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Over-Summering Ecology of the Wheat Curl Mite (*Aceria tosichella* Keifer)

Anthony J. McMechan
University of Nebraska - Lincoln

OVER-SUMMERING ECOLOGY OF THE WHEAT CURL MITE

(*ACERIA TOSICHELLA* KEIFER)

by

Anthony Justin McMechan

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OVER-SUMMERING ECOLOGY OF THE WHEAT CURL MITE (*ACERIA TOSICHELLA* KEIFER)

Anthony Justin McMechan, Ph.D.
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Advisor: Gary L. Hein

The wheat-mite-virus complex is a consistent and significant threat to winter wheat production in the western Great Plains. This complex consists of three viruses (Wheat streak mosaic virus, *Triticum* mosaic virus, and Wheat mosaic virus that are transmitted by the wheat curl mite (*Aceria tosichella* Keifer). Yield impacts from this complex are typically associated with the presence of volunteer wheat that emerges prior to harvest as a result of hail occurring during the heading stages of wheat in early summer. Historical literature on pre-harvest germination has been primarily focused on accelerating breeding programs; however, critical gaps in knowledge exist on pre-harvest germination when evaluating risk for the wheat-mite-virus complex.

A study was designed to evaluate pre-harvest germination potential of winter wheat by collecting heads at 7-9 day intervals beginning at the water-ripe stage until wheat harvest. In addition, risk categories were established based on the speed of germination because field germination will be limited by moisture availability. A second study was conducted in the field to evaluate the impact of environmental conditions on pre-harvest germination. Results indicate that risk for pre-harvest germination begins at the late milk stage with increasingly greater risk for germination up to harvest. In addition, risk for germination is highly dependent on available moisture following hail events.

Historical observations, as well as anecdotal evidence indicate that other hosts besides wheat can support WCM during the over-summering period; however, the risk of these hosts to fall planted wheat is poorly understood. Greenhouse reproductive studies, a field study on mite movement and virus impact, and a weed survey were conducted to evaluate the risk potential of over-summering hosts. Results showed that barnyard grass is a high-risk over-summering host for the wheat-mite-virus complex; however, its frequency is relatively low across the central Great Plains. Green foxtail was comparatively a lower risk host, but it was found in higher frequencies in the weed survey. Foxtail millet, another summer annual, showed significant mite movement under field conditions; however, virus impact was minimal. In addition, greenhouse studies were a good predictor of field potential of all of the over-summering hosts with the exception of foxtail millet. The studies presented in this document provide critical information to better understanding the over-summering ecology and risk of the wheat-mite-virus complex.

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Literature Review

Introduction

The wheat-mite-virus complex is one of the primary causes of yield loss in winter wheat in the western Great Plains. Kansas disease loss estimates indicate that approximately 11 million bushels (2.7%) of wheat was lost due to this complex during the 2015 season (Appel et al. 2015). This complex consists of three viruses (wheat streak mosaic virus (WSMV), *Triticum* mosaic virus (TriMV), and wheat mosaic virus (WMoV)) that are transmitted solely by the wheat curl mite (WCM; *Aceria tosichella* Keifer).

Landscape level impacts from this complex are often localized to a few fields and primarily attributed to the presence of pre-harvest volunteer wheat. However, yield losses in wheat have been reported in areas with minimal volunteer wheat indicating that other grasses may serve as hosts for the wheat-mite-virus complex. There is a need for greater understanding of the factors that allow for pre-harvest wheat establishment. In addition, studies are needed to address the risk of other green-bridge hosts as a source for mites and virus and to assess their potential to cause yield losses in the fall planted winter wheat.

Wheat Curl Mite Classification

The WCM is a member of the family Eriophyidae, and it occurs throughout the world (Oldfield and Proeseler 1996). Within North America, the taxonomic history of the principal species of *Aceria* that occurs on cereals is uncertain (Frost and Ridland 1996). North American mites found on wheat were first identified by Keifer in 1938 as the dry bulb mite, *Aceria tulipae* Keifer because of morphological similarities. Keifer believed that the mites found on wheat were the same species of mite infesting tulips (*A. tulipae)*.

In 1970, Shevtchenko *et al.* proposed that the specific epithet *A. tulipae* belonged only to mites found on Liliaceae and proposed the name *Aceria tritici* for mites infesting wheat. Prior to this publication, Keifer had described a mite on wheat in Yugoslavia that was identical to *Aceria tritici* as *Aceria tosichella* (Keifer 1969). Because Keifer's publication preceded Shevtchenko's publication, the name *Aceria tosichella* Keifer takes precedence. Keifer's publication resulted in the separation of *A. tulipae* and *A. tosichella* into two distinct species (Amrine and Stasny 1994). Although the distinction between *A. tulipae* and *A. tosichella* was made in 1969, it was not adopted into common use until Amrine and Stasny (1994) clarified the historical record. In 1971, Newkirk and Keifer removed mites from *Aceria* and reassigned them to *Eriophyes*, mites in *Eriophyes* were reassigned to *Phytoptus,* and those in *Phytoptus* were assigned to a new genus *Phytocoptella*. Several authors objected to this revision. WCM were restored to the genus *Aceria* in 1989 (Amrine and Stasny 1994). As a result, since 1969 the wheat curl mites have been referred to under multiple species names in the literature including *Aceria tulipae*, *Eriophyes tulipae,* and *Aceria tosichella*.

The complex of viruses the WCM transmits is a major cause of loss in winter wheat production in the Great Plains. To reduce economic impact from this complex, varieties with resistance to the WCM were developed. The first mite resistant wheat variety resulting from a translocation from rye was registered in 1987 and deployed as 'TAM 107' (Porter et al. 1987). TAM 107 in addition to other varieties with the same gene for resistance to the WCM was adopted and widely distributed throughout the west-central Great Plains during the late 1980's and 1990's. WCM populations that were adapted to TAM 107 were identified in Kansas in the mid-1990's (Harvey, Martin, and

Seifers 1995, Harvey, Martin, Seifers, et al. 1995). To determine the extent of this adaptation, Harvey et al. (1999) tested WCM from six distinct geographical locations within the Great Plains. Harvey et al. (1999) placed these mites on varieties of wheat with different genes for WCM resistance (Harvey and Martin 1992, Thomas and Conner 1986, Whelan and Hart 1988, Cox et al. 1999, Sebesta et al. 1994). Results from the study indicated that mites collected from different locations varied in their responses to the different sources of mite resistance (i.e. biotypes).

These same populations were tested for their transmission of WMoV (Seifers et al. 2002). Three populations (Kansas, South Dakota and Texas) were inefficient transmitters of WMoV with transmission rates of 1-6%. Mites in the Montana population were shown to be intermediate in their transmission rate (15%). Mites in the Nebraska population were the most efficient transmitters at a rate of 64% using 10 mites per test plant. The Montana population demonstrated an increased transmission rate (52%) when mixed infections of WMoV and WSMV were used.

Hein et al. (2012) tested these same populations for genetic differences using PCR-RFLP of the mitochondrial cytochrome oxidase subunit I (COI) and cytochrome oxidase subunit II (COII) region and ribosomal DNA. Two distinct populations were identified; type 1 (Kansas, Montana, South Dakota and Texas) and type 2 (Nebraska). The separation between these two types of *A. tosichella* was comparable to their separation with *A. tulipae*, indicating the extent of the differences between the two types. The differences in mite types found within North American mite populations were the same as those found in studies conducted on WCM in Australia (Carew et al. 2009).

WSMV is considered to be the most prevalent of these viruses occurring in part of North America, Europe, the Middle East, North Africa, and Central, East and Southeast Asia (Jones et al. 2005). Annual losses in the Great Plains in North America range from 1% to 5% with localized outbreaks causing yield losses up to 100% (Christian and Willis 1993). WMoV and TriMV are often found in combination with WSMV in the field; however, little is known about the epidemiology of either virus. Studies have indicated that interactions between these viruses can result in increased transmission (WSMV and WMoV) (Seifers et al. 2002) or increased yield impacts on wheat (WSMV and TriMV) (Tatineni et al. 2010, Byamukama et al. 2012).

Wheat Curl Mite Biology and Ecology

Wheat curl mites are white in color with a cigar-shaped body and range in length from 170-250 microns (Keifer 1939). Their small size makes them difficult to see with the naked eye; however, when they accumulate on plants and in mass they can give the impression of a powdery mildew infection (Staples and Allington 1956). Wheat plants that are heavily infested with WCM often display various degrees of chlorosis. Symptomology of mite infestations can be more severe when plants are under drought conditions (Staples and Allington 1956).

The complete life cycle of the WCM requires 7–10 days and includes egg, larva, nymph, and adult stages (Staples and Allington 1956). Eggs take approximately 4 days to hatch at 25°C. Temperature and humidity are critical to egg hatch. The majority of eggs hatch at 25°C with a relative humidity of 100% (Slykhuis 1955). Egg hatch is almost completely arrested below 15°C (Slykhuis 1955). Humidity is critical to egg hatch. Very few eggs hatched at a humidity of 75%, and no eggs hatched at a relative humidity below

50% due to desiccation (Slykhuis 1955). Each immature stage is approximately 36 hours in length at 25°C. Between each of the stages there is a quiescent phase where the mites remain inactive and appear partially translucent, for about 18 hours (Staples and Allington 1956). After an adult emerges, it requires an additional 1-2 day preoviposition period. There are no studies indicating the lifespan of an adult, but it is estimated that adults can live for 20-30 days under ideal conditions. WCM can survive without a host for approximately 48 hours depending on the temperature and humidity (Wosula et al. 2015)

There are some subtle morphological differences between the growth stages of WCMs. In the larval stage, seta located just behind the head face forward; whereas in the nymphal and adult stages, these setae face towards the posterior end. The external reproductive structures only become visible in the adult stage where they appear on the dorsal side towards the anterior end. With the use of a microscope, the genital flap can be used to distinguish females from males. In females the genital flap opens towards the posterior end of the body whereas in males the flap is less pronounced and opens anteriorly (Lindquist et al. 1996).

WCM have an indirect method of sperm transfer (i.e. no copulation occurs). Males deposit spermatophores on the leaf surface and females later locate and pick them up (Oldfield 1970). The mites are haplodiploid and produce males via arrhenotokous parthenogenesis resulting in haploid males. Fertilized females are capable of producing diploid females and haploid males (Helle and Wysoki 1983). When these males emerge and reach reproductive maturity, they produce spermatophores to enable fertilization of the female. A female can lay approximately 12-20 eggs during its lifetime. It has been

estimated that under ideal conditions, the offspring of a single female can result in 3 million mites in 60 days. Optimum reproduction for WCM occurs between 23-27°C (del Rosario and Sill 1965). Reproduction slows at 9°C and stops at 0°C (Staples and Allington 1956).

Mite Movement

Nault and Styer (1969) proposed that significant mite movement occurred only when wheat heads and flag leaves were drying out. Greenhouse studies conducted by Thomas and Hein (2003) showed no correlation between mite movement and plant condition. The study indicated a significant correlation between mite population and mite movement. Healthy host plants supported larger mite populations than deteriorating host plants. Field studies confirmed that healthier hosts supported larger mite populations and as a result, increased mite movement.

WCM move passively between plants and fields via wind dispersal (Sabelis and Bruin 1996). Only adult WCM exhibit dispersal behavior (Nault and Styer 1969). To disperse from plants, adults move to the upper margins of the leaf. At this point they hold their bodies perpendicular to the leaf surface by adhering themselves to the leaf using their caudal sucker. This position raises the mite out of the laminar layer of the leaf surface where wind speeds are higher (Sabelis and Bruin 1996). When plants are heavily infested, mites crawl on one another forming chains through the attachment of their caudal suckers (Nault and Styer 1969). Air movement can stimulate perpendicular standing of WCM and the formation of WCM chains. After dispersing from the host it is estimated that less than 10% of mites will reach their primary host again (Jeppson et al. 1975).

To avoid desiccation, mites migrate to the inner whorl of a newly emerging leaf shortly after landing on a new host. There they feed between the veins of the plant on a thin epidermal layer of tissue known as the bulliform cell. These cells are important in the unrolling of the leaf as it emerges (Esau 1953). WCM feeding prevents the leaf from uncurling, causing subsequent leaves to become trapped. The curled leaf provides an ideal environment for mite survival. WCM will continue to feed on the leaves, migrating to each newly emerging leaf. Mites also colonize the wheat head as it emerges. Within the wheat head, mites live in secluded sites and feed inside the glumes (Kantack and Knutson 1954).

Viruses Transmitted by the Wheat Curl Mite

Wheat Streak Mosaic Virus

Wheat streak mosaic virus (WSMV) was first identified in Nebraska in 1922 as 'yellow mosaic' by Peltier (Staples and Allington 1956). It is the type species of the genus *Tritimovirus* in the family *Potyviridae* (Stenger et al. 1998). WSMV is a single stranded RNA virus with ~9384 nucleotides and is translated as a single polyprotein (Choi et al. 2002). WSMV has distinct resident populations in North America and Eurasia (Rabenstein et al. 2002). However, McNeil et al. (1996) identified 32 distinct RFLP types in five Nebraska counties. The genetic diversity of these RFLP types was greatest among fields rather than between counties. Although the genetic diversity of populations changed over time they remained geographically homogeneous. This indicates extensive mixing of WSMV isolates.

Three WSMV strains within North America have been completely sequenced (Choi et al. 2001). The Type and Sidney 81 strains of WSMV were isolated from wheat

in the Great Plains and share 97.6% of their nucleotide sequence identity. Sidney 81 is considered to be the most dominant strain within the Great Plains. In the central highlands of Mexico, the El Batàn 3 strain was isolated from wheat (Sánchez-Sánchez et al. 2001). It shares only 79% of its nucleotide sequence with the two strains isolated from the Great Plains (Choi et al. 2001). All three of these strains are vectored by the WCM (Brakke 1958, Choi et al. 1999, Hall et al. 2001, Sánchez-Sánchez et al. 2001). WSMV is only transmitted by the wheat curl mite; however, there are some indications that the virus can be transmitted via seed at low levels (ca. 0.5% - 1.5%; Jones et al. 2005). The discovery of WSMV in Australia was hypothesized to occur through the introduction of wheat breeding seed from the United States (Dwyer et al. 2007). WSMV has a wide host range and can infect many plants within the grass family (McNeil et al. 1996). It can infect almost all varieties of wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and oats (*Avena sativa* L.) (Brakke 1971). Sidney 81 and Type strains can be distinguished from one another based on their virulence to the maize inbred line SDP2 (Choi et al. 1999).

Wheat Mosaic Virus

Wheat mosaic virus (WMoV) (genus *Emaravirus,* family Bunyaviridae) was first identified in corn in 1993 (Jensen et al. 1996, McGavin et al. 2012). WMoV, formerly known as High plains virus, is an octapartite segmented, negative-strand RNA virus associated with a 32-kDa protein, double membrane virus-like particles of 80-200 nm in diameter (Ahn et al. 1996, Tatineni et al. 2014). The economic losses associated with WMoV are unknown, but it has a host range consisting of many economically important plants, including wheat and maize (Skare et al. 2006). Field samples that tested positive

for WMoV often had WSMV. These co-infections often have higher symptomatic expression. WMoV cannot be mechanically transmitted, but it can be transmitted by vascular puncture inoculation of corn seeds (Jensen et al. 1996, Louie and Seifers 1996).

WMoV exhibits different rates of transmission depending on the mite source. Nebraska (Type 2) and Montana (Type 1) mites were able to transmit all five WMoV isolates, whereas Kansas (Type 1) mites transmitted only one isolate of WMoV (Seifers et al. 2002), albeit poorly. Montana mites that were virulent for both WSMV and WMoV exhibited higher rates of transmission than avirulent mites with just WMoV.

Only a partial host range of WMoV is currently available because WMoV is not mechanically transmissible. Cheatgrass, corn, barley, oats, rye, green foxtail, yellow foxtail, and wheat are susceptible to WMoV (Seifers et al. 1998). To cause infection, high numbers of WCM had to be transferred to cheatgrass, oats, and rye. WMoV can be separated from WSMV and TriMV through mite transmission onto yellow foxtail plants, because only WMoV will infect this host (Seifers et al. 1998, Skare et al. 2003).

Triticum Mosaic Virus

Triticum mosaic virus (TriMV) (genus *Poacevirus,* family *Potyviridae*) was first identified in wheat in Kansas in 2006 with symptoms almost identical to WSMV (Seifers et al. 2009). Wheat plants infected with TriMV were not geographically localized and were often found in combination with WSMV. The wheat curl mite was identified as the vector of TriMV with a transmission rate of 1.3% using single mite transfers (Seifers et al. 2009). Transmission studies with wheat curl mite populations collected in the Great Plains found that ‘Nebraska’ mites transmitted at 40.3% whereas ‘Kansas’ and ‘Montana’ were only able to transmit TriMV under high mite populations (McMechan et al. 2014).

TriMV has been identified as a single-stranded RNA virus consisting of 10,266 nucleotides with a polyprotein made up of 3,112 amino acids (Tatineni et al. 2009). It is the type member of a new genus *Poacevirus* sharing 49% of its coat protein with *Sugarcane streak mosaic virus* (SCSMV) (Fellers et al. 2009, Tatineni et al. 2009). TriMV shares only 23.2% of its identity with WSMV (Fellers et al. 2009, Tatineni et al. 2009). Although TriMV has been identified as a mite vectored virus and should belong to the genus *Tritimovirus*, it is significantly divergent enough to be placed in a new genus (Fellers et al. 2009, Tatineni et al. 2009). Virion morphology and sequence alignments suggest that TriMV did not originate as recombinants or selection from other viral populations (Fellers et al. 2009, Tatineni et al. 2009)

TriMV has been found in Colorado, Kansas, Nebraska, Oklahoma, South Dakota, Texas, and Wyoming (Burrows et al. 2009). A survey of symptomatic plants collected in the Great Plains region in 2008 indicated that TriMV was positive in 17% of the samples (Burrows et al. 2009). The percentage of positive samples ranged from 57% in Texas to 0% in Montana and North Dakota. TriMV has been shown to impact wheat through reduction in wheat yields and volume weight, but the effect may be cultivar specific (Seifers et al. 2011). Tatineni et al. (2010) showed that TriMV is synergistic in co-infections with WSMV with TriMV exceeding the titer of WSMV late in the infection process. Greenhouse studies conducted by Byamukama et al. (2012) demonstrated that WSMV and TriMV had a negative impact on yield determinants (biomass, tillers, total nitrogen, and total carbon). It was also shown that these effects were more pronounced on the susceptible variety ‘Millennium’ when compared with the resistant variety ‘Mace’.

The host range of TriMV has been evaluated through mechanical inoculation (Seifers et al. 2009, Tatineni et al. 2010). Crops susceptible to TriMV were wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), rye (*Secale cereale* L.), and triticale (*Triticosecale rimpaui* Wittm.) while sorghum (*Sorghum bicolor* (L.) and maize (*Zea* mays L.) were not found to host the virus. Some varieties of barley and triticale were susceptible to TriMV but not WSMV. Several grass species were susceptible; including jointed goatgrass (*Aegilops cylindria* Host.), wild oat (*Avena fatua* L.), cheatgrass (*Bromus secalinus* L.), field brome (*Bromus arvensis* L.), prairie cupgrass (*Eriochloa contracta* Hitchc.), tapertip cupgrass (*Eriochloa acuminate* (J. Presl.) Kunth), and green foxtail (*Setaria viridis* L.).

Virus Transmission

WSMV transmission by WCM is non-transovarial and transtadial (Siriwetwiwat 2006). WCM begin acquiring the virus within 15-20 minutes with a transmission rate of <1% (Orlob 1966a). When WCM were given a period of 16 hours for acquisition of WSMV, they were able to transmit at a rate of 50%. The acquisition phase was similar to the time required for inoculation (Orlob 1966a). WSMV has been detected in the body fluids and gut of the WCM (Paliwal and Slykhuis 1967, Slykhuis 1967, Sinha and Paliwal 1976). Large numbers of WSMV particles were found in the midgut that remained undegraded for at least 5 days. WSMV particles were also discovered in the salivary glands of *A. tosichella* reared on virus infected plants, but the study couldn't be replicated (Paliwal 1980). These findings provide the strongest evidence to date that WSMV is circulated through various body tissues and eventually inoculated through the saliva (Paliwal 1980). Although there is evidence for this type of transmission, regurgitation cannot be ruled out.

Adult WCM must acquire WSMV as an immature in order to transmit the virus (Slykhuis 1955, del Rosario and Sill 1965, Orlob 1966a). Orlob (1966) demonstrated that adult WCM could acquire WSMV but they were unable to transmit the virus. This was determined by mechanically inoculating plants by using macerated WCM that had fed on virus infected plants only after reaching the adult stage. WCM transmit in a semi-persistent manner of transmission because the efficiency of the transmission increases with increased feeding time. However, their ability of WCMs to retain WSMV through molting is indicative of persistent viruses. Once mites have acquired the virus they can continue to transmit it for at least 7 days at room temperature, and up to 61 days when kept at 3°C (Slykhuis 1955, del Rosario and Sill 1965, Orlob 1966a).

Impact of Virus Complex and Wheat Curl Mite

Wheat plants infected with virus often show a yellow mosaic pattern of parallel discontinuous streaks (Wegulo et al. 2008). As the virus progresses, leaves become mottled yellow. Late stages of symptoms can often be confused with *Barley yellow dwarf virus* (BYDV). BYDV symptoms usually start at the tip of wheat leaves and expand towards the middle and base of the leaf. WSMV infected plants usually remain mottled yellow throughout the whole leaf (Wegulo et al. 2008). As WSMV progresses the entire leaf will become pale-yellow similar to that of BYDV, but its symptomatic origin is not from the leaf tip.

The impact of the virus on plant symptomology also depends on the plant stage when wheat is infected. Wheat infected early in its development (early tillering stage) can become stunted, discolored, and rosetted (Wegulo et al. 2008). Infections that occur after

wheat is well tillered are often not as severe. The extent of symptoms in the field can be a good indication of the severity and yield loss.

WCM feeding causes rolling and trapping of wheat leaves. Leaves infested with WCM often remain erect with the edges of the leaves rolled inward towards the mid-rib. As new leaves emerge they can become trapped in the lower leaf, forming a loop. Trapping of wheat leaves can be a good indication of mite presence in volunteer wheat (Wegulo et al. 2008). Leaf trapping can also cause grain heads to become trapped as they emerge (Somsen and Sill 1970).

The impact of viruses transmitted by WCM depends on the time of infection and the density of the mite populations (Wegulo et al. 2008). Wheat plants inoculated with viruses early in the fall are at a higher risk for yield loss (Hunger et al. 1992). Warmer fall temperatures increase the duration of activity for WCM and may increase their secondary spread. Warmer temperatures also increase virus reproduction and titer in virus-infected plants causing an increase in damage potential. Wheat plants inoculated with WSMV and held at 28°C showed symptoms at 5 days whereas plants held at 15°C required 15 days for expression (Sill and Fellows 1953).

Avirulent or non-viruliferous WCM have been shown in field studies to cause yield losses between 1-15% in artificially infested wheat (Harvey et al. 2000). In this study, plots were artificially infested with WCM from the greenhouse and averaged an estimated 8,821±3,814 mites/head resulting in a 17% yield loss when compared to naturally infested plots. Mite populations do not normally reach these levels under natural field conditions. A study conducted by Mahmood et al. (1998) indicated that randomly selected heads from a wheat field averaged around 1,203 mites/head in 1995 and 487

mites/head in 1996 (Mahmood et al. 1998). Samples in the study ranged from 3 to 2,958 mites/head. An outbreak in 1988 showed that mite populations could get as high as 18,000 mites/head (Harvey et al. 1990). These events are uncommon and localized, indicating that avirulent WCM have a limited capacity to cause significant yield loss in wheat.

Alternative Hosts for the Wheat Curl Mite

Wheat is considered to be the primary host for the wheat-mite-virus complex; however, anecdotal and observational evidence indicates that other over-summering hosts may be important for this complex. Christian and Willis (1993) established five characteristics that would be necessary for an over-summering host to have significant risk to fall planted winter wheat. First, the host must thrive in significant populations in or adjacent to fields of wheat. Second, the host should emerge prior to wheat maturing and survive until fall planting of winter wheat. Third, the host should be susceptible to one of the viruses within the wheat-mite-virus complex. Fourth, the host must support a large enough mite population for movement back to wheat. Lastly, WCM must be able to establish back on wheat with potential for secondary spread.

A literature review of over-summering hosts indicates that approximately 197 plant species have been tested for WSMV susceptibility by using mechanical inoculation with 91 species testing positive for WSMV and only 30 of those species being tested by more than one author (see Appendix). Mechanical inoculation with WSMV provides a good estimation of a potential background source for WSMV in the landscape; however, it does not indicate WCM establishment or the ability of WCM to return to fall planted

winter wheat. In contrast, field detection of WSMV has been conducted on 44 plant species with 18 testing positive for WSMV.

A review by Navia et al. (2013) reported 87 plant species as hosts for the wheat curl mite through field observations or lab experiments. We reviewed the literature on WCM and categorized host response to WCM based on Christian and Willis (1993) risk assessment characteristics. Approximately 86 plant species have been tested for WCM reproduction with the large majority of these studies being conducted as short-term (typically 7 days) exposures under controlled conditions using non-quantitative (eg. classification data. Determining a list of potential WCM hosts is inherently difficult due to the nature of the results, but approximately 71 plant species show at least some level of survival of WCM over a short-term period. These studies were also conducted at the early, vegetative stages of plant development. Research is needed to address the long-term reproductive capacity of WCM on the reproductive stages of an alternative host to gain a more accurate estimation of WCM populations under field conditions.

Field observations of WCM have been made on approximately 90 plant species with 66 species having some level of mite presence. Field collections allow for insight into WCM host interaction, natural mite populations, and the potential for mite inoculation of virus. Issues arise in these data when interpreting results between studies and years as the mite population source and host synchronization with winter wheat can vary between regions and years. As an example, Brey et al. (1998) sampled *Poa pratensis* from various locations over three years with 8 - 41% plants being infested by WCM. In addition, these studies require verification of species as other eriophyid mites can be found on grassy plants (Nault and Styer 1969).

Wheat is considered to be the primary host for the WCM with several researchers documenting it as a highly satisfactory host for WCM (Slykhuis 1955, 1956, Connin 1956a, Staples and Allington 1956, Nault and Briones 1968, Harvey et al. 2001). Skoracka et al. (2013) was the first to document reduced WCM reproduction on wheat when transferring specific sources of mites from other hosts to wheat. WCM transferred from wheat to wheat had a population growth rate (PGR) of 50 whereas WCM transferred from *Elymus repens* to wheat had only a PGR of 0.2 – 4 depending on the mite source.

Field collections of volunteer wheat have yielded highly variable results; they have primarily been based on incidence rather than host suitability for reproduction. Staples and Allington (1956) showed that volunteer wheat emerging one week prior to harvest was 100% infested within two weeks of its emergence. In addition, Connin (1956) and Gibson (1957) found an abundance of mites on random samples of volunteer wheat. In contrast, no WCM were found in volunteer wheat emerging three to four weeks after harvest (Staples and Allington 1956). Brey et al. (1998) didn't find WCM on volunteer wheat in two of the three years of the study with a 1% infestation occurring in the last year. In addition, Castiglioni and Navia (2010) found only 4 of 13 locations had volunteer wheat that was infested with WCM. The differences between these studies are likely due to the emergence date of volunteer wheat as indicated by Staples and Allington (1956), outlining one of the potential issues with interpreting field data for other potential alternative hosts.

Harvey et al. (2001) evaluated 29 grass species and found differential survival of WCM on rye (*Secale cereale* L.) depending on the mite source with mites collected from

Kansas having some level of reproduction over a 7 day period whereas Nebraska mites declined rapidly in the same time period. These same populations have been found to have distinct genetic differences (Hein et al. 2012), virus transmission (Siriwetwiwat 2006, McMechan et al. 2014, Wosula et al. 2015), and reproductive rates on virus infected plants (Siriwetwiwat 2006, McMechan 2012).

During the 1984 growing season, Shahwan and Hill (1984) tracked 11 fields that were severely impacted by WSMV and attempted to correlate disease severity with the adjacent fields' cropping and environmental history. Nine of the eleven fields were associated with late season hail resulting in the presence of pre-harvest volunteer wheat. One severely damaged wheat field was planted adjacent to corn (*Zea mays* L.*)* and the other field had been planted adjacent to foxtail millet (*Setaria italica* (L.) P. Beauv.). The study recommended that winter wheat should not be planted within 1 km of corn, foxtail millet, or volunteer wheat to avoid significant damage. Potential severity of WSMV in the presence of corn and foxtail millet combined with lack of evidence for volunteer wheat in these two fields indicates a need for further investigation of these over-summering hosts.

Corn is one of the most documented and tested plants for the wheat-mite-virus complex. Mechanical inoculation with WSMV showed that inbred, hybrid, sweet, and popcorn lines varied in the their response depending on the variety or hybrid line (McKinney 1949, Sill and Connin 1953, Meiners and McKinney 1954, Sill and Agusiobo 1955, Slykhuis 1955, Finley 1957, McKinney et al. 1966, Nault and Briones 1968). In addition, a field study by Gates (1970) showed that mites could transmit WSMV from corn to wheat until about two weeks prior to corn harvest. WCM reproductive studies

indicate that some inbred corn lines were susceptible (How 1963, Orlob 1966b, Nault and Briones 1968) whereas hybrid corn had variable results (How 1963, Connin 1956b, Orlob 1966b, Nault and Briones 1968). A study by Nault and Styer (1969) documented the seasonal population of WCM on two inbred corn lines and found that no mites were present until corn was 76 cm tall. Later in the season, Nault and Styer (1969) observed that mite colonization of the husks was very successful with the population reaching a peak in early to mid September, and mites were last observed on the silks and kernels in late September and October.

Foxtail millet is a common summer annual forage crop grown in the western Great Plains. Baltensperger (2002) indicated that foxtail millet ranks second in world production of millets; however, its primary limitation in the High Plains of the US is that it serves as a carrier for the WCM and WSMV. The susceptibility of foxtail millet to WSMV through mechanical inoculation is unclear with some authors classifying it as immune (Slykhuis 1952, 1961, Sill and Connin 1953) or susceptible (Sill and Agusiobo 1955, Slykhuis 1955, Seifers et al. 1996). Differences in the susceptibility of foxtail millet to WSMV could be attributed to the variety tested or the type of WSMV isolate used. Two short term studies have been conducted to determine WCM reproduction on foxtail millet with only a few mites being present after 7 days of exposure (Slykhuis 1955, 1956). To our knowledge, only observational (Shahwan and Hill 1984) and anecdotal evidence exists for WSMV and WCM survival on foxtail millet under field conditions.

Numerous grassy weeds have been reported as potential hosts for the wheat-mite-virus complex. Barnyard grass and green foxtail were chosen for this study because of

their over-summering presence, frequency and distribution in the Great Plains. Barnyard grass (*Echinochloa crus-galli* (L.) P. Beauv.)) is a stout, C4, summer annual weed readily invading disturbed sites, and it is commonly found in the western Great Plains (Manidool 1992). Barnyard grass has been found to be susceptible (Slykhuis 1952, 1955, Somsen and Sill 1970) and immune (Sill and Agusiobo 1955, Slykhuis and Bell 1963) to WSMV. WCM reproduction studies on barnyard grass showed that few mites were found after 7 days (Slykhuis 1955, 1956) or it has been classified as a susceptible host for WCM (Somsen and Sill 1970). We have found no quantitative evidence of WCM reproduction on barnyard grass. Christian and Willis (1993) found that WSMV presence on barnyard grass in Kansas ranged from 10% in 1988 to 56% in 1989. Only one study has documented the presence of WCM on barnyard grass under field conditions at a rate of 2.2% of plants infected by WSMV (Somsen and Sill 1970).

Green foxtail (*Setaria viridis* (L.) P. Beauv.)) is a summer annual weed that is typically a poor competitor unless in a dense stand which is commonly observed in the Great Plains. Green foxtail is susceptible to WSMV with several studies documenting severe chlorosis and stunting following inoculation (Slykhuis 1952, 1955, Finley 1957, Slykhuis and Bell 1963, Timian and Lloyd 1969, Somsen and Sill 1970). WCM reproductive studies on green foxtail have shown few mites after 7 days (Slykhuis 1955, 1956). Staples and Allington (1956) reported that 2 of 11 plants had WCM one month after infestation; however, no eggs were recovered. Field observations of WSMV on green foxtail show consistent presence of the virus (Staples and Allington 1956, Timian and Lloyd 1969). Christian and Willis (1993) found that 20-40% of plants were positive for WSMV in 1988 and 1989. Field observations of WCM presence on green foxtail

indicate that only a small percentage of plants were infested, but these contained only a few mites (Connin 1956a, Staples and Allington 1956, Timian and Lloyd 1969, Somsen and Sill 1970).

Management of Wheat Curl Mite and Wheat Virus Complex

Pre-harvest volunteer wheat is one of the most important components for the wheat-mite-virus complex as it acts as a source for mites and virus to survive on between harvest in early summer and fall planting of winter wheat. The emergence of volunteer wheat prior to harvest occurs predominantly as a result of hail occurring during wheat head development causing grain to be shattered from the wheat head. With adequate moisture these seeds can germinate prior to the crop reaching full maturity allowing wheat curl mites to move from maturing wheat to the volunteer wheat. If this volunteer wheat is not controlled, mites will move from it onto newly planted wheat in surrounding fields during the fall causing significant yield losses.

Misunderstanding on the risk of volunteer wheat can occur due to differences in the timing of its emergence. Volunteer wheat emerging after harvest (post-harvest volunteer) results in a period without a primary host for the mites to survive on, and thus, poses little risk to adjacent fall planted winter wheat fields. In contrast, the importance of pre-harvest volunteer wheat as a source for mite and virus reinforces the need for detailed information on the pre-harvest period or timeframe during the development stage at which winter wheat could germinate.

The germinability of wheat seeds prior to harvest has been an important topic in winter wheat breeding as a means of accelerating breeding programs and genetics studies (Robertson and Curtis 1967). As a result, a large research effort has been made to better

understand the germinability of immature winter wheat. Studies identified numerous factors such as temperature, drying after collection, handling, variety, and location within the wheat head that can influence the ability of winter wheat seed to germinate prior to harvest (Nutman 1941, Nosatovsky 1957, Aginyan 1958, Kalinin 1959, Robertson and Curtis 1967, Balla 1979).

In general, without any post collection modifications, winter wheat is capable of germinating approximately 9-14 days after pollination with adequate long-term available moisture (Nutman 1941, Nosatovsky 1957, Aginyan 1958, Kalinin 1959, Abramova 1964, Robertson and Curtis 1967, Balla 1979). Temperature is an important component in these evaluations as non-ripened wheat seeds appeared dormant at 20-35°C, but germinated at 10-15°C (Atterberg 1907, Ching and Foote 1961, George 1967). In addition, temperature was found to have a significant affect on the total germination with a higher percentage of seeds germinating at 12°C (80%) compared to 20°C (49%) (Balla 1979).

Drying or desiccating immature wheat heads prior to inducing germination can significantly reduce the number of days from pollination to first germination as well as the percentage of wheat seeds that germinate (Balla 1979). Balla (1979) found that wheat was capable of germinating at 6-8 days after pollination with 12 weeks of drying whereas wheat was unable to germination until 14 days after pollination without any drying.

Post collection handling of immature wheat seeds has been shown to increase their germination potential. Removal of the outer-pericarp from unripened wheat seeds increased their germination (Wellington 1956a, Gordon 1970, Radley 1979, Mitchell et al. 1980). It is hypothesized that the inhibitory effect of the outer-pericarp is due to its

mechanical strength (Wellington 1956b) or the restriction of gas exchange between the embryo and the environment (Radley 1979).

Detailed studies by Wellington (1956a) and Hardesty and Elliott (1956) found that seed location within a wheat head could have a significant impact on its germination, with limited germination occurring at the base of the head unless desiccated prior to germination. This may be in part due to the sequence of pollen shed and fertilization within a wheat head. Pollination first occurs in the middle of the head followed by the top the head, and lastly the base (Wellington 1956a). Percival (1922) observed similar results with a 2-4 day delay in anthesis of basal spiklets.

Seed dormancy or pre-harvest tolerance to sprouting has been tightly linked to seed color, and as a result, cultivars can vary significantly in tolerance to germination prior to harvest. Wellington (1956a) observed a rapid increase in germination of white wheat (88%) at 5-8 weeks after pollination whereas red wheat germinated only at a 7% rate. Nyachiro et al. (2002) tested 10 spring wheat varieties with varying degrees of dormancy at varying temperatures and found that low temperatures could break seed dormancy in tolerant varieties. Mares (1993) tested eight hard white wheat cultivars that varied significantly in their germination at and following harvest. Five hard red winter wheat varieties were evaluated for germination of immature kernels by Robertson and Curtis (1967) in an article brief; however, the authors indicated that there were no differences between the varieties with average germinations occurring within 15 days of pollination. Although a significant amount of work has been conducted, there is a lack of information on germination of grain in early stages of head development and a

comparison of early season germination of grain in varieties based on sprouting tolerance scores.

Chemical Control

Use of acaricides for mite control is limited. Kantack and Knutson (1958) tested over 30 different insecticides on wheat curl mites including many systemic insecticides but had little control without damaging plant health. The high rate of mite reproduction allows populations to respond quickly following an application, if any individuals survive. Mite transmission of plant viruses also limits the effectiveness of acaricides because viruses transmitted by the mites will continue to cause economic damage even if the mites are no longer present. Most importantly, the secluded location of WCM limits effective acaricides to those that are systemic within the plant. Harvey et al. (1979) tested the efficacy of systemic carbofuran (FMC Corporation, Philadelphia, Pennsylvania) and disulfoton (Chemagro, Kansas City Missouri) applied to the soil at planting time. Carbofuran controlled mites during the fall, but it lost its efficacy by spring. However; it was shown to increase wheat yields. Carbofuran is one of the most toxic carbamate pesticides, marketed under the name Furadan. It has been recently cancelled due to its high dietary, worker and ecological risks ("Carbofuran Cancellation Process | Pesticides | US EPA" 2015).

Cultural Control

The most effective management tactic for the control of WCM and its virus complex is the control of pre-harvest volunteer wheat. Controlling volunteer wheat using

herbicides can be an effective management tactic. Herbicides such as paraquat (Zeneca Ag Products, Wilmington, Delware) and glyphosate (Monsanto, St. Louis, Missouri) can be used to destroy the "green bridge" host, diminishing the ability of mites to survive through the summer (Jiang et al. 2005). Paraquat acted rapidly to reduce mite populations, with effects occurring within a few days. Glyphosate was slower than paraquat, but it may be a better option for producers because of its low toxicity to other non-targets (Jiang et al. 2005). Thomas and Hein (2003) indicated that mite movement peaked seven days after a high rate glyphosate treatment. Tillage is also an effective means of controlling volunteer wheat, but it may be less practical in areas where water is limited (Thomas et al. 2004). In dry years, wheat yields in no-tillage systems were 72% to 100% higher than fall chisel plowing and conventional tillage, respectively (Bouzza 1990). Tillage was found to be more effective in controlling mite populations on volunteer wheat than glyphosate (Jiang et al. 2005). Controlling perennial and native grasses is not warranted because they are not likely to allow mite populations to build up in high enough numbers to cause widespread damage (Staples and Allington 1956).

Another method of managing the wheat curl mite and the viruses it transmits is adjusting the planting date of winter wheat. The earlier wheat is planted in the fall the more likely it is to become infested with mites (Wegulo et al. 2008). Planting winter wheat later reduces the time that mites have to build up and reduces time for virus replication. In addition, it reduces the chance for secondary spread of mites within a field. Temperature is an important consideration when planting winter wheat. If temperatures remain warm in the fall and through the winter the wheat may become infested regardless (Staples and Allington 1956). If wheat is planted too late in the fall then yields may be

lower due to agronomic concerns. Hunger et al. (1992) found that planting late in the fall was the best method to avoid WSMV; however, planting late made the wheat in the spring more susceptible to WSMV because of its reduced growth.

Host Plant Resistance

Host plant resistance has been developed against the WCM and the viruses it vectors. Wheat resistance to WCMs has been accomplished through reduced reproduction and colonization by the WCM. TAM 107 developed from rye was the first commercial wheat variety with resistance to WCM colonization (Sebesta and Wood 1978, Thomas and Conner 1986). TAM 107 was released in the late-1980's and was widely grown throughout western Kansas and surrounding states. The variety significantly lowered mite populations in wheat spikes and had a lower incidence of WSMV than any other variety at the time (Harvey et al. 1998). TAM 107 was critical in preventing WCM build up in volunteer wheat. Widespread popularity of TAM 107 resulted in strains of WCM that were adapted to the mite resistant wheat varieties (Harvey et al. 1995, Harvey et al. 1997).

Host plant resistance has also focused on resistance to WSMV. There are currently two known sources of resistance that have been transferred to wheat (Lu et al. 2011). The *Wsm1* gene was transferred from intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth and D. R. Dewey) and confers resistance to WSMV (Wells et al. 1973, 1982, Friebe et al. 1991, Gill et al. 1995). The *Wsm2* gene, was identified in CO960293-2 wheat germplasm and incorporated into 'RonL' (Seifers et al. 2007) and 'Snowmass' (Haley et al. 2002). The exact origin of CO960293-2 is unknown

because both parents exhibited resistance in greenhouse and growth chamber conditions (Haley et al. 2002, Seifers et al. 2006). Both sources of resistance are temperature sensitive, becoming ineffective at temperatures above 24°C (Seifers et al. 2006). These lines are considered to be valuable sources of resistance in areas where temperatures are cool following planting in the fall (Seifers et al. 2006).

Mace was released in 2007 as a hard red winter wheat variety adapted to rain-fed and irrigated wheat in Nebraska and areas in the northern Great Plains (Graybosch et al. 2009). WSMV resistance in Mace is conditioned by the *Wsm*1 gene. Divis et al. (2006) concluded that there were no negative effects associated with the *Wsm*1 gene. Graybosch et al. (2009) tested Mace for its ability to compete with other wheat varieties. Under virus free conditions Mace was comparable to Millennium. Under natural virus conditions Mace yielded significantly more than Millennium and twice the yield of a highly susceptible variety Tomahawk. Mace is not effective against viruses transmitted by the WCM at temperatures above 25°C (Graybosch et al. 2009). Although Mace was released for resistance to WSMV, it has also shown resistance to TriMV (Tatineni et al. 2010, Byamukama et al. 2012).

Risk from the wheat-mite-virus complex begins with presence of suitable host prior to wheat harvest. In many cases, this suitable host is volunteer wheat as a result of pre-harvest hail; however, information is needed on the window time in which germination can occur during wheat head development. In addition, information is needed on the potential of other secondary hosts to support mites and their relative risk to fall planted winter wheat. A better understanding of these risk factors will help producers

and consultants prioritize scouting and management to reduce the likelihood of significant losses from this disease complex.

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Chapter 2

Long-term Reproductive Capability of the Wheat Curl Mite on Alternative Hosts and Reproductive Rates when Returning to Wheat

Introduction

The wheat-mite-virus complex is one of the primary yield limiting diseases in winter wheat (*Triticum aestivum* L.) in the western Great Plains. In 2015, a survey of wheat diseases in Kansas indicated that approximately 11 million bushels of winter wheat were lost as a result of this disease complex (Appel et al. 2015). This complex consists of three viruses (Wheat streak mosaic virus (WSMV), Triticum mosaic virus (TriMV), and Wheat mosaic virus (WMoV)) that are transmitted by the wheat curl mite (WCM; *Aceria tosichella* Keifer).

In the majority of cases, severe yield losses from this complex are localized to areas where volunteer wheat had emerged prior to wheat harvest (pre-harvest volunteer wheat) as a result of pre-harvest hail. This allows mites to move directly from the maturing wheat crop to the volunteer wheat. Once established, WCM populations can build rapidly during the summer months, as long as the volunteer wheat remains viable. In the fall, wheat planted in adjacent fields will become infested with WCM moving from pre-harvest volunteer wheat. Controlling this pre-harvest volunteer wheat is an essential management strategy for the wheat-mite-virus complex; however, situations have occurred in the past where significant yield losses due to virus infection occurred, despite management tactics that were not conducive for the presence of pre-harvest volunteer wheat (Christian and Willis 1993). Yield losses from this complex in the absence of pre-harvest volunteer wheat indicates a need to better understand the capacity for other potential green bridge hosts to support wheat curl mites.

A review by Navia et al. (2013) reported 87 grass species as hosts for the wheat curl mite through field surveys and/or lab reproductive studies. Most reproductive studies have determined short-term survival (e.g. 7 days) under controlled conditions, and they

have used non-quantitative classification methods (e.g. good/fair/poor, resistant/susceptible) to classify host potential. In addition, these studies were conducted only at early, vegetative stages of plant development. Therefore, determining a list of potential WCM hosts from historical literature is inherently difficult; however, approximately 71 plant species show at least some potential as a WCM host from reproductive studies.

Further confusion of past literature on the host range of WCM originates from differences in reproductive ability of distinct mite populations. In the mid-1990's, Harvey et al. (1995, 1999) showed differential survival to several mite-resistant genes in wheat for five mite populations collected across the Great Plains from 'Nebraska' (NE), 'Kansas' (KS), 'South Dakota' (SD), 'Texas' (TX), and 'Montana' (MT). These populations have been classified into two groups based on distinct genetic differences (Type 1: SD, KS, TX, MT and Type 2NE) (Hein et al. 2012). In addition, differences between these types have been found for virus transmission (Seifers et al. 2002, McMechan et al. 2014, Wosula et al. 2015) and reproductive rates on virus infected plants (Siriwetwiwat 2006, McMechan 2012).

Harvey et al. (2001) tested the short-term (7 day) reproductive capacity of KS (Type 1) and NE (Type 2) mites on 28 grass species. Besides the primary host wheat, only secondary hosts jointed goatgrass (*Aegilops cylindrical* Host) and rye (*Secale cereal* L.) were considered hosts for WCM. In addition, only KS (Type 1) mites showed reproductive levels high enough to consider rye as a host. Differential reproduction of mites on rye is likely due to the widespread use of a mite-resistant gene from rye in winter wheat varieties 'TAM 107' and 'PI 47577' (Harvey et al. 1995, 1999, 2001).

Other hosts, such as green foxtail (*Setaria viridis* (L.) P. Beauv.), pearl millet (*Pennistem glaucum* (L.) R. Br.), cheatgrass (*Bromus tectorum* L.), barley (*Hordeum vulgare* L.), tall wheatgrass (*Agropyron elongatum* (Host.) Beauv.), sandbur (*Cenchris pauciflorus* Benth) sorghum (*Sorghum bicolor* (L.) Moench), and corn (*Zea mays* L.) retained mite presence after 7 days, but these were not considered hosts because the mean number of WCM was not statistically greater than the infestation level (Harvey et al. 2001).

Skoracka et al. (2013) tested the assumption that the WCM is a single, highly polyphagous species in Poland. They identified several genetically distinct (mtDNA) lineages of WCM from hosts in Poland, and these populations revealed significant differences in capacity for host colonization ranging from highly polyphagous to more host-specific. Therefore, evaluating the effective host range for distinct mite populations from North America will be critical for accurately determining the host range of the WCM.

Wheat is considered to be the primary host for the WCM (Slykhuis 1955, 1956, Connin 1956a, Staples and Allington 1956, Nault and Briones 1968, Harvey et al. 2001). Short-term reproductive studies often utilize winter wheat as a positive control when comparing other potential hosts for the WCM. Harvey et al. (2001) infested wheat plants with 10 mites and found similar buildup (ca. 40 mites per plant) after 7 days for both Kansas (Type 1KS) and Nebraska (Type 2NE) WCM populations. Longer-term reproductive studies by Siriwetwiwat (2006) found that WCM increased from 10 to approximately 1000 in 21 days.

During the 1979/80 growing season, Shahwan and Hill (1984) tracked 11 fields that were severely impacted by WSMV and attempted to correlate disease severity with

the adjacent fields cropping history. One field was planted adjacent to foxtail millet the previous fall. Very little is known about the reproductive potential of WCM on foxtail millet. Two short term studies to determine WCM reproduction on foxtail millet found no WCM buildup after 7 days (Slykhuis 1955, 1956).

Several summer annual weeds have been listed as potential hosts for the WCM, and these weeds are of particular concern because their occurrence overlaps completely with the green bridge period. Barnyard grass is a summer annual weed that readily invades disturbed sites, and it is commonly found in the western Great Plains (Manidool 1992). Non-quantitative WCM reproduction studies on barnyard grass showed limited mite presence after 7 days (Slykhuis 1955, 1956). However, Somsen and Sill (1970) classified barnyard grass as, "a good host for mites and mosaic [virus] in the greenhouse'. However, there is no known evidence of WCM reproduction on barnyard grass in the literature.

Another summer annual, green foxtail, is typically a poor competitor unless in a dense stand, but it is commonly observed in the Great Plains region (Zimdahl 2007). WCM reproductive studies on green foxtail have shown few mites after 7 days (Slykhuis 1955, 1956). A short-term quantitative study by Harvey et al. (2001) found that 9.4±4.6 and 0.4±0.5 for Kansas (Type 1KS) and Nebraska (Type 2NE) mites, respectively, were present after 7 days indicating that green foxtail is a marginal host at best. Staples and Allington (1956) infested green foxtail with up to 16 mites per plant with only a few mites present one month after infestation. Connin (1956) infested seedlings of green foxtail with an interdeterminate number of mites and noted that mites were never observed more than four days after infestation.

