Epidemiological factors impacting the development of *Wheat streak mosaic virus* outbreaks

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Abstract

Wheat streak mosaic (WSM) is a devastating disease of winter wheat (*Triticum aestivum* L.) in Kansas. Although WSM can cause heavy crop losses, the severity of regional and statewide losses varies by year and location. Wheat streak mosaic is caused primarily by the *Wheat streak mosaic virus* (WSMV) and is spread by the wheat curl mite, *Aceria tosichella* Keifer. To infect fall planted wheat, both the virus and mite require a living, grass host to survive the summer months. The first research objective was to determine the risk of different grass species to serve as a source of WSM. Published experiments and surveys were reviewed to determine the suitability of each host based on a set of criteria. An analysis of the reports from the reviewed literature found 39 species to host both pests. Categorical analysis of these observations suggested that well-studied grass species could be placed in four risk groupings with ten species at high risk of carrying both pests. Furthermore, results from controlled experimentation generally agrees with results from field survey results for both pests.

The second objective was to determine the weather and cropping factors that are associated with regional epidemics of WSM in Kansas. Historic disease observations, weather summaries, soil moisture indices, and cropping statistics were collected from Kansas crop reporting districts from 1995-2013. Binary response variables (non-epidemic case vs epidemic cases) were developed from different thresholds of district losses attributed to WSM. Variables associated with WSM epidemics were identified by a combination of non-parametric correlation, classification trees, and logistic regression. This analysis indicates that the total acres of wheat planted per season was associated with the low frequency of epidemics in Eastern Kansas. Temperature during September appears to influence the yield losses caused by WSM. Wheat planting generally begins during September and continues through October in the state.

Temperature during the winter months (December-February) was also identified as important with warm conditions favoring outbreaks of disease. Dry soil conditions in February was also associated with epidemics of WSM. Models combining these variables correctly classified 60 to 74% of the cases considered in this analysis.

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Dedication

For my patient and loving wife, Molly

Chapter 1 - Literature Review

Introduction

Wheat streak mosaic (WSM) is a significant disease challenge to the major wheat producing regions of the United States. This disease is caused by the grass-infecting pathogen *Wheat streak mosaic virus*. Bread wheat (*Triticum aestivum* L.) is the most agronomically important host for WSM in Kansas. On bread wheat, the symptoms usually develop into yellow, mottled, and discontinuous streaks closest to the tips of newly emerged leaves. Other severe symptoms include stunting, leaf necrosis, and head sterility depending on the time and severity of infection.

WSM has an extensive distribution throughout the world and the United States. The disease has been reported in the Middle East, Australia, Eastern Europe, Central Asia, as well as South, Central and North America (CABI/EPPO 2005). In the United States, WSM has been found as far northwest as Washington stretching southeast to Alabama, but it is especially prevalent in the Great Plains wheat production region (CABI/EPPO 2005; Burrows et al. 2009). Along with its wide distribution, WSM has caused many regional crop epidemics in Kansas. In the years between 2008-2016, the Kansas statewide average losses attributed to WSM ranged from 0.001% to 2.7% and averaged 0.71% (Hollandbeck et al. 2016). During the 2016-2017 season, 5.6% losses were sustained resulting in an estimated 19.3 million bushels lost (Hollandbeck et al. 2017).

The *Wheat streak mosaic virus*

The causal agent of wheat streak mosaic is the *Wheat streak mosaic virus* (WSMV). WSMV has been characterized as a single, filamentous, (+)-sense ssRNA particle (Brakke 1971). *Wheat streak mosaic virus* has been classified in the *Potyviridae* family and the *Tritimovirus* genus. WSM has also been associated with *High Plains wheat mosaic virus* (HPWMoV) (Seifers et al. 1997) and *Triticum mosaic virus* (TriMV)(Seifers et al. 2008), which both cause similar symptoms to WSMV. Although these viruses are present in wheat producing areas, they do not occur with the same frequency as WSMV. WSMV incidence in recent virus surveys of the Great Plains region found WSMV in 35.3% of all surveyed samples, but only 6.2 and 4.3% incidence for TriMV and HPWMoV, respectively (Byamukama et al. 2013). Other surveys have found the incidence at 47, 19, and 17% for WSMV, HPWMoV, and TriMV, respectively (Burrows et al. 2009). These viruses may individually infect wheat but are commonly found in double infections along with WSMV (Byamukama et al. 2013; Burrows et al. 2009). In the case of a double infection of WSMV and TriMV, the negative impacts on susceptible plants is worse than either of the viruses individually (Byamukama et al. 2014).

WSMV infections have many negative effects on plant health. The hallmark symptom of WSMV is the development of long chlorotic streaking increasing in severity from the proximal to distal portion of young developing leaves (McKinney 1937; Slykhuis 1953). Susceptible wheat varieties affected by WSMV generally have reduced leaf chlorophyll levels as measured by SPAD units (Byamukama et al. 2012, 2014; Pradhan et al. 2015), stomatal conductance, transpiration rate, internal CO_2 concentration, and subsequently photosynthetic rate (Pradhan et al. 2015). This reduction in photosynthetic capability is associated with shoot biomass and plant yield (Pradhan et al. 2015). The loss of photosynthetic capacity caused by WSMV appears to have a strong negative effect on both the grain produced by the plant and the aboveground plant structure. The severity of plant symptoms can change drastically depending on the time of infection. When infected prior to vernalization (winter dormancy), winter wheat will have more severe symptoms and negative yield consequences than vernalized wheat. Yield is reduced through a reduction in fertile tillers, thousand kernel weight, and grain weight per tiller (Hunger et al. 1992; Staples and Allington 1956; Rotenberg et al. 2016). Non-symptomatic, WSMV positive tillers were also found to have negative yield effects. A Kansas survey during the 2011-12 growing season found a significant reduction in grain weight per tiller from non-symptomatic, WSMV positive tillers vs. non-symptomatic, WSMV negative tillers (Rotenberg et al. 2016). This effect suggests that WSMV infection may be detrimental to plant health even without apparent visual symptoms.

One reason may be that WSMV has a significant effect on the development and function of roots. Infection of WSMV has been shown to cause significant reduction of root biomass (Price et al. 2010; Pradhan et al. 2015; Byamukama et al. 2012). Along with the reduced root mass, the water-use efficiency (WUE) of the WSMV susceptible inoculated plants diminishes (Price et al. 2010). The WUE is a function of plant biomass per amount of water used. In irrigated wheat, WSMV leads to the underutilization of water in drought prone regions.

The introduction of natural WSMV infections come from two different sources. The wheat curl mite (WCM), *Aceria tosichella* Keifer, is the only described arachnid vector of WSMV, HPWMoV, and TriMV (Slykhuis 1955; Seifers et al. 2009, 1997). The WCM, like WSMV, needs a living host to survive. If the mite does not find a suitable host, it perishes within days (Wosula et al. 2015). In wheat production, the most abundant source of both the WCM and WSMV is volunteer wheat. Although volunteer wheat is the most abundant, new evidence has been shown that WSMV can survive the summer on other weedy grasses (Ranabhat et al. 2018). Once the wheat crop has emerged in the fall, WCMs disperse from over summering sources to infect the crop. This WCM movement generally follows the direction of the prevailing winds and leads to the spread of the virus radiating from the source. If the source of the pests is in an area next to the field, the symptom pattern may exhibit a gradient, radiating away from the region of source plants and resulting in an ‘edge’ effect (Coutts et al. 2008). Although typically WSMV infections occur from local sources of mites from in-field volunteers or those nearby, it has been shown that WCMs can be captured even up to 2 miles away from their original location (Pady 1955). This demonstrates that WCMs have capability of long range dispersal via the wind.

WSMV has also been able to survive within the seed of infected plants (Dwyer et al. 2006). This mode of transmission allows the disease to spread through seed transportation, especially though the dissemination of breeding germplasm. Although this has been as a source of virus in long distance viral introductions, the rates of transmission have been relatively small. In related studies, 0.2 to 0.5% transmission was found across tested genotypes, with the highest being 1.5% in a single genotype (Jones et al. 2005). Due to the low rate of transmission and lack of WCM vector, this method of transmission is not considered a major factor in local or regional outbreaks.

Other than wheat, WSMV has potential to harm other crops, such as proso millet (*Panicum miliaceum* L.), rye (*Secale cereal*e L.), foxtail millet (*Setaria italica* (L.) P. Beauv.), oats (*Avena sativa* L.), barley (*Hordeum vulgare* L.), corn (*Zea mays* L.), sorghum (*Sorghum bicolor* (L.) Moench), pearl millet (*Pennisetum glaucum* (L.) R.Br.), sugar cane (*Saccharum officinarum* L.), and Triticale (*Triticum x Secale*). Of these crops, the effect of WSMV on corn has been the best documented (Sill Jr. and Agusiobo 1955; Connin 1956b; McKinney 1949a; How 1963; Orlob 1966a; Williams et al. 1967). Generally, inbred corn varieties tend to be more susceptible to WSMV than hybrid varieties (How 1963). Comparing types of corn, sweet and popcorn tend to be more susceptible than field and dent corn (McKinney 1949a). Even though corn may be affected by WSMV, it is only considered a major challenge for seed production due to inbred susceptibility.

To survive from season to season, the virus needs a living host. Sixty-nine different species in the family *Poaceae*, including the previously discussed hosts, have been reported as potential hosts in experiments and field observations (McKinney 1937, 1949b, 1949a; Slykhuis 1951; McKinney and Fellows 1951; McKinney and Sando 1951; Slykhuis 1952; Sill Jr. and Connin 1953; Meiners and McKinney 1954; Painter and Schesser 1954; Slykhuis 1955; Sill Jr. and Agusiobo 1955; Connin 1956b; Finley 1957; Bruehl and Keifer 1958; Sill Jr. and del Rosario 1959; Slykhuis 1961; Ashworth Jr. and Futrell 1961; How 1963; McKinney et al. 1966; Orlob 1966a, 1966b; Williams et al. 1967; Timian and Lloyd 1969; Somsen and Sill Jr. 1970; Gates 1970; Christian and Willis 1993; Seifers et al. 1996; Ellis et al. 2004; Coutts et al. 2008; Ito et al. 2012). These reported hosts of WSMV may serve as a reservoir for the virus and be an inoculum source to for the subsequent wheat crop.

The Wheat Curl Mite

The wheat curl mite (*A. tosichella*) has been classified in the family Eriophyidae. The mites cycle through four main life stages: egg, first instar, second instar, and adult (Slykhuis 1955). Mites are generally smaller than can be seen by the naked eye and require a dissecting or compound microscope (40x) to identify. The eggs are 35 x 42μ to 47 x 65μ, first instar nymphs are 33 x 80μ to 47 x 150μ, second instar nymphs are 38 x 140μ to 57 x 206μ, and adults are 38 x 173μ to 63 x 285μ (Slykhuis 1955). Acquisition of WSMV from an infected plant only occurs during the first and second instar stages (Slykhuis 1955; del Rosario and Sill Jr. 1965). Of mites reared on WSMV infected plants, all stages of the mites, except the eggs, could transmit the virus (Slykhuis 1955). No dormant or deutergynous stage of mites have been identified in *A.*

tosichella populations, suggesting that the WCMs require living host for survival (Styer and Nault 1996).

Apart from vectoring viruses, WCMs cause their own separate symptoms on wheat. The WCM causes the longitudinal margin of the leaves to curl over. Leaves at the pre-jointing stage are far more susceptible to severe curling with an appearance similar to the leaves of onions (Slykhuis 1955). Older leaves are more resistant to curling and may only be limited to a portion of the leaf margin. Wheat varieties with genetic resistance to WCM generally reduce reproduction and the incidence of leaf curling (Chuang et al. 2017). Non-viruliferous mites can also cause yield penalties on wheat. On artificially infested plants, high populations of WCM have reduced yields by 17% in 'Ike' wheat (Harvey et al. 2000). Implying a linear effect, the populations of mites could cause 1% loss of yield per 450 mites per spike. The non-viruliferous mites were also able to reduce the test weight and thousand kernel weight (Harvey et al. 2000).

Research on the population dynamics of WCM has produced strong evidence of lineages and biotypes. The earliest indications of WCM biotypes were found through study of separate WCM populations on mite resistant plants. Mites sourced from 'TAM 107' wheat (mite resistant variety) were able reinfest 'TAM 107' and 'Karl' wheat (mite susceptible variety) with the same reproductive capability, but mites sourced from 'Karl' were not able to infest 'TAM 107' with the same reproductive rate as 'Karl' (Harvey et al. 1995). A similar effect was shown from mites sourced from western wheat grass, *Pascopyrum smithii* (Rydb.) Barkworth & D. R. Dewey formerly *Agropyron smithii* Rydb., reducing reproduction potential moving to wheat (Painter and Schesser 1954). Later studies using DNA sequencing of the ITS1, ANT, and 16s rRNA genomic regions identified two distinct biotypes in Australia designated WCM1 and WCM2 (Carew et al. 2009). Genetic analysis of WCM populations in the United States produced similar results using

ITS1 and COI/II mitochondrial sequencing. These researchers named the two genetically separated populations Type 1 and Type 2, equivalent to Australian WCM1 and WCM2, respectively (Hein et al. 2012; Skoracka et al. 2014). Further analysis of mite lineages has shown that three main WCM lineages, deemed MT-1, MT-7, and MT-8, have global distribution (Skoracka et al. 2014). After the discovery of these global lineages, more biological evidence has supported this separation between biotypes/lineages.

Further biological experimentation of populations and biotypes showed that WCM populations varied in their ability to transmit viruses. One study, using different WCM populations across the Great Plains, was able to show that WCM sourced from Nebraska transmitted HPWMoV at significantly higher rates than mites from three other states (Seifers et al. 2002). These varied transmission rates could have been attributed to different biotypes. In Australia, WCM1 were unable to transmit WSMV, while WCM2 transmitted the virus at 76% efficiency (Schiffer et al. 2009). Furthermore, Type 1 populations from the Great Plains have been shown to transmit WSMV at higher efficiencies than Type 2 populations (Wosula et al. 2016).

The reproduction and survival of wheat curl mites are heavily influenced by local environmental conditions. The mites' egg-to-egg life cycle in optimal conditions at 25°C occurs over 7-10 days (Staples and Allington 1956; Slykhuis 1955). Further studies have suggested that the effect of temperature on reproductive rates varies among different populations of WCM. Two globally-distributed WCM lineages have been studied for differences in reproduction. For the MT-1 and MT-8 lineages, the populations increased at temperatures between 12.2 to 40.0°C and 10.4 to 35.7°C, respectively, and decreased at temperatures outside of the ranges (Kuczyński et al. 2016). Along with optimum growth conditions, severe high and low temperatures reduce survivability. WCMs have been able to survive extremely cold temperatures on living wheat. The mites have shown to survive -20°C conditions for a up to a day and endure -5°C conditions for 16 days (Slykhuis 1955). Mites are stressed under temperatures above 35 to 40°C (Kuczyński et al. 2016; Schiffer et al. 2009). Overall, there is a strong effect of temperature on the reproduction and on-host survival of WCM populations.

When the WCM moves off-host, its survival is more dependent on temperature. In high humidity (100%) and low temperature (10°C) situations, mites may survive up to 160 hours off of the host, but in situations of low humidity (2%) and low temperature (10°C), average survival drops to near 43 hours. As the temperature increases (30°C), the interaction between humidity and temperature reduces and results in average survival time dropping to around 27 hours in high humidity and 6 hours in low humidity (Wosula et al. 2015). Overall, the trends show that cool, humid conditions favor WCM survival.

Due to the obligate nature and lack of dormant stage, the WCM requires a living host to survive during summer fallow. This requirement is often referred to as the “green bridge.” The “green bridge” consists of any WCM and WSMV suitable/susceptible host that survives the summer season. In wheat production, the decidedly most important species in the “green bridge’ is volunteer wheat (Connin 1956a). Volunteer winter wheat that germinates within the field before harvest provides a suitable host for WCM and WSMV during a period of major mite migration (Nault and Styer 1969). This means of survival on volunteer wheat through the summer has long been implicated as the major source of the virus for the subsequent winter wheat crops (McKinney 1937; Connin 1956a; Slykhuis 1953). Along with volunteer wheat, cultivated, native, and weedy grass species have been implicated as suitable hosts for both WCM and WSMV. Although there may be debate to the actual risk that these grassy hosts pose, there has been a significant amount of work done to evaluate the potential of different species to carry and increase WCM populations, serve as WSMV sources, and serve as a ‘green bridge’ of both WCM and WSMV (Ito et al. 2012; Sill Jr. and Connin 1953; Christian and Willis 1993; Somsen and Sill Jr. 1970; Slykhuis 1955; Sill Jr. and Agusiobo 1955; Staples and Allington 1956; Connin 1956b; Ranabhat et al. 2018).

To disperse from their infested host and through wheat fields, the WCM utilizes the wind. In its dispersal behavior, the WCM moves out of the curled margins of the leaves and to the edges and tips of the leaves. Once at an optimum location for dispersal, the WCM props itself up perpendicularly using it anal suckers and prepares for eventual release from the plant (Gibson and Painter 1957; Kiedrowicz et al. 2017). Some evidence suggests that aphids also spread mites from plant to plant, but this has not been implicated as a significant means of mite dispersal (Gibson and Painter 1957). WCMs have been captured throughout the spring and summer months, but captures increase drastically around the time of dry down and harvest (Nault and Styer 1969). This shows an association between plant host maturity and large WCM dispersal events. In fields with volunteer wheat, the number of mites captured is reduced after harvest of the wheat crop, but increases later in the summer and early fall. The capture of mites tapers off by late fall and winter (Nault and Styer 1969).

Factors that prompt movement of WCMs away from infested plants include temperature, light, and host plant health. Light and temperature were identified as factors in early studies using growth chambers (Nault and Styer 1969). Lower temperatures as well as dark periods were shown to suppress the movement of mites off the plants. Conversely, higher temperatures and periods of light seemed to stimulate the mites’ dispersal off of the plants (Nault and Styer 1969). Utilizing wind tunnels, it was shown that a decline in host plant health correlated with a decrease in WCM dispersal (Thomas and Hein 2003). Recent work has demonstrated that at high WCM populations, there was no effect of the presence of other insects on WCM dispersal behavior, but with a wind stimulus, a significant proportion of the WCM were standing on anal suckers (Kiedrowicz et al. 2017). Overall, evidence suggests that light, temperature, wind, host maturity and plant health may contribute to the dispersal activity of the WCM.

Weather and Cropping Factors Associated with WSMV Epidemics

In Kansas, major statewide outbreaks of WSMV occurred in 2011, 2012, 2013, 2015, and 2017 (Hollandbeck et al. 2017). These outbreaks led to the loss of millions of bushels and dollars. The sporadic severity of the disease indicates that there are irregular factors that suppress the disease presence. Host resistance to both the mite and the virus has been identified and deployed in some high yielding winter wheat varieties, but the adoption of these varieties has not been widespread in Kansas (Mutti et al. 2011; De Wolf et al. 2017).

