIMMYT, 1979). Triticale was not then grown in Quebec; the screening of triticale collections was initiated only in 1981. The results obtained in the first screening have already generated local interest in triticale breeding and in a research project on the genetics of BYDV resistance in triticale. Although it is premature to draw definite conclusions, some of the initial work and the current research aproach will be discussed here.

The First Trials

Between 1976 and 1978, 12 lines of triticale, mostly from the Winnipeg program, were tested. Although they generally possessed some useful BYDV resistance, they had inferior yield potential; one of the lines was Beagle, reported elsewhere as BYDV resistant (CIMMYT, 1979). In 1981, when testing was begun on the CIMMYT 12th International Triticale Screening Nursery (ITSN), it was expected that most lines of triticale would show some virus resistance, derived from the rye parent. However, it was found that very few triticales showed BYDV resistance. Only nine lines out of 285 were kept for further testing. The next year, when the 13th ITSN was evaluated, 22 out of 172 lines were kept for further testing.

In 1983, the 14th ITSN was tested, and 24 lines retained out of 272. This trend appears to indicate progress towards better resistance in the CIMMYT material, as the 1983 test was very severe and BYDV stress was accompanied by drought stress. The 1983 selections were all significantly better than Beagle, the long-term check in Quebec.

The screening of the 14th ITSN for BYDV resistance showed that Merino, Muskox, Whale, Elk 32, Juanillo and Yogui contained selections with BYDV resistance. On the other hand, very few M2A derivatives possessed adequate BYDV resistance; this is unfortunate as that cross is in the pedigree of a large number of lines. This suggests that M2A derivatives be crossed with BYDV-resistant triticales and selected under BYDV stress if BYDV resistance is an important aim of the program.

At the University of Guelph, screening for BYDV resistance in winter triticales was initiated in 1981. The methodology used for testing winter cereals had to be improved so that virus damage would not be confused with other types of winter damage. Reliable information is now being obtained that indicates that BYDV resistance is slightly better in winter than in spring triticale, at least for the Canadian germplasm. The cultivar OAC Wintri was chosen as the resistant check for future work with winter triticale. Preliminary information shows the heritability of the BYDV resistance derived from Wintri to be satisfactory.

Figure 1. Reaction of winter triticales to BYDV inoculation at the three leaf stage, illustrating extreme cases of resistance and susceptibility. Line GWT 1 (left) produced normal plants with abundant tillering and green color. Line GWT 285 (right) showed stunting, suppressed tillering, low chlorophyll level and yellowing and reddening of leaf tips.

Criteria for Judging Resistance

In a previous report, nine lines of triticale were recommended as resistant parents (Comeau *et al.*, 1984). This selection was based on the observation of grain yield, BYD symptoms and harvest index in BYDV-inoculated plots (Table 1); the use of any of these three criteria have both advantages and disadvantages. Grain yield is the best indicator of resistance when it can be compared in virus-inoculated versus uninoculated plots; however, the use of virus-free plots doubles the amount of work and necessitates frequent aphicide spraying.

Symptom scores are easily obtained; however, it has been observed that the ranking of cultivars on the basis of symptoms varies from week to week. Symptoms possess an unpredictable correlation with yield loss from year to year, and factors other than BYDV can affect leaf color and general plant vigor. The most important of those factors is that of plant maturity, giving rise to large variations in symptom expression.

Harvest index (hi), the ratio of grain yield to dry aerial plant biomass, is also an indicator of BYDV resistance. However, as is the case with grain yield and symptom scores, it is affected by

Table 1. Performances of BYDV-Inoculated Triticales from the 12th ITSN (Averages of 1981 and 1982)[a/]

ITSN number and name		Grain yield	Symptom score	Harvest index	BYDV reaction
15	Delfin 205	3554	4.2	.30	Resistant
20	Bgl"S"-M2A x Cin	3770	4.5	.34	Resistant
83	Goqui-derived[b/]	4079	4.3	.36	Resistant
168	W74.103-Addax/ Bgl"S"-M2A x IRA "Whale"	4880	4.1	.39	Resistant
169	W74.103-Addax/ Bgl"S"-M2A x IRA "Whale"	5421	3.2	.39	Resistant
170	W74.103-Addax/ Bgl"S"-M2A x IRA "Whale"	5116	3.5	.41	Resistant
267	TCCXVI	5473	3.3	.38	Resistant
269	Juanillo"S"	4840	4.1	.39	Resistant
271	Juanillo"S"	4848	4.0	.37	Resistant
4	Beagle	2486	4.8	.24	Intermediate
25	Cananea 79	1078	5.7	.19	Susceptible

[a/] Data from Comeau *et al.*, 1984
[b/] Goqui (IA-M2A x Pi 62/BGL"S")

factors other than BYDV, mainly by the genetic nature of the cultivar which may tend toward a high or low index. Also, the work necessary for determining harvest index is tedious. Harvest index has been found to be rather independent of soil fertility over a broad range (Comeau and Barnett, 1979). The most accurate estimator of BYDV resistance of oats was the harvest index of virus-inoculated plots divided by that of virus-free plots (Cooper and Sorrells, 1983). This criterion of harvest index will be used in the future for making the most accurate comparison of spring triticales. The rationale behind this decision is that, although BYDV-infected plants may sometimes look healthy, the translocation of the photosynthate into the seed is affected; the most accurate statistical information on this phenomenon is obtained from the study of harvest index.

In large-scale screening, observations on symptoms, grain yield and harvest index were integrated into an artificial index called the susceptibility index (SI). In 1982, the formula used for triticale was:

$$SI = 10 - [.001\ y + 12\ hi + .3\ (10 - S)]^{.77}$$

with yield expressed in kg per hectare. Eventually, the best lines chosen through mass screening methods will be reevaluated in trials where yield and harvest index of noninoculated plots will be compared to that of BYDV-inoculated plots.

Experimentation is presently under way using a new method to intensify the expression of BYDV symptoms in winter cereals so that quantitative data become less necessary. This method requires artificial winter protection with glass wool within a polyethylene tunnel. Under such conditions, the prolonged, low temperature virus incubation period (Jones and Catherall, 1979) and alternate cold and heat stress seem to intensify symptom expression.

Prospects for the Future

Although present work on triticale has yielded returns such as the identification of BYDV-resistant lines, it has generated more questions than answers. Some of these questions are presently being studied.

Rye is BYDV resistant, or at least it has always been so considered. If this is true, why are so many triticales susceptible and so few truly resistant? From actual knowledge of triticale cytogenetics, it seems unlikely that the portions of the rye genome involved in BYDV resistance are missing in such a high number of triticales. It is likely,

however, that BYDV resistance of rye is genetically complex and that, in interspecific hybrids such as triticale, the BYDV resistance genes are totally or partially repressed. Methods are being researched for testing the above hypothesis.

Plans are also under way to study the BYDV reaction of rye; such a polymorphic genus as *Secale* may contain variability for BYDV reaction. Preliminary data indicate that the best BYDV-resistant triticales have better resistance than bread wheat or durum wheat.

Due to the present lack of knowledge about the genetics of BYDV resistance in triticale, no prediction can be made as to the difficulty of the transfer of BYDV resistance from triticale to wheat. However, triticale x wheat crosses have been made in the Quebec laboratory with the help of embryo culture, and the genetics of BYDV resistance in triticale itself and in the triticale x wheat hybrids will be studied simultaneously.

The best BYDV-resistant triticales have shown an unexpected agronomic feature; they are, according to CIMMYT reports, generally high yielding worldwide. A similar unexpected association is present for oats in North America and CIMMYT durum wheats. The level of correlation between BYDV resistance and yield is in the 0.40 to 0.55 range, which means that high yielding triticales are seldom very BYDV susceptible and that triticales with high BYDV resistance are seldom low in yield. Nobody understands the reason for this correlation, but research hypotheses should be formulated. Could BYDV resistance become a tool to improve the yield level of certain cereal species? Is BYDV resistance more important worldwide than previously thought? Does selection for BYDV resistance also result in selection for more efficient translocation and other physiological advantages?

The immediate work in Quebec will center on the genetics of BYDV resistance in triticale, but the relationship between yield and BYDV resistance should eventually become a subject of study in itself.

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References

CIMMYT. 1979. CIMMYT Report on Wheat Improvement. P. 57.

Comeau, A., and G. Barnett. 1979. Effect of barley yellow dwarf virus on N, P, K fertilizer efficiency and on the harvest index of oats. Canadian Journal of Plant Science 59:43-54.

Comeau, A., J.-P. Dubuc and C.-A. St-Pierre. 1984. Genetic variability for resistance to barley yellow dwarf virus in spring triticale. Cereal Research Communications (in press).

Cooper, D.C., and M.E. Sorrels. 1983. Greenhouse screening and field evaluation of two oat populations segregating for barley yellow dwarf virus tolerance. Cereal Research Communications 11: 99-105.

Jones, A.T., and P.L. Catherall. 1970. The relationship between growth rate and the expression of tolerance to barley yellow dwarf virus in barley. Annals of Applied Biology 65:137-145.

Status of An Attempt to Transfer the Barley Yellow Dwarf Virus Resistance Gene *Yd2* of Barley to Hexaploid Wheat

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Work is underway at the University of California to transfer the *Yd2* gene found on chromosome 3 of barley (*Hordeum vulgare* L.) to hexaploid wheat (*Triticum aestivum* L.); this gene confers resistance in barley to the barley yellow dwarf virus (BYDV). The procedure being followed is the classical one involving the production of an F_1 plant between the donor and recipient species, treatment to double the chromosome number, recurrent backcrossing to the recipient parent, isolation from the backcross progeny of monosomic addition lines, selfing of those lines to produce stable disomic addition lines, identification of the line possessing the desired gene, determination of whether the gene is expressed, induction of recombination between the added chromosome and a chromosome of the recipient parent and, finally, selection of recombinants which express the transferred gene.

The initial approach involved four barley lines as pollen parents and three cultivars as seed parents. The crosses were made in large numbers (some 50,000 florets pollinated) under field conditions. Hybrid plants were obtained, backcrosses made and monosomic and disomic addition lines accumulated (Jan *et al.*, 1982).

Traditionally, addition lines were first sorted by their morphology and, subsequently, representative plants of each class were intercrossed to identify the added chromosomes by their meiotic pairing behavior. When they were available, genetic markers for specific chromosomes were used to identify lines. More recently, chromosome-specific, electrophoretically identifiable markers and heterochromatin patterns as revealed by C and N-banding have been used.

Both C-banding and electrophoresis for seed storage proteins were used by Jan Dvořák to identify the presumed disomic barley addition lines. However, the added chromosomes were found to be from rye (*Secale cereale* L.) instead of barley. Progenitors of those lines were then studied, and it was found that they, too, possessed no barley chromosomes. Therefore, it was assumed that the original F_1 hybrids originated from accidental pollination of the emasculated wheat florets with rye pollen during the brief periods when the spikes were unprotected for pollination with barley pollen.

In January 1983, to make up for this setback, the present author began the work of again making crosses between barley cultivars and one cultivar of wheat, this time under greenhouse conditions.

(continued)

Materials and Methods

The BYDV-susceptible wheat cultivar Chinese Spring was used as the seed parent. Florets were emasculated, bagged and, one to three days later, pollinated anther-to-floret with one of four barley lines, Ethiopian introductions CI 2376 and CI 3208-4 and California cultivars CM 72 and Atlas 68. All four barleys possess the *Yd2* gene which confers resistance in barley to BYDV. Once a day for three days following pollination, each floret received a drop of gibberellic acid by syringe (75 ppm in distilled water).

When seed set occurred, the seeds were removed from the florets 12 to 15 days after pollination and surface-sterilized in a solution of equal parts commercial bleach and distilled water with a drop of Tween 80 as a surfactant. The seeds were dissected under sterile conditions and, when an embryo was found, it was transferred by the Kruse technique (1973) onto the embryo site of naked barley endosperm from which the embryo had been excised (Jan *et al.*, 1982). This endosperm, which was taken from a seed of approximately the same age as the hybrid seed, was placed on an agar-based nutrient medium, a modification of Gamborg's B5 medium with a 9% sucrose concentration. The culture vials were kept under constant light at 26°C. At the two-leaf stage, the root tips of the plantlets which developed were exised for cytological analysis and the plantlets transferred to soil in pots; a transparent container was inverted over the shoots for about ten days for protection and increased humidity.

At the two-tiller stage, the plants were treated with 0.25% colchicine in distilled water for four hours at room temperature. To do this, the plants were uprooted and the soil washed from the roots which were then folded alongside the shoots so that just the crown could be immersed in the colchicine solution; the roots and shoots were wrapped in moistened paper towels to prevent dessication. At the end of the four hours, the plants were washed and repotted. When the colchicine-treated plants flowered, they were backcrossed with pollen of Chinese Spring without emasculation or gibberellic acid treatment. Embryos were again excised and cultured and root tips excised for cytology at the time of the transfer of the plantlets to soil.

The procedure used for C-banding was that of Dvořák and Appels (1982). The major difficulty with cytological observations on root-tip chromosomes from plantlets in culture is that there is often a rather low mitotic index; therefore, root tips were also collected at the time of colchicine treatment when the roots were washed. The ability to identify barley chromosomes from the F_1 stage onward makes unnecessary the traditional sorting of disomic additions by morphology and intercrossing.

Results

The number of crosses made with each pollen parent varied according to its flowering habit. Under greenhouse conditions CM 72 does not tiller well and anthesis occurs while the heads are still enclosed in the sheath; these factors limit the availability of pollen. Atlas 68 and CI 2376 (the only two-rowed line) were the next to flower after CM 72; CI 3208-4 was very late. The results of two series of crosses, one in January and February and the other in April and May, are summarized in Table 1. Both embryos from the CI 3208-4 parent, the single embryo from the CI 2376 parent, seven of the 18 embryos with an Atlas 68 parent and two of the 13 with a CM 72 parent germinated and differentiated into plantlets. Of the others, most did not grow, some produced callus tissue, and a few differentiated a root or two but experienced no further growth. Changes of medium to lower sucrose levels or to callus-growth media were made but were unsuccessful in rescuing those embryos. No mortality was incurred in the transfer of plantlets from culture vials to soil.

Table 1. Status of Attempted Crosses Between Four Lines of *Hordeum vulgare* and *Triticum aestivum* Cultivar Chinese Spring (CS) and of the Resulting Plants

H. vulgare parent	No. florets pollinated	No. embryos cultured	No. plants obtained and their chromosome constitution
Atlas 68	4357	18	7: 5 were 2n = 21 (CS haploids) 1 was 2n = 23 (CS + barley 4, 7) 1 was 2n = 25 (CS + barley 1,3,4,7)
CI 3208-4	2723	2	2: 1 was 2n = 28 (CS + barley 1,2,3,4,5,6,7) 1 was 2n = 21 (CS haploid)
CI 2376	1166	1	1: 1 was 2n = 25 (CS + barley 2,4,6,7)
CM 72	717	13	2: 2 were 2n = 21 (CS haploids)
Total	8963	34	12: 4 with barley chromosomes 8 CS haploids

As was found in Australia (Islam *et al.*, 1981), there was variation in chromosome number in the plants obtained from the interspecific crosses. Their range of variation was from 2n = 21 to 2n = 36. However, in the cases reported here, no plants with more than the euploid F_1 number of chromosomes, 2n = 28, were obtained. Of the 12 plants obtained, eight were haploids of Chinese Spring and only four possessed any barley chromosomes.

By means of C-banding, the individual barley chromosomes in those plants were identified. The 2n = 23 plant had chromosomes 4 and 7 of Atlas 68. One of the 2n = 25 plants had Atlas 68 chromosomes 1, 3, 4 and 7 and the other had CI 2376 chromosomes 2, 4, 6 and 7. The single euploid F_1 hybrid had all seven barley chromosomes (Figure 1). Thus, only two plants can provide a source of the *Yd2* gene on barley chromosome 3.

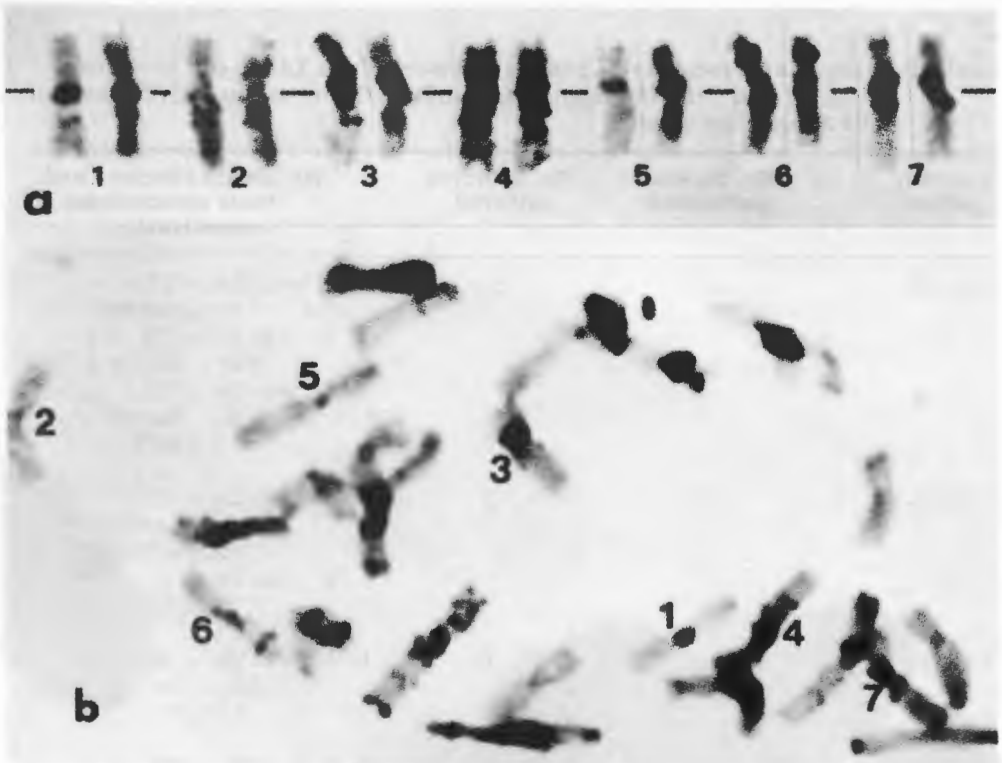

Figure 1. a) C-band karyotype of the chromosomes of barley accession CI 3208-4
b) Root-tip cell of the F1 plant Chinese Spring x CI 3208-4 with the seven barley chromosomes indicated by number

No fertile amphiploid had been reported from a wheat x barley cross despite attempts at doubling the chromosome number of euploid and aneuploid F_1 plants, nor has any been obtained in the present work. The colchicine-treated plants are sufficiently female-fertile to produce seed when backcrossed with wheat pollen but seem to be male-sterile (Table 2). It has been suggested by Islam *et al.* (1981) that barley chromosome 5 conveys a factor which results in self-sterility of hybrid plants with wheat cytoplasm, due to the fact that all hybrid plants with chromosome 5 were self-sterile and no addition line of the chromosome was obtained. However, in the present study, male sterility was also found after colchicine treatment in two of the aneuploid hybrids which lacked chromosome 5.

Each of the two colchicine-treated aneuploid hybrids set three seeds on backcrossing. The euploid hybrid so far has produced 24 seeds from three tillers after backcrossing; one tiller remains to be pollinated. The first spikes to emerge in the three colchicine-treated plants differed in appearance from subsequent spikes. They all had moderate to extreme branching of the rachis and the rachillae were elongated in some spikelets; some first spikes had more than one spikelet at a node. Heads of later tillers were not branched except in the 2n = 25 plant with the Atlas 68 parent. Several morphological characters of barley were evident in the F_1 plants. Lemmas of all spikelets were awned, with longer awns on the higher spikelets. Chinese Spring is not awned, while all barley parents are. The auricles are barley-like as are the characteristics of the sheaths at the bases of the tillers.

Table 2. Status of Backcrosses of Colchicine-Treated F_1 Plants

F_1 chromosome constitution	Barley parent	No. seeds	Back-cross	Selfed	BC chromosome number
2n = 23, barley 4,7	Atlas 68	3	3	0	44,45,46
2n = 25, barley 2,4,6,7	CI 2376	3	3	0	46, ?, ?
2n = 28, all 7 barley	CI 3208-4	24	24	?	?
2n = 25, barley 1,3,4,7	Atlas 68	not yet flowered			

Future Work

Plants with barley chromosome 3 will receive the most attention. Backcrossing will be continued until double monosomic or monosomic lines with chromosome 3 are obtained; these will be selfed to produce addition lines disomic for chromosome 3. The selfed progeny will also be screened for barley telosomics which result from misdivision of monosomics. It seems possible that disomic addition lines of chromosome 3 from Atlas 68 and CI 3208-4 will be obtainable after only two further generations.

The next major hurdle is to determine whether the *Yd2* gene is expressed in the Chinese Spring background of the addition line. *Yd2* in barley is an incompletely dominant gene. Its expression in wheat is anticipated to be affected by dosage effects and by the background genotype of the recipient wheat cultivar. Since Chinese Spring, the recipient, is susceptible, *Yd2* may be masked by the preponderance of susceptible alleles already in wheat. Thus, the value of *Yd2* in improving BYDV resistance in wheat will probably be enhanced by 1) the substitution of barley chromosome 3 for a wheat chromosome or 2) the translocation of the *Yd2*-bearing chromosome arm to a wheat chromosome. Therefore, initial BYDV tests with the addition line might not reveal the ultimate value of *Yd2* in wheat. Secondly, *Yd2* should be introduced into wheat varieties such as Anza that already have measurable resistance to BYDV. In this case, it is expected that *Yd2* will be an effective "enhancer" of resistance.

BYDV tests will be conducted on the addition lines, using wheat/barley 3 in comparison with other wheat/barley chromosome addition lines. At the same time, substitution lines will be developed and translocations as mentioned above will be attemped by manipulating the *Ph* gene system.

In addition to the potential transfer of BYDV resistance, this project will have produced another set of at least six barley disomic addition lines from CI 3208-4; these will be supplemented by some lines from Atlas 68 and CI 2376. These and the ditelosomic additions that are anticipated, in conjunction with Australian material derived from Betzes barley, will be extremely useful cytogenetic tools for investigating such phenomena as nonstructural chromosome differentiation among barley varieties.

Since barley possesses resistance to several other diseases that also attack wheat, these addition lines may yield resistance genes for other diseases for incorporation into wheat. In particular, CI 3208-4 has some resistance to races of powdery mildew and net blotch and CI 2376 has resistance to net blotch and loose smut (Qualset and Moseman, 1966). In general, Ethiopian barley cultivars have demonstrated multiple resistance to several diseases with a greater frequency than random occurrence would predict (Qualset, 1975). This suggests that genetic linkage among resistance genes may have occurred in Ethiopian cultivars while adaptive genes have accumulated without linkage. Linkage between a gene for scald resistance and *Yd2* was shown by Schaller *et al.* (1964) in the Ethiopian cultivar CI 1237.

Acknowledgements

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References

Dvořák, J., and R. Appels. 1982. Chromosome and nucleotide sequence differentiation in genomes of polyploid *Triticum* species. Theoretical and Applied Genetics 63:349-360.

Jan, C.C., C.O. Qualset and J. Dvořák. 1982. Wheat-barley hybrids. California Agriculture 36:23-24.

Islam, A.K.M.R., K.W. Shepherd and D.H.B. Sparrow. 1981. Isolation and characterization of euplasmic wheat-barley chromosome addition lines. Heredity 46:161-174.

Kruse, A. 1973. *Hordeum x Triticum* hybrids. Hereditas 73:157-161.

Qualset, C.O. 1975. Sampling germplasm in a center of diversity: an example of disease resistance in Ethiopian barley. *In* Plant Genetic Resources for Today and Tomorrow, O.H. Frankel and J.G. Hawkes, eds. Cambridge University Press. IBP vol. 2:81-96.

Qualset, C.O., and J.G. Moseman. 1966. Disease reaction of 654 barley introductions from Ethiopia. Preliminary report of the USDA-ARS Crops Research Division, Plant Industry Station, Beltsville, Maryland, USA.

Schaller, C.W., C.O. Qualset and J.N. Rutger. 1964. Inheritance and linkage of the Yd_2 gene conditioning resistance to the barley yellow dwarf virus disease in barley. Crop Science 4:544-548.

The Status of Barley Yellow Dwarf Virus in Maize

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Until recently, barley yellow dwarf virus (BYDV) in maize (*Zea mays* L.) has warranted little attention. Early work, focused on the experimental infection of BYDV in the crop species, included symptom and host range experiments with some maize cultivars and lines (Allen, 1957; Watson and Mulligan, 1957). Initially, it was belived that natural infection of commercial maize plantings was unimportant. In fact, in 1973, BYDV was listed in the *Compendium of Corn Diseases* as a virus only occasionally found or reported (Shurtleff *et al.*, 1973).

Not until 1977 was serious consideration given to the possibility that maize was a reservoir for BYDV (Stoner, 1977). In a study to determine whether maize was a host of BYDV in the USA, virus was recovered from naturally infected maize plants grown in a field nursery. Nonviruliferous *Rhopalosiphum padi* acquired BYDV from the maize and transmitted it to seedlings of Black Hull-less barley (*Hordeum vulgare* L.). Symptoms in maize such as yellowing, reddening and malformation had frequently been seen during field surveys and, in most instances, those symptoms could not be associated with known pathogens or pests or with abnormalities caused by climatic or nutritional factors. Although two host range studies had been made earlier, the susceptibility of maize to BYDV was poorly understood; it appeared that it could only infect maize under very specific experimental conditions.

In the Stoner study (1970), greenhouse and field tests were conducted, using an isolate of BYDV originally obtained from oats near Davis, South Dakota. That isolate was found to be a PAV-like (vector-nonspecific) virus. *R. padi*, collected in South Dakota fields, served as the aphid vector species. Most of the maize selections tested were sweet maize types for human consumption, chosen because they were smaller and more manageable under small container culture than were the field maize types. Briefly, symptoms resulting from experimental infections in the greenhouse and growth chambers consisted of purpling or reddening of the tips of the lower leaves; there was also some slight overall stunting. No symptoms were observed in some maize cultivars even though they were infected. Symptoms in field plants, whether inoculated with the SD (South Dakota) PAV-like virus or naturally infected, closely resembled the experimentally infected plants in the greenhouse or growth chambers.

