Epidemiology of wheat curl mite (Aceria to .) and wheat streak mosaic virus on feral grass species and effect of glyphosate on wheat curl mite dispersal
by Christopher William Brey

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Crop and Soil Science
Montana State University

Abstract:
Wheat streak mosaic virus (WSM) is a devastating virus disease found throughout the Great Plains of the United States and Canada. The wheat curl mite (WCM) Aceria tosichella Keifer, is the only known vector of wheat streak mosaic virus (WSMV). The primary oversummering host for the mite and virus is volunteer wheat. However, in some cases where volunteer wheat was low or absent outbreaks have occurred suggesting feral grasses may be serving as alternate hosts for the mite and virus.

The goal of this project was to examine the role of feral grass species in WCM and WSMV epidemiology. Annual and perennial grasses from a major winter wheat producing area in north central Montana were surveyed for A. tosichella, and assayed by protein antibody sandwich enzyme linked immunosorbent assay (PAS-ELISA) for WSMV during the summers of 1995, 1996, and 1997. Aceria tosichella was collected from Bromus inermis Leys, Poa interior Rydberg, Poa pratensis L., and Triticum aestivum L. Three of the annual grasses, Bromus japonicus Thunb., Bromus tectorum L., and T. aestivum, and five species of perennial grasses, Agropyron cristatum (L.) Gaertn., B. inermis, P. pratensis, Stipa comata Trin. & Rupr., and Stipa viridula Trin., tested positive for the WSMV. None of the grass plants that tested positive had WSM-like symptoms except T. aestivum. The results of the pathogenicity tests indicated that only Aegilops cylindrica Host, and Aven fatua L. were susceptible to both the WCM and WSMV. More importantly, WCMs that acquire the WSMV from these two grass species can transmit the virus to healthy wheat. Bromus inermis, P. pratensis and S. comata were shown to be suitable hosts for WCMs, but in all tests were immune to WSMV. The results of the molecular analysis indicated that WSMV was easily detected by the two serological and two nucleic acid based assays for infected T. aestivum, A. cylindrica and A. fatua grown in the greenhouse and symptomatic T. aestivum plants collected in the field. Although, serological tests indicated P. pratensis exposed to virulifierous WCMs in the laboratory as negative for WSMV infection, the presence of WSMV was detected in immunocapture reverse transcription polymerase chain reaction (IC-RTPCR) test. However, the PCR signal was faint suggesting WSMV detection in WCMs and not the plant host. These findings suggest, with the exception of A. fatua and A. cylindrica, that feral grasses play a limited role in WSMV and WCM epidemology and that volunteer wheat is still the primary host for the mite and virus.

In addition, the effect of glyphosate, a broad spectrum herbicide, was assessed to determine the dispersal response of WCMs on wheat seedlings exposed to field rates of 420 and 840 ml/ha inside a laboratory wind tunnel. The major conclusion of this study was that the recommended rate (840 ml/ha) of glyphosate did increase WCM dispersal within 42 hours of initial application.

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Date 7/27/98

I dedicate this thesis to my parents William and Bernadine Brey and in memory of James Gabor, research entomologist.

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ABSTRACT

Wheat streak mosaic virus (WSM) is a devastating virus disease found throughout the Great Plains of the United States and Canada. The wheat curl mite (WCM) *Aceria tosichella* Keifer, is the only known vector of wheat streak mosaic virus (WSMV). The primary oversummering host for the mite and virus is volunteer wheat. However, in some cases where volunteer wheat was low or absent outbreaks have occurred suggesting feral grasses may be serving as alternate hosts for the mite and virus.

The goal of this project was to examine the role of feral grass species in WCM and WSMV epidemiology. Annual and perennial grasses from a major winter wheat producing area in north central Montana were surveyed for *A. tosichella*, and assayed by protein antibody sandwich enzyme linked immunosorbent assay (PAS-ELISA) for WSMV during the summers of 1995, 1996, and 1997. *Aceria tosichella* was collected from *Bromus inermis* Leys, *Poa interior* Rydberg, *Poa pratensis* L., and *Triticum aestivum* L. Three of the annual grasses, *Bromus japonicus* Thunb., *Bromus tectorum* L., and *T. aestivum,* and five species of perennial grasses, *Agropyron cristatum* (L.) Gaertn., *B. inermis, P. pratensis*, *Stipa comata* Trin. & Rupr., and *Stipa viridula* Trin., tested positive for the WSMV. None of the grass plants that tested positive had WSM-like symptoms except *T. aestivum*. The results of the pathogenicity tests indicated that only *Aegilops cylindrica* Host. and *Aven fatua* L. were susceptible to both the WCM and WSMV. More importantly, WCMs that acquire the WSMV from these two grass species can transmit the virus to healthy wheat. *Bromus inermis*, *P. pratensis* and *S. comata* were shown to be suitable hosts for WCMs, but in all tests were immune to WSMV. The results of the molecular analysis indicated that WSMV was easily detected by the two serological and two nucleic acid based assays for infected *T. aestivum*, *A. cylindrica* and *A. fatua* grown in the greenhouse and symptomatic *T. aestivum* plants collected in the field. Although, serological tests indicated *P. pratensis* exposed to virulifierous WCMs in the laboratory as negative for WSMV infection, the presence of WSMV was detected in immunocapture reverse transcription polymerase chain reaction (IC-RTPCR) test. However, the PCR signal was faint suggesting WSMV detection in WCMs and not the plant host. These findings suggest, with the exception of *A. fatua* and *A. cylindrica,* that feral grasses play a limited role in WSMV and WCM epidemology and that volunteer wheat is still the primary host for the mite and virus.

In addition, the effect of glyphosate, a broad spectrum herbicide, was assessed to determine the dispersal response of WCMs on wheat seedlings exposed to field rates of 420 and 840 ml/ha inside a laboratory wind tunnel. The major conclusion of this study was that the recommended rate (840 ml/ha) of glyphosate did increase WCM dispersal within 42 hours of initial application.