Certain weather events have long been associated with local and regional outbreaks of WSMV. Early studies of outbreaks have associated WSMV with severe hail events (Staples and Allington 1956). In these cases, hail during the late grain filling stages of maturing wheat led to a large population of pre-harvest volunteer wheat that was subsequently infested with WCM from the maturing crop (Staples and Allington 1956). For local sources of WCM and WSMV, wheat fields that have hail damage during late grain filling period may be a significant causal factor for WSMV outbreaks the following year.

Increased precipitation during the summer and fall before the planting of wheat has also been described as a major factor in regional outbreaks. Various outbreaks in Kansas and Nebraska throughout the 1948-1959 wheat seasons were found to be associated with at or above average rainfall during the late summer through the late fall, leading to statewide outbreaks in subsequent wheat harvests (Somsen and Sill Jr. 1970; Staples and Allington 1956). Another major statewide outbreak in North Dakota during the 1988 wheat season was associated with heavy rainfall in the preceding summer (McMullen and Nelson 1989). Rainfall during this period was thought to be associated with large population of volunteer wheat or lush growth of other over summering grasses before planting winter wheat.

Long-term precipitation patterns have been associated with regional and statewide outbreaks. In the Nebraska 1953-4 outbreak, it was noted that drought conditions persisted in January and February of that season (Staples and Allington 1956). The 1988 North Dakota outbreak also described warm, dry conditions through December, as well as a warm and dry spring and summer during the cropping season (McMullen and Nelson 1989). These conditions would be potentially unfavorable for mite hosts and stimulate movement of the WCMs through the crop, as well as reduce snow cover over the winter and create conditions for wind to move WCMs.

Temperature was also identified as a potential factor in WSMV outbreaks. For Kansas and Nebraska outbreaks, cool temperatures were observed in the July and August before the crop was planted, and temperatures in September through November were above average (Somsen and Sill Jr. 1970). The 1953-4 Nebraska outbreak occurred after above average January and February temperatures (Staples and Allington 1956). The 1988 North Dakota outbreak was characterized by warm temperatures through December and warm spring and summer temperatures (McMullen and Nelson 1989). These observations suggest that cool temperatures during the summer months before the outbreak favor the survival and reproduction of mite populations and volunteer wheat, while above average falls and winters favor the reproduction and spread of the mite during the establishment and winter growth of the winter wheat crop.

Warm temperatures during the spring season favor the development of the disease and mites and add additional stress to the affected crop.

Other cropping factors have been noted as contributors to outbreaks of WSMV. During the 1963 Southern Alberta, Canada outbreak, the previous spring had been exceptionally dry, resulting in the delayed emergence and harvest of spring wheat (Atkinson and Slykhuis 1963). This led to long exposure of WCM infested spring wheat with the next season's planted winter wheat and subsequently a major outbreak. Overall, temperature, precipitation, drought, and cropping factors have all been implicated has drivers of WSMV outbreaks.

WSMV Control Strategies in Winter Wheat

For control of WSMV, different strategies minimize the risk of severe viral infections. Management strategies include eradication of inoculum sources, late planting, and host resistance. Since the suspected primary source of WSMV and WCM for fall planted wheat are over-summering wheat volunteers, eradication of volunteers (Connin 1956b). The method of volunteer eradication influences the overall risk of migration of the WCM. If herbicides are used, the time until the weed dies depends on mode of action of the herbicide (Jiang et al. 2005). For example, the time it takes for glyphosate versus paraquat to take effect on the host plant is different. Glyphosate may take up to 4 days longer for complete weed control. This allows WCM to continue dispersing for a longer period of time, lengthening the window of risk. Tillage may also be used to control volunteer wheat. Destroying volunteer plants with tillage may have faster effects on the WCM population than common herbicides with a population decline 5-10 days after a tillage operation. Tillage may not be entirely affective depending on the weather and soil conditions (Jiang et al. 2005). Although there may be variation in control technique, eradication of volunteer wheat in and around a new wheat crop a month before planted is strongly recommended.

Another strategy for preventing early season infections is to adjust planting dates to avoid the highest risk periods of mite movement. Delayed planting has been shown to reduce the incidence of the virus and yield losses from early season WSMV infections (Slykhuis et al. 1956; Staples and Allington 1956). The delay in planting reduces the exposure of wheat to dispersing wheat curl mites, as studies have shown that WCM dispersal activity drops throughout the fall (Staples and Allington 1956; Nault and Styer 1969). This could be attributed to either the decrease in temperature and consequent effects on mite reproduction and dispersal, or the early fall senescence of warm season annual hosts of the mite and virus, such as corn (Nault and Styer 1969; Kuczyński et al. 2016). Although delayed planting may reduce the time that planted fall wheat is exposed to active WCMs, planting too late leads to an increase in WSMV loss causes by spring infections (Hunger et al. 1992). Producers must take both scenarios into account, in addition to other agronomic factors to optimize planting date and minimize yield losses due to WSMV.

The use of chemical controls has not been effective for controlling the WCM or WSMV (Kantack and Knutson 1958; Staples and Allington 1956). In many tests of the early miticides to control WCM, adequate control was achieved only at pesticide levels that ultimately harmed the maturing wheat. Phytotoxicity and reduced germination were noted at pesticide concentrations high enough for control and treatments still did not provide complete control (Kantack and Knutson 1958). Contact miticides are suspected to be ineffective mainly due to the microenvironment produced by the mite. The mites tend to congregate in the leaf sheath or in the curled margins of the leaves, protecting them from contact with the miticidal chemicals. New chemical products have shown early indications of effective control, but replication and economic feasibility studies are still needed (Al-Azzazy et al. 2013).

Along with delayed planting and source eradication, the use of varietal resistant to WCM or WSMV may prevent severe losses from the disease. An early example of WSMV resistance in wheat was the immunity found in the *Agropyron* x wheat hybrid (McKinney and Sando 1951). Within *Triticum aestivum*, there are three named sources of resistance. The resistance genes *Wsm1* and *Wsm3* were introduced into wheat through chromosomal translocation events from *Thinopyrum intermedium* (Host) Barkworth & D. R. Dewey (Liu et al. 2011; Seifers et al. 1995). The third source, *Wsm2*, was identified with unknown origin and provides similar resistance as *Wsm1* (Haley et al. 2002; Seifers et al. 2006). *Wsm1* and *Wsm2* both have resistance to WSMV at lower temperatures (18°C), but at higher temperatures (24°C) the resistance is lost (Seifers et al. 2006, 2007; Liu et al. 2011). The recently discovered *Wsm3* provides temperature dependent resistance as well. There is evidence that the WSMV resistance provided by this gene is retained at higher temperatures, while TriMV resistance is not (Liu et al. 2011). Along with those sources of resistance, other forms of WSMV resistance have been found in synthetic lines derived from *Triticum durum* or *Triticum. diccoides* with *Aegilops tauschii* Coss. (Rupp et al. 2014). Transgenic approaches also appear to be successful in conferring stable resistance to WSMV. An RNAi construct was inserted into wheat that expresses a WSMV coat protein target for gene silencing, and a subsequent reduction in WSMV infection (Cruz et al. 2014). Although present in the wheat breeding germplasm, deployment of the synthetic lines and those developed with RNAi have yet to undergo commercial production.

There have been multiple sources of WCM resistance identified. Early initial resistance was found in lines containing a transfer of genetic material from goat grass *A. taushciii*. This transfer contained two resistance genes named *Cmc1* and *Cmc4* (Thomas and Conner 1986; Cox et al. 1999; Malik et al. 2003). Another WCM resistance gene, *Cmc3*, was sourced from a wheat-rye translocation event (Malik et al. 2003). The resistance gene *Cmc2* originates from a *Thinopyrum elongatum* translocation event into wheat (Martin et al. 1976; Whelan and Hart 1988). Utilizing these sources of mite resistance results in a reduction in the number of mites able to survive on the host and a reduction in yield loss (Harvey et al. 2003). While genetic resistance to WCM shows promise, some resistance has already been overcome. Study of *Cmc3*, sourced from TAM 107, showed that reproduction of some WCM populations are not affected (Harvey et al. 1995; Chuang et al. 2017). Unfortunately, due to the variation within mite populations, mite resistance may not serve as a viable long-term solution to WSMV control.

Currently, there are commercial lines available that resist the mite or the virus. Such varieties include Oakley CL, Clara CL, Joe, and Snowmass (De Wolf et al. 2017). These available varieties have temperature-sensitive WSMV resistance as described earlier and are not resistant to other mite-transmitted viruses, such as TriMV. Mite resistance is available in TAM 107 and derived varieties, such as TAM 112 (Malik et al. 2003). Recent efforts have focused on combining WSMV and WCM resistance into a single variety, though commercial lines are not yet available (Chuang et al. 2017). In conclusion, timely volunteer control, delayed planting, and the virus/vector resistance appear to be the only effective means of control field outbreaks of WSMV.

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Chapter 2 - Categorical Analysis to Determine the Biological Suitability of Grasses for *Wheat streak mosaic virus* and the Wheat Curl Mite

Abstract

Wheat streak mosaic virus (WSMV) and the wheat curl mite (WCM) have long been pests that affect Kansas winter wheat. To survive from the end of wheat harvest to the beginning of the next wheat-growing season, both the mite and the virus require a living host. Controlled experiments and field surveys have implicated many species in the grass family as hosts for both the mite and the virus, but few studies combine available data to develop a more detailed assessment of risk posed by these different grass species. This analysis considered the results of 39 controlled biological experiments and 49 field-based surveys. The first phase of the analysis focused on reports of WSMV or WCM in the various grass species. A subset of the data was then used in a second phase of the analysis, which focused on the potential risk of a grass in aiding the survival of WSMV or WCM. In this analysis, 39 grass species were identified to potentially carry both pests. The analysis also suggested that grass species could be divided into four risk groups and identified ten species most likely to carry both pests. Findings also suggested that reports from controlled experiments generally agreed with results from field observations with 87.5% and 81.7% agreement for WSMV and WCM, respectively. Additionally, there was evidence to suggest that WSMV susceptibility could limit the contribution of a grass species to outbreaks of disease.

Introduction

Winter wheat (*Triticum aestivum* L.) is the primary economic host of *Wheat streak mosaic virus* (WSMV) in the Great Plains. WSMV infection causes systemic infections in wheat with symptoms expressed on all parts of the plant. On the leaves, WSMV causes yellow streaks and mosaic extending from the base to the tip of the leaf. When infected in the fall, the disease stunts the growth of the plant and reduces the number of fertile tillers (Hunger et al. 1992). Underground, the virus reduces root growth and subsequently the water use efficiency of the plant (Price et al. 2010). The disease affects multiple yield components in wheat including number of productive tillers, head size, and kernel weight (Hunger et al. 1992).

At the field level, WSMV can cause yield loss up to 87% in susceptible varieties (Hunger et al. 1992). The disease also causes crop damage on the regional scale. Kansas statewide yield losses attributed to the wheat streak mosaic complex during the period of 2007-2016 varied from 0 to 2.7% with four years of losses greater than 0.7% (Hollandbeck et al. 2016). A recent wheat disease survey in Kansas estimated statewide losses of 5.6%, or 19.3 million bushels (Hollandbeck et al. 2017). Other Great Plains states have experienced similar losses. For example, North Dakota experienced a particularly severe statewide outbreak of WSMV in the 1987-88 season. During this season, growers experienced yield losses leading to losses ranging from 1 to 80% depending on type of wheat with total estimated statewide loss of $40.1 million (McMullen and Nelson 1989).

The wheat curl mite (WCM), *Aceria tosichella* Keifer, is the primary vector of WSMV. WCMs are microscopic, eriophyid mites that feed on living grass hosts. The adult stage of the mites range from 38µ x 173µ to 63µ x 285µ in size (Slykhuis 1955). The feeding of WCMs causes the margin of the wheat leaf to curl. In some cases, this curling makes the leaves appear similar to onion leaves or may traps emerging leaves in the whorl (Slykhuis 1955). The WCM can also transmit two other viruses of wheat, *Triticum mosaic virus* (TriMV) and *High plains wheat mosaic virus* (HPWMoV) (Seifers et al. 1997, 2008). Even without viruses, the feeding of large WCM populations on wheat can cause yield losses and loss of grain quality. Under the assumption of linearity, it has been estimated that 450 WCMs per spike resulted in 1% loss in grain yield (Harvey et al. 2000).

The WCM and WSMV require a living host to survive or reproduce. Before the end of wheat harvest, WCMs move to the head of the wheat plant as the plant matures, and disperse by wind (Nault and Styer 1969; McMechan and Hein 2017). The WCM is vulnerable during the dispersal process and must find a new suitable host where it can find shelter and sustenance. Alternate hosts for the WCM that enable the populations to persist in the absence of the wheat crop are generally referred to as the "Green Bridge". To be a member of the "Green Bridge", a summer plant host should have the following characteristics: large population densities near newly planted wheat, appropriate seasonality (mainly summer annuals and perennials), susceptibility to WSMV, and sustain a large enough WCM population to effectively disperse back to the wheat crop (Christian and Willis 1993).

The best-studied member of the "Green Bridge" is volunteer wheat. Wheat is considered to be "volunteer" when seed is left on the soil after harvest or when grain is knocked out of the maturing wheat heads by high winds or hail. When present in the soil, wheat grain/seed can germinate anytime throughout the spring, summer, and fall (Anderson and Nielsen 1996). Due to its clear suitability for both the vector and virus, and its ubiquity in wheat producing regions, volunteer wheat has been implicated as one of the most important species of the "Green Bridge" (Connin 1956a; Staples and Allington 1956; Thomas and Hein 2003).

Maize (*Zea mays* L.) has also been identified as a summer host for the disease. WSMV has been found to affect primarily sweet corn varieties and inbred lines used for seed production (Finley 1957; How 1963). Some varieties of hybrid field corn have also demonstrated mosaic symptoms in response to inoculation with WSMV (Sill Jr. and Agusiobo 1955). Apart from WSMV, the feeding of the WCM at the reproductive stages of maize is associated with the disease Kernel Red Streak (Nault et al. 1967). Furthermore, dispersal studies demonstrated that WCMs move off the maize crop as it matures in the fall (Nault and Styer 1969). This movement at the time of winter wheat planting makes late-maturing corn a potential source of WCMs and fall infections of WSMV.

Other cereal crops have had mixed reports of WSMV and WCM suitability. For example, mechanically inoculated sorghum [*Sorghum bicolor* (L.) Moench)] exhibited symptoms of WSMV infection in recent studies (Seifers et al. 1996). Although sorghum has been found to be susceptible to WSMV recently, historically sorghum has been understood to be immune or symptomless in response to WSMV infection (Sill Jr. and Connin 1953; Sill Jr. and Agusiobo 1955). Early experiments studying WCM population survival found common oats (*Avena sativa* L.) able to host WCMs with “moderate survival” (Slykhuis 1956). In conflict to this report, a more recent study found two WCM populations unable to establish or survive on common oats (Harvey et al. 2001). Some cereal crop species appear to have the suitability to carry WSMV and the WCM, but variation in the pest and host populations may contribute to conflicting available host information.

Some weedy, introduced grasses of Kansas have also had mixed reports about their ability to carry WSMV and the WCM. A common weed in Kansas, Stinkgrass [*Eragrostis cilianensis* (All.) Vign. ex Janchen], has had evidence of WSMV susceptibility in different experiments and studies (Connin 1956b; Slykhuis 1955; Sill Jr. and Connin 1953; Coutts et al. 2008). Even with many studies indicating stinkgrass is susceptible to WSMV, a recent experiment reported stinkgrass to have no reaction to WSMV mechanical inoculation (Ito et al. 2012). Another introduced weed, quackgrass [*Elymus repens* (L.) Gould], has had many reports of immune/no reaction to WSMV (Sill Jr. and Connin 1953; Slykhuis 1955; McKinney et al. 1966; Somsen and Sill Jr. 1970; Seifers et al. 1996), but new findings have shown manually inoculated quackgrass positive for WSMV using enzyme-linked immunosorbent assay (ELISA) detection methods (Ito et al. 2012). As to the wheat curl mite, smooth crabgrass [*Digitaria ischaemum* (Schreb.) Schreb. ex Muhl] had been reported to increase mite populations from an early study (Connin 1956b). Although the more recent study of WCM populations found no population increase on this species (Harvey et al. 2001). These conflicting reports continue to demonstrate the variation of host suitability for both pests found in cereal crops and complicate management and recommendations.

In the Great Plains, native grasses have also had mixed reports of suitability to WSMV and the WCM. Native grasses can be found in nearby wheat fields and in conservation range program mixtures used by Kansas farm managers (Christian and Willis 1993). Canada wildrye (*Elymus canadensis* L.) has been shown to express WSMV symptoms when manually inoculated (Sill Jr. and Connin 1953; Ito et al. 2012). But using a mite-mediated inoculation, Canada wildrye had varying results (Connin 1956b; Ito et al. 2012). Another native, buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.] was found to be susceptible to WCM in one study, but unable to increase population size in another (Orlob 1966a; Somsen and Sill Jr. 1970). Similar to crops and introduced grass species, natives have had mixed evidence for the biological suitability to carry these pests during the summer.

The conflicting reports for the ability of grass species to host WSMV and the WCM could present some confusion when evaluating the risk of these hosts contributing to local outbreaks of WSMV. Determining the potential risk of grasses to carry both the virus and the mite will helps to rule out potential sources that may be implicated in WSMV crop infections. Recent summaries of the host range of the WCM and WSMV list possible hosts, but did not address conflicting results (Navia et al. 2013; McMechan 2016). In this study, we integrate the results of previous research to develop a more comprehensive assessment of the risk posed by different grass species.

Methods

To categorize the historical evidence for grass species' biological suitability for WSMV and WCMs, 51 published research articles and research bulletins were reviewed in a categorical analysis (Table 2.1). Dissertations were excluded from the review to prevent duplication of information that may have been already included in the published literature. For the purpose of this analysis, a study was defined as an experiment or field survey results included in a research article or bulletin. Studies from published articles and bulletins were comprised of both controlled experiments and survey results for either or both pest(s). If the article separated results of experiments due to multiple populations (biotypes) of WCMs, different methods of inoculation, or surveys over multiple years, the results were considered as separate studies.

The first step of the analysis was to develop a set of criteria to define species suitability for each pest and different type of study. WSMV infection was confirmed based on 5 criteria common across experiments and surveys (Table 2.2). Two categories were used to evaluate the host*pest interaction recorded in the historic studies. If a species fulfilled at least one of the criteria for suitability, an assessment of 1 was given. Conversely, an assessment of 0 was given if none of the suitability criteria was satisfied. The suitability assessments were compiled for each host*pest combination.