Natural field infections occurred in four cultivars of maize tested at Brookings, South Dakota, Aunt Mary's, Early Golden Midget, Golden Sunshine and Rainbow. Alternation of host plants was shown for BYDV in that study when the virus was serially transmitted from the four susceptible maize cultivars to barley and then from barley back to maize. BYDV was also serially transmitted from maize to barley to maize to oats. Symptoms were just as strong in the final barley test plants as they had been in the initial infectivity barley check plants.

From the results of the 1977 study, it was concluded that maize was, in fact, an experimental host for BYDV. As such, it was postulated that the virus could be carried over the summer in field-planted maize and, subsequently, infect autumn-planted small grains. This may explain why no massive reservior of BYDV has ever been found in migrating aphid vectors, native grasses or forbs in epidemic areas.

Recent work (Brown *et al.*, 1983) in the state of Washington again implicates maize as a source of BYDV. The virus causes disease in winter wheat (*Triticum aestivum* L.) and barley grown in the Palouse and Columbia Basin regions of eastern Washington. There, the virus is vectored nonspecifically by four species of cereal aphids; however, *R. padi* and *Macrosiphum (Sitobion) avenae* are the most abundant and efficient vector species. Aphid infestations of small grains increase throughout the spring, decrease by early summer and again increase in the early fall.

The increases of BYDV in fall-planted grains are thought to be associated with an increase in vector populations, since the naturally sparse weeds that survive the arid summer conditions do not support vector populations. Recently, however, expansion of irrigation in the basin has allowed weeds and certain crops to remain green throughout July and August; for example, irrigated maize (sweet, silage and grain) plantings have risen from about 1,500 to 65,000 hectares. Because BYDV is known to attack many graminaceous plants, and maize remains green all summer when winter small grains are drying, it was hypothesized that maize could be a potential source of virus and vector. Thus, to determine if maize is a natural survival host of BYDV between summer harvest and fall planting of small grains, field surveys were undertaken in the Columbia Basin of eastern Washington.

Leaf samples were collected from maize and/or wheat fields in four counties throughout the summer and fall of 1980 and 1981. Developing leaves were collected randomly from five different plants within a field, pooled to constitute a sample and assayed for BYDV by aphid transmission tests. Aphids were also collected from five different plants in a field, pooled and given an acquisition access period on indicator hosts to determine if they were viruliferous.

Virus infectivity assays of detached leaf pieces were accomplished by aphid transmission tests using non-viruliferous, apterous *R. padi* from greenhouse-maintained colonies. Stock aphid colonies were maintained on Luther barley, which served as the BYDV indicator host in all greenhouse tests. Detached leaf pieces were analyzed by confining 10 to 20 *R. padi* with pooled samples in plastic dishes for a 24-hour acquisition-access period. Intact leaf pieces with feeding *R. padi* were transferred to pots containing barley seedlings and then were placed in cages; the aphids were given a three-day inoculation/access period. Inoculated barley was checked periodically during a three-week period for symptom expression. Vector capability of field-collected aphids was tested by pooling apterous aphids and placing them on healthy indicator seedlings, which were also observed for symptom development over a three-week period.

BYDV isolates from field maize were characterized by aphid transmission tests to determine vector specificity; serological comparison was made to four BYDV strains from the state of New York. At Pullman, vector specificity tests were conducted using greenhouse colonies of either

M. avenae, *R. padi* or *Schizaphis graminum*. Additionally, the maize BYDV isolates were tested by ELISA at Ithaca, New York, with antisera prepared against four NY strains of BYDV. Because of past difficulty in detecting BYDV in maize tissue, the maize isolates were transferred by *R. padi* to barley from field and greenhouse-infected maize leaves. Fresh leaves and acetone powders, prepared from fresh or frozen maize or barley leaves, also were tested. Maize seeds for transmission tests were supplied by commercial seed companies, the United States Department of Agriculture Regional Plant Introduction Station, the National Seed Storage Laboratory, or were obtained from a public breeder. Five seeds were planted per pot and the resulting seedlings thinned to three per pot. After a 24-hour acquisition period on detached leaves of BYDV-infected Luther barley, viruliferous *R. padi* (10 to 20 per pot) were transferred to maize seedlings and then caged. The aphids were killed by fumigation three days later, and the inoculated plants maintained in the greenhouse. Inoculated plants were back-indexed to healthy barley indicators, using detached maize leaf pieces and *R. padi* (10 to 20 per plant). Each maize cultivar was tested three times with at least ten plants per experiment.

In 1980, BYDV was recovered from 39, 86 and 50% of fields sampled in July, August and September, respectively; virus was recovered from fields in all of the four counties surveyed. All of the plants from which BYDV was recovered were symptomless. The small number of plants assayed per field did not permit an estimate of infection frequency for each field. Therefore, during August, 50 additional samples were collected randomly from within each of seven maize fields. On the basis of transmission tests of these latter samples, it was determined that the frequency of infection ranged from 4 to 64%. In early July, 1980, low levels of alate and apterous *M. avenae* (two to ten per plant) were noted in 82% of the maize fields surveyed. By contrast, at the same time, *R. padi* was observed in only two out of 23 maize fields surveyed. In early 1980, no *M. avenae* were seen in maize fields but, by mid-August, many colonies of *R. padi* were present in 93% of the fields surveyed. Both alate and apterous aphids were found; 90% were viruliferous when checked by transmission to Luther barley. By September, some of the maize had been harvested, but *R. padi* was observed in all remaining fields, and 38% of the aphids tested were viruliferous. Unharvested maize fields remained somewhat green and supported alate and apterous *R. padi* until harvest or death of the plants due to late September frosts.

The 1980 dryland winter and spring wheat crops in eastern Washington were not heavily infected with BYDV. Since symptoms were associated with less than 15% of the observed fields, it was concluded that those fields were probably not the primary source of virus inoculum for subsequent infections occurring in basin maize or wheat. In July, 1980, *M. avenae* were seen in only one of six spring wheat fields planted next to irrigated maize. Virus was not recovered from any sample of that spring wheat by transmission tests. *R. padi* were not observed in spring wheat fields in July or August of 1980.

In September, 1980, *R. padi* were found in 73% of the winter wheat fields planted in late August and September. BYDV was recovered from 63% of the fields sampled and from 45% of the *R. padi* collected. Mild fall and winter

weather conditions during 1980-81 allowed low numbers of *R. padi* (one to two aphids per 3,000 seedlings) to overwinter in wheat seedlings in the Columbia Basin.

In March, 1981, shortly after winter wheat resumed its growth, BYDV symptoms were discovered in over 50% of the dryland wheat fields in and around the Columbia Basin. In late March, 1981, BYDV was recovered from 55% of the fields surveyed. *M. avenae* were found in all nine maize fields checked in late June, 1981. Most *M. avenae* were viruliferous and BYDV was recovered from 77% of the fields by *R. padi* transmission tests. *M. avenae* were not observed on maize for the remainder of the 1981 crop year.

Unlike the summer of 1980, *R. padi* were not found in maize fields until July of 1981, and only 36% and 11% of the fields surveyed were infested with aphids in July and August, respectively. By early September, *R. padi* were present in 27 out of 30 maize fields surveyed. The increase in *R. padi* occurred after the onset of cooler temperatures, following a prolonged hot summer. BYDV, however, was recovered from the maize fields sampled in June (77%), July (54%), August (63%) and September (100%). When the maize isolate of BYDV was compared to the Washington PAV isolates from small grains and the PAV, MAV, RPV and RMV isolates from New York by transmission tests and/or serological tests, it was determined to be similar to the Washington PAV isolates from small grains. Based on ELISA testing, mild PAV-like homologous reactions occurred with barley leaves infected with the maize isolate. A strong PAV-like reaction occurred in acetone powder preparations of BYDV-infected barley leaves, but not in similarly prepared greenhouse (fresh) or field-inoculated (frozen) maize leaves.

Using *R. padi* as the vector and a Washington PAV isolate from wheat, virus was transferred to and recovered from all of 20 inoculated maize cultivars grown in the Columbia Basin. The virus was also transferred to and recovered from 51 out of 52 other cultivars, lines or hybrids of maize. The virus was recovered both from leaves present at the time of inoculation and those which developed following inoculation. Symptoms were observed in 39 out of 72 cases, and were similar to those described previously for greenhouse-inoculated maize plants. Briefly, symptoms consisted of reddening or yellowing of leaf tips, chlorotic flecking of leaf tips or, rarely, chlorotic spotting. Discoloration began at the tips of the oldest leaves and progressed about halfway down the leaf toward the stock. No symptoms were ever seen in newly developing leaves in the whorl.

In conclusion, results of this study indicate that BYDV and its vector, *R. padi*, probably use summer irrigated maize as a reservoir. It is suspected that BYDV moves directly from infested maize to autumn-planted wheat and barley, since BYDV and *R. padi* were recovered simultaneously from wheat and maize fields planted side by side. Viruliferous *R. padi* from wheat in the Columbia Basin could migrate to surrounding dryland wheat. This appears to be the first report of the recovery of BYDV from naturally infected, yet symptomless plants occurring in commercial fields of maize. The source(s) of BYDV inoculum for maize remains unidentified.

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References

Allen, T.C. 1957. Symptoms of golden bantam corn inoculated with barley yellow dwarf virus. Abstract. Phytopathology 47:1.

Brown, J.K., S.D. Wyatt and D. Hazelwood. 1983. Irrigated corn as a source of barley yellow dwarf virus and vectors in eastern Washington. Phytopathology 74:46-49.

Shurtleff, M.C., *et al.*, eds. 1973. A Compendium of Corn Diseases. American Phytopathological Society, St. Paul, Minnesota, USA.

Stoner, W.N. 1977. Barley yellow dwarf virus in maize. Phytopathology 67:975-981.

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

Rice Giallume, a Disease Related to Barley Yellow Dwarf in Italy

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The earliest record of the occurrence of rice giallume (RG) was reported by Corbetta (1967), who wrote that symptoms of the disease were observed for the first time in northern Italy in 1955. Since 1966, RG has become more common each year (Baldacci *et al.*, 1970; Belli *et al.*, 1974), especially in the northwest, the principal rice growing area. During the period 1966-1980, the disease was generally very widespread, particularly in the provinces of Vercelli, Novara, Milan and Pavia, where it is considered one of the most serious diseases of rice. In Europe, the disease was also recorded in Spain (Batalla, 1969).

All of the most common varieties of rice can be affected by the disease. In susceptible varieties and in certain areas and years, i.e., 1972, 1973 and 1974, the disease affected almost 100% of the rice plants. In 1976, it was calculated that about 46% of the plants of the cultivar Balilla in the Romentino area of northern Italy were infected naturally (Osler *et al.*, 1977). In three different rice areas of the provinces of Novara and Pavia, the average percentage of infected plants was calculated at 43% in 1976, 4% in 1977, 11% in 1978 and 12% in 1979.

Yield losses due to rice giallume are estimated to range from 5% to almost 100%, depending on the area, year and rice variety. Since rice cultivation in Italy covers 184,279 hectares, with an annual production of 10.2 million quintals of rice, the economic importance of a such a disease is evident.

Symptoms of the Disease

Symptoms that occur in RG-infected rice plants vary according to variety, age when infected and environmental and physiological conditions. High light intensity is necessary for symptom development; the strongest symptom expression is seen under greenhouse conditions. Low temperature is important for plant growth and, consequently, for expression of symptoms. The presence of nitrogen in the soil has also been found to stimulate symptom expression (Moletti and Osler, 1979).

The most characteristic symptoms are a yellow to orange leaf color, starting at the tips and the edges; yellowing of the main vein of the leaves; serrated leaf borders; stunting; reduced tillering; blasting of florets and small, erect leaves; necrosis of leaves following discoloration and, in the most serious cases, death of the plant (Baldacci *et al.*, 1970; Belli *et al.*, 1974). Internal symptoms include mytochondria and phloem degeneration, the presence of vesicles and the deposition of opaque material along the walls of phloem cells (Faoro *et al.*, 1978).

(continued)

Causal Agents, Variants and Vectors (Virus-Vector-Plant Relationships)

Because some symptoms resemble those of rice diseases caused by mycoplasma in East Asia (Ling, 1972), giallume was initially considered to be of mycoplasma etiology. However, an isometric virus was detected in infected rice plants as well as in the gut of the aphid vector *Rhopalosiphum padi* (Amici *et al.*, 1974; Belli *et al.*, 1974). The size (25 nm), shape, location and distribution of the virus particles, as well as ultrastructural changes induced in the host tissues, were similar to those described for barley yellow dwarf virus (BYDV) (Amici *et al.*, 1975; Faoro *et al.*, 1978; Faoro and Tornaghi, 1983; Gill and Chong, 1976).

Experimental transmissions conducted with different aphid species led to the consideration of RG as a disease caused by a virus related to BYDV (Osler *et al.*, 1974; Osler, 1980b; 1983). Positive reactions obtained by Rochow and Duffus (1981), using rice giallume virus (RGV), supplied by G. Belli, as an antigen against the antisera obtained by two isolates of BYDV (RPV and MAV), confirmed the hypothesis. Similarities in the ultrastructural alterations caused by RGV in oat and rice plants (Faoro *et al.*, 1978) to those induced by the RPV isolate of BYDV (Gill and Chong, 1976) was a further indication that the agent of rice giallume was a virus belonging to the *R. padi* vector-specific group of BYDV.

After the preliminary transmissions (Osler *et al.*, 1974) obtained with *R. padi* (Osler, *et al.*, 1974), it was found that RGV was also transmitted by *Sitobion avenae* and *Metopolophium dirhodum*; this meant that different virus strains might be present in rice fields (Osler, 1980b, 1984). The presence of an aphid-nonspecific isolate of a virus was discovered in rice plants on the basis of three series of 11 successive comparative transmissions conducted with these three aphid species, as well as with *R. maidis* (Osler *et al.*, 1984). The most efficient vector of RGV is *R. padi*, followed by *S. avenae* and *M. dirhodum*. *R. maidis* and *Sipha glyceriae* failed to transmit RGV (Osler and Longoni, 1975; Osler, 1984).

Transmission of RGV with *R. padi* is of the persistent type; infectivity can be retained for as long as the aphid lives. Ten days after an acquisition period, 50% of the infective aphids held at 20°C were found to be still infective. There is a measurable latent period in the aphid. The acquisition and inoculation threshold is from one to two hours and the transmission efficiency of young *R. padi* for RGV can reach 70% or more.

Using three different aphids species (*R. padi*, *S. avenae* and *M. dirhodum*) and an aphid-nonspecific RGV isolate (PAV type), it has been established that the length of the incubation period of RG in *Avena byzantina* K. varies from 9 to 23 days, according to such factors as cultivar, age of plants and environmental conditions. For the most efficient species, i.e., *R. padi*, the median incubation period (MIP) was two days shorter than that stated for

the other two aphid species (Osler *et al.*, 1984). No difference in MIP was found when different species of aphids were used for infecting the plants used as sources of inoculum.

The response of three rice cultivars having known differences in susceptibility to RGV, when experimentally inoculated with one, three or nine viruliferous *R. padi* per test plant, has been studied. The least susceptible cultivar, G. Marchetti, showed the longest incubation period and the most susceptible, Padano, the shortest. The MIP of RG was inversely proportional to the number of aphids used for the inoculation, further evidence for the dosage response hypothesis (Burnett and Gill, 1976; Boulton and Catherall, 1980; Osler and Moletti, 1982). In comparative inoculations with *R. padi* of 12 rice varieties having different susceptibilities to RGV and at various growth stages, it was possible to establish that early infections induce heavier damage and that, in young plants, the incubation period is shorter (Osler and Moletti, unpublished data).

Host Range and Epidemiology

Cultivated gramineae and weeds, naturally or experimentally infected, have been found to be hosts of the viral agent causing rice giallume; these include *Echinochloa crusgalli* L., *Holcus lanatus* L., *Panicum dichotomiflorum* Michx. and *Leersia oryzoides* Soland, species that do not appear as hosts for BYDV (Amici *et al.*, 1975; Stoner, 1976).

The first symptoms of RG appear in rice about 20 days after emergence of the plant from the water; later it spreads in patches that tend to enlarge, sometimes covering almost all of the rice field. Generally, this typical patchy appearance is correlated with the presence of the perennial weed *L. oryzoides* (Amici *et al.*, 1973; Osler *et al.*, 1977).

The only perennial grass which grows in rice fields is *L. oryzoides*; it is an important host and winter reservoir of the virus. Moreover, *L. oryzoides* is a host of *R. padi* and, in the spring, emerges from the water before the rice. Being attractive to the vector, it becomes a natural source of inoculum for the early spread of infection to rice (Osler *et al.*, 1980b). This grass has become more widespread in rice fields in the last 15 years and is considered a fundamental means by which RGV moves into rice from other gramineae. The annual cycle of the virus is from *L. oryzoides* to rice, with *R. padi* acting as the link (Osler, 1980a).

Field surveys conducted on the dynamics of the alate and apterous populations of *R. padi* (Vidano, 1969) have shown that the alate exules that infest rice plants at the critical initial stage do not play an important role in spreading the disease inside rice fields (Osler *et al.*, 1980; Osler, 1982). The low infectivity (about 0.5%) of the alate exules captured in rice fields and tested on rice plants (Osler *et al.*, 1980b) probably can be attributed to difficulties the insects have in adjusting to the rice host, as they are coming from different species of gramineae (Osler, 1980a; Osler *et al.*, 1980b). Apterous forms of *R. padi* are mainly responsible for spreading the disease within the rice fields.

Control of the Disease

Chemical control—Since 1973, it has been shown, under field conditons, that rice giallume can be controlled with insecticides (Belli *et al.*, 1975; Osler *et al.* 1973; 1977). Epidemiological information obtained on the dynamics of aphid populations and on the disease itself makes possible the choosing of the most suitable period for prophylactic applications of insecticides (Osler, 1982).

Weed control—The use of herbicides against the natural host plants of RVG, applied both within and around the rice fields, has shown that a reduction of disease incidence is associated with a reduction in weeds (Osler *et al.*, 1977). The control of *L. oryzoides*, by herbicides alone or by hand weeding, has reduced the spread of the disease in rice fields to a great extent (Finassi and Noris, 1978; Moletti, 1981).

Use of resistant cultivars—A collaborative program to evaluate the reaction of rice cultivars and lines to infections by RGV was started in 1974 by the Instituto di Patologia Vegetale of the University of Milan and the Ente Nazionale Risi of Milan. Initially, sreening techniques were developed (Osler and De Carolis, 1976). Then, most of the cultivated Italian rice cultivars and pure lines that had been selected for improved agronomic and fungus-resistance traits were tested for resistance. Five cultivars and five lines showed high resistance to RGV infections (Moletti and Osler, 1978; Moletti *et al.*, 1979); four of them showed medium resistance to blast. Field experiments confirmed their resistance. An additional cultivar, Strella (Russo, personal communication), also was found to have good resistance in the field (Osler *et al.*, 1980a). Some susceptible cultivars showed considerable differences in field and greenhouse reactions (Moletti and Osler, 1978), as was also found by Rochow (1961).

Control by insect parasites—Several species of insect parasites of *R. padi* are known in Italy (Olmi, 1969). They can have a marked effect on aphid populations, although they appear after the secondary transmissions have already taken place. Therefore, their efficacy in controlling the disease is not evident during the same year in which the parasites are present; the effect is felt the following year, when only a few *R. padi* survive (Osler, 1982; Osler *et al.*, 1977).

In some areas, such as northeast Italy, it is possible to limit BYDV spead in barley fields through early sowing (Snidaro, 1980). Rice culture in Italy is at the thermal limit for its cultivation; therefore, it is not possible to advance or delay its sowing date. Moreover, in either case, the rice plants would not avoid *R. padi* colonization.

The best practical way to control rice giallume is to combine all the above factors into an integrated control plan to be executed over a large area. Insecticide treatment is advisable only when very susceptible cultivars are planted and in areas where the disease generally has a high incidence.

References

Amici, A., G. Belli, G. Corbetta and R. Osler. 1973. Ricerche sull'epidemiologia de giallume del riso. II. Indagini al microscopio elettronico su piante infestanti della risaia. Il Riso 22:111-118.

Amici, A., F. Faoro and R. Tornaghi. 1975. Subcellular location in different hosts of the virus causing the "giallume" disease of *Oryza sativa*. Il Riso 24:353-358.

Amici, A., R. Osler and G. Belli. 1974. An isometric virus associated with the "giallume" disease of *Oryza sativa*. Phytopathologische Zeitschrift 79:285-288.

Baldacci, E., A. Amici, G. Belli and G. Corbetta. 1970. Il giallume del riso: osservazioni e ricerche su sintomatologia, epidemiologia ed eziologia. Il Riso 19:3-9.

Batalla, J.A. 1969. La enfermedad del arroz llamado "Roja" o "Rocha." Arroz, 31.

Belli, G., A. Amici, G. Corbetta and R. Osler. 1974. The "giallume" disease of rice (*Oryza sativa* L.). Mikrobiologija 11:101-107.

Belli, G., G. Corbetta and R. Osler. 1975. Ricerche e osservazione sull'epidemiologia e sulle possibilitá di prevenzione del "giallume" del riso. Il Riso 4:359-363.

Boulton, R.E., and P.L. Catherall. 1980. The effect of increasing dosage of barley yellow dwarf virus on some resistant and susceptible barleys. Annals of Applied Biology 94:69-75.

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

Corbetta, G. 1967. La "nouva malattia" che colpisce il riso. Il Risicoltore 11:1-3.

Faoro, F., and R. Tornaghi. 1983. Subcellular location of a barley yellow dwarf virus strain in the intestinal epithelium of the aphid *Rhopalosiphum padi*. Abstract. XIII Italian Congress on Electron Microscopy. Pp. 155-156.

Faoro, F., A. Amici and R. Tornaghi. 1978. Cellular ultrastructural alterations as a means of characterizing the virus causing the "giallume" disease of rice. XI Italian Congress on Electron Microscopy. Abstract. Journal of Submicroscopic Cytology 10:126.

Finassi, A., and P. Noris. 1978. Attrezzatura per il diserbo della *Leersia oryzoides* (L.) durante la mietitrebbiatura. Il Riso 27:51-61.

Gill, C.C., and J. Chong. 1976. Differences in cellular ultrastructural alterations between variants of BYDV. Virology 75:33-47.

Ling, K.G. 1972. Rice Virus Diseases. The International Rice Research Institute, Los Baños, Philippines.

Moletti, M. 1981. Difesa fitosanitaria e diserbo nella risicoltura italiana: Giallume. Ente Nazionale Risi, Milano, Italia. 1-1a.

Moletti, M., and R. Osler. 1978. Determinazione della resistenza al "giallume" delle piu importanti varieta di riso italiane mediante inoculazioni sperimentali con l'afide *Rhopalosiphum padi*. Il Riso 1:33-40.

Moletti, M., and R. Osler. 1979. Effetto della concimazione minerale sulla suscetibilita del riso al virus del nanismo giallo dell'orzo, ceppo giallume del riso, inoculato artificialmente con l'afide *Rhopalosiphum padi* L. Il Riso 28:157-162.

Moletti, M., R. Osler and G. Baldi. 1979. Valutazione della resistenza al giallume mediante inoculazioni artificiali con l'afide *Rhopalosiphum padi* in linee di riso migliorate. Il Riso 1:53-61.

Olmi, M. 1969. Studi sulla entomofauna di risaia. III. Primo enfogago di *Sipha glyceriae* (Kaltenbach), il calcidoideo *Aphelinus asychis* Walker (*Hymenoptera Aphelinidae*). Bolletin Sociedad Entomologia Italiana 103(3-4): 47-51.

Osler, R. 1980a. Il giallume del riso: attuali conoscenze sul ciclo di infezione del virus, con particolare attenzione alle piante *Oryza sativa* e *Leersia oryzoides* e all'afiade *Rhopalosiphum padi*. Il Riso 29:217-221.

Osler, R. 1980b. Occurrence of *Sitobion avenae* and *Metopolophium dirhodum* in rice fields of northern Italy and transmission efficiency of the barley yellow dwarf virus strain causing the rice "giallume." *In* Proceedings, Third Conference on Virus Diseases of Graminae in Europe, Harpenden, UK. Pp. 113-118.

Osler, R. 1982. Recenti acquisizioni epidemiologiche in relazione al controllo del giallume del riso. Nota II. Atti Giornate Fitopatologiche, San Remo, 1982. Supplement. Pp. 53-60.

Osler, R. 1983. Indagine sui ceppi del virus del nanismo giallo dell'orzo (BYDV) condotta mediante prove di trasmissione con quattro specie di adidi vettori. Rivista di Patologia Vegetale, S. IV, 19:37-45.

Osler, R. 1984. Caratterizzazione biologica di un ceppo del nanismo giallo dell'orzo (BYDV) agente causale del giallume del riso. Rivista di Patologia Vegetale 19 (in press).

Osler, R., and C. De Carolis. 1976. Prove preliminari di determinazione della resistenza al "giallume" del riso di varieta italiane di riso mediante infezione artificiale. Il Riso 1:59-63.

Osler, R., and C.E. Longoni. 1975. Mancata trasmissione del giallume del riso mediante l'afide *Sipha glyceriae*. Il Riso 25:73-76.

Osler, R., and M. Moletti. 1982. Response of four cultivars of *Oryza sativa* inoculated with different numbers of the aphid *Rhopalosiphum padi* infected with the rice "giallume" strain of barley yellow dwarf virus. Phytopathologische Zeitschrift 105:51-60.

Osler, R., A. Amici and G. Belli. 1974. Transmission of rice 'giallume' by an aphid Rhopalosiphum padi. Rivista di Patologia Vegetale, S. IV, 10:3-10.

Osler, R., A. Amici and G. Belli. 1977. Possible ways of controlling rice "giallume." Annals of Phytopathology 9:347-351.

Osler, R., A. Amici, G. Belli and G. Corbetta. 1973. Ricerche sulla epidemiologia del giallume del riso. I. Dimostrazione della presenza di vettori alati. Il Riso 2:105-110.