Jointed goatgrass is a winter annual weed introduced into North America through contaminated wheat seed (McGregor 1987, Donald and Alex 1991). Due to its temporal overlap with winter wheat, it is not considered important as a green bridge host for mites or virus. However, jointed goatgrass is genetically related to wheat with both having a D chromosome (Maan 1976), and natural crossing between jointed goatgrass and wheat has occurred under field conditions (Johnston and Parker 1929). Mite reproductive studies indicate that jointed goatgrass is a fair-good (Connin 1956) and susceptible host (Somsen and Sill 1970). Harvey et al. (2001) also reported mite counts at 7 days were not significantly different that wheat for both Kansas (Type 1) and Nebraska (Type 2) mites.

A recent study by Skoracka et al. (2013) found that WCM occurring on different hosts in Poland exhibited differential reproductive rates when placed on wheat. Wheat-to-wheat transfers exhibited mite population growth rates of 50 whereas WCM transferred from quackgrass (*Elymus repens* L. Gould) to wheat had a growth rate of 0.2 – 4, depending on the mite source. No potential WCM green bridge hosts in the United States have been tested for their ability to return to wheat. Conducting long-term reproductive studies provides an opportunity to evaluate host adaptation when returning to wheat.

The historical literature on reproductive potential of green-bridge hosts chosen for this study is substantial; however, it lacks critical information necessary to properly evaluate host potential to support mites under field conditions. Long-term reproductive studies that determine survival and reproduction throughout the green bridge period will provide insights into the risk potential of these hosts as sources of mites. The objective of this study was to evaluate the long-term reproductive potential of four wheat curl mite colonies with differing genetic backgrounds on five alternative hosts as well as mite

reproductive potential when returning to wheat. The study focuses on five potential hosts: winter wheat, foxtail millet (*Setaria italic* (L.) P. Beauv.), barnyard grass (*Echinochloa crus-galli* (L.) P. Beauv.), green foxtail, and jointed goatgrass. These hosts were chosen because they have varied anecdotal and experimental evidence for mite reproduction and mite presence under field conditions.

Materials and Methods

Four WCM populations were used in this study. Nebraska (Type 2) mites were collected and maintained as a lab colony since the mid-1990s. This is the same population used to determine differential survival, virus transmission, and host range studies in the mid-1990's through early 2000's (Harvey et al. 1995, 1999, 2001, Seifers et al. 2002, McMechan et al. 2014, Wosula et al. 2015). Two mite populations designated as 'Type 1' and 'Type 2' were collected from four major wheat-producing counties in western Nebraska during the summer of 2011. Naturally infested wheat tillers were placed in cone-tainers (Stuewe & Sons, Inc., Tangent, Oregon, USA) with 14-day old 'Millennium' wheat plants to establish multiple mite colonies. Eggs were transferred from established colonies three to four weeks after infestation of tillers. Clonal mite populations were established from eggs. These populations were genetically characterized based on polymerase chain reaction and restriction digestion of ribosomal internal transcribed spacer region (Hein et al. 2012). Several clonal populations of each of the two types were then merged to form the Type 1 and Type 2 populations. The fourth WCM population was collected during the fall of 2014 from foxtail millet plots. To establish this population, 3-5 mites were transferred to wheat plants in each of nine cone-tianers, and mites were allowed to build up over a period of three weeks. These populations were genetically tested as described above and all cones with mites testing as Type 1 were combined. This population was designated as Type 1F.

All WCM populations were maintained on 'Millennium' wheat in 15-cm-diameter pots with cages. Cages were made of a 15-cm-diameter plastic cylinder with two 8-cm-diameter ventilation holes on opposite sides and the top covered with Nitex® screen (225 x 326 mesh) (BioQuip Products Inc. Compoton, CA). These avirulent wheat

curl mite populations were kept in separate growth chambers with a 14:10 (L:D) cycle maintained at approximately 27°C, and 50 mites were transferred onto new wheat plants every two to three weeks.

Millennium winter wheat, 'Golden German' foxtail millet, barnyard grass, green foxtail, and jointed goatgrass were seeded in pots and caged immediately after planting. Barnyard grass and green foxtail seed was obtained from field sites in east central Nebraska. Jointed goatgrass seed was collected in western Nebraska. Hosts were planted at different times to synchronize the plant development stage at the time of WCM infestation. Barnyard grass was planted 21 days before infestation, and the remaining hosts were planted 10-14 days prior to infestation. To infest plants, infested wheat was inspected under a stereo-microscope at 30-40X, and 10 mites were placed onto a black insect mounting triangle (10 mm x 4 mm) using a human eyelash attached to a wooden dowel. The triangle was then placed in the leaf axil of each of seven test plants within a pot. Only adult mites exhibiting normal mite movement were transferred. After infestation, pots remained in the lab for a period of 10-15 hours to allow mites to settle on the plants. Pots were then transferred to a growth chamber with 14:10 (L:D) cycle maintained at 24-27°C.

One plant was randomly harvested from each pot at 7-day intervals up to 42 days after infestation. Sampled plants were cut at soil level, placed in a Zip-lock bag, and stored at 4°C. The development stage was recorded for each plant, and mites were counted using a stereo microscope (magnification ca. 30-40X). During this time period, reproductive development stages occurred for foxtail millet, green foxtail, and barnyard grass. When they occurred at sampling time, heads from these hosts were placed and

gently pressed onto high definition tape attached to black cardstock with double sided tape (Harvey and Martin 1988). These heads were placed in covered plastic boxes for a minimum of one month to allow the heads to dry and mites to abandon the heads. Heads were removed from the tape, a grid was placed under the tape, and mites on the tape were counted. Wheat plants were only sampled up to 21 days after infestation because extreme population buildup makes accurate population estimation difficult (Siriwetwiwat 2006). Due to the number of treatments and time requirements for counting, this experiment was divided into three separate studies. Wheat, barnyard grass, green foxtail, foxtail millet, and jointed goatrass were used in all studies; however, the number of replications and collection days for these treatments varied between studies. Study 1 compared Type 1 and 2 mites across four runs with 11 replications for all hosts except green foxtail and jointed goatgrass with 8 replications. Study 2 consisted of one run of the experiment to test Type 1, Type 2, and field collected Type 1F mites with three replications for each host. In addition, plants were only collected on day 7, 21, and 35 after infestation. Study 3 consisted of two separate runs to evaluate Nebraska mites designated at 'Type 2NE' with seven replications for all treatment combinations except for jointed goatgrass with four replications.

After 42 days, ten mites were transferred back to wheat from each host with adequate mite populations using the same methods as previously described. Four wheat plants per pot were infested. Wheat plants were harvested in the same manner as previously described with collections occurring every 7 days up to 21 days after infestation for studies 1 and 3. For study 2, plants were only counted at 14-days post-infestation.

Mite counts were analyzed using a type 1 test for fixed effects in PROC GLIMMIX (version 9.22; SAS Institute 2008) with a repeated measures analysis. Studentized residuals indicated that the data were not normally distributed. Variances increased geometrically as a function of the mean indicating a negative binomial distribution. Due to the negative binomial distribution, the subsequent estimations are most appropriate for a mixed model method (Gbur *et al.* 2012). Data were transformed to natural log prior to analysis.

An analysis of variance was run to determine the significance of main effects and interactions. These effects were partitioned over day into linear and quadratic portions to determine which fixed effects remained in prediction models. Non-significant effects were removed from the model. Models with a significant quadratic effect were evaluated for significance for each treatment combination through the solution for fixed effects. Non-significant quadratic parameters were removed from treatment combinations. The analysis of variance was run again containing only the significant effects. Regression equations were obtained from the solution for fixed effects and parameter comparisons were made between treatments by using pairwise contrast statements. In a generalized linear mixed model, R-squares are understood as undefined. However, the correlation between observed values and the values predicted by the regression equations resulting from the analysis above were used to estimate the fit of the equations (PROC CORR; version 9.22; SAS Institute 2008).

Results

Study 1: Type 1 vs. Type 2

An analysis of variance type I test for fixed effects (Table 2.1) indicated that there were no significant differences between colonies. Significant differences occurred between hosts with greatest mean mite populations occurring on wheat (4323) followed by jointed goatgrass (434), barnyard grass (67), green foxtail (5) and foxtail millet (1). The interaction between colony and host was also significant due to greater mean populations of Type 1 mites (634; $t_{88} = 1.97$; $P = 0.0522$) compared to Type 2 (296) mites on jointed goatgrass. In contrast for barnyard grass, Type 2 (200; $t_{88} = 6.53$; $P < .0001$) mites had greater mean mite populations compared to Type 1 (23) mites.

An analysis of regression equations showed differences in the intercepts of equations (Table 2.2) with Type 1 mites on wheat having a greater intercept when compared to barnyard grass and green foxtail whereas no differences occurred for foxtail millet. The lack of intercept differences between Type 1 mites on wheat and foxtail millet is a result of significant decline in mites on foxtail millet after day 7, resulting in a higher intercept (Fig. 2.1). Jointed goatgrass had a lower intercept that was approaching significance when compared to wheat. For Type 2 mites, similar results occurred between wheat and the other alternate hosts with statistically lower intercepts for barnyard grass, green foxtail, and foxtail millet. Unlike Type 1, differences occurred between the foxtail millet and wheat intercepts for Type 2 mites because of a reduction of mite presence on foxtail millet within 7 days of infestation (Fig. 2.2), resulting in a lower intercept compared to Type 1 mites on foxtail millet. No differences in intercepts occurred for Type 2 mites when comparing wheat and jointed goatgrass.

The linear effect (Table 2.1) of day was significant, indicating that mite

populations changed over time. There was no significant interaction between day and colony because the average response of all hosts did not differ between colonies over time. A significant day by host interaction occurred as a result of high reproductive rates for both mite types on wheat, jointed goatgrass and barnyard grass (Table 2.1) whereas a lack of reproduction was observed for foxtail millet. The interaction between day, colony, and host was also significant due to differences in the reproductive rates for Type 1 and Type 2 mites on jointed goatgrass and barnyard grass (Table 2.2).

Significant positive linear slopes were observed for both mite types across all hosts with the exception of foxtail millet, which showed a significant decline for both mite types following infestation. A comparison of linear slopes (Table 2.2) showed the relative rate of increase for mites varied considerably between hosts. Type 1 and 2 mites reproduced at a greater rate of increase on wheat when compared to green foxtail or foxtail millet. In contrast, Type 2 mites had a similar rate of increase on barnyard grass when compared to wheat. However, Type 2 mites on barnyard grass exhibited a significant negative quadratic effect ($t_{321} = -3.44$; $P = 0.0004$) whereas no significant quadratic effect occurred for wheat, making the interpretation of linear parameters less apparent. Jointed goatgrass was the only host that had a greater reproductive rate than wheat for Type 1 mites. However, a significant negative quadratic effect was observed for Type 1 mites on jointed goatgrass ($t_{321} = -5.76$; $P < .0001$), while no significant quadratic effect occurred on wheat ($t_{321} = 0.36$; $P = 0.7136$), making it difficult to properly assess differences in linear parameters. Differences in reproduction between wheat and jointed goatgrass are more apparent using day contrast comparisons of equations. Contrasts indicate that wheat produced more mites at day 7 ($t_{321} = 22.49$; P

<.0001) with an increasingly greater mite population over jointed goatgrass as indicated by a larger F-value at day 21 (t_{321} = 74.04; P <.0001). Significant quadratic effects were also observed for Type 1 (t_{321} = -5.76; P <.0001) and Type 2 (t_{321} = -3.59; P = 0.0007) mites on jointed goatgrass and Type 2 mites on barnyard grass (t_{321} = -3.44; P = 0.0004). No significant quadratics were observed for any other mite type and host combinations. Correlations between predicted and observed values ranged from 0.65 to 0.98 for Type 1 and 0.74 to 0.94 for Type 2 indicating that equations (Table 2.3) were a good representation for observed values.

Study 2: Type 1 vs. Type 2 vs. Type 1F

An analysis of variance for type I test for fixed effects (Table 2.4) showed significant differences between hosts with greatest mean mite populations occurring on wheat (1881) followed by jointed goatgrass (818), barnyard grass (141), green foxtail (3), and foxtail millet (3). However, an interaction between mite type and host occurred due to a greater mean number of Type 2 (401) mites on barnyard grass, compared to Type 1 (29) and Type 1F (22). In contrast, similar mean mites occurred on wheat for all colonies with 1869, 1906, and 1804 mean mite populations for Type 1, Type 2, and Type 1F, respectively. Colonies did not differ from one another due to their differential survival on hosts as indicated in the interaction between colony and host.

Contrasts comparing intercepts (Table 2.5) of all mite types on wheat showed no differences. Within Type 1F (Fig. 3.3), a comparison of wheat with other hosts showed significant differences in intercept for green foxtail and barnyard grass whereas no differences occurred for jointed goatgrass. Within barnyard grass, Type 1F mites had

significantly lower intercepts compared to Type 2 with no differences when compared with Type 1. Intercept comparisons of Type1F to other mite types showed no differences in jointed goatgrass or green foxtail whereas Type 2 intercepts were greater than Type 1F on barnyard grass. Significant differences occurred between all three types on foxtail millet with the greatest intercept occurring for Type 1F, followed by Type 1, and Type 2.

Linear parameter comparisons showed no differences in day due to a balance between reproduction and declining mite numbers across hosts and mite types. Day by host interactions were significant due to consistently high rates of reproduction for mite colonies on wheat whereas mite populations declined for all colonies on foxtail millet. No significant interaction occurred between day, host and colony. Contrasts comparing linear parameters (Table 2.6) for hosts and colonies show that wheat had a greater rate of mite increase when compared to any other hosts with the exception of Type 1F mites on barnyard grass.

Quadratic parameters showed a significant interaction between day and host, as well as day, host and colony. The three-way interaction was due to a significant negative quadratic effect for Type 1 (t_{59} = -2.30; P =0.0247), Type 2 (t_{59} = -2.79; P =0.0070) and Type1F (t_{59} = -2.29; P =0.0255) on jointed goatgrass as well as Type 1F on barnyard grass (t_{59} = -2.97; P = 0.0042). Although linear parameters between wheat and barnyard grass for Type 1F were not significant, the combination of a lower intercept and a significant negative quadratic for barnyard grass resulted in significant differences in mites between hosts at day 7 ($t_{1,59}$ = 5.35; P = 0.0239) and day 21($t_{1,59}$ = 19.90; P <.0001). All other quadratic parameters for mite type and host combinations were not significant. Correlations between the predicted and observed values for Type1F mites ranged from

0.70 for green foxtail to 0.98 for barnyard grass indicating solid predictions.

Study 3: Type 2NE

An analysis of variance type I test for fixed effects (Table 2.7) showed that the effect of host was highly significant with the greatest mean mite populations occurring on wheat (2149) followed by jointed goatgrass (1335), barnyardgrass (457), green foxtail (6), and foxtail millet (2). Regression equations showed that the intercept parameter differed between hosts. Declining mite populations in foxtail millet resulted in a high intercept value that was comparable to wheat, jointed goatgrass, and barnyard grass. Graphical representation of predicted equations (Fig. 3.4) indicates that green foxtail appears to have a different intercept; however, large variation in response over time resulted in a lack of significant differences between other hosts.

Day was also significant indicating that mite populations changed over time. A significant interaction occurred between day and host with wheat, jointed goatgrass, and barnyard grass showing a significant increase in mite populations over time. In contrast, a marginal increase occurred for green foxtail, and mite populations declined on foxtail millet. Intercept contrasts (Table 2.8) between hosts showed no significant differences. Contrasts comparing linear parameters (Table 2.8) show that wheat had a significantly higher linear slope than green foxtail or foxtail millet. Slopes were not significantly different when wheat was compared with jointed goatgrass or barynardgrass. The lack of differences with wheat likely resulted from the significant quadratic effect for jointed goatgrass ($t_{124} = -1.97$; $P = 0.0567$) and barnyardgrass ($t_{124} = -2.34$; $P = 0.0210$). Contrasts comparing wheat to jointed goatgrass showed no significant differences at day 7 ($F_{1,124} =$

1.73; P = 0.1914) whereas mean mite populations were significantly different at day 21 ($F_{1,124}$ = 7.67; P = 0.0065) indicating that the combination of these parameters yielded significant differences over time. Similar results occurred for barnyardgrass with increasing differences with wheat from day 7 ($F_{1,124}$ = 3.56; P = 0.0615) to day 21 ($F_{1,124}$ = 10.24; P = 0.0017). A good correlation was observed between predicted equations (Table 2.2) and observed values with the exception of green foxtail at a correlation of 0.19 due to variations in mite presence over time.

Reestablishment on Wheat

WCM were successfully transferred from wheat, jointed goatgrass and barnyard grass back to wheat plants for each of the three studies. No transfers were made from foxtail millet or green foxtail due to low mite populations. An analysis of type I test for fixed effects of Study 1: Type 1 and Type 2 mites (Table 2.9) indicated that there were significant differences between colonies with more mites occurring for Type 2 (551) than Type 1 (393). Differences also occurred between hosts due to significantly lower populations on barnyardgrass (353) compared to jointed goatgrass (549) or wheat (519). There was no significant interaction between colony and host.

An analysis of regression equations showed that intercepts (Table 2.10) did not differ between colonies and hosts. However, the linear effect of day was highly significant indicating that mite populations changed over time. The interaction between day and colony was significant as well as host and day due to lower reproduction on jointed goatgrass. However, there was a significant interaction between day, host and colony. Linear parameter contrasts (Table 2.10) show that this interaction was due to

lower reproductive rates on wheat for Type 1 mites from barnyard grass compared to Type 2 mites whereas no differences occurred between mites types from wheat or jointed goatgrass. Type 1 mites from barnyard grass produced lower slopes than any other colony and host treatment combination (Fig. 2.5). Equations from solutions for fixed effects (Table 2.11) showed a strong positive linear relationship of mite populations on wheat over time (correlation range 0.95 to 0.97).

Mite transfers back to wheat in study 2 were only evaluated at day 14; therefore, a Type III fixed effects analysis of variance was used to evaluate treatments. There were no differences between colonies ($F_{2,12} = 1.46$; $P = 0.2718$); however, mite populations varied by host ($F_{2,12} = 7.67$; $P = 0.0525$) due to significantly lower mean mite populations on barnyardgrass (641; $F_{1,12} = 7.28$; $P = 0.0194$) compared to wheat (806) and jointed goatgrass (794). The interaction between colony and host was approaching significance ($F_{4,12} = 7.67$; $P = 0.0953$) due to lower mean mite populations on barnyard grass for Type 1 mites (457) whereas mean mite populations ranged from 727 to 855 for all other mite type and host combinations.

An analysis of variance type I test for fixed effects for study 3 using the Type 2NE colony (Table 2.12) showed no significant differences between hosts. Regression analysis showed that there was a significant linear effect of sampling day indicating that mite populations changed over time. No interactions occurred between hosts and days or the quadratic effects of days or host and day. Equations generated from the solution for fixed effects show strong positive linear slopes for all treatment combinations (Table 2.11). Correlations were strong for all equations ranging from 0.95 to 0.97 indicating a good fit between predicted equations and observations.

Discussion

Wheat consistently showed the greatest potential for mite reproduction across all mite types and populations used in this study, further supporting its status as the primary host for the wheat curl mite. For alternative hosts, the linear slope value provided a strong estimation of the reproductive potential and suitability of the host for wheat curl mites. Quadratic parameters provide additional evidence on the holding capacity and potential density of mite populations on alternative hosts, an important characteristic for mite spread (Thomas and Hein 2003). In addition, these long-term studies reduce the carry-over effects from the previous host (wheat), allowing mites to go through multiple generations to gain a better estimation of host suitability for the WCM.

Jointed goatgrass, a winter annual weed with a life cycle similar to winter wheat, was considered a good host for WCM with strong positive linear slopes for both mite types in this study. Although linear slopes were positive for both mite types on jointed goatgrass, Type 1 mites showed consistently greater reproduction than Type 2 mites. Harvey et al. (2001) previously reported no differences in mite numbers for Kansas (Type 1) mites compared Nebraska (Type 2) mites at 7-days after infestation. In addition, jointed goatgrass is significantly different than wheat in its ability support mites and this response varies with mite type. In addition, the differential reproductive rates of mite types on jointed goatgrass was consistent regardless of source for each mite type, with Type 1F mites having similar reproductive rates to Type 1 mites, and Nebraska (Type 2) mites having a similar reproductive potential as Type 2 mites. Quadratic effects provide an indication that mite populations in jointed goatgrass became saturated and began to level off at populations below those for vegetative wheat. Previous research by Siriwetwiwat (2006) showed that WCM could exceed 20,000 per plant after 28 days with

an initial infestation of 10 mites per plant. Population limitations on jointed goatgrass may be due to thinner leaves relative to wheat.

Barnyard grass was the only summer annual host with a WCM reproductive rate similar to jointed goatgrass. Previous literature by Somsen and Sill (1970) had indicated that barnyard grass was "susceptible" to mites; however, there was no quantitative evidence on WCM reproductive capacity. In addition, Somsen and Sill (1970) gave a similar "susceptible" designation to sandbur and green foxtail. Sandbur and green foxtail were shown to have little mite presence after 7 days (Harvey et al. 2001) and this study provided further evidence that green foxtail is a marginal host for the WCM. The differences between barnyard grass and green foxtail clearly shows that previous categorical classifications of hosts for WCM are inadequate for determining the risk potential of over-summering hosts. The seasonal presence of barnyard grass, its susceptibility to wheat streak mosaic (Slykhuis 1952, 1955, Somsen and Sill 1970), and its ability to support large populations of mites increases the need to understand its mite-virus dynamics under field conditions.

Green foxtail showed a significant but relatively limited positive linear slope for all mite types, indicating it was a marginal host for WCM. Harvey et al. (2001) found similar results with differing levels of mites at 7 days depending on mite type. We did not detect differential survival between mite types on green foxtail. Green foxtail was a highly variable host with consistently low populations throughout the sampling period. Staples and Allington (1956) indicated that green foxtail plants infested for one month produced few mites and no eggs could be recovered. In contrast, we observed WCM eggs on green foxtail through the sampling period (data not shown). The slow mite buildup and

presence of mite eggs long after infestation indicates that green foxtail is a suitable host for WCM reproduction. It is likely to have a much lower over-summering risk than barnyard grass; however, further verification of this relationship in the field is warranted.

Mite populations declined on foxtail millet following infestation for all mite types and populations. However, mites and eggs were recovered from foxtail millet 35 days after infestation, indicating low levels of mite reproduction. Isolations of WCM (Type 1F) from wheat trap plants in these plots resulted in a significantly greater intercept compared to other mite types; however, mite populations still declined following infestation. The inability of mites to reproduce on foxtail millet could be to changes in growth habit, plant structure, varietal differences, and/or relative humidity under controlled conditions. Foxtail millet plants produce numerous tillers under field conditions whereas foxtail millet grown in growth chambers rarely produced more than one additional tiller.

Long-term reproductive studies also provided an opportunity to measure potential costs for mite adaptation to alternative hosts. Of all the mite type and host combinations, only Type 1 mites originating from barnyard grass back to wheat exhibited a lower reproductive rate. Skoracka et al. (2013) documented similar reductions in population growth rates when various *A. tosichella* genotypes were transferred from different host species to wheat. In contrast, this study tested mite types with similar reproductive rates on wheat, followed by a temporal period on an alternative host, and their subsequent reestablishment on wheat.

This study is the first to demonstrate the long-term reproductive potential of wheat curl mites on alternative hosts. Long-term studies also allowed for understanding

of mite reproduction through reproductive stages of alternative hosts (barnyard grass, green foxtail and foxtail millet). Such information is important considering that WCM populations on wheat heads can greatly exceed those of vegetative stages of wheat (Byamukama et al. 2015). In addition, long-term reproduction on hosts allows for adaptation and the potential to observe deleterious effects when returning to wheat. To our knowledge, this is the first study to document the long-term reproductive capacity of WCM on alternative hosts, and it provides a frame work for future alternative hosts studies for the WCM. In addition, we identified barnyard grass as a significant host for Type 2 mites, a finding that was previously unreported. Long-term studies also provided a better understanding of green foxtail which supported a relatively low population of mites, with some level of reproduction. Mites returning from alternative hosts to wheat showed little impact on reproduction with the exception of Type 1 mites from barnyard grass. This study provides a baseline for evaluating alternative hosts for wheat curl mites. Future studies are needed to address the interaction between mites and alternative hosts in the presence of virus, as WSMV has been shown to increase mite reproductive rates on wheat (Siriwetwiwat 2006). Given the long-term association between WCM and WSMV it is possible that this virus could counteract plant defenses or increase the nutritional quality of an over-summering hosts allowing mites to establish or allowing for increased reproductive rates on hosts.

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Tables

Table 2.1. Analysis of variance type I test for fixed effects on mite reproduction for colony, host, and sampling day using 10-mite transfers (Colony = Type 1 and Type 2; Host = wheat, jointed goatgrass, barnyard grass, green foxtail and foxtail millet; Day = 7, 14, 21, 28, 35, and 42).

Effect	Num DF	Den DF	F-value	Pr > F
colony	1	88	2.72	0.1025
host	4	88	209.02	<.0001
colony*host	4	88	12.73	<.0001
day	1	321	223.04	<.0001
day*colony	1	321	0.16	0.6933
day*host	4	321	104.54	<.0001
day*colony*host	4	321	4.84	0.0008
day*day	1	321	4.65	0.0318
day*day*colony	1	321	6.25	0.0129
day*day*host	4	321	7.23	<.0001
day*day*colony*host	4	321	2.95	0.0205

Table 2.2. P-values (P>F) for contrasts comparing equation parameters (intercept and linear slope) for five hosts (wheat, jointed goatgrass, barnyard grass, green foxtail and foxtail millet) across Type 1 and Type 2 WCM colonies (P<0.05).

Equation Parameter			Wheat		Jointed goatgrass		Barnyard grass		Green foxtail		Foxtail millet	
		Colony	Type 1	Type 2	Type 1[a]	Type 2[a]	Type 1	Type 2[a]	Type 1	Type 2	Type 1	Type 2
Intercept	Wheat	Type 1	-	-	-	-	-	-	-	-	-	-
		Type 2	0.7090	-	-	-	-	-	-	-	-	-
	Jointed goatgrass	Type 1[a]	0.0885	0.0445*	-	-	-	-	-	-	-	-
		Type 2[a]	0.7341	0.9801	0.0724	-	-	-	-	-	-	-
	Barnyard grass	Type 1	0.0002*	<.0001*	0.1547	0.0005*	-	-	-	-	-	-
		Type 2[a]	0.0896	0.0420*	0.0885	0.0750	0.0779	-	-	-	-	-
	Green foxtail	Type 1	0.0009*	0.0003*	0.2101	0.0016*	0.9447	0.1253	-	-	-	-
		Type 2	0.0027*	0.0009*	0.0971	0.0040*	0.6071	0.2377	0.6926	-	-	-
	Foxtail millet	Type 1	0.1752	0.0828	0.5347	0.1394	0.0102*	0.6134	0.0278*	0.0668	-	-
		Type 2	0.0002*	<.0001*	0.8798	0.0005*	0.6295	0.0501*	0.6204	0.3762	0.6926	-
Linear	Wheat	Type 1	-	-	-	-	-	-	-	-	-	-
		Type 2	0.9675	-	-	-	-	-	-	-	-	-
	Jointed goatgrass	Type 1[a]	0.0257*	0.0241*	-	-	-	-	-	-	-	-
		Type 2[a]	0.3059	0.3175	0.0111*	-	-	-	-	-	-	-
	Barnyard grass	Type 1	<.0001*	<.0001*	<.0001*	0.0122*	-	-	-	-	-	-
		Type 2[a]	0.5699	0.589	0.0257*	0.6561	0.0003*	-	-	-	-	-
	Green foxtail	Type 1	<.0001*	<.0001*	<.0001*	<.0001*	<.0001*	<.0001*	-	-	-	-
		Type 2	<.0001*	<.0001*	<.0001*	<.0001*	<.0001*	<.0001*	0.5826	-	-	-
	Foxtail millet	Type 1	<.0001*	<.0001*	<.0001*	<.0001*	<.0001*	<.0001*	<.0001*	<.0001*	-	-
		Type 2	<.0001*	<.0001*	0.0213*	<.0001*	<.0001*	<.0001*	0.0002*	0.5826	0.1013	-

[a] Indicates the presence of a significant quadratic parameter in equation altering the intercept and linear slope.

Table 2.3. Regression equations after natural log-transformation for Type 1, Type 2, Type 1F, and Nebraska mite colonies for wheat, jointed goatgrass, barnyard grass, green foxtail, and foxtail millet (initial infestation of 10 mites per plant).

WCM Colony	Host	Equation	Correlation	n
Type 1	Wheat	$y = 2.5805 + 0.2557x$	0.98	30
	Jointed goatgrass	$y = 1.5345 + 0.3549x - 0.0047x^2$	0.97	39
	Barnyard grass	$y = 0.7073 + 0.1080x$	0.83	55
	Green foxtail	$y = 0.7432 + 0.0314x$	0.71	39
	Foxtail millet	$y = 1.9045 - 0.0585x$	0.65	57
Type 2	Wheat	$y = 2.7717 + 0.2546x$	0.94	30
	Jointed goatgrass	$y = 2.7863 + 0.2104x - 0.0028x^2$	0.86	39
	Barnyard grass	$y = 1.6321 + 0.2337x - 0.0025x^2$	0.86	56
	Green foxtail	$y = 0.9597 + 0.0394x$	0.74	39
	Foxtail millet	$y = 0.4557 - 0.0395x$	0.77	55
Type 1F	Wheat	$y = 1.9965 + 0.2962x$	0.96	9
	Jointed goatgrass	$y = 2.9104 + 0.1962x - 0.0024x^2$	0.97	9
	Barnyard grass	$y = -0.5332 + 0.2683x - 0.0044x^2$	0.98	9
	Green foxtail	$y = -0.7994 + 0.0412x$	0.70	9
	Foxtail millet	$y = 2.7104 - 0.0515x$	0.86	9
Type 2NE	Wheat	$y = 1.8434 + 0.2773x$	0.97	21
	Jointed goatgrass	$y = 2.5242 + 0.2416x - 0.0026x^2$	0.87	42
	Barnyard grass	$y = 1.8434 + 0.2802x - 0.0039x^2$	0.62	37
	Green foxtail	$y = 0.5729 + 0.0303x$	0.19	42
	Foxtail millet	$y = 2.1575 - 0.0887x$	0.68	24

Table 2.4. Analysis of variance type I test for fixed effects on mite reproduction for colony, host, and day using 10-mite transfers (Colony = Type 1, Type 2 and Type 1F; Host = wheat, jointed goatgrass, barnyard grass, green foxtail, and foxtail millet; Day = 7, 21, and 35).

Effect	Num DF	Den DF	F-value	Pr > F
colony	2	30	1.9	0.1672
host	4	30	168.35	<.0001
colony*host	8	30	4.95	0.0006
day	1	53	3.25	0.0771
day*colony	2	53	1.21	0.3059
day*host	4	53	123.55	<.0001
day*colony*host	8	53	1.35	0.2399
day*day	1	53	0.14	0.7058
day*day*colony	2	53	0.02	0.9850
day*day*host	3	53	3.71	0.0169
day*day*colony*host	6	53	2.23	0.0547

Table 2.5. P-values (P>|F|) for contrasts comparing the intercept parameters of equations for five hosts (wheat, jointed goatgrass, barnyard grass, green foxtail, and foxtail millet) between Type 1 and Type 2 with Type Type1F WCM Colony. (* P<0.05).

Equation Parameter			Type 1F				
		Colony	Wheat	Jointed goatgrass	Barnyard grass	Green foxtail	Foxtail millet
Intercept	Wheat	Type 1F	-	-	-	-	-
		Type 1	0.6859	-	-	-	-
		Type2	0.6333	-	-	-	-
	Jointed goatgrass	Type 1F	0.1645	-	-	-	-
		Type 1	0.4376	0.5641	-	-	-
		Type 2	0.599	0.4244	-	-	-
	Barnyard grass	Type 1F	0.0075*	0.3773	-	-	-
		Type 1	<.0001*	0.0267*	0.2768	-	-
		Type 2	0.2134	0.7358	0.0008*	-	-
	Green foxtail	Type 1F	0.0074	0.0010*	0.8233	-	-
		Type 1	0.0160*	0.0014*	0.5468	0.4248	-
		Type 2	0.1668	0.0151*	0.0992	0.0790	-
	Foxtail millet	Type 1F	0.2378	0.7627	0.0010*	0.0012*	-
		Type 1	0.2383	0.0264*	0.0886	0.0709	0.0365*
		Type 2	0.0214*	0.0025*	0.7351	0.5897	0.0033*

Table 2.6. P-values (P>|F|) for contrasts comparing the linear parameters of equations for five hosts (wheat, jointed goatgrass, barnyard grass, green foxtail and foxtail millet) between Type 1 and Type 2 with Type 1F WCM Colony. (* P<0.05).

Equation Parameter			Type 1F				
		Colony	Wheat	Jointed goatgrass	Barnyard grass	Green foxtail	Foxtail millet
Linear	Wheat	Type 1F	-	-	-	-	-
		Type 1	0.6743	-	-	-	-
		Type2	0.5628	-	-	-	-
	Jointed goatgrass	Type 1F	0.0444*	-	-	-	-
		Type 1	0.2915	0.4551	-	-	-
		Type 2	0.2723	0.4815	-	-	-
	Barnyard grass	Type 1F	0.6958	0.0013*	-	-	-
		Type 1	<.0001*	0.0023*	0.0011*	-	-
		Type 2	<.0001*	0.1205	0.1648	-	-
	Green foxtail	Type 1F	<.0001*	0.0060*	0.0406*	-	-
		Type 1	<.0001*	0.0019*	0.0036*	0.8525	-
		Type 2	<.0001*	0.0002*	0.0018*	0.3282	-
	Foxtail millet	Type 1F	<.0001*	<.0001*	0.0005*	0.0083*	-
		Type 1	<.0001*	<.0001*	<.0001*	0.1005	0.2582
		Type 2	<.0001*	0.4551	0.0002*	0.4658	0.0669

Table 2.7. Analysis of variance type I test for fixed effects on Nebraska mites across hosts and days using 10-mite transfers (Host = wheat, jointed goatgrass, barnyard grass, green foxtail, and foxtail millet; Day = 7, 14, 21, 28, 35, and 42).

Effect	Num DF	Den DF	F-value	Pr > F
host	4	27	186.78	<.0001
day	1	124	41.5	<.0001
day*host	4	124	23.75	<.0001
day*day	1	124	5.75	0.018
day*day*host	4	124	1.9	0.1138

Table 2.8. P-values (P>|F|) for contrasts comparing equation parameters (intercept and linear) for five hosts (wheat, jointed goatgrass, barnyard grass, green foxtail, and foxtail millet) for the Type 2NE WCM Colony. (* P<0.05).

Equation Parameter	Host	Wheat	Jointed goatgrass	Barnyard grass	Green foxtail	Foxtail millet
Intercept	Wheat	-	-	-	-	-
	Jointed goatgrass	0.6965	-	-	-	-
	Barnyard grass	0.3115	0.5513	-	-	-
	Green foxtail	0.1178	0.3349	0.8348	-	-
	Foxtail millet	0.4034	0.7066	0.7809	0.5383	-
Linear	Wheat	-	-	-	-	-
	Jointed goatgrass	0.6751	-	-	-	-
	Barnyard grass	0.9747	0.7205	-	-	-
	Green foxtail	<.0001*	0.0021*	0.0010*	-	-
	Foxtail millet	<.0001*	<.0001*	<.0001*	0.0049*	-

Table 2.9. Analysis of variance type I test for fixed effects on mites for colony, host and day transferred back to wheat using 10-mite transfers (Colony = Type 1 and Type 2; Host = wheat, jointed goatgrass, and barnyard grass; Day = 7, 14, 21).

Effect	Num DF	Den DF	F-value	Pr > F
colony	1	46	8.16	0.0064
host	2	46	6.25	0.0040
colony*host	2	46	1.08	0.3479
day	1	62	3009.32	<.0001
day*colony	1	62	4.08	0.0477
day*host	2	62	3.62	0.0327
day*colony*host	2	62	4.01	0.0230
day*day	1	62	14.64	0.0003
day*day*colony	1	62	0.21	0.6455
day*day*host	2	62	0.51	0.6004
day*day*colony*host	2	62	1.16	0.3200

Table 2.10. P-values (P>|F|) for contrasts comparing equation parameters (intercept and linear slope) on wheat after 42-days on three hosts (wheat, jointed goatgrass, or barnyard grass) across Type 1 and Type 2 mites. (* P<0.05).

Equation Parameter			Wheat		Jointed goatgrass		Barnyard grass	
		Colony	Type 1	Type 2	Type 1	Type 2	Type 1	Type 2[a]
Intercept	Wheat	Type 1	-	-	-	-	-	-
		Type 2	0.6316	-	-	-	-	-
	Jointed goatgrass	Type 1	0.3359	0.1734	-	-	-	-
		Type 2	0.7687	0.4764	0.5445	-	-	-
	Barnyard grass	Type 1	0.7714	0.9127	0.2801	0.6063	-	-
		Type 2	0.386	0.1894	0.8505	0.6338	0.3191	-
Linear	Wheat	Type 1	-	-	-	-	-	-
		Type 2	0.5612	-	-	-	-	-
	Jointed goatgrass	Type 1	0.1125	0.2937	-	-	-	-
		Type 2	0.125	0.3206	0.9525	-	-	-
	Barnyard grass	Type 1	0.0165*	0.0052*	0.0006*	0.0007*	-	-
		Type 2	0.2139	0.5274	0.6118	0.6563	0.0009*	-

Table 2.11. Regression equations after natural log-transformation for Type 1 and 2 mite colonies on wheat after 42-days on wheat, jointed goatgrass, or barnyard grass, with initial infestation of 10 mites per wheat plant.

WCM Colony	Host	Equation	Correlation	n
Type 1	Wheat	y = 2.5091 + 0.2582x	0.96	27
	Jointed goatgrass	y = 2.2161 + 0.2857x	0.95	18
	Barnyard grass	y = 2.6046 + 0.2127x	0.96	14
Type 2	Wheat	y = 2.6413 + 0.2672x	0.97	24
	Jointed goatgrass	y = 2.7863 + 0.2846x	0.97	17
	Barnyard grass	y = 2.2736 + 0.2770x	0.96	26
Type 2NE	Wheat	y = 2.4319 + 0.2996x	0.96	21
	Jointed goatgrass	y = 2.3685+ 0.3009x	0.95	21
	Barnyard grass	y = 2.2651 + 0.3068x	0.97	18

Table 2.12. Analysis of variance type I test for fixed effects of Type 2NE mites transferred back to wheat across host and day using 10-mite transfers (Host = wheat, jointed goatgrass, or barnyard grass; Day = 7, 14, 21).

Effect	Num DF	Den DF	F-value	Pr > F
host	2	9	0.47	0.6383
day	1	42	3445.19	<.0001
day*host	2	42	0.18	0.8379
day*day	1	42	0.17	0.6811
day*day*host	2	42	0.08	0.9210

Figures

Figure 2.1. Reproduction of Type 1 colony mites on wheat, jointed goatgrass, barnyard grass, green foxtail, and foxtail millet (natural log) following initial infestation of 10 mites per plant.

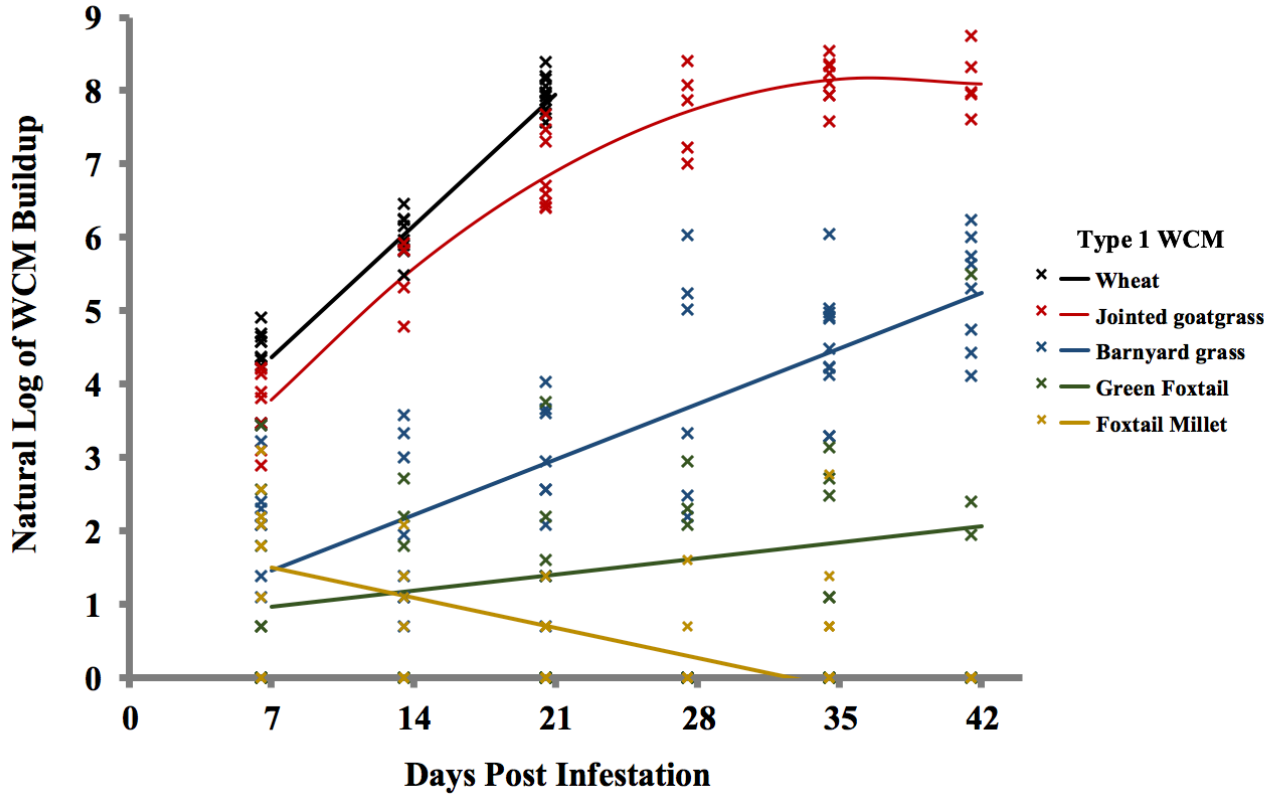


Figure 2.2. Reproduction of Type 2 colony on wheat, jointed goatgrass, barnyard grass, green foxtail, and foxtail millet (natural log) following initial infestation of 10 mites per plant.

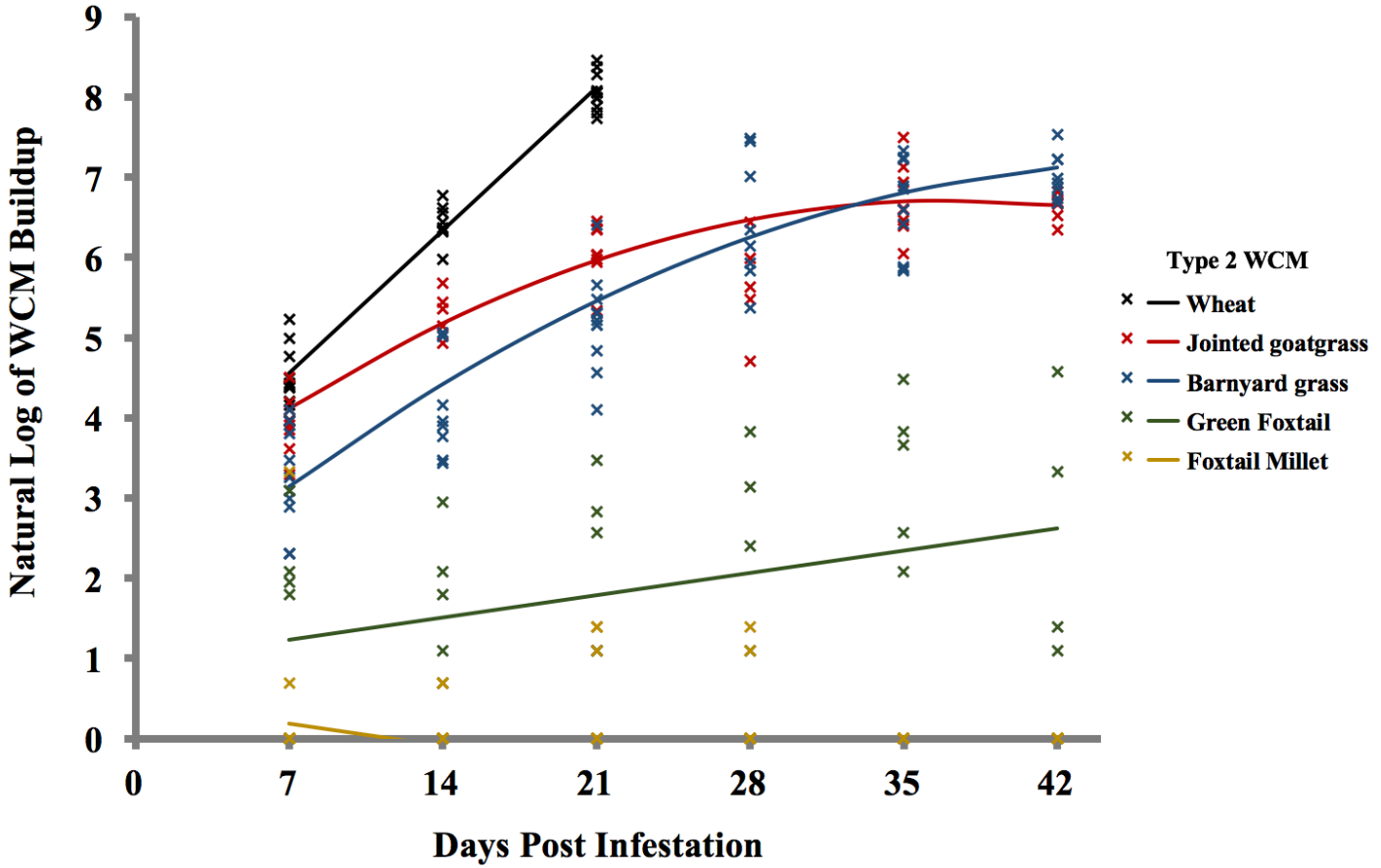


Figure 2.3. Reproduction of Type 1F colony on wheat, jointed goatgrass, barnyard grass, green foxtail, and foxtail millet (natural log) following initial infestation of 10 mites per plant.

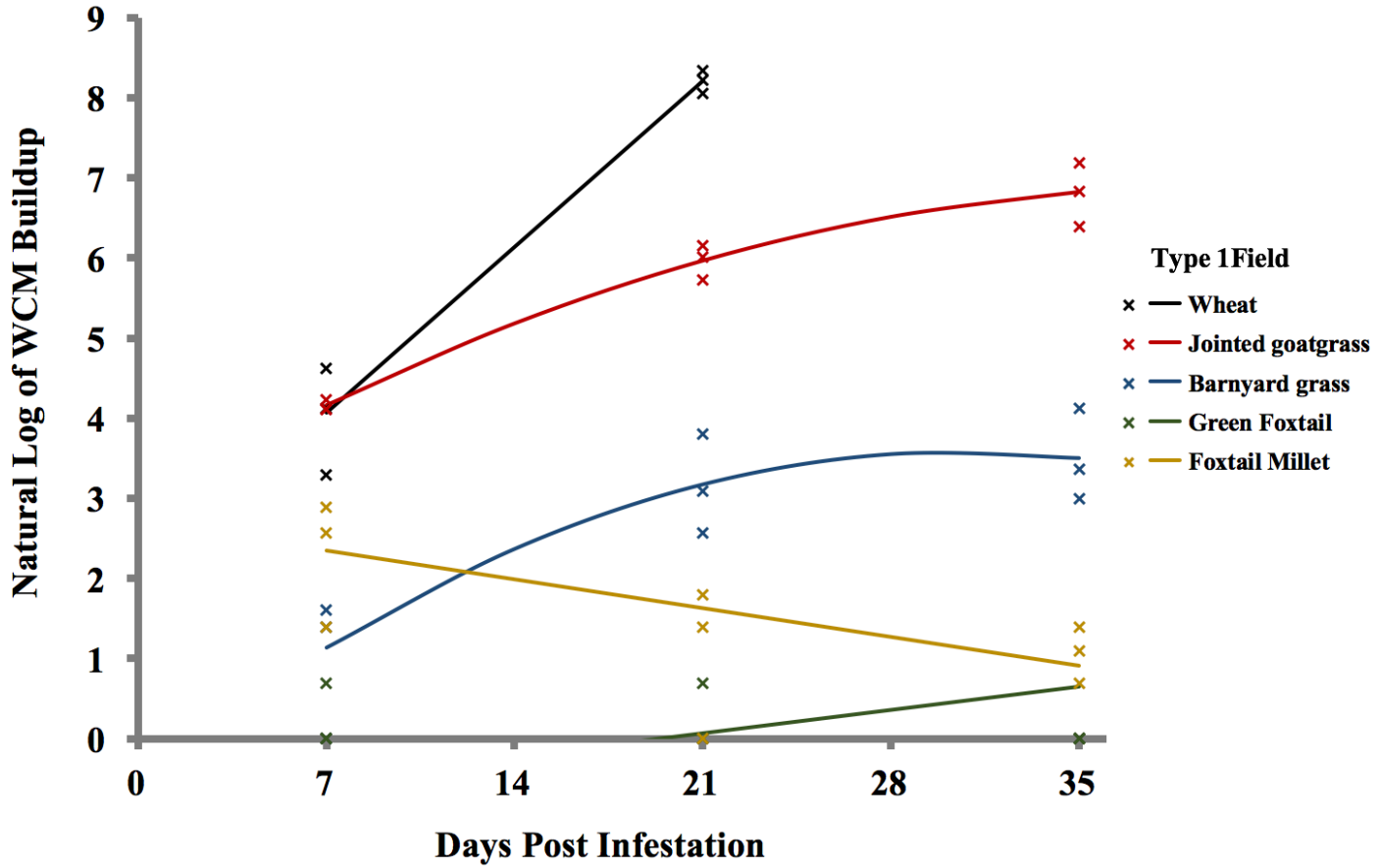


Figure 2.4. Reproduction of Type 2NE colony on wheat, jointed goatgrass, barnyard grass, green foxtail, and foxtail millet after (natural log) following initial infestation of 10 mites per plant.