The report-based analysis considered available reports of grasses as hosts or non-host for WSMV or WCM. If any indication of suitability was found for the host*pest assessment (at least one assessment of 1), the grass species was determined to be a host of the pest, or "+". If the species was included in at least one study and no compatible interaction was found (all assessments 0), the species was considered a non-host for the pest, or "-". The host*pest assessments were then combined for WSMV and WCM to determine if a given species was suitable to both pests. To be considered suitable for both pests, or "+", the species had at least one suitable interaction (assessment of 1, or "+") for both pests. If a species was not a host, or "-", for either or both pests, the species was considered a non-host for both pests, or "-". If one of the pests was not assessed in the literature review, then the species was not included analysis of both hosts.

Contingency tables were developed to explore the relationships between experiments vs. surveys results and individual pest vs. both pests. Reports were generated from experimental and survey results separately for each host*pests, using the method described above. Only species that were assessed in both an experiments(s) and a survey(s) were included in this analysis. Contingency tables were also created to compare host status for each pest individually and combined using findings from the report-based analysis were utilized. Two types of contingency tables were developed compare overall pest results to each other. First, a table comparing the results WSMV and WCM was created. Second, tables were made comparing the individual pests to results of both pests. The tables only included species that have been reported for both pests. For each table, agreement and non-agreement was calculated to compare the degree of agreement between methods used and the individual pest statuses. Agreement was calculated by dividing the number of species that had the same results for both categories by the total number of species included in the table. Non-agreement was calculated by dividing the number of species that had differing results for the two categories by the total number of species included in the table.

This categorical data was also used in an evidence-based analysis to calculate the proportion of studies that indicated a given grass was a host of either WSMV or WCM. Only grass species found in four or more studies for a pest were considered in this analysis. Exact statistics were calculated for the binomial distribution for each host*pest interaction (SAS Version 9.4; SAS Institute, Cary, NC) (Appendix A). A proportion of 0 indicated that the species was a non-host [only non-suitable assessments (0s) recorded], and a proportion of 1 indicated that the species was a host [only suitable assessments (1s) recorded]. The species with host*pest proportions that were between 0 or 1 were determined to be mixed evidence hosts. A two-sided hypothesis test with exact statistics at $\alpha=0.05$ was performed to determine whether a host*pest interaction for mixed evidence hosts were significantly different that $p=0.5$. A cluster analysis that included species with both pest proportions was used to help identify trends of host suitability based on the ward method (JMP Pro Version 11.2.0; SAS Institute, Cary, NC). Results from the cluster analysis was utilized to develop risk groups and thresholds. For verification of the biological significance of the WCM proportion, the WCM proportions were compared with WCM population survival and reproduction data provided by Harvey et al. 2001. The data from Harvey et al. 2001 provided the mean final number of WCM found on the hosts after 7 days start from a starting population of 10 WCM. Mean final population number greater than 10 suggested that host had evidence of mite reproduction, numbers between 10 and 0 suggested evidence of survival, and number of 0 suggested no evidence of mite survival.

Results

The reporting method found that 171 grass species have been assessed for either WSMV, WCMs, or both (Table 2.3). Of the 171 species, 132 have been studied for WSMV, 114 have been studied for the WCM, and 75 have been studied for both. For WSMV, 68 species, or 51.5%, were reported as having evidence of infection. In studies of the WCM, 89 species, or 78.1%, were reported to host the mite. Of the 75 species that were studied for both the WCM and WSMV, 39 species were reported as having evidence for hosting both the WSMV and WCM. Of the remaining 36 species, 25 reported evidence for WCMs and no evidence for WSMV, three reported evidence for WSMV and no evidence for WCMs, and eight had no evidence for both WSMV and WCM (Table 2.4).

Comparisons between experimental and survey results for both pests had strong agreement. Forty species were studied in both WSMV experiments and surveys (Table 2.5 a). Of the 40 species, 21 were reported as hosts in both study types, and 14 were reported as non-hosts. The WSMV experimental and survey results did not agree for 5 species. One species was identified as a non-host in experiments yet determined as a host in survey results, and four were hosts in experimental methods but not found in surveys. A comparison of experiments and surveys for hosts of WCM found similar results (Table 2.5 b). Seventy-one species were assessed for both methods. Fifty-one species were found to be hosts, and 7 were reported having no evidence of hosting WCM for both methods. Four species were identified as non-hosts in WCM experiments while classified as hosts in WCM field surveys, and 9 were reported as having evidence of carrying WCMs in experiments, but not in surveys. For both pests, the comparison of experimental vs. survey results had high levels of agreement (0.875 for WSMV and 0.817 for WCM).

The comparison of the individual pest results vs. combined pest results utilized 75 species that had results for both pests. From WSMV results vs. combined pest results, the comparison found 0.960 of species agreed. The comparison of WCM results vs. combined pest results found only 0.667 of species agreed. From these comparisons, WSMV results has a stronger association with the combined results than WCM results.

The evidence-based analysis resulted in the calculation of 83 host*pest proportions (Prop), 39 species for WCM, 44 for WSMV, and 33 species for both pests (Table 2.7 a-f). For WCM proportions, one was considered a host (Prop=1), three were non-hosts (Prop=0), and 35 were mixed evidence hosts (0<Prop<1). The results from the exact statistic hypothesis testing found four species (*T. aestivum, Z. mays, Setaria virdis*, and *Pascopyrum smithii* (Rydb.) Á. Löve) of these 35 hosts that were significantly different from the proportion of 0.5. The WCM proportions of evidence from the other 31 species were not significantly different from 0.5. For the 44 calculated proportions for WSMV, 14 were considered hosts for WSMV (Prop=1), seven were non-hosts (Prop=0), and 23 were mixed evidence hosts (0<Prop<1). Of the 23 mixed evidence hosts, 11 were significantly different from the proportion of evidence of 0.5, with 10 significantly higher than 0.5 and one lower. The other 12 mixed evidence hosts did not have a proportion of evidence that was significantly different from 0.5.

Cluster analysis results identified thresholds for each pest that would indicate high or low risk of pest suitability. This resulted in the formation of four main groups. First, the species were split into two groups: large (Prop>0.5) and small (Prop<0.5) WSMV proportions. Those two groups were then split into groups that corresponded with large (Prop≥0.63) and small (Prop<0.63) WCM proportions (Figures 2.3 and 2.4). These four risk groupings were designated as high-risk group (High WSMV/High WCM), moderate risk group I (High WSMV/Low

WCM), moderate risk group II (Low WSMV/High WCM), and low-risk group (Low WSMV/Low WCM) (Table 2.7 c-f).

WCM proportions for hosts included in both analyses were compared to the survival and reproduction information of two different mite populations on 26 different species of grasses (Figure 2.2 a,b). Of the species studied, 14 species were considered to be at low risk for WCM (<0.63) and 12 were considered high-risk (≥0.63) from the evidence-based approach. Of the 14 low-risk species, only four species had evidence of survival for both the Kansas (KS) WCM and Nebraska (NE) WCM populations. The remaining 10 low-risk species from the KS and NE mite populations, showed no evidence of mite survival. From 12 high-risk WCM species reaction to the KS population and NE population were: 2 and 0 species had no evidence of survival, 4 and 8 had evidence of survival, and 6 and 4 had evidence of reproduction on the host, respectively.

Discussion

Biologically, both pests require compatible interactions with a suitable host plant to reproduce or survive. From the reported findings, 68 different species of grasses were identified as hosts to WSMV. These identified species have diverse characteristics, such as cool and warm season, annuals and perennials, grain/forage crops and weeds, as well as natives and new introductions to the Great Plains. The summary of WCM reports revealed that 89 species of grasses were suitable hosts for either the survival or reproduction of the mite. Like WSMV, a wide variety of grasses can support populations of the WCM. Although both pests appear to affect a wide distribution of grasses, the WCM appears to have a larger host range both from the absolute number of species and the percentage of studied hosts (71.8 vs. 51.5%) than WSMV.

This analysis is the most recent attempt to determine the suitability of different grasses to host both WSMV and the WCM and to provide a source of virus-carrying WCMs to infect winter wheat or summer volunteer wheat. These findings agree with similar results from recent report-based approaches. A similar review found 91/197 (46.2%) of all species tested with WSMV manual inoculation were positive for WSMV, and 18/44 (40.9%) of all species identified in the field were positive (McMechan 2016). The same review found that 71/86 (83.6%) species in WCM experiments showed some evidence of survival, and 66/90 (73.3%) species in WCM field observations were found to harbor WCMs. In another recent review of WCM hosts, Navia et al. (2013) found almost 90 grass species reported to host the WCM. The variations found between afore mentioned reports of WSMV and WCM hosts, most likely resulted from the inclusion of non-grass species, types of studies considered, the grouping of different synonymous hosts, and differences in articles included in the reviews. Although there is some variation of total number of reported hosts from these recent reviews and the report-based approach in this analysis, both identified similar absolute numbers and percentages of species that could host the WCM and WSMV.

To understand which grass hosts may carry either of these pests, researchers have utilized observations from controlled experiments to predict observations in the broader environment. Using controlled experiments gives pathologists a more efficient method for the screening potential hosts for pests. The analysis of the report based-results with contingency tables had two primary findings. First, results from WSMV and WCM controlled experiments generally agree with WSMV and WCM field survey results. For both pests, these analyses found that host assessments from controlled experiments often agreed with field survey results with relatively strong agreement with 35 of 40 species and 58 of 71 species for WSMV and WCM, respectively (Table 2.5 a,b). The four species found in WSMV experiments and not in surveys could be explained in part by a low number of surveys evaluating these grasses. Kentucky Bluegrass (*Poa* *pratensis* L.) was the only survey report of WSMV that was not supported by experiments under controlled conditions and may be indication of variation within the WSMV population, or differences in the detection methods used (Ito et al. 2012). Of the nine species identified in WCM experimental results, but not found in surveys WCM, most had only one survey assessment. The four species identified as non-hosts in controlled experiments, but found to be WCM host in surveys also had a low number of experimental assessments (less than 3) and could also be explained by variation in WCM populations/biotypes used in the controlled experiments. Overall, from the agreement of experimental and survey results, suggests that controlled experimentation with WSMV and different populations of WCM would likely identify >80% of the grass species that could be viable host of the virus in field situations.

The analysis identified 39 grasses capable of hosting both the WCM and WSMV, and 36 species unable to support at least one of the pests. From the classification analysis comparing the agreement of WSMV and WCM reports vs. both pest results, WSMV was in better agreement than WCM in predicting the host status of both pests (0.960 vs 0.667). The three grass that were WSMV hosts but not WCM hosts were likely associated with the low number of WSMV studies or variability of the WCM populations tested (Table 2.6 a). The 25 grasses that were hosts of WCM but not WSMV were more likely due to the inability to host the WSMV than a low number of studies (mean of 4 WCM studies per entry) (Table 2.6 b). Results from these finding suggest that WSMV host status is generally more associated with green bridge candidates (hosts for both pests) than WCM results. Although it may be due to the threshold for evidence set by the criteria used in the analysis, it could also be due to be linked to the wider adaptation of the WCM on grass hosts. Suitability to WSMV may ultimately be a limiting factor to what species can host WSMV and the WCM and serve as summer source of WSMV.

This review also evaluates the capability of a given grass species hosting either pest by dividing the proportion of studies with evidence of a species hosting the pest by the total number studies considering the species*pest combination. The results from the WSMV proportions suggest that the virus is relatively stable among well studied host species. WSMV host status was consistent (Prop=0 or 1) for 21 of the 44 studied hosts. Of the remaining 23 mixed evidence hosts, 11 were significantly different than Prop=0.5 or equal evidence at $\alpha=0.05$ level from two-tailed hypothesis testing with exact statistics. Furthermore, the frequency distribution of the 44 WSMV proportions is bimodal, suggesting that well-studied species tend to have a consistent host range (Figure 2.1 a). The discovery of previously unknown variants within the population of the virus may explain some of the mixed reports of viral infection. For example, sorghum (WSMV Proportion=0.33) and Kentucky bluegrass (0.17) may have tested by virulent isolates that may not have considered in previous experiments (Seifers et al. 1996; Ito et al. 2012). With the general consistency of assessments, the WSMV proportion could provide a reliable way to evaluate the potential risk that a given grass species contributes to the “green bridge”. The analysis also suggests that WSMV may be more common on annual than perennial grasses. The reasons for this difference are unclear.

In contrast to the WSMV proportions, the distribution of WCM proportions ranges across most possible values but peaks at 0.5. Of these well-studied grasses, most had mixed evidence of WCM suitability. Furthermore, almost all of the species in the WCM evidence-based were significantly different from 0.5 from the two-tailed hypothesis testing with exact statistics. One difference that may contribute to mixed results from the WCM proportion are the differences between WCM populations. A study comparing the survival and reproduction potential of WCM populations found significant differences between populations on different grass hosts (Harvey et al. 2001). This biotype/population effect may explain the number of mixed evidence hosts found in this study.

It also appears that almost all well-studied grass had at least one recorded suitable interaction. Only Indiangrass [*Sorghastrum nutans* (L.) Nash] had no evidence of suitability, suggesting that most grasses are able to harbor at least low populations of WCM. Although many of these well-studied grasses were mixed evidence species, there was still evidence that the WCM proportion did reflect some level of host suitability. From the comparison of WCM proportions to survival and reproduction data from Harvey et al. (2002), it appeared that species with the higher values of WCM proportions (WCM Prop>0.63) were more likely to survive and reproduce than lower values (WCM Prop<0.63) suggesting that the WCM proportion has some relation to WCM suitability of different grass hosts (Figure 2.2 a,b).

The thresholds from the cluster analysis divided species based on evidence of suitability to both WSMV and WCM. The high-risk group included species that are known to be reservoirs of the WSMV (Table 2.7 c). More recent field experiments have also documented species in the high WSMV risk groups throughout the summer including *T. aestivum* L., *S. italica* (L.) P. Beauv., *Echinochloa crus-galli* (L.) P. Beauv., *Z. mays* L., to varying degrees (McMechan 2016; Ranabhat et al. 2018). Although these species have been found more definitively in these experiments, other low to moderate risk groups have not had the benefit of field experiments ruling them out as summer reservoirs. Although grassy weeds and volunteer crops in cultivated fields can often be controlled with herbicides or tillage, grasses found in waterways and conservation reserve programs may provide a larger challenge to control as reservoirs for the virus. Long term regional and field crop protection strategies should continue to include strategies to control both weeds of the cultivated field, as well has limiting the exposure of newly planted wheat to warm fall conditions favoring WCM activity (Nault and Styer 1969; Ranabhat et al. 2018). Further improving wheat varieties to include stable host resistance to both the mite and virus would protect the wheat crop from infection/infestation, and could reduce contribution of volunteer wheat to developing outbreaks of WSM in fall planted winter wheat.

Members of the proposed moderate risk group I are defined by their high-risk to carry WSMV, but low-risk for WCM (Table 2.7 d). Of these species, most are cool season, annuals reducing the potential contribution to the summer ‘green bridge’. Cool season annuals generally do not grow through the summer making them unlikely to carry the mites and virus from one wheat crop to the next in Kansas. In Montana, *Bromus tectorum* L. (a cool season annual) was found in field studies to carry the disease from one wheat season to the next (Ranabhat et al. 2018), but this effect may be limited to climates favoring its over summer survival.

The members of moderate risk group II include species that were low-risk for WSMV and high-risk for WCM (Table 2.7 e). Most of these grasses have some evidence for WSMV suitability (albeit infrequently) and stronger evidence for WCM suitability. This group includes one species of note. Sorghum was associated with this grouping and can be included in crop rotations in the western region of Kansas. In its description, the new virulent isolates of WSMV were discussed primary as a disease of sorghum (Seifers et al. 1996), but in the context of wheat production, sorghum may play a larger risk to wheat than previously thought. More research into the survival and dispersal of WCM and WSMV should provide more insight into the contribution of sorghum to WSM in winter wheat. The low-risk group has species that are thought to be poor hosts for both pests (Table 7 f). Although the group varies in the WCM proportion, no evidence of WSMV suitability has been described in this group. Further survey work and experimentation could be performed to monitor for potential changes in the host range of WSMV.

Three main conclusions should be taken from the reporting and analysis. First results from the report-based analysis suggest WSMV suitability may be the limiting factor to the number of suitable hosts that can successfully carry both pests and serve as a member of the green bridge. Second, results from controlled experiments generally agree with field survey results for both pests. Therefore, in cases of limited information, controlled experiments may be adequate to identify grass hosts for these pests. Finally, both WSMV and WCM have extensive suitable host ranges and may survive on the native and introduced grasses of the Great Plains in the cultivated field as well as native and restored prairies. This may provide a substantial challenge in limiting the degree to which managers could utilize eradication of host species to completely eliminate the risk of WSMV infection for fall planted wheat. Future development of stable resistant wheat varieties number of suitable hosts for the summer “green bridge” and protect the planted crop from hard to manage sources of disease.