Osler, R., A. Amici, G. Belli and M. Moletti. 1980a. Recenti acquisizioni epidemiologiche in relazione al controllo del giallume del riso. Atti Giornate Fitopatologiche 1980, Siusi (BZ). Supplement 2:41-49.

Osler, R., A. Amici and C.E. Longoni. 1980b. *Leersia oryzoides*, a natural host and winter reservoir of the rice "giallume" strain of barley yellow dwarf virus. Phytopathologische Zeitschrift 97:242-251.

Osler, R., C.E. Longoni and S. Prati. 1984. Determinazione del periodo di incubazione del giallume del riso (RG), una malattia indotta dal virus del nanismo giallo dell'orzo (BYDV). Rivista di Patologia Vegetale (in press).

Rochow, W.F. 1961. The barley yellow dwarf virus disease of small grains. Advances in Agronomy 13:217-248.

Rochow, W.F., and J.E. Duffus. 1981. Luteoviruses and yellows disease. *In* Handbook of Plant Virus Infections and Comparative Diagnosis, E. Kurstak, ed. Elsevier/North Holland, Amsterdam. Pp. 147-170.

Snidaro, M. 1980. Virosi del nanismo giallo dell'orzo. L'Informacion Agrario 36:11937-11941.

Stoner, W.N. 1976. Reaction of some grasses to barley yellow dwarf virus. Plant Disease Reporter 60:593-596.

Vidano, C. 1959. Sull'anolociclo del Rhopalosiphum padi. Memorias, Sociedad de Entomologia Italiana 38:188-196.

The Barley Yellow Dwarf Research Program at CIMMYT

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Barley yellow dwarf (BYD) is a ubiquitous disease. The symptoms of BYD in bread wheat, durum wheat and triticale are, firstly, not particularly apparent and, secondly, not well-recognized, even by experienced cereal workers. It has only recently become apparent how widespread this disease is. Unfortunately, a great deal of the diagnostic ability for BYD is currently found in the developed world.

BYD could be considered a second generation or second level disease. Severe rust, septoria or scald epidemics can totally mask diseases such as BYD and, historically, have probably done so. However, once resistance has been developed to those diseases, the effects of the second generation diseases become apparent. BYD, like the rusts, is not a problem every year; it has a third biological variable, the aphid vector, and conditions that influence the aphid vectors influence the spread and epidemiology of BYD.

Germplasm development and distribution is the essential task of CIMMYT and, after the 1980 Barley Yellow Dwarf Workshop sponsored by CIMMYT at the El Batan headquarters in Mexico, a proposal was prepared for the development of a BYD project. The objectives of the project, in general, were to:

- Conduct epidemiological studies on BYD, looking in particular at the cropping systems used for wheat (both bread and durum), barley and triticale;
- Identify virus strains;
- Identify the species of aphids that are the vectors of BYD;
- Identify BYD-resistant germplasm by screening cereal collections. Included would be hybridization of resistant lines and distribution to areas with particular BYD problems. The whole system would cycle with site-specific evaluations being taken into account in the hybridization;
- Evaluate cultivars and elite breeding lines for resistance to BYD, assuring free access to the material for cooperators and others with interest in the program;
- Determine the genetic basis of BYD resistance;
- Run site-specific evaluations on material selected for BYD resistance;
- Train researchers in BYD methodology, and
- Set up workshops and ensure the dissemination of information through publications.

Since the 1980 workshop, CIMMYT, and particularly the bread wheat and barley programs, have noted lines reported to be resistant to BYD by cooperators, and have utilized Toluca, with its natural epidemics of BYD, as a winter site for selecting BYD-resistant material.

The winter cycle testing site at Toluca initially worked well for bread wheat but less well for barleys; after the distribution of the first nursery it became apparant that the site did not permit complete differentiation between winter hardiness and BYD resistance. Currently, there is an additional problem with the site; infestation with the aphid *Diuraphis noxia* was so severe in the winter of 1983 that the symptoms it caused completely masked BYD symptoms on both wheat and barley. It is not known whether Toluca will be usable as a winter BYD screening site in the future.

Lines selected in Toluca in 1982 were utilized to form initial BYD nurseries and, through the cooperator network, they were sent to specific sites for preliminary evaluation. Although it would be extremely helpful if all cooperators could inoculate their plots with viruliferous aphids in the way described by A. Comeau in these proceedings, most cooperators have to depend on natural infestations of aphids, making epidemics inconsistent from year to year. It is felt that, if cooperators would seed their plots as if they were spaced plants, the results obtained under natural epidemics could be greatly enhanced. It may be possible for some cooperators to increase infection by providing borders of BYD-susceptible cereals to act as reservoirs for aphids and virus for the inoculation of nurseries in the way described by C.O. Qualset in these proceedings. Most CIMMYT nurseries, with the exception of yield trials, are sown as a single plot. Again, it is felt that the reliability of results obtained from a BYD nursery would be greatly enhanced by replication.

The preliminary BYD bread wheat nursery was obtained for initial screening at Toluca. It contained 89 entries, including two check lines with every 20 entries, and was sent to six selected sites. So far, usable data has been received from only two screening sites, New Zealand (J.M. McEwan) and Canada (A. Comeau). Table 1 lists the scores from those entries that were checked as being good in Canada and that had a rating of 5 and below in New Zealand; the mean score of the checks is also given. It should be stresed that all of these entries appeared to have a high level of resistance in the initial screening in Toluca. It can be seen that there is a large variation in resistance over sites. However, some entries show good resistance at both sites, e.g., entries 47, 54, 63 and 71.

BYD epidemics are natural at the Palmerston North site in New Zealand and, therefore, are not nearly as severe as those created at the Quebec screening site.

Currently, all wheat nursery reports received by CIMMYT are surveyed, and any entry that is rated BYD-resistant from any site will be considered for inclusion in the next BYD bread wheat nursery to be distributed in 1985-86.

The barley lines for inclusion in the initial BYD barley nursery were also selected in Toluca. That preliminary nursery consisted of 169 entries (129 spring and 40 winter barleys) and was distributed in 1982. To date, only three reports have been received from cooperators, again from Canada (A. Comeau) and New Zealand (J.M. McEwan), as well as from Spain (J. Hernando Velasco). Table 2 lists the spring materials that exhibit resistance at any of the sites. There are a number of entries that exhibit good resistance at all sites, but it is apparent that there are still many notable reversals; a line that is resistant at one site often appears susceptible at another. This again points out the neccessity for multisite testing.

Table 1. BYD Scores for Entries in the Preliminary BYD Bread Wheat Nursery, from Cooperators at Two Sites[a/]

Entry no.	Cross	Saint-Foy Quebec, Canada (A. Comeau)	Palmerston North, New Zealand [b/] (J.M. McEwan)
1	R37-GHL121 x KAL-BB	7.7	5
2	FLN-ACC x ANA	6.9	3
5	KEA "S"	8.0	5
6	PRL "S"	7.5	5
8	PRL "S"	7.4	3
9	PRL "S"	7.6	4
17	[JUP(7C-PATO(B)/LR64-INIA x INIA-BB)]ANA	7.0[c/]	6
18	GH "S"	7.0[c/]	7
19	TI RESEL-HUAC "S"	7.6	5
22	MAYA-NAC	7.7	4
23	JUP-BJY "S"	7.7	5
24	JUP-BYJ "S"	7.7	3
25	BJY "S"-JUP	7.5	5
27	NKT "S"	7.7	4
28	NKT "S"	7.6	4
29	NKT "S"	7.5	5
30	NKT "S"	7.7	3
31	DGA-BJY "S"	8.2	3
32	DGA-BJY "S"	7.5	3
33	DGA-BJY "S"	7.6	5
35	DGA-BJY "S"	7.6	3
36	DGA-BJY "S"	7.6	3
37	[58.57 (MAYA "S"-CGN/CC-INIA x CAL)	7.5	5
38	YACO "S"7.7		5
39	YACO "S"	7.7	5
43	YACO "S"	7.8	4
44	YD "S"/TOB-ERA x TOB-CNO67	7.6	5
45	BAYA "S"	7.6	5
47	TOB-CNO67 x TOB-ERA/NAC	7.4[c/]	4
48	CNO67-MFD x MON "S"	7.4	4
51	F35.70-MO x NAC	8.0	4
52	F35.70-MO x NAC	8.2	5
54	BBY2-BJY "S" x JUP	7.5[c/]	4
55	JUP-EMU "S" x GJO "S"	7.7	4
56	JUP-EMU "S" x GJO "S"	7.3	4
57	JUP-EMU "S" x GJO "S"	7.6	4
58	JUP-EMU "S" x GJO "S"	7.0	4
63	DODO "S"	7.4[c/]	4
65	COQ "S"-PVN "S"	7.6	5
67	PF70354-MUS "S"	7.6	4
68	PF70354-MUS "S"	7.7	5
69	CAR853-COC x VEE "S"	7.6	4
70	BAGE-HORK "S" x ALDAN "S"	7.6	5
71	ERA-MN69146 x PVN "S"	6.6[c/]	5
73	DOVE "S"-CNT7 [ALD "S" (BB-GLL x CN067-7C/KVZ-TI)]	7.5	5
75	P.AR-H567.71	6.9	4
76	GOF "S"-ALD "S"	7.8	5
77	S SEAFOAM x SOTY-JN(3)	7.0	5
79	B7455	7.2	5
87	IAS63-ALD "S" x GTO-LV	7.6	5
88	IAS63-ALD "S" x GTO-LV	7.8	5
89	IAS63-ALD "S" x GTO-LV	7.8	5
Checks	Anza	7.5	4
	Nacozari 76	8.0	4.75

[a/] Scoring system 0 to 9 (0 fully resistant, 9 fully susceptible) as described by C.O. Qualset, these proceedings

[b/] All entries scoring 5 and below selected as having good resistance in New Zealand

[c/] Entries selected as having good resistance in Canada

Table 2. BYD Scores for Entries in the Initial BYD Barley Nursery, from Cooperators at Three Sites[a/]

Entry no.	Cross	Saint-Foy, Quebec, Canada (A. Comeau)	Palmerston North, New Zealand (J.M. McEwan)	Madrid, Spain (J. Hernando)
1	PRO	5.8	2[b/]	3
2	CQ-UN6, UN3	5.0[b/]	7	3
3	HOR728	5.3[b/]	5	5
9	COMA "S"	6.5	7	1[b/]
11	NABO "S"	6.7	7	1[b/]
12	API-CM67 x ORE	6.0[b/]	6	1
14	CACO "S"	5.5[b/]	2[b/]	1
16	HD-ATHS x PYO-DL 70/APM-5106	6.5[b/]	8	3
29	SUTTER	6.5[b/]	0[b/]	5
31	79AN-MN	6.5[b/]	8	5
34	BEN-4D	6.0[b/]	2[b/]	3
35	CEDRO "S"	9.0	2[b/]	0
36	CHINO "S"	5.0[b/]	3	0
37	BREA "S"-SUTTER x F_3 BULK HIP	6.5	1[b/]	1
43	SOT-ABN x GAS-ORE "S"	5.5[b/]	4	1
44	POCHE "S"	6.7	2[b/]	3
47	ABN	6.7	0[b/]	3
48	NIGRINUDUM	7.3	2[b/]	0
50	PI382406	6.7	0[b/]	1
51	GOB "S"	8.7	3	0
52	PYO-RM1508 x DOR DIST/EMIR	7.7	4	3[b/]
53	DEIR ALLA 105	9.3	3[b/]	3
58	DRAGO "S"	6.5[b/]	9	7
61	ASSE-NACKTA x VILLA ROBLEDO/PYO	5.0[b/]	1[b/]	0
63	BFL "S"	6.0[b/]	5	0
64	BREA "S" x MCU377. 24D-BEN/NPL x BCO. MR-GVA	6.5[b/]	3	1
67	OJL "S"	6.5[b/]	2[b/]	0
68	OJL "S"	6.5[b/]	1[b/]	1[b/]
70	LIMA PERU581 x BCO. MR-AS46/BREA "S"-DL70	6.5[b/]	7	0
79	LIGNEE640	7.0[b/]	1[b/]	0
80	HOBO "S"	7.5	6	0[b/]
85	P.STO "S"	8.0	0[b/]	0
88	BGS-10876.1	6.5[b/]	7	3
95	(BURK^2-APRO x 11016.2/BREA "S") G134-APM x NACKTA	7.0	8	5[b/]
97	BUSSELL	7.3	6	1[b/]
102	U.SASK HARVEY 143-BAL16/BCO.MR-AVT x CEL	6.7	1[b/]	7
103	U.SASK HARVEY 144-BAHTIM10 x CEL-CI3909.2	5.7	1[b/]	7
105	11012.2-MZQ x MZQ-BEN	7.0	8	3[b/]
106	CI424 x G134- APM/BDGC-GAS x APM-HC1905	6.3	7	0[b/]
111	(API-CM67 x APM-II965/API-CM67 x II266.L2966.69) BEN	6.7	3[b/]	3
113	API-CM67 x DL71/ROW906.73	5.7[b/]	7	3
115	ALAMO "S"	6.0[b/]	4	3
118	ORE"S" x API-CM67	5.0[b/]	3	3
125	ORE"S" x INDIAN DWARF-CM67	6.5	1[b/]	3
127	API-CM67 x AGER	6.7[b/]	1[b/]	3
128	APM-GVA x POR-U.SASK1800/API-CM67 x DS-APRO	6.5[b/]	4	5

a/ Scoring system 0 to 9 (0 fully resistant, 9 fully susceptible) as described by C.O. Qualset, these proceedings

b/ Entries selected by cooperators as having good resistance

A second BYD barley nursery has now been distributed. It contains 43 spring barleys, including California Mariout and Atlas 57 as susceptible checks and CM 67 and Atlas 68 as resistant checks; results are not expected from this nursery until late 1984 or early 1985. The lines included were selected from the first BYD nursery on the basis of data from reports received from cooperators on other CIMMYT barley nurseries. Spring x winter barley crosses are now being made in Mexico in an attempt to transfer the BYD resistance in winter material (D.T. Sechler, these proceedings) to spring material.

Strong links to programs that are screening germplasm are being developed. Currently, there is more interest in materials that are relatively well-adapted, since they are readily usable; wild relatives, however, will be used if they supply good resistances. Screening of materials for BYD resistance, will be done at CIMMYT, providing coordination for groups doing germplasm screening around the world. CIMMYT is in a good position to act as a clearing house for obtaining, adding to and distributing material for further BYD screening.

From preliminary results, it appears that screening at different sites is important as there appears to be much between-site variation in resistance. Resistance from different sites should be intercrossed and subsequently distributed for further testing. Current data is preliminary and further testing is required at a greater range of sites before more reliable data can be expected. The real strength of the CIMMYT BYD program will depend, to a great extent, on the feedback from its cooperators.

The Barley Yellow Dwarf Research Program in Missouri

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Barley yellow dwarf (BYD) first attracted major attention in Missouri in 1959. Until then, except for 1949 when a heavy red leaf infection was observed on oats in southwest Missouri, damage of this nature had apparently been spasmodic and scattered. In 1959, the loss in oat yield was estimated at 37%, with estimates ranging from 2 to 70% in different areas of the state (Sechler *et al.*, 1959). Since 1959, major BYD epidemics have occurred in 1964, 1967, 1974, 1976 and 1978; damage, however is evident every year.

Epidemics of BYD have not been confined to Missouri. Murphy (1959) reported BYD to be the most destructive disease affecting oats throughout the USA in 1959. He stated that the epiphytotics of BYD in earlier years, such as those of 1907 and 1948, doubtless resulted in greater total loss to the national oat crop than that of 1959.

While various reports indicate that BYD has been present for many years, it has been recognized as a virus disease of cereals only since 1951 when it was identified by Oswald and Houston. Since then, much research has been concentrated on the problem.

Symptoms

BYD has been shown to affect several agronomic traits of small grains in Missouri. Sechler *et al.* (1959) obtained highly significant negative correlations for leaf damage and yield in evaluations of 97 oat strains that varied in susceptibility to BYD. Weerapat *et al.* (1974) found a high positive correlation for plant height, panicle number and grain yield in genetic studies of progenies from crosses among five cultivars that differed in barley yellow dwarf virus (BYDV) resistance. A high negative correlation was obtained for leaf discoloration versus the other characters. Percent leaf discoloration, variability in height of tillers and blasting of the spikelets are currently used in the field as visual indicators to rate oat lines for BYDV tolerance. The stage of plant growth at the time of BYDV infection affects symptom expression. Seedling plants are more severely damaged than plants of more advanced maturity.

An early symptom of BYD on the barley plant is the presence in the older leaves of a golden yellow color starting at the tip, progressing along the margins and gradually enveloping the entire leaf (Poehlman *et al.*, 1982). Infections of young plants of susceptible strains may result in severely stunted or dwarfed plants which tiller profusely, yet produce few seed-bearing spikes. Later infections may result in reduced height and lower than normal yield, but stunting does not occur. Root systems of fall-infected plants are reduced in size, making the plants more susceptible to drought or winter injury.

In wheat, BYDV symptom expression is less vivid. However, lines may be rated for susceptibility on the basis of leaf discoloration. As with barley, discoloration starts at the leaf tip, but varies among susceptible cultivars from yellow to red or purple. Fall infections result in more extensive leaf discoloration than spring infections, as well as more reduction in plant height and root development.

Vectors

In collections of aphids colonizing fields of small grains near Columbia, Missouri, both in the fall and spring from 1977 to 1980, Grafton *et al.* (1982a) found *Rhopalosiphum padi*, *R. maidis* and *Schizaphis graminum*. Aphids collected from 208 of 210 of the colonies transmitted a virus that produced typical BYD symptoms on Grundy oat seedlings. An additional species, *R. rufiabdominalis*, was identified on barley in the fall of 1982 by Bourne (unpublished data).

Alternate Host Plants

Since small grains are not grown during the summer months (July to September), alternate host species are important if volunteer small grain plants are not present. Many species have been shown to host BYDV (Bruehl, 1961). Since tall fescue (*Festuca arundinacea*) is the major pasture grass in Missouri, it is potentially the most prevalent natural reservoir. Grafton *et al.* (1982a) found that 81 of 136 symptomless tall fescue plants collected along roadbanks from 90 Missouri counties were infected with a virus that was transmitted by *R. padi* and produced symptoms typical of infection by BYDV on Grundy oat seedlings. Although tall fescue normally shows no BYD symptoms in Missouri, Weerapat *et al.* (1972) showed that, under certain environmental conditions, Kentucky 31 tall fescue will express symptoms of leaf yellowing when seedlings are infested by English grain aphids carrying the BYDV isolate Champaign 6.

Effects of BYDV

In a controlled greenhouse experiment with wheat, Renkoski (1978) showed that the feeding of nonviruliferous aphids was associated with slightly reduced tillering and grain yield. The feeding of aphids carrying BYDV significantly reduced tillering as well as grain yield. When the aphids carried the virus, the number of kernels per spike was significantly reduced (sterility increased), as was the 100-kernel weight. Increased variability in plant height was also associated with the disease. Gellner and Sechler (1982), looking at BYDV inoculation techniques in oats, found that prolonged feeding of viruliferous aphids and increased aphid populations were associated with increased BYD symptom expression in a BYD-tolerant oat genotype.

Grafton *et al.* (1982b) conducted field experiments in which cages were placed around plantings to either confine or exclude vectors. They found that BYDV infections reduced winter survival, plant height, the number of spike-bearing tillers, total dry weight, grain yield and seed size in winter barley. These reductions were related to the amount of BYDV injury in the eight lines observed. In Post, the entry with the least BYDV injury, none of the traits were reduced significantly while, in severely injured Harrison and Durra, all traits were severely reduced by the disease. The data confirm that fall infection by BYDV predisposes plants to winter injury, stunting and reduced tillering, seed size and grain yield.

To observe the effect of macro-environment on symptom expression in four oat cultivars differing in resistance to BYDV, both uninoculated and BYDV-infected plants were transplanted and covered with mesh screened cages at three diverse field locations in Missouri (Gellner, 1982). Since the three-way interaction of location x cultivar x virus was not significant, it appeared that the environment effected the disease reaction of each cultivar in a similar manner.

Gellner (1982), in a path-coefficient analysis, found that the major direct effects on yield from BYDV-inoculated oat plants were from either tiller number or numbers of spikelets per tiller. Number of seeds per spikelet and weight per seed were less affected.

Breeding for Resistance to BYDV

The inheritance of BYDV resistance in oats was studied by Brown and Poehlman (1962). Utilizing lines which had shown varying levels of tolerance to BYDV in the Missouri environment, they found the inheritance of resistance to BYDV to be quantitative. Heritability estimates ranged from 23% for the susceptible x susceptible cross to 51% for the susceptible x resistant cross.

From crosses among five oat lines differing in resistance to BYDV, Weerapat (1974) isolated lines superior to the best parent in BYDV resistance and grain yield. The superior combining ability of Pettis in the study indicated that cultivars comparable in BYDV resistance may differ in their ability to transmit resistance to their progenies. From one of the crosses, Pettis (resistant to BYD) x Florida 500 (intermediate in resistance), the cultivar Bates was selected (Sechler and Poehlman, 1978).

In a two-generation analysis experiment, the inheritance of BYDV resistance in oats, manifested by plant height, tiller number, seed yield and percent leaf reddening, was determined to be complex since significant epistasis was present (Gellner, 1982).

In the small grain breeding program in Missouri, plant selections in segregating populations are made from spaced plants grown under normal field conditions and where BYDV is relatively prevalent. Concentrated aphid feeding on spaced plants results in more severe BYD symptoms than those observed in normal seedings. This technique provides a situation in which more BYD-tolerant lines can be identified. The barley cultivar Perry (Poehlman and Sechler, 1979), a cultivar with relatively good BYDV resistance, was selected from a segregating population in this manner, as was the wheat cultivar Hart (Sechler *et al.*, 1977).

Efforts are underway to identify lines with the *Yd2* gene for BYDV resistance in segregates of crosses of the Ethiopian spring barley, CI 14088, to the Perry and Harrison cultivars of winter barley. Since BYDV tolerance appears to be quantitatively inherited both in oats and wheat, a modified recurrent selection program is underway to accumulate genes for nonspecific resistance.

References

Brown, G.E., and J. Poehlman. 1962. Heritability of resistance to barley yellow dwarf virus in oats. Crop Science 2:259-262.

Bruehl, G.W. 1961. Barley yellow dwarf, a virus disease of cereals and grasses. Monograph no. 1. The American Phytopathological Society.

Gellner, J.L. 1982. Studies of barley yellow dwarf disease in oats. PhD Dissertation. University of Missouri, Columbia, Missouri, USA.

Gellner, J.L., and D.T. Sechler. 1982. Dosage effect in barley yellow dwarf diseased oats. Oat Newsletter 32:61-63.

Grafton, K.F., J.M. Poehlman, O.P. Sehgal and Dale Sechler. 1982a. Tall fescue as a natural host and aphid vectors of barley yellow virus in Missouri. Plant Disease 66:318-320.

Grafton, K.F., J.M. Poehlman, D.T. Sechler and O.P. Sehgal. 1982b. The effect of barley yellow dwarf virus infection on winter survival and other agronomic traits in barley. Crop Science 22:596-600.

Murphy, H.C. 1959. The epidemic of barley yellow dwarf on oats in 1959. Plant Disease Reporter Supplement 262:316.

Oswald, J.W., and H.R. Houston. 1951. A new virus disease of cereals, transmissible by aphids. Plant Disease Reporter 35:471-475.

Poehlman, J.M., and Dale T. Sechler. 1979. Registration of Perry barley. Crop Science 19:742.

Poehlman, J.M., Dale T. Sechler and K.F. Grafton. 1982. Barley yellow dwarf virus (BYDV): breeding for resistance in winter barley. *In* Proceedings, Fourth International Barley Genetics Symposium, Edinburg, Scotland, 1981.

Renkoski, M.A. 1978. A study of floret sterility in three winter wheat cultivars. M.S. Thesis. University of Missouri, Columbia, Missouri, USA.

Sechler, Dale, and J.M. Poehlman. 1978. Registration of Bates oats. Crop Science 18:525.

Sechler, Dale, J.M. Poehlman and R.P. Pfiefer. 1977. Registration of Hart wheat. Crop Science 18:980.

Sechler, Dale, J.M. Poehlman, M.D. Whitehead and O.H. Calvert. 1959. The barley yellow dwarf virus-bacterial blight complex on oats in Missouri in 1959. Plant Disease Reporter Supplement 262:351-353.

Weerapat, P., D.T. Sechler and J.M. Poehlman. 1972. Host study and symptom expression of barley yellow dwarf virus in tall fescue (*Festuca arundinacea*). Plant Disease Reporter 56:167-168.

Weerapat, P., D.T. Sechler and J.M. Poehlman. 1974. Barley yellow dwarf virus resistance in crosses with Pettis oats. Crop Science 14:218-220.

The Barley Yellow Dwarf Research Program in the USA

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Losses caused by the aphid transmitted disease, barley yellow dwarf (BYD), in wheat, barley, oats and other small grains are viewed with considerable concern in the USA. Five years ago, a preliminary plan in the Agricultural Research Service (ARS), United States Department of Agriculture, was drafted to establish a screening program to serve state experiment stations and ARS wheat, barley and oat breeding programs. The plan was to use a minimum of two locations so that both winter and spring genotypes could be field tested with specific isolates of the virus, using controlled inoculation procedures. Unfortunately, ARS funds were not obtained and, therefore, there is little likelihood that such a barley yellow dwarf virus (BYDV) screening program will materialize. Service-type programs are not high priority items in the new ARS strategic and implementation program plans.

In a very limited but very important way, H. Jedlinski and C.M. Brown have provided a cooperative ARS-University of Illinois screening service for other programs working toward resistance to BYDV in spring oats and winter wheat. At the same time, they have conducted their own joint research program on pathology and breeding for resistance to BYDV. They have had truly remarkable success with spring oats, and are now making some progress toward the development of winter wheats with tolerance to BYDV.

D.T. Sechler and J.M. Poehlman have selected for BYDV tolerance in wheat, oats and barley at the University of Missouri, under field conditions with natural infection. The virus persists in grass hosts which are widely distributed throughout the area.