CHAPTER 1

LITERATURE REVIEW

Distribution of Wheat Streak Mosaic Disease

Wheat streak mosaic (WSM) is one of the most important and widely distributed virus diseases of wheat (*Triticum asetivum* L.). First observed in Nebraska in 1922 by Peltier (1), it is now recognized throughout the Great Plains of North America, eastern Europe, and regions of the Ukraine (2). It is most prevalent in the central and western parts of North America, where severe damage to winter and spring wheat crops occurs annually. Since 1949, WSM has caused heaviest wheat yield losses in Kansas (3,4,5) and southern Alberta, Canada (6,7) and from time to time has caused serious economic loses in Nebraska (8), South Dakota (9), North Dakota (10), Colorado (11), Wyoming (12), and Montana (13, 14). Although less severe, WSM has been reported in Idaho (15), Washington (16), California (17), Oklahoma (18), and Texas (19). Outside North

America, WSM has been identified in Rumania, Jordan, Yugoslavia, Russia and Turkey (20, 21).

Economic Importance

In the Great Plains, WSM is estimated to reduce annual wheat yields by 2% each year. However, localized losses of up to 100% are not uncommon in some endemic regions (22). Greatest losses over the past 20 years have occurred in Kansas. From 1976 to 1987, the state averaged 2.5% wheat yield loss annually, and in 1988 estimated statewide losses were 13%, or 42 million bushels (23). From 1988 to 1991, losses in the state have averaged 15.5 million bushels per year (3). One of the most severe WSM epidemics in the northern Great Plains occurred in North Dakota in 1988. Statewide wheat yield losses that year were approximately $40.1 million (10). Since 1954, when the first case of wheat streak mosaic was observed in Montana, major outbreaks have occurred in 1964, 1981, 1993 and 1994 (13). The most recent (1993-1994) wheat streak epidemic in Montana caused severe crop losses valued at $50 million (J. Riesselman, Department of Plant Pathology, Montana State University, personal communication).

Disease Symptomology

The first symptoms of WSM consist of a faint green mottling of the leaves, followed by the development of light green and yellow blotches or streaks running

parallel to the leave veins. As the disease progresses, a general stunting of the plant can be detected (8). In addition, plants are prostrate and produce an abnormally large number of tillers. At a distance, severely diseased wheat appears lighter in color and by casual examination may be misinterpreted as nitrogen deficiency (8, 24). Severely infected plants tend to be less upright and do not produce heads; less seriously infected plants may produce sterile heads containing shriveled kernels. Symptoms may vary depending on virus strain, variety of wheat, plant health, time of infection, soil fertility, co-infection with another virus (i.e., High Plains virus) and temperature (8, 14, 24).

Etiological Agent: Wheat Streak Mosaic Virus

Wheat streak mosaic virus (WSMV), *Marmor virgatum* McK., is a member of the genus *Rymovirus* (25) in the family Potiviridae. A recent submission to reclassify WSMV based on its coat protein and 3' non-coding region into a separate genus, *Whestervirus*, has been proposed (26). The virus is a long (700 nm X 13 nm) flexous, rod shaped viron containing a single-stranded RNA genome of approximately 8,500 base pairs. The nucleotide sequence of the 3' poly (A) terminal region encoding the capsid gene protein is known, but the majority of the genome has not yet been characterized (27). At least two characteristics distinguish WSMV from other potyviruses: 1) the virus is vectored solely by the wheat curl mite (WCM), *Aceria tosichella* Keifer (28), and 2) the capsid protein is larger than the 32 to 36 Kda coat protein reported for most potyviruses. However, WSMV has also been known to be transmitted in the field

between infected and healthy wheat plants through abrasive leaf action during high winds (29). Despite these differences WSMV is currently classified as a member of the mite transmitted subgroup 3 potyvirus (30) because, similar to other potyviruses, it induces the production of pinwheeled shaped cytoplasmic inclusion bodies composed of a 66 Kda protein (31). Under field conditions an individual infected wheat plant may be co-infected with High Plains virus (HPV) (32), Wheat spot mosaic virus (WspMV) (33) and agropyron mosaic virus (AgMV) (34).

Description and Biology of the Wheat Curl Mite

Aceria tosichella, a member of the family Eriophyoidea, is the only known vector of WSMV. Originally the WCM was designated *Aceria tulipae* (Keifers), described from tulips, however since 1970 the mite occurring on wheat has been renamed *Aceria tosichella* Keifer (35, 36). Adult mites are (length: ca. 250 μm) wingless, white, cigar-shaped arthropods with two pairs of legs near their anterior cephalic region (8). They prefer to feed near the edges of wheat leaves causing the leaves to curl and bend inward producing a protective microhabitat. The mites reproduce by laying eggs. Females are capable of laying 8 to 12 eggs during their lifetime (8). The shortest life cycle from egg to egg was reported to be seven days at 25°C (37). The normal life cycle from egg to egg occurs between 10 to 12 days (8). Like many other eriophyids, *A. tosichella* has two nymphal instars. The virus is not transmitted transovarially, but by both adult and nymphal stages (37). Wheat streak mosaic virus is transmitted by *A. tosichella* in a

persistent manner, that is mites removed from a virus source are still able to transmit the virus after 7 days (38). Approximately 15 minutes are required for the mite to acquire the virus, and it may remain infective for 7-9 days through molts without additional acquisitions (37). The primary mode of mite dispersal from plant to plant is by wind. Other insects such as aphids and leaf hoppers have been reported to transport mites from plant to plant (39, 40). In addition to WSMV, *A. tosichella* has transmitted High Plains virus (32, 40), WspMV (33) and brome streak mosaic virus (42).

Methodologies for Detection of WSMV in Native and Cereal Grasses

Since WSMV was first recognized in Nebraska (1), researchers have used a variety of methods for detecting the virus in Gramineae species. Techniques for the diagnosis of WSMV infection in feral and cultivated grasses have ranged from the use of indicator plants to the molecular technique of reverse transcription polymerase chain reaction (RT-PCR). Detection tests for WSMV include indicator plants, immunological specific electron microscopy (ISEM), enzyme linked immunosorbent assays (ELISA), dot blots, and RT-PCR are described below.