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Tables and Figures

Table 2.1 Publications and Related Information for Report and Evidence-Based Analyses

Publication Info		WSMV Experimental			WSMV Survey		WCM Experimental	WCM Survey
Author(s)	**Year**	**N[a]**	**Inoculation[d]**	**Method[e]**	**N**	**Method**	**N**	**N**
McKinney	1937	1	Man	ManW	0	NA	0	0
McKinney (V)	1949	1	Man	Visual	0	NA	0	0
McKinney (T)	1949	1	Man	Visual	0	NA	0	0
Slykhuis	1951	1	Man	ManW	1	ManW	0	0
McKinney & Fellows	1951	1	Man	ManW	1	ManW	0	0
McKinney & Sando	1951	1	Man	Visual	0	NA	0	0
Slykhuis	1952	1	Man	Visual	0	NA	0	0
Sill & Connin	1953	1	Man	ManW	0	NA	0	0
Keifer	1954	0	NA	NA	0	NA	0	1
Meiners & McKinney	1954	1	Man	Visual	0	NA	0	0
Painter & Schesser	1954	0	NA	NA	1	ManW	0	1
Slykhuis	1955	2	Man/WCM	ManW	0	NA	1	1
Sill & Agusiobo	1955	1	Man	ManW	0	NA	0	0
Staples & Allington	1956	0	NA	NA	0	NA	1	1
Connin (H)	1956	1	WCM	Visual	0	NA	1	0
Connin (O)	1956	0	NA	NA	0	NA	0	1
Slykhuis	1956	0	NA	NA	0	NA	1	0
Finley	1957	1	Man	Visual	1	ManW/Visual	0	0
Bruehl & Keifer	1958	0	NA	NA	1	Visual	0	1

Publication Info		WSMV Experimental			WSMV Survey		WCM Experimental	WCM Survey
Author(s)	Year	N[a]	Inoculation[d]	Method[e]	N	Method	N	N
Sill and del Rosario	1959	1	WCM	Visual	0	NA	1	0
Ashworth & Futrell	1961	0	NA	NA	1	ManW	0	1
Slykhuis	1961	1	Man	ManW	0	NA	0	0
Slykhuis	1962	0	NA	NA	0	NA	0	1
How	1963	1	Man	Visual	3	WcmW/ManW	1	0
Slykhuis & Bell	1963	1	Man	Visual	0	NA	0	0
McKinney et al.	1966	1	Man	Visual	0	NA	0	0
Orlob (EH)	1966	2	Man/WCM	ManW	1	ManW	1	1
Orlob (EV)	1966	1	WCM	WcmW	0	NA	0	0
Watts & Bellotti	1967	0	NA	NA	0	NA	0	1
Williams et al.	1967	1	Man	Visual	1	ManW	0	0
Nault & Briones	1968	0	NA	NA	0	NA	1	0
Nault & Styer	1969	0	NA	NA	0	NA	0	1
Timian & Lloyd	1969	0	NA	NA	1	WcmW	0	1
Gates	1970	0	NA	NA	1	WcmW	0	1
Somsen & Sill	1970	1	U	Visual	3	Visual	1	1
Flechtmann & Davis	1971	0	NA	NA	0	NA	0	1
Peterson	1989	0	NA	NA	0	NA	0	1
Christian & Willis	1993	0	NA	NA	2	ELISA	0	0
Seifers et al.	1996	2	Man/WCM	ELISA/ WcmW	1	ELISA/WcmW	0	0
Gillespie et al.	1997	0	NA	NA	0	NA	0	1
Brey et al.	1998	0	NA	NA	0	NA	0	3

Publication Info		WSMV Experimental			WSMV Survey		WCM Experimental	WCM Survey
Author(s)	**Year**	**N[a]**	**Inoculation[d]**	**Method[e]**	**N**	**Method**	**N**	**N**
Kozlowski	2000	0	NA	NA	0	NA	0	0
Harvey et al.	2001	0	NA	NA	0	NA	2	0
Skoracka et al.	2001	0	NA	NA	0	NA	0	1
Golya et al.	2002	0	NA	NA	0	NA	0	1
Skoracka & Magowski	2002	0	NA	NA	0	NA	0	1
Ellis et al.	2004	0	NA	NA	1	RTPCR	0	0
Halliday & Knihinicki	2004	0	NA	NA	0	NA	0	1
Coutts et al.	2008	0	NA	NA	2	ELISA	0	2
Carew et al.	2009	0	NA	NA	0	NA	0	1
Ito et al.	2012	2	Man/WCM	ELISA/ WcmW	2	ELISA	0	0

[a] Number of the type of study included in the research article or bulletin

[b] Inoculation Methods: Man-Manual inoculation method, WCM- Virus carrying Wheat Curl Mite inoculation method, U- Unspecified inoculation method

[c] Confirmation Methods: Visual- Assessed for WSMV by visual symptoms of the host, ManW- Tested for WSMV by inoculating wheat with infected host tissue, WCMW– Tested for WSMV by inoculating wheat with surviving WCM from infected host, ELISA- Host tissue tested with ELISA based testing methods for WSMV virus, RTPCR- Host tissue tested with RTPCR testing for viral nucleic acid

Table 2.2 Criteria for Categorical Assessments

Criteria for Categorical Assessment					
Assessment	Pest	WSMV		WCM	
	Type	Controlled Experiment	Field Observation	Controlled Experiment	Field Observation
0	No Evidence	**Visual-** No symptoms of viral infection **ManW-** No symptoms of viral infection and sap from species unable to reinfect wheat (Not a symptomless carrier) **WCMW-** WCM from species unable to transmit symptoms back to wheat **ELISA-** Species negative for WSMV using serological techniques	**Visual-** No symptoms of viral infection from field survey **ManW-** Sap from species unable to reinfect wheat (Not a symptomless carrier) **WCMW-** WCM from species unable to transmit symptoms back to wheat **ELISA-** All surveyed species negative for WSMV using serological techniques **rtPCR-** All surveyed species negative for WSMV rtPCR	WCM unable to survive on species	WCM not found on species during field survey
1	Evidence	**Visual-** Symptoms of viral infection including: Mosaic, Mottling, Stunting, and Local Lesions **ManW-** Sap from species able to reinfect wheat (Symptomless carrier) **WCMW-** WCM from species able to transmit symptoms back to wheat **ELISA-** Species positive for WSMV using serological techniques	**Visual-** Symptoms of viral infection including: Mosaic, Mottling, and Local Lesions from surveyed field **ManW-** Sap from species able to reinfect wheat (Symptomless carrier) **WCMW-** Surviving WCM from species able to transmit symptoms back to wheat **ELISA-** Species positive for WSMV using serological techniques **rtPCR-** Species positive for WSMV using rtPCR	WCM able to survive or reproduce on species	Reported as WCM species or WCM found during field survey

Table 2.3 Results of Species from Report-based Approach

Scientific Name	Common Name	Report WSMV	Report WCM	Report Both
Achnatherum hymenoides (Roemer & Schultes) Barkworth	Indian Ricegrass	+[a]	+	+[b]
Oryzopsis hymenoides (Roem. & Schult.) Ricker ex Piper[c]				
Aegilops crassa Boiss.	Persian Goatgrass	+		
Aegilops cylindrica Host	Jointed Goatgrass	+	+	+
Aegilops ovata L.	Ovate Goatgrass	+		
Aegilops triuncialis L.	Barb Goatgrass	+		
Aegilops ventricosa Tausch	Swollen Goatgrass	+		
Agropyron amurense Drobrow		-		
Agropyron ciliare (Trin.) Franch.	Wildrye	-		
Agropyron cristatum (L.) Gaertn.	Crested Wheatgrass	-	+	-
Agropyron dasystachyum (Hook.) Scribn. & J.G. Sm.	Thickspike Wheatgrass	-		
Agropyron desertorum (Fisch. ex Link) Schult.	Desert Wheatgrass	-	-	-
Agropyron divaricatum Boiss. & Bal.		-		
Agropyron inerme (Scribn. & J.G. Sm.) Rydb.	Beardless Wheatgrass	-		
Agropyron junceum (L.) P. Beauv p.p.	Russian Wheatgrass	-		
Agropyron lasianthum Boiss.		+		
Agropyron pertenue (C.A. Mey.) Nevski		-		
Agropyron pungens auct. non (Pers.) Roem. & Schult.	Tick Quackgrass	+		
Agropyron rigidum (Schrad.) P. Beauv.	Tall Wheatgrass	-		
Agropyron semicostatum Ness ex Steud.	Drooping Wildrye	-		
Agropyron sibiricum (Willd.) P. Beauv.	Siberian Wheatgrass	-		
Agropyron spicatum Pursh	Bluebunch Wheatgrass	-		
Agropyron trichophorum (Link) K. Richt.	Stiffhair Wheatgrass	-		
Agrostis alba auct. non L.	Redtop	-	-	-
Alopecurus carolinianus Walter	Carolina Foxtail		-	
Alopecurus pratensis L.	Meadow Foxtail	-	+	-
Andropogon gerardii Vitman	Big Bluestem	-	+	-
Andropogon hallii Hack.	Sand Bluestem	-		
Andropogon saccharoides Sw.	Silver Beardgrass	-		
Aristida adscensionis L.	Sixweeks Threeawn		-	
Aristida oligantha Michx.	Prairie Threeawn	-		
Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl	Tall Oatgrass	-	+	-
Avena fatua L.	Wild Oat	+	+	+
Avena sativa L.	Common Oat	+	+	+
Beckmannia syzigachne (Steud.) Fernald	American Sloughgrass	-	+	-
Bothriochloa ischaemum (L.) Keng	Yellow Bluestem	-		
Andropogon ischaemum (L.)				
Bothriochloa macra (Steudel) S.T. Blake	Redgrass		+	
Bouteloua curtipendula (Michx.) Torr.	Side-oats Grama	-	+	-
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	Blue Grama	-	+	-
Bouteloua hirsuta Lag.	Hairy Grama	+	+	+
Bromus arvensis L.	Field Brome	+		
Bromus catharticus Vahl	Rescuegrass	-	+	-
Bromus diandrus Roth	Great Bromegrass		+	
Bromus inermis Leyss.	Smooth Brome	-	+	-
Bromus japonicus Thunb.	Japanese Brome	+	+	+
Bromus marginatus Nees ex Steud.	Mountain Brome		+	
Bromus secalinus L.	Rye Brome	+	+	+
Bromus tectorum L.	Downy Brome	+	+	+
Buchloe dactyloides (Nutt.) Engelm.	Buffalograss	-	+	-
Calamovilfa longifolia (Hook.) Scribn.	Sand Reedgrass		-	
Cenchrus echinatus L.	Southern Sandbur	-		
Cenchrus pauciflorus Benth.	Sandbur	+	+	+
Chloris truncata R. Br.	Windmillgrass		+	
Chloris verticillata Nutt.	Tumble Windmillgrass		-	

Scientific Name	**Common Name**	**Report WSMV**	**Report WCM**	**Report Both**
Coix lacryma-jobi L.	Job's Tears	-		
Cortaderia selloana (Schult. & Schult. f.) Asch. & Graebn.	Pampasgrass	-		
Cynodon dactylon (L.) Pers.	Bermudagrass	+	+	+
Dactylis glomerata L.	Orchardgrass	-	+	-
Digitaria ischaemum (Schreb.) Schreb. ex Muhl.	Smooth Crabgrass	+	+	+
Digitaria sanguinalis (L.) Scop.	Hairy Crabgrass	+	+	+
Distichlis spicata (L.) Greene	Inland Saltgrass	+	+	+
Distichlis stricta (Torr.) Rydb.				
Echinochloa crus-galli (L.) P. Beauv.	Barnyardgrass	+	+	+
Ehrharta calycina Sm.	Perennial Veldtgrass	-		
Eleusine indica (L.) Gaertn.	Goosegrass	-	+	-
Eleusine tristachya (Lam.) Lam.	Spike Goosegrass	+		
Elymus canadensis L.	Canada Wildrye	+	+	+
Elymus condensatus J. Presl	Giant Wildrye	+		
Elymus elymoides (Raf.) Swezey	Squirreltail	+	+	+
Sitanion hystrix (Nutt.) J.G. Sm.				
Elymus giganteus Vahl	Mammoth Wildrye	+		
Elymus lanceolatus (Scribn. & J.G. Sm.) Gould	Thickspike Wheatgrass	-		
Elymus nevskii Tzvelev		+		
Agropyron ugamicum Drobow				
Elymus repens (L.) Gould	Quackgrass	+	+	+
Agropyron repens (L.) P. Beauv.				
Elymus trachycaulus (Link) Gould ex Shinners	Slender Wheatgrass	+	+	+
Agropyron trachycaulum (Link) Malte				
Elymus virginicus L.	Virginia Wildrye	+	+	+
Eragrostis cilianensis (All.) Vign. ex Janchen	Stinkgrass	+	+	+
Eragrostis curvula (Schrad.) Ness	Weeping Lovegrass	+		
Eragrostis pilosa (L.) P. Beauv.	Indian Lovegrass		-	
Eragrostis reptans (Michx.) Nees	Creeping Lovegrass		-	
Eragrostis sessilispica Buckley	Tumble Lovegrass	-		
Eragrostis trichodes (Nutt.) Alph. Wood	Sand Lovegrass	+	-	-
Erianthus ravennae (L.) P. Beauv.	Ravennagrass		-	
Eriochloa contracta Hitchc.	Prairie Cupgrass	+	-	-
Euchlaena mexicana Schrad.	Teosente	+	+	+
Festuca elatior L.	Tall Fescue	-	-	-
Festuca rubra L.	Red Fescue	-	-	-
Glyceria striata (Lam.) Hitchc.	Fowl Mannagrass		-	
Haynaldia villosa (L.) Schur	Mosquitograss	+		
Hesperostipa comata (Trin. & Rupr.) Barkworth	Needle-and-thread	-	+	-
Stipa comata Trin. & Rupr.				
Hordeum gussoneanum Parl.	Mediterranean Barley	+		
Hordeum jubatum L.	Foxtail Barley	-	+	-
Hordeum leporinum Link	Hare Barley		+	
Hordeum murinum L.	Mouse Barley	+		
Hordeum pusillum Nutt.	Little Barley	-	+	-
Hordeum vulgare L.	Common Barley	+	+	+
Koeleria macrantha (Ledeb.) Schult.	Prairie Junegrass		+	
Koeleria cristata (L.) Pers.				
Leptochloa fascicularis (Lam.) A. Gray	Bearded Sprangletop		-	
Leptochloa filiformis (Lam.) P. Beauv.	Red Sprangletop		-	
Lolium multiflorum Lam.	Italian Ryegrass	+	+	+
Lolium oldenburgicum			+	
Lolium perenne L.	Perennial Ryegrass	-	+	-
Lolium rigidum Gaudin	Rigid Ryegrass	+	+	+
Miscanthus sinensis Andersson	Chinese Silvergrass		-	
Muhlenbergia mexicana (L.) Trin.	Bearded Wirestem Muhly		+	
Muhlenbergia wrightii Vasey ex J.M. Coult.	Spike Muhly		+	

Scientific Name	**Common Name**	**Report WSMV**	**Report WCM**	**Report Both**
Munroa squarrosa (Nutt.) Torr.	False Buffalograss		+	
Nassella viridula (Trin.) Barkworth	Green Needlegrass		+	
Stipa viridula Trin.				
Oryza sativa L.	Rice		+	
Panicum capillare L.	Witchgrass	+	+	+
Panicum dichotomiflorum Michx.	Fall Panicum	+		
Panicum effusum R. Br.	Hairy Panicgrass		+	
Panicum hallii Vasey	Hall's Panicum	+		
Panicum maximum Jacq.	Guineagrass	-		
Panicum miliaceum L.	Proso Millet	+	+	+
Panicum virgatum L.	Switchgrass	-	+	-
Pascopyrum smithii (Rydb.) Á. Löve	Western Wheatgrass	-	+	-
Agropyron smithii Rydb.				
Paspalidium gracile (R. Br.) Hughes	Slender Panic		+	
Pennisetum clandestinum Hochst. ex Chiov.	Kikuyugrass	-		
Pennisetum glaucum (L.) R. Br.	Pearl Millet	+	+	+
Pennisetum setaceum (Forssk.) Chiov.	Crimson Fountaingrass	-		
Phalaris arundinacea L.	Reed Canarygrass	-	+	-
Phalaris paradoxa L.	Hood Canarygrass	+		
Phleum pratense L.	Timothy	-	+	-
Poa annua L.	Annual Bluegrass	-	+	-
Poa bulbosa L.	Bulbous Bluegrass	+		
Poa compressa L.	Canadian Bluegrass	+	+	+
Poa interior Rydb.	Inland Bluegrass		+	
Poa nervosa (Hook.) Vasey	Wheeler Bluegrass		+	
Poa pratensis L.	Kentucky Bluegrass	+	+	+
Poa secunda J. Presl	Sandberg Bluegrass		-	
Poa stenantha Trin.	Northern Bluegrass	+		
Polypogon monspeliensis (L.) Desf.	Rabbitfoot Polypogon		-	
Psathyrostachys juncea (Fisch.) Nevski	Russian Wildrye	-		
Elymus junceus Fisch.				
Puccinellia airoides (Schult.) Hitchc.	Nuttall Alkaligrass		-	
Saccharum officinarum L.	Sugar Cane	+		
Schedonnardus paniculatus (Nutt.) Trel.	Tumblegrass	-	+	-
Schizachyrium scoparium (Michx.) Nash	Little Bluestem	-	-	-
Andropogon scoparius Michx.				
Secale cereale L.	Cereal Rye	+	+	+
Secale montanum Guss.	Rye	+		
Setaria faberi Herrm.	Giant Foxtail	+		
Setaria italica (L.) P. Beauv.	Foxtail Millet	+	+	+
Setaria jubiflora (Trin.) R.D. Webster	Warrengograss		+	
Setaria magna Griseb.	Giant Foxtail	+		
Setaria pumila (Poir.) Roem. & Schult.	Yellow Foxtail	-	+	-
Setaria glauca (L.) P. Beauv.				
Setaria lutescens (Weigel) F.T. Hubbard				
Setaria verticillata (L.) P. Beauv.	Bristly Foxtail	+	+	+
Setaria viridis (L.) P. Beauv.	Green Foxtail	+	+	+
Sorghastrum nutans (L.) Nash	Indiangrass	-	-	-
Sorghum almum Parodi	Columbusgrass	-		
Sorghum bicolor (L.) Moench	Sorghum	+	+	+
Sorghum vulgare Pers.				
Sorghum halepense (L.) Pers.	Johnsongrass	-	+	-
Sorghum versicolor Andersson	Black-seed Wild Sorghum	-		
Sorghum x dummondii	Sudangrass		+	
Spartina pectinata Bosc ex Link	Prairie Cordgrass		+	
Spodiopogon sibiricus Trin.	Frost grass	-		
Andropogon sibiricus (Trin.) Steud.				

Scientific Name	**Common Name**	**Report WSMV**	**Report WCM**	**Report Both**
Sporobolus airoides (Torr.) Torr.	Alkali Sacton	-	-	-
Sporobolus compositus (Poir.) Merr.	Tall Dropseed	-		
Sporobolus asper (P. Beauv.) Kunth				
Sporobolus cryptandrus (Torr.) A. Gray	Sand Dropseed	-	-	-
Sporobolus neglectus Nash	Puffsheath Dropseed	+	+	+
Stipa robusta (Vasey) Scribn.	Sleepygrass	+		
Thinopyrom ponticum (Podp.) Barkworth & D.R. Dewey	Tall Wheatgrass	+	+	+
Agropyron elongatum (Host) P. Beauv.				
Thinopyrum intermedium (Host) Barkworth & D.R. Dewey	Intermediate Wheatgrass	+	-	-
Agropyron intermedium (Host) P. Beauv.				
Tragus australianus S.T. Blake	Small Burrgrass	+		
Tripsacum dactyloides (L.) L.	Eastern Gamagrass	-	+	-
Triticum aestivum L.	Common Wheat	+	+	+
Triticum dicoccum (Schrank) Schübl.	Rivet Wheat		+	
Triticum durum Desf.	Durum Wheat		+	
Triticum timopheevi (Zhuk.) Zhuk.	Timopheev's Wheat		+	
Triticum x Agropyron		+	+	+
Triticum x Secale	Triticale		+	
Urochloa maxima (Jacq.) R. Webster	Guineagrass	-		
Urochloa panicoides P. Beauv.	Liverseed		+	
Vulpia bromoides (L.) Gray	Brome Fescue		+	
Zea mays L.	Corn (Combined)	+	+	+
	Field Corn	+	+	+
	Hybrid Corn	+	+	+
	Inbred Corn	+	+	+
	Pop Corn	+		
	Sweet Corn	+	+	+
Total Species Reported Hosts		**68**	**89**	**39**
Total Species Reported Non-Hosts		**64**	**25**	**36**

[a] Reported as: + Host (at least one assessment for the species-pest interaction was 1);
- Non-Host (all assessments for the species-pest interaction were 0);
“ ” Not found in any reference

[b] Reported as: + Host for both WSMV and WCM;
- Non-Host for either WSMV or WCM;
“ ” Either WSMV, WCM, or both missing

[c] Synonymous named found in WSMV Review

Table 2.4 Comparison of WSMV Results vs. WCM Results

		WSMV		
		Host (+)	Non-Host (-)	
WCM	Host (+)	39 Species	25	64
	Non-Host (-)	3	8	11
		42	33	N=75

Agreement[a]: 47 of 75 Species
Non-Agreement[b]: 28 of 75 Species

[a] Agreement is the proportion of species that were confirmed to be uniformly classified as hosts or non-hosts of both WSMV and WCM
[b] Non-Agreement is the proportion of species found to be hosts for either WSMV or WCM but not both.