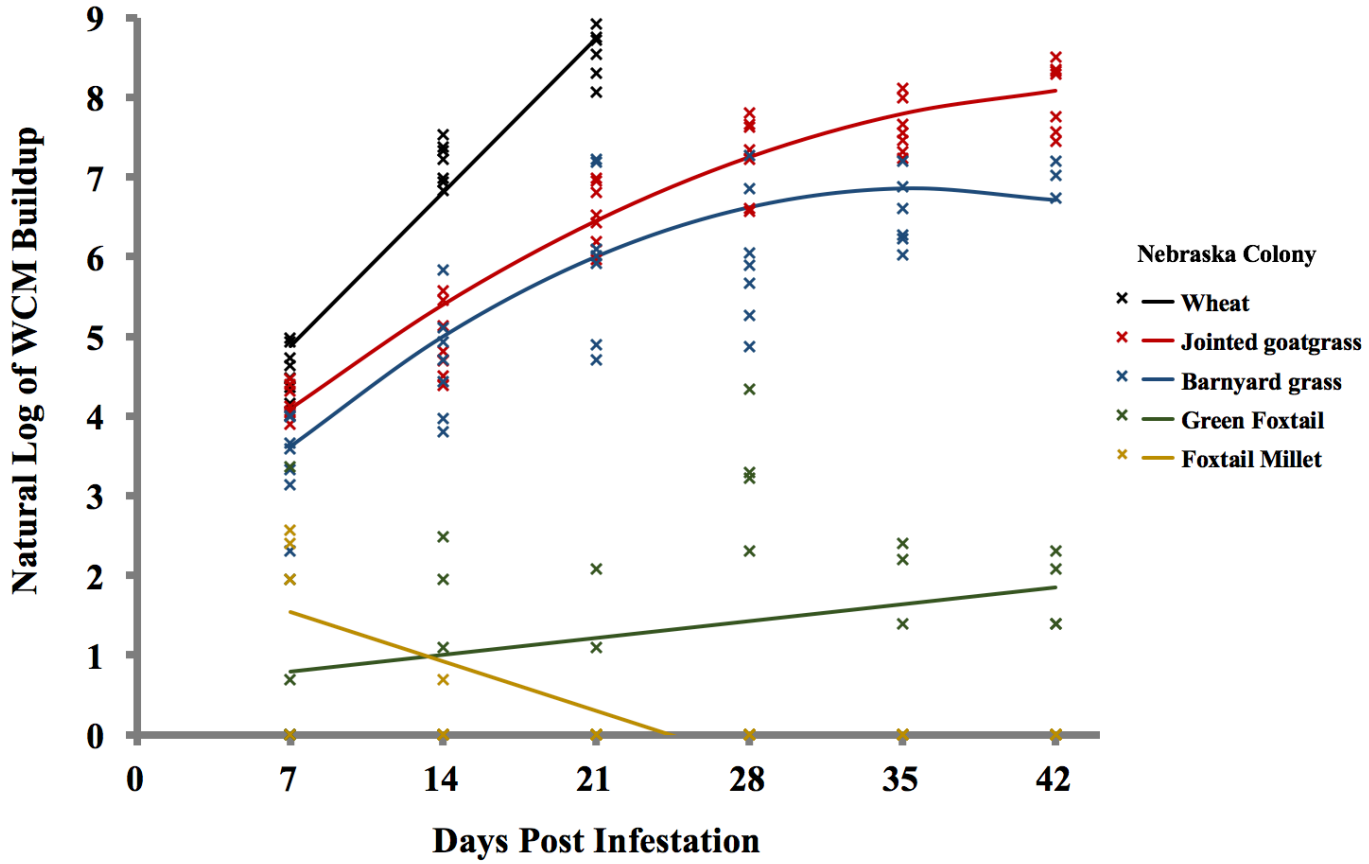
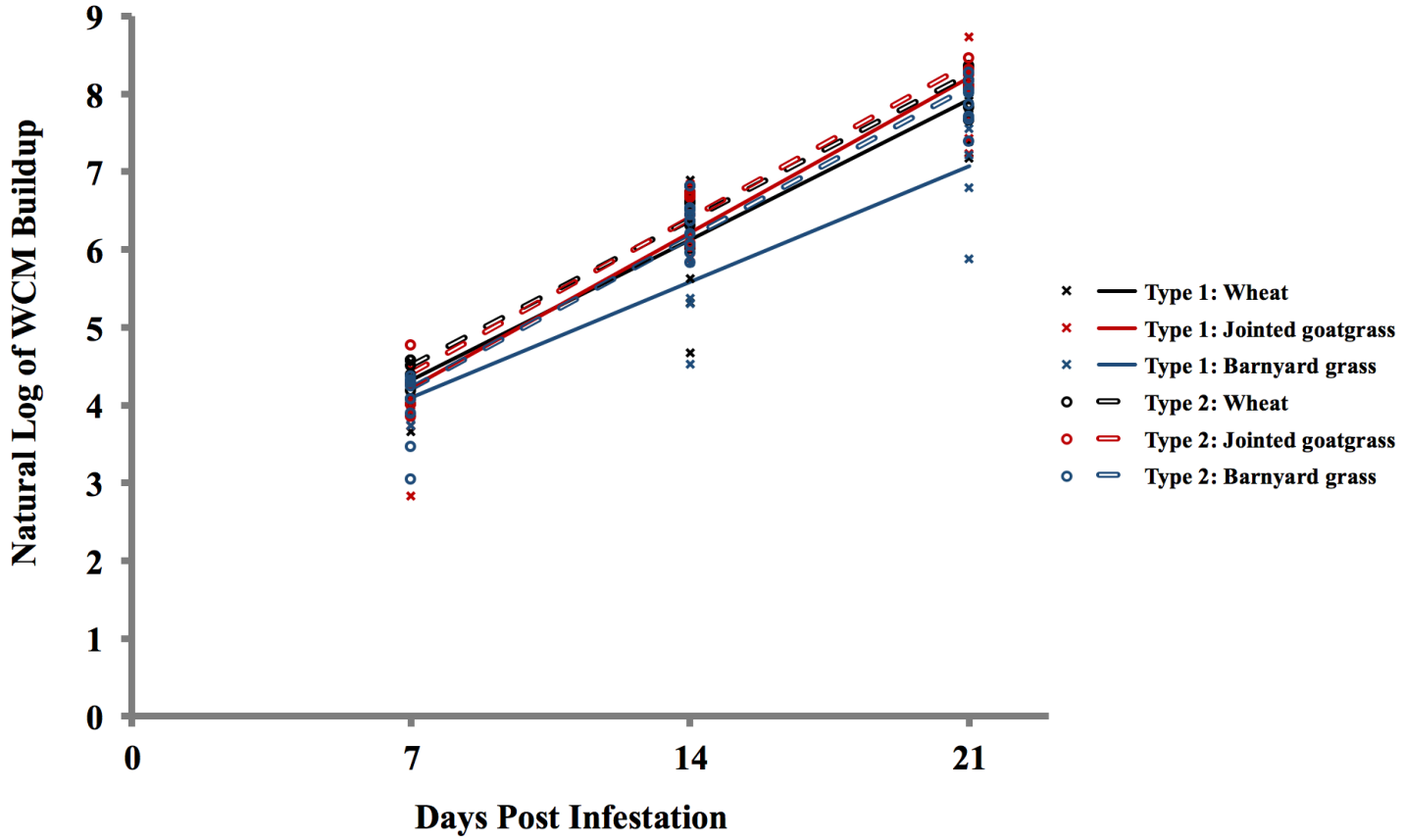


Figure 2.5. Reproduction of Type 1 and Type 2 colonies on wheat after 42-days on wheat, jointed goatgrass, or barnyard grass (natural log) following initial infestation of 10 mites per plant.



CHAPTER 3

Establishing Risk of Over-Summering Hosts for the Wheat Curl Mites and its Associated Viruses

Introduction

The wheat-mite-virus complex is one of the primary yield limiting diseases in winter wheat (*Triticum aestivum* L.) in the western Great Plains. This complex consists of three viruses (*Wheat streak mosaic virus* (WSMV), *Triticum mosaic virus* (TriMV), and *Wheat mosaic virus* (WMoV)) that are transmitted by the wheat curl mite (WCM; *Aceria tosichella* Keifer). Severe yield losses from this complex are often localized to areas where pre-harvest wheat had emerged during the previous year. Controlling pre-harvest volunteer wheat is one of the most effective management strategies for this complex; however, situations have occurred in the past where significant yield losses due to virus infection have occurred despite management tactics that were not conducive for the presence of pre-harvest volunteer wheat (Shahwan and Hill 1984, Christian and Willis 1993). These situations indicate the need to better understand the risk potential for other grasses to serve as mite and virus hosts during the critical over-summering period between winter wheat harvest and fall planting.

Previous research indicates that there are approximately 90 reported hosts for the wheat curl mite (Amrine and Stasny 1994); however, not all of these hosts pose a risk to winter wheat. Christian and Willis (1993) established five characteristics that would be necessary for an alternative host to be a significant risk as a source for mites and virus to winter wheat. First, the host must thrive in significant populations in or adjacent to fields of winter wheat. Second, the host should emerge prior to wheat maturing and survive until fall planting of winter wheat. Third, the host should be susceptible to one of the viruses within the wheat-mite-virus complex. Fourth, the host must support a large

enough mite population to enable significant movement back to wheat. Lastly, WCM must be able to re-establish on wheat with potential for secondary spread.

Historically, the risk assessment of alternative hosts has focused on the presence of WSMV through mechanical inoculation, WCM reproduction, and/or the detection of mites and virus from field-collected samples. Wheat is considered the primary host for the WCM with several researchers documenting it as a highly satisfactory host for WCM (Slykhuis 1955, 1956, Connin 1956a, Staples and Allington 1956, Nault and Briones 1968, Harvey et al. 2001). Field collections of volunteer wheat have had highly variable results depending on the timing of emergence. Staples and Allington (1956) showed that volunteer wheat emerging one week prior to harvest was 100% infested within two weeks of emergence. In contrast, no WCM were found in volunteer wheat emerging three to four weeks after harvest (Staples and Allington 1956).

Harvey et al. (2001) found differential survival of WCM on wheat varieties with different genes for mite resistance depending on the mite source with mites collected from Kansas having some level of reproduction over a 7 day period whereas Nebraska mites declined rapidly in the same time period. These same populations have been found to have distinct genetic differences (Carew et al. 2009, Hein et al. 2012), virus transmission (Seifer et al. 2002, McMechan et al. 2014, Wosula et al. 2015), and reproductive rates on virus infected plants (Siriwetwiwat 2006). Wheat is susceptible to WSMV (Staples and Allington 1956) ,WMoV (Skare et al. 2006), and TriMV (Seifers et al. 2009).

During the 1984 growing season, Shahwan and Hill (1984) tracked 11 fields that were severely impacted by WSMV and attempted to correlate disease severity with the

adjacent field's cropping and environmental history. Nine of the eleven fields were associated with pre-harvest hail resulting in the presence of volunteer wheat. One severely damaged field was planted adjacent to corn (*Zea mays* L.) and the other field had been planted adjacent to foxtail millet (*Setaria italica* (L.) P. Beauv.). The study recommended that winter wheat should not be planted within 1 km of corn, foxtail millet, or volunteer wheat to avoid significant damage. Potential severity of WSMV in the presence of corn and foxtail millet in those fields indicates a need for further investigation of these over-summering hosts.

Corn is one of the most tested plants for the wheat-mite-virus complex. Mechanical inoculation with WSMV showed that inbred, hybrid, sweet, and popcorn lines varied in response (McKinney 1949, Sill and Connin 1953, Meiners and McKinney 1954, Sill and Agusiobo 1955, Slykhuis 1955, Finley 1957, McKinney et al. 1966, Nault and Briones 1968). A field study by Gates (1970) showed that mites could transmit WSMV from corn to wheat until about two weeks prior to corn harvest. WCM reproductive studies indicate that some inbred corn lines were susceptible (How 1963, Orlob 1966, Nault and Briones 1968) whereas hybrid corn had more variable results (How 1963, Connin 1956b, Orlob 1966, Nault and Briones 1968). A study by Nault and Styer (1969) documented the seasonal population of WCM on two inbred corn lines and found that no mites were present until corn was 75 cm tall. Later in the season, Nault and Styer (1969) observed that mite colonization of the husks was very successful and peaked in early to mid-September, and mites were last observed on the silks and kernels in late September and October.

Foxtail millet is a common summer annual forage crop grown in the western Great Plains. Baltensperger (2002) indicated that foxtail millet ranks second in world production of millets; however, its primary limitation in the High Plains of the US is that it serves as a carrier for the WCM and WSMV. The susceptibility of foxtail millet to WSMV through mechanical inoculation is unclear with some authors classifying it as immune (Slykhuis 1952, 1961, Sill and Connin 1953) or susceptible (Sill and Agusiobo 1955, Slykhuis 1955, Seifers et al. 1996). Differences in the susceptibility of foxtail millet to WSMV could be attributed to the variety tested or the type of WSMV isolate used. Two short term studies have been conducted to determine WCM reproduction on foxtail millet with only a few mites present after 7 days of exposure (Slykhuis 1955, 1956). To our knowledge, only observational (Shahwan and Hill 1984) and anecdotal evidence exists for WSMV and WCM on foxtail millet under field conditions.

Numerous grassy weeds have been reported as potential hosts for the wheat-mite-virus complex. Barnyard grass (*Echinochloa crus-galli* (L.) P. Beauv.), is a stout, C4, summer annual weed that readily invaded disturbed sites, and it is commonly found in the western Great Plains (Manidool 1992). Barnyard grass has been found to be susceptible (Slykhuis 1952, 1955, Somsen and Sill 1970) and immune (Sill and Agusiobo 1955, Slykhuis and Bell 1963) to WSMV. WCM reproduction studies on barnyard grass showed that few mites were found after 7 days (Slykhuis 1955, 1956), but it has also been classified as a susceptible host for WCM (Somsen and Sill 1970). We have found no quantitative evidence of WCM reproduction on barnyard grass. Christian and Willis (1993) found that WSMV presence on barnyard grass in Kansas ranged from 10% in 1988 to 56% in 1989. Only one study has documented the presence of WCM on

barnyard grass under field conditions at a rate of 2.2% plants infested (Somsen and Sill 1970).

Green foxtail (*Setaria viridis* (L.) P. Beauv.) is a summer annual weed that is typically a poor competitor unless in a dense stand which is commonly observed in the Great Plains. Green foxtail is susceptible to WSMV with several studies documenting severe chlorosis and stunting following inoculation (Slykhuis 1952, 1955, Finley 1957, Slykhuis and Bell 1963, Timian and Lloyd 1969, Somsen and Sill 1970). WCM reproductive studies on green foxtail have shown few mites after 7 days (Slykhuis 1955, 1956). Staples and Allington (1956) reported that only 2 of 11 plants had WCM one month after infestation, and no eggs were recovered. Field observations of WSMV on green foxtail show consistent presence of the virus (Staples and Allington 1956, Timian and Lloyd 1969). Christian and Willis (1993) found 20-40% of plants positive for WSMV in 1988 and 1989. Field observations of WCM presence on green foxtail indicate that only a small percentage of plants were infested, but these contained only a few mites (Connin 1956a, Staples and Allington 1956, Timian and Lloyd 1969, Somsen and Sill 1970).

Historical efforts have provided valuable insight into the potential for some alternative hosts to support WCM and virus; however, much more detailed research is needed to assess the actual risk of these hosts to fall planted winter wheat. Addressing these risks in the field greatly limits the number of hosts that can be evaluated. For this study, we have chosen five hosts (wheat, corn, foxtail millet, barnyard grass, and green foxtail that vary in their anecdotal and experimental evidence for risk to fall planted winter wheat with regard to the Christian and Willis (1993) criteria. The objectives of this

study were to determine the potential for wheat curl mites to survive on these alternative hosts during the summer under field conditions and evaluate the impact on fall planted winter wheat that these hosts as sources of mites and virus. This is the first study to document the season long mite activity for these hosts and the risk from these hosts to surrounding fall planted winter wheat.

Materials and Methods

Six over-summering grass hosts were evaluated for risk to fall planted winter wheat, including two winter wheat treatments. Winter wheat treatments differed by timing of emergence with one wheat treatment emerging prior to the maturation of the surrounding winter wheat crop (pre-harvest wheat), and the other planted two weeks after harvest (post-harvest wheat). Additional hosts were corn (Cropland 3337), foxtail millet (FTM; Golden German Millet), barnyard grass (BYG), and green foxtail (GFT). All treatments were seeded into small plots (ca. 1.5 m by 1.5 m) separated by 4.5 m and arranged in a randomized complete block design with six replications. Corn was planted on the 22 and 18 May of 2013 and 2014, respectively. Pre-harvest wheat, foxtail millet, barnyard grass, and green foxtail were planted the last week in May during both years of the study. Plant stand densities of over-summering hosts were taken two to three weeks after emergence, and stands for green foxtail and barnyard grass were thinned to population densities of 30-50 plants/m^2, approximately two weeks after emergence.

WCM movement was quantified as winter wheat matured each year to determine the potential for initial infestation of over-summering hosts. A trap pot was placed on each of the four sides of the study area to monitor WCM activity. Each trap pot consisted of three cone-tainers (4 cm in diameter; Steuwe and Sons Inc., Tangent, Oregon, USA), and each cone-tainer contained three 'Millennium' wheat plants. Plants were reared under artificial lights and covered with plastic cages (5 cm in diameter and 50 cm in height) with two to three vents, covered with Nytex® screen for 14 days prior to field exposure. In the field, trap pots consisted of a 4 L bucket buried to a level even with the soil surface. A 30-cm square plywood board was placed over the bucket with a 15-cm-

diameter hole in the center. A pot (15 cm in diameter; Hummert International, Topeka, Kansas, USA) with the bottom cut out was placed through the hole of the plywood board. A 15-cm-diameter insert was cut from white wall board (0.090 fiberglass reinforced plastic), and four holes (3.2-cm diameter) were drilled at equal distance from one another within the insert. The insert was then placed within the lid 15-cm pot. The bucket was filled with water prior to placement of the trap pots. Trap pots were exposed in the field by placing them into one of the four holes in the insert and removing the cage. Trap cone plants were exposed for seven days, and new plants were exposed weekly from early June (2^{nd}-5^{th}) until two weeks after winter wheat harvest. Each trap pot was covered with 0.8-cm mesh cone-shaped hardware cloth with the bottom buried below the soil to deter herbivores. Winter wheat development was recorded weekly, and over-summering host development stages were recorded at harvest.

After wheat harvest, trap pots were placed in the center of each plot with three cone-tainers per pot. The fourth hole in the insert was covered to reduce water loss from the bucket. Trap pots were exposed every other week for seven days through mid- to late October. A fourth cone-tainer was added to the trap pots twice during the season to evaluate virus presence. For this sampling, two cones were evaluated for mites and the other two for WSMV presence. Cone-tainers that were evaluated for virus were covered with cages in the field and held in the greenhouse for 3-4 weeks. At that time, plants were sampled for subsequent double-antibody sandwich enzyme linked immunosorbent assay (DAS-ELISA) testing as described in (Byamukama et al. 2014). To monitor mites on the cone-tainer plants, three plants per cone-tainer (9/plot) were cut at soil level, placed in Zip-lock bags, and stored at 4°C until mites could be counted under a stereo microscope

at 30X-40X. In 2013, mites were collected from trap pots during each of the collection dates and placed in vials containing 100% alcohol to determine mite type using PCR-RFLP as described by Hein et al. (2012).

To evaluate potential virus spread into surrounding winter wheat, the variety 'Pronghorn' was seeded in 0.3-m row spacing around each plot on 20 Sept., 2013 and 9 Sept., 2014. In the spring, a SPAD-502 Chlorophyll Meter (SPAD; Konica Minolta Sensing Inc., Ramsey, NJ) was used to quantitatively evaluate virus symptomology, and ELISA testing was used to determine virus presence. Each SPAD reading consisted of an average of 10 flag leaf readings per row. SPAD readings were taken from each of the six rows adjacent to the plot in all four cardinal directions during the early milk stage. Ten flag leaves were sampled for virus assay via ELISA testing from each row directly adjacent to each plot in all four cardinal directions as well as rows three and five to the east of each plot. WSMV presence in flag leaves was tested as a composite of the 10 leaves via ELISA. ELISA sensitivity for composite samples was verified through known ratios (1:9, 3:7, 7:3, 9:1) of WSMV infected to healthy tissue.

Mite movement data from trap pots were analyzed by using two response variables (proportion of infested wheat plants and average number of mites per plant) to determine frequency and abundance of mites on trap plants through PROC GLIMMIX (SAS Institute 2008) with repeated measures. Studentized residuals indicated that proportion data were not normally distributed, with the response variable limited between 0 and 1, thus a beta distribution was used in the analysis. For repeated measure analysis, covariance models on inference (CS, AR(1), ANTE(1), and UN) were tested to determine the model with the lowest Akaike information criterion corrected value. Analysis of

variance of fixed effects was used to determine differences in year, host, and time effects. Random effect was replication. T-tests were used to test for differences between years, host, and time.

SPAD readings were analyzed in PROC GLIMMIX to determine differences between hosts (fixed effects) and repeated measures to determine difference for direction and row, with replication as a random effect. Covariance models were run in the same manner as described for mite movement data. ELISA absorbance values were divided into two separate analyses. The first analysis compared virus impact using absorbance values from the row directly adjacent to the plot to test the fixed effects of host, direction, and their interaction. The second analysis evaluated ELISA absorbance values with distance from the plot using the rows east of the plot (1, 3, and 5) with fixed effects of host, row, and their interaction. T-tests and contrasts were used to determine differences between hosts, rows, and directions. Correlation coefficients were used to compare mite movement parameters with virus symptoms (SPAD) and virus presence (DAS-ELISA) data using PROC CORR (SAS Institute 2008). Environmental data were obtained from the High Plains Regional Climate Center (hprcc.unl.edu; University of Nebraska-Lincoln). Weather data originated from an established weather station located less than 1 km from the plot site.

Results

Average mean monthly temperatures and total precipitation (Table 3.1) varied between the two years of the study. The largest differences in temperature occurred during the month of October with an average temperature of 14.1°C and 19.7°C for 2013 and 2014, respectively. Total precipitation from September to November was highest in 2014 (225.0 mm) and lowest in 2013 (106.2 mm). Spring temperatures varied considerably for the month of March with highest temperatures in 2015 (15.8°C) compared to 2014 (10.5°C). Total precipitation during the spring and summer (March-August) also varied widely between the two years with 159.5 mm in 2014 to 422.9 mm in 2015.

Border trap pots (Fig. 3.1) showed extensive and significant mite movement into the over-summering host study with 99% and 96% trap plants infested as winter wheat reached the hard dough stage in 2013 and 2014, respectively. As a result, pre-harvest wheat plots showed severe virus symptoms and leaf curling from mite infestations within a week of winter wheat harvest in both years. Five tillers were taken from each pre-harvest wheat plot and dissected to determine the number of mites per tiller under a stereo microscope. Pre-harvest wheat tillers averaged 29 (±6) and 132 (±18) mites per tiller during 2013 and 2014, respectively. Due to the high mite infestation levels, pre-harvest wheat was destroyed just after harvest to prevent mite infestation from these plots to other over-summering host plots. These plots were then designated as "bare" plots for the remainder of the season.

Over-summering host development stages (Table 3.2) were more mature at wheat harvest during the summer of 2014 compared to 2013. The most notable differences

occurred for corn with V13 (14 leaves) and VT (tassel present) at harvest for 2013 and 2014, respectively. Only slight differences occurred for the remaining hosts in the study with most plants ranging between tillering and jointed at harvest.

An analysis of mite movement data from trap pots located within each plot showed a significant year, host, and time interaction for both the proportion of infested mites ($F_{25, 350.1} = 5.47$; $P<.0001$) and average number of mites per trap plant ($F_{25, 345.3} = 4.85$; $P<.0001$). These interactions were a result differing seasonal values in the proportion infested plants and average mites per trap plant each year; therefore, each year of the study was analyzed separately.

ELISA sensitivity for composite samples through known ratios (1:9, 3:7, 7:3, 9:1) of WSMV infected to healthy tissue showed that a 10-leaf sample containing a single WSMV-infected leaf produced absorbance values 10 times greater than healthy controls. These results indicate excellent sensitivity of this sampling process.

2013-14: Mite activity

Proportion of infested plants (Fig. 3.2a) varied between hosts ($F_{5,30} = 21.05$; $P <.0001$) with greatest activity occurring from barnyard grass (0.53), followed by foxtail millet (0.41), green foxtail (0.17), corn (0.06), post-harvest wheat (0.01) and bare ground (0.01). Collection dates also differed ($F_{5,142} =2.06$; $P = 0.0734$) with the proportion of infested plants reaching its peak during the first (0.15) and third (0.16) week in September but then declining in October. The interaction between host and collection date was not significant ($F_{25,142} = 0.86$; $P = 0.6561$).

The most important time period for mite movement from summer hosts back to winter wheat would be in late Sept. and October. Orthogonal contrasts (Table 3.3)

between over-summering hosts (corn, FTM, GFT, and BYG) and wheat plots (post-harvest wheat and bare plots) indicate greater mite activity for over-summering hosts in October week 1 ($F_{1,142} = 9.03$; $P = 0.0031$), but no differences were seen in week 3 ($F_{1,142} = 3.03$; $P = 0.0841$). Similar differences occurred when contrasting corn vs. foxtail millet, green foxtail, and barnyard grass with corn having less activity during week 1 ($F_{1,142} = 9.12$; $P = 0.0030$) whereas all hosts showed reduced activity and no differences in week 3 ($F_{1,142} = 1.99$; $P = 0.1603$) of October. Contrasts of foxtail (foxtail millet and green foxtail) vs. barnyard grass indicate the barnyard grass had significantly greater mite activity than foxtail grasses during week 3 ($F_{1,142} = 16.5$; $P = 0.0070$) of September compared to a lack of differences in week 1 ($F_{1,142} = 1.67$; $P = 0.1979$) of October as a result of increasing mite activity from foxtail millet. Increased activity from foxtail millet compared to green foxtail is evident from the lack of difference in week 3 ($F_{1,142} = 2.71$; $P = 0.1017$) of September compared to significant greater activity in foxtail millet during week 1 ($F_{1,142} = 12.91$; $P = 0.0005$) of October. Week 3 of October showed no differences for any of the possible orthogonal contrasts (Table 3.3) indicating that mite activity had declined for the season.

Similar results were obtained for average mites per plant (Fig. 3.2b); however, the magnitude of these differences varied between the two response variables. Average mites per plant differed between hosts ($F_{5,28.2} = 20.19$; $P < 0.0001$) and collection dates ($F_{5,111} = 9.04$; $P < 0.0001$). Barnyard grass (2.17) had the greatest average number of mites per trap plant, followed by foxtail millet (0.85), green foxtail (0.40), corn (0.10), bare ground (0.02) and post-harvest wheat (0.01). Collection dates showed average mite numbers per trap plant increasing from 0.88 to 1.22 for weeks 1 and 3 of September,

respectively. Average mites per trap plant declined for the last sampling period to 0.07. A significant interaction between host and collection date occurred ($F_{25,123.7} = 5.93$; $P < 0.0001$). This interaction was primarily due to increased mite activity in barnyard grass during September (5.02) compared to the average of foxtail millet and green foxtail (1.04) in week 3 (Table 3.3; $F_{1,155.9} = 93.07$; $P<.0001$) of September whereas no differences occurred between these hosts in week 1 (Table 3.3; $F_{1,155.9} = 0.05$; $P = 0.8258$) of October.

WCM collected from trap pots across the over-summering period and evaluated for mite type using PCR varied in the percentage of Type 1 and 2 mites depending on the host. Of the 15 mites collected from border pots, 47% were Type 1 and 53% were Type 2, indicating that comparable level of Type 1 and 2 mites infested the study. Mites collected from corn and green foxtail trap pots showed little preference for mite type with 55% (6/11) and 67% (6/9) being Type 1 and and 45% (5/11) and 33% (3/9) Type 2 for green foxtail and corn, respectively. In contrast, the 15 mites collected from barnyard grass were 93% (14/15) Type 2. The opposite occurred for foxtail millet with 81% (21/25) of mites testing as Type 1.

Trap pots exposed in the field from 28 August to 4 September and held for virus detection showed that only plants from barnyard grass (11/12: 92%) and foxtail millet (3/12: 36%) plots were positive for WSMV. A second sample taken in early October found that only trap plants from barnyard grass plots tested positive for WSMV (7/12: 58%).

2013-14: Virus impact

Relative chlorophyll content or SPAD readings (Fig. 3.3a) were different between hosts ($F_{5,25}$ = 4.81; P = 0.0032) with barnyard grass (45.4; t_{25} = -2.23; P = 0.0351) having significantly lower SPAD values or greater virus symptomology than green foxtail (46.4), followed by foxtail millet (47.2), corn (47.3), and post-harvest wheat (47.5). Bare plots (48.2; t_{25} = -2.31; P = 0.0297) had significantly higher SPAD values than green foxtail. Direction from host plots was also significant ($F_{3,90}$ = 2.59; P = 0.0574) with north (47.2), east (46.6), and south (46.7) having significantly ($F_{1,90}$ = 5.49; P = 0.0213) lower SPAD values compared to west (47.7) indicating that mite movement and virus spread was not equal in all directions from the hosts. Rows were also different ($F_{5,497}$ = 23.77; P < 0.0001) with the wheat row directly adjacent to the host plot (Row 1; 45.0) (t_{587} = -2.21; P = 0.0278) having lower SPAD values than row two (45.9). In addition, row two (t_{587} = -3.36; P = 0.0008) had lower SPAD values than row three (47.4). No differences occurred between rows four (47.7), five (48.3), and six (48.1) indicating that virus impact was primarily limited to the first two- to three-rows adjacent to the plot.

The interaction between host and direction was significant ($F_{15,497}$ = 1.81; P = 0.0574). Contrasts comparing the east to the average of all other directions for each host found significant differences for barnyard grass ($F_{1,90}$ = 21.56; P < 0.0001) whereas no differences were found for corn ($F_{1,90}$ = 0.30; P = 0.5865), foxtail millet ($F_{1,90}$ = 0.02; P = 0.8991), green foxtail ($F_{1,90}$ = 0.28; P = 0.5984), post-harvest wheat ($F_{1,90}$ = 0.03; P = 0.8712) or bare ($F_{1,90}$ = 0.05; P = 0.8156). These differences indicate that barnyard grass had significant mite movement and virus spread relative to the other over-summering hosts.

The host by row interaction was also significant ($F_{25,497} = 23.77$; $P < 0.0001$). Contrasts of row one vs. the remaining rows for each host indicated significant differences for barnyard grass ($F_{1,497} = 114.77$; $P < 0.0001$), corn ($F_{1,497} = 10.17$; $P = 0.0015$), foxtail millet ($F_{1,497} = 14.52$; $P = 0.0002$), and green foxtail ($F_{1,497} = 10.61$; $P = 0.0012$) indicating virus impact adjacent to these hosts. In comparison, no differences occurred for post-harvest wheat ($F_{1,497} = 0.04$; $P = 0.8381$) and bare ($F_{1,497} = 0.51$; $P = 0.4750$) indicating a lack of virus impact or gradient from these hosts.

The interaction of row by direction was also significant ($F_{15,497} = 2.20$; $P = 0.0058$) with the direction east of the plots being significantly different than the average of all other directions between rows one ($F_{1,497} = 4.23$; $P = 0.0402$) and three ($F_{1,497} = 6.53$; $P = 0.0109$) but no differences occurred for rows two ($F_{1,497} = 0.42$; $P = 0.5154$), four ($F_{1,497} = 0.03$; $P = 0.8673$), five ($F_{1,497} = 2.32$; $P = 0.1280$) and six ($F_{1,497} = 1.01$; $P = 0.3145$). The interaction between host, row, and direction was not significant ($F_{75,497} = 1.02$; $P = 0.4427$).

ELISA absorbance values on all rows directly adjacent to the plot differed between hosts ($F_{5,25} = 7.91$; $P = 0.0001$) with barnyard grass (0.79; $F_{1,25} = 35.6$; $P < 0.0001$) having significantly higher absorbance values and greater virus presence than all other hosts. Only numerical differences were observed between green foxtail (0.40), corn (0.36), foxtail millet (0.31), post-harvest wheat (0.25) and bare (0.21). Direction was also significant ($F_{3,71} = 4.56$; $P = 0.0056$) with north (0.52; $F_{1,71} = 10.5$; $P < 0.0018$) having greater absorbance values than east (0.28), south (0.34) or west (0.39). Hosts also varied by direction ($F_{15,71} = 2.18$; $P = 0.0149$) with barnyard grass having higher absorbance

values than all other hosts on the north and west sides but not the south and east sides of the plot.

ELISA absorbance values (Fig. 3.3b) analysis on east rows one, three and five of the plots differed by host ($F_{5,25} = 2.56$; $P = 0.0467$) with barnyard grass (0.42) having greater virus presence than corn (0.23), foxtail millet (0.22), green foxtail (0.22), post-harvest wheat (0.26) and bare ground (0.21). These results indicate that mites coming from barnyard grass may have greater virus transmission rates than mites from other hosts. There was no difference between rows ($F_{2,38} = 1.88$; $P = 0.1669$), or for the interaction between host and row ($F_{10,38} = 0.92$; $P = 0.5250$).

2014-15: Mite activity

Proportion of WCM-infested plants (Fig. 3.4a) was different between hosts ($F_{5,30}= 24.13$; $P <.0001$) with greatest activity occurring from barnyard grass (0.65), followed by foxtail millet (0.48), green foxtail (0.31), corn (0.09), post-harvest wheat (0.02) and bare ground (0.02). Differences also occurred between collection dates ($F_{5,141} = 2.29$; $P = 0.0489$) as a result of reduction in activity between week 2 (0.23) and week 4 (0.09) of October. A significant interaction occurred between host and collection date ($F_{25,141} = 2.98$; $P < .0001$). Late season interactions were primary due to significantly greater mite activity from barnyard grass (0.78) compared to the average of foxtail grasses (0.46) during week 2 ($F_{1,141} = 9.25$; $P = 0.0028$) of October whereas no differences occurred during week 4 ($F_{1,141} = 2.03$; $P = 0.1560$) of the same month. All other orthogonal contrasts (Table 3.3) with the exception of bare ground vs. post-harvest wheat showed significant differences for the last three collection dates. Mites per plant (Fig. 3.4b) were

fewer in 2013-14 and data were nearly identical in terms of significant main effects and orthogonal contrasts (Table 3.3).

Trap pots exposed to the field from 12 to 19 August and held in a greenhouse for virus detection showed WSMV positive samples for barnyard grass (4/9: 44%), corn (6/11; 55%), green foxtail (4/5; 80%), post-harvest wheat (0/11; 0%) and bare (0/12; 0%). Foxtail millet had only one sample during this period due to a large amount of herbivory. The second virus collection occurred from 23 to 30 September with the following results: barnyard grass (10/11; 91%), corn (0/12; 0%), foxtail millet (0/11; 0%), green foxtail (2/10; 20%), post-harvest wheat (0/12; 0%) and bare ground (0/12; 0%).

2014-15: Virus Impact

Relative chlorophyll content or SPAD readings (Fig. 3.5a) showed significant differences between hosts ($F_{5,25} = 2.46$; $P = 0.0602$) with barnyard grass (37.6; $F_{1,25} = 9.33$; $P = 0.0053$) having significantly lower readings than post-harvest wheat (39.4), green foxtail (39.7), corn (40.6), foxtail millet (40.7), and bare ground (41.1). SPAD values also differed by direction ($F_{3,90} = 3.47$; $P = 0.0195$) from plots with the north (39.6), east (39.6), and south (39.6) having significantly lower SPAD readings ($F_{1,90} = 10.39$; $P = 0.0018$) than the west (40.6). Rows also differed ($F_{5,598} = 2.64$; $P = 0.0226$) with contrasts showing that rows one (39.3) and two (39.4) had lower SPAD values ($F_{1,598} = 11.28$; $P = 0.0008$) than rows three (40.1), four (39.9), five (40.4), and six (40.0). This indicates that mite movement and virus spread originated from host treatments and that hosts were unlikely to cause significant impact on neighboring host plots.

The host by row interaction was also significant ($F_{25,598} = 5.96$; $P < 0.0001$). Contrasts comparing rows one, two and three to rows four, five and six for each host showed significant differences for barnyard grass ($F_{1,598} = 91.21$; $P < 0.0001$) and corn ($F_{1,598} = 6.45$; $P = 0.0133$) whereas no differences occurred for foxtail millet ($F_{1,598} = 0.58$; $P = 0.4467$), green foxtail ($F_{1,598} = 0.42$; $P = 0.5172$), post-harvest wheat ($F_{1,598} = 0.01$; $P = 0.9122$) or bare ground ($F_{1,598} = 1.59$; $P = 0.2083$). Interactions of host by direction ($F_{15,90} = 1.11$; $P = 0.3572$), row by direction ($F_{15,598} = 1.27$; $P = 0.2186$) and host, row, and direction ($F_{75,598} = 0.89$; $P = 0.7258$) were not significant.

ELISA absorbance values for WSMV on rows directly adjacent to the plot differed between hosts ($F_{5,25} = 6.75$; $P = 0.0004$) with barnyard grass (0.68; $F_{1,25} = 25.12$; $P < 0.0001$) having greater absorbance values than all other hosts. In addition, foxtail millet (0.41; $F_{1,25} = 7.75$; $P = 0.0101$) had greater values than post-harvest wheat (0.16) and bare ground (0.12). No differences occurred between corn ($F_{1,25} = 1.45$; $P = 0.2392$) or green foxtail ($F_{1,25} = 3.00$; $P = 0.0956$) when compared with post-harvest wheat and bare ground. ELISA absorbance values also varied by direction ($F_{3,90} = 5.25$; $P = 0.0022$) with the east (0.46; $F_{1,90} = 10.86$; $P = 0.0014$) having greater absorbance values than north (0.34), west (0.28), and south (0.19). The interaction between host and direction was not significant ($F_{15,90} = 1.26$; $P = 0.2437$).

ELISA values for east rows one, three and five (Fig. 3.5b) differed between hosts ($F_{5,25} = 7.78$; $P = 0.0002$) with barnyard grass (0.94; $F_{1,25} = 31.37$; $P < 0.0001$) having higher absorbance values compared to corn (0.41), foxtail millet (0.37), green foxtail (0.40), post-harvest wheat (0.15) and bare ground (0.11). Corn ($F_{1,25} = 4.77$; $P = 0.0386$) and green foxtail ($F_{1,25} = 4.20$; $P = 0.0510$) had significantly greater absorbance values

and foxtail millet ($F_{1,25} = 3.37$; P = 0.0784) was approaching significance when compared to the average of post-harvest wheat and bare ground plots. Rows were approaching significance ($F_{2,60} = 2.41$; P = 0.0982) with row one (0.45) having numerically but not significantly ($F_{1,60} = 2.41$; P = 0.0861) higher absorbance than rows three (0.32) and five (0.40). The interaction between host and row was not significant ($F_{10,60} = 1.42$; P = 0.1919).

Mite Movement and Virus Impact Correlations

To evaluate the relationship between mite movement and virus impact, we correlated mite movement parameters (proportion of plants infested and average number of mites per plant) with virus symptomology (SPAD values) and presence (ELISA absorbance) for each year of the study (2013-14 and 2014-15) (Table 3.4). Mite movement parameters were further divided into two categories based on season long mite movement and movement occurring after falling planting of wheat (after Sept. 15). Virus symptomology (SPAD) and virus presence (ELISA) were divided into three categories to evaluate correlations with different spatial relationships around the plots and included:1) average of the row directly adjacent to the plot in each cardinal direction (row 1, 2) average of the rows sampled for ELISA east of the plot (east rows 1, 3, and 5), and 3) all rows sampled for ELISA (row 1 in all directions, plus rows 3 and 5 to the east of the plot).

In 2013-14, the average number of mites per plant across the entire season provided the strongest correlation with virus symptomology and presence. A strong negative correlation was found with SPAD at -0.64, -0.58, -0.63 and a similar positive

correlations was obtained for ELISA with 0.63, 0.52, 0.68 for row one, east rows and all rows parameter, respectively. A poor relationship was found for mite movement parameters of the post planting period with a range of -0.17 to -0.19 and 0.10 to 0.12) across all spatial parameters for virus symptomology and presence, respectively. The proportion of plants infested with mites showed a slightly lower but similar correlation to the average number of mites for whole season movement when compared with SPAD values ranging from -0.50 to -0.53. ELISA absorbance values with the proportion of plants infested for the whole season were similar for row 1 (0.51) and all rows (0.53); however, correlation values were reduced for east rows (0.32). Correlations were lower for all virus impact parameters when compared to mite movement data from the post planting period.

In 2014-15, the strength of correlations varied considerably when comparing SPAD and ELISA. In general, stronger correlations were found between the proportion of infested plants and ELISA absorbance readings ranging from 0.58-0.65. Similar correlations were found between the average number of mites per plant and ELISA readings for row one (0.61), east rows (0.58), and all rows (0.64). SPAD correlations with mite movement parameters were lower than those for ELISA parameters. Correlations with post planting data were lower than those for entire season data; however, these values were not as variable as those in 2013-14.

Discussion

Consistent and significant mite movement occurred from neighboring winter wheat fields to the study site during both years (Fig. 3.1). Peak mite movement coincided with the soft- and hard-dough stages of winter wheat and then declined rapidly after harvest. Over-summering hosts, with the exception of post-harvest wheat, were at various stages of vegetative development (Table 3.2) during the peak mite movement period providing substantial opportunity for mites to infest and become established on over-summering hosts. The relative pressure of mites on over-summering hosts is supported by the high frequency and large population of mites found on pre-harvest wheat within a week of harvest. Extensive infestation of pre-harvest wheat necessitated its destruction to eliminate its potential to infest other host plots. After destroying pre-harvest wheat, plots were designated as 'bare ground' plots, and they provided a measure of background mite activity for the remainder of the season. Trap pots in bare ground plots had minimal mite presence in both years, indicating that there was no significant background or interplot movement of mites. Thus, mite spread and virus impact within and around an individual plot would be representative for that host.

Mite activity and virus impact from over-summering hosts varied between the two study years, primarily as a result of continued mite movement during the fall of 2014. Similar environmental conditions were reported each fall, with the exception of warmer temperatures during October 2014. Warm temperatures may have allowed for continued growth of over-summering hosts and reproduction of mites leading to an extended period of mite movement. Virus impact on fall planted wheat was greater in 2014 when compared with 2013 and was likely a result of an earlier planting date and warmer

temperatures during the 2014 season. In 2013, heavy rains during early-September delayed planting with wheat emerging during early-October.

Of the over-summering hosts evaluated, barnyard grass provided the greatest mite movement (Fig. 3.3a,b; 3.5a,b), virus symptomology (Fig. 3.4a, 3.6a), and virus presence (Fig. 3.4b, 3.6b) during both years of the study. The potential risk of barnyard grass as a source of mites and virus was not anticipated based on historical literature. Somsen and Sill (1970) indicated that only 2.2% of barnyard grass plants surveyed were found to be infested with WCM. The reduced mite presence they saw could be due to a lack of mite pressure in the areas surveyed or differences in timing of emergence of barnyard grass relative to winter wheat harvest. Christian and Willis (1993) documented greater potential for barnyard grass with WSMV infection rates ranging from 10% in 1988 to 56% in 1989. However, high WSMV infection rates on barnyard grass indicates that mites have fed on the host and that the plants are susceptible to virus, but it does not indicate mite presence or potential for mite movement back to wheat in the fall. The high risk of mite and virus presence in barnyard grass in this field study and the conflicting data from previous research, indicates the value of conducting field studies to evaluate the risk characteristics stated in Christian and Willis (1993).

Foxtail millet showed consistent and significant mite movement during both years of the study with increasing mite activity during the fall of 2014. Virus presence on trap pots was less consistent with only one collection period with 36% WSMV positive trap plants. Low virus presence in trap pots corresponded with limited virus presence around the plots. WSMV was detected via ELISA on the surrounding wheat plants, but absorbance values were not greater than those for post-harvest wheat or bare ground plots

in either season. The lack of virus spread from foxtail millet may be a related to the differential susceptibility of foxtail millet varieties to WSMV as reported by Slykhuis 1952, 1955, 1961, Sill and Connin 1953, Sill and Agusiobo 1955, Seifers et al. 1996). This study provides the first field based evidence of mite movement and virus spread from foxtail millet, adding critical supporting evidence for previous anecdotal and field based observations (Shahwan and Hill 1984). Historical inconsistences of virus impact around foxtail millet fields may correspond to the timing of foxtail millet harvest or its ability to support WSMV. The presence and importance of foxtail millet in the western Great Plains region indicates the need for additional studies to better understand the relationship between timing of foxtail millet harvest, differences in virus susceptibility of current varieties, and its status relative to the emergence of fall planted winter wheat.

Green foxtail showed a low but significant level of mite activity throughout the summer with 19 and 32% of trap plants infested with mites in 2013 and 2014, respectively. Mite presence corresponded with virus symptomology (Fig. 3.3a) and presence (Fig. 3.3b), but virus presence was limited to the first row in 2013. In 2014, virus symptomology (Fig. 3.5a) and presence (Fig. 3.5b) spanned multiple rows. An earlier planting date and warmer fall temperatures in 2014 likely contributed to increased virus presence. Previous literature has shown a consistent but low number of WCM on green foxtail plants under field conditions; however, its potential impact on winter wheat was unknown. The literature contains several potential over-summering hosts with low levels of mite activity indicating a need for such hosts to be evaluated in a similar manner to properly estimate their risk to wheat.

Corn had relatively low levels of mite activity during the over-summering period for both seasons with peak mite activity occurring during mid- to late September. Nault and Styer (1969) documented the presence of mites on corn after the V8 leaf stage. During both years, corn development was beyond the V8 stage at wheat harvest, increasing the potential to be become infested. Mite activity from corn was generally lower than anticipated. This could be due to structural differences of corn compared to other over-summering hosts in this study. Mites are generally found within the husks and ears of corn during the latter half of the season (Nault and Styer 1969). Corn ear height, reduced vegetation density in the lower canopy, and small plot size may have limited the mite activity in the lower part of the canopy where the trap pots were located. Higher mite activity in the canopy is further supported by the distribution of virus presence around the plots with greater virus damage at row five than row one during the spring of 2015. Future studies should consider placing additional trap pots at intervals away from the corn plots to provide an estimation of differences in mite activity based on trap pot location for structurally taller hosts. Virus impact around plots in combination with historical literature indicates caution when planting winter wheat next to corn that has not been harvested.

Correlations between mite movement and virus symptoms (SPAD) or virus presence (ELISA) varied considerably between the two years of the study. The greatest and most consistent correlations across both years of the study occurred when the average number of mites per plant across the whole season was combined with ELISA absorbance values for all rows. In 2013-14, the average number of mites per plant had a better correlation with virus impact due to the large number of mites per trap plant from

the trap pots and virus impact from barnyard grass. The differences between SPAD and ELISA were relatively small for either of the mite movement parameters when using whole season mite movement data.

Poor correlations in 2013-14 occurred when mite movement was limited to the post-planting date. This likely resulted from delayed planting and emergence of the winter wheat and a reduction in mite activity from over-summering hosts for the last sample period. In contrast, correlations for mite movement after planting provided a good correlation for SPAD and ELISA during 2014-15 with the highest correlations occurring for ELISA absorbance values; however, these correlations were lower than the full season correlations. A reduction in correlations for SPAD readings during 2014 could be due to the timing of SPAD reading or the presence of other chlorophyll limiting diseases or abiotic factors in the field study.

The results from this study demonstrate the ability of barnyard grass, green foxtail, and foxtail millet to support mites under field conditions and cause significant virus impact to fall planted winter wheat. Establishing plots and allowing for natural infestation of mites and virus allowed for better representation of natural infestation potential of over-summering hosts. Monitoring mite movement into the study area provides an indication of the extent and timing of mite movement with synchrony of over-summering host stage of development. In addition, monitoring movement from each host provided an understanding of the temporal ability of an over-summering host to support mites, and provided additional information on its risk potential during the fall period. Virus impact around host plots was fundamental to understanding risk as foxtail millet supported a large number of mites but showed reduced virus impact relative to

barnyard grass. The combination of mite movement and virus impact provides the most complete picture of over-summering host risk as source of mites and virus to fall planted winter wheat.

Conducting over-summering host studies under field conditions provided an opportunity to evaluate mite type differences between hosts. Our results indicate that mite types varied by host; as a result, future studies should consider mite types when conducting field or greenhouse experiments. Our results may provide some resolve in the differences in mite survival reported in previous studies.

The ability of barnyard grass and green foxtail to support mites and cause damage to fall planted wheat indicates a need for a better understanding of the distribution and frequency of these hosts in the western Great Plains. Such information would also provide an understanding of other potential hosts that may be important the wheat-mite-virus complex.

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Tables

Table 3.1. Average monthly, fall (Sept. – Nov.), and spring/summer (April – Aug.) temperatures in (°C) and total monthly precipitation (mm) during the winter wheat growing season and over-summering period between harvest and planting for Sidney, NE. Data provided by the High Plains Regional Climate Center, University of Nebraska-Lincoln.