Indicator Plants

McKinney (43) first described the carborundum method for determining monocotyledonous plants infected with WSMV. This procedure involves the mechanical inoculation of sap from the suspected source plant to an indicator plant, (i.e., a host plant

that expresses disease symptoms when infected). Since then, researchers have used this method for distinguishing WSMV infection in feral grasses (44, 45) and for the separation of virus strains based on symptom expression in cereals (46, 47). Indicator plants such as, *Agropyron intermedium* L., *Hordeum jubatum* L. and *Avena sativa* L. have been used to aid in the differentiation of WSMV, AgMV, and an unrecognized hordeum mosaic virus found in Canada, respectively (48).

Immunological Specific Electron Microscopy (ISEM)

Immunological specific electron microscopy, more commonly known as leaf-dip serology, first reported by Ball and Brake (49) has become a fast, efficient, and popular method for virus identification (50). Carroll et al. (47) employed this technique to distinguish WSMV infection from barley yellow dwarf and nitrogen deficiency in diseased spring and winter wheat plants collected from commercial fields in Montana. Leaf-dip serology was used to aid in WSMV identification in several wheat cultivars in Colorado (46). Langenberg (51) discovered antigen reaction to WSMV antiserum in leaf-dips depended on the age of the wheat leaf. He found that the young fully expanded leaves reacted completely or partially with antiserum, whereas virons from older leaves did not react. He also observed that histologically fixed WSM virons in ultrathin sections could be immunolabelled in leaves of all ages. He attributes this negative antiserum reaction in the leaf-dip test to the degradation of virons in the older leaves during the extraction step.

Enzyme Linked Immunosorbent Assay (ELISA)

Clarke and Adams (52) first reported the use of ELISA as a very effective detection assay for plant viruses. Many variations of this basic procedure have been used in an attempt to optimize the test for a specific purpose. The basic method is very economical and sensitive for detecting virus concentrations as low as 1-10 nanograms per ml (53).

Direct double antibody sandwich ELISA (52), involves a solid phase (i.e., polystyrene microtiter plate) which is first coated with virus antibody in the immunoglobulin (IgG) form. Next, the IgG traps the virus antigen. The trapped virus is then revealed by an enzyme-labeled specific antibody that reacts when a substrate is added to give rise to a visible product which can be measured in a spectrophotometer. Two major disadvantages of this procedure are: 1) it is highly strain specific and 2) requires a different enzyme-conjugated antibody for each virus that is tested.

Indirect double antibody sandwich ELISA involves the final detection step to be conjugated to an antiglobulin IgG (54) or protein A (55). In this procedure, antivirus IgG is prepared in two animal species; one to trap (raised in a rabbit) and one to detect (chicken antirabbit globulin) the virus with enzyme conjugate specific for the latter. Thus, one conjugated IgG can be used to assay a range of related viruses.

Various modified ELISA procedures have been used by many researchers for WSMV detection in feral grasses (56, 57) and cereals such as spring and winter wheat cultivars, maize, barley, and sorghum crops (58, 59, 60, 61, 62). Christian and Willis (57) used an indirect ELISA assay as described by Lommel et al. (63) to determine which

grass species were infected with WSMV in Kansas. Montana et al. (56) employed a direct antigen plating ELISA to detect agropyron mosaic virus and WSMV in grasses near the periphery of wheat fields in Oklahoma. A case reported by Hunger and Sherwood (60) showed that a polyclonal antibody to WSMV cross-reacted with healthy wheat. To remedy this situation they substituted the polyclonal antiserum with a monoclonal antibody and reaction to healthy wheat was eliminated.

Dot Blot and Leaf Squash Assays

Both the dot blot (review: 64, 65) and leaf squash (review: 66) methods are simpler, faster, and cheaper assays than ELISA, but they allow quantification of virus only when bound antibody is monitored by radioactivity (64). Bottacin and Nassuth (64) used these procedures to detect levels of WSMV infection in mechanically inoculated wheat, barley, maize, and oats grown under laboratory conditions in Canada. They found that both assays revealed a positive correlation between symptom severity and amount of virus that accumulated in the four cereals. Also, they found grinding a small amount of young leaf tissue in a mortar and pestle in buffer and then blotting this material onto nitrocellulose paper was sufficient to transfer enough WSMV antigen to be detected by a WSMV antibody. An earlier comparison studied by Sherwood (67) also concluded that filter paper immunobinding assay (similar to dot blot assay) was easier, faster, and cheaper to use than both western blotting and ELISA when detecting WSMV, but ELISA was the best assay for virus quantification. Makkouk and Jarikji (62) reported ELISA to be

1000X more sensitive then double immunodiffussion (similar to dot blot assay) in detecting WSMV in purified and wheat plant extracts.

Reverse Transcription Polymerase Chain Reaction

Reverse transcription polymerase chain reaction (review: 68, 69) has become an important molecular technique for detecting low titer RNA viruses and generally has been found to be more sensitive than any of the other protein, nucleic acid, and serological based assays (70). A comparative study conducted by Mathews et al. (71) showed that RT-PCR was more reliable then ELISA at detecting citrus triteza virus in trees in the field during months of nonoptimal titer. They reported RT-PCR detected citrus triteza virus when ELISA could not, and that ambiguous ELISA readings could be retested with RT-PCR to resolve the erroneous ELISA results. There has been a concerted effort to develop RT-PCR assays for many of the pathogenic plant RNA viruses. RT-PCR assays have been developed for apple chlorotic leaf spot and apple stem grooving virus (70), soybean mosaic virus (72), tomato spotted wilt tospovirus (73), cucumber mosaic virus (74) zucchini yellow mosaic virus (75), barely yellow dwarf virus (76) and WSMV (77, 78).