At Purdue University, another cooperative ARS-University team is concentrating on various aspects of BYDV-related research. R.M. Lister and J.E. Foster are using the enzyme-linked immunosorbent assay (ELISA) test to measure antigens to BYDV in infected plants, with the hope that this procedure can provide a rapid and effective screening method for tolerance to BYDV. They are also using this procedure to study the virus in corn and grass hosts. H.W. Ohm and G.E. Shaner are working toward the development of resistant varieties of oats and soft red winter wheat.

Breeding progress for tolerance to BYDV has already been made in the soft red winter wheat class. Cultivars like Caldwell from the Purdue-ARS program, Roland from the University of Illinois-ARS program and Hart from the University of Missouri program have decidely more tolerance to BYDV than the older Arthur types.

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At the University of California at Davis, C.O. Qualset, C.W. Schaller and their colleagues conduct wheat and barley breeding programs, respectively, for resistance to BYDV. They have screened part of the National Small Grains Collection for reaction to BYDV and will be involved in future evaluation for resistance from spring and fall plantings in field plots.

R.W. Kieckhefer at the ARS Northern Grain Insects Laboratory, Brookings, South Dakota, is studying the effect of other insect predators on the regulation of aphid populations under natural conditions. The BYDV virus persists in numerous grass reservoirs from which aphids transmit the virus to growing cereal crops.

W.F. Rochow has conducted basic research in a cooperative ARS-Cornell University research program for a number of years. His primary objective is to provide information on virus-vector specificity, variation that occurs within the virus, the vector and the host plant, and the role specificity plays in the spread of the virus in nature.

In the state of Washington, K.S. Pike and S.D. Wyatt are monitoring transmission of BYDV in a cycle involving both winter and spring wheat, grass hosts, irrigated corn, and wheat grown as a cover crop during what was previously a "green-free" period. They are involved with the identification of sources of the virus and vectors and how BYDV is spread to winter wheat. A similar program in Idaho is conducted by R.L. Forster and G.W. Bishop.

In a special integrated pest management (IPM) proposal developed for the Western Regional Coordinating Committee (WRCC-34), the small grains subcommittee selected BYDV as the most important pest complex needing research attention in the 11 participating western states. Although anticipated funding did not materialize, the plan still includes BYDV research as the top priority need for small grains.

T.W. Carroll and colleagues at Montana State University surveyed aphid vectors and have determined that various strains of the virus occur in Montana where the leading varieties of winter wheat are susceptible to BYDV. Most damage occurs in early planted winter wheat (planted in August and the first part of September). Late planting (after the tenth of September or the first hard freeze) is emphasized as an effective management procedure for control of BYDV.

R.G. Timian of ARS at North Dakota State University works with barley, oat and wheat breeders toward a better understanding of the epidemiology of BYD and in the development of tolerant varieties. N.D. Williams and L.R. Joppa are involved in testing a number of *Triticum* species for reaction to BYDV under controlled inoculation with viruliferous aphids in the field.

The US wheat production area most affected by BYDV is the Midwest, with most losses occurring in Illinois, Missouri and Indiana. Severity of the disease seems to be increasing in the Plains States or, perhaps, losses from BYD were formerly attributed to other production problems.

Barley yellow dwarf is on the increase in the Southeast where the wheat area has increased dramatically during the past two to three years. There, earlier maturing wheat varieties with better straw strength and more disease resistance make possible double cropping with soybeans. More wheat acreage in the Southeast, plus the fact that BYDV transmitting aphids can be active the year around, translates into more potential loss from the disease.

Barley yellow dwarf is also on the increase in the Pacific Northwest, primarily because of increased irrigation and changes in cropping practices that favor the aphid vectors of the virus. Wheat is grown during the entire year in large irrigation areas in the Columbia Basin of Washington and Oregon. It is often seeded as a cover crop following potatoes in July or August, providing the aphids with an ideal host during a time of the year that is usually critical for their survival. Significant amounts of corn are produced in the area, and it also serves as a very effective host for aphids during the same period. Early fall planting of wheat (August and early September) and late planting of spring wheat (late May and June) makes these crops especially vulnerable to BYD in the Pacific Northwest.

In California, BYDV has been important for many years, both in wheat and in barley. Areas planted to wheat have increased markedly during the last two to three years, so the extent of the BYD problem has similarly increased.

The 1983 US farm program, known as payment in kind (PIK), requires that acres taken out of wheat production be a part of some conservation-type program. In many cases, farmers have planted winter wheat in the spring as a cover crop or have used some other small grain to serve as a deterrant to soil erosion; grain cannot be harvested from those acres. The net result is green growth, including weeds, which harbors aphids and other insects and diseases; this problem has been encountered nationwide. Several reports indicate an increase in BYDV, indirectly ascribable to the PIK program.

Symptoms of BYD are much less noticeable in wheat than in oats or barley. It is likely that the US wheat farmer suffers considerable loss each year from this often insidious virus disease. Since symptoms are generally subtle, BYD in wheat is often mistaken for nitrogen deficiency, effects of drought or even root or crown rot infection. When symptoms are more evident, infected wheat plants are stunted to varying degrees, they have a generally unhealthy appearance with yellowish leaves and yield is greatly reduced.

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Members of the US National Wheat Improvement Committee (NWIC), an informal committee made up of federal, state and private industry wheat research scientists, discussed the need for expanded research on BYDV in 1980 and, at their annual meeting that year, passed a resolution emphasizing that need. Similar resolutions were again passed in 1981, 1982 and at the 1983 meeting just last month. These resolutions have been forwarded to ARS administrators, to State Experiment Station Directors, Wheat Commissions and Wheat Growers Associations and to the National Association of Wheat Growers.

A similar resolution was drawn up and distributed by the National Barley Improvement Committee in 1982. In addition, some members of the Barley Committee carried the message personally to ARS administrators and to selected Senators and Congressmen.

This latter approach had been used earlier by members of the Oat Improvement Council who, each year for the past five years, have appeared in Washington before appropriate Senators and Congressmen and the Agriculture Appropriation Subcommittees of the Senate and House of Representatives, as well as before ARS administrators. These wheat, barley and oat research committees have been successful in obtaining additional funds in support of germplasm programs but, so far, have not seen positive results for BYD research.

A major thrust in the National Small Grains Collection program is the evaluation of all accessions for a series of descriptors which wheat research scientists have declared as high priority needs. Among the disease and insect descriptors, reaction to BYDV ranks high. Plans called for the first evaluation of winter wheat accessions for BYDV tolerance to take place during the 1984 season, but the tests have had to be postponed for at least one year. Approximately 1,000 spring oats have been evaluated during 1983, and more will be tested in 1984.

The Barley Yellow Dwarf Research Program in the People's Republic of China

Zhou Guang-he, Zhang Xing-cai, Guian You-ting, Zhang Shu-xiang, Cheng Zhuo-min and Chen Guan, Chinese Academy of Agricultural Sciences, People's Republic of China

For determining how aphid vectors of barley yellow dwarf (BYD) oversummer and overwinter in China, field observations and greenhouse tests have been made in the People's Republic over the past five years.

Field monitoring in summer seasons in Xin-Xiang, Henan Province, have shown that vectors such as *Metopolophium dirhodum* and *Rhopalosiphum maidis* oversummer easily. Although *Schizaphis graminum* and *Sitobion avenae* are very susceptible to high temperatures, they can, nevertheless, be found in shady places. Aphid numbers increase with the decrease in temperature in September. In the autumn of 1980, in Linfen, Shanxi Province, plants were inoculated with alates of *S. graminum*, *S. avenae* and *R. padi* collected from grasses and volunteer wheat. Some of the aphids were found to be viruliferous and, a few weeks later, typical BYD symptoms were observed on the volunteer wheat.

In the winter wheat area, reservoirs of BYDV were also found; there the virus overwinters in wheat seedlings and its vectors. The spread of the virus depends on vector movement. In the spring, the activity of aphids which have overwintered as adults or nymphs on winter wheat or grasses increases and so causes virus spread. In contrast, in the Ningxia autonomous region, eggs of *S. graminum* and *M. avenae* have rarely been found in spring wheat and oats, and there are no overwintering perennial grasses to act as virus hosts.

In years of severe BYD outbreaks, there appears to be a relationship between winter and spring wheat growing areas. After heavy BYD infection in the winter wheat areas, spring wheat and oats also show severe infection. As a result, much cooperative work has been done in the two areas over the last ten years.

In late April or early May, alates of *S. avenae* are the first aphids found in fields of spring wheat and oats. For example, in 1982, in Shuoxian County in Shanxi Province, the population of winged aphids were found to increase suddenly during May 9 and 10 and May 25 to 27; the number of alates of *M. avenae* trapped in one black lamp increased during those periods from 1 to 220 and from 8 to 19,740, respectively. At the same time, alates were found over wide areas of the spring wheat and oats. Fifteen to twenty days after the alates were widely distributed, typical BYD symptoms were found on wheat and oat seedlings. However, in Feng-Zhen County in the Nei Monggol autonomous region, the results of inoculations with 1,000 *S. avenae* alates from May 23 to 26, 1982, showed that not all alates were viruliferous.

An analysis of weather records for May, 1982, showed that conditions were particularly favorable for long-range aerial transport of aphids, most likely enabling them to be carried from winter to spring wheat growing areas. In 1976, several alates of *S. graminum* and *S. avenae* were trapped on the top of

Liu Pan Mountain, at an elevation of 2840 meters and between the winter and spring cereal areas, further suggesting that the source of BYDV in spring wheat comes from the winter wheat area.

Factors effecting BYD epidemiology were investigated by monitoring aphid populations over the whole crop growing season and correlating their abundance with meteorological records. Results of the study showed that September rainfall and October temperature were the principal factors in initial infection in winter wheat. In spring wheat, the population of aphid vectors, particularly *S. graminum*, prior to the start of winter, the percentage of infected plants, and the January temperatures were the three determining factors for the intensity of spring epidemics; seeding date and cultural practices could also be factors.

In 1982, Chinese isolates of BYDV were compared with the four luteoviruses previously characterized by Dr. Rochow in New York. Wheat and oat plants, collected from six provinces and autonomous regions, were chopped, dried and sent to Ithaca, New York, for serological assay; each sample was tested by enzyme-linked immunosorbent assay (ELISA). Results of the tests allowed the samples to be divided into five groups. One group (99 samples) was similar to the MAV-like isolate of New York and one (17 samples), to the RPV-like isolate; a third group (3 samples) appeared similar to the RMV-like isolate. A fourth group of 45 samples was more similar to the PAV-like isolate, transmitted nonspecifically by *R. padi* and *S. avenae*, than to any of the others, but its identification was doubtful. Test results of 143 samples were negative, possibly reflecting the presence of a luteovirus serologically distinct from the four known in the USA. This hypothesis would seem to be borne out by the fact that the resistant California cultivar, Anza, was intermediately susceptible in China.

Because the principal BYDV problem in China has been in wheat, the search for resistant or tolerant cultivars has taken place only in wheat. About 2,000 cultivars have been screened since 1973, none of which have been found to be resistant; some, however, show tolerance to the virus.

Serological Detection of Cucumber Mosaic Virus in South African Cereal Crops: Seed-Borne CMV in Barley

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In the course of investigating viruses affecting Gramineae in South Africa, brome mosaic virus (BMV) has been found to be perhaps the most important cause of disease of wheat and grasses in the Orange Free State. The virus also occurs in barley, although serious natural infections have been noticed in only a few isolated instances. Field-grown barley which tests BMV negative often exhibits severe yellowing, dwarfing and necrotic leaf spotting, symptoms reminiscent of barley yellow dwarf virus (BYDV) infection. However, the disease appears to be seed transmitted (von Wechmar, unpublished data), which would seem to rule out BYDV as the disease agent. It has been shown that BMV can mimic BYDV symptoms in small grains (von Wechmar, unpublished data); it is interesting to discover that still another agent can act similarly in barley.

During preliminary investigations of diseases of small grains, several field isolates of BMV were propagated on barley in the laboratory and antisera raised against them. Some of the antisera appeared to react with more than one virus in precipitin tests; subsequent testing by enzyme-assisted immunoelectroblotting (IEB) (Rybicki and von Wechmar, 1982b) revealed that the antisera reacted strongly with both a local and a foreign strain of cucumber mosaic virus (CMV) (von Wechmar, unpublished data). This finding prompted a thorough investigation of the incidence of CMV in barley and other small grains, especially since it appeared to be seed-borne. CMV had not previously been reported to cause severe disease in small grains, although it was known to occur in maize (Damsteegt, 1981; Tien-Po *et al.*, 1982). As with previous investigations on BMV and other viruses (von Wechmar and Rybicki, 1981; Rybicki and von Wechmar, 1982a; von Wechmar *et al.*, 1984; Erasmus *et al.*, 1983), it was found necessary to rely less on symptoms and more on relatively sophisticated serological techniques in order to detect what were often very low concentrations of virus.

Materials and Methods

The seed utilized in the study was that of the barley (*Hordeum vulgare*) cultivar Clipper, which was obtained from commercial suppliers, and the cultivars Comma, Swanneck and Loerie obtained through the Small Grain Centre, Bethlehem. Antisera to a South African and to an Israeli isolate of CMV (isolated from *Nicotiana tabacum*, decorative species, and *Nicotiana glauca*, respectively) were used. They were prepared in rabbits as described elsewhere (Lupuwana *et al.*, 1984). Formalinized CMV was used for immunization.

Among the serological methods utilized were radial immune diffusion tests (von Wechmar *et al.*, 1984). The enzyme-linked immunosorbent assay (ELISA) was also performed, essentially using the method of Clark and Adams (1977). The preparation of seedsoaks have been described elsewhere (von Wechmar *et al.*, 1984) but, briefly, individual seeds were soaked in 0.6 ml PBS or PBS/0.05% Tween-20, 0.2% BSA (PBS-T-BSA) for 18 hours at room temperature, then placed on moist cotton and allowed to germinate.

Individual coleoptiles cut from germinated seeds, or embryos cut from ungerminated seeds, were crushed in small volumes of PBS-T-BSA. Seed washings and crushed extracts were incubated in IgG-coated trays (2 µg per ml) for two hours at 37°C or overnight at 4°C. Conjugated anti-CMV globulin preparation was diluted 1 to 500 (2 µg per ml) in PBS-T-BSA, and incubated in the trays for two hours at 37°C. Conjugate reaction was assayed by the addition of one mg per ml p-nitrophenyl phosphate in 10% (v/v) diethanolamine, pH 9.8, and subsequent absorbance readings made at 405 nm on a Titertek Multiskan plate reader (Flow Laboratories, UK). The normal background reading was less than 0.05 absorbance units. Samples with absorbance readings of 0.1 and above were considered positive.

Extracts giving positive ELISA scores were also checked by IEB (Rybicki and von Wechmar, 1982b). No false positives were detected; all ELISA positives produced a protein band at the correct position for CMV coat protein (NW = 24,500) (results not shown).

Results

Preliminary serological testing of seeds by radial immunodiffusion (RID) (von Wechmar *et al.*, 1984) showed some batches of barley seed reacting strongly with anti-CMV antiserum. However, similar tests on barley seed for barley stripe mosaic virus (BSMV), using specific serum as well as normal rabbit pre-immune serum, revealed a relatively high incidence of nonspecific positives; this was in contrast to wheat seed testing, where false positive results were rare. Accordingly, it was decided to rely on nonprecipiting serological tests, i.e., ELISA, in order to investigate the occurrence of CMV in barley seed and seedlings and in field-grown plants.

Table 1 illustrates the incidence of CMV on seed surfaces and in coleoptiles grown from the same seeds. It is evident that, in all cases, more coleoptiles were CMV positive than the parent seed surfaces; this, also, is in direct contrast to the case of BMV in wheat seed (von Wechmar *et al.*, 1984), and indicates that the majority of CMV virions associated with barley seed are perhaps internally located rather than adsorbed to the seed surface as is the case with BMV and wheat. The barley cultivars listed in Table 1 were selected for testing as a result of poor performance in the field and/or laboratory; the alarmingly high incidence of CMV in emergent coleoptiles may explain the lack of performance as well as symptoms observed in the field.

CMV-positive seedlings have been grown to maturity, the symptoms observed and extracts tested for mechanical transmissibility of the disease. Clipper barley appears distinctly dwarfed, with much dead

Table 1. ELISA Tests for CMV on Seed Surfaces and Emergent Coleoptiles

Barley cultivar	ELISA testing for CMV[a]	
	Seed surface	Coleoptile[b]
Clipper 1	2/15	7/13[c]
Clipper 2	0/15	3/15
Swanneck	5/15	14/14[c]
Heine	5/15	[c]
Loerie	2/12	10/12[c]

a/ Background A_{405} values were typically 0.01 to 0.05; only values of 0.1 and higher were considered positive

b/ Coeoptiles were cut from single germinated seeds at 4 to 6 cm, and crushed for ELISA

c/ Discrepancies between seed and coleoptile test totals due to nongermination of seeds tested

foliage and uniformly yellowed leaf blades. Older plants (at heading stage) develop dark necrotic patches on the leaves. Sap prepared by homogenization of diseased leaves in potassium phosphate buffer is infective, and causes more severe symptoms than those described above.

It was interesting that anti-BMV antisera, both that in the Cape Town laboratory (Rybicki and von Wechmar, 1981) and that obtained from the University of Nebraska, USA, reacted specifically with CMV (Figure 1). The implication is that CMV may have been transmitted through the seedlings on which the BMV isolates were propagated, both in South Africa and in the USA. Unless specifically tested for, such antibodies, although unnoticed, may cause nonspecific background readings or false positive readings in the ELISA test.

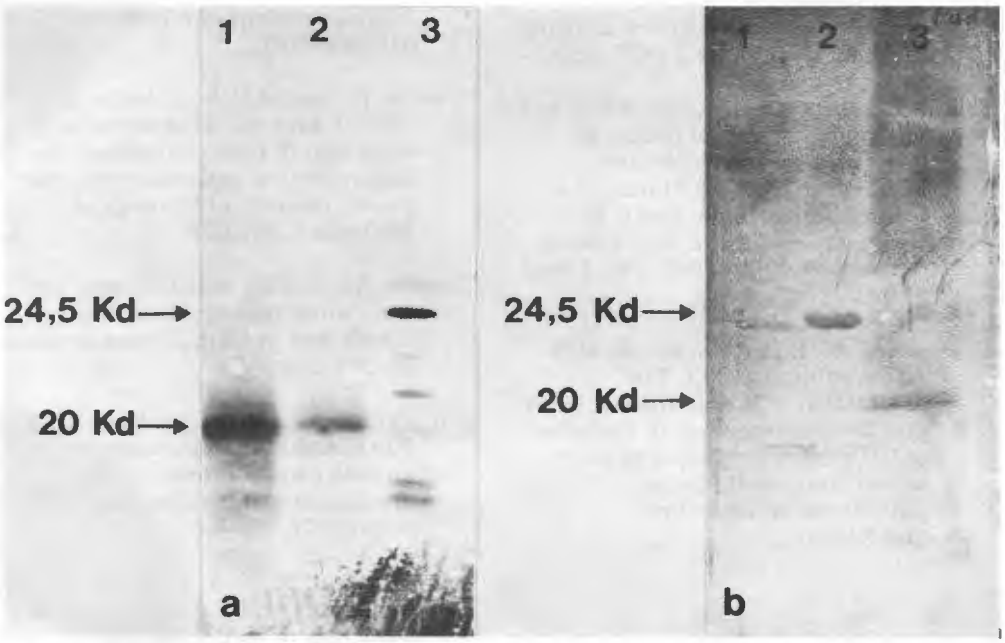

Figure 1. Immunoelectroblot of cereal samples probed with anti-BMV antisera (arrows indicate position and molecular weight of BMV (20 kd) and CMV (24.5 kd) proteins in the electropherograms.

a) Blot probed with Nebraska anti-BMV serum

Samples:

Track 1: 10 µg of purified BMV
Track 2: Homogenized leaf from barley co-infected with barley stripe mosaic virus (BSMV) and BMV
Track 3: *N. tabacum* isolate of CMV (5 µg)

b) Blot probed with Cape Town anti-BMV serum (propagated in barley)

Samples:

Track 1: *N. glauca* (Israel) isolate of CMV (5 µg)
Track 2: *N. tabacum* isolate of CMV (10 µg)
Track 3: Homogenized leaf sample of BMV-infected maize plant

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References

Clark, M.F., and A.N. Adams. 1977. Characteristics of the microplate method of enzyme-linked immunosorbent assay for detection of plant viruses. Journal of General Virology 34:475-483.

Damsteegt, V.D. 1981. Exotic virus and viruslike diseases of maize. *In* virus and Viruslike Diseases of Maize in the United States, D.T. Gordon, J.K. Knoke and G.E. Scott, eds. Southern Cooperative Series Bulletin no. 247. Pp. 110-123.

Erasmus, D.S., E.P. Rybicki and M.B. von Wechmar. 1983. The association of brome mosaic virus and wheat stem rust: II. Detection of BMV in/on uredospores of wheat stem rust. Phytopathologische Zeitschrift 108:34-40.

Lupuwana, P., A. Kaufmann and M.B. von Wechmar. 1984. Characterization and identification of local isolates of cucumber mosaic virus. Abstract. 22nd Annual Congress of the South African Society for Plant Pathology.

Rybicki, E.P., and M.B. von Wechmar. 1982a. Characterization of an aphid-transmitted virus disease of small grains. Isolation and partial characterization of three viruses. Phytopathologische Zeitschrift 103:306-322.

Rybicki, E., and M.B. von Wechmar. 1982b. Enzyme assisted immune detection of plant virus proteins electroblotted onto nitrocellulose paper. Journal of Virological Methods 5:267-278.

Tien-Po, A.L.N. Rao and T. Hatta. 1982. Cucumber mosaic virus from cornflower in China. Plant Disease 66:337-339.

Von Wechmar, M.B., and E.P. Rybicki. 1981. Aphid transmission of three viruses causes Freestate Streak disease. South African Journal of Science 77:488-492.

Von Wechmar, M.B., A. Kaufmann, F. Desmarais and E.P. Rybicki. 1984. Detection of seed transmitted brome mosaic virus by ELISA, radial immuno-diffusion and immunoelectroblotting test. Phytopathologische Zeitschrift 109:341-352.

Aphid Transmission of Cereal Viruses Causes Freestate Streak Disease

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The aphid *Diuraphis noxia* (Figure 1) was first noticed in South Africa in the spring of 1978 and, since then, has been present in wheat fields in the Orange Free State (OFS). Abnormal symptoms associated with the presence of the aphid were initially referred to as Freestate streak disease; however, as some of the components of the disease were later identified, that name was abandoned. Initially, *D. noxia* was found only in eastern OFS, but entomologists monitoring the movement of the aphid showed that it had migrated to virtually every wheat growing area in the country within the two following seasons. Further studies have shown that the aphid appears to prefer the climatic conditions prevailing in the OFS; its occurrence in other regions is less significant. Most of this early work has been reviewed thoroughly (von Wechmar and Rybicki, 1981; Rybicki and von Wechmar, 1982a).

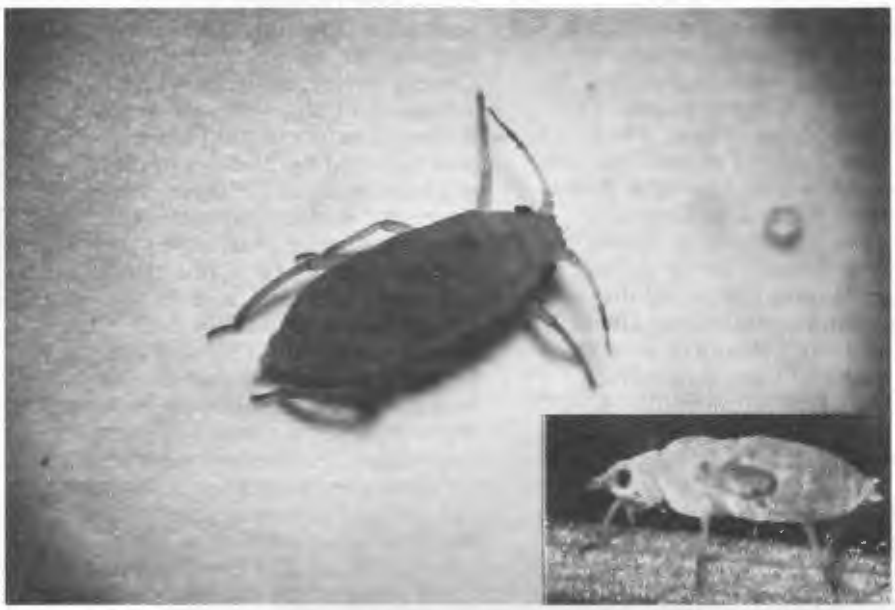

Figure 1. *Diuraphis noxia* **aphids are distinguished by their oblong body shape and double cauda**

Aphid Damage

Plants colonized by the *D. noxia* aphid are readily recognizable by the broad and narrow white stripes running along the midrib of the younger leaves. The aphids are packed in colonies inside the leafwhorl of the youngest unfolding leaf, giving it a rolled and spindled appearance. Wheat and barley are the preferred hosts but, in the off-season, the aphid is also found on oats and bromus grass (*Bromuscatharticus*). It is tolerant to cold and can be found in leafwhorls throughout the winter as well as in times of light frost; there is a marked population increase with the rising temperatures of spring. Clones have been maintained for up to five years in the laboratory by alternating night/day temperatures from 5 to 10°C, respectively.

The aphid is known to have a phytotoxic effect on its host. This is characterized by tightly rolled leafwhorls and prostrating of the growth habit in tillering plants. The shoots of Scheepers, a local wheat variety, often discolor to pink-maroon. As plants develop and mature, shoots return to the vertical and appear normal; close examination, however, reveals white streaks along the midrib of younger leaves, indicating the presence of the aphid. Some affected leaves and young shoots of severely infested plants die prematurely. Recovering plants often exhibit a stiff upright growth habit, reminiscent of that of small grains infected by virus. Barley plants, in particular, often yellow and stunt following early aphid infestation, symptoms also associated with barley yellow dwarf virus (BYDV) infection. During the early stages of investigation, it was not possible to distinguish between aphid phytotoxicity and symptoms caused by virus infection. Once virus-free aphid clones were obtained, however, it was clear that symptoms of phytotoxicity were distinct from those resulting from infection with one or more viruses.