	2012-13		2013-14		2014-15	
Month	Temp. (°C)	Precip. (mm)	Temp. (°C)	Precip. (mm)	Temp. (°C)	Precip. (mm)
Sept.	27.0	11.7	26.0	187.2	25.3	78.7
Oct.	15.7	8.9	14.1	37.9	19.7	19.8
Nov.	13.6	0.0	10.0	0.0	7.9	7.6
Sept. - Nov.	**18.8**	**20.6**	**16.7**	**225.0**	**17.6**	**106.2**
Mar.	10.5	0.0	10.3	0.0	15.8	3.6
Apr.	11.3	0.3	16.0	5.8	16.3	96.0
May	21.1	63.3	20.4	88.1	16.4	189.5
June	28.4	63.0	27.2	3.8	26.9	63.0
July	30.1	90.2	30.4	11.7	29.6	58.4
Aug.	30.9	27.9	30.1	50.0	22.5	12.4
Mar. – Aug.	**22.0**	**244.6**	**22.4**	**159.5**	**22.5**	**422.9**

Table 3.2. Development stage of hosts (pre-harvest and post-harvest wheat, barnyard grass, green foxtail, foxtail millet, and corn) at harvest and fall planting of winter wheat for 2013 and 2014.

Host	Wheat Harvest		Fall Planting	
	2013	2014	2013	2014
Pre-harvest wheat	Z29+	Z29+	-	-
Post-harvest wheat	-	-	Z24	Z28
Corn	V13	VT/R1	R6	R5.25
Foxtail millet	Z32	Z32	Z59	Z59
Barnyard grass	Z29	Z31	Z57-59	Z55-59
Green foxtail	Z26	Z28	Z57-59	Z59

*Z = Zadoks scale used to assess plant development for pre-harvest, post-harvest, foxtail millet, barnyard grass, and green foxtail. Corn staged according to leaf collar method (Abendroth et al. 2011).

Table 3.3. Orthogonal contrasts for proportion of mite infested trap plants and average mites per trap plant for over-summering hosts (corn, foxtail millet (FTM), green foxtail (GFT), barnyard grass (BYG), destroyed pre-harvest wheat (bare), and post-harvest wheat. Significant differences between contrasts indicated as * = P<0.05 and ** = P<0.01.

	2013-14				2014-15			
	Prop. Infested		Avg. # Mites		Prop. Infested		Avg. # Mites	
Orthogonal Contrasts	**d.f.**	**F-value**	**d.f.**	**F-value**	**d.f.**	**F-value**	**d.f.**	**F-value**
		Wk 3 Sept. 2013				*Wk 4 Sept. 2014*		
1. corn, FTM, GFT, BYG vs. post-harvest and bare	1, 142	12.3**	1, 150	34.72**	1, 141	13.7**	1, 140	7.5**
2. corn vs. GFT, FTM, BYG	1, 142	13.0**	1, 150	35.46**	1, 141	17.9**	1, 140	17.0**
3. GFT and FTM vs. BYG	1, 142	7.5**	1, 150	93.07**	1, 141	7.1**	1, 140	10.3**
4. GFT vs. FTM	1, 142	2.7	1, 150	0.00	1, 141	15.2**	1, 140	10.2**
5. bare vs. post-harvest	1, 142	0.5	1, 150	0.05	1, 141	0.6	1, 140	0.0
		Wk 1 Oct. 2013				*Wk 2 Oct. 2014*		
1. corn, FTM, GFT, BYG vs. post-harvest and bare	1, 142	9.0**	1, 150	4.88*	1, 141	21.7**	1, 140	15.8**
2. corn vs. GFT, FTM, BYG	1, 142	9.1**	1, 150	4.05*	1, 141	20.1**	1, 140	15.2**
3. GFT and FTM vs. BYG	1, 142	1.7	1, 150	0.05	1, 141	9.3**	1, 140	7.9**
4. GFT vs. FTM	1, 142	12.9**	1, 150	5.59*	1, 141	9.1**	1, 140	7.4**
5. bare vs. post-harvest	1, 142	0.0	1, 150	0.00	1, 141	0.5	1, 140	0.0
		Wk 3 Oct. 2013				*Wk 4 Oct. 2014*		
1. corn, FTM, GFT, BYG vs. post-harvest and bare	1, 142	3.0	1, 150	0.14	1, 141	8.7**	1, 140	14.0**
2. corn vs. GFT, FTM, BYG	1, 142	2.0	1, 150	0.10	1, 141	8.7**	1, 140	14.0**
3. GFT and FTM vs. BYG	1, 142	0.2	1, 150	0.00	1, 141	2.0	1, 140	1.8
4. GFT vs. FTM	1, 142	0.6	1, 150	0.10	1, 141	11.2**	1, 140	24.3**
5. bare vs. post-harvest	1, 142	0.0	1, 150	0.00	1, 141	0.0	1, 140	0.0

Table 3.4. Correlations between mite movement parameters (proportion of infested trap pot plants and average number of mites per trap pot) across two different times periods (season long and post-planting) and virus symptomology (SPAD) or virus presence (WSMV ELISA) with three different spatial areas (row 1, east rows, and all rows). Significant differences between contrasts indicated as * = P<0.05, ** = P<0.01, and *** = P<0.0001 (n =36).

Mite Movement Parameter		SPAD (Relative Chlorophyll)			WSMV ELISA Absorbance		
		Row 1[1]	East Rows[2]	All Rows[3]	Row 1[1]	East Rows[2]	All Rows[3]
2013-2014 Season							
Proportion Infested Plants	**Season[4]**	-0.52**	-0.50**	-0.53***	0.51**	0.32*	0.53***
	Planting[5]	-0.41*	-0.36*	-0.40*	0.26	0.19	0.29
Average # Mites/Plant	**Season[4]**	-0.64***	-0.58***	-0.63***	0.63***	0.52**	0.68***
	Planting[5]	-0.18	-0.17	-0.19	0.10	0.11	0.12
2014-2015 Season							
Proportion Infested Plants	**Season[4]**	-0.56***	-0.37*	-0.46**	0.64***	0.60***	0.65***
	Planting[5]	-0.52***	-0.35*	-0.43**	0.63***	0.58***	0.63***
Average # Mites/Plant	**Season[4]**	-0.48**	-0.31	-0.38*	0.61***	0.58***	0.64***
	Planting[5]	-0.39*	-0.23	-0.29	0.51***	0.49**	0.53***

[1] Row 1: average of rows in all directions directly adjacent to the plot
[2] East Rows: average of rows 1, 3, 5 east of plot
[3] Rows 1,3,5: average of row 1 in all directions, and row 3, 5 east of plot
[4] Season: average of all collection dates
[5] Planting: collections occurring after fall planting of wheat

Figures

Figure 3.1. WCM movement into the study area as an average of percent of trap plants infested across four locations at each cardinal direction from the study for each year (2013 and 2014 season).

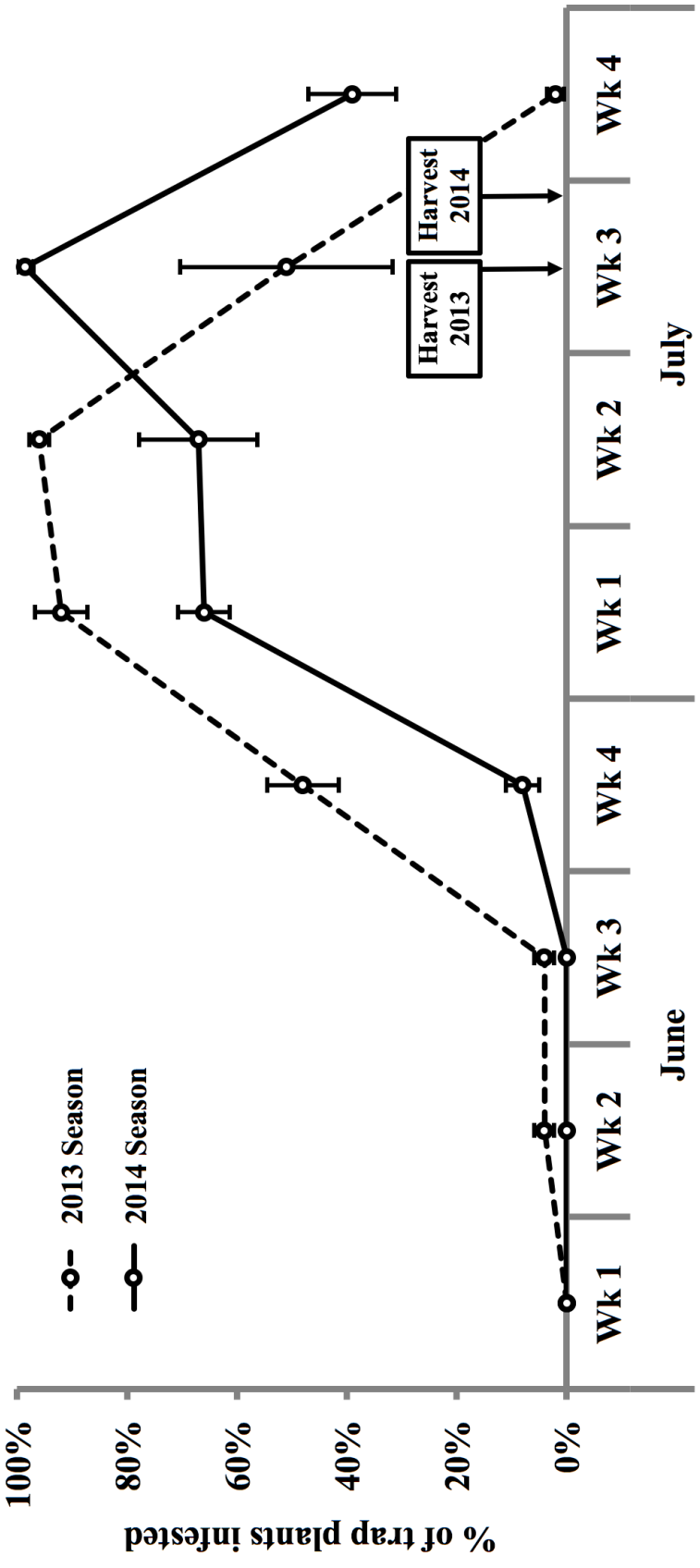


Figure 3.2. Proportion of infested trap plants (a) and average number of wheat per trap plant (b) for 2013-14 season from one week after wheat harvest until late October for six hosts (barnyard grass, corn, foxtail millet, green foxtail post-harvest wheat, and pre-harvest wheat / bare).

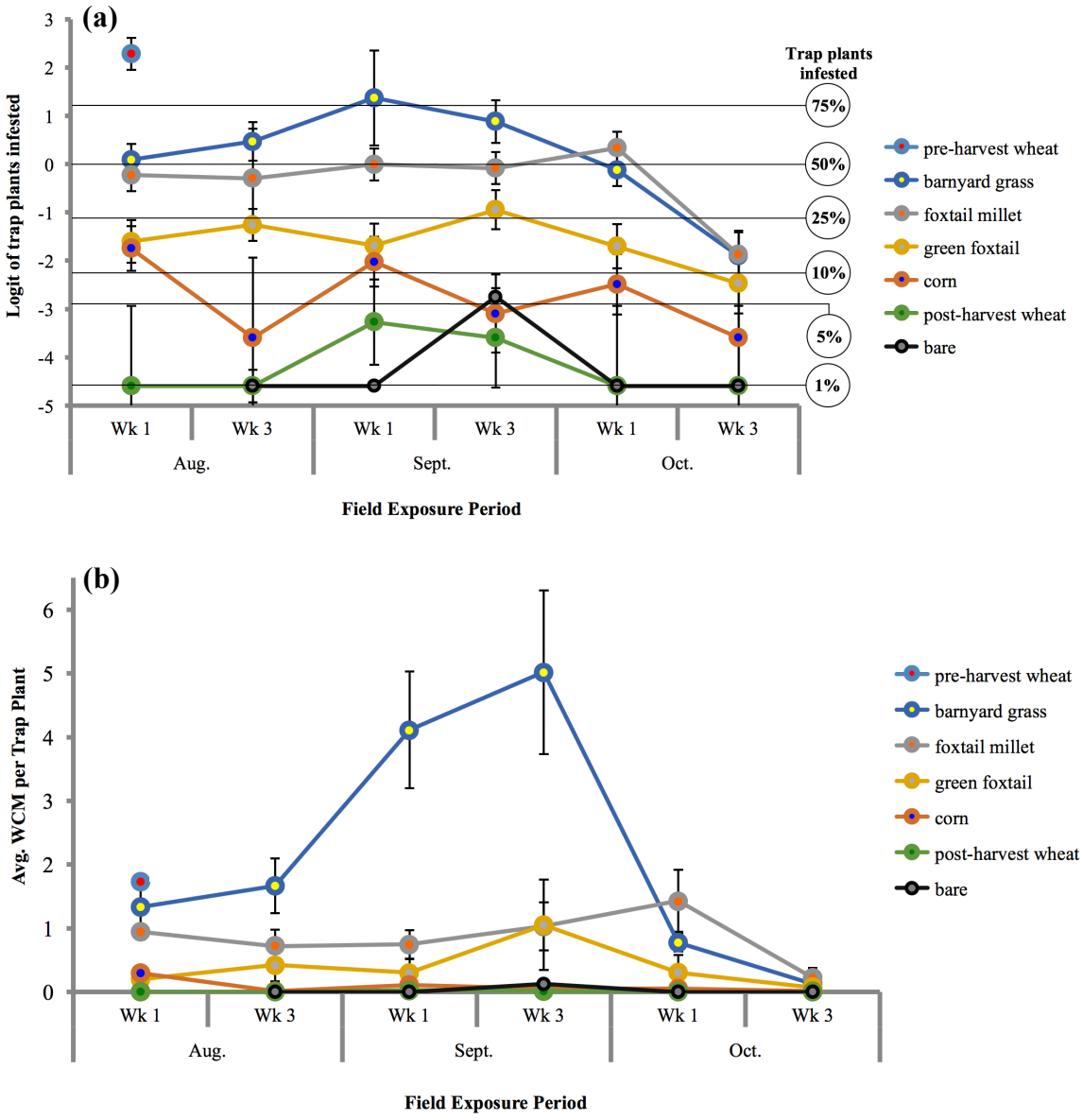


Figure 3.3. Virus symptomology (SPAD: relative chlorophyll content) and presence (WSMV ELISA absorbance) for wheat surrounding the over-summering plots (spring 2014).

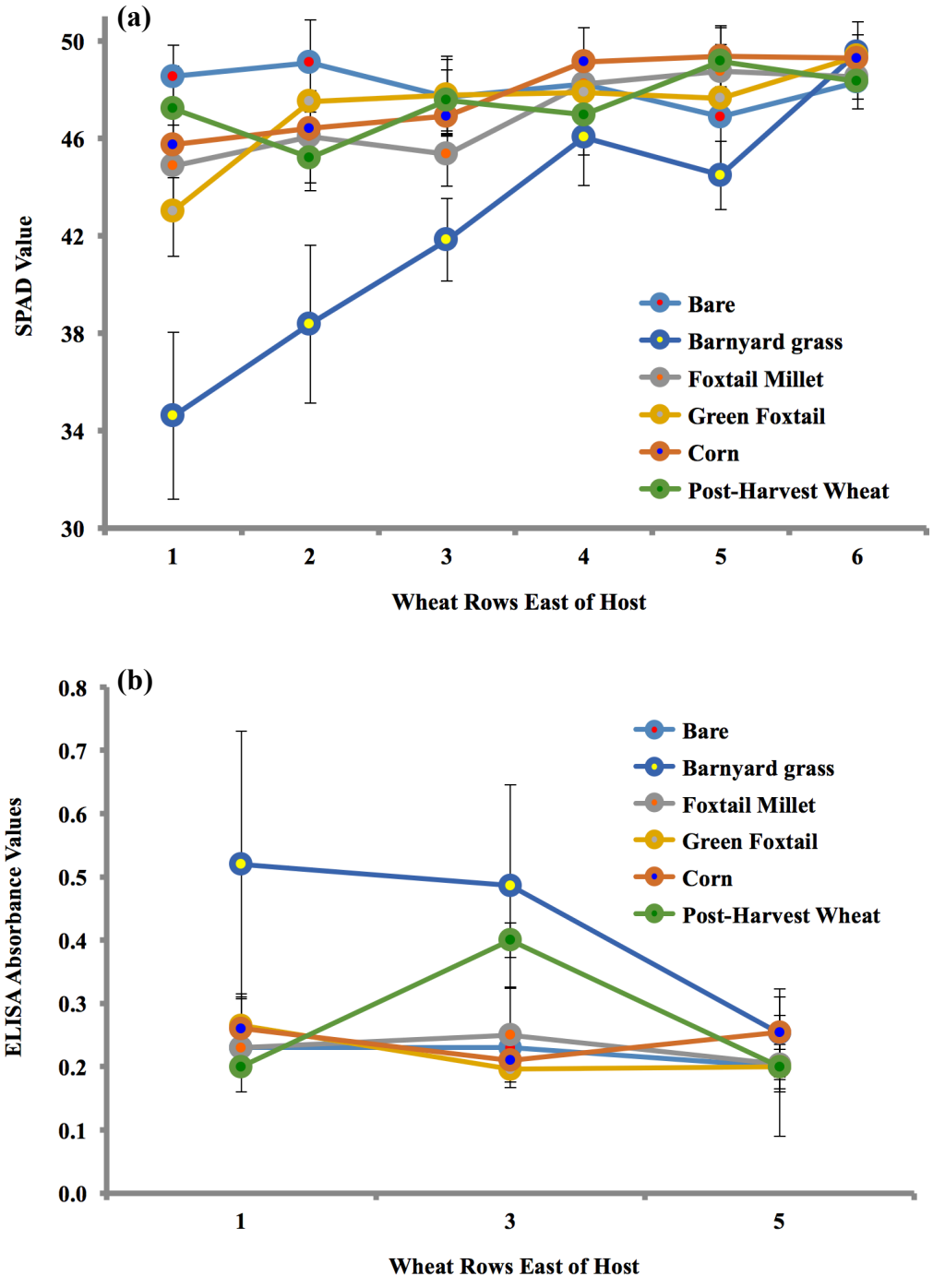


Figure 3.4. Logit of infested trap plants (a) and average number of wheat per trap plant (b) for 2014-15 season from one week after wheat harvest until late October for six hosts (barnyard grass, corn, foxtail millet, green foxtail post-harvest wheat, and pre-harvest wheat / bare).

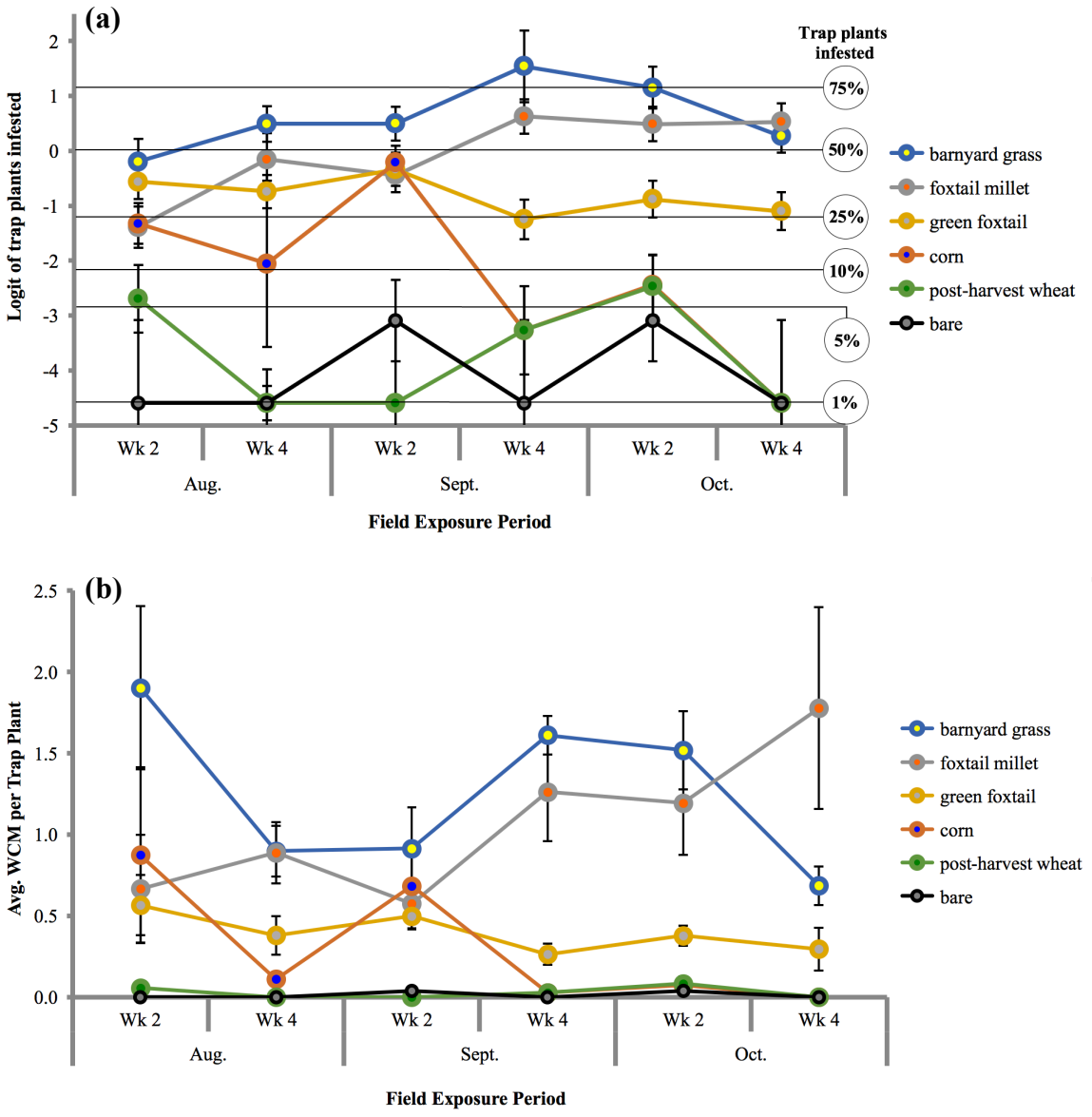
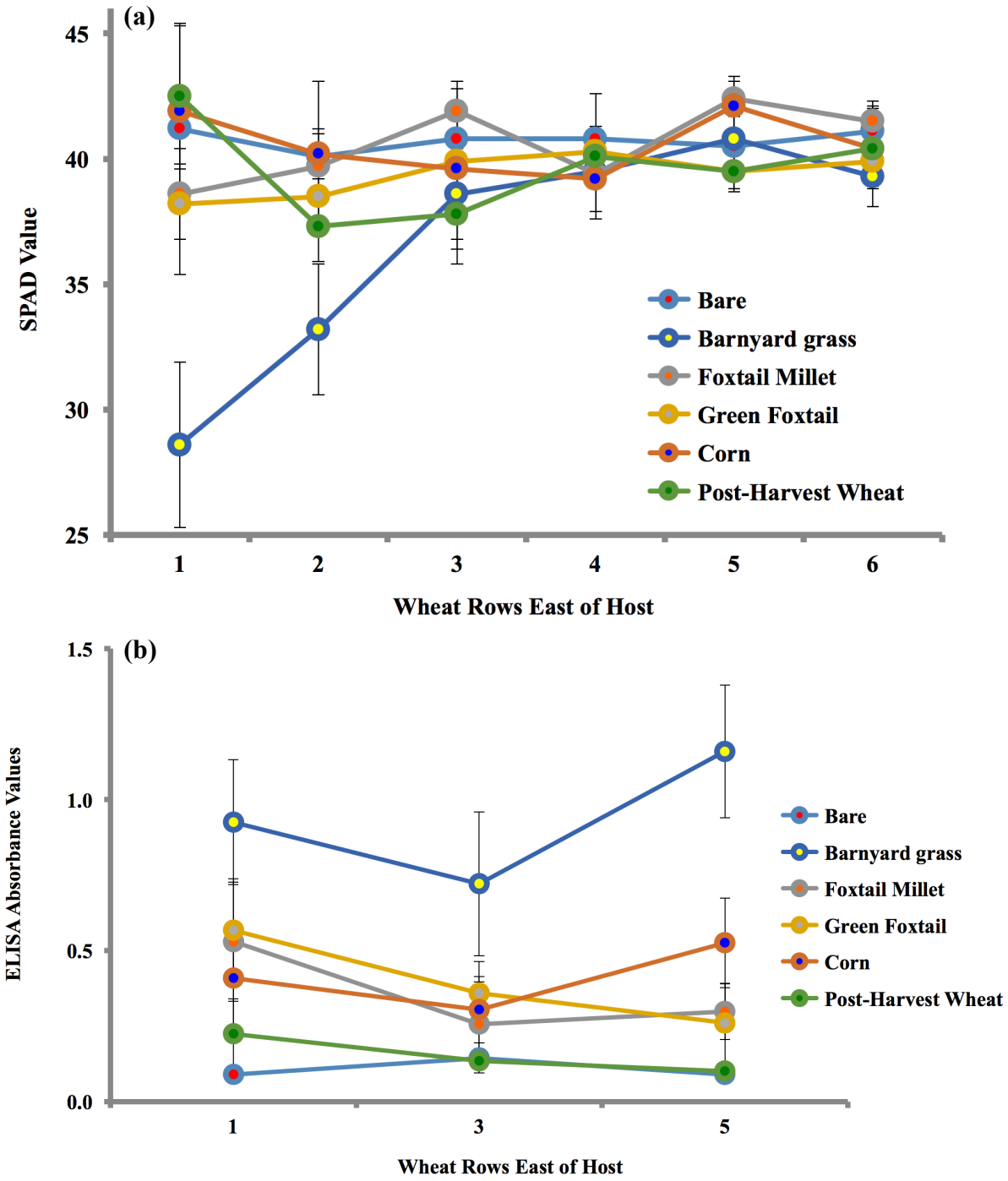


Figure 3.5. Virus symptomology (SPAD: relative chlorophyll content) and presence (WSMV ELISA absorbance) for wheat surrounding the oversummering host plots (spring 2015).



CHAPTER 4

Window of Risk for Germination of Pre-Harvest Volunteer during the Heading Stages of Winter Wheat

Introduction

The wheat-mite-virus complex is one of the primary yield limiting diseases in wheat in the western Great Plains. Kansas disease loss estimates indicate that approximately 11 million bushels (2.7%) of wheat was lost as a result of this complex during the 2015 season (Appel et al. 2015). This complex consists of three viruses (*Wheat streak mosaic virus* (WSMV), *Triticum mosaic virus* (TriMV), and *Wheat mosaic virus* (WMoV)) that are transmitted by the wheat curl mite (WCM) (*Aceria tosichella* Keifer). Landscape level impacts from this complex are not equally distributed throughout the Great Plains. Yield impacts are usually localized to a few fields and are primarily attributed to the presence of pre-harvest volunteer wheat.

Risk of pre-harvest volunteer wheat as a source of mites and virus requires a sequence of events beginning prior to winter wheat maturing in early summer. Risk begins with wheat seeds being dislodged from wheat heads usually as a result of hailstorms occurring during the heading stages of winter wheat. Hailstorms are often accompanied by rain, resulting in adequate moisture to germinate the dislodged seeds. Volunteer wheat germinating prior to winter wheat maturing (pre-harvest volunteer wheat) allows mites to move directly from the maturing wheat crop to the volunteer wheat. Once established, WCM populations can build rapidly during the summer months, as long as the volunteer wheat remains viable. Wheat planted in adjacent fields will gradually become infested with WCM from pre-harvest volunteer wheat. The timing of the mite infestation and virus inoculation, presence of resistant varieties, and prevailing environmental conditions will determine the yield impact on winter wheat.

The risk potential for volunteer wheat to serve as a source of mites and virus depends on the timing of its emergence. This is due to the limited off-plant survival of the WCM of only less than 1-2 days under warm temperatures and low humidity conditions (Wosula *et al.* 2015). As a result, volunteer wheat emerging after harvest results in a break in the green bridge period without a viable host for WCM. This break reduces the potential for mites to infest volunteer wheat and dramatically reduces the risk potential to fall planted wheat.

The importance of the pre-harvest volunteer wheat in the epidemiology and impact of the wheat-mite-virus complex reinforces the need for detailed information on the winter wheat head development stage at which winter wheat could germinate. Such information is critical for determining the window of time where hail events could result in germination of pre-harvest volunteer wheat. Information on the window for germination can help concentrate grower and consultant efforts in scouting and evaluating potential high-risk fields.

The germination of immature wheat prior to crop maturity has been an important topic in winter wheat breeding as a means of accelerating breeding programs and genetics studies (Robertson and Curtis 1967). Researchers have identified numerous factors that can influence the ability of winter wheat seed to germinate prior to harvest, such as temperature, drying after collection, handling, variety, and location within the wheat head (Nutman 1941, Nosatovsky 1957, Aginyan 1958, Kalinin 1959, Robertson and Curtis 1967, Balla 1979).

Without post collection modifications, winter wheat is capable of germinating approximately 9-14 days after pollination with adequate long-term available moisture

(Nutman 1941, Nosatovsky 1957, Aginyan 1958, Kalinin 1959, Abramova 1964, Robertson and Curtis 1967, Balla 1979). Temperature is an important component in these evaluations as non-ripened wheat seeds appear dormant at 20-35°C whereas germination can occur at 10-15°C (Atterberg 1907, Ching and Foote 1961, George 1967). In addition, temperature was found to have a significant effect on the total germination with a higher percentage of seeds germinating at 12°C (80%) compared to 20°C (49%) (Balla 1979).

Drying or desiccating immature wheat heads prior to inducing germination can significantly reduce the number of days from pollination necessary for germination, as well as the percentage of wheat seeds that germinate (Balla 1979). Balla (1979) found that wheat was capable of germinating at 6-8 days after pollination with 12 weeks of drying. In contrast, wheat was unable to germinate until 14 days after pollination without drying (Balla 1979).

Post collection handling of immature wheat seeds has been shown to increase its germination potential. Removal of the outer-pericarp from unripened wheat seeds increased their germination (Wellington 1956a, Gordon 1970, Radley 1979, Mitchell et al. 1980). It is hypothesized that the inhibitory effect of the outer-pericarp is due to its mechanical strength (Wellington 1956b) or the restriction of gas exchange with the embryo (Radley 1979).

Detailed studies by Wellington (1956a) and Hardesty and Elliott (1956) found that seed location within a wheat head could have a significant impact on its germination with limited germination occurring at the base of the head unless desiccated prior to germination. This may be in part due to the sequence of fertilization within a wheat head. This first occurs for seeds in the middle of the head followed by those at the top, and

lastly, the seeds located at the base of the wheat head are fertilized (Wellington 1956a). Percival (1922) observed similar results with a 2-4 day delay in anthesis of the basal spikelet.

Seed dormancy or pre-harvest tolerance to sprouting has been tightly linked to seed color, and as a result, cultivars vary significantly in tolerance to germination prior to harvest. Wellington (1956a) observed a rapid increase in germination of white wheat (88%) at 5-8 weeks whereas red wheat was only 7% germinated. Nyachiro et al. (2002) tested 10 spring wheat varieties with varying degrees of dormancy at different temperatures and found that low temperatures could break seed dormancy in tolerant varieties. Mares (1993) found that eight hard white wheat cultivars varied significantly in their germination at and following harvest. Five hard red winter wheat varieties were evaluated for germination of immature kernels by Robertson and Curtis (1967); however, the authors indicated that there were no differences between the varieties with average germinations occurring within 15 days of pollination with green wheat. Although a significant amount of work has been conducted on pre-harvest germination there is a lack of information on germination of early stages of head development on current wheat varieties without drying and a comparison of early season germination of varieties based on sprouting tolerance scores.

A recent study by Graybosch et al. (2013), evaluated genetic markers for prediction of pre-harvest sprouting in winter wheat. Commercially available hard red winter wheat varieties showed a wide variation in sprouting tolerance with the greatest tolerance occurring in ‘Camelot’ and lowest tolerances occurring in ‘Pronghorn’. An analysis of marker alleles across several wheat varieties revealed that *QPhs. pseru-2B1*

provided a significant contribution to pre-harvest tolerance in the white winter wheat ‘Rio Blanco’ (Graybosch et al. 2013). The identification of genes for pre-harvest tolerance tosprouting and screening methods for selecting sprout-tolerant wheat varieties provides an opportunity to determine whether or not these characteristics could be important for pre-harvest germination of wheat following natural hail events.

Wheat germination research has been primarily focused on early season harvest of winter wheat to shorten breeding cycles and not as a means of determining risk for pre-harvest volunteer development. The goal of this study was to evaluate the germination of winter wheat from varieties with varying degrees of pre-harvest sprouting, establish a first germination date based on thresholds for each variety, and determine a window of risk for the development of highly risky volunteer wheat. Unlike previous studies, this research was done over a number of seasons to gain an understanding of the impact of the crop growth environment on germination, and determine if variety could be used as a means of reducing the potential for pre-harvest volunteer wheat. Previous studies have only documented the number of days since anthesis and not the stage of wheat development at first germination. Days after anthesis is an accurate description under controlled conditions; however, the head development of wheat will progress at different rates under field conditions due to temperature and moisture availability. Such information is critical for producers and consultants to evaluate the risk for this serious disease under field conditions.

Materials and Methods

Germination for Wheat Head Collections

Wheat heads were collected from fields over three separate growing seasons at two locations per season in conjunction with the Winter Wheat State Variety Trials conducted by the University of Nebraska-Lincoln. The 2011-12 and 2013-14 samples were collected from Cheyenne and Deuel County, Nebraska. The 2012-13 samples were collected from Cheyenne and Kimball County. Two wheat varieties were chosen based on their tolerance to pre-harvest sprouting, 'Pronghorn' (susceptible) and 'Camelot' (resistant) (Graybosch et al. 2013). These varieties were grown in a randomized complete block design with five replications. Each plot consisted of 6, 6-m rows with 0.3-m spacing between rows. Plots were sampled every 7-9 days beginning at the water-ripe stage until harvest with 5-8 collections occurring during each season. Three wheat heads were randomly selected from the far right row of each plot. Wheat heads were staged based on a seed selected from the middle of each wheat head. After staging, wheat heads were each placed in separate clear plastic clamshell food containers (10 x 10-cm) to evaluate germination. Awns were cut back to the glumes on each head and seeds were separated from the rachis. Seeds were spread across the soil surface and sprayed with 12 mL of water. Containers were sealed and held at 18 – 24°C and germination was evaluated every three days up to 21 days. The numbers of seeds per head were counted during the final sample for each variety to determine the total seeds available for germination.

Risk of volunteer wheat germination was evaluated in four separate analyses, to evaluate variety germination characteristics, risk groups, time-to-event for first

germination, and pre-harvest germination regressions. Germination variety characteristics were determined by analyzing the germination potential of sprouting tolerant and susceptible wheat varieties at each stage of head development with access to continuous moisture. The second analysis was to determine three risk groups with differing levels of potential access to moisture as an indication of likelihood that germination could occur in the field. The third analysis utilized the risk groups and a 1% germination threshold to determine the window of risk for germination prior to harvest. The last analysis focused on the relationship between germination and pre-harvest date through regression equations. Prior to the analyses, germination counts were converted to proportion of germination. Studentized residuals indicated that proportion data were not normally distributed, with the response variable limited between 0 and 1, thus a beta distribution was used in the analysis.

Variety Germination Characteristics

Germination characteristics between wheat varieties and stages were analyzed with a type I test for fixed effects by using PROC GLIMMIX (version 9.22; SAS Institute 2009). These fixed effects were partitioned over sampling day into linear and quadratic portions to determine fixed effects in prediction models. Non-significant effects were removed from the model. Significant quadratic effects were further analyzed in the solution for fixed effects and individual treatments were removed from equations if they were non-significant. Equation parameters were obtained from the solution for fixed effects. Correlations between observed values and the values predicted by the regression equations were used to estimate the fit of the equations (PROC CORR; version 9.22; SAS

Institute 2008). Contrasts were used to compare intercept, linear, and quadratic parameters between equations.

Risk Groups

An analysis was undertaken to compare germination potential across varieties for various days of incubation in clamshell containers by treating day as a categorical variable. Available moisture is one of the primary constraints to germination of immature wheat seeds under field conditions; therefore, limited time to germination in clamshell containers would represent a greater likelihood of germination under field conditions. Risk groups of 6, 9 and 12 days were chosen based on differences between days and a minimum threshold for germination. Day 6 germination in clamshell containers represented limited access to moisture under field conditions whereas days 9 and 12 represented increasing greater access to moisture following a hail event. These risk groups were used in the time-to-event analysis and pre-harvest germination regressions to evaluate the risk of volunteer wheat establishment with varying levels of available moisture following a hail event.

Time-to-Event

A time-to-event analysis was run to determine the earliest pre-harvest date at which germination could occur using a 1% germination threshold for each risk group (Day 6, Day 9, and Day 12). Prior to the analysis a germination was averaged across the three heads within each plot. Germination values exceeding a threshold of 1% were given the corresponding pre-harvest date when the threshold was exceeded. Studentized

residuals indicated that the response variable of pre-harvest date was normally distributed. An analysis of variance type III test using PROC GLIMMIX (version 9.22; SAS Institute 2008) with an F-test was done to determine significant effects for variety and risk groups. Differences within risk groups and varieties were determined through t-tests. Random effects were years and locations.

Pre-harvest Germination Regressions

A regression analysis was used to determine germination from the time of first germination to harvest. This analysis was done using the same methods as the variety characteristics regression analysis to test the fixed effects of variety and risk group. These variables were partitioned over pre-harvest dates into linear and quadratic effects. Equations were obtained from the solutions for fixed effects after non-significant parameters were removed. Correlations were used to determine fit of equations and contrasts were run to determine differences in parameters.

Results

The seasonal growth and development of winter wheat varied significantly between years, primarily as a result of extreme drought conditions during the 2011-12 growing season. The water ripe (Zadoks 71) stage for winter wheat occurred on 24 May 2012, 10 June 2013, and 12 June 2014. In addition, the developmental time between water ripe and harvest was 35, 40, and 42 days for 2012, 2013, and 2014, respectively. This variation in maturity and development of wheat was primarily due to low precipitation combined with high temperatures in 2012 (19.5mm, 30.1°C) during the head development period compared to 2013 (60.1mm, 26.5°C) and 2014 (76.7mm, 25.9°C).

Variety Germination Characteristics

An analysis of year, variety, and days in germination containers showed no interaction for year by variety ($F_{2,325} = 0.39$; $P = 0.6789$), or year for the linear ($F_{2,325} = 0.03$; $P = 0.9682$), or year for the quadratic ($F_{2,325} = 0.39$; $P = 0.8691$); therefore, years were combined for the analysis.

An analysis of variety and stage (Table 4.1) showed a significant interaction between stage and variety with increasing greater germination for Pronghorn compared to Camelot through hard dough and a reduction in both varieties at the harvest ripe stage. Germination first occurred in Pronghorn in the early milk stage at 0.6%. Increasing germination was observed in Camelot and Pronghorn in the middle milk (0.5%, 1.1%), late milk (0.6%, 2.5%) stages, early dough (0.9%, 9.6%), soft dough (1.2%, 13.0%), hard

dough (2.5%, 21.1%), respectively. Germination declined to 1.8% for Camelot and 12.4% for Pronghorn at the harvest ripe stage.

For regression comparisons between variety and stages across days in germination containers, both linear and quadratic parameters had a significant interaction with variety and stage (Table 4.1). Quadratic parameter evaluation for individual treatment combinations showed that only soft dough, hard dough, and harvest ripe had a significant quadratic effect for Camelot whereas Pronghorn quadratic parameters were significant from the late milk through harvest ripe stages (Table 4.2; Fig. 4.1, 4.2). Regression equations for varieties and stages were a good fit of observed values with correlations ranging from 0.73 to 0.99 for Pronghorn and 0.70 to 0.98 for Camelot (Table 4.2).

Pairwise contrasts comparing Camelot and Pronghorn at each development stage showed a greater intercept (Table 4.3) for Pronghorn at late milk, soft dough, and hard dough compared to Camelot at the same stages. In addition, linear parameter contrasts (Table 4.4) showed greater slopes for Pronghorn compared to Camelot at middle milk and late milk. Quadratic parameters (Table 4.5) showed no differences between varieties at the same stage of development, indicating similar onsets of dormancy near wheat harvest. However, for Pronghorn the quadratic parameter for late milk was significantly higher than for the remaining stages, and the quadratic parameter for hard dough was significantly lower than for the remaining stages (Table 4.5). Parameter comparisons between varieties for the harvest ripe stage showed no difference for intercepts, linear, or quadratic parameters. However, the combination of these parameters resulted in significant differences between varieties for the harvest ripe stage at day 12 ($F_{1,342} = 6.74$; $P = 0.0097$) with increasing differences through day 21 ($F_{1,342} = 34.78$; $P < .0001$).

Establishing Risk Groups

To establish risk groups for pre-harvest germination, we assumed that more rapid germination or fewer days to germination would represent a greater likelihood of germination under field conditions, and this would result in greater risk potential for volunteer wheat development following a hail storm. Overall, germination increased across the days held in containers, and for both varieties and growth stages, the treatments that germinated earliest also increased to the greatest levels of germination by 21 days (Fig. 4.1, 4.2). The effect of days was highly significant ($F_{6,70} = 27.66$; P <.0001) with germination increasing from 0.7% at day 3 to 18.0% at day 21. The low proportion of germination at day 3 was less than 0.5% for most stages; therefore, it was considered too low to utilize as a risk category. A comparison of day 3 and 6 (1.7%) showed that germination was approaching significance ($t_{70} = -1.83$; P = 0.0722). As a result, day 6 was chosen as the highest risk category because it represented the earliest germination to occur at significant levels. Day 9 germination (3.9%) was significantly greater ($t_{70} = -2.32$; P = 0.0232) than day 6, and it was categorized as medium risk. Lastly, day 12 (7.7%) was greater ($t_{70} = -2.77$; P = 0.0071) than day 9. The time to germination at day 12 represents greater requirements for available moisture following a natural hail event under field conditions. The risk categories (Day 6, 9, 12) from this analysis were used to generate different risk potentials for germination in subsequent analyses.

Time-to-Event Analysis

Window of risk for germination prior to harvest was evaluated using a 1% threshold for each of the risk groups (day 6, 9 and 12) established in the previous analysis. An evaluation of the days before harvest for initial germination in the germination containers was done using an analysis of variance type III test (Table 4.6) to test the fixed effects variety, risk group, and year. Results showed no significant difference between years for pre-harvest germination date; however, differences occurred between varieties with first germination occurring at 21 and 11.5 days prior to harvest for Pronghorn and Camelot, respectively. In addition, risk groups were different from one another with day 12 germination (21.6 days) occurring earlier ($t_{16} = 3.36$; $P = 0.0040$) than day 9 (-15.5 days), which occurred earlier ($t_{16} = 4.85$; $P = 0.0002$) than day 6 (-11.3 days). No interactions occurred between risk group, year, variety or the three-way combination. The lack of interaction between variety and risk group was due to a similar reduction in the number of days prior harvest (Fig. 4.4) from low to high risk for each variety.

Pre-harvest Germination Regressions

A regression analysis was conducted to determine the relationship between germination and pre-harvest date following first germination. An analysis of year, variety, risk group, and pre-harvest day showed a significant year by pre-harvest interaction ($F_{2,160} = 3.13$; $P = 0.0465$) as a result of increasing germination in 2011-12 (Fig. 4) and a decline in germination prior to harvest in 2012-13 and 2013-14 (Fig. 4.5) due to pre-harvest dormancy. This interaction combined with the abnormal weather

conditions resulted in a separate analysis for the 2011-12 growing season for pre-harvest germination equations.

2011-12 season: An analysis of variance type I test for fixed effects (Table 4.7) showed significant main effects (variety, risk group), but there was a significant interaction between variety and risk group. This interaction occurred due to a significant increase in germination between risk groups for Pronghorn with the day 6 germination (1.9%; $t_{29} = -3.95$; P = 0.0005) having greater germination compared to day 9 (6.5%), and day 9 having greater germination that the day 12 germination (25.2%%; $t_{29} = -9.06$; P<.0001) risk group. In contrast, day 6 (0.6%; $t_{29} = -1.50$; P=0.1448) and day 9 (1.9%; $t_{29} = -9.06$; P=0.3591) risk groups were not significantly different from day 12 (1.3%) risk group for Camelot.

Linear effects also showed a significant interaction with variety and risk group (Table 4.7) as a result of greater slope values for Camelot compared to Pronghorn for day 6 germination whereas Pronghorn had greater slopes for day 9 germination. Quadratic effects were not significant for the interaction between variety and risk group; however, the solutions for fixed effects (Table 8) showed a significant quadratic effect for both varieties for the day 12 germination group. Equations (Table 8) were a good predictor of observed values with correlations ranging from 0.87 to 0.99 for across all varieties and risk groups.

Intercept comparisons (Table 4.9) are a reflection of differences in germination at wheat harvest. These contrasts showed that Pronghorn had greater germination than Camelot for each risk group comparison. Within variety, risk group comparisons of intercepts were only significant when comparing day 9 and 12 germination, with greater

values for day 9 germination as a result of a significant quadratic effect for the low risk group. Linear contrasts (Table 4.9) showed greater slopes for Pronghorn compared to Camelot in the high-risk group. No differences in slopes occurred for the other risk groups when comparing varieties. Within Camelot, significant differences occurred between day 6 and day 9 risk groups with a greater slope value (Table 4.9) for the day 9 risk group. For Pronghorn, differences in slopes occurred between all risk groups with greatest slope values occurring for the day 12 risk group, followed by day 9 and day 12 risk groups. Graphical representation of these equations shows that the combination of parameters can make linear slopes difficult to interpret. The combination of these parameters showed that day 6 germination (Fig. 4.4) increased from <0.5% at 25 days to 25.2% for Pronghorn prior to harvest. Increasing germination also occurred for day 9 and 12 groups; however, these increases were lessened by greater germination at 25 days before harvest.

2012-13/ 2013-14 Season: An analysis of variance type I test for fixed effects (Table 4.10) for the 2012-13 and 2013-14 showed differences between varieties and risk groups; however, there was no interaction between these main effects. Although there was no interaction, there was a significant increase in germination between risk groups for Pronghorn at 2.6%, 8.3%, and 16.9% for day 6, 9, and 12, respectively. In contrast, Camelot germination did not differ between risk groups at 0.7%, 1.1%, and 1.9%. Although the interaction term was not significant, its p-value suggest an impact on the regression model and was retained in the regression equation.

Intercept contrast comparisons (Table 4.11) showed no significant differences between risk groups for Camelot whereas all risk groups differed in their intercepts for

Pronghorn. Contrasts between varieties within the same risk group showed significant differences for day 6 germination with greater intercept values for Pronghorn. Linear contrasts (Table 4.11) were only significant for Pronghorn between high and low risk groups; however, low and medium risk comparisons were approaching significance with greater linear parameter for day 12 compared to day 9 risk group. Linear contrasts are inherently difficult to interpret due to the strong quadratic effects that occurred. Quadratic contrasts (Table 4.11) were very similar between risk groups within Camelot whereas significant differences occurred between risk groups for Pronghorn as a result of a reduction in dormancy from high risk to medium and low risk groups (Fig. 4.5). Correlations were lower in 2012-13/2013-14 compared to 2011/12; however, they were a good fit of the observed data ranging from 0.64 to 0.95.

Discussion

Regardless of the differences in environmental conditions between years 'Pronghorn' consistently exhibited greater germination than 'Camelot' with access to continuous moisture by wheat development stage (Fig. 4.1, 4.2) and in the days prior to wheat harvest (Fig. 4.4, 4.5). In addition, the pre-harvest date for first germination (Fig. 4.3) shows that the window of risk for pre-harvest germination began 28 days prior to harvest for Pronghorn whereas risk window for Camelot occurred only 15 days prior to harvest.

The response and characteristics of pre-harvest germination of susceptible and tolerant wheat varieties used in this study corresponded with pre-harvest sprouting tolerance scores established by Graybosch et al. (2013). Selection of wheat lines by plant breeders and the increased perception by growers to proactively manage risk for pre-harvest germination could reduce the potential for the presence of pre-harvest wheat as a potential source for the wheat-mite-virus complex. In addition, the similarities between sprouting tolerance and pre-harvest germination implies that sprouting tolerance scores could be used as a means of selecting varieties for a reduced window of risk for pre-harvest germination. It's important to note that this study was conducted under controlled conditions, and likely provides the greatest potential window for pre-harvest germination. Previous research by Biddulph et al. (2005) showed that pre-harvest dormancy or tolerance of wheat was strongly influenced by environmental conditions such as temperature and rainfall. Results from previous studies imply a need for field studies to better understand and validate the role of these varieties and their window of risk for pre-harvest germination.

The earliest germination by winter wheat occurred at the early milk stage; however, this was only observed for Pronghorn with long-term (15-days) access to moisture. In contrast, the first germination for Camelot did not occur until the middle milk stage. The occurrence of first germination in this study relates well to previous studies that showed germination occurring approximately 9-14 days after pollination with adequate long-term available moisture (Nutman 1941, Nosatovsky 1957, Aginyan 1958, Kalinin 1959, Abramova 1964, Robertson and Curtis 1967, Balla 1979). However, this study documents the development stage of wheat that corresponds with first germination as well as the potential for wheat varieties with high tolerance scores to delay the development stage at which first germination occurs.

Germination peaked for both wheat varieties at the hard dough stage, indicating that this stage provides the greatest potential for establishment of pre-harvest volunteer wheat. For Camelot (Fig. 4.1), hard dough was the only development stage to achieve 1% germination after 6 days on moist soil. In contrast, predicted equations for Pronghorn per wheat development stage (Fig. 4.2) showed that germination exceeded 1% after 6 days on soil at the early dough stage and continued through the harvest ripe stage. Such differences indicate significantly greater potential for pre-harvest germination for Pronghorn.