Dependent on the choice of primers, RT-PCR facilitates the detection of a broad group of related or specific virus strains. For instance, differentiation of strains of cucumber mosaic virus (74) and citrus tristeza virus (71) have been enhanced by primers derived from the variable region of their genomes and then differentiated by further

analysis of amplified products by the use of restriction endonuclease and restriction fragment length polymorphism (RFLPs). A similar study by McNeil et al. (77) used RT-PCR and RFLP technique to characterize genomic differences in WSMV isolates collected from within and among wheat fields in six Nebraska wheat counties. They found three main and twenty nine minor linages of WSMV co-circulating in the region over two years. This was one of the first studies to report virus variation from plant to plant in nature.

Cereals as Hosts for the Wheat Curl Mite and Wheat Streak Mosaic Virus

Wheat streak mosaic virus and WCM have a broad host range encompassing many cereal crops. They employ all varieties of wheat, rye, barley, and oats as hosts (79). Several varieties of maize (80, 81), sorghum (61), rice (82) and millet (39) are also susceptible to both the mite and virus. However, winter wheat is the primary overwintering host harboring both the WCM and WSMV, and volunteer wheat germinating before or after harvest is the most important oversummering host for the mite and virus (8, 83).

Annual Grasses as Hosts for the Wheat Curl Mite and Wheat Streak Mosaic Virus

Many native annual grass species have been reported susceptible to manual inoculation with WSMV and/or viruliferous WCMs (refer to Table 1.1 for host summary). In order to be important in WSM epidemiology, it is not only necessary that annual grasses provide a source of virus, but also be a suitable host for the mite. Several annual grasses such as *Aegilops cylindrica* (83), *Digitaria sanguinalis* (84), and *Setaria viridis* (37) have been documented to support both the WCM and WSMV naturally in the field, apparently posing a potential threat to wheat (Table 1.2).

McKinney and Fellows (85) isolated WSMV from *A. cylindrica* growing along roadways in western Kansas, while Connin (86) collected WCMs from this species in several central Kansas counties. Greenhouse studies indicate *A. cylindrica* to be a fair to good host for WCM survival and reproduction (86). Although actual mite numbers were not reported, he did observe the characteristic rolling and trapping of leaves in this species. He also found that WCMs from *A. cylindrica* could transmit WSMV to wheat. Similar results were obtained in a greenhouse study by Burns et al. (14). *Aegilops cylindrica* is genetically related to wheat (87); it is a winter annual with a life-cycle that parallels winter wheat. Many have speculated that it is probably not an important host in WSM epidemiology (8, 84, 85). However, in some cases before winter wheat matures, *A. cylindrica* may have the potential to be an important early summer host (green period May to June) (45).

Table 1.1. Susceptibility of annual grass species to wheat curl mite (WCM) infestation and wheat streak mosaic virus (WSMV) infection under laboratory conditions.

Scientific name	Common Name	Increase of WCM	WSMV Transmission		Authority
			Mannual Inoculation	WCM Infestation	
Aegilops crassa Boiss.			Susceptible		(3, 4)
Aegilops cylindrica Host.	Jointed goatgrass	Fair-Good	Susceptible	Immune, Susceptible	(2, 3, 4, 11, 12)
Aegilops ovata L.			Susceptible		(3, 4)
Aegilops triuncialis L.	Barb goatgrass		Susceptible		(3, 4)
Aegilops venticosa Tausch.			Susceptible		(3, 4)
Aristida adscensionis L.	Sixweek threeawn	Resistant			(2)
Aristida oligantha Mich.	Prarie threeawn		Immune	Immune	(7)
Avena fatua L.	Wild oats	None	Susceptible	Susceptible	(1, 2, 4, 11)
Beckmannia syzigachne (Steud.) Fernald	American sloughgrass	Susceptible	Immune		(2)
Bromus japonicus Thumb.	Japanese brome	None	Susceptible	Susceptible	(1, 2, 3, 4, 12)
Bromus tectorum L.	Cheatgrass brome	None, Susceptible	Susceptible	Immune	(1, 2, 11, 12)
Carex L.	Sedge	Susceptible	Immune		(2)
Cenchrus pauciflorus Benth.	Sandbur	Good	Susceptible	Susceptible	(2, 4, 7, 11, 12)
Coix lacryma-jobi Toun.	Job's tears		Immune		(1, 4)
Digitaria ischaemum (Schreb)	Smooth crabgrass	Fair-good	Susceptible	Susceptible	(3, 4, 11, 12)
Digitaria sanguinalis (L.) Scop.	Crabgrass	None, Susceptible Very-poor	Susceptible	Susceptible, Immune	(1, 2, 4, 7, 11, 12)
Echinochloa crusgalli (L.) Beauv.	Barnyard grass	Poor	Susceptible	Susceptible	(1, 2, 4, 7, 11, 12)
Eleusine indica (L.) Gaertn.	Goosegrass	None	Immune	Immune	(2, 4, 11, 12)
Eragrostis cilianenis (All.)	Stinkgrass	Poor, Susceptible Poor, None	Susceptible, Immune Susceptible	Susceptible Susceptible, Immune	(1, 2, 4, 11, 12)
Eragrostis pilosa (L.) Beauv.	Indian lovegrass	Resistant			(2)

Table 1.1. (continued)

Scientific name	Common Name	Increase of WCM	WSMV Transmission: Mannual Inoculation	WSMV Transmission: WCM Infestation	Authority
Euchlaena mexicana Schrad.	Teosinte	Poor, Resistant	Immune	Immune	(2, 11, 12)
Eriochloa contracta Hitch.	Praire cupgrass			Susceptible	(7)
Haynaldia villosa Schur.			Susceptible		(3, 4)
Hordeum gussonianum Parl.	Mediterranean barley		Susceptible		(3, 4)
Hordeum jubatum L.	Wild barley		Immune		(4)
Hordeum murinum Huds			Susceptible		(3, 4)
Panicum capillare L.	Witchgrass	None, Susceptible	Susceptible, Immune	Susceptible	(1, 2, 4, 8, 11, 12)
Panicum dichotomiflorum Mchx.	Fall panicum			Immune	(7)
Phalaris paradoxa			Susceptible		(1, 3, 4)
Phleum pratense L.	Ttimothy	Poor	Susceptible		(2)
Poa annua L.	Annual bluegrass	Poor	Susceptible		(2)
Schedonnardus paniculatus (Nutt.) Trel.	Tumblegrass			Immune	(7)
Setaria faber Herrm.	Giant foxtail			Susceptible	(7)
Setaria lutescens (Weigel) Hubb.	Yellow foxtail	None	Immune	Immune	(1, 4, 9, 12)
Setaria verticillata Beauv.	Bristly foxtail	Poor	Susceptible	Susceptible	(1, 2, 4, 12)
Setaria viridis (L.) Beauv. Hermgreen	Foxtail	None, Poor	Susceptible	Susceptible	(1, 3, 4, 7, 9, 11, 12)