Isolation of Barley Yellow Dwarf Virus

The presence of the aphid and the yellow, dwarfed appearance of cereals made BYDV a prime suspect, and clean aphid clones of *D. noxia* were started for transmission studies. Field-collected plants suspected of being infected with virus were colonized with clean aphids and, after three days acquisition feeding, the aphids were transferred to Clipper barley, Scheepers and Betta wheat and Langewens oat seedlings for a three-day inoculation feeding. This was followed by 21 days in plant growth rooms at 20°C and high light intensity. A clean clone of *Rhopalosiphum padi* (also occurring naturally in the OFS, but in lesser numbers) was also used for transmission studies; *R. padi* is a known vector of BYDV and has no phytotoxic effect on its host. Virus transfer was successful for both aphids when judged by visual symptom expression. Purified concentrated preparations of the plants contained icosahedral virus particles with a sedimentation coefficient of approximately 114 Svedberg and protein MW of 21 kd. The yields were small, 20 to 100 µg per kg leaf (Rybicki and von Wechmar, 1982a). Serological tests with anti-BYDV serum (obtained from C.C. Gill of Canada) were positive (Rybicki, unpublished data).

Isolation of Other Viruses

Further fractionation of similar concentrated virus preparations on sucrose gradients revealed two additional components, one banding higher and one lower than the BYDV band. The top band was identified as brome mosaic virus (BMV) and the bottom band as an aphid-pathogenic virus, now known as *R. padi* virus (RhPV) (Rybicki and von Wechmar, 1982). Table 1 summarizes some physical properties of the three components.

This three-virus complex was maintained by aphid transmission over a long period. One source of Clipper barley was used throughout for aphid and virus maintenance, but a range of wheat, oats and barley cultivars were used for virus propagation to establish whether any local cultivar might be more suitable for BYDV propagation. Results showed that the relative concentration of the viruses in the complex was determined by the specific host used. For instance, some sources of Scheepers wheat supported an increase in the BMV fraction while others did not; in oat cultivars, the proportion of BMV in the complex decreased. In Heine barley, BMV increased to a level that eliminated the other components; Heine was subsequently shown to contain a high percentage of seed transmitted BMV.

Examination of extracts prepared from control plants grown in the absence of aphids or, alternatively, colonized with nonviruliferous aphids, in some cases showed small quantities of BMV, but never the three-virus complex. After examining many cultivars and several seed sources of particular cultivars, it became evident that the presence and quantity of BMV fluctuated according to cultivar and the origin of the seed of a particular cultivar. No BMV was extracted from control Clipper plants, grown either in the presence or absence of aphids.

Table 1. Some Physical Characteristics of Particles in the Aphid-Transmitted Virus Complex

	BMV	BYDV	RhPV
Morphology	Isometric	Isometric	Particles degraded
Diameter in mm	±28	±28	—
Sedimentation coefficient (Svedbergs)	72	114	165 ±5
Serological identity	BMV	BYDV	RhPV[a/]
Protein MW (kd)	20	22	28;30;31
Nucleic acid MW x 10^6	1;0.7;0.3	1.8	2.86

[a/] Antiserum obtained from C.J. D'Arcy, Illinois

Seed-Transmitted Brome Mosaic Virus

The above findings pointed to the possible presence of seed transmitted BMV, a fact not previously reported. The results of the work of this author (von Wechmar *et al.*, 1984) show that BMV is borne on the seedcoat and in the embryo of wheat seed; plants grown from such seed will contain low levels of BMV. The following immunological tests were used to detect seed associated BMV with anti-BMV serum prepared against a South Africa isolate and serum obtained from E. Moorhead-Ball, Nebraska, in 1965:

- Radial immune diffusion (RID) in agar gel for detecting virus on the seedcoat and the embryo (Figure 2);
- Enzyme-linked immunosorbent assay (ELISA) on single seed washings, coleoptiles of single seeds and excised embryos of nongerminating seeds;
- Immune electron microscopy on seed washings, and
- Immunoelectroblotting (Rybicki and von Wechmar, 1982b) on whole seed extracts, single seedlings and precipitin reactions in agar cut from RID tests.

The RID test is simple and rapid, so that large numbers of seed can be tested. With wheat, the test is specific but, with barley, nonspecific precipitations occur, making it less reliable. The average percentage of contaminated seed found in commercial seed batches is low. Seed from areas with severe aphid infestations and severe BMV infection show a higher percentage of contamination. Laboratory tests have shown that extracts of plants grown from contaminated seed that have been exposed to feeding of both *D. noxia* and *R. padi* for prolonged periods contain a much higher concentration of BMV than control plants grown in the absence of aphids (von Wechmar *et al.*, 1984).

Symptomatology

Plants grown from BMV contaminated seed seldom show any characteristic symptoms during the early growth stages. At ear emergence, severely infected plants can be distinguished by the emergence of white, empty ears and the yellowing of the whole plant,

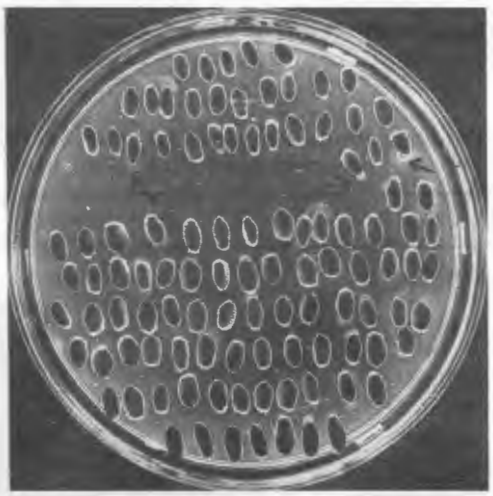

Figure 2. Radial immunodiffusion test with wheat seed embedded in agar containing anti-BMV serum; precipitin reactions around the ends of seed embryos (see arrows) indicate seed contaminated with BMV

beginning at the flagleaf (Figure 3). The plant is usually dwarfed by about one-third in comparison with surrounding uninfected plants and has a bunched, compacted appearance similar to that of barley yellow dwarf. In the spring, the hot, dry conditions may enhance early leaf death. Symptom expression varies among cultivars, but aphid and seed-transmitted BMV causes no visible mosaic.

Summary

The presence of the aphid *D. noxia* in small grain gives rise to symptoms similar to those of BYD. Examination of infected plants has shown that aphids can transmit a three-virus complex (BMV, BYDV and RhPV) from field-collected plants and that this virus complex can be maintained by aphid transmission over a long period. Aphids also transmit BMV alone, either from mechanically inoculated hosts or from plants grown from BMV-contaminated seed. Such plants do not exhibit mosaic symptoms, but appear yellow and dwarfed, symptoms that can easily be confused with the BYD disease.

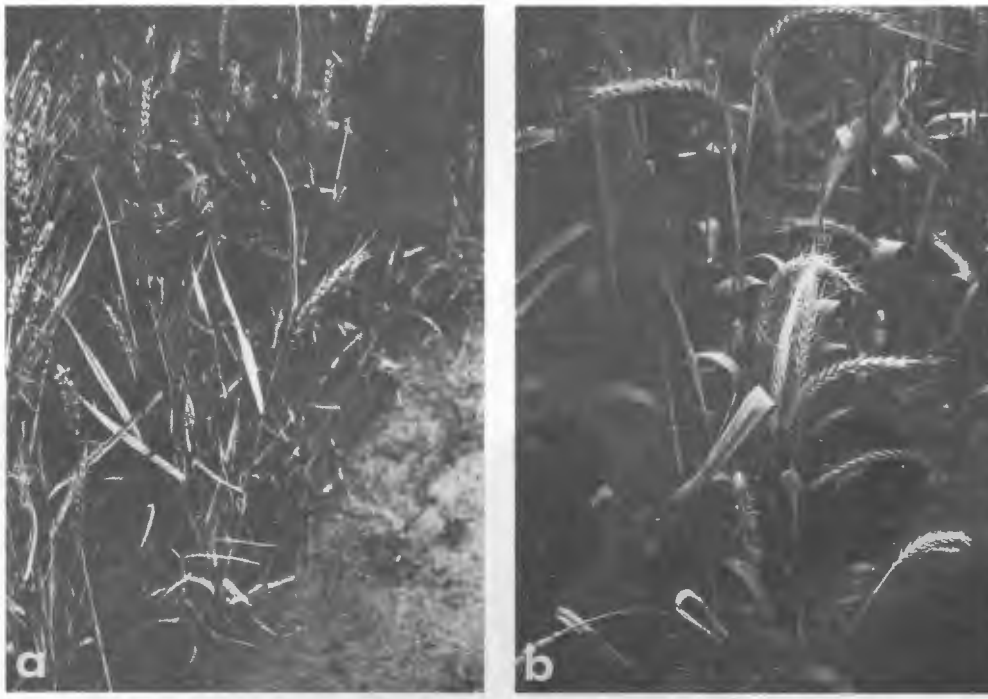

Figure 3. Plants exhibiting symptoms of brome mosaic virus (light colored leaves in the photographs indicate severe yellowing)

a) Wheat plant infected with brome mosaic virus and colonized by *D. noxia* at an early age; yellowing and dwarfing resemble symptoms of barley yellow dwarf infection

b) Triticale plant exhibiting yellow flagleaves, dead heads and dwarfing, symptoms often associated with plants grown from seed infected with brome mosaic virus

References

Von Wechmar, M.B., and E.P. Rybicki. 1981. Aphid transmission of three viruses causes Freestate streak disease. South African Journal of Science 77:488-492.

Ribicki, E.P., and M.B. von Wechmar. 1982a. Characterization of an aphid-transmitted virus disease of small grains: isolation and partial characterization of three viruses. Phytopathologische Zeitschrift 103:306-322.

Ribicki, E.P., and M.B. von Wechmar. 1982b. Enzyme-assisted immune detection of plant virus proteins electroblotted onto nitrocellulose paper. Journal of Virological Methods 5:267-278.

Von Wechmar, M.B., A. Kaufmann, F. Desmarais and E.P. Rybicki. 1984. Detection of seed-transmitted brome mosaic virus by ELISA, radial immunodiffusion and immunoelectroblotting tests. Phytopathologische Zeitschrift 109:341-352.

The Extent of Freestate Streak and *Diuraphis noxia* in Mexico

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In 1980, previously unobserved symptoms were noted on the occasional plant in cereals sown at the El Batan research station of CIMMYT in the State of Mexico. In 1981, the symptoms were widely distributed in cereals at the station. These same symptoms were observed on the Central Plateau in 1982 and in Toluca and Saltillo in 1983; it is now known that similar symptoms had been observed in the Bajio in 1980. Figure 1 shows symptom distribution in Mexico, with both test and commercial plantings of bread and durum wheat, barley and triticale showing symptoms of the Freestate streak disease.

The affected plants had whitish yellow streaks on the leaves and, in some cultivars, reddening was observed. This was usually accompanied by stunted growth. The affected leaves were characteristically curled and had the appearance of an onion leaf; at times there was severe leaf deformation and corkscrewing. Badly affected plants sometimes exhibited a prostrate growth habit.

When barley plants with symptoms headed, they sometimes showed badly distorted curved heads with curled awns (Figures 2 and 3). In wheat, the heads generally were erect except in very severe cases when the spikes also curved; they were sterile in the upper part of the spike (Figure 4).

Figure 1. Distribution of symptoms of Freestate streak in Mexico

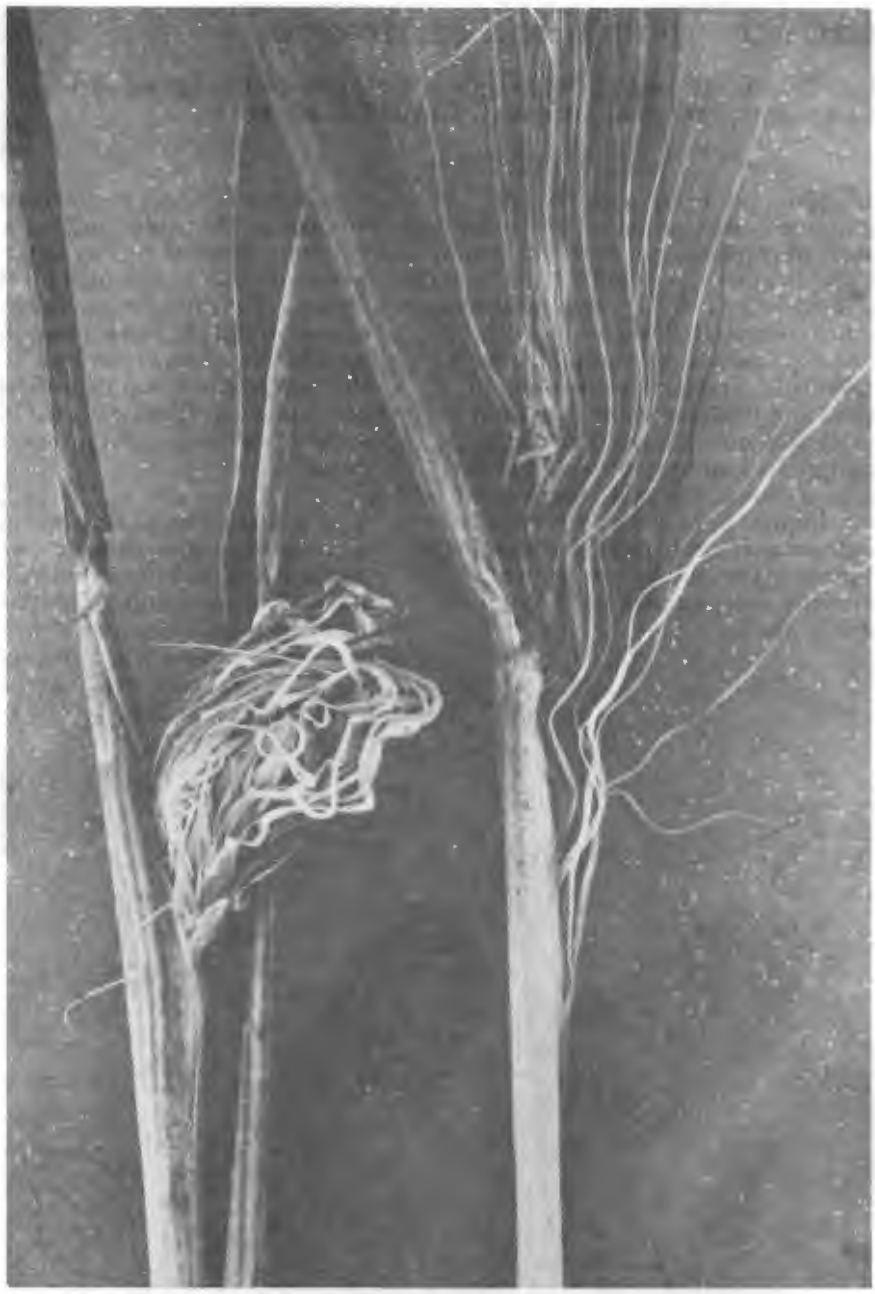

Figure 2. Barley spikes distorted as a result of Freestate streak

Figure 3. Barley plants in the field, showing stunting and head distortion due to Freestate streak

Figure 4. Wheat with streaked leaf and spike showing sterility in the upper part as a result of Freestate streak

Identification of the Problem

On plants showing these symptoms, an unknown species of aphid was found, one that had not been observed in the area. Aphid feeding tests were made on healthy plants under greenhouse conditions and, after 48 hours, chlorotic discolorations appeared; characteristic streaks developed after five to ten days.

The aphid was found to feed within the base of the curled leaves. As the plant matured, the aphid began to feed on the tender tissues of the spike in the jointing stage. After spike emergence, the aphid usually left the plant.

Identification of the Aphid and the Causal Agent

In 1981, Dr. J. Holman of the Institute of Entomology of Prague, Academy of Science, Czechoslovakia, identified the aphid as being of the genera *Diuraphis* and, in 1982, Dr. H.J.R. Durr of the Department of Entomology, University of Stellenbosch, Cape Town, South Africa, confirmed his findings and identified the species as *Diuraphis noxia*.

It was thought that the problem could result from an aphid transmitted virus and/or direct aphid feeding damage. In an attempt to obtain virus-free colonies of the aphid, aphids were isolated and unfed, newborn nymphs were fed on test seedlings of Morocco wheat. This experiment proved that all of the aphids were capable of causing symptoms, although not all of the same severity. If a virus was involved, it was being transmitted transovarially. Because of the rapidity of symptom development, it was hypothesized that the symptoms were being caused by a toxin from the aphid. However, the idea that a virus or even viruses might be involved was not rejected.

An experiment was carried out in which plants were subjected to various feeding periods by single aphids, which

Figure 5. Wheat spike curled as a result of very severe Freestate streak

were then killed with insecticide (Table 1). Symptoms appeared more rapidly in those treatments where the aphid had a longer feeding time; the intensity of the symptoms were also more severe with longer feeding times. The symptoms appeared in those leaves where the aphid had access for feeding and became more severe while the aphid was present or a few hours after it was removed. The growth that occurred after the aphid was eliminated was green, vigorous and symptomless. The plants were kept under observation for one month after the elimination of the aphids, and no additional symptoms were observed.

Mechanical Transmissions

Studies in South Africa [where the disease was named Freestate streak (FSS)] suggest that this aphid can be a potential vector for three viruses, barley yellow dwarf virus (BYDV), brome mosaic virus (BMV) and a third one designated as Component B, now known as *R. padi* virus (RhPV) (von Wechmar and Rybicki, these proceedings). Component B is transmitted transovarially to the aphid progenies and from them to the barley cultivars such as Clipper and Heine (von Wechmar and Rybicki, 1981). These authors suggest that BMV and BYDV are associated and that the two viruses may cause damage to cereals in South Africa. They found BMV to be transmitted by *D. noxia* , *Rhopalosiphum padi, R. maidis* and *Schizaphis graminum*, as well as being seed borne. Subsequent mechanical transmission of aphid-transmitted BMV gave rise to red discolorations, symptoms characteristic of field infections; coloration lessened with additional transmissions.

Table 1. Number of Inoculated Wheat Seedling Showing Symptoms of Freestate Streak Disease and Levels of Symptoms[a/]

D. noxia feeding time(hr)	Hours after *D. noxia* feeding							
	12	14	16	18	24	32	48	72
0	0	0	0	0	0	0	0	0
0.5	0	0	1A	5A	5A	5A	3A	2A
1	0	0	1A	2A	5A	6A	6A	6B-D
2	0	0	8A	8A	9A	9B-D	9B-D	9B-D
4	0	0	6A	8A	8B	9B	9B	9B-D
7	0	0	6A	7A	8B	8B-D	8B-D	9B
8	0	0	7A	8A	9B	9B	9B	9B-D
10	0	0	7A	9A	9B	9B-D	9B-D	9B-D
12	8A	8A	9B	9B	9B	9B	9B	9B-D-E-F
24	8B	8B	9B	9b	9D	9C-D	9C-D	9B-D-E-F
36	9B	9B	9B	9C	9D	9C-D	9C-D	9B-D-E-F
48	9B	9B	9B	9C	9D	9C-D	9C-D	9B-D-E-F

[a/] Nine seedlings inoculated per treatment with two first-stage nymphs

Visual scoring system used:
A Small diffuse blotchy discolorations in one area of the leaf
B More noticeable discolorations than A
C Similar discolorations to B but in two areas of the leaf
D The same discolorations as C with streaking on the first leaf
E The same discolorations as C with marked streaking on the first and second leaves
F The same as E with the addition of leaf rolling

Tests were carried out in Mexico for the presence of BMV in cereals. Mechanical transmissions were made from seedlings and adult plants of bread wheat, barley, durum wheat and triticale brought from fields in Saltillo, El Bajio, El Batan and Toluca. Besides plants with streaks, special care was taken to obtain plants with red discoloration. The extract of sap obtained (with sterile water and a phosphate buffer of pH 6.0) was used to inoculate Clipper barley, *Chenopodium quinoa*, Golden Bantam sweet corn and beans (*Phaseolus vulgaris*), plants that are differential indicators for BMV. The results of the test were negative for all samples (Table 2).

Testing with Various Aphids of the Species *D. noxia*

To test whether transmission of any symptom takes place with aphids other than *D. noxia*, insects of the species *R. padi*, *R. maidis*, *S. avenae* and *Metopolophium dirhodum* were allowed to feed for one week on plants where *D. noxia* aphids were feeding at the same time and where severe symptoms had appeared. At the end of the week, the aphids were moved to healthy plants where they were held for one month for observation. In none of the tests were symptoms produced that would indicate an aphid transmitted virus. However, this work will be continued and expanded.

Table 2. Mechanical Transmissions for Detection of Brome Mosaic Virus in Samples from Various Localities in Mexico

Origin of sample	Species collected	Growth stage	Results of inoculation
El Bajio[a/]	Barley Bread wheat Durum wheat	Flowering Heading	Negative
El Batan[b/]	Barley Bread wheat	Heading	Negative
Valley of Mexico[a/]	Barley Triticale	Heading	Negative
Saltillo[a/]	Barley Durum wheat Triticale	Heading	Negative
Toluca[b/]	Barley Bread wheat Durum wheat Triticale	Seedlings Heading	Negative

a/ Symptoms of streaking and purple discolorations
b/ Symptoms of streaking only

Currently, work is in progress on the possible transmission of a virus through seed. Seed harvested from field plants with severe symptoms of FSS produces some abnormal seedlings. However, symptoms disappear with growth. Serological evaluation will be carried out.

Observations by Electron Microscopy

In premilimary studies it has not yet been possible to detect any virus particles in preparations made from diseased plants or from early attempts at purification. This work, however, is still in very preliminary stages.

Screening Germplasm

The screening of lines and cultivars in the field has been started to see if some field resistance can be found. Quite marked differences have been noted in susceptibility.

Yield Loss Studies

Preliminary yield loss studies have also been begun with a comparison of yields from sprayed versus unsprayed plots. If crops are sprayed with insecticide at the first sign of symptoms, the symptoms can be eliminated. That does not mean, however, that the possibility of the presence of a virus has been eliminated.

References

Smith, K.M. 1972. A Textbook of Plant Virus Diseases, 3rd ed. Academic Press, New York.

Von Wechmar, M.B., and E.P. Rybicki. 1981. Aphid transmission of three viruses causing Freestate streak disease. South African Journal of Science 77:488-492.

The Research Program for Combating the Russian Wheat Aphid (*Diuraphis noxia* Mordwilko) in South Africa

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Aphids have been actively researched worldwide only in the past 20 years. In South Africa, *Schizaphis graminum* reached pest proportions in the Orange Free State in the 1950s, while *Sitobion avenae* has been a sporadic pest in the western and southern Cape, especially on dryland wheat, since 1971. Other species which occur sporadically on wheat are *Metopolophium dirhodum* and *Rhapolosiphum padi*. Apart from the damage caused as a result of sap extraction, the aphids also act as vectors for the transfer of viruses.

In September, 1978, a new aphid, *Diuraphis noxia*, was discovered on wheat in the Orange Free State in the districts of Paul Roux and Bethlehem. In 1979, the pest spread over the entire state and to parts of the Transvaal, Natal and Lesotho. In 1980, it also spread to the southwestern Cape and, by 1981, it was found throughout the Republic of South Africa. As the pest was unknown in the country and was accompanied by great crop loss, its occurrence led to much confusion and even panic among farmers. Initial losses were difficult to evaluate, but crop loss assesments showed that up to 90% yield losses could have been incurred. A conservative estimate revealed that 600,000 hectares of wheat were sprayed in 1980 at an estimated cost of R8 million ($6.8 million US).

D. noxia is a relatively small (less than 2 mm long) green aphid with an elongated, spindle-shaped body. It can easily be distinguished from other aphids infesting wheat in southern Africa by the extremely short antennae, a characteristic projection above the cauda or tail, i.e., a "double tail" and, to the naked eye, the absence of the prominent siphunculi which are typical of other aphids. This aphid is indigenous to southern Russia (hence the common name Russian wheat aphid), countries bordering the Mediterranean, Iran and Afghanistan.

In 1979, the Department of Agriculture assembled a research group with the specific aim of launching a coordinated program aimed at controlling *D. noxia*. The program was set up and accorded the highest priority rating for research in the following fields:

- Evaluation of insecticides for use in combating the pest, including soil systemics for use at planting time;
- Determination of economic thresholds, i.e., the maximum infection level at which chemical control is economically feasible;
- Development of resistant wheat varieties;
- Study of the nature of the toxin secreted by the aphid;
- Influence of natural enemies on the survival of the aphid, and
- The role of the viruses transmitted by the pest.

Evaluation of Insecticides

In the use of insecticides, the producer has two options, namely, preventive control through the application of a soil systemic insecticide at planting or corrective spraying during the growing season when infestation justifies such action.

In the case of winter wheat planted in May and June, research has shown that the application of a soil systemic insecticide at planting offers limited protection against attack from the Russian wheat aphid. As winter wheat is grown mostly in the Orange Free State, with a planting date of from May 1 to 15, the application of soil systemics usually affords protection up to mid-August. Because the aphid normally reaches pest proportions between that date and mid-September (see economic threshold trial data), this form of control usually has to be followed by corrective chemical control. With later planting dates of up to mid-July (as in eastern Orange Free State), the use of soil systemics usually has the beneficial effect of delaying the build-up of a large aphid population. It is recommended that such wheat be sprayed only once, prior to flag leaf emergence, at growth point stage (gps) 14 on the Joubert Scale (Joubert, 1974).

The recommended soil systemics are:

- Phorate 10% granules as a row treatment at planting at 35 grams per 100-meter row, or
- Disulfoton 5% granules: broadcast treatment at 15 grams per hectare or row treatment at 10 kg per hectare.

The decision of whether to use a soil systemic or not is dependent on economic considerations.

Corrective Spraying

Wheat planted during the period from the end of April to June is normally subject to very low infestation during the winter months. Infestations start increasing in August, and there is a rapid increase in infestation when the wheat reaches gps 14. Aphid numbers usually reach a peak during the period between ear emergence (gps 18) and flowering (gps 20); research has shown that the greatest damage takes place between gps 14 and gps 18. It has also been found that spraying at gps 12 is economically justified, provided 10% or more of the plants are infested. Control at gps 12, if infestation exceeds 10%, prevents a build-up of damaging aphid numbers in the initial period between gps 14 and gps 18. In the case of winter plantings, infestation before gps 12 has no effect on yield, provided a spray is applied at gps 12. To spray before gps 12, therefore, gives no additional advantage, but only increases costs.