The methods for wheat head staging and post-collection handling used in this study are important for interpreting results. Seeds selected from the middle of wheat heads represent the most developed portion of the head (Wellington 1956a, Hardesty and Elliott 1956), reinforcing the connection between wheat stage and germination. This method was critical for determining the earliest stage for germination, as the wheat

development stages designated in this study reflect the most developed seeds within the wheat head. In addition, previous literature indicates that our methods of post-collection handling and seed preparation methods may have increased the potential for germination of immature wheat kernels. The process of mechanically separating seeds from the rachis prior to placing them on soil surface could have potentially damaged the outer-pericarp, increasing the potential for early season germination (Wellington 1956a, Gordon 1970, Radley 1979, Mitchell et al. 1980). Damage to the outer-pericarp of wheat seeds in this study is uncertain; however, it is possible that mechanical separation of seeds in this study is similar to the damage incurred during natural hail events as a result of hailstones dislodging seeds from wheat heads. Previous studies also implied that seeds appear dormant at temperatures above 20°C (Atterberg 1907, Ching and Foote 1961, George 1967). Clamshell containers for germination were held between 18 and 24°C, indicating that pre-harvest germination potentials for these wheat varieties are likely conservative based on historical data. In addition, the proportion of germination obtained in this study exceeded those from previous studies, implying a shift towards increased tolerance to higher temperatures for pre-harvest germination of wheat varieties. Further studies are needed to compare historical and current wheat varieties to further determine these factors.

Regression equations following first germination through wheat harvest varied between years. During the drought of the 2011-12 season, both wheat varieties exhibited increasing rates of germination through harvest for high and medium risk groups. In contrast, 2012-13/2013-14 data showed the onset of dormancy as indicated by significant quadratic parameters for all risk groups with high-risk in Camelot showing a

significant reduction in the window of germination prior to harvest. Previous studies by Mares (1993) and Biddulph et al. (2005) show that the influence of rainfall and temperature on sprouting tolerance is not well understood and results vary between studies. Our results provide supporting evidence for Mares' (1993) research, indicating that reduced rainfall and/or increased temperature resulted in minimal pre-harvest tolerance to sprouting. The differences with Biddulph et al. (2005) could be due to the removal of wheat heads from hot-dry conditions to sealed containers with continuous moisture for an extended period. The potential impact of environmental factors demonstrates the need for additional understanding of this relationship.

A comparison of the time-to-event analysis and the days to harvest regression equations shows differences in the window of risk for pre-harvest germination using a 1% threshold. Differences between these analyses are a reflection of the fit of the equation to observed values for regressions whereas the time-to-event analysis was triggered by individual observations exceeding the 1% threshold within the data set. Regression equations for both years, with the exception of the high risk group for Camelot in 2012-13/2013-14 show that germination consistently exceeded the 1% threshold following first germination. This indicates that after first germination the likelihood of germination remains high through the rest of the wheat head development until harvest with the exception of day 6 germination declining below 1% for Camelot prior to harvest in 2012-13 and 2013-14 (Fig. 5).

The results from the study demonstrate the potential window of risk for pre-harvest germination of wheat. This is the first study to draw a link between pre-harvest sprouting tolerance scores and pre-harvest germination following grain shatter that could

result in volunteer wheat. Understanding this relationship increased the value of pre-harvest sprouting scores as a measure for evaluating varieties to reduce pre-harvest germination of wheat. Wheat head collections over three seasons also provided additional information on the role of environmental conditions and their influence on germination. Regardless of these variations, we found no differences between years for pre-harvest date at which first germination occurs (Fig. 4.3), indicating that it remains relatively stable across the wide range of conditions observed in this study. In addition, first germination data show that the pre-harvest date for germination is strongly influenced by wheat variety. The large differences in the window of risk for germination between pre-harvest susceptible Pronghorn and tolerant Camelot implies that producers may be able to use variety to establish the likelihood of establishment of pre-harvest volunteer, and thus, elevated risk for virus disease the following year. Previous studies as well as this study show a strong influence by environmental conditions on regression equations following first germination. This study provides strong evidence that consultants and growers should prioritize scouting for pre-harvest germination in wheat fields hailed during the late milk stage. In addition, fields hailed within three weeks of harvest (early dough) have a greater likelihood of germinating with less available moisture. Lastly, fields hailed at soft dough or within 15 days of harvest provide the greatest potential for pre-harvest germination. These risk windows for germination varied by variety, providing a potential for proactive management of pre-harvest germination.

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Tables

Table 4.1. Analysis of variance type I test for fixed effects for varieties (Camelot and Pronghorn), wheat stages (water ripe, early milk, middle milk, late milk early dough, soft dough, hard dough, ripe) and days (3 – 21) in containers with access to continuous moisture.

Effect	Num DF	Den DF	F-value	P-value
variety	1	45	73.08	<.0001
stage	7	45	28.61	<.0001
variety*stage	7	45	3.82	0.0025
day	1	334	349.12	<.0001
day*variety	1	334	29.66	<.0001
day*stage	7	334	11.41	<.0001
day*variety*stage	7	334	5.59	<.0001
day*day	1	334	15.97	<.0001
day*day*variety	1	334	0.77	0.3808
day*day*stage	7	334	1.65	0.1215
day*day*variety*stage	7	334	1.62	0.1291

Table 4.2. Regression equations in logit for pre-harvest germination at each stage of wheat head development (water ripe, early milk, middle milk, late milk, early dough, soft dough, hard dough, and harvest ripe) and varieties (Camelot and Pronghorn) (y = germination in logit; x = pre-harvest date) *All P-values for correlations were less than 0.01.

Wheat Stage	Variety	Equation (logit)	Correlation*	N
Early Milk	Pronghorn	$y = -7.352 + 0.127x$	0.73	28
Middle Milk	Camelot	$y = -6.592 + 0.047x$	0.70	28
	Pronghorn	$y = -7.370 + 0.231x$	0.90	28
Late Milk	Camelot	$y = -6.934 + 0.107x$	0.91	28
	Pronghorn	$y = -10.586 + 0.834x - 0.019x^2$	0.83	28
Early Dough	Camelot	$y = -6.640 + 0.147x$	0.95	28
	Pronghorn	$y = -6.592 + 0.540x - 0.012x^2$	0.96	28
BSoft Dough	Camelot	$y = -8.566 + 0.486x - 0.011x^2$	0.98	28
	Pronghorn	$y = -5.725 + 0.462x - 0.009x^2$	0.94	28
Hard Dough	Camelot	$y = -6.593 + 0.398x - 0.010x^2$	0.98	28
	Pronghorn	$y = -3.675 + 0.283x - 0.005x^2$	0.93	28
Ripe	Camelot	$y = -7.515 + 0.433x - 0.010x^2$	0.98	28
	Pronghorn	$y = -6.379 + 0.532x - 0.011x^2$	0.97	28

Table 4.3. P-values for contrasts comparing intercepts from logit equations for each stage of wheat development (EM – early milk, MM – middle milk, ED – early dough, SD – soft dough, HD – hard dough, and R – ripe) and wheat variety (Camelot and Pronghorn) (* = P-value <0.05).

Variety		Camelot						Pronghorn						
	Stage	MM	LM	ED	SD	HD	R	EM	MM	LM	ED	SD	HD	R
Camelot	MM	-	-	-	-	-	-	-	-	-	-	-	-	-
	LM	0.7200	-	-	-	-	-	-	-	-	-	-	-	-
	ED	0.9553	0.7170	-	-	-	-	-	-	-	-	-	-	-
	SD	0.1377	0.2082	0.1176	-	-	-	-	-	-	-	-	-	-
	HD	0.9993	0.6957	0.9507	0.1210	-	-	-	-	-	-	-	-	-
	R	0.3924	0.5770	0.3595	0.4472	0.3601	-	-	-	-	-	-	-	-
Pronghorn	EM	0.4484	0.6642	0.4117	0.3598	0.4118	0.8801	-	-	-	-	-	-	-
	MM	0.2441	0.4004	0.1879	0.4924	0.2020	0.8645	0.7205	-	-	-	-	-	-
	LM	0.0017*	0.0031*	0.0008*	0.1776	0.0010*	0.0197*	0.0102*	0.0159*	-	-	-	-	-
	ED	1	0.6699	0.9439	0.1072	0.9992	0.3301	0.3764	0.1639	0.0006*	-	-	-	-
	SD	0.2932	0.1236	0.1631	0.0206*	0.2340	0.0568	0.0551	0.0119*	<.0001*	0.1779	-	-	-
	HD	0.0008*	<.0001*	<.0001*	0.0001*	0.0002*	0.0001*	<.0001*	<.0001*	<.0001*	<.0001*	0.0012*	-	-
	R	0.7979	0.4832	0.6952	0.0736	0.7720	0.2272	0.2529	0.0933	0.0003*	0.7446	0.2979	<.0001*	-

Table 4.4. P-values for contrasts comparing linear parameter from logit equations for each stage of wheat development (EM – early milk, MM – middle milk, ED – early dough, SD – soft dough, HD – hard dough, and R – ripe) and wheat variety (Camelot and Pronghorn) (* = P-value <0.05).

Variety		Camelot						Pronghorn						
	Stage	MM	LM	ED	SD	HD	R	EM	MM	LM	ED	SD	HD	R
Camelot	MM	-	-	-	-	-	-	-	-	-	-	-	-	-
	LM	0.2676	-	-	-	-	-	-	-	-	-	-	-	-
	ED	0.0344*	0.3213	-	-	-	-	-	-	-	-	-	-	-
	SD	0.0042*	0.0123*	0.0228*	-	-	-	-	-	-	-	-	-	-
	HD	<.0001*	0.0004*	0.0011*	0.5925	-	-	-	-	-	-	-	-	-
	R	0.0008*	0.0037*	0.0088*	0.7694	0.7883	-	-	-	-	-	-	-	-
Pronghorn	EM	0.1603	0.7047	0.6325	0.0181*	0.0011*	0.0069*	-	-	-	-	-	-	-
	MM	0.0003*	0.0048*	0.0161*	0.0883	0.0332*	0.0667	0.0252*	-	-	-	-	-	-
	LM	<.0001*	<.0001*	<.0001*	0.0641	0.0017*	0.0116*	<.0001*	<.0001*	-	-	-	-	-
	ED	<.0001*	<.0001*	<.0001*	0.7234	0.1093	0.3588	<.0001*	<.0001*	0.0220*	-	-	-	-
	SD	<.0001*	<.0001*	<.0001*	0.8745	0.4540	0.8004	<.0001*	<.0001*	0.0031*	0.2333	-	-	-
	HD	<.0001*	0.0003*	0.0009*	0.1786	0.1554	0.1804	0.0023*	0.2361	<.0001*	<.0001*	0.0013*	-	-
	R	<.0001*	<.0001*	<.0001*	0.7629	0.1241	0.3919	<.0001*	<.0001*	0.0174*	0.9029	0.2689	<.0001*	-

Table 4.5. P-values for contrasts comparing quadratic parameter from logit equations for each stage of wheat development (EM – early milk, MM – middle milk, ED – early dough, SD – soft dough, HD – hard dough, and R – ripe) for wheat varieties (Camelot and Pronghorn) (* = P-value <0.05).

Variety		Camelot			Pronghorn				
	Stage	SD	HD	R	LM	ED	SD	HD	R
Camelot	ED	-	-	-	-	-	-	-	-
	SD	-	-	-	-	-	-	-	-
	HD	0.8552	-	-	-	-	-	-	-
	R	0.8281	0.9444	-	-	-	-	-	-
Pronghorn	LM	0.1898	0.0445*	0.0697	-	-	-	-	-
	ED	0.8944	0.5849	0.6153	0.0698	-	-	-	-
	SD	0.7346	0.809	0.9157	0.0138*	0.2865	-	-	-
	HD	0.2673	0.1123	0.2628	0.0005*	0.0034*	0.0491*	-	-
	R	0.9401	0.8381	0.8132	0.0357	0.647	0.539	0.0113*	-

Table 4.6. Analysis of variance type III test for fixed effects of year, variety and risk group. (year = 2011-12, 2012-13, and 2013-14, variety = Camelot and Pronghorn, risk group = high (day 6), medium (day 9), low (day 12)).

Effect	Num DF	Den DF	F-value	P-value
year	2	3	0.47	0.6646
variety	1	16	93.42	<.0001
year*variety	2	16	2.62	0.104
risk group	2	16	34.47	<.0001
risk group*year	4	16	1.32	0.3065
risk group*variety	2	16	1.31	0.2961
risk group*year*variety	4	16	0.32	0.8595

Table 4.7. Analysis of variance type I test for fixed effects on variety, risk group and preharvest date for 2011-12 season. (Variety = Camelot and Pronghorn, Risk group = high (day 6), medium (day 9), low (day 12), preharvest date = -25 – 0).

Effect	Num DF	Den DF	F-value	P-value
variety	1	6	50.09	0.0004
risk group	2	6	18.95	0.0026
variety*risk group	2	6	4.06	0.0769
preharvest	1	24	75.25	<.0001
preharvest*variety	1	24	0.36	0.5558
preharvest*risk group	2	24	0.45	0.641
preharvest*variety* risk group	2	24	5.90	0.0083
preharvest*preharvest	1	24	0.52	0.4795
preharvest*preharvest*variety	1	24	0.00	0.9849
preharvest*preharvest* risk group	2	24	4.20	0.0273
preharvest*preharvest*variety* risk group	2	24	0.71	0.5027

Table 4.8. Regression equations after logit transformation for pre-harvest germination for risk group (low, medium, high) and variety (Camelot and Pronghorn) for 2011-12 and 2012-13/ 2013-14. *All P-values for correlations were less than 0.01.

Year	Risk Group	Variety	Equation (logit)	Correlation*	N
2011-12	Low (Day 12)	Camelot	$y = -3.434 - 0.219x - 0.014x^2$	0.94	8
		Pronghorn	$y = -1.475 - 0.166x - 0.008x^2$	0.93	8
	Medium (Day 9)	Camelot	$y = -2.082 + 0.145x$	0.96	8
		Pronghorn	$y = -0.035 + 0.169x$	0.99	8
	High (Day 6)	Camelot	$y = -3.999 + 0.0648x$	0.87	8
		Pronghorn	$y = -0.449 + 0.045x - 0.008x^2$	0.98	8
2012-13 and 2013-14	Low (Day 12)	Camelot	$y = -4.357 - 0.205x - 0.009x^2$	0.75	15
		Pronghorn	$y = -1.564 - 0.054x - 0.003x^2$	0.70	15
	Medium (Day 9)	Camelot	$y = -5.226 - 0.236x - 0.009x^2$	0.69	15
		Pronghorn	$y = -2.901 - 0.190x - 0.008x^2$	0.83	15
	High (Day 6)	Camelot	$y = -6.122 - 0.251x - 0.009x^2$	0.64	15
		Pronghorn	$y = -5.499 - 0.431x - 0.016x^2$	0.95	15

Table 4.9. P-values for contrasts comparing parameters from logit equations (intercept and linear) for risk groups (low = day 12, medium = day 9, and high = day 6) and wheat varieties (Camelot and Pronghorn) for 2011-12. (* = P-value <0.05).

			Camelot			Pronghorn		
Parameter	**Variety**	**Stage**	**High**	**Medium**	**Low**	**High**	**Medium**	**Low**
Intercept	**Camelot**	**High**	-	-	-	-	-	-
		Medium	0.0703	-	-	-	-	-
		Low	0.6438	0.2322	-	-	-	-
	Pronghorn	**High**	0.0052*	0.0368*	0.0227*	-	-	-
		Medium	0.0024*	0.0099*	0.0114*	0.4215	-	-
		Low	0.0235*	0.3662	0.0945	0.1162	0.0267*	-
Linear	**Camelot**	**High**	-	-	-	-	-	-
		Medium	0.2109	-	-	-	-	-
		Low	0.0936	0.0313*	-	-	-	-
	Pronghorn	**High**	0.0084*	0.0812*	0.008*	-	-	-
		Medium	0.0701	0.6414	0.0212*	0.0709	-	-
		Low	0.0037*	<.0001*	0.7469	<.0001*	<.0001*	-

Table 4.10. Analysis of variance type I test for fixed effects on year, variety and preharvest date for 2012-13 and 2013-14 seasons. (Variety = Camelot and Pronghorn, Risk group = high (day 6), medium (day 9), low (day 12), preharvest date = -30 – 0).

Effect	Num DF	Den DF	F-value	P-value
variety	1	18	39.33	<.0001
risk group	2	18	7.82	0.0036
variety*risk group	2	18	0.94	0.4108
preharvest	1	54	4.59	0.0368
preharvest*variety	1	54	0	0.9765
preharvest*risk group	2	54	0.36	0.6975
preharvest*variety* risk group	2	54	0.28	0.7577
preharvest*preharvest	1	54	17.83	<.0001
preharvest*preharvest*variety	1	54	0	0.9566
preharvest*preharvest* risk group	2	54	0.69	0.5053
preharvest*preharvest*variety* risk group	2	54	0.77	0.4668

Table 4.11. P-values for contrasts comparing equation parameters (intercept, linear, and quadratic) from logit equations for risk groups (low, medium, and high) and wheat varieties (Camelot and Pronghorn) for 2012-13 and 2013-14. (* = P-value <0.05).

			Camelot			Pronghorn		
Parameter	**Variety**	**Stage**	**Low**	**Medium**	**High**	**Low**	**Medium**	**High**
Intercept	**Camelot**	**Low**	-	-	-	-	-	-
		Medium	0.6713	-	-	-	-	-
		High	0.3420	0.5295	-	-	-	-
	Pronghorn	**Low**	0.7393	0.8753	0.3596	-	-	-
		Medium	0.0714	0.0751	0.1427	0.0198*	-	-
		High	0.0130*	0.0069*	0.0061*	0.0007*	0.0406*	-
Linear	**Camelot**	**Low**	-	-	-	-	-	-
		Medium	0.9587	-	-	-	-	-
		High	0.8645	0.8915	-	-	-	-
	Pronghorn	**Low**	0.5073	0.3866	0.2316	-	-	-
		Medium	0.8023	0.8130	0.9200	0.1061	-	-
		High	0.4161	0.3391	0.2973	0.0086*	0.1156	-
Quadratic	**Camelot**	**Low**	-	-	-	-	-	-
		Medium	0.9471	-	-	-	-	-
		High	0.9623	0.9772	-	-	-	-
	Pronghorn	**Low**	0.4582	0.4452	0.3543	-	-	-
		Medium	0.9396	0.8519	0.8500	0.0709	-	-
		High	0.4806	0.3462	0.2530	<.0001*	<.0001*	-

Figures

Figure 4.1. Graphical representation of equations in logit and % germination equivalents for pre-harvest germination of sprouting resistant (Camelot) variety across six stages of head development with 21-days of access to continuous moisture across two years (2011-12, 2012-13 and 2013-14) and locations (Cheyenne, Deuel, and Kimball).

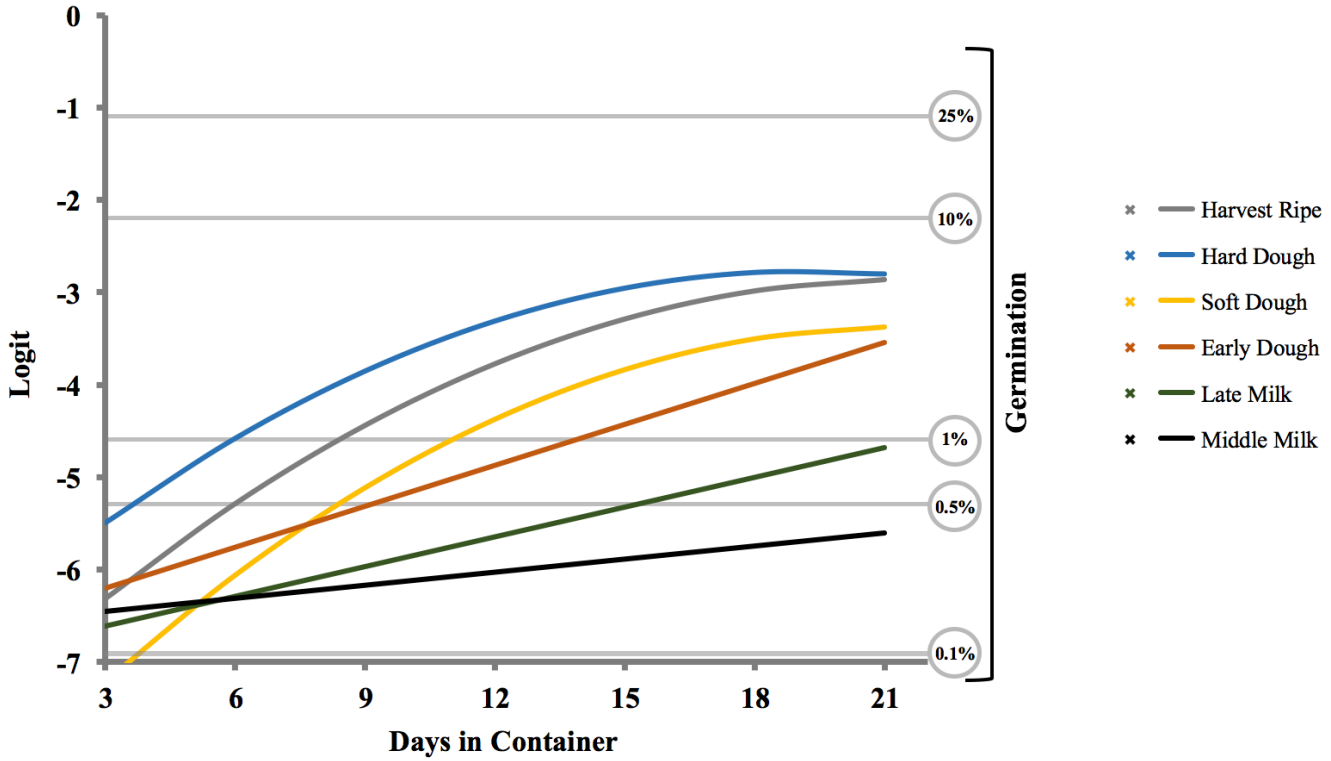


Figure 4.2. Graphical representation of equations in logit and % germination equivalents for pre-harvest of sprouting susceptible (Pronghorn) variety across six stages of head development with 21-days of access to continuous moisture across two years (2012-13 and 2013-14) and locations (Cheyenne, Deuel, Kimball).

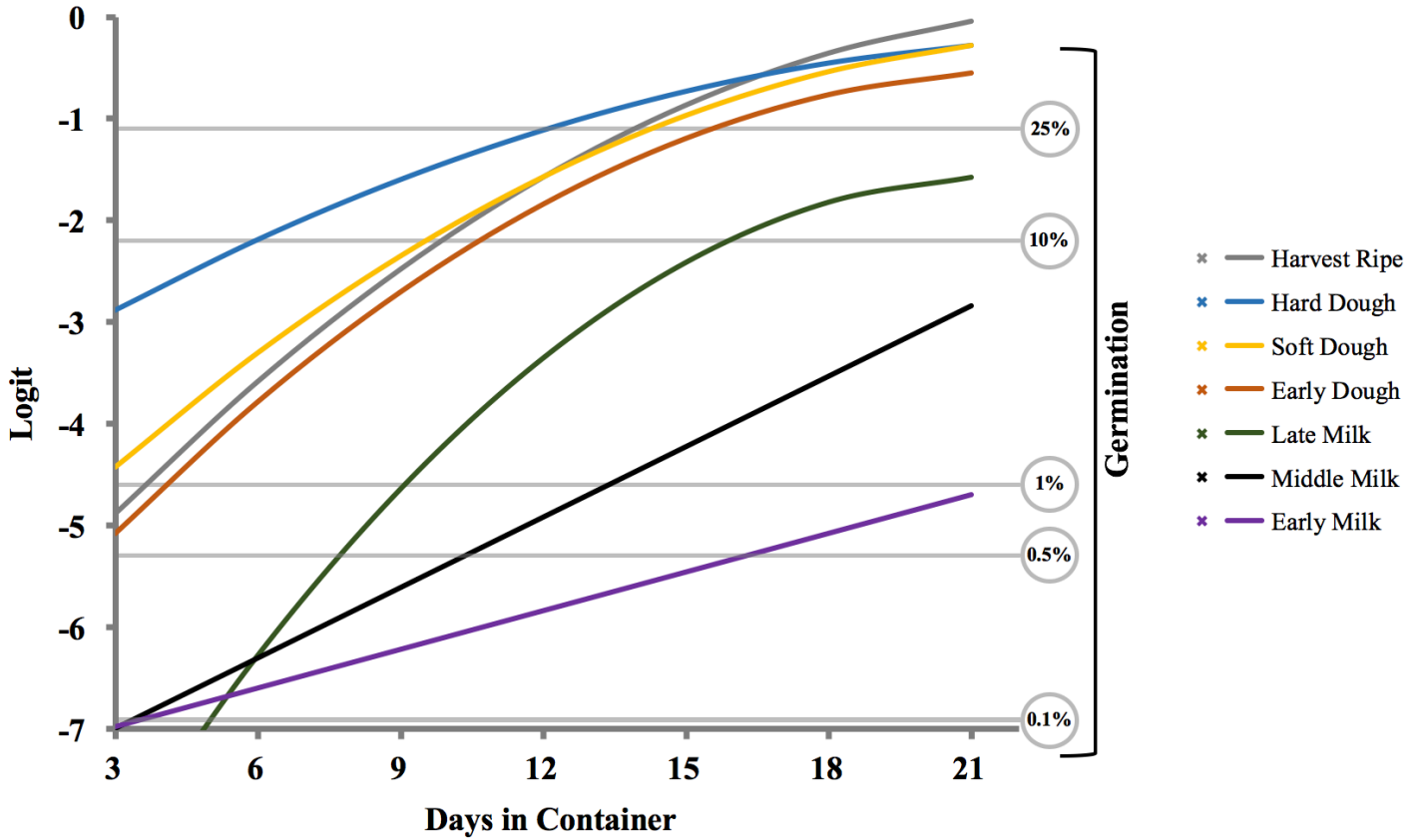


Figure 4.3. Pre-harvest date for first germination of wheat with threshold of 1% for risk group (high, medium, low) and variety (Camelot, Pronghorn) across all three years of the study (2011-12, 2012-13 and 2013-14). (Letters indicate significant differences at P<0.05).

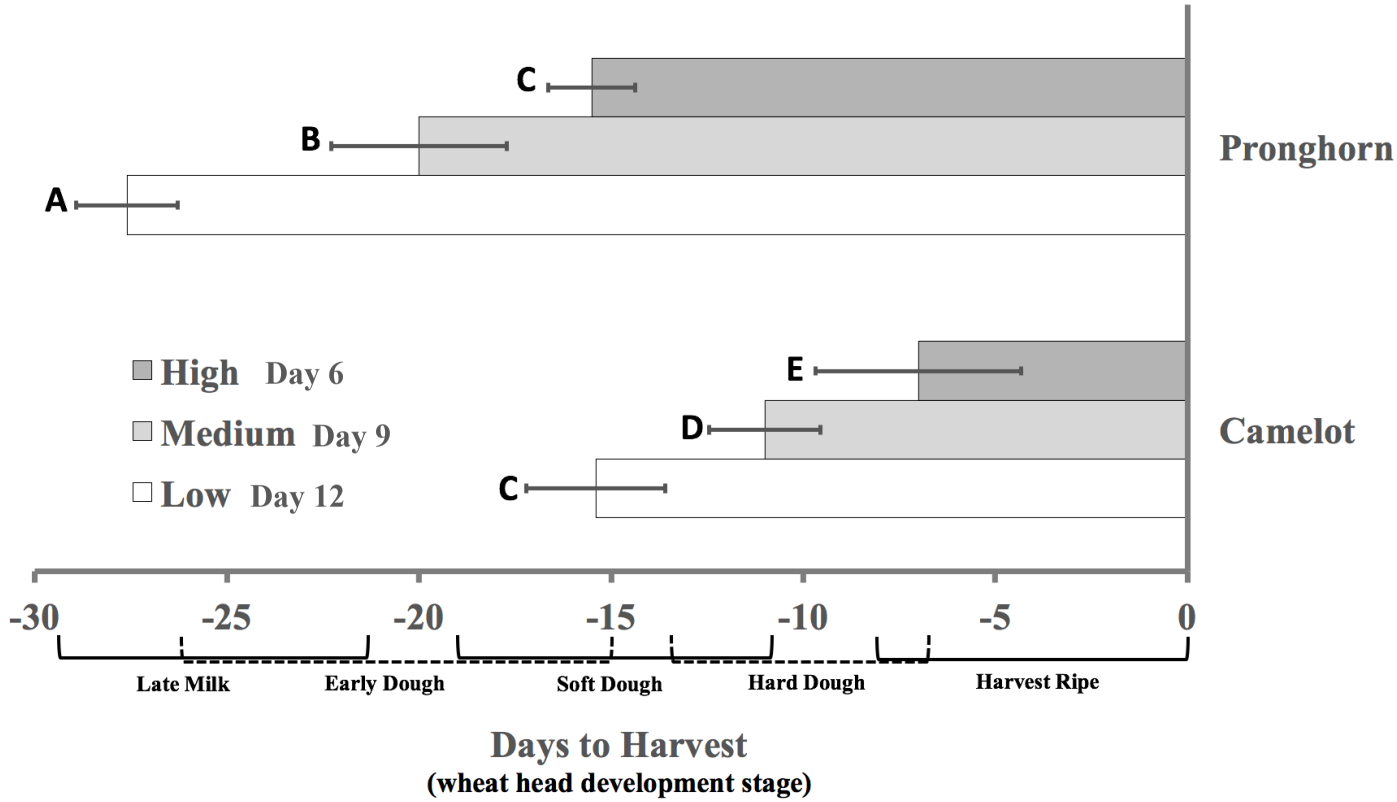


Figure 4.4. Graphical representation of equations in logit and % germination equivalents for wheat varieties (Camelot and Pronghorn) for each risk group (high, medium and low) from 25 – 3 days prior to harvest during 2011-12 season.

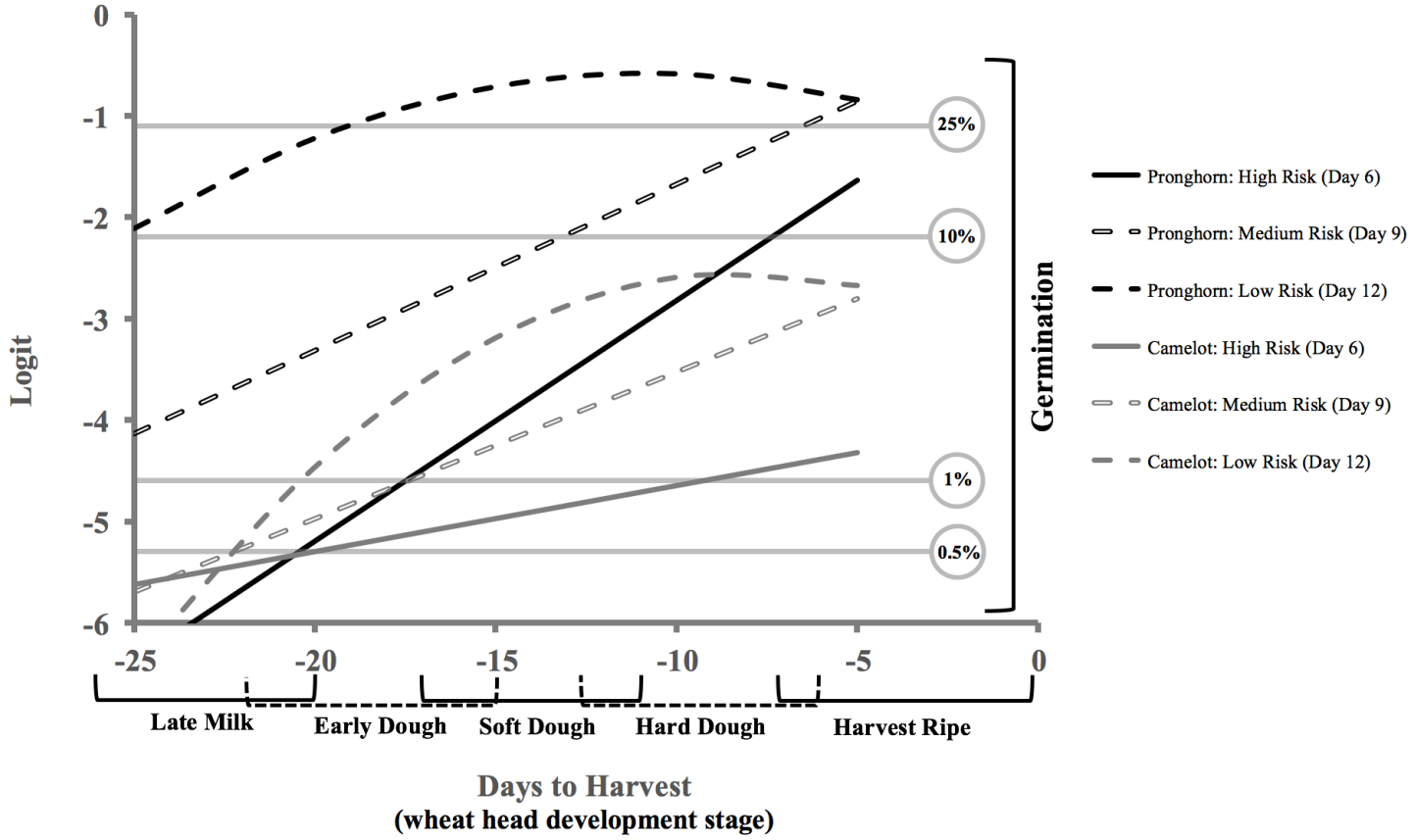
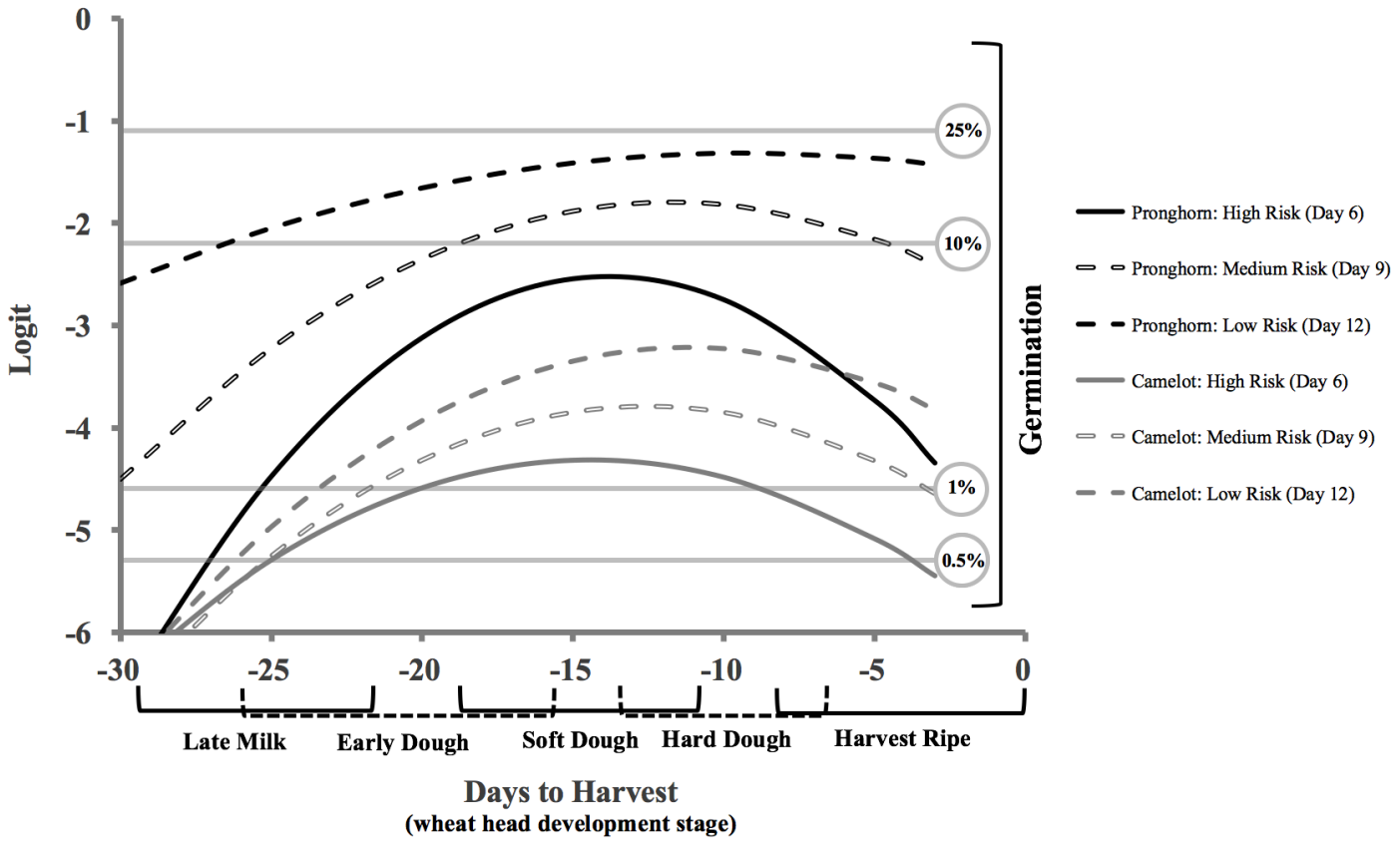


Figure 4.5. Graphical representation of equations in logit and % germination equivalents for wheat varieties (Camelot and Pronghorn) for each risk group (high, medium and low) from 30 – 3 days prior to harvest during 2012-13 and 2013-14 seasons.



CHAPTER 5

Effects of simulated hail on pre-harvest germination of winter wheat under field conditions

Introduction

The wheat-mite-virus complex is a consistent and significant threat to wheat production in the western Great Plains. This complex consists of three viruses (*Wheat streak mosaic virus* (WSMV), *Triticum mosaic virus* (TriMV), and *Wheat mosaic virus* (WMoV)) that are transmitted by the wheat curl mite (WCM) (*Aceria tosichella* Keifer). Average annual losses have been estimated at 1.4% over the past decade (Appel et al. 2015). However, these yield losses are not uniformly distributed across the western Great Plains, with localized yield losses of up to 100%. Areas with significant yield losses from this complex are typically associated with the presence of volunteer wheat emerging prior to wheat harvest.

A sequence of events must occur for volunteer wheat to pose a significant threat to fall planted winter wheat. Risk typically begins with hailstorms occurring during heading of wheat that dislodge seeds from wheat heads. In many cases, severe storms are accompanied with significant rain that enhances germination of the dislodged seeds. Once the volunteer wheat is established, mites are able to infest the volunteer wheat from the maturing wheat crop, and mite populations build rapidly during the summer months, as long as the volunteer wheat remains viable. Wheat crops planted in adjacent fields during the fall will gradually become infested with WCM from the infested pre-harvest volunteer wheat. The timing of mite infestation and virus inoculation, presence of resistant varieties, and prevailing environmental conditions will determine the yield impact on winter wheat. To reduce risk, producers must control volunteer wheat at least 14 days prior to fall planting (Wegulo et al. 2008).

The risk of volunteer wheat as a source of mites and virus is highly dependent on the timing of its emergence and mite movement off of wheat heads. Wheat head collections from water ripe to harvest show a consistent increase in mite populations with populations peaking in the hard dough stage (see Chapter 6). Mite movement is dependent on mite population densities on wheat plants, indicating that wheat germinating prior to harvest will become infested with mites. In contrast, wheat emerging one week after harvest has significantly lower risk due to the limited off-plant survival of the WCM. Wosula et al. (2015) found that WCM could survive for only 1-2 days under low humidity conditions, indicating that mites must find a viable host prior to winter wheat harvest.

Pre-harvest wheat is a critical component for the epidemiology of the wheat-mite-virus complex, and its presence possesses the greatest threat to fall planted winter wheat. This reinforces the need for detailed information on the window of time during wheat head development when pre-harvest germination can occur. The understanding and identification of this risk period would allow producers and consultants to concentrate scouting efforts to identify and manage those fields with the greatest risk for subsequent disease development. In addition, such information could contribute to risk models by taking into account the likelihood of developing pre-harvest volunteer based on the timing of hail occurrence and the stage of wheat development.

Previous research has identified several abiotic factors that are fundamental for determining the germination of immature wheat seeds. Temperature is an important component for non-ripened wheat seeds which can appear dormant at 20-35°C whereas these same wheat stages are capable of germinating at 10-15°C (Atterberg 1907, Ching

and Foote 1961, George 1967). Gosling et al. (1981) found that wheat harvested 18 days after flowering was unable to germinate at 20°C; however, germination readily occurred for the same wheat collection when held at 10°C to 18°C. In contrast, wheat collected 25 days after flowering readily germinated at 20°C, indicating that less developed wheat seeds are more negatively impacted by higher temperatures (Gosling et al. 1981). In addition, temperature has been found to have a significant effect on the total germination with a higher percentage of seeds germinating at 12°C (80%) compared to 20°C (49%) (Balla 1979). Research has also shown that the environmental conditions during wheat head development can affect dormancy (Mares 1993). Wheat plants held at a maximum temperature of 26°C during head development exhibited greater dormancy than those exposed to 34°C (Mares 1993). In addition, other studies have found that rainfall during head development was also a major contributor to dormancy (Biddulph et al. 2005). Such findings indicate that our understanding of the impact of environmental conditions on germination at harvest or during head development are not well understood.

Drying or desiccating immature wheat heads prior to inducing germination can significantly reduce the number of days from pollination necessary for germination as well as the percentage of wheat seeds that germinate (Balla 1979). Balla (1979) found that wheat was capable of germinating at 6-8 days after pollination with 12-weeks of drying. In contrast, wheat was unable to germination until 14 days after pollination without any drying (Balla 1979).

A recent paper Graybosch et al. (2013) evaluated hard red and white wheats for pre-harvest sprouting and found that current commercial wheat varieties vary greatly in

their pre-harvest sprouting tolerance. Hard red winter wheat variety 'Camelot' showed the greatest mean tolerance score for pre-harvest sprouting whereas 'Pronghorn', a wheat of the same market class showed a very low sprouting tolerance (Graybosch et al. 2013). These wheat varieties were evaluated for sprouting by collecting wheat heads at harvest; therefore, studies are needed to address their relevance to germination tolerance prior to harvest. Such studies would provide an indication of the potential to utilize wheat varieties to reduce the likelihood of pre-harvest wheat establishment.

Previous studies on germination are primarily focused on early season harvest of winter wheat to accelerate breeding programs or to reduce the likelihood of sprouting after wheat has ripened. The differential response of wheat varieties to sprouting provides an indication that such mechanisms could be useful for reducing pre-harvest establishment of volunteer wheat. The objective of this study was to evaluate sprouting tolerant and susceptible varieties for their differences in pre-harvest germination under field conditions at different stages of head development. In addition, drying conditions were altered by placing cages over plots to determine the potential role of temperature and relative humidity on pre-harvest germination. Such studies will provide an indication of the window of time during wheat head development when germination could occur and the environmental factors that influence pre-harvest germination and volunteer wheat establishment.

Materials and Methods

Simulated hail studies were conducted over two years at the High Plains Agricultural Lab near Sidney, NE. In 2013, hail was applied to pre-harvest sprouting tolerant, Camelot and susceptible Pronghorn (Graybosch et al. 2013) wheat varieties in a randomized complete block design with six replications. Three split-plot treatments consisted of timing of hail application with hail applied at early dough (Zadoks 83), soft dough (Zadoks 85), and hard dough (Zadoks 87) stages. The split-split-plot treatments were uncaged and caged (2m x 2m x 2m) metal frames covered with an Amber lumite screen (20x20 mesh) to represent rapid and slow drying conditions, respectively. Approximately 19 mm of water was applied using a garden hose and handheld sprinkler to each plot within a few hours of the hail application. Cages were placed over plots one day after the hail treatment and removed seven days later. In 2014, the study was conducted using only Pronghorn wheat with four hail dates applied at middle milk (Zadoks 75), early dough, soft dough, and hard dough stages in a randomized complete block design with eight replications. Water was applied at 0, 2, and 4 days after the hail application with approximately 25.4 mm for each application. Data loggers (HOBO U23 Pro v2; Onset Computer Corporation, Bourne, MA) were used to measure temperature and relative humidity within the plots from the day before to 7 days after each hail application for all treatments in two randomly selected reps in 2013 and four randomly selected reps in 2014 to evaluate differences in environmental conditions between varieties, hail dates, as well as caged and uncaged treatments.

Wheat heads were counted in 0.3 m of wheat row at six random locations within each plot prior to hail applications. Five heads were collected from each plot to estimate

the total number of seeds per row foot. Leaf area index readings were taken using an LAI 2000 Plant Canopy Analyzer (Licor Inc., Lincoln, NE) at five locations within each plot just prior to the hail event and one day after the hail treatment to provide an estimation of hail damage.

Hail treatments were applied with a hail simulator attached to and powered by a tractor. For each plot, five 9-kg ice bags were placed in a hopper at the top of the machine and fed into a vertical feeder housing containing a rotating horizontal cylinder with spikes that crushed the ice into 1-3 cm pieces. Powered by a hydraulic air seeder fan, ice was propelled from the machine through a 20-cm diameter hose at approximately 170 km/h at the hose opening. The hose was directed toward the wheat and across the entire plot in a continuous motion at a 45-degree angle to provide uniform damage within a plot. Eighteen locations were marked within each plot prior to the hail application. Six of these locations were randomly selected for germination counts taken at 7, 14, and 21 days after hail was applied. Five volunteer wheat plants were sampled from each plot during mid-August and inspected under a stereo microscope at 30X-40X for mites.

Leaf area index data was averaged per plot and analyzed using a type III test for fixed effects (PROC GLIMMIX; SAS Institute Inc., Cary, NC, Version 9.3) to determine the impact of hail application with fixed effects of hail date, variety, and pre/post LAI values. LAI readings were analyzed with repeated measures. Random effects were replication, hail date, and variety. Temperature and relative humidity were averaged per plot over the 7 days following the hail application to evaluate the fixed effects of hail date, variety, and cage using a Type III test for fixed effects (PROC GLIMMIX; SAS

Institute Inc., Cary, NC, Version 9.3). Random effects were replication, hail date, variety, and cage depending on the fixed effect being tested.

Germination count data were averaged across the six locations within each plot, and percent germination was obtained by dividing the count data by the average number of seeds per row foot determined from the head sampling data taken prior to the hail event. Non-normal proportional germination data were corrected using a beta distribution. An analysis of variance type I test for fixed effects (PROC GLIMMIX) was used to determine differences between hail date, variety, and cage. These effects were partitioned over days into linear and quadratic portions to determine fixed effects for prediction models. Non-significant effects were removed from the model. Quadratic parameters were evaluated for each treatment combination to determine significance from zero, non-significant quadratic treatment combinations were removed from the model. A final model was run containing only the significant effects.

Regression equations were obtained from the solution for fixed effects. Correlations between observed and predicted values from regression equations were used to evaluate fit (PROC CORR; SAS Institute Inc., Cary, NC, version 9.3). Parameters in equations were evaluated using contrasts to compare intercept, linear, and quadratic components. Environmental data were obtained from the High Plains Regional Climate Center (hprcc.unl.edu; University of Nebraska-Lincoln). Weather data originated from an established weather station located less than 2 km from the plot site.

Mite count data were analyzed using a type III test for fixed effects in PROC GLIMMIX to determine differences in variety, hail date, and cage. Random effect was

replications. Proportion of infested seedlings per plot was adjusted using a beta distribution. Differences within treatments were evaluated using t-tests.

Results

Hail damage, post-water application, environmental conditions, and treatment combinations varied between seasons; therefore, each year of the study was analyzed separately. Greater damage occurred from the hail applications during the 2014 season due to increased hydraulic power for the tractor that was used. In addition, post-watering applications in 2014 were made after cages were placed over plots allowing for reduced water loss and increased water availability for immature wheat seeds.

Hail Study 2013

Leaf area index (LAI) readings varied by hail date ($F_{2,10} = 9.86$; $P = 0.0043$) with the highest readings occurring for the early dough (1.91) and soft dough (1.84) stages whereas significantly ($F_{1,10} = 10.85$; $P = 0.0081$) lower LAI readings occurred during the hard dough (1.45) stage. Differences also occurred between readings taken before and after the hail application ($F_{1,28} = 203.58$; $P < .0001$) with lower values for post hail readings (1.45) compared to pre-hail readings (1.98), indicating significant structural damage to wheat as a result of the hail application. However, a significant interaction occurred between hail date and timing of LAI readings ($F_{2,28} = 26.18$; $P < .0001$) due to a large reduction ($t_{28} = 4.56$; $P < .0001$) in LAI from 2.30 to 1.39 in early dough for pre- and post-hail readings whereas a smaller, albeit significant reduction ($t_{28} = 3.92$; $P = 0.0002$) occurred for soft dough from 1.99 to 1.71. No significant differences occurred between varieties ($F_{1,15} = 2.81$; $P = 0.1145$), or their interaction with hail date ($F_{2,15} = 1.19$; $P = 0.3307$), timing of LAI reading ($F_{1,28} = 0.11$; $P = 0.7474$), or the three-way interaction ($F_{2,28} = 0.10$; $P = 0.9013$).

One of the temperature and humidity monitors failed to collect data following the first hail application, and it was removed from the data set. Temperatures varied following each hail application ($F_{2,2}$ = 104.43; P = 0.0036) with 7-day average temperatures of 20.9°C, 23.6°C, and 25.2°C after early dough, soft dough, and hard dough applications, respectively. Differences also occurred between cages ($F_{1,4}$ = 127.62; P <.0001) with lower temperatures in caged (22.4°C) plots compared to uncaged (24.1°C) plots. No differences occurred between varieties ($F_{1,3}$ = 0.10; P = 0.7693) or their interaction with hail date ($F_{2,3}$ = 0.48; P=0.6593). In addition, cages showed no interactions with hail date, variety or for the three-way interaction. Similar differences were found for the relative humidity data with differences between hail dates ($F_{2,2}$ = 106.75; P = 0.0093) as a result of greater average humidity in early dough (75.3%), followed by hard dough (65.0%) and soft dough wheat (61.0%). Differences also occurred between cages ($F_{1,4}$ = 18.70; P = 0.0124) with greater humidity in caged (68.8%) plots compared to uncaged (65.3%) plots. No differences in humidity occurred for variety or its interaction with other treatments.