1: Slykhuis 1955
2: Somsen & Sill 1970
3: McKinney & Fellows 1951
4: Sill & Connin 1953
5: Gibson 1957
6: Anderson 1971
7: Christian 1993
8: Brake et al. 1990
9: Staples & Allington 1956
10: Gibson & Painter 1957
11: Connin 1956
12: Wehing 1956

Table 1.2. Annual grasses reported to be naturally infected with the wheat streak mosaic virus (WSMV) and/or infested with wheat curl mites (WCM).

Scientific name	Common name	WSMV	WCM	Authority
Aegilops cylindrica Host	Jointed goatgrass	Susceptible	Fair-good	(1, 2, 3)
Avena fatua L.	Wild oats	Susceptible	None	(1)
Bromus japonicus Thunb.	Japanese brome	Susceptible	Fair	(1, 2, 3)
Bromus secalinus L.	Cheatgrass	Susceptible	Poor	(2)
Bromus tectorum L.	Downy brome	Susceptible	Poor	(1, 3, 4)
Cenchrus pauciflorus Benth.	Sandbur	Susceptible	Poor	(1, 2, 5, 6)
Digitaria sanguinalis (L.) Scop.	Crabgrass	Susceptible	Fair-good	(2, 5, 6)
Echinochloa crusgalli (L.) Beauv.	Barnyard grass	Susceptible	Poor	(1, 2, 5, 6, 7)
Eragrostis cilianensis (All.) Lutati.	Stinkgrass	Susceptible	Fair-poor	(1, 2, 5, 6, 9)
Eriochloa contracta Hitchc.	Prairie cupgrass	Susceptible	No data	(7)
Panicum capillare L	Common witchgrass	Susceptible	Fair-poor	(1, 2, 5, 6, 7, 9)
Panicum dichotomiflorum Michx.	Fall panicum	Susceptible	No data	(8)
Setaria faberi Herrm.	Giant foxtail	Susceptible	No data	(7)
Setaria viridis (L.) P. Beauv.	Green foxtail	Susceptible	Fair-good	(1, 2, 4, 5, 6, 7)
Setaria verticillata L.	Bristly foxtail	Susceptible	Poor	(6)

1: Slykhuis 1955
2: Somsen & Sill 1970
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8: Brake et al. 1990
9: Staples & Allington 1956

Digitaria sanguinalis has been found to be frequently infected with WSMV in nature and easily infected with the virus in the greenhouse (45). Gibson (84) reported thriving populations of *A. tulipae* (the nomenclature has since been changed to *A. tosichella*) on several *D. sanguinalis* plants collected in a shaded basement well at the Kansas State University Agriculture Experiment Station in Colby, Kansas. McKinney and Fellows (85) found *D. sanguinalis* to give mosaic symptoms by manual inoculation. Sill and Connin (45) reported WCM reproduction to be very poor on *D. sanguinalis*, whereas Somson and Sill (83) and Connin (86) found this species to be an acceptable WCM host. Interestingly, Connin (81) discovered the few mites that survived on *D. sanguinalis* when transferred to wheat were still able to transmit the virus. *D. sanguinalis* is a warm weather troublesome grass species found in temperate and subtropical areas of North America. In Montana, it is known to be common throughout the state (88). It reaches maturity in late summer before senescing in early fall. As the plant dies in early fall, mites are forced to leave the plant in search of a more succulent host. Dispersed by wind currents, they may land in adjacent wheat fields initiating a WSM outbreak (85).

Setaria viridis is probably the most frequent WSMV virus infected grass (83). A recent grass survey in Kansas seriologically confirmed this species to be infected with WSMV in the field (57). McKinney and Fellows (85) reported *S. viridis* as susceptible to mechanical inoculation, and Slykhuis (37) found this species to be successfully inoculated with virus both manually and with mites. Connin (86) and Slykhuis (28) were unable to establish a WCM population on this species in the greenhouse, while del

Rosario and Sill (89) reported fair colonies on 85% of the 40 *S. viridis* plants infested. They postulated that different biotypes of *A. tosichella* exist which may account for their successful colonization of WCMs on *S. viridis* (previous attempts had failed). *S. viridis* has been found to be naturally infested with WCMs in Kansas (84, 85) while researchers in Nebraska have found only one or two mites on many sampled *S. viridis* (24, 45). However, there have been a few isolated outbreaks of WSM in Nebraska traced to *S.viridis* (90). Since *S. viridis* is cool season grass that grows from July through September, it may provide a suitable intermediate host for the mite and virus during the most critical period between the harvest and planting of winter wheat (83).

The general opinion in the scientific community is that the majority of annual grasses are probably not important in WSM epidemology (8, 24). Although many grasses can be infected with WSMV in the greenhouse by WCMs and/or mechanical inoculation, the combination of poor mite hosts and plant host life-cycle (i.e., *A. cylindrica* and *D. sanguinalis*) are not conducive to contributing to a WSM epidemic. However, it is possible that under the right circumstances, a few viruliferous mites from annual grasses (i.e., *S. viridis*) might establish a foci in volunteer wheat or in cultivated wheat and cause a local outbreak.