Tables 2.5 a,b Comparison of Experimental Results vs Survey Results for WSMV (a) and WCM (b)

(a)		WSMV Experimental		
		Host (+)	Non-Host (-)	
WSMV Survey	Host (+)	21 Species	1	22
	Non-Host (-)	4	14	18
		25	15	N=40

Agreement[a]: 35 of 40 Species
Non-Agreement[b]: 5 of 40 Species

(b)		WCM Experimental		
		Host (+)	Non-Host (-)	
WCM Survey	Host (+)	51 Species	4	55
	Non-Host (-)	9	7	16
		60	11	N=71

Agreement: 58 of 71 Species
Non-Agreement: 13 of 71 Species

[a] Agreement is the proportion of species classified as hosts were controlled experiments and surveys addressing WSMV and WCM agree.
[b] Non-Agreement is the proportion of species were experimental and survey evidence do not agree

Tables 2.6 a,b Comparison of Individual Pest Results vs. Combined Pest Results

(a)

		WSMV		
		Host (+)	Non-Host (-)	
Both Reported	Yes	39 Species	0	39
	No	3	33	36
		42	33	N=75

Agreement[a]: 72 of 75 Species
Non-Agreement[b]: 3 of 75 Species

(b)

		WCM		
		Host (+)	Non-Host (-)	
Both Reported	Yes	39 Species	0	39
	No	25	11	36
		64	11	N=75

Agreement: 50 of 75 Species
Non-Agreement: 25 of 75 Species

[a] Agreement is the number of species with the same results for each category
[b] Non-Agreement is the number of species with different results for each category

Figure 2.1 a,b Frequency Distribution of WSMV(a) and WCM (b) Proportions

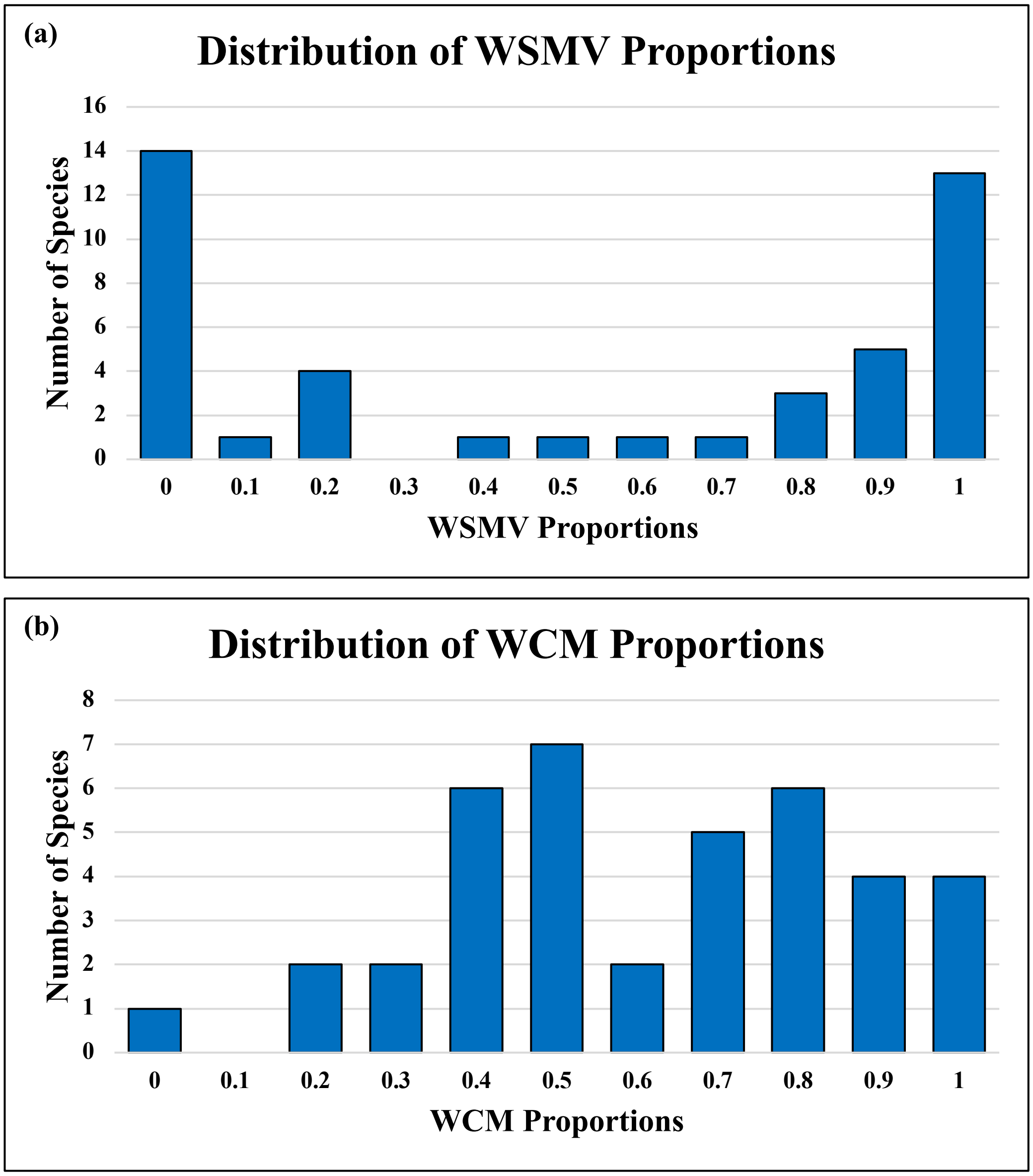

Figure 2.2 a,b Scatter Plot of WCM Proportion vs Mean Number of WCM from Starting Populations of 10 WCMs from Kansas (KS) Sourced Mites (a) and Nebraska (NE) Sourced Mites (b) After 7 days on 26 Different Grass Species

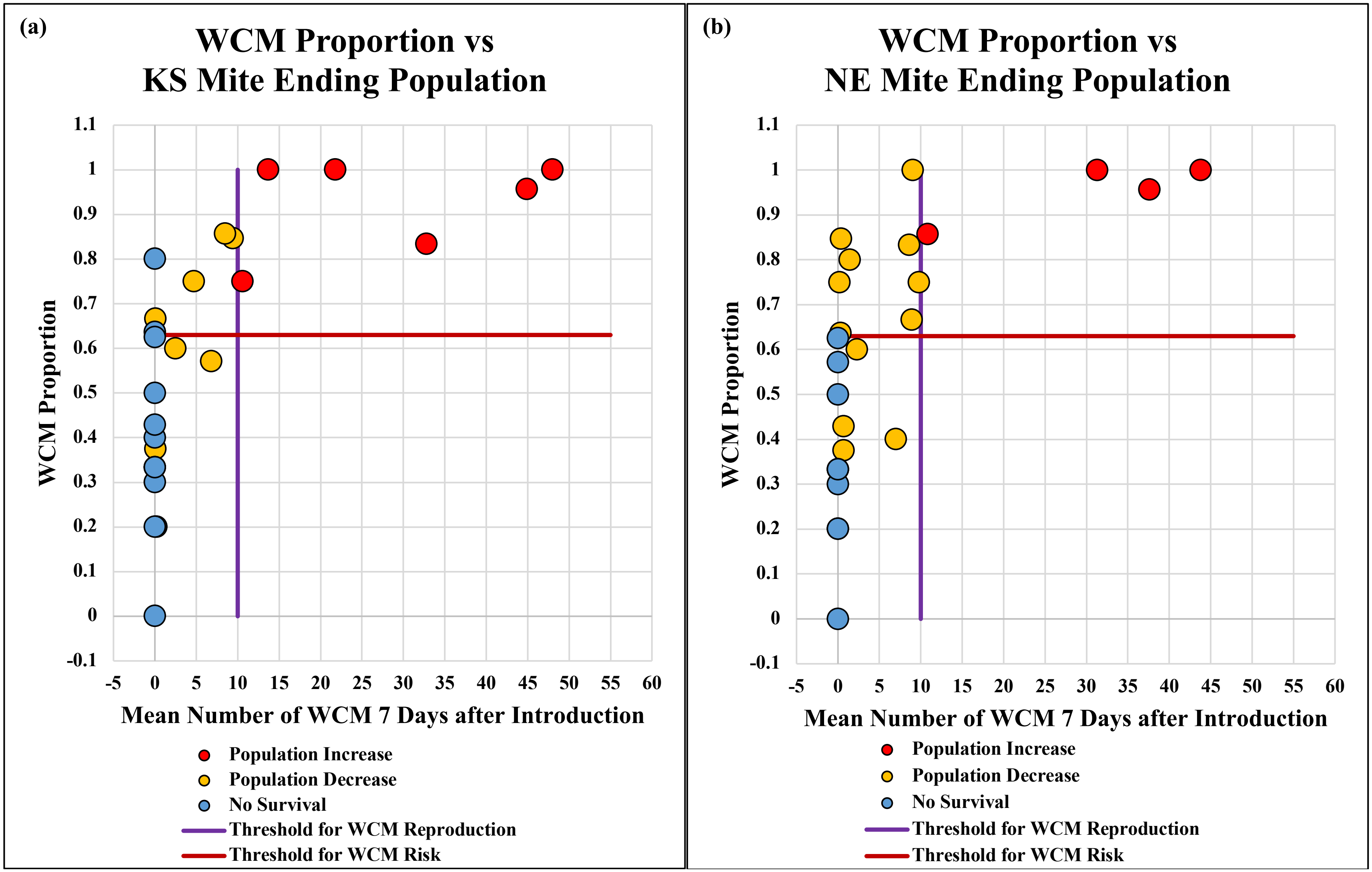

Figure 2.3 Dendrogram from Cluster Analysis of WCM and WSMV Proportions of Evidence by Ward Method and Proposed Risk Groupings

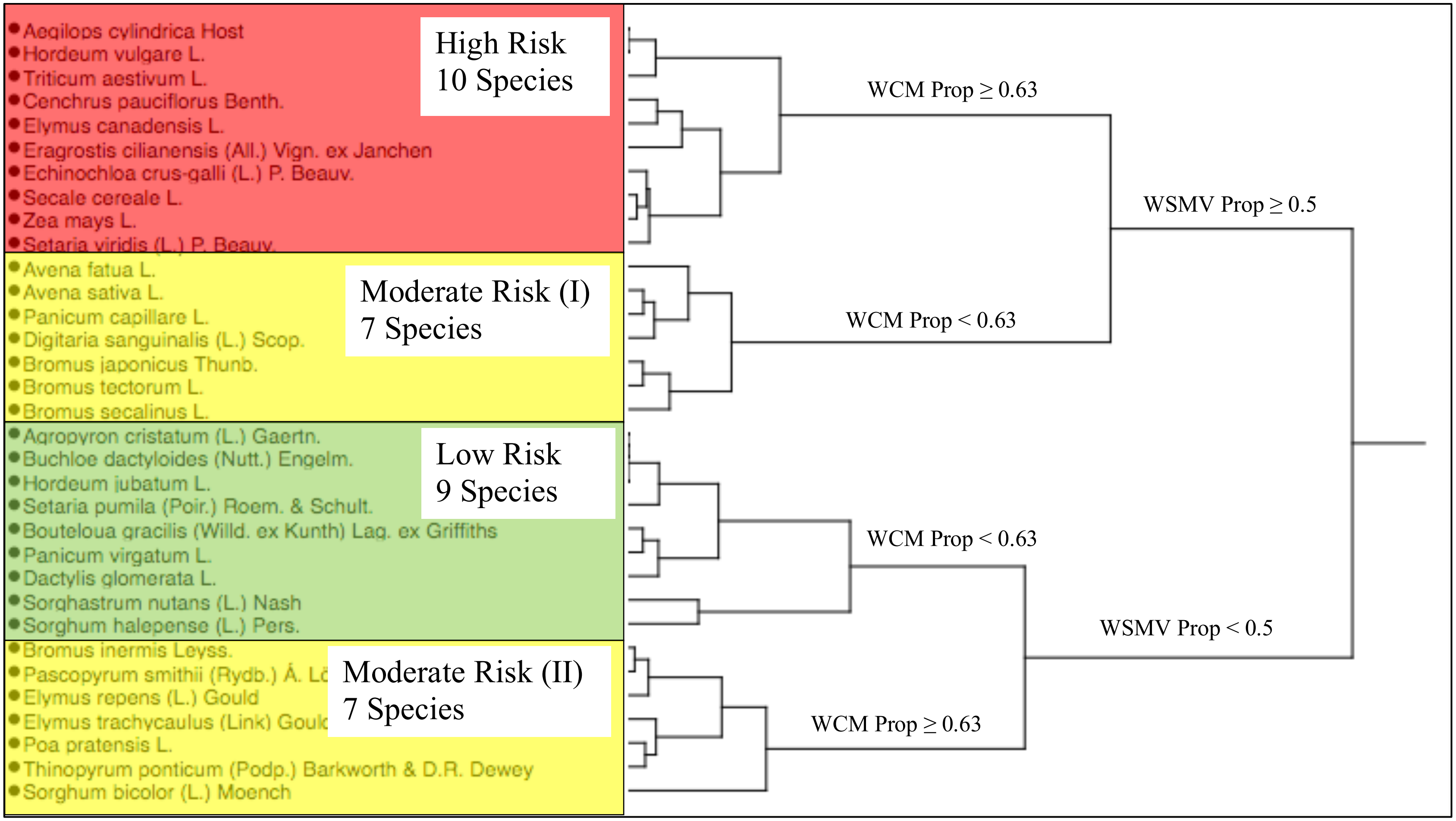

Figure 2.4 Scatter Plot of WCM Proportion of Evidence vs WSMV Proportion of Evidence with Proposed Risk Groupings from Cluster Analysis and Total Assessments (N of WCM Assessments + N of WSMV Assessments) represented by the Size of the Marker

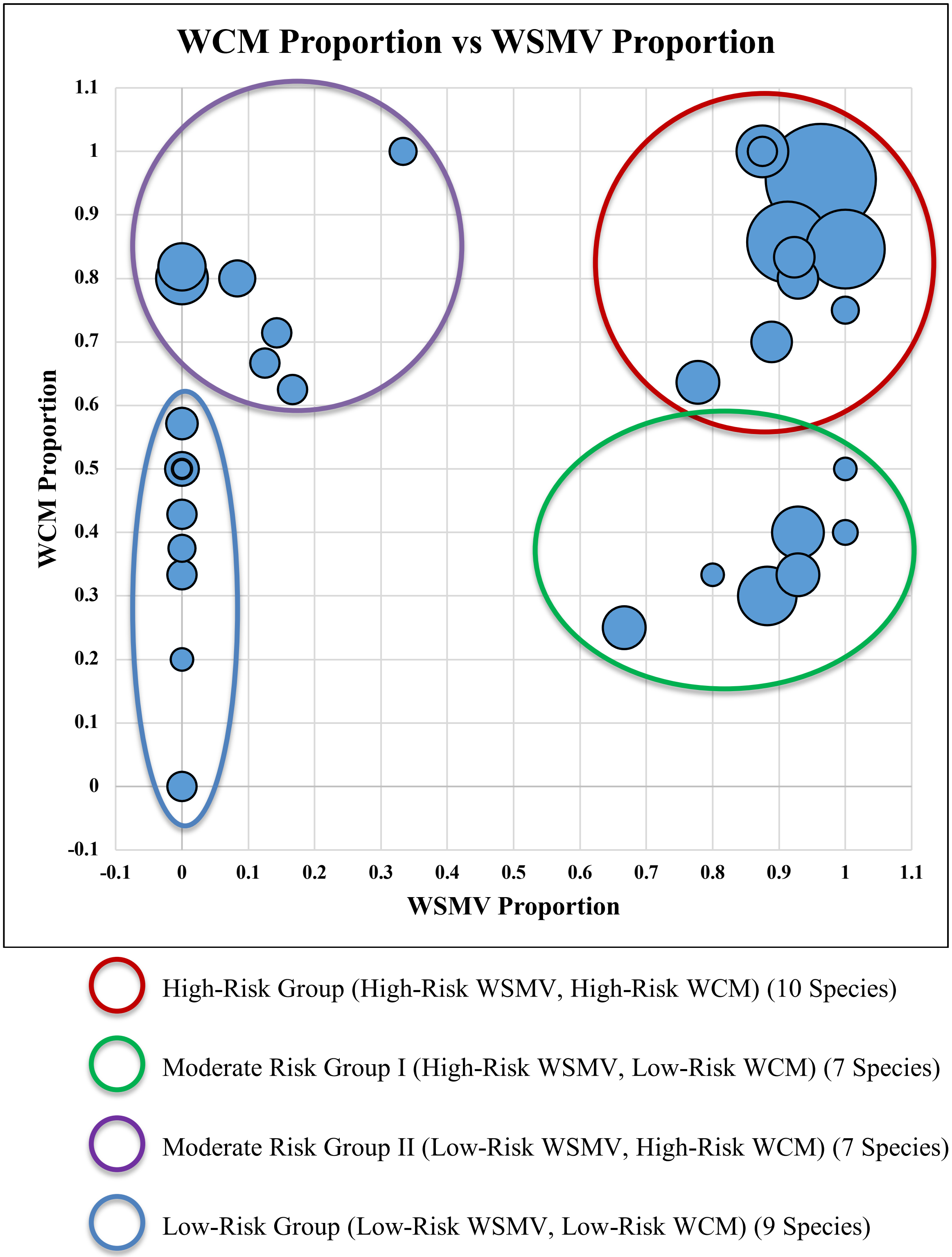

Table 2.7 a-f Results of Evidence-Based Approach

(a)