Regardless of the differences in environmental conditions between caged and uncaged plots, we found no differences in germination between caged and uncaged plots ($F_{1,40}$ = 0.84; P = 0.3670) or their interaction with variety ($F_{1,40}$ = 1.08; P = 0.3078), hail date ($F_{2,120}$ = 0.33; P = 0.6783), or the three-way interaction ($F_{4,120}$ = 0.57; P = 0.5726).

An analysis of germination following hail application using type I test for fixed effects (Table 5.1) showed that germination varied by variety with Pronghorn (0.1%) having greater germination compared to Camelot (0.01%). Differences also occurred between hail dates with hard dough (0.2%) having greater germination (t_{20} = 6.71; P

<.0001) than soft dough (0.01%). Wheat hailed at the soft dough stage was similar (t_{20} = 0.23; P = 0.8183) to wheat at early dough (0.01%). However, a significant interaction occurred between variety and hail date with similar germination between varieties during the soft dough stage (t_{20} = 1.38; P = 0.1842) whereas Pronghorn (1.5%) had greater germination (t_{20} = 6.36; P <.0001) than Camelot (0.02%) when hailed at the hard dough stage (Fig. 5.1). Germination also varied by day with a numerical increase in germination between day 7 (0.01%) through 14 (0.02%) and a significant increase (t_{60} = 4.17; P <.0001) by day 21 (0.1%). The day by hail date interaction was also significant due to similar germination between day 7 and 14 for soft dough (t_{60} = 0.11; P = 0.9101) stages whereas hard dough showed a significant increase (t_{60} = 10.57; P <.0001) from 0.06% at day 14 to 6.8% at day 21.

Contrasts comparing varieties, hail dates and days (Table 5.2) showed that Pronghorn hailed at the hard dough stage had greater germination than all other hail dates and evaluation days. In addition, Camelot had greater germination when hailed at the hard dough stage for day 21 evaluations when compared to early or soft dough stages in Pronghorn. These differences were primarily due to heavy rains 13 days after the final hail application.

Hail Study 2014

Leaf area index readings varied by hail date ($F_{3,21}$ = 15.43; P <.0001) with middle milk (1.56) and early dough (1.44) having greater readings ($F_{1,21}$ = 43.94; P<.0001) than soft dough (1.15) and hard dough (1.13). Greater differences were observed between readings taken before and after the hail application ($F_{1,28}$ = 618.51; P <.0001) with a

significant reduction in LAI values for post-hail (0.70) compared to pre-hail (1.94) readings. No significant interaction occurred between hail date and timing of readings ($F_{3,28} = 1.88$; $P = 0.1566$)

Average 7-day temperature varied between hail dates ($F_{3,9} = 154.95$; $P < .0001$) with increasing temperatures from middle milk (19.2°C) through early dough (20.1°C), and soft dough (24.6°C) stages. In contrast, temperatures declined significantly for the hail application occurring during the hard dough stage (21.1°C). Cages also varied in temperature ($F_{1,12} = 92.12$; $P < .0001$) with lower temperatures for caged plots (20.4°C) compared to uncaged plots (22.2°C). Differences in average humidity also occurred across hail dates ($F_{3,9} = 58.07$; $P < .0001$) with the highest humidity occurring in hard dough (85.2%) followed by early dough (77.2%), middle milk (77.1%) and soft dough (71.1%). Average humidity also varied by cage with uncaged plots (76.5%) having lower humidity than caged plots (78.7%). There was no significant interaction between hail date and cage for temperature ($F_{3,12} = 1.48$; $P = 0.2699$) or relative humidity ($F_{3,12} = 1.48$; $P = 0.8438$).

An analysis of germination following hail applications showed no differences between caged and uncage plots ($F_{1,28} = 3.17$; $P = 0.0857$), or their interaction with hail date ($F_{3,28} = 2.18$; $P = 0.1125$), day ($F_{2,112} = 0.03$; $P = 0.9749$), or the three-way interaction ($F_{6,112} = 1.02$; $P = 0.4166$). Therefore, cages were averaged prior to the analysis.

An analysis of germination following hail application using type I test for fixed effects showed that germination varied by hail date ($F_{3,21} = 50.24$; $P < .0001$) with greatest germination occurring in wheat hailed at the hard dough stage (7.1%), followed by soft

dough (1.7%) and early dough (0.9%). Wheat hailed at early dough had greater germination (t_{21}= 2.21; P = 0.0380) when compared to middle milk (0.0%) which showed no germination over the 21 days of evaluation, indicating that significant germination occurred when wheat was hailed at the early dough stage. The interaction between hail date and day was also significant ($F_{6,56}$ = 4.89; P = 0.0004) due, in part to a significant increase (t_{56}= 5.93; P<.0001) in germination for hard dough (Fig. 5.2) between day 14 and 21 whereas wheat hailed at the soft dough stage declined (t_{56}= 2.81; P = 0.0068) over the same period. Contrasts comparing hail dates and days (Table 5.3) showed that soft dough and hard dough had significantly greater germination than when hailed at the middle milk stage. In addition, a comparison of soft dough and hard dough at the same evaluation date showed that germination at hard dough was greater than at soft dough for all dates. Evaluation dates within the hard dough stage showed a significant increase in germination with each evaluation date. In contrast, no differences occurred between dates within the early dough stage. Mean germinations across hail dates exceed 0.1% for all hail dates and days with the exception of day 7 for early dough and all evaluation days for middle milk.

Discussion

Regardless of the variation in environmental conditions between seasons, the greatest potential for pre-harvest germination and resulting volunteer wheat occurred when wheat was hailed at the hard dough stage. Wheat varieties with differing sprouting tolerance scores (Graybosch et al. 2013) exhibited similar differences in their potential for pre-harvest germination with sprouting-susceptible Pronghorn exhibiting a greater rate of germination compared to sprouting-tolerant Camelot. In addition, Pronghorn exhibited low levels of germination at the early and soft dough stages (Table 5.2, 5.4) during both years of the study whereas no germination occurred within 21 days of the hail event for Camelot at either of these stages. The differences between these varieties have significant implications for the management of pre-harvest volunteer to reduce risk to fall planted wheat. However, studies are needed to address the differences in susceptible and tolerant varieties over a range of temperature and rainfall conditions to assess the durability sprouting tolerant varieties.

The earliest applications of hail occurred at the middle milk stage with no detectable germination within 21 days of hail. Instead, wheat hailed at this stage exhibited a strong tendency for the development of secondary tillers. An extension publication by Staples et al. (n.d.) supports our finding, indicating that early hailed wheat can produce secondary tillers; however, the exact stage was not stated. The risk of secondary tillered wheat as a result of hail storms during the early stages of wheat heading poses little to no threat to fall planted wheat as it matures prior to fall planting. It is possible that secondary tillered wheat could act as a source of post-harvest wheat; however, studies are needed to address this.

Early and soft dough stage wheat was strongly impacted by available moisture. In 2013, a single application of water was made after early and soft dough treatments, and this resulted in very low levels of germination (Fig. 5.1). However, multiple water applications on the same variety and wheat stages in 2014 resulted in a greater proportion of germinated seeds within 21 days (Fig. 5.2). In 2013, a large rain event that occurred on 24 July resulted in a rapid increase in germination for hard dough stage wheat. It is possible that germination could have occurred for other hail dates; however, the heavy rains during 2013 occurred after their final evaluation dates for wheat hailed at early and soft dough.

Plant collections on 16 August 2013 showed that volunteer wheat had germinated in early and soft dough stage wheat. The presence of mites on this volunteer wheat indicates that it had emerged prior to harvest. The ability of this wheat to germinate long after a hail event is supported by previous literature. Balla (1979) found that wheat removed from the plant within 6-8 days of pollination was able to germinate if heads were held under dry conditions for three months and then wetted. In this study, wheat was hailed at early dough which corresponds with 23-26 days after pollination. It is possible that more mature wheat seeds would require less drying time to allow for germination. This result shows the importance of heavy rains to induce germination of wheat hailed during the earlier stages of head development. As a result, producers and consultants should scout hailed fields for the presence of volunteer wheat within a week of harvest to determine the risk potential to adjacent fields that are to be planted to wheat in the fall.

Volunteer wheat present prior to harvest is likely to be infested with mites as indicated by trap pots collected at weekly intervals through wheat heading (see Chapter 3) and mite populations in wheat heads with peak populations at hard dough (see Chapter 6). The low mite infestation levels across all hail dates in this study (9-23% infested plants) would pose a significant threat to wheat, as mite populations can build and spread rapidly. Producers should control pre-harvest volunteer wheat at least 14 days prior to fall planting, to avoid significant economic losses from this complex.

Temperature data obtained from this study indicate that immature wheat seeds were likely under considerable stress based on temperature studies in previous literature. Several studies have indicated that wheat can appear dormant at 20-35°C (Atterberg 1907, Ching and Foote 1961, George 1967). Our results show that average temperatures were between 19 and 25°C. However, these temperatures were based on a 7-day average temperature and don't account for fluctuations over the course of an individual day, with temperatures ranging between 14°C and 36°C. The impact of fluctuating temperatures on germination is not well understood as historical studies on germination have held temperatures relatively constant. In addition, temperatures taken from HOBO data loggers don't reflect micro environments at the soil level or areas shaded by residue.

The methods used in this study provide a realistic representation of natural hail events in wheat fields. The application of ice with high winds allowed for destruction of the wheat canopy, as indicated by a 27% and 64% in reduction in LAI values between pre- and post-hail readings for 2013 and 2014, respectively. This alteration allows for the inclusion of changes in microclimates at the soil surface as a result of vegetation being broken and laid between rows. In many cases, germinated wheat was confined to the

area around the original wheat row, allowing seeds to fall into cracks in the soil. These secluded locations allowed for a longer contact with water from subsequent artificial and natural rainfall events. In addition, we observed increasing germination between rows where large amounts of plant biomass accumulated likely due to increased shading of immature wheat seeds by wheat stalks.

The study demonstrates the potential for wheat to germinate between the early and hard dough stages. In addition, it demonstrates the differences in germination between sprouting tolerant (Camelot) and susceptible wheat (Pronghorn), validating sprouting tolerance as a potential management strategy for managing volunteer wheat. Rainfall and beneficial microclimate were critical components for the germination of immature wheat, indicating that producers and consultants should scout low-lying areas of hail damaged fields for first signs of germination. Scouting of low-lying areas is primarily a function of greater biomass to shade the soil surface and a potential site for accumulation of water following hail, increasing the likelihood of wetter conditions at the soil surface over a long period of time. Both years of this study showed low levels of germination for early dough stage wheat, increasing the importance of determining how the population densities of volunteer wheat contribute to mite spread and virus impact in adjacent wheat fields. In addition, the potential for wheat to germinate well after a hail event increases the importance that producers and consultants scout fields at harvest for the presence of volunteer wheat just prior to harvest to determine risk.

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Tables

Table 5.1. Analysis of variance type I test for fixed effects for variety (Camelot and Pronghorn), hail date (early dough, soft dough and hard dough) and days (7, 14, and 21) sampled for germination after hail application for the 2013 season.

Effect	Num DF	Den DF	F-value	P-value
variety	1	5	17.23	0.0089
hail date	2	20	34.75	<.0001
variety*hail date	2	20	6.82	0.0055
day	2	60	14.85	<.0001
day*variety	2	60	0.46	0.6343
day*hail date	4	60	18.02	<.0001
day*variety*hail date	4	60	0.51	0.7255

Table 5.2. P-values showing differences in contrasts comparing varieties (Camelot and Pronghorn), hail date (ED: early dough, SD: soft dough, and HD: hard dough) across days (7, 14, and 21) sampled for germination after hail application. *ND = not determined due to a lack in germination for either treatment combination.

			Pronghorn											
	Stage		ED/SD	HD		ED			SD			HD		
		Day	7/14/21	7/14	21	7	14	21	7	14	21	7	14	21
Camelot	ED/SD*	7	-	-	-	-	-	-	-	-	-	-	-	-
		14	ND*	-	-	-	-	-	-	-	-	-	-	-
		21	ND	-	-	-	-	-	-	-	-	-	-	-
	HD	7	0.8696	-	-	-	-	-	-	-	-	-	-	-
		14	0.8696	-	-	-	-	-	-	-	-	-	-	-
		21	<.0001	<.0001	-	-	-	-	-	-	-	-	-	-
Pronghorn	ED	7	0.6681	0.5423	<.0001	-	-	-	-	-	-	-	-	-
		14	0.4543	0.3480	<.0001	0.7129	-	-	-	-	-	-	-	-
		21	0.4543	0.3480	<.0001	0.7129	1	-	-	-	-	-	-	-
	SD	7	0.9935	0.8644	<.0001	0.6701	0.4529	0.4529	-	-	-	-	-	-
		14	0.1520	0.1020	<.0001	0.2492	0.3951	0.3951	0.1341	-	-	-	-	-
		21	0.2060	0.1428	<.0001	0.3412	0.5271	0.5271	0.1868	0.7980	-	-	-	-
	HD	7	0.0010	0.0005	0.0002	0.0011	0.0018	0.0018	0.0011	0.0107	0.0066	-	-	-
		14	0.0001	<.0001	0.0022	0.0002	0.0003	0.0003	0.0002	0.0030	0.0016	0.0132	-	-
		21	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	-

Table 5.3. P-values showing differences in contrasts for hail date (MM: middle milk, ED: early dough, SD: soft dough, and HD: hard dough) across days (7, 14, and 21) sampled for germination after hail application for wheat variety Pronghorn. * All ED and SD comparisons for Camelot were resulted in P-value = 1 due to a lack of germination for 7,14, 21 day evaluations.

Stage		MM	ED			SD			HD		
	Day	7/14/21	7	14	21	7	14	21	7	14	21
MM	7	-	-	-	-	-	-	-	-	-	-
	14		-	-	-	-	-	-	-	-	-
	21	ND	-	-	-	-	-	-	-	-	-
ED	7	0.3049	-	-	-	-	-	-	-	-	-
	14	0.1591	0.422	-	-	-	-	-	-	-	-
	21	0.1474	0.3687	0.916	-	-	-	-	-	-	-
SD	7	0.0098	0.0004	0.0006	0.0007	-	-	-	-	-	-
	14	0.0013	<.0001	<.0001	<.0001	<.0001	-	-	-	-	-
	21	0.0029	<.0001	<.0001	<.0001	0.0011	0.0068	-	-	-	-
HD	7	0.0006	<.0001	<.0001	<.0001	<.0001	0.1258	0.0042	-	-	-
	14	0.0002	<.0001	<.0001	<.0001	<.0001	0.0015	<.0001	<.0001	-	-
	21	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	-

Figures

Figure 5.1. Germination in logit with equivalent % germination for varieties (Camelot and Pronghorn), hail date (early dough, soft dough and hard dough) evaluated at 7, 14, and 21 days after hail was applied. For contrasts comparing va ies, hail date, and evaluation day (days post-hail application), see Table 2.

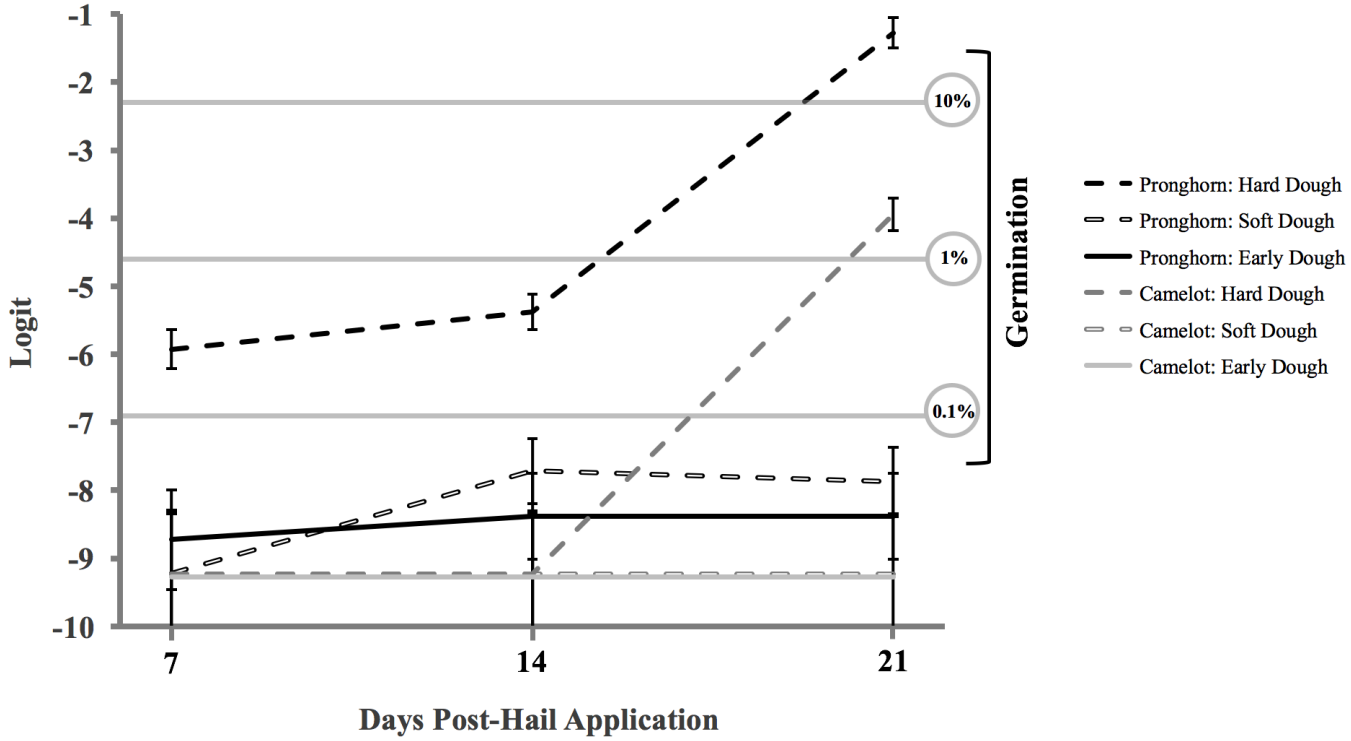
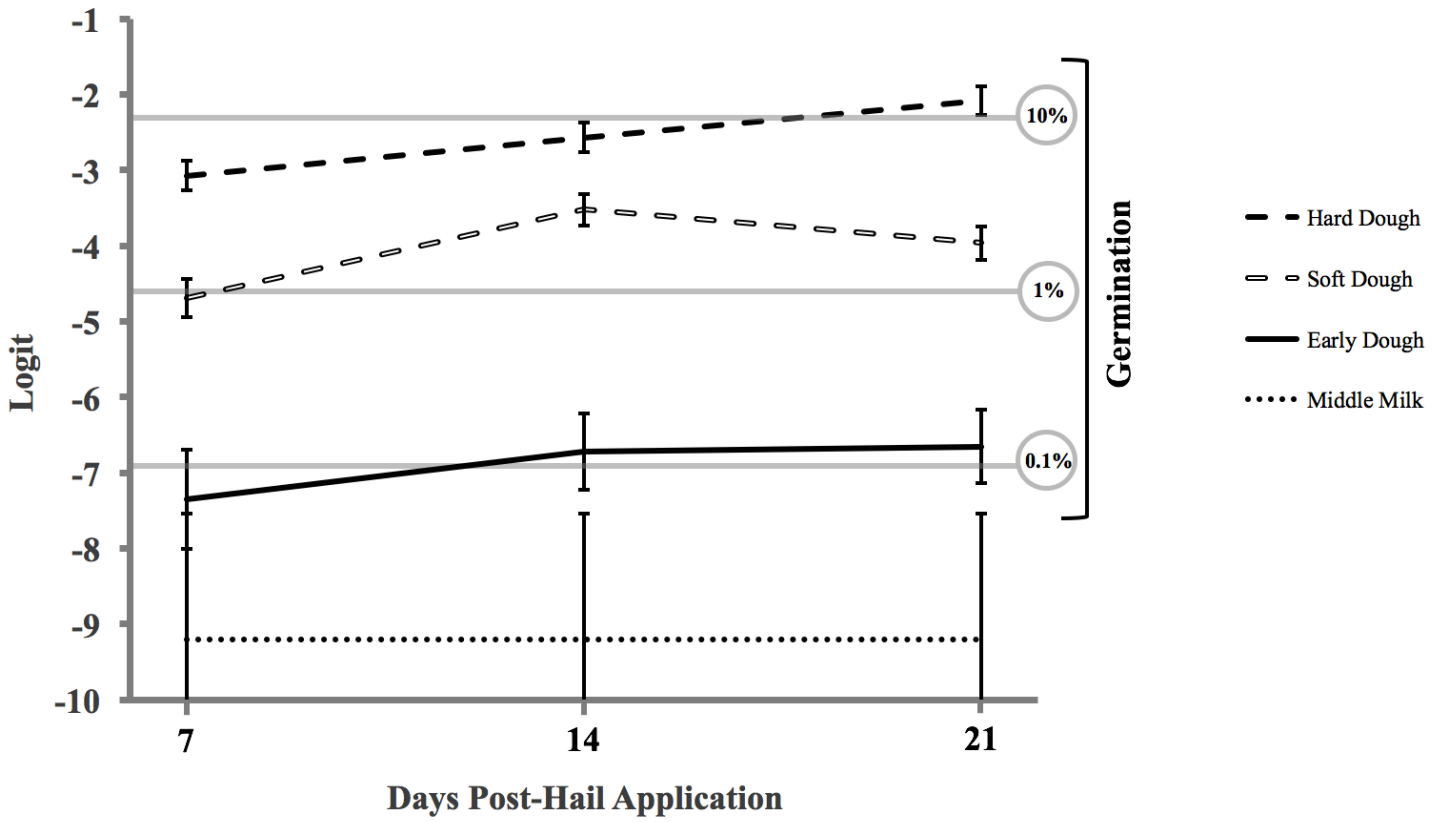


Figure 5.2. Germination in logit with equivalent % germination for variety Pronghorn for hail dates (middle milk, early dough, soft dough and hard dough) evaluated at 7,14, and 21 days after hail was applied. For contrasts comparing hail dates, and evaluation day (days post-hail application), see Table 3.



Chapter 6

Impact of Rainfall, Population Density and Direct Infestation of Seedlings by Wheat Curl Mites during the Heading Stages of Winter Wheat

Introduction

Wheat is a staple food crop worldwide, and it is a core component of many dryland cropping systems in the western Great Plains of North America. The wheat-mite-virus complex is a consistent and significant threat to wheat production in this region. During the 2015 season, Kansas estimated yield losses of approximately 11 million bushels (2.7%) across the state from this disease complex (Appel et al. 2015). This complex consists of three viruses (*wheat streak mosaic virus* (WSMV), *Triticum mosaic virus* (TriMV) and *wheat mosaic virus* (WMoV)) that are transmitted to wheat by the wheat curl mite (WCM: *Aceria tosichella* Keifer).

Yield impacts from this disease complex are not equally distributed throughout the Great Plains region, with significant yield losses concentrated to localized areas where volunteer wheat has emerged prior to wheat harvest (pre-harvest volunteer). The occurrence of pre-harvest volunteer wheat is often associated with severe hail storms occurring during the heading stages of winter wheat. Hail dislodges immature seeds from wheat heads, and these seeds germinate in the presence of adequate moisture. As the wheat crop matures, mites move via wind from maturing wheat fields to the newly germinated volunteer wheat. Once the volunteer wheat is infested, mite populations can build rapidly throughout the summer months. In the fall, mites disperse from the volunteer wheat to adjacent newly planted wheat fields, and they transmit viruses to the wheat, causing significant yield losses.

The potential for mite infestation and virus impact on fall-planted winter wheat is strongly linked to the presence of viable hosts for mites prior to wheat harvest. This temporal overlap in hosts is important for the epidemiology of the wheat-mite-virus complex due to the limited off-plant survival of WCM. According to Wosula et al. (2015), the maximum time period for mite survival without a host is 7 days at 10°C and 95% humidity. Lowering the

humidity to 2% reduced the survival to two days (Wosula et al. 2015). In addition, increasing temperatures to 30°C reduced survival to 30 and 6 hours for high and low humidity, respectively (Wosula et al. 2015). In western Nebraska, average July temperatures over the last 30 years are typically around 23°C with maximum temperatures around 30°C (High Plains Regional Climate Center – University of Nebraska). Limited off plant survival increases the importance of understanding the characteristics of mite build up on wheat heads and their ability to transition to a suitable over-summering host.

Previous studies have documented the abundance and presence of wheat curl mites on wheat heads at the soft and hard dough stages of head development. Mahmood et al. (1998) found that randomly selected wheat heads from fields in western Nebraska averaged 1,203 mites/head in 1995 and 487 mites/head in 1996 (Mahmood et al. 1998). Mite populations varied significantly between wheat fields with averages ranging from 23 to 1,872 mites/head (Mahmood et al. 1998). Byamukama et al. (2015) collected wheat heads from fields from three distinct regions across Nebraska and found greater mite populations in the Panhandle (380 mites/head) compared to west-central (200 mites/head) and southeast (50 mites/head) during the 2011 growing season. In 2012, greater mite numbers were observed across all regions of the state ranging from 800 to 1,200 mites per head; however, no significant differences were found across the three regions (Byamukama et al. 2015). Both of these studies documented wide fluctuations in the mean number of mites between years across a broad geographic region, indicating that certain environmental factors may be important for determining mite population densities on wheat heads. The relative increase in average number of mites per wheat head across Nebraska between the 2011 and 2012 seasons coincided with widespread drought in 2012, indicating that variations in the frequency or abundance of rainfall during heading stages could

be an important factor for determining mite population densities on wheat heads. In addition, the gradient in rainfall patterns across Nebraska indicate that greater mite populations may be present under drier climates. Observations on the correlation between rainfall and mite populations are confounded by an increasing number of wheat acres over this same geographic region. In addition, the variation in precipitation patterns on specific fields makes interpretations of rainfall impacts difficult, indicating the need for specific studies to evaluate the impact of rainfall on mite populations in headed wheat. To our knowledge, no studies have been conducted to evaluate the impact of rainfall on mite populations during the vegetative or reproductive stages of winter wheat.

Mite population densities have been found to be an important component for determining mite movement. A study by Thomas and Hein (2003) found a strong relationship between increasing mite population densities on wheat plants and mite movement off of wheat plants. Other studies have documented a flush of mites following glyphosate application during vegetative stages of wheat development (Brey 1998). For reproductive stages of wheat, mite movement has been correlated with the senescence of flag leaves and wheat heads (Nault and Styer 1969).

Previous research has documented the prevalence and density of mite populations on maturing wheat heads; however, these studies have been conducted during the soft/hard dough stage of wheat. No information is currently available on the the seasonal dynamics of mite populations on wheat heads. The goal of this study was to evaluate mite population densities at different stages of wheat head development to determine the wheat stages wheat curl mites are most abundant and the relative increase in mite populations across those development stages. In addition, a study was designed to evaluate the potential for mites to infest germinated wheat

directly from infested grain under isolated conditions. This would provide additional information on alternative methods of mite infestation of pre-harvest wheat. The final portion of this study was to determine the impact of rainfall on mite populations during the heading stages of wheat.

Materials and Methods

Mite Population in Wheat Heads

Wheat heads were collected from fields over three separate growing seasons at two locations per season in conjunction with the Winter Wheat State Variety Trials conducted by the University of Nebraska-Lincoln. The 2011-12 and 2013-14 samples were collected from Cheyenne and Deuel County, Nebraska. The 2012-13 samples were collected from Cheyenne and Kimball County. Four wheat varieties (Pronghorn, Mace, Millennium, and Camelot) were sampled during the 2011-12 and 2012-13 growing seasons whereas only two varieties (Pronghorn and Camelot) were sampled in 2013-14. Wheat varieties were grown in a randomized complete block design with five replications. Each plot consisted of 6, 6-m rows with a 0.3 m spacing between rows. Plots were sampled every 7-9 days beginning at the water ripe stage until harvest with 5-8 collections occurring during each season. For each sample, five wheat heads were randomly selected from the far right row of each plot. Wheat heads were cut 1-2 cm below the lowest spikelet and placed in Ziploc bags on ice. Heads were individually staged based on a seed selected from the middle of each wheat head. After staging, two of the five heads were placed on high definition tape that was secured to black cardstock (7-cm by 29-cm) with double sided tape to determine WCM population per head (Harvey and Martin 1988, Byamukama et al. 2015). Awns of wheat heads were firmly pressed against the tape to ensure contact with wheat head. Wheat heads were placed in plastic shoe boxes and covered with lids to prevent air movement around the heads for a period of 6 weeks before counting. Mite counts were made by using a stereomicroscope at 30X-40X magnification. Total heads collected varied between seasons with 400, 440, and 260 heads counted during 2012, 2013, and 2014.

For the remaining three wheat heads, the awns of each head were clipped back to the glumes, seeds were mechanically separated and spread into individual clear plastic clamshell containers containing 30 grams of sterilized greenhouse soil. The soil surface was sprayed with 12 ml of distilled water and sealed. Containers were held at 18-24°C and five randomly selected plants were harvested from germinated containers at 21-days to determine mite presence. Mite presence was evaluated under a stereo-microscope at 30-40X. A total of 600, 660, and 390 heads were placed on soil for germination during the 2012, 2013, and 2014 season.

Rainfall Study

A simulated rainfall machine as designed by Meyers and Harman (1979) was used to apply rain during the heading stages of winter wheat to evaluate the impact of rainfall on mite populations. This study was conducted over two years (2013, 2014) in commercial wheat production fields planted to 'Settler CL' at the University of Nebraska's High Plains Agricultural Lab near Sidney, Nebraska. The study consisted of four artificial rainfall applications (no rain, early application, late application, and both early and late application) in a randomized complete block design with six replications. Each plot consisted of four wheat rows with a 0.3 m row spacing and row lengths of 2.4 m.

Wheat plants were artificially infested with mites 3 weeks prior to the first rainfall application during each season to increase mite numbers and the frequency of infested heads. In 2013, half of the replications were infested with mites from a field with pre-harvest volunteer wheat. Volunteer wheat plants were cut at soil level and inspected at 30X-40X magnification under stereomicroscope for mites. Plants were cut into 2-4 cm leaf sections containing 30-40 mites per leaf piece. An individual leaf section was attached to each of 15 randomly selected

wheat heads in the center two rows of each plot at wheat flowering. Metal paper clips were used to attach infested leaves and tags were placed on the stems of each infested head. In 2014, mites were reared on 'Millennium' wheat in pots under greenhouse conditions for four weeks prior to field infestation. Individual wheat plants contained in excess of thousands of mites per plant at the time of field infestation. To infest field plots, individual wheat plants from pots were cut at the soil level and placed on the top of wheat plants in the field during the boot stage. The middle two rows of each plot were infested by laying the infested wheat end-to-end, covering approximately 1 m per row.

A rainfall simulator, electrically powered and controlled by a gas generator was used to apply rainfall treatments. A gas powered Honda WB20XT water pump provided water pressure through a 15.8-mm garden hose at 41 kpa and a height of 3 m from the soil surface as suggested by Meyer and Harmon (1979). Aluminum catch pans on either side of the application area collected excess water and distributed it away from the study site. Teejet nozzles (80150) passed between catch pans in approximately 0.5 s passes with the duration of time spent in each catch pan determining the rainfall rate per hour. The machine was calibrated to apply 19 mm of rain in 8 min per rainfall treatment during the 2013 season and 25 mm of rain in 11 minutes per rainfall treatment during the 2014 season. Wheat head collections occurred prior to and following rainfall applications to measure the impact of rainfall on mite populations with a total 30 heads per rainfall treatment (5/plot) for each of four collections per season. Heads were kept at 4°C until they could be placed on high definition tape as described previously.

Mite count data from the rainfall study were analyzed using PROC GLIMMIX (SAS Institute 2008) with repeated measures to test the fixed effects of rainfall application, collection date, and infestation method. Random effects were collection date and replication. Mite counts

from wheat heads were averaged for each treatment plot prior to analysis. Variances increased geometrically as a function of the mean indicating a negative binomial distribution. Covariance models on inference (CS, AR(1), ANTE(1), and UN) were tested to determine the model with the lowest Akaike information criterion corrected value, and degrees of freedom were adjusted using Kenward and Rogers methods to reduce test statistics biases. Environmental data were obtained from the High Plains Regional Climate Center (hprcc.unl.edu; University of Nebraska-Lincoln). Weather data originated from an established weather station located less than 2 km from the plot site.

Winter wheat variety trial mite count data were analyzed as described for the rainfall study by using the average number of wheat curl mites per plot for each stage of head development. No differences occurred between varieties; therefore, varieties were averaged prior to the analysis. Fixed effects were wheat development stage and site nested within year. Years and sites were not analyzed separately because not all sites were represented during each year of the study. Random effects were replications. Least significant mean differences were used to determine differences within and between main effects. Proportion of infested wheat heads was also reported to determine the frequency of infested heads in wheat fields for each development stage and site year combination. The direct infestation of germinated seedlings was reported as a percentage of total plants evaluated. No statistical analysis was conducted on this data due to the low frequency of infested plants.

Results

Mite Populations in Wheat Heads

The number of wheat curl mites per wheat head (Fig. 6.1) varied for each site year combination ($F_{5,94}$ = 15.15; P <.0001) with the greatest average occurring in Deuel County during 2012 (590) and 2014 (218) followed by Kimball County (94) in 2013. Average number of mites per head was lowest in Cheyenne County at 20, 48, and 55 mites/head for 2012, 2013, and 2014, respectively. Mite numbers also varied by wheat development stage ($F_{7,408}$ = 21.74; P <.0001) with the average number of mites per head increasing from water ripe (1) through early milk (8), middle milk (12), late milk (39), early dough (267), soft dough (269), and hard dough (548) stages. Mite populations declined significantly (t_{408} = 5.62; P <.0001) between the hard dough and harvest ripe (135) stage. A significant interaction occurred between site year and stage ($F_{35,408}$ = 6.68; P <.0001) due to the greater increase in mite populations at the hard dough stage for Deuel County during 2012 (1819) and 2014 (730) compared to Cheyenne County during 2012 (89), 2013 (212), and 2014 (231) or Kimball County in 2013 (403). In contrast, mite populations were less than 100 mites per head for all counties and years with the exception of Deuel County during 2012 at 1010 mites/head.

The proportion of wheat heads (Fig. 6.2) infested with mites at peak infestation reached 100% for every site year with the exception of Cheyenne County during 2014 (84% infested). In addition, the proportion of infested wheat heads was in excess of 40% for both Deuel County in 2012 and 2014 during the water ripe stage.

Mite Infestation of Seedlings

Of the 4037 plants evaluated, 61 plants were found to be infested with WCM, demonstrating that mites were able to directly infest germinated wheat seedlings from infested grains under controlled conditions. Seedling infestation from infested grain varied by site year and wheat development stage (Table 6.1). Mites were found on seedlings in four of the six site years with the greatest percentage of mites occurring in Deuel County during 2012 (47/921: 5%) and 2014 (7/398: 2%). In Cheyenne County, only 3 and 7 plants were found to be infested during 2012 and 2013, respectively. Of the seven stages of head development, mites were first observed during the early dough stage (8/1163: 1%), with increasing levels of infestation for soft (20/889: 2%) and hard (31/467: 7%) dough stages. Only 2 of 727 plants were found to be infested with mites during the harvest ripe stage.

Rainfall Study

Mite infestation method, natural rainfall, as well as application timing and amount of rain applied varied between the two years of the study; therefore, each year was analyzed separately. In 2013, limited natural rainfall occurred (Fig. 6.3a) during wheat heading with the exception of 45 mm of rain on 22 June. More frequent rainfall occurred during the 2014 season (Fig. 6.3b) following the early rainfall application date with 9 of the 10 days after the application having some level precipitation. However, the natural rainfall events during this 10-day period were low (2 – 15 mm). For the late season application in 2014, only 2 of the 9 days following the 2nd rainfall application had precipitation with rainfall of less than 5 mm on either day.

An analysis of variance for the fixed effect of infestation method during the 2013 season showed no significant interactions with rainfall treatments ($F_{3,17.7} = 0.10$; $P = 0.9564$), therefore

infestation methods were combined for the analysis. In 2013, mite populations on wheat heads (Fig. 6.4a) varied by collection date ($F_{3,20}$ = 18.86; P <.0001) with increasing mite populations for collection one (1.5), two (16.2), and three (65). Mite populations declined in the final collection (13.6) period. Rainfall applications showed differences in mite populations ($F_{3,18}$ = 6.50; P = 0.0036); however, these differences were not consistent with simulated rainfall treatments. The greatest number of mites across all collection dates occurred with early (51) and late (39) rainfall applications followed by no rainfall (29) and the combination rainfall application (22). The interaction between rainfall application and collection date was not significant ($F_{9,25.3}$ = 1.73; P = 0.1333).

Artificial infestation of wheat heads during the 2014 season (Fig. 6.4b) resulted in extensive mite populations on wheat heads with some in excess of 16,000 mites/head. Mite populations on wheat heads varied by collection period ($F_{3,20}$ = 46.04; P <.0001) with increasing mite populations from collection one (463), two (1063), and three (6054). Mite populations declined significantly (t_{20} = 2.53; P = 0.0200) between collection dates three and four (4484). No differences were observed between rainfall applications ($F_{3,18.1}$ = 0.72; P = 0.5502) or for the interaction between rainfall application and collection date ($F_{9,25.4}$ = 0.73; P = 0.6819).

Discussion

Mite populations on wheat heads (Fig. 6.1) collected from winter wheat variety trials in the western Panhandle of Nebraska varied considerably between site years. This variation and the average number of mites per wheat head were consistent with results reported by Mahmood et al. (1998) and Byamukama et al. (2015). Regardless of the variation between site years, this study demonstrated a consistent and significant increase in mite populations as wheat heads advanced through development stages.

Early season head collections from the water ripe through the late milk stages showed relatively low levels of mite populations. However, the proportion of infested plants at the water ripe stage (Fig. 6.2) varied considerably between locations at 0 and 50%, indicating a greater frequency of infested wheat heads in some fields soon after head emergence. During 2012 and 2014, we received and validated reports of significant yield loss from the wheat-mite-virus complex in Deuel County within a 15 km radius of the field site, indicating the potentail for a low level of mite infestation during the fall. Mite populations at the Deuel county sites were the highest recorded for the study; however, these populations did not conincide with a significant virus impact. Yield data from the winter wheat variety trials during 2012 show that virus resistant ‘Mace’ (1550 kg/ha) had lower grain yields than commercially susceptible ‘Camelot’ (2020 kg/ha), indicating a lack of significant pressure fromt wheat-mite-virus complex (Regassa et al. 2012). Mace was not present in 2014; however, yields for Camelot were at 3030 kg/ha, indicating virus pressure was minimal (Regassa et al. 2014). In addition, no virus sympotms were observed in these variety trials.

The results from this study demonstrate that not all wheat heads are infested with mites during the early stages of head development. This could be due to the inability to detect low mite

populations in wheat heads through the sticky tape method. The rapid and continued increase in the proportion of infested heads further supports the notion that low populations of mites were present within wheat heads. With the exception of Cheyenne County in 2013, all other site years reached 100% infestation level, indicating that all wheat fields are likely to become infested with mites in the weeks prior to wheat harvest. Under the most conservative levels, average mite populations of 50 mites/head would result in mite populations of 269 million per hectare assuming 164 heads per meter of wheat row. These large mite populations conicide with significant mite activity from wheat fields (see Chapter 3), reinforcing the concept by Thomas and Hein (2003) that mite movement is strongly linked with mite population densities on wheat heads. In addition, Nault and Styer (1969) reported increasing mite movement from wheat fields with peak activity near harvest, as a result of declining host suitability.

Greater mite populations on wheat heads also corresponded with direct infestation of germinated volunteer wheat seedlings under controlled conditions. This had not been previously documented. Direct mite infestation of wheat seedlings first occurred during the early dough stage with an increasing number of infested plants through the soft and hard dough stages with a rapid decline at the harvest ripe stage. Controlled conditions likely increased mite survival due to the maintenance of adequate moisture for seedling germination. Such conditions are not impossible under field conditions as hail damage typically destroys wheat stands, increasing the potential for dense vegetation next to the soil surface. Situations with lower humidity levels are likely to decrease direct infestation of newly germinated wheat, due to a reduced survival period for mites (Wosula et al. 2015). This is apparent from the diminishing ability of mites to survive on harvest ripe wheat as reflected in the decline in mite populations from wheat heads that were placed on high definition tape. Greater infestation of mites in hard dough compared to harvest

ripe indicates that mites continue to feed on seeds until germination occurs. This is based on the assumption that as wheat approaches harvest seeds dry down rapidly and become unsuitable for mite feeding. Rainfall applications had no consistent impact on mite populations during either year of the study. The rainfall simulator used in this study was designed to produce raindrops of similar size and energy to those coming from natural rain events. The reproducibility of natural events increases the likelihood that rain during wheat heading has little impact on mite populations. A lack of impact on mite populations could be due to the physical structure of wheat heads, precluding rain drops from collecting within the glumes of the wheat head where mites are typically found. In the case of 2014, high mite populations may have been reduced but only minimally, allowing mites to rebound rapidly due to their high reproductive rates following rainfall application. Similar studies are needed to address the impact of rainfall on mite populations during the earlier, vegetative stages of wheat development when the mites are not protected within the heads.

The results from this study demonstrate the seasonal buildup of mite populations with peak populations occuring during the soft and hard dough stages of winter wheat. The ability of mites to directly infest germinated wheat from infested grain under controlled conditions was demonstrated; however, this was limited to late stages of wheat development (early dough through hard dough) resulting in low levels of infestation for all these late stages. Mite infestation of seedlings was also associated with high populations on wheat heads with Deuel County accounting for 54 of the 61 plants with direct seedling infestation. Our results show a lack of impact from rain applied during the heading stages of wheat, likely as a result of mites being protected from the direct impact of rain drops. The importance of mite population

densities for mite movement indicates a need for further research, especially regarding the role of rainfall on mite populations in the vegetative stages of wheat development.

Figures

Figure 6.1. Average number of wheat curl mites per head during different heading stages of wheat (water ripe, early milk, middle milk, late milk, early dough, soft dough, hard dough, ripe) across site years (2012 Deuel, 2012 Cheyenne, 2013 Cheyenne, 2013 Kimball, 2014 Cheyenne, and 2014 Deuel).

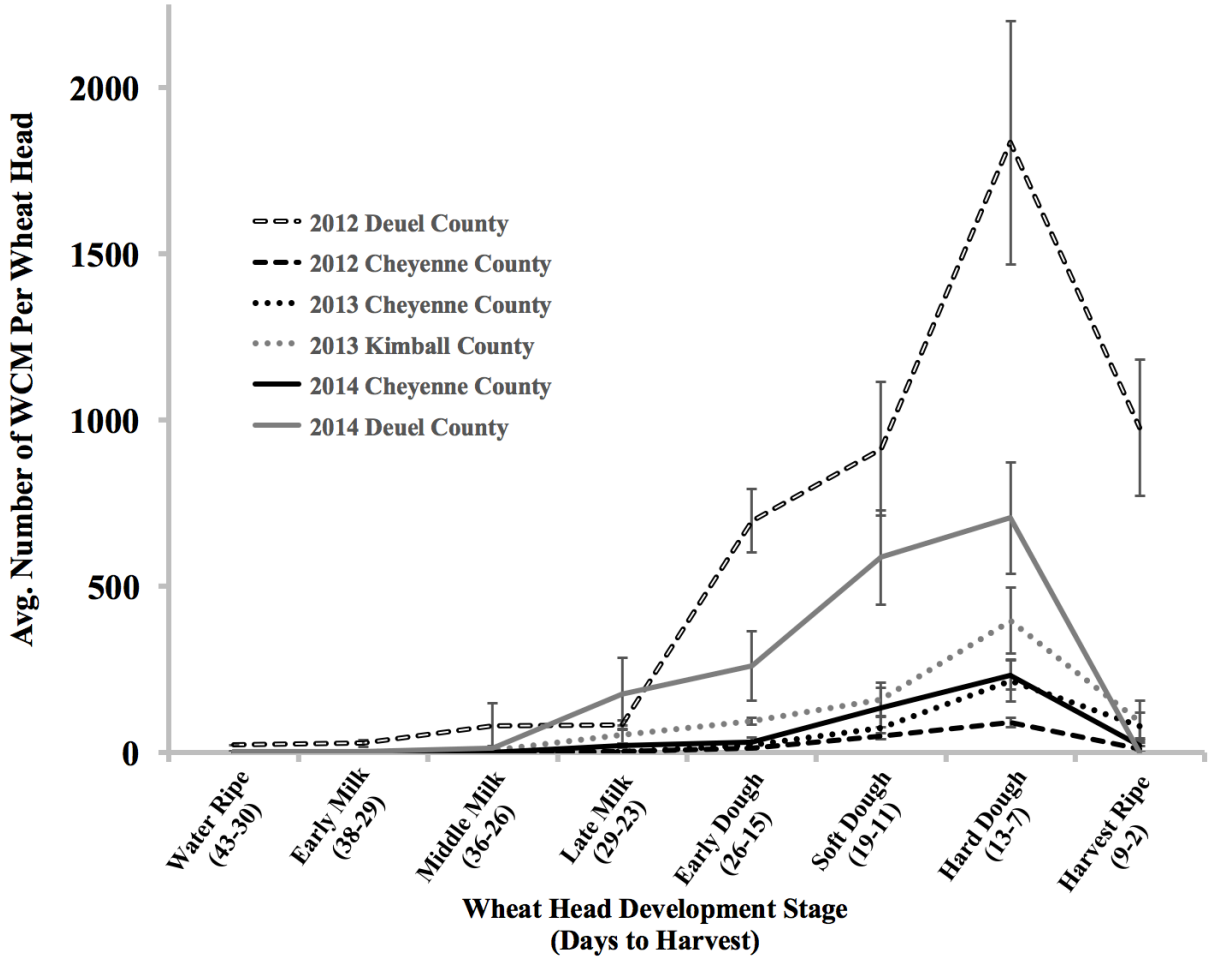


Figure 6.2. Proportion of mite infested wheat heads during different heading stages of wheat (water ripe, early milk, middle milk, late milk, early dough, soft dough, hard dough, ripe) across years (2012, 2013, 2014) and locations (Cheyenne, Deuel, and Kimball Counties).

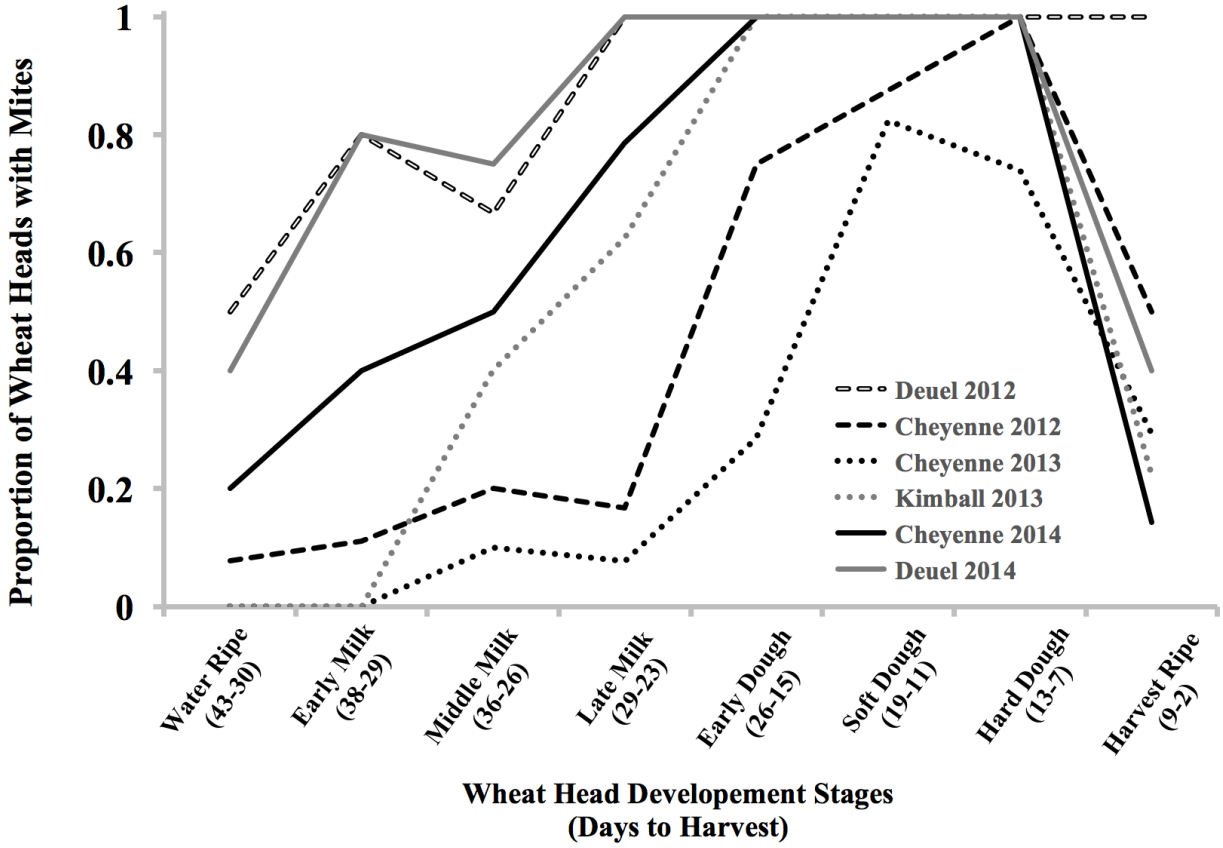


Figure 6.3. Natural rainfall totals per day, wheat head sample collection dates, and dates of rainfall applications (early and late) for 2013 (a) and 2014 (b) growing seasons. Wheat was infested on June 6th in 2013, and May 24th in 2014.