Perennial Grasses as Hosts for the Wheat Curl Mite and Wheat Streak Mosaic Virus

Numerous species of perennial grasses have been reported susceptible to WSMV and WCM in the greenhouse (refer to Table 1.3 for host summary). A few perennial grasses have been shown to be natural hosts for the mite or virus (Table 1.4), but only *Elymus canadensis, Elymus virginicus, Bouteloua hirsuta, Lolium perenne*, and *Sitaton hystrix* have been reported as hosts for both. Although, *Pascopyrum smithii* is immune to the virus, it is believed to be the most important perennial grass host for the wheat curl mite (83).

Elymus canadensis is an important range and pasture species often infected with the virus (45, 85). This species rarely carries large populations of mites, but occasionally some heavily infested plants are found (83). A grass survey in western Nebraska found *E. canadensis* to have flourishing WCM populations on only two young plants sampled (8). Slykhuis (37) was able to achieve mite virus infection in *E. canadensis* despite failure to establish a WCM colony on this grass species. He ascertained that a strain difference in the mite may account for this vector-host barrier. Connin (86) however was able to obtain fair mite infestations on *E. canadensis*, but was unable to obtain virus infection by mites. McKinney and Fellows (80) reported *E. canadensis* as being either a symptomless carrier, or exhibiting local lesions or mosaic symptoms when mechanically inoculated with the virus. *Elymus canadensis* is a hardy perennial grass that may serve as

Table 1.3. Susceptibility of perennial grass species to wheat curl mite (WCM) infestation and wheat streak mosaic virus (WSMV) infection under laboratory conditions.

Scientific name	Common Name	Increase of WCM	WSMV Transmission		Authority
			Manual Inoculation	WCM Infestation	
Agropyron cristatum (L.) Gaertn	Fairway wheatgrass	Susceptible	Immune		(10)
Agropyron dasystachyum (Hook.) Scribn.	Thickspike wheatgrass		Immune		(10)
Agropyron elongatum Beauv.	Tall wheatgrass	None	Immune	Immune	(10, 12)
Agropyron lasianthum Boiss.			Susceptible		(10)
Agropyron repens (L.) Beauv.	Quackgrass	Susceptible	Immune		(10)
Agropyron rigidum Beauv.			Immune		(10)
Agropyron trachycaulum (Link) Malte	Slender wheatgrass	Susceptible	Immune		(10)
Agropyron trichophorum (Link) Richt.	Stiffhair wheatgrass		Immune		(10)
Alopercurus pratensis L.	Meadow foxtail	None	Immune	Immune	(12)
Andropogon gerardii Vitm.	Big bluestem	Susceptible	Immune	Immune	(10)
Andropogon scoparius Michx.	Little bluestem	None	Immune	Immune	(10)
Arrhenatherum elatius L. Beauv.	Tall oatgrass	Poor	Immune	Immune	(12)
Bouteloua hirsuta Lag.	Grama	Good	Symptomless Immune	Susceptible, Immune	(10)
Bromis inermis Leyss.	Smooth brome	Very poor	Immune	Immune	(10, 12)
Bromis tectorum L.	Downy brome	Susceptible	Susceptible		(2)
Buchloe dactyloides (Nutt.) Engelm.	Buffalograss	None, susceptible	Immune	Immune	(2, 7, 12)
Cynodon dactyon (L.) Pers.	Bermudagrass	Susceptible	Susceptible	Immune	(2, 7)
Dactylis glomerata L.	Orchard grass	None	Immune	Immune	(11, 12)
Distichlis stricta (Torr.) Rydb.	Inland saltgrass	Susceptible	Susceptible		(2)
Elymus canadensis L.	Canada wildrye	Fair	Susceptible	Immune, Susceptible	(2, 3, 4, 11, 12)
Elymus condensatus Presl.	Giant wildrye		Susceptible		(3, 4)

Table1.3. (continued)

Scientific name	Common Name	Increase of WCM	WSMV Transmission: Mannual Inoculation	WSMV Transmission: WCM Infestation	Authority
Eragrostis sessilispica Buckl.	Tumble lovegrass		Immune	Immune	(7)
Eragrostis trichodes (Nutt.) Wood	Sand lovegrass		Susceptible		(2, 3, 4)
Festuca L.	Fescue	Susceptible		Immune	(3)
Festuca rubra L.	Red fescue		Immune		(4)
Hordeum pusillum Nutt.	Little barley	Susceptible	Immune		(2)
Koeleria cristata (L.) Pers.	Prairie junegrass	Susceptible			(2)
Lolium perenne L.	Perennial ryegrass	Susceptible			(2)
Muhlenbergia mexicana (L.) Trin.	Bearded wirestem mugly	Susceptible			(2)
Munroa squarrosa (Nutt.) Torr.	False buffalograss	Susceptible			(2)
Oryzopsis hymenoides (Roem. & Schult) Ricker	Indian ricegrass	Poor	Symptomless	Susceptible	(3, 4, 12)
Panicum virgatum L.	Switchgrass	None, Susceptible	Immune	Immune	(2, 3, 4, 11, 12)
Phalaris arundinacea L.	Reed canary grass	None	Immune	Immune	(4, 11, 12)
Pascopyrum smithii Rybd.	Western wheatgrass	Poor-Fair	Immune	Immune	(10, 12)
Phleum pratense L.	Timothy	Susceptible	Immune		(2, 4)
Poa annua L.	Annual bluegrass		Susceptible		
Poa bulbosa L.	Bulbous bluegrass		Susceptible		(3, 4)
Poa compressa L.	Canada bluegrass		Susceptible		(3,4)
Poa pratensis L.	Kentucky bluegrass	Susceptible	Immune		(2, 4)
Poa stenantha Trin.			Symptomless		(3, 4)
Puccinellia airoides (Nutt.)	Nuttall alkaligrass	Resistant			(2)
Schedonnardus paniculatus (Nutt.) Trel.	Tumblegrass	None			(2)
Setaria pumila (Poir.) Roem. & Schult.	Yellow foxtail	Susceptible	Susceptible, Immune		(2, 7)
Sitanion hystrix (Nutt.) J.G. Smith	Bottlebursh	None	Susceptible		(2)
Elymus giganteus Vahl.			Susceptible		(3, 4)

Table 1.3. (continued)