Only WCM Group

Scientific Name	**Common Name**	**WCM Proportion[a]**	**N of WCM[b]**	**Season**	**Habit**	**Origin[c]**	**KS Distribution[d]**
Alopecurus pratensis L.	Meadow Foxtail	0.2	5	Cool	Perennial	Introduced	E, C, W
Digitaria ischaemum (Schreb.) Schreb. ex Muhl.	Smooth Crabgrass	0.5	4	Warm	Annual	Introduced	E, C
Eleusine indica (L.) Gaertn.	Goosegrass	0.6	5	Warm	Annual	Introduced	E, C
Hesperostipa comata (Trin. & Rupr.) Barkworth	Needle-and-thread	0.5	6	Cool	Perennial	Native	E, C, W
Nassella viridula (Trin.) Barkworth	Green Needlegrass	0.67	6	Cool	Perennial	Native	W
Phalaris arundinacea L.	Reed Canarygrass	0.75	4	Cool	Perennial	Native/ Introduced	E, C, W

[a] Number of positive WCM assessments divided by the total number of WCM assessments

[b] Total number of assessments for WCM

[c] Native or introduced to the Great Plains of the United States

[d] Distribution throughout the State of Kansas (E-Present in the Eastern third, C-Present in the Central third, W-Present in the Western third)

(b)

Only WSMV Group

Scientific Name	Common Name	WSMV Proportion[e]	N of WSMV[f]	Season	Habit	Origin	KS Distribution
Andropogon gerardii Vitman	Big bluestem	0	5	Warm	Perennial	Native	E, C, W
Bouteloua curtipendula (Michx.) Torr.	Side-oats Grama	0	5	Warm	Annual	Native	E, C, W
Elymus virginicus L.	Virginia Wildrye	1	5	Cool	Perennial	Native	E, C, W
Eragrostis trichodes (Nutt.) Alph. Wood	Sand Lovegrass	1	6	Warm	Perennial	Native	E, C, W
Euchlaena mexicana Schrad.	Teosente	0.5	4	Warm	Annual	Introduced	NA
Panicum miliaceum L.	Proso Millet	0.89	9	Warm	Annual	Introduced	E, C, W
Pennisetum glaucum (L.) R. Br.	Pearl Millet	0.60	5	Warm	Annual	Introduced	E, C, W
Schizachyrium scoparium (Michx.) Nash	Little Bluestem	0	5	Warm	Perennial	Native	E, C, W
Setaria italica (L.) P. Beauv.	Foxtail Millet	0.71	7	Warm	Annual	Introduced	E, C, W
Setaria verticillata (L.) P. Beauv.	Bristly Foxtail	1	5	Warm	Annual	Introduced	E
Thinopyrum intermedium (Host) Barkworth & D.R. Dewey	Intermediate Wheatgrass	0.17	6	Cool	Perennial	Introduced	NA

[e] Number of positive WSMV assessments divided by the total number of WSMV assessments

[f] Total number of assessments for WSMV

(c)

High-Risk Group (High WSMV/High WCM)

Scientific Name	Common Name	WSMV Proportion	N of WSMV	WCM Proportion	N of WCM	Season	Habit	Origin	KS Distribution
Aegilops cylindrica Host	Jointed Goatgrass	0.88	8	1	6	Cool	Annual	Introduced	E, C, W
Cenchrus pauciflorus Benth.	Sandbur	1	5	0.75	8	Warm	Annual	Native	E, C, W
Echinochloa crus-galli (L.) P. Beauv.	Baryardgrass	0.93	14	0.8	5	Warm	Annual	Introduced	E, C, W
Elymus canadensis L.	Canadian Wildrye	0.89	9	0.7	10	Cool	Perennial	Native	E, C, W
Eragrostis cilianensis (All.) Vign. ex Janchen	Stinkgrass	0.78	9	0.64	11	Warm	Annual	Introduced	E, C, W
Hordeum vulgare L.	Barley	0.88	16	1	8	Cool	Annual	Introduced	E, C, W
Secale cereale L.	Rye	0.92	13	0.83	6	Cool	Annual	Introduced	E, C, W
Setaria viridis (L.) P. Beauv.	Green Foxtail	1	23	0.85	13	Warm	Annual	Introduced	E, C, W
Triticum aestivum L.	Wheat	0.96	27	0.96	23	Cool	Annual	Introduced	E, C, W
Zea mays L.	Corn	0.91	23	0.86	14	Warm	Annual	Introduced	E, C, W

(d)

Moderate Risk Group I (High WSMV/Low WCM)

Scientific Name	Common Name	WSMV Proportion	N of WSMV	WCM Proportion	N of WCM	Season	Habit	Origin	KS Distribution
Avena fatua L.	Wild Oat	0.67	12	0.25	8	Cool	Annual	Introduced	E, C, W
Avena sativa L.	Common Oat	0.93	14	0.33	6	Cool	Annual	Introduced	E, C, W
Bromus japonicus Thunb.	Japanese Brome	1	7	0.4	5	Cool	Annual	Introduced	E, C, W
Bromus secalinus L.	Rye Brome	1	7	0.5	4	Cool	Annual	Introduced	E, C
Bromus tectorum L.	Downy Brome	0.93	14	0.4	10	Cool	Annual	Introduced	E, C, W
Digitaria sanguinalis (L.) Scop.	Hairy Crabgrass	0.8	5	0.33	6	Warm	Annual	Native	E, C, W
Panicum capillare L.	Witchgrass	0.88	17	0.3	10	Cool	Annual	Native	E, C, W

(e)

Moderate Risk Group II (Low WSMV/High WCM)

Scientific Name	Common Name	WSMV Proportion	N of WSMV	WCM Proportion	N of WCM	Season	Habit	Origin	KS Distribution
Bromus inermis Leyss.	Smooth Brome	0	11	0.82	11	Cool	Perennial	Introduced	E, C, W
Elymus repens (L.) Gould	Quackgrass	0.08	12	0.8	5	Cool	Perennial	Introduced	E
Elymus trachycaulus (Link) Gould ex Shinners	Slender Wheatgrass	0.14	7	0.71	7	Cool	Perennial	Native	W
Pascopyrum smithii (Rydb.) Á. Löve	Western Wheatgrass	0	9	0.8	15	Cool	Perennial	Native	E, C, W
Poa pratensis L.	Kentucky Bluegrass	0.17	6	0.63	8	Cool	Perennial	Introduced	E, C, W
Sorghum bicolor (L.) Moench	Sorghum	0.33	9	1	4	Warm	Annual	Introduced	E, C, W
Thinopyrum ponticum (Podp.) Barkworth & D.R. Dewey	Tall Wheatgrass	0.13	8	0.67	6	Cool	Perennial	Introduced	W

(f)

Low-Risk Group (Low WSMV/Low WCM)

Scientific Name	Common Name	WSMV Proportion	N of WSMV	WCM Proportion	N of WCM	Season	Habit	Origin	KS Distribution
Agropyron cristatum (L.) Gaertn.	Crested Wheatgrass	0	8	0.5	8	Cool	Perennial	Introduced	W
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	Blue Gramma	0	5	0.38	8	Warm	Perennial	Native	E, C, W
Buchloe dactyloides (Nutt.) Engelm.	Buffalograss	0	5	0.5	4	Warm	Perennial	Native	E, C, W
Dactylis glomerata L.	Orchardgrass	0	7	0.43	7	Cool	Perennial	Introduced	E, C, W
Hordeum jubatum L.	Little Barley	0	4	0.5	6	Cool	Perennial	Native	E, C, W
Panicum virgatum L.	Switchgrass	0	8	0.33	6	Warm	Perennial	Native	E, C, W
Setaria pumila (Poir.) Roem. & Schult.	Yellow Foxtail	0	8	0.57	7	Warm	Annual	Introduced	E, C, W
Sorghastrum nutans (L.) Nash	Indiangrass	0	8	0	6	Warm	Perennial	Native	E, C, W
Sorghum halepense (L.) Pers.	Johnsongrass	0	6	0.2	5	Warm	Perennial	Introduced	E, C, W

Chapter 3 - Weather Patterns Associated with Regional Wheat Streak Mosaic Epidemics in Kansas

Abstract

Wheat streak mosaic (WSM) is a major, albeit erratic, threat to the hard red winter wheat producing regions of the United States. The magnitude of yield losses to WSM in Kansas, for example, range from 0.0 to 18.1% across years and crop reporting districts. The goal of this research was to identify weather patterns that influence the annual and regional epidemics of WSM in Kansas based on yield loss observations recorded for the years 1995-2013. Yield loss was coded as a binary variable with >0.7% loss considered to be an epidemic (coded as 1). Another series of binary variables were also developed to characterize a range of district losses. These regional yield losses were paired with summaries of weather and other factors likely to influence outbreaks of WSM. The resulting data set (n=171) was evaluated with non-parametric correlation, recursive partitioning, and logistic regression analysis. Results indicate that outbreaks of WSM are positively correlated with the amount of wheat production within a region and favored by warm temperatures during September wheat planting. The analysis also suggests that warm winter temperatures (December - February) and dry soil conditions in February increase the risk of severe WSM epidemics. Logistic regression models based on these variables correctly classified 66-74% of cases considered in this analysis. The weather patterns identified in this analysis are consistent with conditions that favor the survival, reproduction, and dispersal of the wheat curl mites that vector the *Wheat streak mosaic virus*.

Introduction

The disease wheat streak mosaic (WSM) and its causal agent, the *Wheat streak mosaic virus* (WSMV), have been devastating winter wheat (*Triticum aestivum* L.) in Kansas and throughout the Great Plains of the United States. Yield losses to WSMV are influenced by the host resistance and time of infection. Under severe disease conditions, yield losses in susceptible fields can be to be as high as 87% (Hunger et al. 1992). Apart from field scale losses, WSM has also been the cause of sporadic regional and statewide disease losses. In Kansas, statewide losses to WSM have ranged from 0.001% to 5.6% over the last ten years, and losses of at least 1% have occurred in five of those ten years (Hollandbeck et al. 2017). Although heavy statewide losses may be sustained in some years, these events have been unpredictable. Even in the earliest descriptions of WSM by McKinney (1937), it was "noteworthy that theses western mosaics do not recur with certainty." The goal of this research is to better understand weather patterns and cropping factors that contributed to major epidemics of WSM in Kansas.

The symptom expression of wheat streak mosaic is influenced by temperature. Early studies of WSMV showed that warm temperatures decreased the incubation period of manually inoculated plants. Plants incubated at 28, 24, 20, and 16°C took 5, 7, 9, and 15 days, respectively, to express viral symptoms (Sill Jr. and Fellows 1953). The severity of stunting also increased as temperatures increased with major stunting occurring at temperatures above 16°C. Further study of temperature in relation to WSMV symptom expression led to the discovery of a cumulative growing degree days model associated with confirmed WSMV field samples. The researchers found that samples collected at dates with greater than 700 cumulative degree days above 0°C from January 1st were more likely to be positive for WSMV (Burrows et al. 2016). Further, studies of temperature effects on WSMV indicated that high temperatures could diminish the effect of WSMV resistance genes, *Wsm1* and *Wsm2*. Lines containing the resistance gene *Wsm1* or *Wsm2* were resistant to WSMV at 18°C, but not at 24°C (Seifers et al. 2007, 2006).

Since its discovery as the vector of WSMV, many studies have characterized the effect of environment on the wheat curl mite (WCM). Early studies of off-host survival showed that the mite requires a living host to survive and cannot persist off of the host at any life stage (Slykhuis 1955; Nault and Styer 1969). When removed from the host plant, mite survival is influenced by environmental conditions. Early studies demonstrated the best WCM survival on detached leaves occurred at relative humidity greater than 75% and temperatures less than 15°C (Slykhuis 1955). A more recent study of WCM off host survival revealed that survival was greater at 95% RH than at 2% RH, and that survival increased as temperature decreased from 30°C to 10°C (Wosula et al. 2015). The same study noted that WCM became inactive at temperatures below 15°C. Field studies of WCM dispersal activity indicated that aerial populations tend to diminish as fall transitions to winter (Staples and Allington 1956; Nault and Styer 1969). The reproduction of the WCM is strongly influenced by temperature. Recent studies looking at two common WCM lineages, MT1 and MT8, demonstrated that on-host populations increased at temperatures between 12 and 40°C for MT1 and 10 and 36°C for MT8. The population growth peaked at 36 and 32°C for MT1 and MT8, respectively (Kuczyński et al. 2016).

For survival between wheat crops, the WCM requires a living host to survive the summer months. In multiple studies, volunteer wheat was identified as the primary source of WSM infections (Staples and Allington 1956; Connin 1956a; Somsen and Sill Jr. 1970). Factors influencing the timing of volunteer wheat presence and germination have long been associated with local outbreaks of WSMV. Hail damage in pre-harvested wheat has been associated with early germination of volunteer wheat (Staples and Allington 1956). The danger of this pre-harvest volunteer wheat comes from the presence of young plants present within a mite infested crop during the period of highest mite dispersal (Nault and Styer 1969; McMechan and Hein 2017). This crossover of pre-harvest volunteer and late maturing wheat increases the risk of WSMV infection during the fall planting season for winter wheat. The following analysis of weather and cropping factors could provide Kansas wheat producers information about weather conditions and time periods that favored WSM epidemics.

Methods

Historic Disease Observations/Response Development

District annual percent losses (DAPL) to WSM were compiled from wheat disease surveys for the 9 crop reporting districts (CRD) of Kansas from 1995-2013 (Figure 3.1). Details of the Kansas wheat disease survey methodology can be found in Bockus et al. 2001. DAPL was converted from a continuous variable to a binary response variable with epidemic cases (coded as 1) and non-epidemic cases (coded as 0). A location-year was considered an epidemic case when $\text{DAPL} \geq 0.7\%$ yield loss. This value represented the median value of cases from Central and Western CRDs in years with reported disease loss.

Explanatory Variable Candidates

Yearly crop statistics were collected from the USDA - National Agricultural Statistics Survey quick stats database. Cropping statistics included the acres of wheat planted, acres of wheat harvested, previous year’s acres of wheat planted, previous year’s acres of wheat harvested, previous year’s acres of corn planted, previous year’s acres of sorghum planted, and the estimated percentage of CRD area for each of cropping statistics. Hourly temperature (°C), relative humidity (%), and precipitation (mm) was obtained from weather stations within crop reporting districts from 1994-2013 (Figure 3.1). Monthly mean temperature, mean relative humidity, and sum of precipitation were calculated from hourly weather data for a period of 17 months from the previous year's March through July of the season considered.

Specific conditions from experiments and studies of WSMV and WCM described in the introduction were used to develop monthly variables describing biological processes of WCM and WSMV. Temperature variables included: the sum hours below 10°C, the sum hours between 10 and 35°C, the sum hours above 35°C, cumulative degree day (10°C low threshold and 35°C high threshold), the sum hours below -20°C, the sum hours above 20°C, sum hours between 15 and 30°C, the sum of hours below 15°C, as well as a temperature derived simulated mite growth rate for the first 28 days of each month (SMR). Relative humidity monthly variables included: the sum of hours greater than 75% RH and the sum of hours less than 50% RH. The monthly Standard Precipitation Index (SPI), monthly Palmer Z-Index (ZNDX), and monthly Palmer Drought Severity Index (PDSI) were collected to describe soil moisture conditions within each district. These soil moisture indices were retrieved from National Oceanic and Atmospheric Administration - National Climatic Data Center climate resource.

Variable Selection

Preliminary evaluation of the historic observations indicated that WSM yield losses were more common in Central and Western CRDs than in the Eastern third of the state. Classification tree analysis of the full dataset (all 9 CRDs) (JMP Pro Version 11.2.0; SAS Institute, Cary, NC) identified that variables describing the acres or density of wheat planted could explain a large part of this regional variation within the state. The classification trees provided the likelihood-ratio chi square (G^2), misclassification rate (MR), and receiver operator characteristics (AUC) for the select variables. Based on these results, the subsequent analysis accounted for these regional differences by initially focusing of weather patterns influencing disease related yield losses in Central and Western CRDs. The final stage of the analysis returns to the full data set and integrates earlier results regarding the influence of both intensity of wheat production and weather patterns.

The potential influence of weather and cropping factors on the epidemics of WSM in the Western two-thirds of Kansas was evaluated with non-parametric correlation and classification tree analysis. These analyses were initially conducted using the DAPL≥0.7% base response variable. Results from classification tree analysis with a likelihood ratio chi square greater than 15.0 are presented. Then, the analyses were expanded to consider a range of binary response variables from observations of Central and Western CRDs with slightly different thresholds of DAPL. These different DAPL thresholds represented 20-quantiles values from the Central and Western CRDs (Table 3.1). This resulted in eleven binary response variables. The relation of weather and crop variables with each of these response variables was evaluated with non-parametric correlation analysis, Kendall's tau (JMP Pro Version 11.2.0; SAS Institute, Cary, NC) and classification tree analysis as described above. The top five variables with the greatest absolute Kendall's tau and G^2 statistics were recorded for each binary response. Variables correlated with highly associated variables also were not advanced because they represented similar information from time periods or types of information (temp, moisture) already represented by variables with greater absolute Kendall's tau and G^2 values. Trends in the type of information and critical time periods were identified by frequency at which variables representing this information were selected based on Kendall's tau and G^2. Variables with the highest frequency in the table were selected for further analysis. The variable selection procedure identified the temperature during the winter season (December through February) as potentially useful indicators of disease risk. Because these variables potentially represented a response to temperature spanning multiple months, we elected to create additional variables covering this time period including: number of hours that temperature was below 10°C and 15°C, and the hours that temperature was above 20°C for December through February.

Models of disease risk were developed using the data set representing all 9 CRDs and the DAPL≥0.7% response. In this analysis, classification trees were used as a guide for identifying potentially useful combinations of variables previously found to have a relationship to WSM losses. The acres of wheat planted was included in all models with the tree procedure identifying weather-based variable that might compliment this information. Logistic regression was then used to model the influence of these variables on regional epidemic at DAPL≥0.7% (SAS Version 9.4; SAS Institute, Cary, NC). The fit of the resulting models was evaluated based on Akaike's Information Criterion (AIC), area under the receiver operator characteristics curve (AUC), percent correct, specificity, and sensitivity.

Results

Historic Disease Observations

Kansas disease loses over the entire state included 171 location-years from nine CRD over 19 years. For the following analyses, district annual percent loss (DAPL) greater than or equal to 0.7% was used as the threshold for the categorical response variable. At this threshold, there were 137 non-epidemic cases and 34 epidemic cases corresponding to 80.1 and 19.9% of cases, respectively. At the CRD level, the frequency of epidemic cases ranged from 0 to 36.8%. Excluding Eastern Kansas, there were 114 location-years from six CRD. For DAPL≥0.7% there were 82 non-epidemic cases and 32 epidemic cases, corresponding to 71.9 and 28.1% of cases, respectively. At the CRD level, the percent of epidemic cases ranged from 21.1% (Northwestern and Northcentral CRDs) to 36.8% (Southwestern CRD).