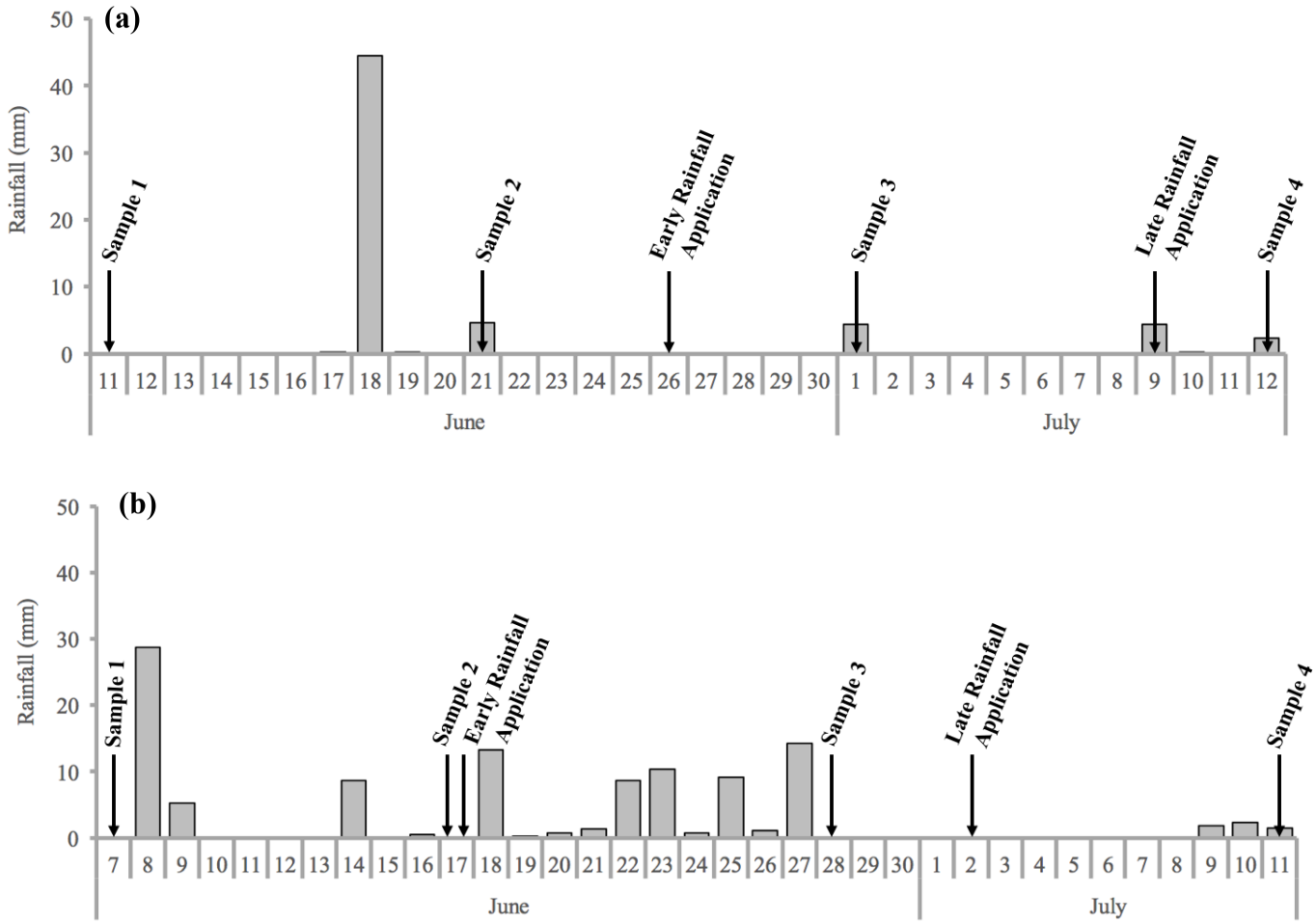
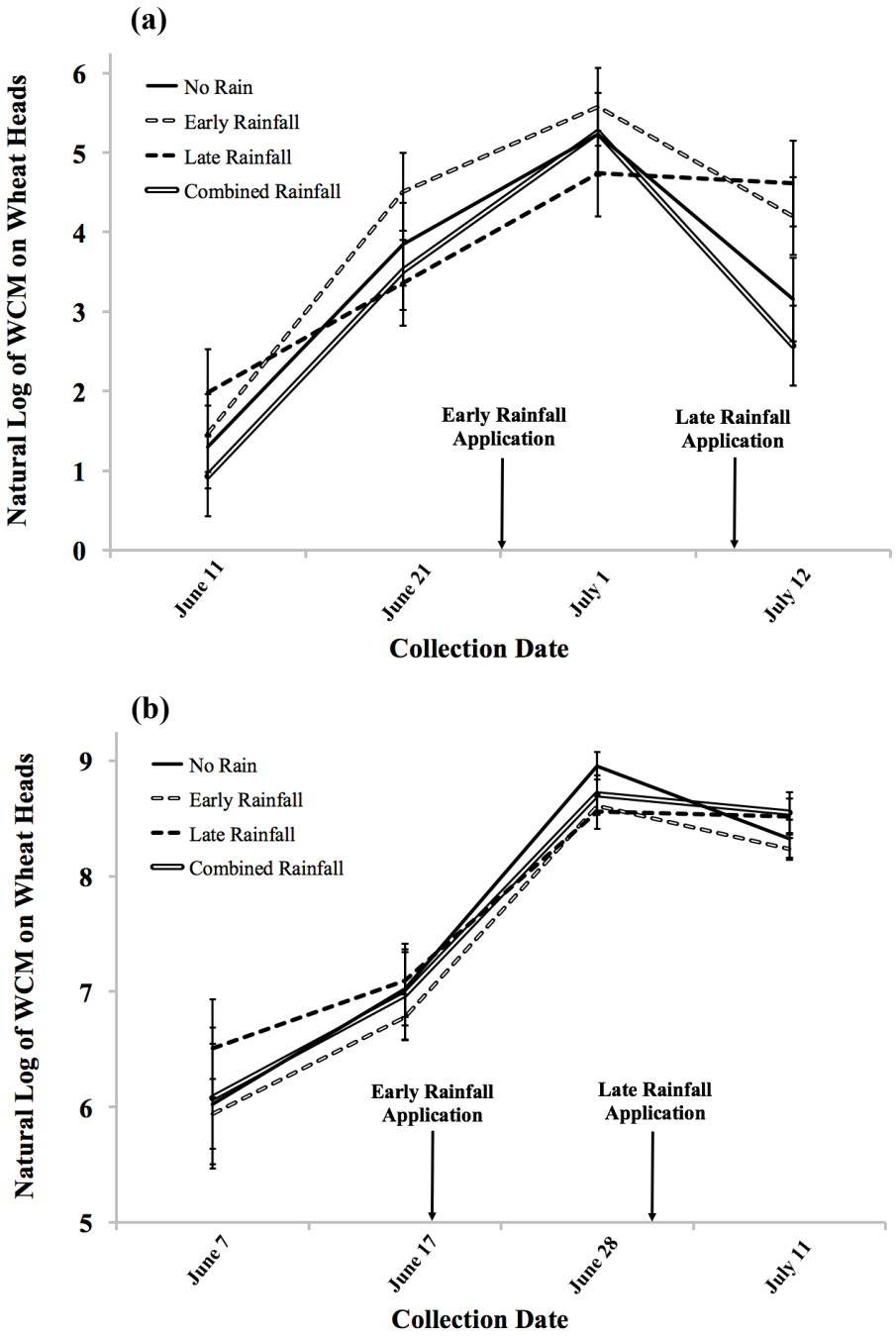


Figure 6.4. Natural log of WCM populations on wheat heads across rainfall applications (No rain, early, late, and combined) and collection periods for simulated rainfall study during the 2013 (a) and 2014 (b) seasons.



Tables

Table 6.1. Mite presence on germinated wheat seedlings from seven wheat head development stages (early milk, middle milk, late milk, early dough, soft dough, hard dough and harvest ripe) across three years (2012, 2013, and 2014) and three locations (Cheyenne, Kimball and Deuel County).

		No. of Plants with Mites/ Total Plants Evaluated							
		Wheat Head Development Stage							
Year	Location	Early Milk	Middle Milk	Late Milk	Early Dough	Soft Dough	Hard Dough	Harvest Ripe	**Total per Year/Location**
2012	Cheyenne	0/2 (0%)	0/46 (0%)	0/237 (0%)	0/370 (0%)	3/181 (2%)	0/19 (0%)	N/A	**3/874 (0.3%)**
	Deuel	0/31 (0%)	0/69 (0%)	0/150 (0%)	8/423 (2%)	15/140 (11%)	23/63 (37%)	1/45 (2%)	**47/921 (5.1%)**
2013	Cheyenne	0/7 (0%)	0/16 (0%)	0/50 (0%)	0/118 (0%)	0/211 (0%)	3/195 (2%)	1/267 (0%)	**4/864 (0.4%)**
	Kimball	0/5 (0%)	0/14 (0%)	0/36 (0%)	0/112 (0%)	0/118 (0%)	0/91 (0%)	0/216 (0%)	**0/592 (0.0%)**
2014	Cheyenne	N/A	0/9 (0%)	0/56 (0%)	0/42 (0%)	0/161 (0%)	0/41 (0%)	0/79 (0%)	**0/388 (0.0%)**
	Deuel	N/A	0/34 (0%)	0/10 (0%)	0/98 (0%)	2/78 (3%)	5/58 (9%)	0/120 (0%)	**7/398 (1.8%)**
Total per Stage		**0/64 (0%)**	**0/188 (0%)**	**0/539 (0%)**	**8/1163 (0.7%)**	**20/889 (2.2%)**	**31/467 (6.6%)**	**2/727 (0.3%)**	**61/4037 (1.5%)**

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Chapter 7

Frequency and Density of Weeds in Winter Wheat Stubble Fields in the central High Plains

Introduction

Historically, weed surveys in winter wheat fields have been used to investigate the performance of herbicides (Wicks et al. 2003), estimate weed control problems (Loux and Berry 1991), or evaluate changes in weed species composition or their abundance with varying management practices (Wicks et al. 2000). In some cases, weeds can support arthropods and plant pathogens, increasing their potential to cause economic losses in agricultural crops that share the same pest/pathogen host range. Risk assessments of weedy hosts are primarily based on their ability to support arthropods or diseases, as well as their distribution, frequency and temporal occurrence in regions where susceptible crops are grown.

The wheat-mite-virus complex is one of the primary yield limiting diseases in the central High Plains of North America. This complex consists of three viruses (*Wheat streak mosaic virus* (WSMV), *Wheat mosaic virus* (WMoV), and *Triticum mosaic virus* (TriMV)) that are transmitted by the wheat curl mite (WCM; *Aceria tosichella* Keifer). Yield losses from this complex are typically associated with the presence of volunteer wheat that emerges prior to wheat harvest, usually as a result of hailstorms during wheat heading. However, historical evidence and observations indicate that other secondary hosts, such as summer annual grasses, could be important for the over-summering survival of mites and virus leading to the subsequent impact of this complex on fall planted winter wheat (Christian and Willis 1993).

Unlike most eriophyid mites, the WCM has a broad host range, occurring on approximately 90 different grass species (Amrine and Stasny 1994, Navia et al. 2013). In part, this wide host range is due to a build-up in mite populations on wheat heads

(Byamukama et al. 2015) that later emigrate from wheat fields around harvest. In addition, WCM move randomly with wind currents as they are not capable of directed movement after leaving a host plant. The combination of these two factors results in WCM being introduced to a wide range of plant species as wheat nears maturity. Suitable host plants are critical for the over-summering survival of mites as they cannot survive for more than a few days without a host (Wosula et al. 2015). Several studies have been conducted to determine host suitability for WCM and the viruses they transmit through field observations, short-term reproductive studies, and mechanical inoculations (see Appendix A). In Chapter 2 and 3, we identified the long-term reproductive potential of WCM on barnyard grass and green foxtail, and validated their risk as a source of mites and virus to fall planted winter wheat under field conditions. Barnyard grass (*Echinochloa crus-galli* (L.) Beauv.) showed high reproductive rates for WCM under greenhouse conditions and significant virus impact on fall planted winter wheat when compared with other hosts. In contrast, green foxtail showed low levels of reproduction and some virus spread under field conditions. Given the difference in risk potential of these potential over-summering hosts, it is important to understand the frequency and density of these hosts, and identify additional potential mite and virus hosts. The objective of this study was to survey weed presence in winter wheat stubble across winter wheat growing areas in western Nebraska, northwest Kansas, and northeast Colorado.

Materials and Methods

Winter wheat fields were surveyed during early to mid-August over two years across 18 counties in the Panhandle and southwestern Nebraska, northwestern Kansas, and northeastern Colorado (Fig. 7.1). This geographic region was chosen based on changes in crop rotations and management options that occur across the study area to gain a better understanding of weed species and abundance in this region.

In 2013, three fields were sampled per county with ten locations within each field whereas six fields were sampled per county with five locations per field in 2014. CropScape, a product of the United States Department of Agriculture – National Agricultural Statistics Service, was used to identify regions where winter wheat was grown. GPS waypoints were selected throughout these wheat-growing regions and random numbers were generated to determine stops in each county to survey fields for weeds.

Within a field, survey locations were taken at 30-40 meter intervals with samples beginning at approximately ten meters from the field edge. A 1-m^2 frame made of polyvinyl tube with ½ and ¼ meter dividers was used to evaluate weed species and population densities at each location within a field. To determine population density for a given weed species, plant counts were made at ¼, ½, and 1-m^2 areas, depending the on the number of plants counted per unit area. If plant counts exceeded 50 plants per ¼ or ½ m^2 areas, then the number of plants was recorded as well as the unit area at which the evaluation was made. Weeds with less than 50 plants per ½ meter were evaluated across a 1-m^2 area.

The frequency of each weed species was reported as a percentage of total fields evaluated. Weed densities were calculated by converting all counts to a per m^2 area basis and then averaging the mean number of plants per m^2 for each field.

Results

Volunteer wheat (*Triticum aestivum* L.) had the highest occurrence (Table 7.1) in winter wheat stubble at 68.6% and 48.6% occurrence in fields and densities of 40.8 and 40.5 plants/m^2. Averages densities for volunteer wheat were similar between years, however, individual wheat stubble fields ranged between 0.6 and 212 plants/m^2. In nearly all cases, the volunteer wheat had originated as a result of a direct loss of seed during the harvesting process and later germinated with post-harvest rains. This assumption was based on the lack of hail damage in the area, distribution of germinated wheat in the field, and absence of significant WCM or virus pressure on volunteer wheat at the time of the survey.

Of the summer annual grasses identified, stinkgrass (*Eragrostis cilianensis* (All.) E. Mosher) was most frequently found with presence in 70.6% and 42.9% of fields during 2013 and 2014, respectively. Stinkgrass occurrence in wheat stubble was similar to volunteer wheat; however, its densities (20.0 and 14.7 plants/m^2) were lower than volunteer wheat. Green foxtail and witchgrass (*Panicum capillare* L.) were also present in more than 30% of wheat stubble fields for either species over the two years of the survey. All other grass species had relatively low frequencies with barnyard grass found in 9.8% and 6.7% of fields with a wide range in population densities from 26.6 to 4.3 plants/m^2 in 2013 and 2014, respectively. The highest densities of barnyard grass were found during 2013 at 112 plant/m^2 with peak numbers occurring within the low-lying areas.

The remaining grass species identified in this survey were found in less than 4% of fields during either year of the survey. Of these grasses, longspine sandspur (*Cenchrus longispinus* (Hack.) Fern) had the highest population density with 32.1 plants/m^2. In most cases, fields with longspine sandspur had relatively low population densities with the exception of a single field in

Garden County in Nebraska with populations densities of 49.6 plants per m^2 across the five locations evaluated.

Even though no broadleaf plants have been found to host wheat curl mites, broadleaf plants (Table 7.1) were also evaluated for their frequency and density in these wheat fields. The most frequent plants seen were kochia, Russian thistle, and *Amaranthus spp.* (redroot pigweed, tumble pigweed, and tall waterhemp). In general, densities of broadleaf species were lower than those of grasses, with average densities less than 12 plants/m^2.

Discussion

The frequency and density of grass hosts found in this survey provides critical information on the risk potential of previously identified over-summering hosts for the wheat-mite-virus complex. Barnyard grass, a high risk host (see Chapter 2, 3) for WCM and virus was relatively infrequent in winter wheat stubble; however, high population densities (max. 112 plants/m^2) of this host were found in some low-lying areas. In contrast, green foxtail a comparatively lower risk host was frequently found in winter wheat stubble; however, its population densities were relatively low at 8.6 and 7.5 plants/m^2. These results provide a potential explanation for the ability of high-risk hosts such as barnyard grass to evade detection in previous studies (Christian and Willis 1993). Stinkgrass and witchgrass were present in more than 40% of fields during each year the survey was conducted. WCM reproductive studies on stinkgrass indicate that it is a poor host for WCM with few mites present (Slykhuis 1955, 1956, Connin 1956, Staples and Allington 1956); however, some studies have indicated that it is susceptible to WCM with 28.8% of plants infested under field conditions (Somsen and Sill 1970). Reproductive studies on witchgrass show no mites present 7 days after infestation (Slykhuis 1955, Connin 1956, Harvey et al. 2001) with only 1.4% of plants infested with mites under field conditions (Somsen and Sill 1970).

Wicks et al. (2003) conducted the most recent survey of weeds in winter wheat fields in western and southern Nebraska. A comparison of the two studies shows that green foxtail, stinkgrass, and witchgrass had consistently high frequencies in both surveys. Difference in host frequencies occurred for volunteer wheat which was found in only 6% of fields in 1998 whereas 68.6% and 48.6% of fields had volunteer wheat during 2013 and 2014, respectively in this study. In addition, barnyard grass was found in 27% of wheat stubble fields in 1998 compared to 9.8%

and 6.7% of fields over the two years of this study. Differences between weed surveys are not uncommon as Wicks et al. (2003) reported a 54 and 42% increase in the occurrence of longspine sandspur and stinkgrass, respectively, when compared to surveys conducted in 1980-81 (Buhler et al. 1985). In addition, a 16 and 37% increase in longspine sandspur and stinkgrass, respectively, was found by Wicks et al. (2003) compared to a survey conducted in 1986 (Wicks et al. 1989). The differences between the current study and the previous surveys could be a result of the methods used to evaluate fields for weeds. Wicks et al. (2003) evaluated a 1.5-m area, approximately 50 meters from the field edge for weed population density whereas the frequency of weeds was reported based on an evaluation of plants found in a 0.8 hectare area around the sample site. Such methods would have allowed for the detection of less frequent hosts that may have evaded the methods used in this study.

This study provides important parameters for evaluating the risk potential of hosts, such as barnyard grass and green foxtail, that were previously characterized as sources of mites and virus. In addition, this survey will help prioritize the selection of plants for future host range studies. A comparison of historical data indicates a need to conduct these surveys at regular intervals, as they provide a baseline of information for risk assessment and impact of weeds in agricultural crops.

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Tables

Table 7.1. Frequency of weeds in winter wheat stubble across 52 fields in 2013 and 105 fields in 2014 in the Panhandle and southwestern Nebraska, northwestern Kansas, and northeastern Colorado during early- to mid-August.

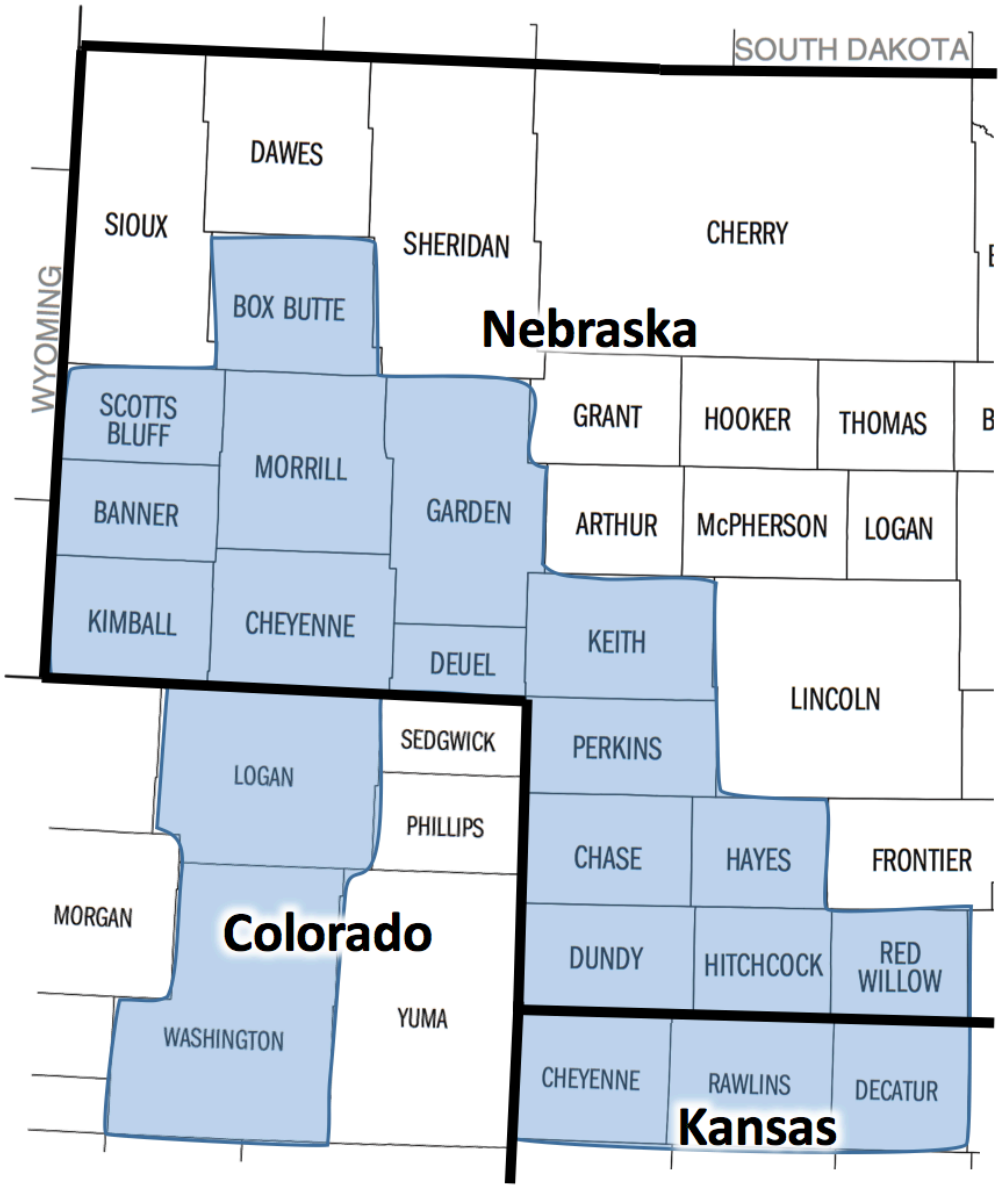
Common Name	Latin Name	Code	2013	2014
	Grasses			
Volunteer Wheat	*Triticum aestivum* L.	TRAE	68.6%	48.6%
Stinkgrass	*Eragrostis cilianensis* (All.) E. Mosher	ERACN	70.6%	42.9%
Green Foxtail	*Setaria viridis* (L.) Beauv.	SETVI	52.9%	32.4%
Witchgrass	*Panicum capillare* L.	PANCA	39.2%	41.0%
Barnyard grass	*Echinochloa crus-galli* (L.) Beauv.	ECHCG	9.8%	6.7%
Large crabgrass	*Digitaria sanguinalus* (L.) Scop.	DIGSA	3.9%	0.0%
Longspine Sandbur	*Cenchrus longispinus* (Hack.) Fern	CCHPA	2.0%	1.9%
Corn	*Zea mays* L.	ZEAMX	2.0%	1.9%
Yellow Foxtail	*Setaria pumila (Poir.) & Shult.*	SETLU	0.0%	1.9%
Proso Millet	*Panicum miliaceum* L.	PAMI2	2.0%	0.0%
Volunteer Oats	*Avena fatua* L.	AVESA	0.0%	1.0%
	Broadleaf			
Kochia	*Kochia scoparia* (L.) Schrad	KCHSC	58.8%	41.0%
Russian Thistle	*Salsola tragus* L.	SATR12	49.0%	46.7%
Pigweed/Waterhemp	*Amaranthus spp.*	.	64.7%	27.6%
Buffalobur	*Solanum rostratum Dun.*	SOLCU	39.2%	19.0%
Common Lambsquarters	*Chenopodium album* L.	CHEAL	27.5%	15.2%
Carpetweed	*Mullugo verticillata* L.	MOLVE	19.6%	20.0%
Common Purslane	*Portulaca oleracea*L.	POROL	9.8%	18.1%
Puncturevine	*Tribulus terrestris* L.	TRBTE	15.7%	2.8%
Wild Buckwheat	*Polygonum convolvulus* L.	POLCO	15.7%	1.9%
Common Sunflower	*Helianthus annuus* L.	HELAN	5.9%	0.0%
Prickly Lettuce	*Lactuca serriola* L.	LACSE	0.0%	3.8%
Horseweed	*Conyza canadensis* (L.) Cronq.	ERICA	0.0%	2.8%
Venice Mallow	*Hibiscus trionum* L.	HIBTR	0.0%	1.9%
Velvet Leaf	*Abutilon theophrasti* Medik.	ABUTH	0.0%	0.9%
Common Ragweed	*Ambrosia artemisiifolia* L.	AMBEL	0.0%	0.9%

Table 7.2. Density of weeds in winter wheat stubble across 52 fields in 2013 and 105 fields in 2014 in the Panhandle and southwestern Nebraska, northwestern Kansas, and northeastern Colorado during early- to mid-August.

Common Name	Scientific Name	2013	2014
	Grasses		
Volunteer Wheat	*Triticum aestivum* L.	40.8 ± 6.4	40.5 ± 9.2
Stinkgrass	*Eragrostis cilianensis* (All.) E. Mosher	20.0 ± 4.8	14.7 ± 3.1
Green Foxtail	*Setaria viridis* (L.) Beauv.	8.6 ± 1.8	7.5 ± 2.5
Witchgrass	*Panicum capillare* L.	3.6 ± 1.0	7.6 ± 1.5
Barnyard grass	*Echinochloa crus-galli* (L.) Beauv.	48.9 ± 40.8	4.3 ± 1.1
Large crabgrass	*Digitaria sanguinalus* (L.) Scop.	2.3 ± 4.1	-
Longspine Sandbur	*Cenchrus longispinus* (Hack.) Fern	1.0	32.1 ± 29.1
Corn	*Zea mays* L.	0.2	0.2 ± 0.2
Yellow Foxtail	*Setaria pumila (Poir.) & Shult.*	-	6.7
Proso Millet	*Panicum miliaceum* L.	8.3	-
Volunteer Oats	*Avena fatua* L.	-	0.6
	Broadleaf		
Kochia	*Kochia scoparia* (L.) Schrad	2.1 ± 0.3	3.2 ± 0.8
Russian Thistle	*Salsola tragus* L.	2.1 ± 0.5	3.2 ± 0.4
Pigweed/Waterhemp	*Amaranthus spp.*	6.8 ± 1.9	3.3 ± 0.6
Buffalobur	*Solanum rostratum Dun.*	2.0 ± 0.5	1.6 ± 0.2
Common Lambsquarters	*Chenopodium album* L.	1.9 ± 0.6	1.7 ± 0.3
Carpetweed	*Mullugo verticillata* L.	2.4 ± 0.6	3.2 ± 0.6
Common Purslane	*Portulaca oleracea*L.	6.6 ± 5.4	4.8 ± 1.3
Puncturevine	*Tribulus terrestris* L.	11.9 ± 7.8	2.3 ± 0.8
Wild Buckwheat	*Polygonum convolvulus* L.	2.2 ± 0.8	2.2 ± 0.8
Common Sunflower	*Helianthus annuus* L.	3.1 ± 1.2	-
Prickly Lettuce	*Lactuca serriola* L.	-	4.3 ± 1.3
Horseweed	*Conyza canadensis* (L.) Cronq.	-	1.3 ± 0.3
Venice Mallow	*Hibiscus trionum* L.	-	3.0 ± 0.6
Velvet Leaf	*Abutilon theophrasti* Medik.	-	1.0 -
Common Ragweed	*Ambrosia artemisiifolia* L.	-	2.0 -

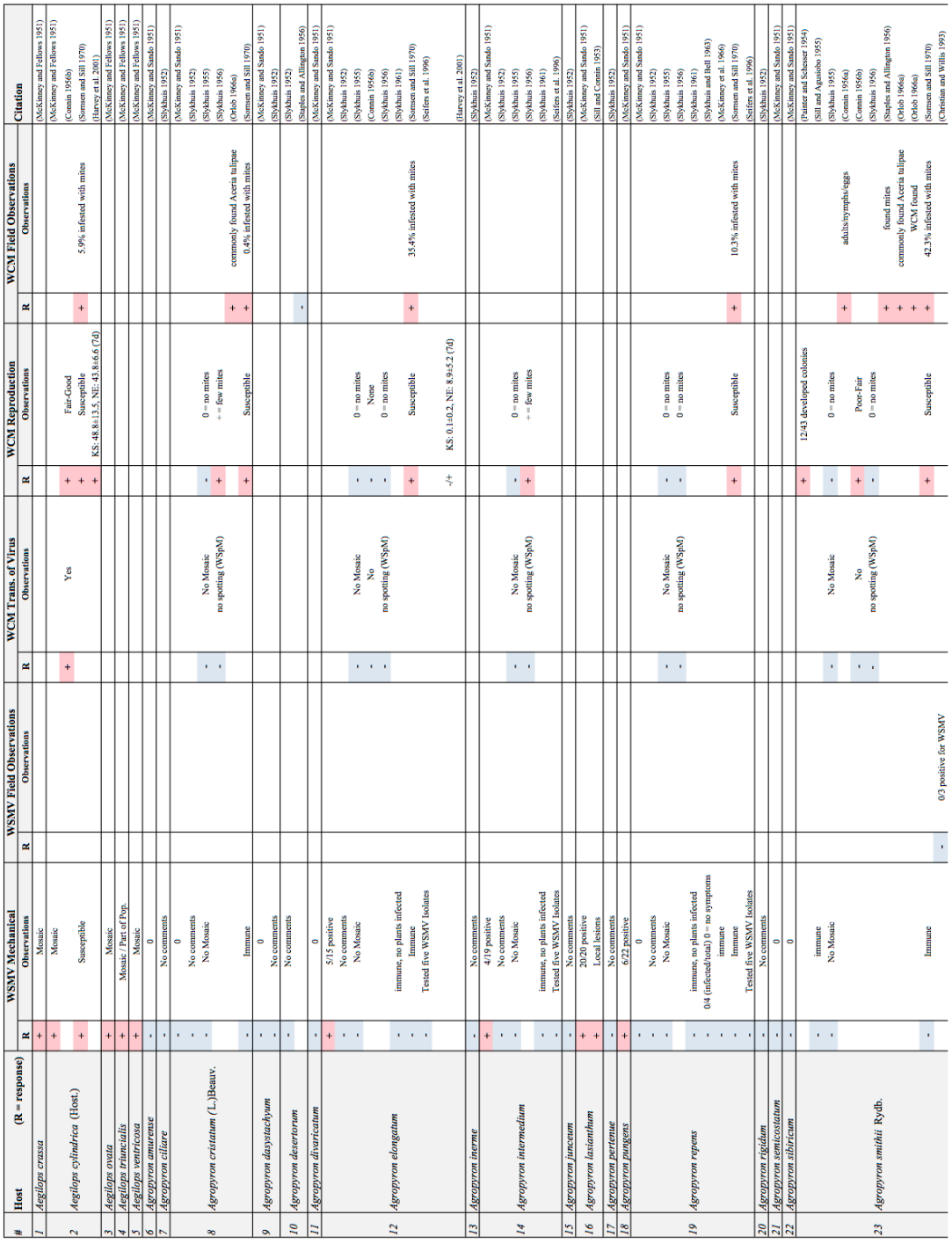
Figures

Figure 7.1. County map for Nebraska, Kansas, and Colorado with area highlighted where winter wheat fields were surveyed for weed frequency and density during the fall of 2013 and 2014. (3 fields per county in 2013; 6 fields per county in 2014).



Appendix

Appendix A. Literature on hosts tested for the wheat streak mosaic virus and the wheat curl mite.



#	Host (R = response)	WSMV Mechanical		WSMV Field Observations		WCM Trans. of Virus		WCM Reproduction		WCM Field Observations		Citation
		R	Observations	R	Observations	R	Observations	R	Observations	R	Observations	
1	*Aegilops crassa*	+	Mosaic									(McKinney and Fellows 1951)
2	*Aegilops cylindrica* (Host.)	+	Mosaic Susceptible			+	Yes	+ + +	Fair-Good Susceptible KS: 48.8±13.5, NE: 43.8±6.6 (7d)	+	5.9% infested with mites	(McKinney and Fellows 1951) (Connin 1956b) (Somsen and Sill 1970) (Harvey et al. 2001)
3	*Aegilops ovata*	+	Mosaic									(McKinney and Fellows 1951)
4	*Aegilops triuncialis*	+	Mosaic / Part of Pop.									(McKinney and Fellows 1951)
5	*Aegilops ventricosa*	+	Mosaic									(McKinney and Fellows 1951)
6	*Agropyron amurense*	-	0									(McKinney and Sando 1951)
7	*Agropyron ciliare*	-	No comments									(Skyhuis 1952)
8	*Agropyron cristatum* (L.)Beauv.	- - -	0 No comments No Mosaic Immune			- -	No Mosaic no spotting (WSpM)	- +	0 = no mites + = few mites Susceptible	+ +	commonly found Aceria tulipae 0.4% infested with mites	(McKinney and Sando 1951) (Skyhuis 1952) (Skyhuis 1955) (Skyhuis 1956) (Orloh 1966a) (Somsen and Sill 1970)
9	*Agropyron dasystachyum*	-	0									(McKinney and Sando 1951)
10	*Agropyron desertorum*	-	No comments							-		(Skyhuis 1952) (Staples and Allington 1956)
11	*Agropyron divaricatum*	-	0									(McKinney and Sando 1951)
12	*Agropyron elongatum*	+ - - - -	5/15 positive No comments No Mosaic immune, no plants infected Immune Tested five WSMV Isolates			- - -	No Mosaic No no spotting (WSpM)	- - - + -/+	0 = no mites None 0 = no mites Susceptible KS: 0.1±0.2, NE: 8.9±5.2 (7d)	+ -	35.4% infested with mites	(McKinney and Sando 1951) (Skyhuis 1952) (Skyhuis 1955) (Connin 1956b) (Skyhuis 1956) (Skyhuis 1961) (Somsen and Sill 1970) (Seifers et al. 1996) (Harvey et al. 2001)
13	*Agropyron inerme*	-	No comments									(Skyhuis 1952)
14	*Agropyron intermedium*	+ - - -	4/19 positive No comments No Mosaic immune, no plants infected Tested five WSMV Isolates			- -	No Mosaic no spotting (WSpM)	- +	0 = no mites + = few mites			(McKinney and Sando 1951) (Skyhuis 1952) (Skyhuis 1955) (Skyhuis 1956) (Skyhuis 1961) (Seifers et al. 1996)
15	*Agropyron junceum*	-	No comments									(Skyhuis 1952)
16	*Agropyron lasianthum*	+	20/20 positive									(McKinney and Sando 1951)
17	*Agropyron pertenue*	+	Local lesions No comments									(Sill and Connin 1953) (Skyhuis 1952)
18	*Agropyron pungens*	+	6/22 positive									(McKinney and Sando 1951)
19	*Agropyron repens*	- - - - - - -	0 No comments No Mosaic immune, no plants infected 0/4 (infected/total) 0 = no symptoms immune Immune Tested five WSMV Isolates			- -	No Mosaic no spotting (WSpM)	- -	0 = no mites 0 = no mites Susceptible	+ +	10.3% infested with mites	(McKinney and Sando 1951) (Skyhuis 1952) (Skyhuis 1955) (Skyhuis 1956) (Skyhuis 1961) (Skyhuis and Bell 1963) (McKinney et al. 1966) (Somsen and Sill 1970) (Seifers et al. 1996)
20	*Agropyron rigidum*	-	No comments									(Skyhuis 1952)
21	*Agropyron semicostatum*	-	0									(McKinney and Sando 1951)
22	*Agropyron sibiricum*	-	0									(McKinney and Sando 1951)
23	*Agropyron smithii* Rydb.	- - - -	immune No Mosaic Immune	-	0/3 positive for WSMV	- -	No Mosaic No no spotting (WSpM)	+ - + -	12/43 developed colonies 0 = no mites Poor-Fair 0 = no mites	+ + + + + +	adults/nymphs/eggs found mites commonly found Aceria tulipae WCM found 42.3% infested with mites	(Painter and Scheser 1954) (Sill and Agusiobo 1955) (Skyhuis 1955) (Connin 1956a) (Connin 1956b) (Skyhuis 1956) (Staples and Allington 1956) (Orloh 1966a) (Orloh 1966a) (Somsen and Sill 1970) (Christian and Willis 1993)

#	Host (R = response)	WSMV Mechanical		WSMV Field Observations		WCM Trans. of Virus		WCM Reproduction		WCM Field Observations		Citation
		R	Observations	R	Observations	R	Observations	R	Observations	R	Observations	
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
24	*Agropyron smithii*							-	KS: 0.0±0.0, NE: 1.4±1.3 (7d)			(Harvey et al. 2001)
25	*Agropyron spicatum*	-	0									(McKinney and Sando 1951)
26	*Agropyron spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
27	*Agropyron trachycaulum*	+	2/22 positive									(McKinney and Sando 1951)
		-	No comments									(Slykhuis 1952)
		-	No Mosaic			-	No Mosaic	-	0 = no mites			(Slykhuis 1955)
						-	no spotting (WSpM)	-	0 = no mites			(Slykhuis 1956)
										-		(Staples and Allington 1956)
		-	Immune					+	Susceptible	+	8.3% infested with mites	(Somsen and Sill 1970)
		-	No comments									(Slykhuis 1952)
		+	Local lesions									(Sill and Connin 1953)
						-	no spotting (WSpM)	-	0 = no mites			(Slykhuis 1956)
28	*Agropyron ugamicum*	+	4/14 positive									(McKinney and Sando 1951)
29	*Agrostis alba*	-	No Mosaic			-	No Mosaic	-	0 = no mites			(Slykhuis 1955)
						-	no spotting (WSpM)	-	0 = no mites			(Slykhuis 1956)
30	*Agrotricum spp.*	+	Some immune, res., susc., segregating									(Sill and Connin 1953)
		+	erratic response									(Sill and Agusiobo 1955)
						-	variable response	+	mites present after a week			(Slykhuis 1956)
		+	4/6 varities susceptible									(Finley 1957)
										+	field infested	(Bruehl and Keifer 1958)
31	*Allium cepa*	-	probably immune									(Sill and Agusiobo 1955)
32	*Alopecurus carolinianus*	-	Immune							-	0/1 plants	(Somsen and Sill 1970)
33	*Alopecurus pratensis*	-	immune									(Sill and Agusiobo 1955)
						-	No	-	None			(Connin 1956b)
										-	0/1 plants	(Somsen and Sill 1970)
								-	KS: 0.2±0.1, NE: 0.0±0.0 (7d)			(Harvey et al. 2001)
34	*Amaryllis sp.*	-	probably immune									(Sill and Agusiobo 1955)
35	*Andropogon gerardii*							+	low population after 7 days			(Orlob 1966a)
								+	Susceptible (poor host)	+	0.2% infested with mites	(Somsen and Sill 1970)
				-	0/22 positive for WSMV							(Christian and Willis 1993)
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
36	*Andropogon hallii*	-	immune									(Sill and Agusiobo 1955)
37	*Andropogon saccharoides*			-	0/8 positive for WSMV							(Christian and Willis 1993)
38	*Andropogon schaemum*	-	immune									(Sill and Agusiobo 1955)
39	*Andropogon scoparius*							-	no mites			(Orlob 1966a)
								-	Resistant	-	0.0% infested with mites	(Somsen and Sill 1970)
				-	0/15 positive for WSMV							(Christian and Willis 1993)
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
40	*Andropogon sibircus*	-	immune									(Sill and Agusiobo 1955)
41	*Andropogon spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
	Aristida sp.									-	no mites found	(Carew et al. 2009)
42	*Aristida oligantha*			-	0/3 positive for WSMV							(Christian and Willis 1993)
43	*Arrhenatherum elatius*	-	immune									(Sill and Agusiobo 1955)
						-	No	+	Poor			(Connin 1956b)
										-	0.0% infested with mites	(Somsen and Sill 1970)
44	*Avena fatua*	-	No comments									(Slykhuis 1952)
		+	Mosaic / Few Plants with Symptoms			+	Mosaic / Few Plants with Symptoms	-	0 = no mites			(Slykhuis 1955)
						-	no spotting (WSpM)	+	+ = few mites			(Slykhuis 1956)
		+	4/6 infected/total) + = mild mosaic									(Slykhuis and Bell 1963)
		+	Susceptible					-	Resistant	-	0.0% infested with mites	(Somsen and Sill 1970)
		+	Tested five WSMV Isolates									(Seifers et al. 1996)
				+	2006: 30% positive (20 plants tested)							(Coutts et al. 2008)
				-	2007: 7 plants tested							(Coutts et al. 2008)
										+	6 WCM, all WCM2 Type	(Carew et al. 2009)
45	*Avena sativa*	+	5/9 vareities positive									(McKinney 1949)
		+	8 varieties, 7.9 - 79.5% positive									(Slykhuis 1952)
		+	most symptomless / mild or carriers									(Sill and Connin 1953)
		+	systemic infection									(Sill and Agusiobo 1955)
		+	Mosaic			+	Mosaic	-	0 = no mites			(Slykhuis 1955)
						+	Yes	-	All but one with very poor			(Connin 1956b)
						-	no spotting (WSpM)	+	+ = few mites			(Slykhuis 1956)
		+	1/3 varieties suceptible									(Finley 1957)
		+	moderate susceptibilty, some not infected									(Slykhuis 1961)
		+	9/10 (infected/total) + = mild mosaic									(Slykhuis and Bell 1963)

#	Host (R = response)	WSMV Mechanical		WSMV Field Observations		WCM Trans. of Virus		WCM Reproduction		WCM Field Observations		Citation
		R	Observations	R	Observations	R	Observations	R	Observations	R	Observations	
		+	susceptible to mechanical 3a virus							-	mites not found (A. hystrix)	(Orlob 1966a)
												(Williams et al. 1967)
								-	KS: 0.0±0.1, NE: 0.0±0.0 (7d)			(Harvey et al. 2001)
				-	57 plants tested							(Coutts et al. 2008)
46	*Beckmannia syzgachne*	-	Immune					+	Susceptible	+	11.8% infested with mites	(Somsen and Sill 1970)
47	*Belamcanda chinensis*	-	probably immune									(Sill and Agusiobo 1955)
48	*Beta spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
48	*Bothriochloa macra*									+	3 WCM, all WCM2 Type	(Williams et al. 1967)
		+	Carrier No Symp.									(McKinney and Fellows 1951)
49	*Bouteloea hirsuta*	+	Symptomless/ Symptomless Carrier									(Sill and Connin 1953)
				-	0/3 positive for WSMV							(Christian and Willis 1993)
						-	No	-	None			(Connin 1956b)
								+	medium population after 7 days			(Orlob 1966a)
50	*Bouteloua curtipendula*	-	Immune					+	Susceptible	+	0.2% infested with mites	(Somsen and Sill 1970)
				-	0/19 positive for WSMV							(Christian and Willis 1993)
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
						-	No	-	None			(Connin 1956b)
										-		(Staples and Allington 1956)
								+	low population after 7 days			(Orlob 1966a)
51	*Bouteloua gracilis*							+	Susceptible	-	0.0% infested with mites	(Somsen and Sill 1970)
				-	0/4 positive for WSMV							(Christian and Willis 1993)
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
								-	KS: 0.1±0.1, NE: 0.7±0.7 (7d)			(Harvey et al. 2001)
52	*Bouteloua hirsuta*	+	Symptomless Carrier					+	Susceptible	+	15% infested with mites	(Somsen and Sill 1970)
53	*Bouteloua sp.*					+	Yes	+	Good			(Connin 1956b)
										-		(Staples and Allington 1956)
	Bromus catharticus									+	15 WCM, all WCM2 type	(Carew et al. 2009)
	Bromus diandrus											
		-	No comments									(Slykhuis 1952)
		-	immune									(Sill and Agusiobo 1955)
		-	No Mosaic			-	No Mosaic	-	0 = no mites			(Slykhuis 1955)
						-	No	+	Very Poor			(Connin 1956b)
						-	no spotting (WSpM)	-	0 = no mites			(Slykhuis 1956)
										-		(Staples and Allington 1956)
54	*Bromus inermis*									+	mites found, problem until destroyed	(Bruehl and Keifer 1958)
										+	mites found	(Timian and Lloyd 1969)
		-	Immune					+	Susceptible	+	6.2% infested with mites	(Somsen and Sill 1970)
				-	0/14, 0/34 positive for WSMV							(Christian and Willis 1993)
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
										+	1995: 175 plants, 1% inf., 1 WCM	(Brey et al. 1998)
										+	1996: 150 plants, 5% inf., 1±2 WCM	(Brey et al. 1998)
										+	1997: 475 plants, 5% inf., 1±2 WCM	(Brey et al. 1998)
		+	Mosaic									(McKinney and Fellows 1951)
		+	No comments									(Slykhuis 1952)
55	*Bromus japonicus*	+	Mosaic / Few Plants with Symptoms			+	Mosaic / Few Plants with Symptoms	-	0 = no mites			(Slykhuis 1955)
						-	no spotting (WSpM)	-	0 = no mites			(Slykhuis 1956)
		+	3/6 (infected/total) + = mild mosaic									(Slykhuis and Bell 1963)
		+	Susceptible (and/or B. tectorum)					+	Susceptible (and/or B. tectorum)	+	22.3% infested(and/or B. tectorum)	(Somsen and Sill 1970)
56	*Bromus marginatus*									+	mites found	(Bruehl and Keifer 1958)
		+	No comments									(Slykhuis 1952)
		+	Mosaic			+	Mosaic	-	0 = no mites			(Slykhuis 1955)
57	*Bromus secalinus*					-	no spotting (WSpM)	-	0 = no mites			(Slykhuis 1956)
		+	1/1 (infected/total) ++ = mod. mosaic									(Slykhuis and Bell 1963)
		+	Susceptible					+	Susceptible	+	7.7% infested with mites	(Somsen and Sill 1970)
58	*Bromus spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
		+	No comments									(Slykhuis 1952)
		+	Mosaic / Few Plants with Symptoms			+	Mosaic / Few Plants with Symptoms	-	0 = no mites			(Slykhuis 1955)
						-	No	-	None			(Connin 1956b)
						-	no spotting (WSpM)	-	0 = no mites			(Slykhuis 1956)
										-		(Staples and Allington 1956)
59	*Bromus tectorum*	+	15/15 (infected/total) + = mild mosaic									(Slykhuis and Bell 1963)
										-	mites not found (A. hystrix)	(Orlob 1966a)
				+	found with WSMV							(Orlob 1966b)
		+	Susceptible (and/or B. japonicus)					+	Susceptible (and/or B. japonicus)	+	22.3% infested(and/or B. tectorum)	(Somsen and Sill 1970)
								-/+	KS: 0.0±0.0, NE: 7.0±6.6 (7d)			(Harvey et al. 2001)
								+	low population after 7 days			(Orlob 1966a)