All currently registered insecticides for use in South Africa afford effective control, provided the application procedure is carried out correctly. Experience has shown that tractor applications are more effective, as the large volume of water allows the contact insecticides, especially, to penetrate the rolled-up leaves.

(continued)

Efficiency of aerial spraying is dependant on temperature and humidity at the time of spraying. The following insecticides are registered for use against the Russian wheat aphid:

- Chlorpyrifos 48% emulsifiable concentrate (ec) at 1 lt per ha;
- Demeton-S-methyl 25% ec at 500 ml plus parathion 50% ec at 650 ml per ha;
- Monocrotophos 40% ec at 500 ml plus dichlorvos 100% ec at 200 ml per ha;
- Monocrotophos 40% ec at 500 ml plus parathion 50% ec at 650 ml per ha;
- Monocrotophos 40% ec at 650 ml plus mevinphos 15% ec at 500 ml per ha;
- Heptenophos 50% ec at 100 ml plus parathion 50% ec at 220 ml per lt water applied at 300 lt spray mixture per ha;
- Thiometon 25% ec at 550 ml per ha plus parathion 50% ec at 650 ml per ha;
- Dimethoate (24%) and parathion (20%) in an emulsifiable mixture at 1.6 lt per ha;
- Dimethoate 40% ec at 750 ml per ha in the winter rainfall region only;
- Thiometon 25% ec at 550 ml per ha (winter rainfall region only);
- Phosphamidon 50% wettable powder (wp) at 500 ml plus parathion 50% ec at 650 ml per ha, and
- Demeton-S-methyl 25% ec at 500 ml per ha (winter rainfall region only).

Determination of Economic Thresholds

The object of these investigations, which were begun in 1980, was to determine the infestation levels and growth stages which cause an economic reduction in wheat yield; this was done in order to establish economic threshold values for chemical control. Trials were conducted at the Small Grain Centre, Bethlehem, from 1980 through 1983.

The treatments in the trials included sprayed and unsprayed plots (see spraying schedule below) in a randomized design; the plots were of six rows 10 meters long and 35 cm apart. The seeding density was 15 kg per hectare, the recommended density for wheat in the Orange Free State at the time of year of the trials. All the treatments, except the aphid-free controls, were infested at the two to three-leaf stages. Infestations were terminated by spraying at the following infestation levels and growth stages:

- Treatment A^1 and A^2 at approximately 25% (gps 11)
- Treatment B^1 and B^2 at approximately 36% (gps 12)
- Treatment C^1 and C^2 at approximately 70% (gps 14)
- Treatment D^1 and D^2 at approximately 80% (gps 15)
- Treatment E^1 and E^2 at approximately 96% (gps 20)

Prior to spraying, the percentage of infected plants and the mean number of aphids per infested plant were determined. The data from two consecutive years were as follows:

- The increase in infection followed a logistic trend, thus making it possible to predict increases in infestation and determine threshold values;
- The greatest increase in infestation took place at gps 12;
- An infestation between flag leaf emergence (gps 15) and complete ear emergence (gps 19) caused a drastic reduction in yield, and
- Chemical control at gps 12 prevented damaging numbers of aphids at the critical stage.

The effect on yield of reinfestation after spraying at gps 12 warrants further study.

Development of Resistant Cultivars

The above studies showed that economic chemical control measures exist for *D. noxia* . However, the cost is considerable; more permanent control would result from the development of cultivars resistant to the pest.

As in the case of any new invader, little is known about the biotic or abiotic factors affecting the biology of the aphid, its alternate hosts, natural enemies, off-season movement and the effect of the environment on its fecundity and survival. In addition, there appears to be little relationship between visual symptoms and yield loss in the host. The effect of the toxin on the growth and development of the host plant is also unknown, especially since streaking symptoms are known to disappear upon removal of the aphid. The role of virus in the whole syndrome is still unclear.

In order to screen quantities of cereals, it was necessary to find a method which was fast, accurate and highly repeatable. After considering various alternatives, it was decided to use the embryo count method, which at least satisfied the requirements of accuracy and repeatability. This method is based on the assumption that aphid fecundity is directly related to the acceptability of the feeding substrate of the host plant. Prior to counting the embryos, aphids were conditioned on each host plant by rearing three generations of aphids prior to actually counting the embryos. In each trial, the bread wheat cultivar Betta was used as the susceptible host and the oat cultivar Witteberg as the resistant host.

The general impression gained from these studies would be that currently available wheat germplasm has a very limited genetic variability regarding resistance to *D. noxia*. On a more optimistic note, it can be inferred that certain of the allied wheat species, for example, *T. monococcum*, *T. timopheevi*, *Ae. squarrosa*, rye and *T. dicoccoides* appear to posses levels of tolerance which would make them possible candidates for use in a cross-breeding program. As all of these species have genomic and chromosomal complementarity with hexaploid wheat, currently available cytological procedures could be employed in making the crosses.

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Ecology and Habits of the Pest

Studies directed toward a better understanding of the ecology and habits of *D. noxia* revealed that newly planted wheat was colonized predominantly by apterae from volunter wheat and brome grass species. The infestation in the wheat field was spread by apterae which probably walked or were blown from plant to plant. The increase in population density of aphids during August and September was correlated with the improved nutritive status of plants in gps 10. This growth stage is characterized by high photosynthetic rates, a prerequisite for ear filling. It was also shown that the preferred feeding site of *D. noxia* was at the base of the leaf. Feeding causes the leaf to roll up in a cylindrical fashion; the diameter is largest at the base of the leaf, furnishing a well-protected space in which the colony can develop.

Studies on biological control of *D. noxia* under South African conditions revealed that several species, i.e., *Aphidius colemani* and *Aphelinus asychus*, were parasitizing *D. noxia*. However, their numbers were so low that they had little or no effect in the control of the aphid. By far the most abundant naturally occurring predator was the coccinellid beetle *Adonia variegata*. However, due to the low temperatures in the Orange Free State during August and September, the numbers of the beetle were also too low to have any significant effect in controlling the pest. Therefore, an attempt was made to breed an artificial colony of coccinellid species which would be better adapted to cool conditions. Four species, *Adalia bipunctata, Coccinella septempunctata, Huppodamia convergens* and *Coleomegilla manilata*, were imported from the USA, UK and Israel and reared under quarantine at the Plant Protection Research Institute in Pretoria. After breeding in the laboratory, eggs were released in the field. However, of all of the species, only *A. bipunctata* adults were found, and they were found in the town center of Bethlehem.

Currently, trials are underway to attempt to create large populations of coccinellids in close proximity to wheat fields. One way is by growing Japanese radish on which the endemic *Adonia variegata* usually appears in large numbers. Also, there will be an attempt to diminish the initial *D. noxia* populations by growing oats and wheat in alternating strips. Data on these trials will be available toward the end of the season.

Nature of the Virus and its Effect of the Plant

Infestation of wheat by the Russian wheat aphid results in a change in the pigmentation of the leaves. Interveinal chlorotic yellow and purple streaks on leaves are typical symptoms. Laboratory experiments showed that changes occurred in the cell organization of wheat tissue treated with an aphid extract. Initially, the orderly peripheral arrangement of the chloroplasts in the cytoplasm was disrupted and, subsequently, the chloroplast membranes desintegrated; after a period of five hours no chloroplast could be distinguished. It would thus appear that the primary sites of feeding damage are the chloroplast membranes and the photosynthetic pigments.

Trials showed that aphid infestation of wheat plants had a pronounced affect on the chlorophyll content of leaves. The chlorophyll concentration in infested leaves was only 35% that of the concentration in healthy leaves, and the chlorophyll concentration in the proximal half of the infested leaves was only 15% that of healthy leaves. This reduction in chlorophyll content may be due to disruption of the thykaloid membranes, thus setting free the membrane-bound chlorophyll molecules. A reduction in chlorophyll content of leaves of up to 85%, as measured in these investigations, has an adverse effect on photosynthesis and, consequently, metabolism in general. Studies on the primary effect of the virus on photosynthesis showed it to be linked to an almost 50% increase in the 0_2 evolution rate.

Conclusions

The foregoing data are the result of a cooperative research program encompassing certain divisions of the Department of Agriculture and the Universities of the Orange Free State, Cape Town and Stellenbosch. The results achieved thus far have not only been of great practical use in the control of the Russian wheat aphid in South Africa, but have had implications for other areas and pests as well. This knowledge, as is evident from this workshop, is of value to CIMMYT, particularly in Mexico where *D. noxia* has become a pest in the last two years. It is hoped that an international collaborative research program can be launched to learn more about *D. noxia* and to find a way to control it.

References

(These contributions are taken from the proceedings of the Russian Aphid Work Group, University of the Orange Free State, Bloemfontein, South Africa, May 5-6, 1982 (in press).

Aalbersberg, Y.K., M.C. Walters and N.J. van Rensburg. 1982. The status and potential of biological control studies on *Diuraphis noxia* (Aphididae).

Butts, P.A., and K.W. Pakendorf. 1982. Wheat breeding for resistance to *Diuraphis noxia*: methodology and progress.

Butts, P.A., and K.W. Pakendorf. 1982. The utility of the embryo count method in characterizing cereal crops for resistance to *Diuraphis noxia*.

Butts, P.A., and M.C. Walters. 1982. Seed teatment with systemic insecticides for the control of *Diuraphis noxia* (Aphididae).

Du Toit, F. 1982. The use of two soil systemic insecticides against *Diuraphis noxia* on winter wheat.

Du Toit, F., and M.C. Walters. 1982. Damage assessment and economic threshold values for the chemical control of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) on winter wheat.

Fouché, A., R.L. Verhoeven, P.H. Hewitt, M.C. Walters, C.F. Kriel and J. de Jager. 1982. Russian aphid (*Diuraphis noxia*) feeding damage on wheat, related cereals and *Bromus* grass species.

Hewitt, P.H., G.J.J. van Niekerk, M.C. Walters, M.C. Kriel and A. Fouché. 1982. Aspects of the ecology of the Russian wheat aphid (*Diuraphis noxia*) in the Bloemfontein district. I. The colonization and infestation of sown wheat, identification of summer hosts and cause of infestation symptoms.

Kriel, C.F., P.H. Hewitt, J. de Jager, M.C. Walters, A. Fouché and Van der Westhuizen. 1982. Aspects of the ecology of the Russian wheat aphid (*Diuraphis noxia*) in the Bloemfontein distric. II. Population dynamics.

Krüger, G.H.J., and P.H. Hewitt. 1982. The effect of Russian wheat aphid (*Diuraphis noxia*) extract on photosynthesis of isolated chloroplasts.

Other References

Joubert, G.D. 1974. The influence of cold treatment and photoperiod on photosynthesis in wheat. PhD Thesis. University of Stellenbosch, Republic of South Africa.

Situation Reports

Argentina

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Wheat, rye, barley and oat production totals eleven million hectares in Argentina. Barley yellow dwarf (BYD) has been known to be a disease affecting those crops since 1978, when aphid transmission tests were carried out by INTA to assess the incidence of the disease in Argentina.

Positive transmission of barley yellow dwarf virus (BYDV) was obtained to Coast Black oats (*Avena byzantina* Koch) by using the aphid species *Metopolophium dirhodum, Schizaphis graminum, Rhopalosiphum padi* and *R. rufiabdominalis.* Two aphid species which occur in Argentina but which have not yet been tested as vectors of BYDV are *Sitobion avenae* and *R. maidis.* The inoculum sources for these tests were diseased samples of cereals from various parts of the country.

Observations on the incidence of BYD have been carried out for several years in the province of Buenos Aires, the largest cereal producing province in Argentina. Symptoms were general and the incidence of BYD was found to decrease as the vector population decreased. In 1981, the disease was epiphytotic in commercial crops in the Balcarce area, and high losses were experienced in experimental plots at Castelar. One of the most effected areas in the province was in the west (Guamini), where sandy soils made the symptoms more obvious; another was in the southeast, including Balcarce, where some durum wheat crops were grown and where colonies of *M. dirhodum* were frequently found.

Isolated observations in other locations showed BYD symptoms on oats, barley and triticales in Anguil (La Pampa) and on wheat and oats in Paraná (Entre Rios). No symptoms were observed on wheat in Marcos Juárez in 1977 or in 1981. There are important cereal growing areas in Argentina where nothing is yet known about the incidence and distribution of BYD.

To determine the inoculation pressure of alate aphids, pots of Coast Black oats were exposed to aphid flights for weekly periods in a bare soil area at the meteorological station near the experimental field in Castelar for two periods during the year. The highest rates of infection were obtained during the period of August to November when the *M. dirhodum* population was high. The infection of the trap plants was lower during the March to June period when the *S. graminum* population increased.

A methodology has now been developed for estimating the effects of the virus on yield without the use of exclusion cages; results are still being evaluated.

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Germplasm evaluation assays have routinely been made in the IICA-BID-SOUTH CONE program. Anza, CNT 9, Londrina, San Agustín INTA, Tucunduva, V 23 and Yecorá showed a lower susceptibility to BYDV at Castelar in 1981; the most susceptible cultivars were Buck Ñandú, Klein Toledo, Labrador INTA, LE 1787, LI 887, Nobre and Trigal 800. The differences observed in one component of yield, the 1000-grain weight, could have been produced by both the virus and the heavy aphid infestation.

Many questions still need to be answered about the status of BYD in Argentina. Among them are: 1) effects of BYD on yield, 2) virus isolates present, 3) effects of BYD on grasses (*Lolium*), and 4) the effect of the increase in *S. graminum* populations on the epidemiology of BYDV on summer crops like sorghum. More equipment and human resources are needed to achieve these objectives. However, the interest in BYD among scientists involved in cereal production has increased, and this is a promising factor for BYD research in Argentina.

Brazil

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Barley yellow dwarf (BYD) was identified in Pelotas, Rio Grande do Sul, in southern Brazil in 1967 and, since then, has been studied intensely in that state where it is one of the main wheat diseases, responsible for production losses of between 20 and 30%. In the remaining wheat producing states in the country the virus has also been found to be present; although surveys have been discontinuous in time, they indicate that BYD is an economically important disease. This disease is also present in barley, oats and triticale where it causes damage similar to that of wheat. It has been observed in pastures, but practically nothing has been done so far to assess losses and possible solutions.

The research program developed in 1967 has the goals of establishing the economic importance of the disease, learning about its epidemiology and setting up methods of control for minimizing losses in wheat, barley, oats and triticale. In order to reach those objectives, the following aspects are studied: 1) levels of damage in the principal cultivars, 2) sources of tolerance to both virus and vector, 3) fluctuations in aphid vectors and hosts of both vectors and virus, and 4) the economic feasibility of chemical control. Additionally, studies on predators have been broadened and new parasite species introduced aimed at reducing the aphid population, both in commercial fields and in their surroundings.

At present, the evolution of interactions occurring in the complex process of achieving a balance among vector populations, cultivars and environmental conditions is being assessed. In so doing, it will be possible to update recommendations aimed at integrated control for maximum economic benefit.

Greater emphasis is now being placed on breeding for resistance or tolerance to barley yellow dwarf virus (BYDV) in wheat, barley and triticale. In wheat, lines have already been developed that, in tests under controlled conditions, have shown reduction in yield loss similar to the one obtained in barley with the *Yd2* gene, i.e., less than 10%. In triticale, using inoculations of a mixture of the isolates transmitted by *Rhopalosiphum padi* and *Metopolophium dirhodum*, plants of lines PFT 7880 and PFT 7882 were selected; it has not been possible to detect symptoms or recover virus from detached leaves 30 days after inoculation. The transfer of such resistance to wheat is now being attempted through backcrossing, with apparent success in the third backcross.

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In tests involving field inoculations, resistance to the vector has been shown to be an important trait. Lines having resistance to *M. dirhodum*, *Sitobion avenae* and *R. padi* in the young plant stage have suffered less damage than lines having greater tolerance to BYDV but more susceptibility to the vectors. Field tests under Passo Fundo conditions, however, were not conclusive due to the high natural occurrence of the virus most years, which made keeping the checks free from virus very difficult. For that reason, tests for both resistance and tolerance are now carried out in nylon netting screen houses with controlled inoculation and adequate checks. A lack of relationship between symptoms and damage has been observed in many cultivars; therefore, it is important to assess the affects on productivity under uniform conditions of treatment. For example, the varied use of insecticides among inoculated lines or cultivars and checks may mask the fact that a lowering of production in many cultivars may be due to the phytotoxicity of the insecticides.

In barley, the resistance of cultivar WPGM 626-46-25, one which has performed very efficiently for the virus isolates existing in southern Brazil, has been incorporated into other lines by backcrossing. The most advanced lines in this program are already being tested and it is expected that, in the next few years, new lines will be available for production purposes.

So far, no studies on BYDV isolates with either the electron microscope or serology have been carried out in Brazil. However, isolates differentially transmitted by *R. padi*, *R. maidis*, *S. avenae*, *M. dirhodum*, and *Schizaphis graminum*, as well as nonspecific isolates, have been detected. Differing reactions of cultivars to isolates transmitted by *R. padi* and *M. dirhodum* have been observed; for example, the cultivar Nobre is tolerant to the isolates transmitted by *M. dirhodum* but shows little tolerance to those transmitted by *R. padi*; the cultivar Maringá has the exact opposite reaction. Similar variation in isolate response has been observed in Anza.

Vector-specific isolates vary in their symptom severity, some cause rosetting and death of the barley cultivar Black Hull-less, while others cause only mild symptoms. This evidences a pathogenic variability among vector-specific isolates, making necessary a broader assessment of the sources of resistance and tolerance under study.

Breeding work for BYDV resistance in wheat is being carried out in Brazil in collaboration with O. de Sousa Rosa, in barley with E. Minella and in triticale with A.C. Baier. Mrs. G.E.L. Marques is working on resistance to vectors and D.N. Gassen and F.J. Tambasco on biological and chemical control of BYD.

Chile

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Barley yellow dwarf (BYD), an important disease of cereals in Chile, has been observed since 1972. In 1975, it appeared in epidemic form, causing severe damage. The estimates of losses in wheat production ranged between 10 and 60% in various parts of the country during 1975, 1976 and 1977. Although BYD is observed every year in all of the wheat growing regions of Chile, its incidence varies from locality to locality. The aphid-virus complex seems to be more concentrated in the northern part of the country where it causes severe crop losses; there the central irrigated valley suffers more damage than the humid Pacific coast.

In 1977 and 1978, surveys were made to determine the main wheat diseases in north central Chile. Observations were based on periodic visits to given wheat fields, from the Aconcagua Valley to Curicó. BYD and septoria leaf blotch were found to be the most prevalent diseases in the central plain, and septoria leaf blotch and yellow leaf spot on the coast.

Three aphid species, *Metopolophium dirhodum*, *Sitobion avenae* and *Rhopalosiphum padi* were found to be primarily responsible for barley yellow dwarf virus (BYDV) transmission to cereals in Chile. In the central valley, major damage is caused by *M. dirhodum*; the other two predominate in the coastal region. The PAV-like isolate is most prevalent in the north, and a mixture of PAV and MAV-like isolates in the south.

In the summer, the three main vector species are found in the Andean ranges and in ravines where spontaneous gramineae are abundant. Aphid colonization in the north central valley starts in February, with the population increasing during the fall. In the winter, population levels are reduced, but spring brings a population increase which, in the last few years, has reached a peak in November. The wheat crop matures in December, after which the aphids migrate to the Andean uplands and to the south. In June or July, after the crops have been established, the aphids migrate to the coastal area; before that, due to the absence of rainfall, host plants are not present.

The appearance of BYD has caused a significant change in the cultivars grown in Chile. Wheat cultivars such as Huelquén and Candealfén, both very susceptible to BYDV, have been replaced by more tolerant cultivars, such as Aurifén and SNA-1(Anza). One cultivar, Tolbay-INIA, has shown a high level of tolerance in tests in Chile and Brazil; it shows average losses to BYD of less than 5% per year.

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From 1976 to 1982, there was a decrease in aphid populations in the country as a whole. In the north central area, this decrease was from about 40 aphids per tiller on farmers' fields to less than 10, mainly due to lowered population levels of *M. dirhodum* and *S. avenae*. This has led to a change in the proportion of cereal aphid species, with an increase in the relative abundance of *R. padi*. The lower incidence of *M. dirhodum* and *S. avenae* may be related to the introduction of several micro-hymenoptera parasites into the country by the INIA Biological Control Program; at least three of the species have become well established. These natural enemies appear to be so effective that direct feeding damage historically caused by *M. dirhodum* and *S. avenae* has nearly disappeared.

Since 1976, INIA has worked on various aspects of the BYD problem, aphid populations and species, losses due to the virus and the aphid-virus complex, and a program for integrated biological and cultural control. Research is now being concentrated on artificial inoculations of BYDV to test the levels of tolerance of the various phenotypes within the national breeding program.

The Andean Region, with Special Emphasis on Ecuador

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Although observations indicate that economic losses due to barley yellow dwarf (BYD) occur in Colombia, Ecuador, and Peru periodically, national as well as international resources do not permit major efforts in BYD research. Indeed, since resources are not even adequate for the general cereal breeding programs, it is doubtful that much effort will be placed on BYD research without specific international support.

Periodic visits to experiment stations as well as to farmers' fields in the Andean region indicate that *Metapolophium dirhodum* and *Sitobion avenae* are most common in wheat fields. To a lesser degree, *Rhopalosiphum padi* and *R. maidis* have also been observed; *Schizaphis graminum* is common in Bolivia. As far as can be ascertained, barley yellow dwarf virus (BYDV)-vector relationships have not been investigated in any of those countries.

In Peru, during 1980, drought in the highlands appeared to be associated with increased incidence of BYD in the Huaylas Valley, a major wheat and barley growing area. Many irrigated fields of wheat and barley showed incidence levels of more than 90%, based on symptoms. The most common aphids were *M. dirhodum* and *S. avenae*. It was hypothesized that the aphids were moving from dying weeds, and perhaps maize, to the irrigated cereals.

In Ecuador, work with BYD has had two goals, the establishment of the etiology of the disease and the determination of its effect on on-farm research, especially as related to fertilizer trials and recommendations.

In addition to *M. dirhodum* and *S. avenae*, the most numerous aphids in Ecuador, a *Rhopalosiphum* sp., probably *R. padi*, is present to a lesser extent; *R. maidis* has also been identified. Observations show that aphids in the wheat growing area continuously reproduce asexually; thus, viruliferous aphids are present all through the year.

Thirty-three samples of wheat, barley, oats, rye and triticale, collected principally at the Santa Catalina Experiment Station near Quito in 1981, were tested for BYDV by R.M. Lister of Purdue University, using ELISA. Only PAV-Ig and RPV-Ig were used. Sixty-four percent of the samples were positive for either PAV-like isolates, RPV-like isolates or mixed. The other 12 samples could have carried other isolates or could have been the result of misdiagnoses of symptoms in the field. Wheat samples contained only the PAV-like isolate. It is probable that both *M. dirhodum* and *S. avenae* are transmitting the RPV-like isolate.

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During June, 1977, severe BYD-like symptoms were observed in the north of Ecuador and at the Santa Catalina Experiment Station (INIAP). Since the on-farm research program was beginning to establish experiments in that area, there was concern that BYD could increase the variability in the data obtained. Therefore, in 1980, experiments were established for controlling aphids with systemic insecticides and for determining the extent of loss due to BYD. These were carried out in conjunction with experiments dealing with technology generation at the farm level. Losses combined over three sites and attributed to BYD showed that the cultivar Chimborazo showed a loss of 20% in yield potential and the cultivar Altar, 17%.

Similar data were obtained in other years. An independent loss determination in one field of the cultivar Chimborazo, where 100 healthy plants and 100 plants with BYD symptoms were randomly sampled, is shown in Table 1. Incidence of BYD was determined to be 42%.

Yield loss due to BYD was estimated to be about 17%; only grains per spike and grain weight were significantly affected. Observations indicated that infection occurred well into the stem elongation growth stage. Confirmation of loss levels independently of insecticide trials tended to preclude bias due to the interaction of cultivars and insecticides. Unsprayed checks were observed for the presence of other

Table 1. Effect of BYD on Components of Yield of Wheat Cultivar Chimborazo, Cayambe, Ecuador, 1980

	Yield components		
	Spikes/plant	**Grains/spike**	**100-grain wt (g)**
Without BYD symptoms	4.05	46.74	3.13
With BYD symptoms	4.28	33.22	2.65
Difference	0.23NS	13.52***	0.48***

NS Non-Significant
** Significant (P=0.001)

insects and nematodes to ascertain if they were affecting yields; none were found. Although number of aphids per plant was seldom checked, counts were generally low, discounting any significant effect on losses due to aphids alone.

The concern about the effect of BYD on fertilizer trials in growers' fields prompted the confirmation of this information by other experiments. In 1983, two of four replications of on-farm fertilizer trials were protected with systemic insecticides to estimate the effects of BYD. Each replicate contained 17 fertilizer treatments; the experiments were carried out at five sites. Data presented in Table 2 show a selected, representative portion of the treatments.

Again, losses attributable to BYD were within the range observed over the years, i.e., 10 to 30%. It is obvious that, without insecticide protection, there is a significant effect of BYD but, since the on-farm experiment represents farmer reality, plots used for deriving recommendations will not be sprayed in the future. The on-farm effort will investigate the economic feasibility of insecticide use for reducing the effects of BYD but, even if it is found to be economical, it is hoped that insecticides will be only a stop-gap measure. Within the economic realities of the Andean region, breeding for resistance is the recommended solution.

Table 2. Combined Analysis of Fertilizer Trials for BYD Loss Determination (Two Replications Sprayed and Two Unsprayed)

Fertilizer treatment (kg/ha)	Yield (kg/ha)		Yield loss (%)
	Sprayed	Unsprayed	
0- 0-0	736	658	11
40-40-0	1216	891	27
80-40-0	2255	1559	31
120-40-0	2446	1998	18
160-40-0	2715	2022	26
Mean of all 17 treatments a/	2134	1587	26
LSD .01 = 346 kg		CV 32.3%	

a/ Data combined from five sites and all cultivars

Mexico

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Barley yellow dwarf (BYD) has been observed for the last 30 years in northwest and central Mexico, especially in barley grown either under irrigation or dryland conditions. The incidence of the disease has been less in wheat, oats and triticale.