Variable Selection

Comparing the Eastern three Kansas CRD to the Western six CRD at the DAPL≥0.7% threshold, only two epidemic cases and 55 non-epidemic case have been reported in the eastern third of the state. This represents only 5.9% of the epidemic cases from the entire state, but it also includes 40.1% of the non-epidemic cases from the entire state. Furthermore, measurable loss (DAPL>0) has only occurred in three location-years in the Eastern CRDs of Kansas. In relation to the cropping statistics for each district, the eastern three CRD plants fewer acres of wheat (acres of winter wheat planted ≤ 690,000 acres; mean=305,630 acres) vs. the western six CRD plants of the state (acres of winter wheat planted ≥ 938,000 acres; mean=1.52 million acres).

The Kendall's τ-based analysis of weather from Western and Central Kansas found most of the entries were in winter months with some association with the late fall and spring of the season (Figure 3.2 a). Of the different types of variables, temperature had the greatest number of variables present (Figure 3.2 b). Soil moisture (drought) indices had the second highest number of entries followed by relative humidity. These three types of variables were selected across the available range of response thresholds. The classification tree-based analysis of weather also found the winter season most associated with WSM epidemics, with PY spring and fall, and the summer of the season also showing fewer associated variables (Figure 3.2 a). As for the type of variable, temperature had greatest association across the response thresholds. Drought also had a large number of variables present (Figure 3.2 b). Direct measures of precipitation and crop statistics did not have substantial associations in this analysis.

From classification tree analysis, a specific node at AWP≥690,001 split epidemic cases by high wheat producing regions (Western/Central Kansas) vs. low wheat producing regions (Eastern Kansas). Within the low producing wheat production group, only two cases were misclassified. The high wheat production group had 114 total cases with 82 epidemic and 32 non-epidemic cases. This single variable partition model had an AUC of 0.6713 and misclassification rate of 0.1988. Classification tree analysis from the general monthly summaries and soil moisture indices for the high production districts of Kansas at DAPL≥0.7% found some associated factors. Only results that had a likelihood chi square value greater than 15 are discussed. Temperature conditions in the previous year's (PY) September, PY November, PY December along with January during the season had some association with highest value in January (Figure 3.3 a). Relative humidity in June in the season considered had association with regional epidemics (Figure 3.3 b). The three drought indices had varying associations with epidemics. The standard precipitation index indicated that February had association with epidemics (Figure 3.3 d). Palmer's Z- Index had association during PY November and February of the season (Figure 3.3 e). Direct measure of precipitation, palmer's drought severity index, and cropping statistics were not strongly associated with epidemics of greater than 0.7% loss (Figure 3.3 c,f).

Mean temperature in January (ATJan), Palmer's Z-Index in February (ZNDXFeb), and hours below 15°C during the winter months (Win<15) were selected for further analysis with logistic regression modeling based on the top results from both the classification trees and the weather analyses from Central and Western Kansas. Recursive partitioning further selected the standard precipitation index in previous year's October (SPIPYOct) as a third term for ATJan, hours below 15°C in the previous year's September (T<15PYSep) for ZNDXFeb, and the simulated mite rate in the previous year's September (SMR_PYSep) for Win<15. For logistic regression models, all two term models improved model performance from the single term models with AWP (Table 3.2). Hours below 15°C during the winter months had the lowest AIC value (147), highest AUC value (0.80), and most cases correctly classified at a balanced specificity and sensitivity (73.1 percent correct). Of monthly variables, mean temperature in January had the lowest AIC value (153) and Palmer's Z-Index in February had the highest AUC (0.77) and best accuracy at a balanced specificity and sensitivity (69.0 percent correct). Of three term models, only acres of wheat planted (AWP), Z-Index in February, and hours below 15°C in the previous year's September with an interaction between monthly variables had the better performances by AIC value (139) and AUC value (0.81) of all three term models and four term models (with interactions). Although this model was a better fit by AIC and AUC, the percent correct, sensitivity, and specificity were only slightly improved from the two variable models with Palmer's Z-Index.

Discussion

Within Kansas, the spatial position of the CRD with the amount of wheat planted was a major determinant of frequency of epidemic cases. The Eastern three CRD of Kansas have planted fewer acres of wheat than the Central and Western six CRD. Of the years considered, all eastern CRDs have planted at least 55,500 acres of wheat but no more than 690,000, while western and central CRDs have planted at least 938,000 acres of wheat and at the most 2,675,000 acres. The fewer acres of wheat planted in the eastern portion of the state could reduce the number fields with summer volunteer wheat. These lower numbers of infested fields would reduce the possibility that a winter wheat fields would be planted near WCM carrying volunteer wheat. This factor could help explain the reduced frequency of region wide epidemics in the Eastern portion of Kansas.

Warmer temperatures in September were also found to be associated with WSM. In this analysis, higher average temperature, fewer hours below 15 °C in September, and simulated WCM reproduction rates were both found to be associated with epidemics in Kansas. In the Kansas winter wheat crop, this is the time of planting and germination (United States Department of Agriculture National Agricultural Statistics Service 1997). Warm temperatures during this time could result in increased activity of WCMs during the earliest stages of the winter wheat crop. This is consistent with previous research which indicated that temperatures above 10°C promoted the increase of multiple mite populations (Kuczyński et al. 2016). Dispersal studies have shown that the activity of dispersing populations tends to decrease throughout the fall and into the winter, likely corresponding with the decreases in temperature (Staples and Allington 1956; Nault and Styer 1969). More recent dispersal studies showed that mean temperature during this period was positively associated with both WCM infestation and WSMV infection of trap plants during the late summer and early fall (Ranabhat et al. 2018).

This time period also corresponds to the key WSM management decision for the wheat crop. Studies have found that wheat planted at later dates in the fall were less likely to be impacted by WSM (Slykhuis et al. 1956). Later planting dates typically correspond with cooler temperatures, decreasing the risk of mites dispersing from summer hosts to newly planted winter wheat. Along with WCM activity, winter wheat does not express symptoms of WSMV until the crop breaks dormancy in the spring (Burrows et al. 2016). In a year with exceptionally warm fall temperatures, viral symptoms can express in the fall. A recent example, exceptionally warm temperatures in the fall of 2016 led to fall symptom development and identification of WSMV within the establishing wheat crop. Earlier disease development would naturally increase the negative impacts of viral infection.

Warm temperatures throughout the winter were also strongly associated with losses from WSM. Above average temperatures during this time could favor continued WCM survival, dispersal, and reproduction. This agrees with the findings Slykhuis (1955) who reported that exposure to extended periods of sub-zero temperatures can reduce the survival of WCM. Those studies identified that extended periods of subzero temperatures reduced both the survival and the egg hatchability of the WCM. Additional research is needed to more fully characterize the influence of low temperature on the survival of WCM populations.

Drought and low soil moisture conditions during the month of February were also strongly associated with heavy disease losses. This month generally corresponds to the wheat crop breaking of dormancy and spring tillering of the wheat crop. As to the impacts of the disease, WSMV has an impact on the development and function of the roots. WSMV-affected plants have reduced root biomass and reduced water use efficiency (Price et al. 2010). Reduced root biomass and reduced root functionality could exacerbate stresses on the crop during this period. Drought stress may also reduce the plant health and subsequently stimulate WCM movement. As the crop deteriorates from drought stresses, WCM may be stimulated to move off of the stressed host plant and further into the effected field. Reduced precipitation during this time may also correspond to reduced snow cover. Reduced snow cover would expose WCM sources to wind and increase the chance of mite movement during this period. Further support of drought and moisture in February comes from the last major statewide outbreak which occurred during the 2016-2017 season. Statewide losses attributed to WSM were estimated at 5.6% of the total winter wheat crop, or 19.3 million bushels (Hollandbeck et al. 2017). During that season, the February Palmer's Z-Index indicated similar moderate drought conditions associated with historic epidemics in the analysis. This most recent observation provides more compelling evidence for the importance of precipitation during this time period.

All of the associated weather factors before spring of the wheat season could correspond to movement and spread of WSMV during a sensitive stage for the winter wheat crop. WSMV infection before the jointing stage of wheat has been shown to cause significantly higher losses for the wheat crop. In Oklahoma, it was shown that fall inoculation led to significantly lower yields than spring inoculation (Hunger et al. 1992). Further study revealed reduction in the shoot biomass, stem dry weight, water use efficiency, and yield with infection at or before wheat jointing (Pradhan et al. 2015). In conclusion, weather or factors simulating WCM movement and WSMV infection before this key physiological period in the wheat crop would suggest that the wheat crops' susceptibility before jointing is key to heavy losses during an epidemic.

From this analysis of regional WSM epidemics in Kansas, no variables were strongly associated in the late spring or summer conditions of the previous year (likelihood ratio chi square greater than 15). No strongly associated summer variables suggest the favorable conditions for the green bridge are usually present in high wheat production regions. Grass species other than volunteer wheat have been identified in CRP and grassy swales to carry WSMV over the summer (Christian and Willis 1993). These other grasses may provide sources for WSMV in years that favor mite activity and winter survival. More recent field experiments have been done to show that other grassy weeds and crops can successfully carry both pests throughout the summer through normal wheat planting dates (Ranabhat et al. 2018). These recent experiments and surveys along with further study may continue to show other viable, non-volunteer wheat sources of WSMV found near wheat fields.

This research identified weather patterns, cropping factors, and time frames associated with major epidemics of WSM. The amount of wheat planted appears to have a strong association with both the intensity and the distribution of regional WSM epidemics in Kansas. Warm temperatures throughout the winter and late winter drought also influence epidemics of WSM. In combination with those conditions, mite-favorable conditions during September were also associated with epidemics. Additional research is needed to better characterize the role of weather on the activity of WCM and outbreaks of WSM

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Tables and Figures

Figure 3.1 Kansas Crop Reporting and NOAA Climate Districts and Approximate Weather Station Locations (Relevant Weather Stations Denoted by Crosshair Symbol)

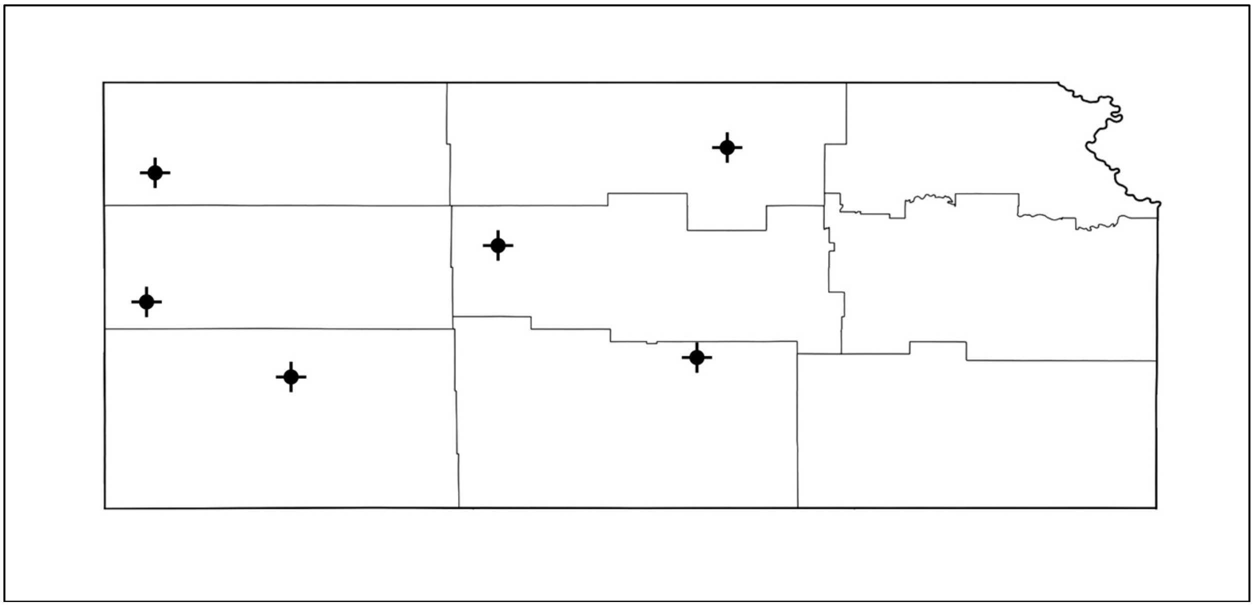


Table 3.1 Eleven Response Variables Developed from 20-Quantile Values for the Central and Western Kansas Crop Reporting Districts, 1995-2013

Variable Information		Type of Statistic	Frequency of Observation	
Variable Notation	Variable Description (Value)	Numeric/ Categorical	Non-Epidemic Cases	Epidemic Cases
DAPL	District Annual Percent Loss	Numeric	Total Cases 114[a]	
Q45[b]	DAPL ≥ 0.032%	Categorical[c]	51 (44.7)[d]	63 (55.3)
Q50 (Median)	DAPL ≥ 0.118%	"	57 (50.0)	57 (50.0)
Q55	DAPL ≥ 0.21%	"	63 (55.3)	51 (44.7)
Q60	DAPL ≥ 0.266%	"	68 (59.6)	46 (40.4)
Q65	DAPL ≥ 0.51425%	"	74 (64.9)	40 (35.1)
Q70	DAPL ≥ 0.6755%	"	80 (70.2)	34 (29.8)
Q75 (Quartile)	DAPL ≥ 0.93925%	"	86 (75.4)	28 (24.6)
Q80	DAPL ≥ 1.3%	"	92 (80.7)	22 (19.3)
Q85	DAPL ≥ 1.961%	"	97 (85.1)	17 (14.9)
Q90	DAPL ≥ 2.661%	"	103 (90.4)	11 (9.6)
Q95	DAPL ≥ 4.92825%	"	109 (95.6)	5 (4.4)

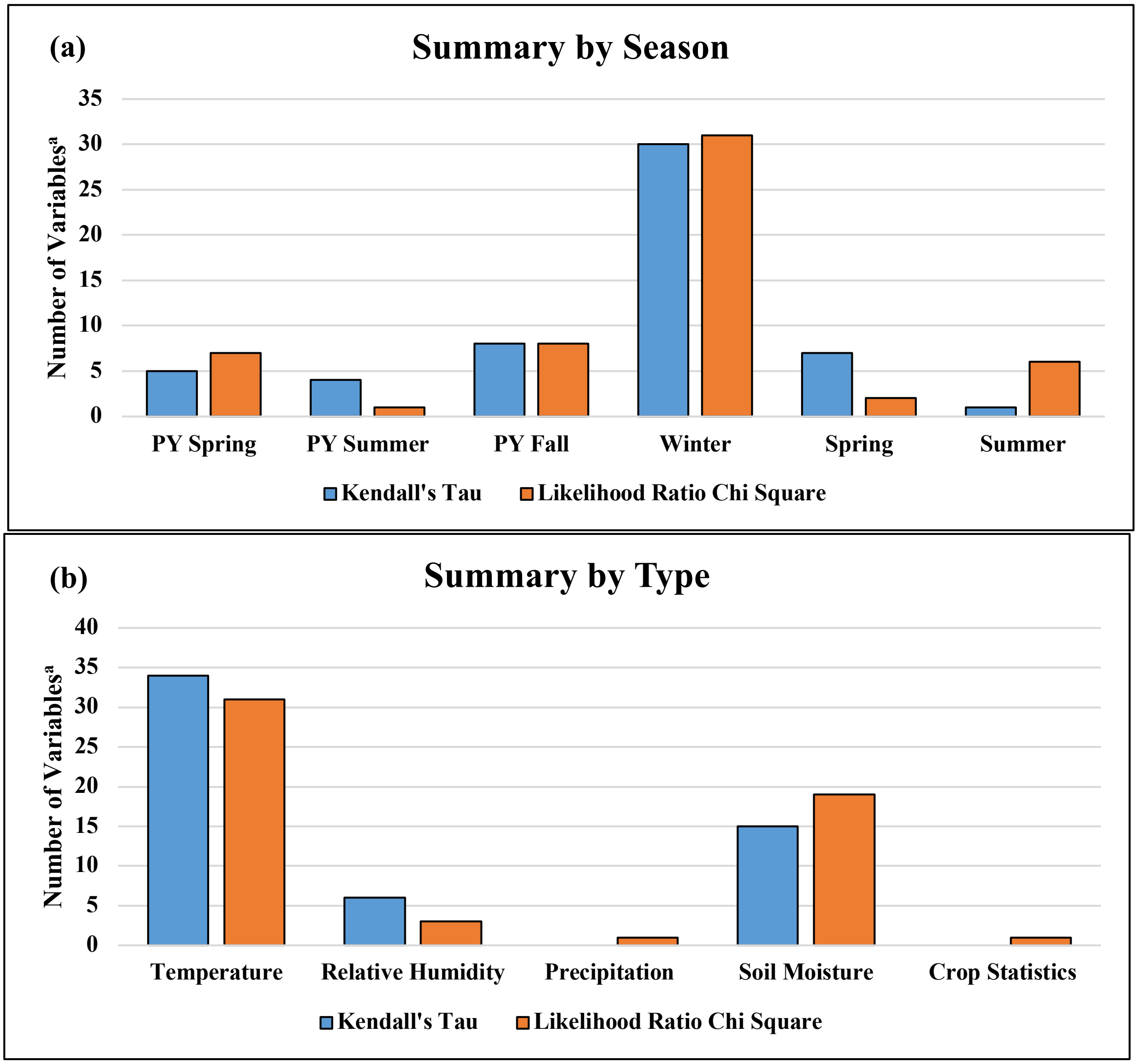
[a] Data includes cases from 1995-2013 from all KS CRDs

[b] Quantiles notation includes the percentile used to establish the variable threshold

[c] Numeric variable converted into a categorical, binary variable with values above the described threshold. Values above the threshold given a designation of 1 (Epidemic Case) and all others 0 (Non-Epidemic Case) and treated as two separate categories.