Scientific name	Common Name	Increase of WCM	WSMV Transmission: Manual Inoculation	WSMV Transmission: WCM Infestation	Authority
Elymus virginicus L.	Virginia wildrye	Susceptible	Susceptible		(2, 3, 4)
Sorghastrum nutans (L.) Nash	Indian grass	None	Immune	Immune	(2, 3, 4, 7, 12)
Sorghum halepense L.	Johnson grass	Good, None	Immune	Immune	(2, 4, 11, 12)
Sporobolus asper (Michx.) Kunth.	Tall dropseed		Immune	Immune	(7)
Sporobolus cryptandrus (Torr.) A. Gray	Sand dropseed		Immune	Immune	(7)
Sporobolus neglectus Nash	Puffsheath dropseed	Suspectible	Susceptible		(2)
Stipa comata Trin. & Rupr.	Needle & thread	Susceptible			(2)
Stipa robusta (Vasey) Scribn.	Sleepygrass		Susceptible		(3, 4)
Stipa viridula Trin.	Green needlegrass	Susceptible			(2)
Tripsacum dactyloides (L.) L.	Eastern gamagrass	Resistant	Immune		(2)

1: Slykhuis 1955
2: Somsen & Sill 1970
3: McKinney & Fellows 1951
4: Sill & Connin 1953
5: Gibson 1957
6: Anderson 1971
7: Christian 1993
8: Brake et al. 1990
9: Staples & Allington 1956
10: Gibson & Painter 1957
11: Connin 1956
12: Wehing 1956

Table 1.4. Perennial grasses reported to be naturally infected with the wheat streak mosaic virus (WSMV) and/or infested with wheat curl mites (WCM).

Scientific name	Common name	WSMV	WCM	Authority
Agropyron repens (L.) Beauv.	Quackgrass	Immune	Fair-good	(2)
Bouteloua hirsuta Lag.	Hairy grama	Susceptible	Fair	(6, 8)
Buchloe dactyloides (Nutt.) Englem.	Buffalograss	Immune	Fair	(2)
Cynodon dactylon (L.) Pers.	Bermudagrass	Immune	Fair	(2)
Elymus canadensis L.	Canada wildrye	Susceptible	Fair	(2, 4, 6, 7)
Elymus virginicus L.	Virginia wildrye	Susceptible	Fair	(1, 2, 3, 4, 5, 6)
Hordeum pusillium Nutt.	Little barley	Immune	Fair	(2)
Lolium perenne L.	Rryegrass	Susceptible	Fair	(9)
Pascopyrum smithii Rydb.	Western wheatgrass	Immune	Fair-good	(2, 5,7)
Poa nervosa Hook	Wheeler's bluegrass	Immune	Fair	(7)
Oryzopsis hymenoides R & S	Indian ricegrass	Immune	Fair	(3, 7)
Seteria lutescens (Weigel) Hubb.	Yellow foxtail	Immune	Fair	(5, 7)
Sitanon hystrix Nutt.	Bottlebrush squirrtail	Susceptible	Fair	(1)
Stipa comata Trin. & Rupr.	Needle-&-threadgrass	Immune	Poor	(7)

1: Slykhuis 1955
2: Somsen & Sill 1970
3: McKinney & Fellows 1951
4: Sill & Connin 1953
5: Gibson 1957
6: Anderson 1971
7: Staples & Allington 1956
8: Gibson & Painter 1957
9: Connin 1956

alternate for the virus and mite during adverse periods (78). This species is widely distributed in Montana (83).

Elymus virginicus, a less common perennial, has been shown to be naturally infected with WSMV in Kansas (45). McKinney and Fellows (85) found this species to display mosaic symptoms when subject to mechanical inoculation with WSMV. However, *E. virginicus* seldom harbors large populations of WCMs in the field (83). The importance of this grass host to other perennials may diminish based on its inability to support populations of mites and its relatively low abundance in certain locations.

Bouteloua hirsuta may be a very important host because WCMs reproduce well on it, and it is susceptible to WSMV (86). Connin (86) found this species to be susceptible to virus through mite transmission. He stated that of the 14 perennial grasses tested, mites transmitted WSMV only to an undetermined *Bouteloua* species. Similar to previous perennial grass hosts for the mite and virus, *Bouteloua* is capable of serving as an intermediate host during adverse periods (83).

Lolium perenne and *Sitaton hystrix,* may be important hosts in WSM epidemiology. Although reports of these two species as naturally infected with WSMV in the field, there has been no mention whether WCMs were found on these grasses (45, 86).

Pascopyrum smithii is widely distributed, green, and succulent during most of the summer and is common along the borders of wheat fields. This is the most widely studied perennial grass as a host for the WCM (83, 91). This grass species is important in maintaining mite populations, but because it is immune to the virus, it is not capable of

producing viruliferous WCMs for infecting wheat. However, because it has been reported to harbor significant mite populations from May through September, it is considered a serious host in WSM epidemiology (86). A host response study by del Rosario and Sill Jr. (89) found that when WCMs from *P. smithii* were placed on wheat the mites adapted poorly to wheat. In addition to harboring WCMs, other eriophyoids, *Aceria agropyronis* (Keifer), *A. slykhuis* (Hall) and *Aculus mckenzie* (Keifer) have been reported to inhabit this grass species (92).

Because perennial grasses provide green host plant material year round, they are more prone than annual grasses to serve as reservoirs for the WCM and WSMV. As yet no perennial grass species that harbors the mite and virus has been shown to be a serious source of infection for wheat in the field (93). However, under the right climatic and growing conditions, viruliferous mites may be carried from a perennial to an adjacent cultivated wheat field or volunteer wheat patch. Thus, WSMV spread from perennial grasses need not be a frequent occurrence to be significant in virus epidemiology. Also, WSMV infection depends on whether viruliferous mites that land directly onto wheat can transmit the virus.