The aphid species *Rhopalosiphum padi*, *R. maidis*, *R. rufiabdominalis*, *Shizaphis graminum*, *Metopolophium dirhodum*, *Sitobion avenae* and *Diuraphis noxia* are found widely distributed in cereal crops. However, nothing is known of the relative ability of those species to transmit barley yellow dwarf virus (BYDV).

The production losses caused by the disease have not been determined for any of these four small grains. No research priority has been given to BYD in Mexico although, in the national breeding programs, the new improved cultivars are checked for resistance to the barley yellow dwarf virus.

USA

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Significant progress has been made in reducing the impact of barley yellow dwarf (BYD) on the production of barley and wheat in California during the 32-year interval since its first recorded occurrence and subsequent identification in 1951. The first two tolerant barley cultivars possessing the *Yd2* gene, CM 67 and Atlas 68, were released in 1967. The subsequent releases of four additional tolerant cultivars with varying agronomic characteristics (UC 566, CM 72, Sutter and Prato, all with *Yd2*) have provided California growers with a choice of tolerant barley cultivars. During the 16-year period since the first release of cultivars possessing the *Yd2* gene, there has been no indication of any reduction in its effectiveness; it appears to provide protection against all isolates present in California.

All wheat and barley cultivars grown in California in 1951 were highly susceptible to BYD, and a screening program yielded only moderately tolerant types from the USDA World Collection. One source, CI 13232, was useful in the breeding program, but the derived resistance was little or no better than that of Anza, which was shown to have tolerance in 1969. Anza and Yecora Rojo have been the dominant wheat cultivars in California for the past five years, planted in about equal acreages. Although the tolerance of Anza is not as high as desired, it has been effective in reducing BYD damage, a contributing factor to its high productivity, especially in the Sacramento Valley. Although Yecora Rojo, the predominant cultivar in the San Joaquin valley, shows substantial BYD symtoms, it possesses some tolerance; this is readily apparent when it is compared with the susceptible cultivar, Ramona 50, the predominant variety in 1951. However, like Anza, its tolerance is not adequate for complete protection.

Oats are grown primarily as a hay crop in California and BYD damage is severe most years; all cultivars are susceptible. A screening and breeding program is now in progress. (The highest level of tolerance identified thus far comes from the Brown-Jedlinski program in Illinois.)

Prior to the release of tolerant cultivars of barley and wheat, losses were reduced to some extent by avoiding early fall and late spring planting. An indication of the widespread distribution of BYD in California and the losses that can occur under field conditions, and conversely, the contribution of tolerant cultivars, is provided by the comparative yields of the two isogenic barley cultivars (California Mariout-susceptible and CM 67-tolerant) when tested in widely scattered locations throughout the principal cereal areas of California. In 19 location x yield comparisons, the tolerant cultivar had a mean yield superiority of 19% over its susceptible counterpart, with individual test differences as high as 60%. This yield differential is attributable to the difference in their reactions to BYD.

Although tolerant cultivars have been grown in California for a number of years, the BYD virus continues to be widespread throughout the state, as indicated by symptom expression on wild oats, an important component of the annual grasses of winter rangelands. The endemic nature of BYD in California could be expected since the major small grain areas are

encompassed by rangelands whose native vegetation serves as a reservoir for both the virus and the vectors. Hence, the continued development and utilization of tolerant cultivars is imperative.

Recent studies by F. Gildow (formerly University of California, Berkeley) have shown that the PAV-like isolate is the most common in California (75%), followed by the MAV-like (19%) and the RPV-like (6%). Prato barley, which possesses the Yd_2 gene derived from CM 67, is tolerant to all three isolates. The oat cultivar, Kanota, was shown to be tolerant to the most prevalent isolate, PAV, but is susceptible to the other two.

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Barley yellow dwarf (BYD) is a disease of small grains of regional and national importance. It is most devastating to oats, barley and wheat, especially very early planted winter wheat and barley and late planted spring small grains.

Severe epiphytotics have been recognized in the USA almost every year since 1907, with the one in 1959 causing a 28% decrease in total oat production in Illinois; similar losses were recorded for other states. In tests in Illinois, wheat yields decreased an average of 63% after fall infection with barley yellow dwarf virus (BYDV) and 41% after spring infection, although the symptoms often were not readily recognizable.

Research at the University of Illinois represents different disciplines and involves both basic and practical approaches. It is a cooperative effort between the Illinois Agricultural Experiment Station and the Agricultural Research Service of the USDA. Plant pathologists and plant breeders working with different isolates of the BYD virus and its aphid vectors have developed and released highly tolerant oat germplasm and oat cultivars such as Brave, Jaycee, Lang, Larry, Ogle and Otee for use by growers and plant breeders. Those varieties have significantly increased oat yields in the United States during the past ten years.

Much less progress has been made with winter wheat. No outstanding sources of tolerance to BYDV have been discovered to date among the over two thousand selections tested at Urbana. However, field research has shown winter wheats to differ in their response to BYDV, and it is believed that the level of tolerance can be improved genetically and that productive wheat germplasm lines and cultivars with better BYDV tolerance should be available in the future.

Following are some of the major objectives that will be pursued in this effort:

- To screen wheat germplasm (cultivated wheats and wild relatives of wheat) for sources of BYDV tolerance;
- To determine the level of BYDV tolerance in presently grown cultivars of winter wheat (evaluations to include advanced experimental lines from various wheat breeding programs with field evaluations being made under Illinois conditions using Illinois virus isolates);

- To determine the nature and extent of the interactions of wheat cultivars and germplasm with date of BYDV infection (fall versus spring) and how the infection interacts with other factors such as soil-borne and air-borne pathogens and winter damage;
- To evaluate, with the additional funds available for germplasm enhancement, the USDA collections of winter wheat and spring oats for BYDV tolerance;
- To continue research on other virus-vector-host interactions, and
- To participate in uniform BYDV nurseries that may be developed, especially those for winter wheat but possibly also some for spring wheat, barley and oats.

J.E. Foster, USDA, Purdue University, and R.M. Lister, Purdue University (Indiana)

Since the severity of a problem generally determines the effort devoted to its solution, some time has been spent in the Purdue-USDA small grains improvement program demonstrating the losses in wheat yield that can be attributed to barley yellow dwarf (BYD). Those had been largely overlooked since symptom expression in wheat is usually not as obvious as it is in oats and barley. It is believed that there is always a 10% loss in wheat yield due to BYD; even when relatively little evidence of the disease is evident. Various workers have shown BYD-related yield losses in wheat as high as 86%, clearly showing it to be a major disease requiring an intense research effort.

The historically severe yield losses from BYD in 1907, 1949 and 1959 sparked research in Indiana. It was observed that winter wheat there sustained substantial losses in yield in 1972, 1973 and 1976, indicating a need for expanded research. Therefore, a detailed series of experiments was set up to determine the effect of BYD on winter wheat yields, using controlled infestations with viruliferous aphids and planting dates set to escape natural infestations; comparisons were made using several cultivars and experimental lines. Measured losses ranged from a low of 5% by a resistant cultivar when infested in the spring to 85% for a susceptible cultivar infested in the fall. There were wide differences between cultivars in the extent of symptom expression and in degree of loss sustained. Since nearly all currently grown cultivars of soft wheat in Indiana are highly susceptible, it is felt that the estimate of a 10% yield loss each year is very conservative.

The 1983 season was the first in Indiana for commercial production of the new BYDV-resistant wheat cultivar, Caldwell. As a result, there were many reports by farmers of yields in excess of 6,800 kg per hectare. The existing wheat yield record in Indiana of 6,450 kg per hectare was established in 1961 and, it is interesting to note, that record held until this BYDV-resistant cultivar was released.

D.T. Sechler,
University of Missouri

Barley yellow dwarf (BYD) first attracted major attention in Missouri in 1959. Until then, except for 1949 when a heavy red leaf infection was observed on oats in southwest Missouri, damage from the disease had apparently been spasmodic and scattered. In 1959, the loss in oat yield was estimated at 37%, with estimates ranging from 2 to 70% in different areas of the state. Since 1959, major BYD epidemics have occurred in 1964, 1967, 1976 and 1978; some damage is evident every year.

The most serious damage from BYD occurs in spring-seeded oats, although winter barley can also be severely damaged. Leaf discoloration, variability in tiller height, and blasting of the florets is common in oats; these symptoms of barley yellow dwarf virus (BYDV) infection have been associated with reduced grain and/or forage yield and quality. Fall infection of winter barley with BYDV can result in stunting. In more tolerant cultivars, symptom expression is usually in varying degrees of leaf discoloration; root systems are reduced and plants are more susceptible to winter injury and/or drought. The damage to wheat is less obvious. Fall infections result in leaf discoloration (yellow to red depending on the cultivar), height variation and reduced root development. Reductions in grain yield are more drastic from fall than from spring infections. The yield reduction in wheat is usually less than that in oats or barley but, because of the magnitude of the wheat area, the economic loss is greater.

While wheat acreage in Missouri has increased to about 1.2 million hectares, oat and barley acreages have decreased to less than 81,000 ha. Factors other than disease were largely responsible for this shift, although the severity of BYD on oats and barley and its impact on relative performance were also undoubtedly influencing factors.

Small grains occupy less than 7% of the cultivated area in Missouri and are not grown during the summer months (July-September). On the other hand, tall fescue is grown as a perennial hay and pasture grass on over 1.62 million hectares and is the most prevalent grass on roadbanks. Studies utilizing tall fescue plants collected at random from roadbanks in 90 Missouri counties found 60% of the plants to be infected with a virus that was transmitted by *Rhopalosiphum padi* and showed symptoms typical of infection by BYDV on Grundy oat seedlings. Tall fescue is the major pasture grass in Missouri and apparently is a reservoir for BYDV infection. Although BYD symptoms are not normally observed in field plantings, Kentucky 31 tall fescue seedlings, under controlled environmental conditions, have been found to express leaf yellowing when infested by *Sitobion avenae* carrying BYDV isolate Champaign 6.

Not only are host plants for BYDV generally present in all areas of the state, but the aphid vectors are also commonly identified. In systematic monitoring at Columbia, Missouri, over a three-year period, *R. padi*, *R. maidis* and *Schizaphis graminum* were

collected in both fall and spring. Aphids collected from 99% of the colonies transmitted a virus that produced typical BYD symptoms on Grundy oat seedlings. In the fall of 1982, an additional species, *R. ruflabodminalis*, was identified on barley.

The magnitude of the economic loss in small grains from BYD and the inadequacy of alternative control measures necessitates the highest priority being given to the incorporation of genetic resistance to BYDV in oat and barley cultivars for Missouri. In wheat, other diseases have received greater emphasis in the breeding program, although improved BYDV tolerance is also an important goal.

T.W. Carroll,
Montana State University

In 1980, barley yellow dwarf virus (BYDV) caused an epidemic in winter wheat in the central Montana counties of Judith Basin and Fergus; August and early September plantings were most severely affected. About 25,000 hectares were involved, and the loss was estimated conservatively at $1.8 million. The approach adopted to control the disease was to delay planting of winter wheat until after the tenth of September, thus avoiding large numbers of aphid vectors.

In 1981, there was a second barley yellow dwarf (BYD) epidemic in central Montana, with the virus present in about 50,000 hectares of early planted winter wheat in Pondera and surrounding counties. Loss could not be estimated with any degree of accuracy since much of the area was also severely infected by wheat streak mosaic virus. Again, planting after the tenth of September was recommended for controlling BYD.

In 1982 and 1983, there was only a low incidence of BYDV in spring barley and wheat in central Montana. No virus was recovered from winter wheat, presumably because most of the crop had been planted after mid-September. Since field surveys have determined that BYD has been a problem only in early planted winter wheat in that region of the state, it is believed that the proper choice of planting date can keep the disease at an acceptable economic level in all small grains. Losses due to the virus since 1981 have been minimal.

Future BYDV work by the Montana Agricultural Experiment Station will be limited to some surveillance of small grain fields in central Montana. High priority will be given to the development of barley, and perhaps wheat, populations having tolerance to BYDV; the latter effort will be funded by a research contract with US A.I.D.

Canada

A. Comeau, Agriculture Canada

Observations in Canada between 1965 and 1983 indicate that a barley yellow dwarf (BYD) epidemic in spring cereals takes place about every four years. Recent work (1978-1983) indicates that BYD on winter cereals may also be very serious in Quebec and Ontario. There was 100% barley yellow dwarf virus (BYDV) infection on winter cereals in the Quebec area in October, 1982, contributing to heavy winter kill. As a result, farmers almost stopped growing winter cereals and BYDV resistance is needed for winter wheat to return to being a viable crop in Quebec.

BYDV research in Quebec is concentrated on the rearing of BYDV-infected aphid vectors for the use of plant breeders. Studies of the epidemiology of BYDV have also been pursued. In evaluating germplasm, a global approach has been used, for example, all of the species of the genus *Avena* are tested. *Avena sterilis* from a large number of geographical locations have also been tested in the attempt to locate species having greater resistance to BYDV. An international approach has been one of the goals, and collaborators from the United States (C.O. Qualset and H. Jedlinski), New Zealand (J.M. McEwan) and Brazil (V. Caetano) have helped in establishing collections of resistant germplasm.

The late Dr. Anderson of CIMMYT requested that CIMMYT material be tested in Canada and, in 1981, the International Development Research Centre of Canada gave its support to a joint project between Laval University and Agricultural Canada for testing CIMMYT and ICARDA breeding materials for BYDV reaction.

Rapid progress was made in barley with Ethiopian barleys as resistant parents. In oats, Illinois oats and *Avena sterilis* were used. In triticale, some lines have shown good resistance and, in bread wheat, Anza and BuckBuck selections and Brazilian wheats have had some value. However, interspecific hybrids have given much better results, and large collections of wheat x *Agropyron*, wheat x *Elymus* and wheat x triticale are tested using international sources and the results of local interspecific hybridization work.

Recent academic studies have dealt with the inheritance of BYDV resistance in oats (interspecific), barley and winter wheat; triticale and wheat x triticale and wheat x *Agropyron* are now being tested. There has been more emphasis on the development of major genes than in the pyramiding of minor genes in Quebec, although both approaches have been used.

Britain

R.T. Plumb, Rothamsted Experimental Station

Barley yellow dwarf (BYD) is the most important virus disease of cereals in Britain. Surveys of spring-sown barley from 1967 to 77 and winter-sown wheat from 1971 to 77 showed that up to 90% of the crops were infected in any one year. Autumn-sown cereals are especially damaged by BYDV if infected when young; autumn-sown barley infected before it tillers can be killed. The recent increase in the area of barley sown in autumn and the trend to early sowing (September) has increased the exposure of this crop to infection.

BYDV is ubiquitous in grasses, which provide its principal perennial source. *Lolium* spp. are the most commonly sown grasses in Britain, and all *Lolium* cultivars are susceptible to BYDV. Maize is also infected and may be a locally important source of infective aphids in the autumn, although it is not grown widely enough to increase the inoculum significantly.

Several aphid vectors of BYDV are regularly present, although their numbers fluctuate from year to year. The principal vectors are *Rhopalosiphum padi, Sitobion avenae* and *Metopolophium dirhodum;* other vectors are *S. fragariae, M. festucae, R. insertum* and *R.maidis.* BYDV is usually introduced into crops, especially in the autumn, by *R. padi,* but that aphid may also spread virus during the early part of the winter. *S. avenae* also introduces virus and, in some years, can damage crops directly when it feeds on ears in large numbers. *M. dirhodum* rarely introduces virus and, although it can spread virus when its numbers are large, this normally occurs too late to cause serious crop loss.

Strains of BYDV have long been recognized by the efficiency of their vectors in transmitting them and by their hosts. Recently, serological studies have shown that the strains are serologically as well as biologically distinct. Detailed studies may reveal strains that have specific aphid vectors but, while the importance of strains in virus epidemiology is without doubt, the recognition of only two nonspecific strains, B and F, has proved of great value in Britain. Strain B is the more damaging and its efficiency of transmission by single aphids is, approximately, *R. padi,* 90%, *S. avenae,* 40%, *M. dirhodum,* 25% and *M. festucae,* 5%. Strain F efficiency is *R. padi,* 20%, *S. avenae,* 70%, *M. dirhodum,* 100% and *M. festucae,* 30%. When young plants are infected, the losses caused by strain B are at least twice those of strain F. Antisera to the two strains reacted with more than 90% of the British BYDV isolates tested, as well as with isolates from Australia and Chile.

(continued)

There are regional differences in the incidence of the two strains. B-type strains are predominant in western, especially southwestern, Britain, while the F-type strains are most prevalent in the eastern regions. This difference in distribution is probably related to the ability of the vectors, especially *R. padi*, to survive the winter on hosts of BYDV.

There are large differences in virus incidence between years and regions. Infection can result in complete crop failure, especially when autumn sowing follows a grass sward that has been incompletely destroyed; this, however, is exceptional. Recently, an increase in volunteers, especially of winter barley, and grassy stubble has resulted from minimal tillage and the early harvest of winter-sown barley. This has increased the risk of early, damaging virus infection caused by aphid transfer from volunteers or grasses to the emerging cereal.

Autumn-sown crops in some regions of England and Wales have been designated as virus-prone, principally in the south, southwest and southeast coastal regions. In those regions, farmers are advised to spray all September-sown crops with aphicide. Optimum spraying time is the end of October and the first two weeks of November. Until now, BYDV has caused little apparent damage to cereals in Scotland.

Because of regional and seasonal differences, it would not be very informative to give a figure for average yield losses due to BYD, even if one were known. However, as the cereal crop in England and Wales is worth approximately £ 2,500 x 10^6 ($3,675 x 10^6 US), even a 1 to 2% yield loss is worth preventing, either through the use of pesticides or by sowing after aphid flights have ended.

Most research effort has concentrated on virus epidemiology, and a forecasting system is now in operation for autumn-sown crops. During October and November, advice is given about which crops are likely to benefit from autumn aphicide spraying. This advice is based on measurements obtained at nine sites in England and Wales on numbers of aphids caught in suction traps, on aphid infectivity and on crop-growth stage. In contrast, spring-sown crops are most at risk when sown late; those sown after mid-April are especially at risk.

There has never been a large program on breeding for resistance to BYDV, principally because of the success of chemicals in controlling virus spread and the difficulty in getting expression of the Yd_2 gene in cultivars adapted to British conditions. Because of cuts in government-funded agricultural research, it seems likely that even the small current breeding effort will stop.

Ireland

M.J. Foxe, University College of Dublin, and A.M. Feeney, Oakpark Research Centre

Barley yellow dwarf (BYD) has become an increasingly important problem in cereal crops in Ireland, largely due to increased emphasis on the growing of winter cereals in recent years. Both autumn-sown barley and wheat have increased in popularity because of their high yields and the generally better weather conditions for sowing. Barley yellow dwarf virus (BYDV) infection of these crops has become increasingly serious with significant yield reductions reported. Still further losses due to BYD are predicted because of the tendency by growers to sow crops as early as possible in September, thus encouraging severe aphid infestations in October. Because of the potential threat of BYD, growers are beginning to routinely spray for aphids, although there is not yet sufficient information available on the infectivity of the aphid populations present.

Although BYDV appears to be widespread in Ireland, little is yet known as to the strains of the virus that predominate; research is currently under way for the identification of the major strains through the use of the enzyme-linked inmunosorbent assay (ELISA). So far, both PAV and MAV-type isolates have been encountered in barley, wheat and oat samples. There is also a lack of information regarding the major vectors, although *Sitobion avenae* and *Rhopalosiphum padi* have been identified as the primary vectors in Ireland.

There is considerable interest in identifying the predominant strains of BYDV, determining the distribution of BYDV in winter and spring cereals and in ascertaining the major vectors. Research in the three areas is under way, with an early goal being that of a monitoring system to determine the risk to early-sown winter crops of aphid infestation and, thus, to assess the necessity for spraying.

With the increasing amount of BYDV infection in Ireland, particularly in winter cereals, growers are concerned about potential losses and the possibilities for limiting the spread of BYDV. Other research areas under current investigation include the purification of strains of BYDV and the development of methods for increasing the sensitivity of the ELISA detection system for testing plants and aphid vectors. Future goals include the development of monoclonal antibody systems for antiserum production for the different strains of BYDV.

Italy

R. Osler, Universitá di Udine

Barley yellow dwarf virus (BYDV) was detected for the first time in Italy in 1958, but damage began to be economically important only after 1960. Barley yellow dwarf (BYD) now represents a serious problem for a few crops and its incidence is on the rise.

Fall-sown barley suffers heavy loss to the disease, and BYD has become one of the most important diseases of rice in the country. In wheat, BYDV infection is more prevalent each year. Until a few years ago, maize was just a possible host for BYDV but, at present, there is some worry that the pure lines of maize especially may experience yield loss because of the disease. Perennial ryegrass (*Lolium perenne* L.) and oats often show some damage. Factors that may have contributed to the spreading of the disease in recent years are an increasing aphid population found on gramineae, earlier fall sowing by farmers and milder autumn weather.

The principal BYD aphid vector in Italy is *Rhopalosiphum padi* followed, in that order, by *Sitobion avenae* and *Metopolophium dirhodum*. The strains of BYDV present are PAV-like and RPV-like, i.e., the strains connected with *R. padi*. They are found in maize as well as in the small grains. Three suction traps have been operating in Italy since 1981, permitting the collection of data on the winged aphid populations and their infectivity.

BYDV, especially in maize, has been studied with electron microscopy, in crude extracts and in ultrathin sections, and by serological tests, mainly using ELISA techniques. Other studies have been carried out on the comparative transmissions by aphid vectors maize-to-maize and maize-to-other gramineae. SEM X-ray microanalysis has supplied interesting data about K^+ content in the reddish portions of infected maize leaves.

In natural and experimental tests, it has been possible to detect rice cultivars and lines resistant to BYDV. No resistant barley cultivars have been found. Maize hybrids and wheats have shown good tolerance to infection. Epidemiological observations have led to good results in preventing infection in barley crops by late fall sowing.

At present, research on BYDV in Italy is concentrated in three main areas: 1) further study of the disease as it effects maize; 2) the acquisition of more information on epidemiology, and 3) the search for resistant or tolerant varieties.

Iberian Peninsula

S. Fuentes, CIMMYT, Portugal

Due to severe drought in the 1982-83 crop season in Portugal and southern Spain, symptoms of barley yellow dwarf (BYD) were difficult to assess in commercial wheat crops. Abundant aphids in the screening nurseries at Elvas, Portugal, caused extensive yellowing but no stunting in triticales (3 to 4 on the conventional scale). Durums were more damaged than bread wheats, but effective screening was not possible due to the heavy incidence of yellow rust and septoria.

High BYDV incidence was recorded in May, 1983, at the Experiment Station of Lerida, north of Barcelona, Spain, where extensive fruit orchards and grasses provide a reservoir for the vectors. In the 10th IBON, a CIMMYT nursery, 90% of the entries showed reactions of 4 to 9. The most resistant entries (reaction = 1.0) with excellent agronomic type were 39, 72, 176 and 237. In the 16th IBWSN, also a CIMMYT nursery, 86% of the entries had readings of 4 to 9; the most resistant (reaction = trace to 1.0) were the following: 9, 11, 42, 55, 88, 162, 198 and 199.

Spain

A. Alfaro, Universidad Politécnica de Valencia, and F. Montes, Instituto Nacional de Investigaciones Agrícolas

Barley yellow dwarf (BYD) was described in literature in Spain for the first time in 1978-79 as a result of a study performed on paddy rice in the Valencia region on the east coast, an area far from other cereal growing areas. However, the disease was already well-known there, having appeared as endemic on transplanted rice for at least the last sixty years. There was a positive diagnosis of BYD on wheat and barley in Lerida in northeastern Spain at the same time and, in 1980, it was identified in Seville in southern Spain and in Alcalá de Henares in the central part of the country. The records from those areas corresponded to those of experimental farms where breeding or cereal nurseries were maintained.

Annual records have been carefully kept in Spain and show that the prevalence of BYD is quite recent. The first report of the disease on cereals other than rice had been from Alcalá de Henares where it appeared in the winter of 1971-72; it did not show up again there until 1976.

The degree of dispersal of BYD on cereals seems to be quite different in the three areas. It does not show up in open fields at Alcalá de Henares and it has a scattered distribution in the Lerida area; it appears more widely in southern Spain.

In the Valencia study, *Rhopalosiphum padi*, fed through membrane on purified extracts of diseased cereals and rice, transmitted the disease to graminaceous hosts. This aphid is generally the dominant early species in the effected areas, and its flight incidence was the one which fitted the timing of the disease outbreaks in rice in 1979-1980. No attempt was made to estimate the infectivity of individual aphids.

The incidence of the disease on rice has been drastically reduced as a result of the crop being sown directly from seed instead of being transplanted. Systematic experiments show that this reduction is due to the resulting difference in sowing dates.

Records that had been kept on disease intensity on experimental stands at the Arrocera Station at Sueca, Valencia, made possible a successive multiple regression test comparing that information to meteorological data (15 x 38 matrix). The 75% of variability was explained by a linear equation with a single variable, the number of days in November and April with mean temperatures below 10°C.

Nursery data obtained from southern Spain over the last three years indicate that the collections of durum wheat show BYD symptoms much more frequently than do those of bread wheat.

Egypt and the Near East

T. Abdel-Hak, Agriculture Research Center

As early as the 1940s and 50s in Egypt, barley yellow dwarf (BYD) was common on barley and wheat; wheat striate mosaic was common on wheat only. In general, infections of BYD were found in late seeded fields (December) and infection of wheat striate mosaic in early plantings (early November). At that time, the main method for controlling BYD was that of aphid control through the use of the insecticide, nicotine sulphate.

In 1961, a severe epidemic of wheat striate mosaic reached an infection level of 70% in some wheat fields as a result of favorable environmental conditions, earlier planting dates than normal and the highly susceptible commercial cultivars of the time, including Giza 145, Giza 147, Giza 148 and Mokhtar. Since then, screening for resistance to BYD and wheat striate mosaic, as well as to the rusts and smuts, has been routine in Egypt.