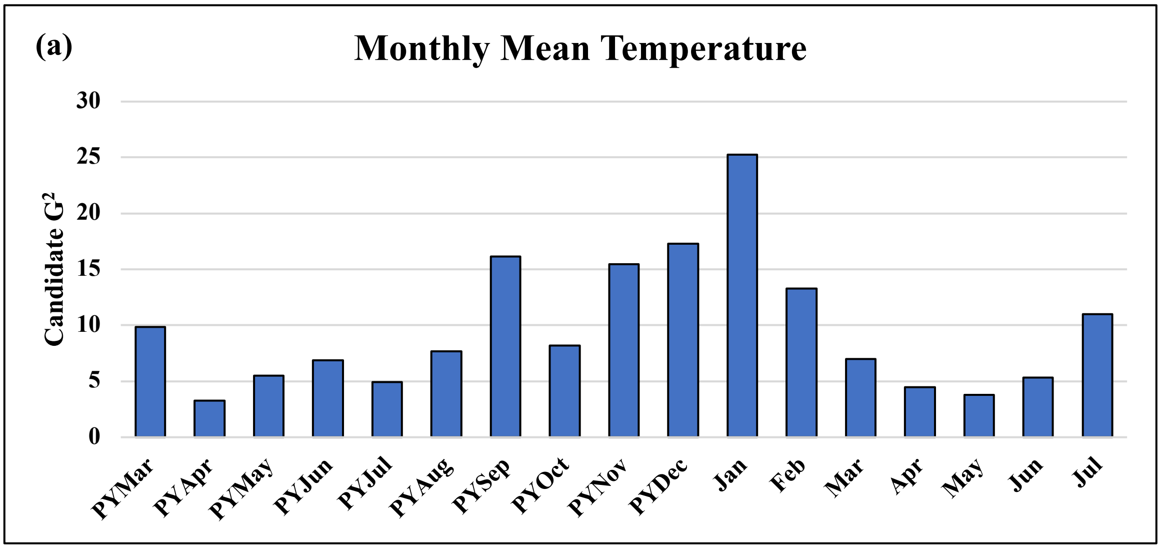
[d] Number of Cases (Percent of Cases)

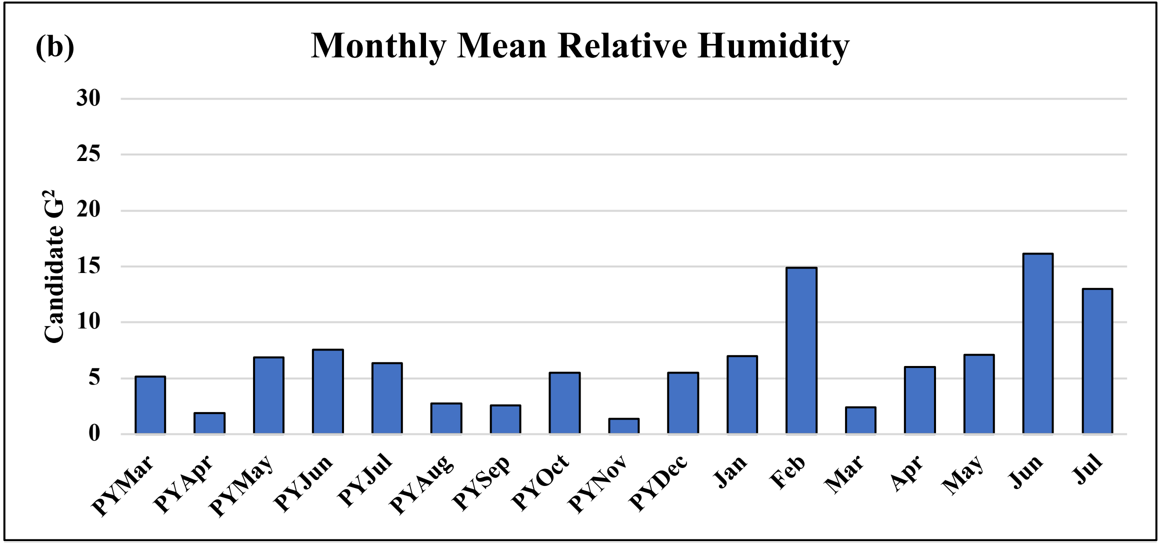
Figure 3.2 a,b Analysis of Season (a) and Type (b) from 11 Different Loss Thresholds using Kendall's |τ| and Likelihood Ratio Chi Square for Central and Western Kansas Crop Reporting Districts, 1995- 2013

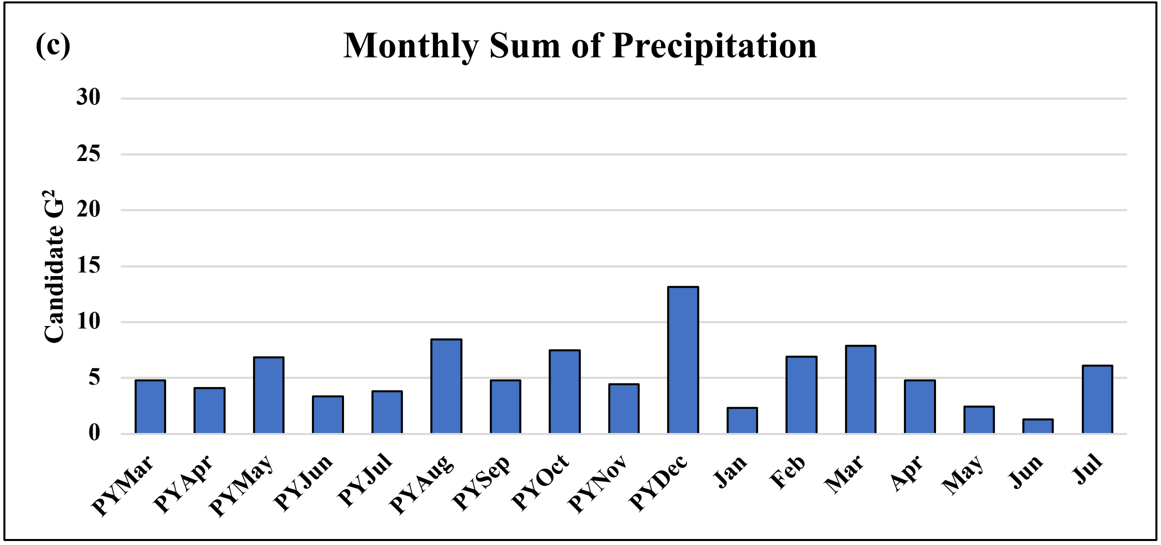


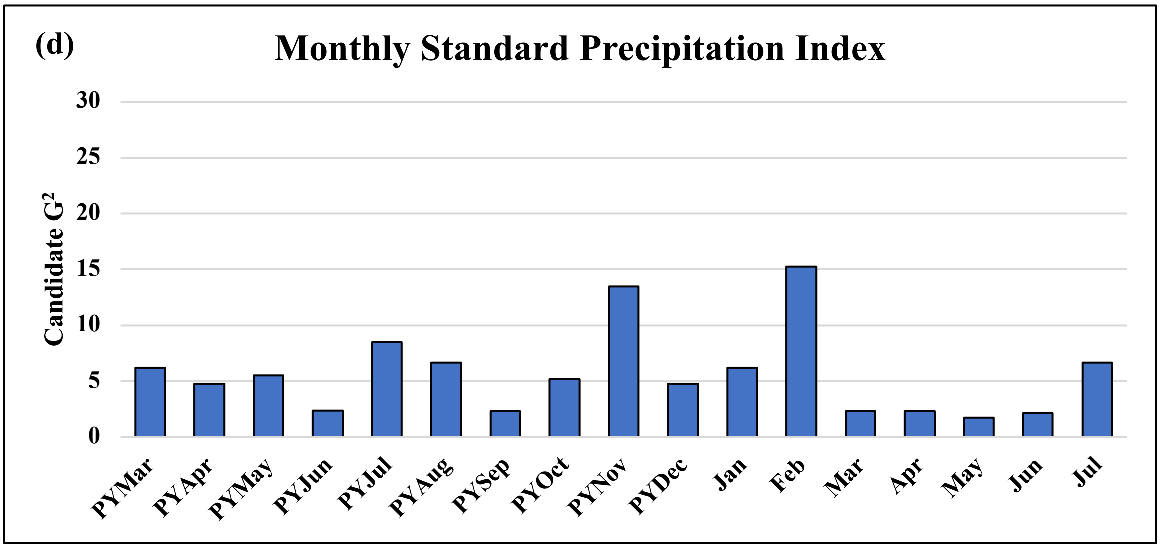
[a] Number of variables identified by analyzing all monthly weather, soil moisture, and crop statistics at eleven response variables with Kendall's |τ| and likelihood ratio chi square and considering the top 5 variables of the different month and type at each response (n=55)

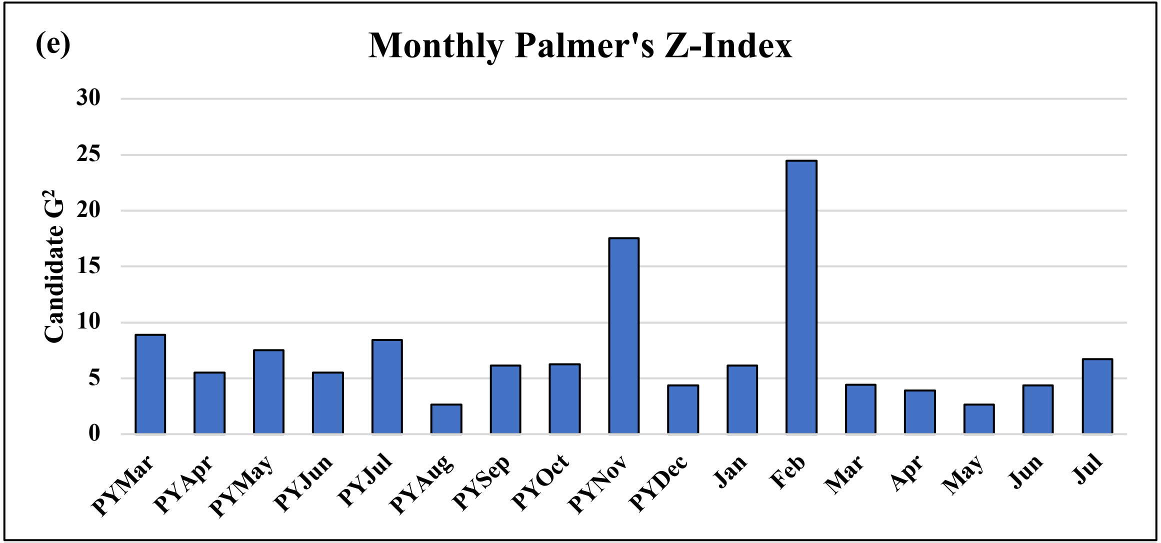
Figure 3.3 a-f Calculated Likelihood Ratio Chi Square (Candidate G^2) for Monthly Explanatory Variables for Central and Western Kansas CRDs at DAPL≥0.7% Response


(a) Monthly Mean Temperature


(b) Monthly Mean Relative Humidity


(c) Monthly Sum of Precipitation


(d)
Monthly Standard Precipitation Index
Candidate G²
0
5
10
15
20
25
30
PYMar
PYApr
PYMay
PYJun
PYJul
PYAug
PYSep
PYOct
PYNov
PYDec
Jan
Feb
Mar
Apr
May
Jun
Jul


(e)
Monthly Palmer's Z-Index
Candidate G²
0
5
10
15
20
25
30
PYMar
PYApr
PYMay
PYJun
PYJul
PYAug
PYSep
PYOct
PYNov
PYDec
Jan
Feb
Mar
Apr
May
Jun
Jul

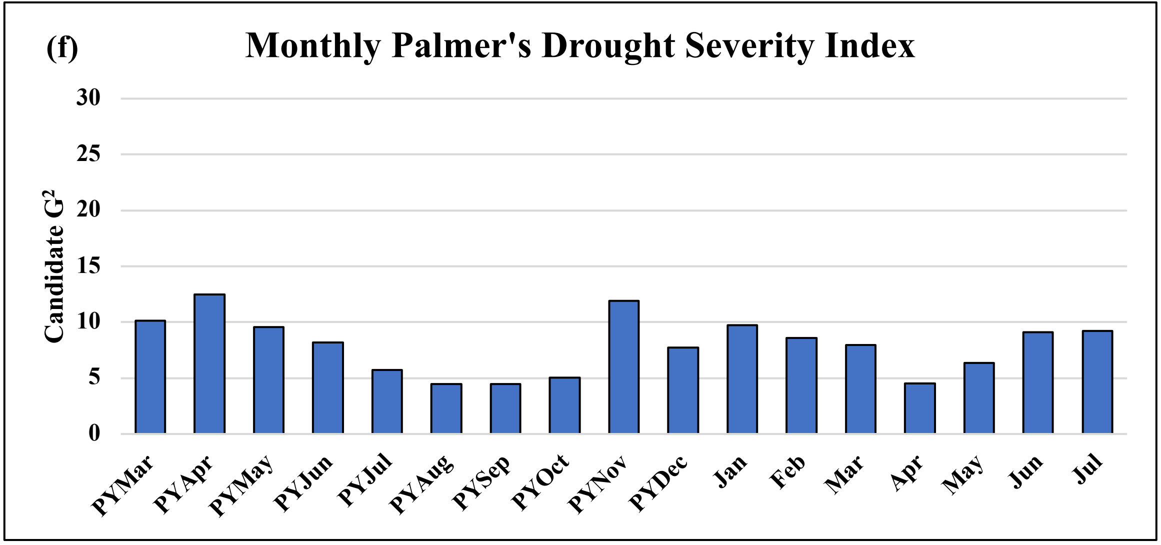

(f)
Monthly Palmer's Drought Severity Index
Candidate G²
0
5
10
15
20
25
30
PYMar
PYApr
PYMay
PYJun
PYJul
PYAug
PYSep
PYOct
PYNov
PYDec
Jan
Feb
Mar
Apr
May
Jun
Jul

Table 3.2 Results from Logistic Regression Analysis of the Epidemic Cases of WSM at the DAPL≥0.7% Response

First Term	Second Term	Third Term	Fourth Term	AIC[a]	AUC[b]	Percent Correct[c]	Sensitivity[d]	Specificity[e]
AWP[f]				163	0.68	60.8	64.7	59.9
AWP	ATJan[g]			153	0.74	66.1	64.7	66.4
AWP	SPIPYOct[h]			164	0.69	62.6	50.0	65.7
AWP	ATJan	SPIPYOct		153	0.75	67.3	64.7	67.9
AWP	ATJan	SPIPYOct	ATJan*SPIPYOct	154	0.75	64.9	64.7	65.0
AWP				163	0.68	60.8	64.7	59.9
AWP	ZNDXFeb[i]			153	0.77	69.0	70.6	68.6
AWP	T<15PYSep[j]			164	0.71	63.7	64.7	63.5
AWP	ZNDXFeb	T<15PYSep		154	0.76	67.8	67.6	67.9
AWP	ZNDXFeb	T<15PYSep	ZNDXFeb*T<15PYSep	139	0.81	68.4	70.6	67.9
AWP				163	0.68	60.8	64.7	59.9
AWP	Win<15[k]			147	0.80	73.1	76.5	72.3
AWP	SMR_PYSep[l]			164	0.71	64.3	61.8	65.0
AWP	Win<15	SMR_PYSep		149	0.80	74.9	70.6	75.9
AWP	Win<15	SMR_PYSep	Win<15*SMR_PYSep	151	0.80	74.9	70.6	75.9

[a] Akaike's Information Criteria (AIC) estimates fit of the model and considers the number of parameters utilized to prevent overfitting. Models with lower AIC values are preferred to ones with higher values.

[b] Area under the receiver operating characteristics curve (AUC) estimate describes the relationship of model sensitivities to specificities. Values range from 0.5 to 1 with models of higher value better classifying cases.

[c] Percent correct is percent of correctly identified cases

[d] Sensitivity is the percent of correctly identified epidemic cases

[e] Specificity is the percent of correctly identified non-epidemic cases

[f] Acres of wheat planted (AWP)

[g] Mean January temperature (ATJan)

[h] Standard precipitation index previous year's October (SPIPYOct)

[i] February Palmer's Z-Index (ZNDXFeb)

[j] Hours below 15C previous year's September (T<15PYSep)

[k] Winter hours below 15C (Win<15)

[l] Simulated mite rate previous year's September (SMR_PYSep)

Chapter 4 - Conclusions

This research set out to identify factors that influence the development of wheat streak mosaic (WSM) epidemics at the regional level. These results point to potential sources of *Wheat streak mosaic virus* (WSMV) and the wheat curl mite (WCM) as well as highlight certain cropping factors and weather patterns that were associated with historic losses to the disease in Kansas. The first chapter reviews the previous research on the factors that influence the severity of WSMV infection, influences on the activity and reproduction of the WCM, epidemiological factors associated with WSM outbreaks, and management strategies for the prevention and control of the disease.

The second chapter reviewed the historic observations of the grasses that could serve as hosts for WSMV and the WCM. Previous reviews of the WSMV and WCM host ranges utilized reports found in the literature but did not utilize observations of non-suitability to describe possible variation in the hosts or pest populations. The results from this chapter included both report-based and categorical analysis of the host range for both pests, specifically pertaining to grass species. A report-based analysis found similar results to previous reviews and identified 39 grass species that have been reported to host both pests. A categorical analysis defined 4 risk groups and 10 grass species that are highly likely to be suitable for WSMV and WCM. Further field testing is needed to better verify the proposed risk groupings and threats to newly planted wheat.

The third chapter studies the historical association of cropping practices and weather variables or patterns to regional epidemics of WSM. A comparison of the acres of wheat planted showed an association with low frequency of epidemics in the eastern three Kansas crop reporting districts (CRD). This suggested that larger amounts and frequency of wheat planted may influence the development of regional outbreaks. Continued analysis focused on the western six CRDs showed that warm temperatures in September and throughout the winter months (December through February) and dry conditions in February were associated with regional epidemics of WSM. These conditions stress plants and stimulate the movement of the WCM. With further development, the information in this work could clarify the potential role of different grass species and weather on the development of WSM epidemics in Kansas.

Appendix A - SAS Code for Pest Suitability Categorical Analysis

```
Data Assessments;
      input entry $ pub $ Genspe $ Gen $ Pest $ Type $ Inoc $ Conmeth $ Quan Cat;
      datalines;
1     McK37     Triaes     Tri     Wsm     Exp     Man     ManW     2     1
2     McK37     Elyrep     Ely     Wsm     Exp     Man     ManW     0     0
3     McK49     Triaes     Tri     Wsm     Exp     Man     Visual     2     1
…


…
1030     Ito12     Agrcri     Agr     Wsm     Obs     NA     ELISA     0     0
1031     Ito12     Aegcyl     Aeg     Wsm     Obs     NA     ELISA     0     0
1032     Ito12     Broine     Bro     Wsm     Obs     NA     ELISA     0     0
;
Proc sort data=Assessments;
      by Genspe Pest Decending Cat;
      Run;

Proc freq order=data noprint;
      output out=new binomial;
      tables Cat/ binomial (Level="1" exact) alpha=.05;
      exact binomial/MIDP;
      by Genspe Pest;
      run;

data new2;
set new;
if n<4 then delete;

proc print;
run;
```