Control of Wheat Streak Mosaic Disease

Control of WSM depends primarily on disrupting the life cycle of the WCM (33, 84, 94). Because the vector can only survive for 4-6 days without a green host, any disruption of host succession (2-3 wks) will cause a reduction in the incidence of WSM

(95). Prevention of infestation is paramount to any successful management program, because once cultivated wheat fields are infested nothing can be done to salvage them (90). Over the last half century there have been a series of successful management strategies used to combat WSM outbreaks. These strategies include: 1) scouting potential wheat and grass reservoirs for WCM and WSMV, 2) implementation of resistant wheat cultivars, 3) delay in planting date, 4) complete destruction of volunteer wheat and other potential grass and weed sources for the mite and virus. The use of miticides and insecticides have been unsuccessful in controlling the wheat curl mite (96, 97, 98).

Randomly collecting wheat plants from cultivated wheat fields in the fall and spring has facilitated forecasting potential WSM outbreaks. Somsen and Sill (83) found randomly surveying fields in Kansas for WCMs was a very good tool for predicting potential epidemics. Early predictive schemes involved monitoring wheat plants in the greenhouse transplanted from the field for development of WSMV symptoms (99). Recently, ELISA assays have been used for measuring WSMV titers in wheat varieties grown in South Dakota (100). Another method for predicting disease outbreak is the examination of individual wheat plants (cultivated and volunteer) for the presence of WCMs.

Plant resistance to the WCM is a primary tactic used in an integrated WSM management program (101). Wheat lines resistant to the WCM have been developed primarily from chromosome substitutions from *Agropyron* (3) and *Secale* (6) grass

species. Resistant wheat varieties can not withstand a WSM disease epidemic, but moderate resistance or field tolerance is valuable in reducing wheat loses (3). Recently TAM 107, a winter wheat variety that previously showed promising WCM resistance, has been reported to be susceptible to WCM populations in the field and laboratory (101).

The importance of planting date on the severity of WSM has been documented. Willis (102) summarized a 10 year study conducted by W. S. Gardner in South Dakota, who concluded that WSM was most severe in early planted winter wheat, and that late planting decreased the disease dramatically. Fellows and Sill (99) determined that winter wheat must be infected early in the fall when plants are young before serious yield loses occur and that spring infection in winter wheat causes little or no winter wheat loss. Thus, wheat plants infected early in the fall stage have a greater risk of becoming infected with the disease than plants infected in the spring. The later winter wheat is planted, the less it is exposed to viruliferous WCMs in the fall. However, the effectiveness of late planting is predicated on the extent of warm weather and moisture in the fall. Because of variable growing seasons, the recommended planting date is different for each wheat producing state or region. However, the general rule for planting winter wheat is two weeks following the harvest of spring wheat and/or the destruction of volunteer wheat (94). Thus, there is no danger of serious mosaic infection in winter wheat regardless of planting date if there are no susceptible hosts for the vector and virus nearby (103).

Destruction of volunteer wheat or other potential mite and virus reservoir grass

hosts before planting effectively controls WSMV (83). Volunteer wheat plants are controlled by conventional tillage or herbicide applications. Slykhuis (103) reported that the use of mouldboard plow was more than sufficient to destroy volunteer wheat plants and eliminate any possibility of WSMV infection in adjacent wheat fields. A contact herbicide, such as glyphosate, has been used to control volunteer wheat in north central Montana.

Summary

Wheat streak mosaic is a serious virus disease of winter and spring wheat. It can occur anywhere wheat is grown. Wheat yield losses attributed to WSM have ranged from partial to complete in some regions. Wheat streak mosaic is caused by the wheat streak mosaic virus (WSMV), *Marmor virgatum* McK. which is vectored solely by the wheat curl mite (WCM), *Aceria tosichella* Keifer. Although numerous grass species have been implicated as hosts for both the mite and virus, the primary oversummering (volunteer) and overwintering (winter) host is winter wheat. The mite and virus can only survive for 4 to 6 days off of a green host. The main WSM control tactic is destroying potential reservoir hosts before planting the next wheat crop.

The absence of volunteer wheat after a WSM outbreak introduces two important questions which have not been thoroughly addressed. First, do resident grasses serve as oversummering reservoirs for the mite and virus ? Second, if host grasses can support WCMs and WSMVs can they serve as an intermediary bridge host to wheat ? Many

studies have tested WCM and WSMV susceptibility and examined mite virus transmission to a range of grass species. However, nobody has examined the WCM and WSMV epidemiology through a combination of field surveys, laboratory transmission and acquisition tests, and sensitive serological and molecular assays for WSMV detection in field and laboratory grass samples. The following chapters represent an accumulation of field and laboratory data that addresses these questions for 13 potential grass species relative to their importance in WSMV and WCM epidemiology.

Chapter 2 and 3 describe an extensive WCM and WSMV grass survey over three summers (1995 to 1997) in a selected area in north central Montana that has had a recent history of significant WSM outbreaks. Chapter 4 expands on theses grasses by attempting to develop infection by mechanical and viruliferous WCM transmission using a Montana WSMV and WCM source. Chapter 5 presents serological and nucleic acid based assays on field and laboratory grasses for WSMV detection, and Chapter 6 describes a wind tunnel test on WCM to determine what effect glyphosate has on mite dispersal.

In conclusion, understanding the host range of WSMV and WCM is essential for further development of pest and pathogen management control strategies. Wheat streak mosaic epiphytotics are not a yearly occurrence in Montana. However, acquiring knowledge of where the mite and virus are residing during non-outbreak years when limited volunteer wheat is available is very important in understanding the WSM disease cycle.

Objectives

1. Determine which species of grasses are infested with WCMs and infected with WSMV in areas bordering wheat fields, if infected grass hosts could maintain virus infection and support WCM populations from year to year, and whether early detection of commonly infected grasses may facilitate predicting a WSM outbreak in Montana.

2. Evaluate the susceptibility of 13 common grass species to a Montana WCM and WSMV, and if susceptible can viruliferous WCMs from grasses transmit WSMV to wheat.

3. Compare the sensitivity of serological and nucleic acid based assays for the detection of WSMV in field collected and laboratory infected Gramineae species.

4. Ascertain the dispersal response of WCMs on wheat seedlings exposed to glyphosate a broad spectrum herbicide.

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