As a result of extensive tests, the cultivar Giza 155 was produced with resistance to wheat rusts, bunt and flag smuts, BYD and wheat striate mosaic. This variety was released about 16 years ago and is still successfully grown without any damage from rusts and smuts or from virus diseases. In fact, both BYD and wheat striate mosaic have been of minor importance since the 1970s; the latter disease, has disappeared but for very rare infections in late plantings of some recently developed wheat cultivars.

During the last few years, BYD has become more of a problem due to the increase in aphid populations in some governorates. BYD has been found in barley fields in almost all governorates but, in general, the infection is still slight except where large aphid populations are found. Controlling the aphids with Malathion and other insecticides has been recommended. The recorded insect vectors in Egypt are *Rhopalosiphum padi* and *R. maidis*.

Screening for resistance to BYD in wheat was carried out at the Sakha Experiment Station beginning in 1978. Three hundred seventy-one of the lines or cultivars which were found free from virus infection were tested in two successive seasons and then were tested in the greenhouse at Giza under artificial infestation with aphid vectors. The lines and cultivars selected continue to show stability in their resistance.

Fourteen commercial barley cultivars were also tested at 14 localities in Egypt during the 1978 growing season and at 16 sites in 1979 to 1981. From these studies it was concluded that the barley cultivars Giza 121, Giza 24, Borgel-Arab, Bahteem 52 and Marsi Matrouh were resistant to BYD under Egyptian conditions.

Reports indicate that BYD effects wheat and barley in most countries throughout the Near East. However, it seems that little damage results from the disease.

ICARDA Region

O.F. Mamluk and J. van Leur, International Center for Agricultural Research in the Dry Areas, Syria

Little work has been done in the ICARDA region on cereal viruses in general and on barley yellow dwarf virus (BYDV) in particular; most available information originates from reports of visiting consultants or of pathologists in the various national programs. The information is based mainly on visual field diagnosis, an insufficient basis for reliable diagnosis of viral diseases. However, the presence of BYDV in cereals, as well as other viruses on leguminous crops, is causing increasing concern in the region.

Barley yellow dwarf (BYD) seems to be widespread on wheat, barley and oats in Morocco. A very high incidence of the disease was reported in 1980 in the Tessaout area on two wheat cultivars, Nasma 149, 75%, and Kyperounda, 95%. Research on the disease is now being carried out within the Moroccan national program.

In Tunisia, where oats are grown on a large scale as a fodder crop in mixtures with vetch, BYD has been encountered on barley at a low level. Host, vector and environmental conditions favor the propagation and spread of the disease.

In Egypt, where aphids are a major pest of cereal crops, BYDV could be of great importance. The outbreak of the virus, together with that of the wheat striate mosaic (WSM), resulted in a 10% reduction in yield in the early sixties and is a warning of what could happen again.

The quantitative survey of barley cultivation in Syria in April and May of 1982 showed that 7.6% of the fields checked exhibited BYD symptoms. The incidence of the disease ranged from 0.1 to 5.5% with a severity of 0.2 to 0.6 on a 0 to 9 scale. The affected area was estimated as having a yield loss of about 9%, with the highest incidence and severity detected in zone 3 (>250 mm annual precipitation), followed by zone 4 (200 to 250 mm annual precipitation). Scattered BYD occurrence of low severity has been reported at Tell Hadya Station and off-stations.

Virus diseases are thought to be of minor importance at this time in the ICARDA region except for Morocco. In the rest of the region, BYD occurrence is discontinuous and of low severity; however, no systematic or quantitative studies are known to have been conducted to estimate losses due to BYD.

Barley in the ICARDA region is grown mainly in areas with 400 mm and less annual precipitation. In those dry, rainfed areas with a crop season and a weed-free season, the build-up of virus diseases may be low. However, cultivated maize and grasses, grown under wetter conditions next to the dry areas where barley is cultivated, constitute likely aphid and virus reservoirs for the survival of BYDV. The type of barley grown in the Near and Middle East, mainly two-rowed and with relatively rapid growth and early maturity, offers a good chance for the development of BYD.

The main vectors, *Rhopalosiphum padi, R. maidis, Sitobion avenae, Schizaphis graminum* and *Metopolophium dirhodum* are very common in the Near East. However, population density and colonization of the host are greatly dependent on weather conditions which prevail in the spring and those vary considerably from year to year.

Although cereal viruses were not included among the eight most important diseases of the ICARDA region, nine viruses were described as of possible concern. Of those nine, three, BYDV included, were chosen as warranting attention. At present, advanced breeding material is screened for resistance to the major diseases in the region in about 50 sites (Key Location Disease Nursery, Initial Disease Nursery and Observation Nursery).

In 1983, data was received at ICARDA on BYDV resistance in durum wheat under natural field infections from Elvas, Portugal, and Sevilla, Spain.

The Center receives invaluable support from Montana State University and A. Comeau of Agriculture Canada, Quebec, in evaluating ICARDA germplasm material for BYDV. In the third year of collaboration with Quebec, data provided on BYDV resistance in barley and wheat have been very useful. The material sent in the 1981-82 season represented the regional crossing blocks of barley and durum and bread wheat, since this material is suggested to the national programs as parents in their crossing programs.

Recently, ICARDA signed an agreement with IPO, Wageningen, The Netherlands, with phased development of work in viruses proposed. In the beginning, the Center will have support from IPO laboratories and expertise, and a plant virologist will be posted at ICARDA's principal station. His primary tasks will be to survey and identify viruses on crops of the region and to assist plant breeders in sceening for resistance to viruses.

The status of BYD as a problem in the Middle East has not been properly investigated and, hence, could be under-estimated. The recent disease situation, discontinuous and with low incidence and severity, may change with changing farming systems, e.g., year-round cultivation through irrigation and the introduction of pastures and forages in the fallow. The disease could become more widespread and destructive and should be watched carefully.

Turkey

E. Kinaci and K. Yakar, Central Anatolian Research Institute

Cereals, especially wheat and barley, have historically been the most important crops in Turkey; they constitute, in fact, the main food source for the people as well as feed for livestock. Approximately 75% of the arable land in the country is devoted to cereals. In a given year, 66% of the total cereal area is planted and 34% is under fallow.

Research activities in cereals were initiated in the 1920s with the establishment of research stations whose goals were the improvement of varieties and cultural practices. Studies on cereal diseases, particularly wheat rusts and bunt, were initiated in the 1930s and, with the establishment of the Wheat Research and Training Project in 1969, a nationwide, multidiciplinary research program was started. One of the main objectives of the project was the development of new, high yielding varieties with better disease resistance.

There are two major environments in Turkey where wheat is grown, the winter wheat area and the spring wheat area; a considerable amount of facultative wheat is also grown. Because of the widely differing wheat environments, new cultivars and farming practices and changes in disease patterns and pathogens often result. Therefore, a disease monitoring system was necessary for the Wheat Research Project, and a nationwide disease surveillance program was started in 1971.

In 1973, barley yellow dwarf (BYD) occurrence in Central Anatolia was first reported. It was found in several farmers' fields there as well as in low incidence in Ankara Province. Although BYD has been found almost everywhere that cereals are grown, it was not reported again until 1975 when, in a survey of cereal diseases transmitted by aphids and leaf hoppers in the Aegean region, it was reported quite frequently.

In the 1982-83 growing season, rainfall came late in the spring causing drought in Central Anatolia. Plants were under stress and dryland root and foot rots were present on a large scale. Because of the general yellowing, stunting and drying of plants, possible BYD symptoms were not noticed at the early growing stages. In the spring, during the regular survey program, typical BYD symptoms were found in field edges on grasses.

In June, 1983, BYD symptoms were found on the widely grown durum cultivars Kunduru 1149 and Bezostaja 1 in Ankara Province. It was also noted on Kunduru 1149 and on Berkmen in Cankiri Province. In some fields, more than 50% of the plants showed symptoms. Aphids were often found in the leaflets and occasionally on leaf sheaths and were identified as *Rhopalosiphum padi* and *R. maidis*, recognized vectors of barley yellow dwarf virus (BYDV). According to farmers who experienced BYD damage in their fields, yield losses were considerable, with Kunduru 1149 and Berkmen suffering the most damage.

Eastern, Central and Southern Africa

E. Torres, CIMMYT, Kenya

The striking damage to cereals by rusts and other fungi tends to obscure the impact of cereal viruses as yield-reducing factors in eastern, central and southern Africa, and there has been a scarcity of research conducted on wheat and triticale viruses in the region. Apart from barley yellow dwarf (BYD), maize streak is the only virus disease that has been regarded as a constraint in wheat production anywhere in the area.

Maize streak has been reported as a serious and constant disease of wheat along the southern boundary of the region, in Swaziland, Zimbabwe and the southern province of Zambia. *Digitaria horizontalis*, a wild African grass, plays host to the virus and its vectors in the genus *Cicadulina* (Cicadellidae). Hence, the epidemic spread of the disease may be an example of an insect-transmitted virus causing a serious crop disease when a crop is introduced into an area where the virus-vector complex is already established and adapted.

Studies related to barley yellow dwarf virus (BYDV) are very scanty. Transmission of the virus from Egyptian grasses by the aphids *Rhopalosiphum padi, R. maidis, Schizaphis graminum* and *Sitobion avenae* have been reported. A survey of cereal aphids in Ethiopia showed the occurrence of the above species as well as *Metopolophium dirhodum* and *Diuraphis noxia*.

In October, 1983, during a visit to Gopher Meda State Farm on the eastern escarpment of the Rift Valley in Ethiopia, a field of wheat of the variety Enkoy was observed with the typical distribution pattern and plant symptoms of BYD. Aphid populations had reached high levels before being controlled by insecticide sprays. Enkoy is the most widely grown wheat variety on state farms, with an estimated acreage of 50,000 hectares.

In 1978, there was a severe outbreak of *D. noxia* on bread wheat in Ethiopia, resulting in a crop loss on over 5,000 hectares. Aphid populations and their direct and indirect damage to wheat become more pronounced under mild droughts, rainfall acting as a natural population control. Wheat researchers have seen, over the years, sporadic occurrences of BYD in Kenya, but there has never been a severe outbreak.

All of this scattered information shows that BYD is not an obvious yield constraint and, therefore, is not a current research target in breeding or disease control in the region. However, data and observations suggest the presence of virus and vector complexes that may cause problems when cropping patterns change. The fact that weather conditions effect aphid populations may influence disease levels of a pathogen like BYD.

South Africa

M.B. von Wechmar and E.P. Rybicki, University of Cape Town

In South Africa little basic research has been conducted on the barley yellow dwarf virus (BYDV) as such, so that reference to it in this paper relates to the observation of an aphid transmissible disease that expresses symptoms normally associated with the virus. It has been shown, however, that a small isometric virus (+24 nm diameter) is associated with an aphid transmitted yellows disease; serological strain identification has not been done. The virions are infectious in membrane feeding studies and are not related to brome mosaic virus (BMV).

Barley yellow dwarf (BYD) was first recorded in the mid-sixties after being observed on barley, oats and wheat in the west and southwestern Cape regions. A survey conducted at the time showed that the disease was aphid transmissible (*Rhopalosiphum padi, R. maidis, Macrosiphum granarium* and *Schizaphis graminum*) and that it could be recovered by aphid transfer to indicator hosts from 48 out of 73 field samples collected over a wide area. A recent field survey (September, 1983) in the mayor production regions reinforced the earlier observations that the disease was most prevalent (noticeable) in the Swartland.

The presence of barley yellow dwarf was highlighted once more when severe infestations with *Diuraphis noxia* aphids, an aphid species new to South Africa, were noticed for the first time in small grains in the Orange Free State in 1978. Low levels of *R. padi, R. maidis, S. graminum* and *Myzus persicae* were also present. Although the predominant crop in the region is wheat, particularly strong symptoms of yellowing and dwarfing were exhibited in barley and triticale following aphid infestation; wheat, although infected, showed less characteristic symptoms.

The only data available on crop losses were obtained from controlled field experiments conducted at Stellenbosch from 1965 to 1967. Results clearly indicated that the disease could greatly limit the yield of barley, oats and wheat in the western Cape region. Severe yield reductions were recorded for oats and barley, particularly when sown early (late autumn). Differences in cultivar susceptibility were also demonstrated. More recent crop loss evaluations are not available for the reason that BYD has been shown to occur and be transmitted as the result of a complex of viruses. However, the continued presence of high aphid levels, particularly in wheat grown in the Orange Free State, points out the necessity for BYD being given high research priority.

People's Republic of China

Zhou Guang-he, Zhang Xing-cai, Quian You-ting, Zhang Shu-xiang, Cheng Zhou-min and Chen Quan, Chinese Academy of Agricultural Sciences

Barley yellow dwarf (BYD), usually called wheat yellow dwarf in China, is one of several important virus diseases of wheat and oats and has been known as a virus disease of wheat for at least 30 years. Little attention was paid to the disease, however, before 1966, when it caused a serious reduction in wheat yield. Since then, in 1970, 1973 and 1978, epidemics were recorded in northern and northwestern China in Gansu, Shaanxi, Shanxi, Henan, Hebei and Shandong provinces and in the Ningxia and Nei Monggol autonomous regions.

Yield losses from BYD have approached 100% when plants are infected early; winter wheat can even be killed as a result of fall infection. In 1970, yield losses caused by BYD in Shaanxi and Gansu provinces and the Ningxia autonomous regions were estimated at 50,000 tons.

The five aphid species that have been identified as barley yellow dwarf virus (BYDV) vectors in China are *Schizaphis graminum, Sitobion avenae, Metopolophium dirhodum, Rhopalosiphum padi* and *R. maidis.* Among them, *S. graminum* and *S. avenae* are the most important.

According to greenhouse biological tests, two isolates of BYDV have been identified. One is an MAV-like isolate transmitted by *M. avenae.* The other is an isolate transmitted by *S. graminum*; this isolate has been found to be the most destructive.

In order to discover where aphid vectors and BYDV oversummer in areas where winter wheat is grown, and overwinter in areas of spring wheat or oats, observations in the field and biological tests in the greenhouse have been carried out for five years. Results from greenhouse inoculation tests show that, besides wheat, barley, oats, rye and some varieties of maize, BYDV can also infect other grasses, such as *Bromus japonicus, Eragroseis poacoides, Briza maxima, B. media* and *Chloris virgata,* with resulting clear symptoms.

Long and short-term forecasting of aphid flights has been attempted over the last four years in an attempt to learn when vector aphid control is neccessary to reduce BYD damage in wheat. This vector control has not been particularly economical or effective in controlling BYDV. However, cultural control in the form of avoidance of early autumn or late spring seeding has helped in reducing initial BYDV infection. Also, since 1965, the use of systemic organophosphorous insecticides for seed treatment has been effective in reducing the secondary spread of BYDV in the Zhang Ye region of Gansu province.

While the best control measure for BYD would be the use of resistant cultivars, it has not yet been possible to find a BYDV-resistant source of wheat in China, although a few cultivars have been found to be tolerant. The BYD-resistant cultivar, Anza, which was introduced from California, was susceptible under Chinese conditions. Therefore, it is considered that BYDV isolates in China are different from those in the USA.

The Philippines

D.B. Lapis, University of the Philippines

After listening to the reports from the participants here regarding the presence in their countries of barley yellow dwarf virus (BYDV), I began to ask myself if I was at the right place. I could also envy those people who made the reports--they had something to justify their presence at this workshop I have almost nothing to report as barley yellow dwarf (BYD) has not been observed or identified in the Philippines. This is probably due to the facts that 1) barley, oats and triticale are not grown commercially in the Philippines, 2) wheat production on the commercial scale was begun only this year and covers only some 100 hectares, and 3) weather conditions in the country are probably not conducive to virus infection.

However, most of the aphids that are vectors of BYDV are present, as well as the various host plants, both cultivated plants and grasses. BYD symptoms have not been observed on rice but, after seeing the symptoms of the disease on corn as shown by R. Osler of Italy, I suspect that the virus might be present, especially on maize; this remains to be seen on my return. I will attempt to do some transmission studies and hope that, at our next meeting, I will have something to report on the situation of BYD in the Philippines.

Just before coming here, a telegram was received from E. Saari of CIMMYT,Thailand, asking me to report that some symptoms appearing to match those of BYD have been seen there. Aphids have also been found on wheat and barley there and have been identified as *Rhopalosiphum padi*, *R. rufiabdominalis*, *Schizaphis hipersiphonata*, *Histeroneura setariae*, *Sitobion* spp., *R. maidis*, *Melanaphis sacchari* and *Aphis craccivora*.

Australia

R.J. Sward, Plant Research Institute

In Australia, the three principal grain cereals, wheat, barley and oats, are grown primarily in areas of dryland farming where the annual rainfall is 250 to 500 mm. In those areas, the incidence of barley yellow dwarf (BYD) is low most years; in a survey of eastern Australia in 1963, the average loss was calculated to be 2%. However, a major BYD epiphytotic is recorded on the average of every five to seven years and, those years, the losses are far higher. In field trials conducted in dryland areas with wheat infected prior to tillering, losses in grain yield of almost 80% have been measured.

A small proportion of cereal crops, mainly malting barley and oats for stock feed, are grown in areas receiving more than 500 mm annual rainfall; there the incidence of BYD is high most years. In barley crops in the wetter areas of Victoria and Western Australia, natural infection causes reductions in grain yield of 35% and 22%, respectively. Local severe outbreaks have led to almost 100% of plants becoming infected at an early growth stage, resulting in grain yield losses of up to 60%.

In Australia, five species of cereal aphids have been recorded. They are *Rhopalosiphum padi, R. maidis, R. rufiabdominalis, R. insertum* (first recorded in 1983) and *Sitobion miscanthi* (until recently identified as *Macrosiphum avenae miscanthi*). Of these, *R. padi* is by far the most common, regularly transmitting a very severe, RPV-like isolate of BYDV. In one cereal-growing area of Victoria, over 60% of the alate *R. padi* trapped were infective. The other four aphid species have been shown to transmit some isolates of BYDV. Although the isolates present in Australia have not been fully determined, they have been tentatively characterized as PAV-like, MAV-like and RMV-like.

The sources and reservoirs of BYDV are widespread and varied. A range of native and introduced grasses are known hosts and, in the dryland areas, many of these survive over summer in damp roadside ditches and beside irrigation channels and watercourses.

In the wetter areas, perennial ryegrass (*Lolium perenne* L.), a major component of permanent pastures, is another reservoir of BYDV. In the southeast, where peak aphid flights occur in early autumn (March and April) and in the spring (September to November), cereal crops emerging during those periods are commonly severely infected with BYDV. Gradients of infection can be measured in crops, often with the highest levels occurring adjacent to infected pastures or stands of graminaceous weeds. Volunteer cereals also act as a virus source; they played an important role in the spread of BYDV during an epiphytotic in southeastern Australia in 1983.

Over the last 25 years, a number of major BYD epiphytotics have been monitored in Victoria and, thus, there the disease has been given a high research priority. The southern part of Western Australia, with a Mediterranean-type climate, has high levels of BYD and the research priority is moderately high; it is considerably lower in most other parts of Australia. In the warmer climate of Queensland, it is thought that aphid parasites and predators significantly restrict cereal aphid numbers; there BYD is considered a low priority problem. In the other two cereal growing states, New South Wales and South Australia, the incidence and importance of BYD are poorly defined and the research priority is low.

Until recently, BYD had not been considered a major problem in Tasmania; its cold wet climate is not conducive to large autumn aphid flights. However, Paul Guy, in his work on luteoviruses, has found a 15 to 70% incidence of BYDV in perennial ryegrass in pastures, with the main isolate appearing to be vector-nonspecific (PAV-like). A survey of wheat crops in Tasmania is now being planned.

New Zealand

J.M. McEwan, Department of Scientific and Industrial Research

Barley yellow dwarf (BYD) was first reported in New Zealand cereal crops in 1955, although it may have been present considerably earlier. Early experimental work on its control in autumn-sown wheat crops in Canterbury showed that significant losses in yield could occur, although the effect was dependent upon season and cultural practices.

Species of *Lolium*, the main grasses used for sown pasture in New Zealand, constitute the principal reservoir of the disease; they also serve as the winter refuge for viruliferous aphids. *Rhopalosiphum padi* has been shown to be the principal vector.

The trapping of flying aphids was begun in the 1960s. Those in Canterbury revealed some regular patterns, with the principal infestation from autumn aphid flights found to be avoidable by delaying the sowing of cereal crops until the middle of May. The resulting recommendation was implemented to good effect in the control of BYD in those crops. Spring aphid flights were less predictable and, due to a significant reduction in yield by delaying the sowing of spring cereals, control of the problem by the use of aphicide sprays was recommended.

The establishment of a breeding program for spring cereal crops in the North Island led to an appraisal of the BYD situation in the area. Field observations supplemented by some aphid trapping indicated that significant flights of aphids occurred through the month of October and that a relatively high proportion of the aphids were viruliferous. Wheat crops are usually sown some time prior to that period and the use of CIMMYT material, particularly Karamu (synonym Anza), has led to a significant level of tolerance to BYDV within the gene pool of the breeding program.

Barley, being traditionally later sown, is more at risk to BYDV infection, and commercially significant losses from the disease occur. The *Yd2* gene has been incorporated into the breeding program and a search for alternative types of resistance continues. Selection in oat, durum and triticale breeding material has also revealed useful variation in the direction of BYDV tolerance. Results of field trials carried out in the late 1960s on the effect of aphids and BYD on the established crop indicated that significant and economic increases in yield were possible with control measures using organophosphate aphicide sprays.

The persistent occurrence of BYDV infection in the North Island has resulted in a series of investigational studies. A cooperative breeding program on BYDV tolerance in oats has been established with Agriculture Canada and includes a genetic study on the basis of resistance; research on resistance factors in barley, other than that of the *Yd2* gene, has been established with the University of California, Davis.

Appendix I

Letter from W.F. Rochow, Research Plant Pathologist, United States Department of Agriculture, Agricultural Research Service; Plant Pathology Department, Cornell University, Ithaca, New York, USA, Discussing the Identification and Naming of the Luteoviruses that Cause Barley Yellow Dwarf

November 9, 1983

Dr. Peter Burnett
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Dear Peter,

. . . .

Since you asked for suggestions of further areas for discussion, I will send one along. I think your group of experts should consider useful ways to identify and name the different luteoviruses that cause barley yellow dwarf. I am enclosing a copy of a letter I wrote in 1981 when I was a member of the Plant Virus Subcommittee of ICTV. Nothing ever came of this letter because that group does not deal with nomenclature problems at this level. The letter is still reasonably current. The evidence for the two groups discussed is even stronger now that we have the work with dsRNA (F.E. Gildow) and the current studies with cDNA (M. Zaitlin and P. Palukaitis).

. . . .

Barley yellow dwarf is a disease of many grains and grasses caused by a group of plant luteoviruses. There has always been a problem to find a useful way to identify and name these viruses. Since interest in barley yellow dwarf has grown in recent years, this problem will increase. Moreover, recent discovery of a small, isometric virus of one of the aphid vectors will complicate the situation . . . .

My approach to this problem has always been to try to follow the most simple option and to do the thing least likely to cause confusion. Thus, I have long avoided the use of "strains" because we have known so little about relationships among these viruses. I use the term "isolate" because it is the most direct, simple way I know to describe each of the five characterized virus cultures we study in Ithaca. I have designated each of these five isolates with a three letter "name," based on identity of the aphid vector, the property that first permitted differentiation among the viruses. Although these letters indirectly identify vectors, they are not direct abbreviations of anything, a concept some editors have trouble understanding. Thus, MAV is my designation of a virus isolate transmitted specifically by *Macrosiphum avenae*, but MAV does not stand for "*Macrosiphum avenae* virus." (Now that we have aphid viruses, I'm glad I have stuck to this!) I use these letters only because they seem the most simple approach to me. Others prefer different approaches. For example, Gill uses four digit numerals to identify his virus isolates. Some of the problems associated with use of my three-letter designations are that it restricts use of the letters for others who might wish to use a similar system, the names are mis-used by people as designations of groups rather than of specific virus isolates, and the names become less useful as the names

of vectors change. For example, the current name for *Macrosiphum avenae* is *Sitobion avenae*. In recent years we have learned some things about relationships among these five virus isolates, and similar isolates others have studied.

As indicated on the list of luteoviruses in the fourth report of ICTV, isolates of BYDV fall into two groups, on the basis of both serological studies and cytological effects on cells as observed by Gill and his colleagues in Winnipeg. The two groups are as follows:

I. MAV, PAV, and SGV
II. RPV, RMV, and rice giallume

One dilemma reinforced by our current understanding is the simple question of what is barley yellow dwarf virus? These two groups are serologically distinct, although probably not absolutely unrelated. But it is a bit awkward to have serologically distinct viruses all called isolates of barley yellow dwarf virus. The problem is what names could be used to help the situation rather than complicate it. In 1974 P.L. Catherall (Plant Pathology 23:116-117) suggested that "ryegrass chlorotic streak virus" might be a more appropriate name for isolates similar to RPV. Since RPV is especially closely related to some isolates of beet western yellows virus, a more logical argument is that RPV-like isolates should be called beet western yellows virus! Since many of the characterized luteoviruses are serologically related, it is still probably premature to try to arrange them in groups until we know more about the degree of relationships.

One approach that could be suggested is to circulate workers who deal with barley yellow dwarf viruses and see if there is any interest in developing a standarized way to identify isolates. For example, my five isolates could be designated as follows:

NY-MAV-1
NY-PAV- 1
NY-SGV- 1
NY-RPV- 1
NY-RMV-1

In this scheme, Henry Jedlinski (Illinois, USA) could designate his Champaign 6 isolate as IL-PAV-1, Gill's 6407 (Manitoba, Canada) could be MAN-MAV-1, etc. As work develops on insect viruses in aphids, it will be important to avoid confusion between plant luteoviruses and aphid viruses.

Another possibility would be to encourage workers to stress use of the two virus groups. Since this separation into groups is based on a range of virus properties, it seems likely that it will continue to be useful. We could write about group I or group II barley yellow dwarf luteoviruses, or maybe just group I luteoviruses, etc. Perhaps a name should be devised for each group, but I think it is still too soon for that.

. . . .

Sincerely,
W.F. Rochow
Research Plant Pathologist

Appendix II

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