#	Host (R = response)	WSMV Mechanical		WSMV Field Observations		WCM Trans. of Virus		WCM Reproduction		WCM Field Observations		Citation
		R	Observations	R	Observations	R	Observations	R	Observations	R	Observations	
60	*Buchloe dactyloides*	-	Immune					+	Susceptible	+	3.4% infested with mites	(Somsen and Sill 1970)
				-	0/4 positive for WSMV							(Christian and Willis 1993)
61	*Camalovifa longifolia*									-		(Staples and Allington 1956)
62	*Canna sp.*	-	probably immune									(Sill and Agusiobo 1955)
63	*Capsicum spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
64	*Carex sp.*	-	Immune					+	Susceptible	+	0.6% infested with mites	(Somsen and Sill 1970)
65	*Cenchrus echinatus*			-	52 plants tested via ELISA							(Coutts et al. 2008)
66	*Cenchrus pauciflorus*	+	Symptomless			+	Yes	+	Good			(Sill and Connin 1953)
												(Connin 1956b)
										-		(Staples and Allington 1956)
		+	used to inoculate wheat	+	less common					-	negative	(Ashworth and Futrell 1961)
										+	WCM found	(Orlob 1966a)
		+	Susceptible					+	Susceptible	+	3.4% infested with mites	(Somsen and Sill 1970)
				+	1/12 positive for WSMV							(Christian and Willis 1993)
								+	KS: 10.6±14.5, NE: 9.8±13.8 (7d)			(Harvey et al. 2001)
67	*Chenopodium album*	-	immune									(Meiners and McKinney 1954)
		-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
68	*Chloris spp.*			-	174 plants tested via ELISA							(Coutts et al. 2008)
69	*Chloris verticillata*									-	0/22 plants	(Somsen and Sill 1970)
70	*Codiacum variegatum*	-	immune									(Sill and Agusiobo 1955)
71	*Coix lacryma-jobi*	-	immune									(Sill and Agusiobo 1955)
72	*Convallaria majalis*	-	probably immune									(Sill and Agusiobo 1955)
73	*Cortaderia selloana*	-	immune									(Sill and Agusiobo 1955)
74	*Crocus sp.*	-	probably immune									(Sill and Agusiobo 1955)
75	*Cucumis spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
76	*Cucurbita spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
77	*Cynodon dactylon*	+	Susceptible					+	Susceptible	+	2.6% infested with mites	(Somsen and Sill 1970)
				-	504 plants tested via ELISA							(Coutts et al. 2008)
78	*Cyperus alternifolius*	-	probably immune									(Sill and Agusiobo 1955)
79	*Cyperus esculentus*	-	probably immune									(Sill and Agusiobo 1955)
				-	0/2 positive for WSMV							(Christian and Willis 1993)
80	*Cypripedium sp.*	-	probably immune									(Sill and Agusiobo 1955)
81	*Dactylis glomerata*	-	immune									(Sill and Agusiobo 1955)
						-	No	-	None			(Connin 1956b)
		-	No									(Finley 1957)
		-	immune, no plants infected									(Slykhuis 1961)
		+	0/9 (infected/total) 0 = no symptoms									(Slykhuis and Bell 1963)
		-	Immune					-	Resistant	-	0/30 plants	(Somsen and Sill 1970)
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
								-	KS: 0.0±0.0, NE: 0.7±0.8 (7d)			(Harvey et al. 2001)
82	*Dactylis spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
83	*Digitaria ischaemum*	+	Mosaic									(McKinney and Fellows 1951)
										+	adults	(Connin 1956a)
						+	Yes	+	Fair - Good			(Connin 1956b)
								-	KS: 0.0±0.0, NE: 0.0±0.0 (7d)			(Harvey et al. 2001)
84	*Digitaria sanguinalis*	+	No comments									(Slykhuis 1952)
		+	symptoms in 7 - 9 days									(Meiners and McKinney 1954)
		+	Mosaic / Few Plants with Symptoms			+	Mosaic / Few Plants with Symptoms	-	0 = no mites			(Slykhuis 1955)
						+	Yes	+	Very Poor			(Connin 1956b)
						-	no spotting (WSpM)	-	0 = no mites			(Slykhuis 1956)
		+	6/20 (infected/total) ++ = mod. Mosaic									(Slykhuis and Bell 1963)
								-	KS: 0.0±0.0, NE: 0.0±0.0 (7d)			(Harvey et al. 2001)
85	*Digitaria spp.*	+	Susceptible					+	Susceptible	+	3.6% infested with mites	(Somsen and Sill 1970)
86	*Distichlis stricta*	+	Susceptible					+	Susceptible	+	2.2% infested with mites	(Somsen and Sill 1970)
87	*Echinochloa crus-galli*	+	No comments									(Slykhuis 1952)
		-	probably immune									(Sill and Agusiobo 1955)
		+	Mosaic / Few Plants with Symptoms			+	Mosaic	+	+ = few mites			(Slykhuis 1955)
						-	no spotting (WSpM)	+	+ = few mites			(Slykhuis 1956)
				+	less common							(Ashworth and Futrell 1961)
		+	0/9 (infected/total) 0 = no symptoms									(Slykhuis and Bell 1963)
		+	Susceptible					+	Susceptible	+	2.2% infested with mites	(Somsen and Sill 1970)
				+	1/10, 28/50 positive for WSMV							(Christian and Willis 1993)
88	*Ehrharta calycina*			-	109 plants tested via ELISA							(Coutts et al. 2008)
89	*Eleusine indica*	-	Immune			-	No	-	None			(Connin 1956b)
								+	Susceptible	-	0.0% infested with mites	(Somsen and Sill 1970)
								-	KS: 2.5±1.5, NE: 2.3±3.3 (7d)			(Harvey et al. 2001)

#	Host (R = response)	WSMV Mechanical		WSMV Field Observations		WCM Trans. of Virus		WCM Reproduction		WCM Field Observations		Citation
		R	Observations	R	Observations	R	Observations	R	Observations	R	Observations	
90	*Eleusine tritachya*			+	symptomatic, verified by RT-PCR							(Ellis et al. 2004)
91	*Elymus canadensis*	+	Carrier No Symp./ Local/Mosaic									(McKinney and Fellows 1951)
		+	Local / Symptomless / Mosaic									(Sill and Connin 1953)
		-	No Mosaic			+	Mosaic	-	0 = no mites			(Slykhuis 1955)
										+	adults	(Connin 1956a)
						-	No	+	Fair			(Connin 1956b)
						-	no spotting (WSpM)	-	0 = no mites			(Slykhuis 1956)
								+	young plants	+	mites found	(Staples and Allington 1956)
								+	low population after 7 days	+	WCM found	(Orlob 1966a)
		+	Susceptible					+	Susceptible	+	1.4% infested with mites	(Somsen and Sill 1970)
92	*Elymus condensatus*	+	Local Lesions / Part of Pop.									(McKinney and Fellows 1951)
		+	Local / Part of Population									(Sill and Connin 1953)
93	*Elymus giganteus*	+	Local Lesions / Part of Pop.									(McKinney and Fellows 1951)
		+	Local / Part of Population									(Sill and Connin 1953)
94	*Elymus junceus*	-	Tested five WSMV Isolates									(Seifers et al. 1996)
95	*Elymus virginicus*	+	Mosaic									(McKinney and Fellows 1951)
		+	Mosaic Symptoms									(Sill and Connin 1953)
		+	1/6 (infected/total) + = mild mosaic									(Slykhuis and Bell 1963)
		+	Susceptible					+	Susceptible	+	20% infested with mites	(Somsen and Sill 1970)
96	*Eragrostis cilianensis*	+	No comments									(Slykhuis 1952)
		+	Mosaic / Few Plants with Symptoms			+	Mosaic / Few Plants with Symptoms	+	+ = few mites			(Slykhuis 1955)
						+	Yes	+	Poor			(Connin 1956b)
						+	moderate spotting (WSpM)	+	+ = few mites			(Slykhuis 1956)
				+	virus detected			-	1 month: no mites, no eggs	-	no mites found	(Staples and Allington 1956)
										-		(Ashworth and Futrell 1961)
		+	Susceptible					+	Susceptible	+	28.8% infested with mites	(Somsen and Sill 1970)
								-	KS: 0.0±0.0, NE: 0.3±0.3 (7d)			(Harvey et al. 2001)
				+	2% positive, 50 plants tested							(Coutts et al. 2008)
97	*Eragrostis curvula*			+	symptomatic, verified by RT-PCR							(Ellis et al. 2004)
				-	Date 1: 25 plants tested via ELISA							(Coutts et al. 2008)
				-	Date 2: 1005 plants tested via ELISA							(Coutts et al. 2008)
98	*Eragrostis pilosa*							-	Resistant	-	0.0% infested with mites	(Somsen and Sill 1970)
99	*Eragrostis reptans*									-	0/8 plants	(Somsen and Sill 1970)
100	*Eragrostis sessilispica*			-	0/2 positive for WSMV							(Christian and Willis 1993)
101	*Eragrostis trichodes*	+	Mosaic									(McKinney and Fellows 1951)
		+	Mosaic Symptoms									(Sill and Connin 1953)
								+	medium population after 7 days			(Orlob 1966a)
		+	susceptible to mechanical 3a virus									(Williams et al. 1967)
		+	Susceptible									(Somsen and Sill 1970)
102	*Erianthus ravennae*									-	0/4 plants	(Somsen and Sill 1970)
103	*Eriochloa contracta*									-	0/1 plants	(Somsen and Sill 1970)
				+	3/8, 25/71 positive for WSMV							(Christian and Willis 1993)
104	*Euchlaena mexicana*	+	local and system infection									(Sill and Agusiobo 1955)
						-	No	+	Poor			(Connin 1956b)
		+	susceptible to mechanical 3a virus									(Williams et al. 1967)
		-	Immune					-	Resistant	-	0/1 plants	(Somsen and Sill 1970)
105	*Festuca elatior*	-	No Mosaic			-	No Mosaic	-	0 = no mites			(Slykhuis 1955)
						-	no spotting (WSpM)	+	++ = moderate survival of mites			(Slykhuis 1956)
106	*Festuca rubra*	-	No comments									(Slykhuis 1952)
		-	No Mosaic			-	No Mosaic	-	0 = no mites			(Slykhuis 1955)
						-	no spotting (WSpM)	+	+ = few mites			(Slykhuis 1956)
107	*Festuca sp.*	-	Immune					+	Susceptible	+	10% infested with mites	(Somsen and Sill 1970)
		-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
108	*Ficus elastica*	-	immune									(Sill and Agusiobo 1955)
109	*Gladiolus sp.*	-	probably immune									(Sill and Agusiobo 1955)
110	*Glyceria striata*									-	0.0% infested with mites	(Somsen and Sill 1970)
111	*Glycine max*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
112	*Gomphrena spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
113	*Hallii canna*	-	.									(Sill and Agusiobo 1955)
114	*Haynaldia villosa*	+	Mosaic									(McKinney and Fellows 1951)
115	*Helianthus annuus*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
116	*Hordeum gussonianum*	+	Mosaic									(McKinney and Fellows 1951)
117	*Hordeum jubatum*	-	No comments									(Slykhuis 1952)
		-	No Mosaic			-	No Mosaic	-	0 = no mites			(Slykhuis 1955)
										+	0.1% infested with mites	(Somsen and Sill 1970)
118	*Hordeum murinum*	+	Mosaic / Part of Pop.									(McKinney and Fellows 1951)

#	Host (R = response)	WSMV Mechanical		WSMV Field Observations		WCM Trans. of Virus		WCM Reproduction		WCM Field Observations		Citation
		R	Observations	R	Observations	R	Observations	R	Observations	R	Observations	
119	*Hordeum pusillum*	-	Immune					+	Susceptible	+	11.2% infested with mites	(Somsen and Sill 1970)
120	*Hordeum sp.*	+	Mosaic									(McKinney and Fellows 1951)
121	*Hordeum vulgare*	+	2nd incolation for infection									(McKinney 1949)
		+	4/5 var. positive, 0 -23.8% infected									(Slykhuis 1952)
		+	most symptomless / mild or carriers									(Sill and Connin 1953)
		+	all systemic infection									(Sill and Agusiobo 1955)
		+	Mosaic			+	Mosaic	+	+ = few mites			(Slykhuis 1955)
						+	Yes	+	Favorable			(Connin 1956b)
						+	slight spotting (WSpM)	+	++ = moderate survival of mites			(Slykhuis 1956)
		+	2/2 varieties susceptible									(Finley 1957)
		+	moderate susceptibilty, some not infected									(Slykhuis 1961)
		+	8/12 (infected/total) + = mild mosaic									(Slykhuis and Bell 1963)
		+	yellow local and systemic spindle shaped									(McKinney et al. 1966)
										-	mites not found (A. hystrix)	(Orlob 1966a)
		+	susceptible to mechanical 3a virus									(Williams et al. 1967)
								+	KS: 21.8±17.1, NE: 31.3±25.2 (7d)			(Harvey et al. 2001)
				-	42 plants tested							(Coutts et al. 2008)
122	*Hungaria canna*	.	.									(Sill and Agusiobo 1955)
123	*Iris sp.*	-	probably immune									(Sill and Agusiobo 1955)
124	*Kalanchoe sp.*	-	immune									(Sill and Agusiobo 1955)
125	*Koeleria cristata*							+	Susceptible	+	1.5% infested with mites	(Somsen and Sill 1970)
126	*Leersia sp.*									-	0/21 plants	(Somsen and Sill 1970)
127	*Leptochloa fascicularis*									-	0/1 plants	(Somsen and Sill 1970)
128	*Leptochloa filiformis*									-	0/1 plants	(Somsen and Sill 1970)
129	*Lilium candidum*	-	probably immune									(Sill and Agusiobo 1955)
130	*Lolium multiflorum*	+	moderate susceptibilty, some not infected									(Slykhuis 1961)
		+	3/26 (infected/total) + = mild mosaic									(Slykhuis and Bell 1963)
131	*Lolium perenne*	-	immune, no plants infected									(Slykhuis 1961)
		-	0/14 (infected/total) 0 = no symptoms									(Slykhuis and Bell 1963)
								+	Susceptible	+	9.0% infested with mites	(Somsen and Sill 1970)
				-	Date 1: 10 plants tested via ELISA							(Coutts et al. 2008)
				-	Date 2: 11 plants tested via ELISA							(Coutts et al. 2008)
132	*Lolium rigidum*			+	2006: 65% positive, 20 plants tested							(Coutts et al. 2008)
				+	2007: 10% positive, 10 plants tested							(Coutts et al. 2008)
133	*Lolium spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
134	*Lycopersicon spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
135	*Marantina bicolor*	-	probably immune									(Sill and Agusiobo 1955)
136	*Medicago sativa*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
137	*Melica sp.*									-	0/6 plants	(Somsen and Sill 1970)
138	*Miscanthus sinensis*									-	0/2 plants	(Somsen and Sill 1970)
139	*Muhlenbergia mexicana*							+	Susceptible	+	4.4% infested with mites	(Somsen and Sill 1970)
	Muhlenbergia wrightii									+	sig. damage to plant, malformation	(Watts and Bellotti 1967)
140	*Munroa squarrosa*							+	Susceptible	-	0/5 plants	(Somsen and Sill 1970)
141	*Musa sp.*	-	probably immune									(Sill and Agusiobo 1955)
142	*Muscari armeniacum*	-	probably immune									(Sill and Agusiobo 1955)
143	*Nicotiana spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
144	*Orchis sp.*	-	probably immune									(Sill and Agusiobo 1955)
145	*Ornithogalum sp.*	-	probably immune									(Sill and Agusiobo 1955)
146	*Oryza sativa*							-	KS: 0.0±0.0, NE: 0.4±0.7 (7d)			(Harvey et al. 2001)
147	*Oryzopsis hymenoides*	+	Carrier No Symp. / Part of Pop.									(McKinney and Fellows 1951)
		+	Symptomless Carrier / Part of Population									(Sill and Connin 1953)
		+	Symptomless			+	Symptomless	++	++ = moderate survival			(Slykhuis 1955)
										+	mites found	(Staples and Allington 1956)
		+	Susceptible					-	Resistant			(Somsen and Sill 1970)
148	*Panicum capillare*	+	No comments									(Slykhuis 1952)
		+	Mosaic / Few Plants with Symptoms			+	Mosaic / Few Plants with Symptoms	-	0 = no mites			(Slykhuis 1955)
						+	Yes	-	None			(Connin 1956b)
						-	no spotting (WSpM)	-	0 = no mites			(Slykhuis 1956)
				+	virus detected			-	1 month: no mites, no eggs	+	one mite found	(Staples and Allington 1956)
				+	symptoms common					-		(Ashworth and Futrell 1961)
		+	11/25 (infected/total) ++ = mod. mosaic									(Slykhuis and Bell 1963)
										-	mites not found (A. hystrix)	(Orlob 1966a)
						+	virus to wheat, 8 days isolation					(Orlob 1966b)
		+	susceptible to mechanical 3a virus									(Williams et al. 1967)
		+	Susceptible					+	Susceptible	+	1.4% infested with mites	(Somsen and Sill 1970)
				+	0/8, 4/55 positive for WSMV							(Christian and Willis 1993)

#	Host (R = response)	WSMV Mechanical		WSMV Field Observations		WCM Trans. of Virus		WCM Reproduction		WCM Field Observations		Citation
		R	Observations	R	Observations	R	Observations	R	Observations	R	Observations	
				+	2007: 5% positive, 70 shoots			-	KS: 0.0±0.0, NE: 0.0±0.0 (7d)			(Harvey et al. 2001) (Coutts et al. 2008)
149	*Panicum cenchrus*											(Ashworth and Futrell 1961)
150	*Panicum dichotomiflorum*			-	0/10 positive for WSMV							(Christian and Willis 1993)
151	*Panicum hallii*	+	susceptible to mechanical 3a virus									(Williams et al. 1967)
152	*Panicum maximum*	- -	immune Tested five WSMV Isolates									(Sill and Agusiobo 1955) (Seifers et al. 1996)
153	*Panicum miliaceum*	- + + + +	No comments Mosaic / Streak : 80% infected Mosaic / Few Plants with Symptoms 5/7 (infected/total) +++ = severe mosaic susceptible to mechanical 3a virus			+ -	Mosaic / Few Plants with Symptoms no spotting (WSpM)	- -	0 = no mites 0 = no mites			(Slykhuis 1952) (Sill and Agusiobo 1955) (Slykhuis 1955) (Slykhuis 1956) (Slykhuis and Bell 1963) (Williams et al. 1967)
154	*Panicum ramosum*	+	Mosaic : 20% infected									(Sill and Agusiobo 1955)
155	*Panicum spp.*	-	not susceptible to Ohio 3a virus	+	symptomatic, verified by RT-PCR							(Ashworth and Futrell 1961) (Williams et al. 1967) (Ellis et al. 2004)
156	*Panicum virgatum*	- - -	immune Immune Tested five WSMV Isolates	- -	0/15 positive for WSMV	- 	No	- - + -	None no mites Susceptible KS: 0.0±0.0, NE: 0.0±0.0 (7d)	+ 	0.4% infested with mites	(Sill and Agusiobo 1955) (Connin 1956b) (Orlob 1966a) (Somsen and Sill 1970) (Christian and Willis 1993) (Seifers et al. 1996) (Harvey et al. 2001)
157	*Pedilanthus tithmaloides*	-	immune									(Sill and Agusiobo 1955)
158	*Pennisetum clandestinum*			-	32 plants tested							(Coutts et al. 2008)
159	*Pennisetum glaucum*	-	immune									(Sill and Agusiobo 1955)
160	*Pennisetum setaceum*			-	462 plants tested							(Coutts et al. 2008)
161	*Pennistem glaucum*	+	lines repsonded diff. depending on isolate	+	variety trial , verified with ELISA	+	5 mites, tranmission to wheat (100%)	 +	 KS: 16.1±20.4, NE: 5.7±6.5 (7d)	+	18.0% infested with mites	(Somsen and Sill 1970) (Seifers et al. 1996) (Harvey et al. 2001)
162	*Peperomia sp.*	-	immune									(Sill and Agusiobo 1955)
163	*Phalaris arundinacea*	- -	No comments immune			 -	 No	 -	 None			(Slykhuis 1952) (Sill and Agusiobo 1955) (Connin 1956b)
								-	KS: 4.7±3.8, NE: 0.2±0.3 (7d)			(Harvey et al. 2001)
164	*Phalaris paradoxa*	+	Mosaic / Part of Pop.									(McKinney and Fellows 1951)
165	*Philodendron sp.*	-	probably immune									(Sill and Agusiobo 1955)
166	*Phleum pratense*	- -	No comments No Mosaic			- -	No Mosaic no spotting (WSpM)	- + +	0 = no mites ++ = moderate survival of mites Susceptible	 -	 0.0% infested with mites	(Slykhuis 1952) (Slykhuis 1955) (Slykhuis 1956) (Somsen and Sill 1970)
167	*Poa annua*			-	10 plants tested			+	Susceptible	-	0.0% infested with mites	(Somsen and Sill 1970) (Coutts et al. 2008)
168	*Poa bulbosa*	+ +	Local Lesions / Mosaic Local lesions / Mosaic Symptoms									(McKinney and Fellows 1951) (Sill and Connin 1953)
169	*Poa compressa*	+ + +	Mosaic / Part of Pop. Mosaic Symptoms / Part of Population May develop mosaic symp.			 + -	 May develop mosaic symp. no spotting (WSpM)	 ++ +	 ++ = moderate survival + = few mites	 +	 mites found, caused problem until destroyed	(McKinney and Fellows 1951) (Sill and Connin 1953) (Slykhuis 1955) (Slykhuis 1956) (Bruehl and Keifer 1958)
170	*Poa interior*									+	1996: 10 plants, 50% inf., 8±7 WCM	(Brey et al. 1998)
171	*Poa nervosa*									+	only one sample with mites and eggs	(Staples and Allington 1956)
172	*Poa pratensis*	- - - -	No comments No Mosaic 0/10 (infected/total) 0 = no symptoms Immune			- -	No Mosaic no spotting (WSpM)	- - + -	0 = no mites 0 = no mites Susceptible KS: 0.0±0.0, NE: 0.0±0.0 (7d)	 + + + + 	 19.2% infested with mites 1995: 120 plants, 41% inf., 3±2 WCM 1996: 200 plants, 35% inf., 4±6 WCM 1997: 1,150 plants, 8% inf., 6±8 WCM 	(Slykhuis 1952) (Slykhuis 1955) (Slykhuis 1956) (Slykhuis and Bell 1963) (Somsen and Sill 1970) (Brey et al. 1998) (Brey et al. 1998) (Brey et al. 1998) (Harvey et al. 2001)
173	*Poa stenantha*	+ +	Carrier No Symp. / Part of Pop. Symptomless Carrier / Part of Population									(McKinney and Fellows 1951) (Sill and Connin 1953)
174	*Polygonatum sp.*	-	probably immune									(Sill and Agusiobo 1955)
175	*Polypohon monspeliensis*									-	0.0% infested with mites	(Somsen and Sill 1970)

#	Host (R = response)	WSMV Mechanical R	WSMV Mechanical Observations	WSMV Field Observations R	WSMV Field Observations Observations	WCM Trans. of Virus R	WCM Trans. of Virus Observations	WCM Reproduction R	WCM Reproduction Observations	WCM Field Observations R	WCM Field Observations Observations	Citation
176	*Puccinellia airoides*							-	Resistant	-	0.0% infested with mites	(Somsen and Sill 1970)
177	*Rhoeo discolor*	-	probably immune									(Sill and Agusiobo 1955)
178	*Saccharum officinarum*	+	Local Chlorotic Lesions									(Sill and Connin 1953)
		-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
179	*Sagittaria monte-vidensis*	-	probably immune									(Sill and Agusiobo 1955)
180	*Sansevieria thyrsiflora*	-	probably immune									(Sill and Agusiobo 1955)
181	*Schedonnardus paniculatus*							+	Susceptible	+	3.2% infested with mites	(Somsen and Sill 1970)
182	*Secale cereale*	+	1/41 positive									(McKinney and Sando 1951)
		-	0/4 varieties positive									(Slykhuis 1952)
		+	most symptomless / mild or carriers									(Sill and Connin 1953)
		+	susceptible / erratic response									(Sill and Agusiobo 1955)
		+	Mosaic / Few Plants with Symptoms			+	Mosaic / Few Plants with Symptoms	+	+ = few mites			(Slykhuis 1955)
						+	slight spotting (WSpM)	+	++ = moderate survival of mites			(Slykhuis 1956)
		.										(Finley 1957)
		+	slightly susceptible, or few plants infected									(Slykhuis 1961)
		+	susceptible to mechanical 3a virus									(Williams et al. 1967)
								+	KS: 32.8±17.0, NE: 8.6±7.2 (7d)			(Harvey et al. 2001)
183	*Secale montanum*	+	1/18 positive									(McKinney and Sando 1951)
184	*Setaria faberi*			+	1/11, 19/61 positive for WSMV							(Christian and Willis 1993)
185	*Setaria italica*	-	No comments									(Slykhuis 1952)
		-	Symptomless or immune									(Sill and Connin 1953)
		+	Mosaic / Stunting / Streaks: 100% infected									(Sill and Agusiobo 1955)
		+	WSMV H94FM, H95, H88 isolates positive									(Seifers et al. 1996)
186	*Setaria magna*	+	susceptible to mechanical 3a virus									(Williams et al. 1967)
187	*Setaria pumila*	-	No comments									(Slykhuis 1952)
		-	No Mosaic			-	No Mosaic	-	0 = no mites			(Slykhuis 1955)
								-	1 month: no mites, no eggs	+	one mite found	(Staples and Allington 1956)
		+	Susceptible					-	Immune	+	6.4% infested with mites	(Somsen and Sill 1970)
				-	0/6, 0/54 positive for WSMV							(Christian and Willis 1993)
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
								+	KS: 6.6±6.1, NE: 0.0±0.0 (7d)			(Harvey et al. 2001)
188	*Setaria verticillata*	+	severe chlorosis and stunting									(Slykhuis 1952)
		+	Mosaic / Few Plants with Symptoms			+	Mosaic	+	+ = few mites			(Slykhuis 1955)
						+	moderate spotting (WSpM)	+	+ = few mites			(Slykhuis 1956)
		+	5/18 (infected/total) ++ = mod. mosaic									(Slykhuis and Bell 1963)
				+	symptomatic, verified by RT-PCR							(Ellis et al. 2004)
189	*Setaria viridis*	+	severe chlorosis and stunting									(Slykhuis 1952)
		+	Mosaic / Few Plants with Symptoms			+	Mosaic	+	+ = few mites			(Slykhuis 1955)
										+	adults	(Connin 1956a)
						+	Yes	-	None			(Connin 1956b)
						+	moderate spotting (WSpM)	+	+ = few mites			(Slykhuis 1956)
				+	virus detected			+	1 month: 2 infested plants, no eggs	+	11 plants, 1-2 mites per plant	(Staples and Allington 1956)
		+	Yes									(Finley 1957)
		+	WSMV transmitted to test plants	+	WSMV symptoms					+	mites found	(Timian and Lloyd 1969)
				+	15/38, 30/148 positive for WSMV							(Christian and Willis 1993)
								+/-	KS: 9.4±4.6, NE: 0.4±0.5 (7d)			(Harvey et al. 2001)
				+	symptoms common					-		(Slykhuis 1955)
		+	3/10 (infected/total) ++ = mod. mosaic									(Slykhuis 1956)
						+	virus to wheat, 16 days isolation					(Slykhuis 1961)
		+	Susceptible					+	Susceptible	+	2.1% infested with mites	(Ashworth and Futrell 1961)
190	*Seteria italica*	+	Mosaic / Few Plants with Symptoms			+	Local Chlorotic Spots / Mosaic	+	+ = few mites			(Slykhuis and Bell 1963)
						+	moderate spotting (WSpM)	+	+ = few mites			(Orlob 1966b)
		-	immune, no plants infected									(Somsen and Sill 1970)
191	*Sitanion hystrix*	+	Susceptible					-	Resistant	-	0.0% infested with mites	(Somsen and Sill 1970)
192	*Smilacina sp.*	-	probably immune									(Sill and Agusiobo 1955)
193	*Solanum spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
194	*Sorghastrum nutans*	-	immune									(Sill and Agusiobo 1955)
						-	No	-	None			(Connin 1956b)
								+	low population after 7 days			(Orlob 1966a)
		-	Immune					-	Resistant	-	0.0% infested with mites	(Somsen and Sill 1970)
				-	0/18 positive for WSMV							(Christian and Willis 1993)
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
								-	KS: 0.0±0.0, NE: 0.0±0.0 (7d)			(Harvey et al. 2001)
195	*Sorghum almum*	-	immune									(Sill and Agusiobo 1955)
						-	No	+	Suitable			(Connin 1956b)
		-	0/2 varieties susceptible									(Finley 1957)

#	Host (R = response)	WSMV Mechanical		WSMV Field Observations		WCM Trans. of Virus		WCM Reproduction		WCM Field Observations		Citation
		R	Observations	R	Observations	R	Observations	R	Observations	R	Observations	
196	*Sorghum bicolor*									+	remained for 26 days, some eggs	(Gibson 1957)
				+	7-56% transmission to field Sorghum			+	0 - 10.6 mites after 3-7 days	+	infestations 18 - +100 mites per plant	(Harvey and Seifers 1991)
		+	lines repsonded diff. depending on isolate			+	5 mites, tranmission to wheat (40-66%)					(Seifers et al. 1996)
								+	KS: 13.7±9.4, NE: 9.0±16.5 (7d)			(Harvey et al. 2001)
197	*Sorghum halepense*	-	All tested - immune									(Sill and Connin 1953)
		-	immune									(Sill and Agusiobo 1955)
						-	No	+	Good			(Connin 1956b)
												(Staples and Allington 1956)
		-	Immune					-	Resistant	-	0.0% infested with mites	(Somsen and Sill 1970)
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
								-	KS: 0.0±0.0, NE: 0.0±0.0 (7d)			(Harvey et al. 2001)
198	*Sorghum officinarum*	-	immune									(Sill and Agusiobo 1955)
199	*Sorghum spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
200	*Sorghum versicolor*	-	immune									(Sill and Agusiobo 1955)
201	*Sorghum vulgare*	-	No comments									(Slykhuis 1952)
		-	All tested - immune									(Sill and Connin 1953)
		-	immune									(Sill and Agusiobo 1955)
202	*Sorghum X drummondii*					.	Not recorded	+	Poor - Fair, decreased as matured			(Connin 1956b)
203	*Spartina pectinata*									+	1.3% infested with mites	(Somsen and Sill 1970)
204	*Sporobolus airoides*							+	medium population after 7 days			(Orlob 1966a)
205	*Sporobolus asper*			-	0/6 positive for WSMV							(Christian and Willis 1993)
206	*Sporobolus cryptandrus*									-		(Staples and Allington 1956)
								+	medium population after 7 days			(Orlob 1966a)
				-	0/3 positive for WSMV							(Christian and Willis 1993)
207	*Sporobolus neglectus*	+	Susceptible					+	Susceptible	+	3.7% infested with mites	(Somsen and Sill 1970)
208	*Stipa comata*					-	no spotting (WSpM)	-	0 = no mites			(Slykhuis 1956)
										+	1-6 mites found, no eggs	(Staples and Allington 1956)
								-	no mites			(Orlob 1966a)
								+	Susceptible	+	2.2% infested with mites	(Somsen and Sill 1970)
209	*Stipa robusta*	+	Mosaic									(McKinney and Fellows 1951)
		+	Mosaic Symptoms									(Sill and Connin 1953)
210	*Stipa viridula*									-		(Staples and Allington 1956)
								+	Susceptible	+	0.6% infested with mites	(Somsen and Sill 1970)
211	*Trifolium spp.*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
212	*Tripsacum dactyloides*	-	Resistant					-	Resistant	+	2.2% infested with mites	(Somsen and Sill 1970)
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
213	*Triticum aegilopoides*	+	100% infected									(McKinney and Sando 1951)
214	*Triticum aestivum*	+	all varieties positive									(McKinney 1949)
		+	100% infected									(McKinney and Sando 1951)
		+	Susceptible									(Sill and Connin 1953)
		+	symptoms in 4 - 8 days									(Meiners and McKinney 1954)
						+	Yes	+	Highly Satisfactory			(Connin 1956b)
						+	severe spotting (WSpM)	+	+++ = abundace of mites			(Slykhuis 1956)
								+	500+ mites, 100+ eggs			(Staples and Allington 1956)
		+	2/2 susceptible									(Finley 1957)
						+	mites transmitted WSMV from corn					(Sill and del Rosario 1959)
												(Ashworth and Futrell 1961)
		+	highly susceptible, all plants infected									(Slykhuis 1961)
												(How 1963)
		+	18/18 (infected/total), severe mosaic									(Slykhuis and Bell 1963)
		+	typical WSMV symptoms									(McKinney et al. 1966)
										+	usually less than 20 mites	(Orlob 1966a)
		+	susceptible to mechanical 3a virus									(Williams et al. 1967)
								+	200-250 to 1000-4000 in 10 days			(Nault and Briones 1968)
										+	found overwintering on vol. wheat	(Nault and Styer 1969)
		+	WSMV transmitted to test plants	+	WSMV symptoms					+	mites found	(Timian and Lloyd 1969)
				+	WSMV trans. until 2wks from harvest							(Gates 1970)
				+	5/29 positive for WSMV							(Christian and Willis 1993)
								+	KS: 44.9±17.9, NE: 37.6±19.1 (7d)			(Harvey et al. 2001)
				-	231 plants tested							(Coutts et al. 2008)
215	*Triticum aestivum (cultivated)*									-	1995: 320 plants, 0% infested	(Brey et al. 1998)
										-	1996: 85 plants, 0% infested	(Brey et al. 1998)
										+	1997: 550 plants, 1% inf., 1 WCM	(Brey et al. 1998)
216	*Triticum aestivum (postharvest)*									+	preharvest wheat heavily infested	(Gibson 1957)
217	*Triticum aestivum (preharvest)*									+	percentage decreased after ripening	(Gibson 1957)
218	*Triticum aestivum (spring)*	+	Mosaic			+	Mosaic	+	+++ = abundant			(Slykhuis 1955)

#	Host (R = response)	WSMV Mechanical		WSMV Field Observations		WCM Trans. of Virus		WCM Reproduction		WCM Field Observations		Citation
		R	Observations	R	Observations	R	Observations	R	Observations	R	Observations	
219	*Triticum aestivum (volunteer)*									+	"early volunteer" had abundant pop.	(Connin 1956a)
										-	1995: 70 plants, 0% infested	(Brey et al. 1998)
										+	1996: 25 plants, 1% infested, 1 WCM	(Brey et al. 1998)
										+	1997: 350 plants, 1% inf., 1 WCM	(Brey et al. 1998)
220	*Triticum aestivum (winter)*	+	Mosaic			+	Mosaic	+	+++ = abundant			(Slykhuis 1955)
221	*Triticum dicoccoides*	+	100% infected									(McKinney and Sando 1951)
222	*Triticum dicoccum*	+	93% infected									(McKinney and Sando 1951)
		+	Mosaic			+	Mosaic	+	++ = moderate survival			(Slykhuis 1955)
						+	severe spotting (WSpM)	+	++ = moderate survival of mites			(Slykhuis 1956)
223	*Triticum durum*	+	100% infected									(McKinney and Sando 1951)
		+	Mosaic			+	Mosaic	+	+++ = abundant			(Slykhuis 1955)
						+	severe spotting (WSpM)	+	+++ = abundace of mites			(Slykhuis 1956)
224	*Triticum monococcum*	+	100% infected									(McKinney and Sando 1951)
225	*Triticum orientale*	+	100% infected									(McKinney and Sando 1951)
226	*Triticum persicum*	+	100% infected									(McKinney and Sando 1951)
227	*Triticum polonicum*	+	100% infected									(McKinney and Sando 1951)
228	*Triticum spelta*	+	100% infected									(McKinney and Sando 1951)
229	*Triticum sphaerococcum*	+	100% infected									(McKinney and Sando 1951)
230	*Triticum timopheevi*	+	100% infected									(McKinney and Sando 1951)
		+	Mosaic			+	Mosaic	+	++ = moderate survival			(Slykhuis 1955)
						+	severe spotting (WSpM)	+	++ = moderate survival of mites			(Slykhuis 1956)
231	*Triticum turgidum*	+	100% infected									(McKinney and Sando 1951)
232	*Triticum vulgare*	+	No comments									(Slykhuis 1952)
233	*Tulip sp.*	-	probably immune									(Sill and Agusiobo 1955)
234	*Typha latifolia*	-	probably immune									(Sill and Agusiobo 1955)
235	*Vicia villosa*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)
236	*Yucca glauca*	-	Not a Host									(Sill and Connin 1953)
		-	probably immune									(Sill and Agusiobo 1955)
237	*Zea mays*	-	No Mosaic			+	Local Chlorotic Spots / Mosaic	-	0 = no mites			(Slykhuis 1955)
						+	moderate spotting (WSpM)	+	+ = few mites			(Staples and Allington 1956)
								+	40 - 90% developed mite colonies			(Sill and del Rosario 1959)
		+/-	Ohio 28: susceptible, Va. 35: resistant									(McKinney et al. 1966)
		+	susceptible to mechanical 3a virus	+	large area of Ohio							(Nault and Briones 1968)
		-	Tested five WSMV Isolates									(Seifers et al. 1996)
								+	KS: 8.5±2.1, NE: 10.8±3.4 (7d)			(Harvey et al. 2001)
238	*Zea mays (field)*	+	8/9 varieties : 9.5 - 52% infected									(McKinney 1949)
		+	Few - suscepible, Many - immune									(Sill and Connin 1953)
		+	Immune to susc. variety									(Sill and Agusiobo 1955)
								+	Poor - Fair			(Connin 1956b)
239	*Zea mays (hybrid)*							+	11 - 24 mites per plant			(How 1963)
								+	high pop. wih decline at 21 days			(Orlob 1966a)
								+	200-250 to 200-250 in 10 days			(Nault and Briones 1968)
		-	largerly resistant									(Timian and Lloyd 1969)
				+	WSMV trans. until 2wks from harvest							(Gates 1970)
240	*Zea mays (inbred)*	+	1/2 suscetible									(Finley 1957)
								+	too numerous to count			(How 1963)
								+	high population after 21 days			(Orlob 1966a)
								+	200-250 to 1,200-5,600 in 10 days			(Nault and Briones 1968)
										+	not found until mid-whorl stage	(Nault and Styer 1969)
		+	susceptible to resistant response					+	readily colonized 2-4 week seedlings			(Timian and Lloyd 1969)
241	*Zea mays (Pop)*	+	Most resistant / few susceptible									(Sill and Agusiobo 1955)
242	*Zea mays (sweet corn)*	+	2/2 susceptible							+	field infestations	(Finley 1957)
		+	9/13 varieties : 4.8 - 68 % infected									(McKinney 1949)
		+	symptoms in 7 - 18 days									(Meiners and McKinney 1954)
		+	Immune to susc. variety									(Sill and Agusiobo 1955)
								+	Poor-Fair			(Connin 1956b)
243	*Zebrina pendula*	-	probably immune									(Sill and Agusiobo 1955)
244	*Zinnia elegans*	-	not susceptible to Ohio 3a virus									(Williams et al. 1967)

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Appendix B. 2012-13 data for establishing risk of over-summering hosts for the wheat-virus complex.

Extreme drought occurred during the 2012-13 season leading to lack of germination and establishment of barnyardgrass and green foxtail during the spring of 2012. Pre-harvest wheat had poor establishment leading to repeated supplemental plantings within plots from May 22nd through June 30th. Foxtail millet established from single planting on May 22nd. Corn was planted on May 10th.

WCM movement into plots (Figure 1) peaked one month earlier in 2012 compared to 2013 and 2014 with activity peaking at 72.9%, approximately one week before harvest. Mite activity from plots are represented as proportion of plants infested (Figure 2a) and average number of mites (Figure 2b). Virus symptomology (Figure 4) (SPAD; relative chlorophyll) and virus presence (Figure 5; WSMV ELISA) show spring impact from host plots.

Figure 1. WCM movement into the study area as an average of percent of trap plants infested across four locations at each cardinal direction from the study for each year (2012, 2013 and 2014 season).

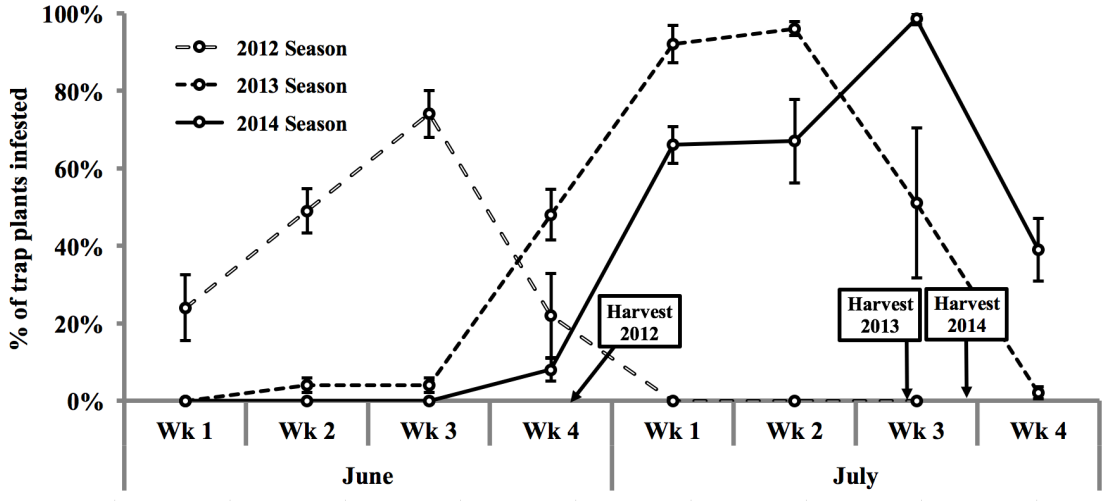


Figure 2. Proportion of infested trap plants (a) and average number of wheat per trap plant (b) for 2012-13 season from one week after wheat harvest until late October for six hosts (corn, foxtail millet, green foxtail, wheat (artificially infested).

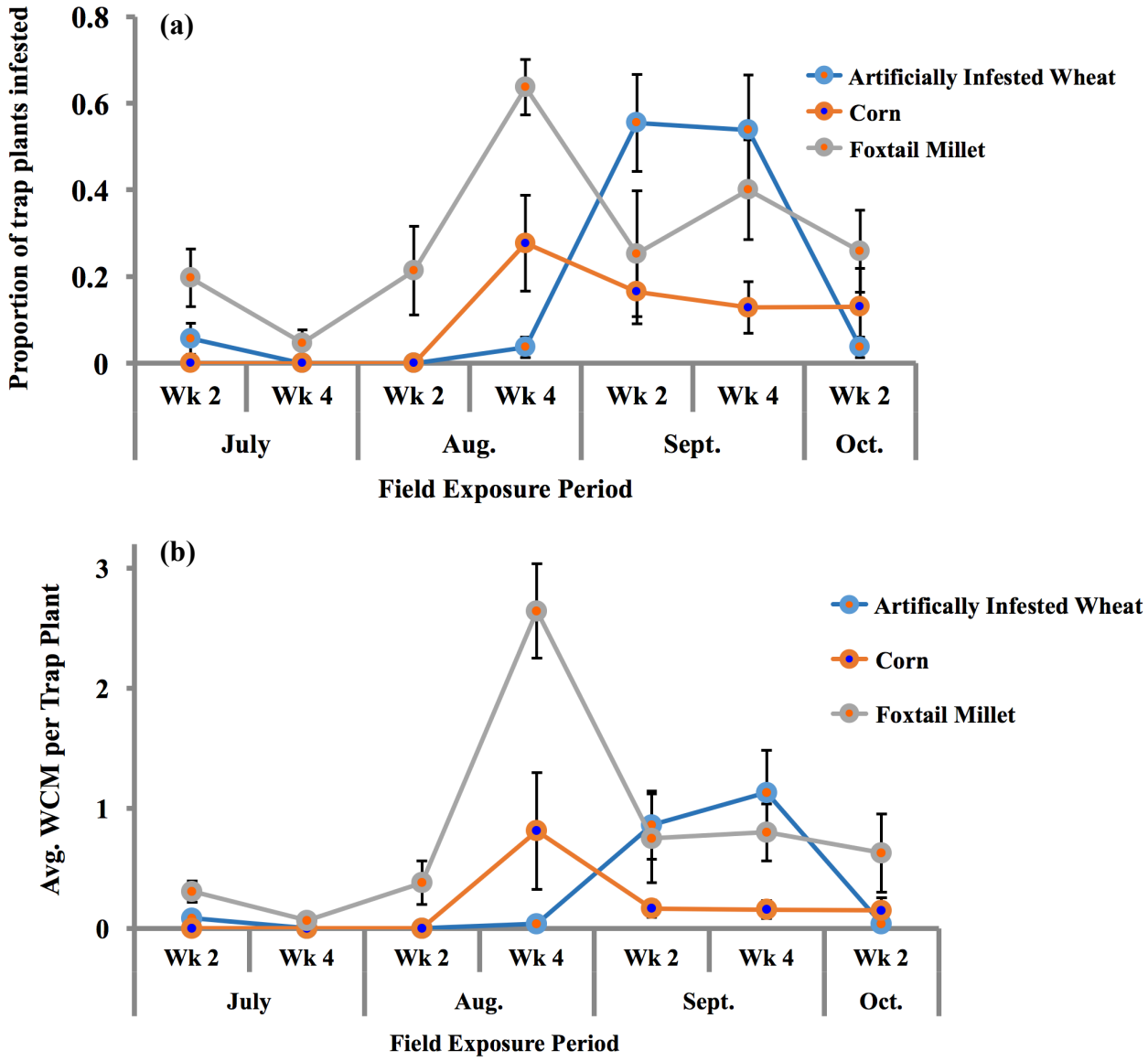
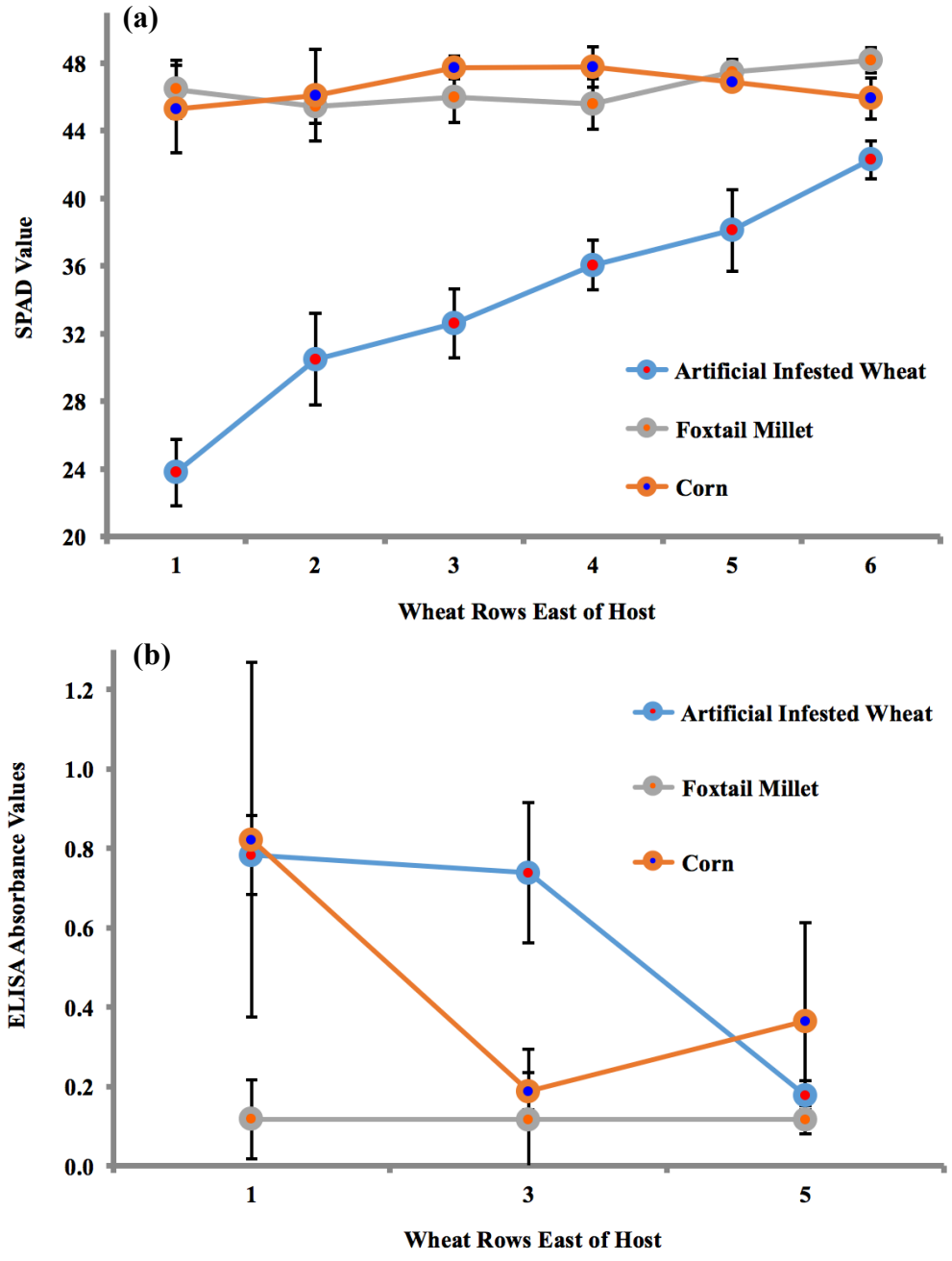


Figure 3. Virus symptomology (a) (SPAD: relative chlorophyll content) and presence (b) (WSMV ELISA absorbance) for wheat surrounding the over-summering plots (spring 2013).



Appendix C. SAS-Code for Regression and Proportion Data Analysis

```
*ANOVA for evaluation of main effects and interactions;

proc glimmix data=reproductivestudy;
class colony host rep run;
model adult=colony|host|day|day/ solution htype=1 dist=negbin;
random run*colony*host*rep;
nloptions maxiter=1000;
run;

*Remove non-significant effects from model through solution for fixed
effects;
*Rerun model containing only significant effects;
*Add "noint" to obtain intercepts for equations;

proc glimmix data=reproductivestudy;
class colony host rep run;
model adult=colony*host day(colony*host) day*day(colony*host)/ noint solution
htype=1 dist=negbin;
random run*colony*host*rep;
nloptions maxiter=1000;
run;

*Evaluate individual quadratic effects for significance and remove individual
treatment combination if not significant from zero;
*q=1 for significant quadratic, q=0 for non-significant quadratic;
*Add q to model to knockout quadratic effect;

title 'Type 1 vs. 2 Analysis';
proc glimmix data=reproductivesortOnlyType;
if colony ="Type1" and host="BYD" then q=0;
if colony ="Type1" and host="GF" then q=0;
if colony ="Type1" and host="FM" then q=0;
if colony ="Type1" and host="JG" then q=1;
if colony ="Type1" and host="W" then q=0;
if colony ="Type2" and host="BYD" then q=1;
if colony ="Type2" and host="GF" then q=0;
if colony ="Type2" and host="FM" then q=0;
if colony ="Type2" and host="JG" then q=1;
if colony ="Type2" and host="W" then q=0;
class colony host rep run;
model adult=colony*host day day(colony*host) day*day*q(colony*host)/ noint
solution htype=1 dist=negbin;
random run*colony*host*rep;
output out=yhats1 pred(ilink)=p; *output predicted values from model;
run;

*Correlation between observed and predicted values;

proc print data=yhats1; run;
proc corr data=yhats1;
by colony host;
var adult p;
run;
```