

6-9-2015

The Effect of Temperature, Relative Humidity, and Virus Infection Status on off-host Survival of the Wheat Curl Mite (Acari: Eriophyidae)

E. N. Wosula

University of Nebraska–Lincoln, ewolsula2@unl.edu

A. J. McMechan

University of Nebraska–Lincoln, justin.mcmechan@gmail.com

G. L. Hein

University of Nebraska–Lincoln, ghein1@unl.edu

Follow this and additional works at: <http://digitalcommons.unl.edu/entomologyfacpub>



Part of the [Entomology Commons](#)

Wosula, E. N.; McMechan, A. J.; and Hein, G. L., "The Effect of Temperature, Relative Humidity, and Virus Infection Status on off-host Survival of the Wheat Curl Mite (Acari: Eriophyidae)" (2015). *Faculty Publications: Department of Entomology*. 421.

<http://digitalcommons.unl.edu/entomologyfacpub/421>

This Article is brought to you for free and open access by the Entomology, Department of at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Publications: Department of Entomology by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

The Effect of Temperature, Relative Humidity, and Virus Infection Status on off-host Survival of the Wheat Curl Mite (Acari: Eriophyidae)

E. N. Wosula, A. J. McMechan, and G. L. Hein

Department of Entomology, University of Nebraska–Lincoln, Lincoln, NE 68583

Corresponding author — E. N. Wosula, email ewosula2@unl.edu

Abstract

The wheat curl mite, *Aceria tosichella* Keifer, is an eriophyid pest of wheat, although its primary economic impact on wheat is due to the transmission of *Wheat streak mosaic* (WSMV), *Wheat mosaic* (also known as High Plains virus), and *Triticum mosaic* (TriMV) viruses. These viruses cause significant annual losses in winter wheat production throughout the western Great Plains. Temperature and humidity are factors that often influence arthropod survival, especially during dispersal from their hosts, yet the impact of these two factors on off-host survival has not been documented for wheat curl mite. Pathogen-infected host plants often influence the biology and behavior of vectors, yet it is not known if virus-infected wheat affects off-host survival of wheat curl mite. The objectives of this study were to 1) determine if temperature, relative humidity, and mite genotype impact off-host survival of wheat curl mite and 2) determine the effect of WSMV- and TriMV-infected host plants on off-host survival of wheat curl mite. Temperature and relative humidity significantly affected off-host survival of wheat curl mite. Length of survival decreased with increasing temperature (106.2 h at 10°C and 17.0 h at 30°C) and decreasing relative humidity (78.1 h at 95 and 21.3 h at 2%). Mites from TriMV-infected host plants had ~20% reduction in survival at 20°C compared with those from WSMV-infected plants. The duration of off-host survival of wheat curl mite is influenced by environmental conditions. Management strategies that target a break in host presence will greatly reduce mite densities and virus spread and need to account for these limits.

Keywords: wheat, *Aceria tosichella*, Wheat streak mosaic virus, *Triticum mosaic virus*

The wheat curl mite, *Aceria tosichella* Keifer (1969), is a microscopic and phytophagous eriophyid mite commonly associated with cereals worldwide (Amrine and Stasny 1994, Frost and Ridland 1996). Although wheat is its primary host, wheat curl mite has been recorded on >80 grass species in 46 Poaceae genera (Slykhuis 1955, Connin 1956, Somsen and Sill Jr. 1970, Harvey et al. 2001, Carew et al. 2009, Skoracka et al. 2013). The wheat curl mite is white in color, cigar-shaped, and measures ~250 microns in length and 75 microns in width (Keifer 1938). Under favorable conditions, the mite has a high reproductive potential. It can complete its life cycle in 8 to 10 d (egg, larval, nymphal, and adult stages), and each female can lay up to 12 eggs (Staples and Allington 1956, del Rosario and Sill Jr. 1958).

The wheat curl mite causes characteristic leaf rolling and occasional trapping of wheat leaves. Yield loss may occur under heavy mite infestation (Harvey et al. 2002). However, the economic importance of this mite is due to its ability to transmit three viruses in wheat, *Wheat streak mosaic virus* (WSMV), *Triticum mosaic virus* (TriMV), and *Wheat mosaic virus* (WoMV; also known as High Plains virus), which commonly are found in wheat in the Great Plains (Slykhuis et al. 1955, Seifers et al.

1997, 2009). These viruses cause an average annual yield loss of ~2% in the Great Plains (Appel et al. 2007); however, localized yield losses up to 100% are common (Wegulo et al. 2008).

In North America, two distinct genotypic lineages of wheat curl mite have been identified and designated as Type 1 and Type 2 (Hein et al. 2012). The original designation of these two types was made from Australian mite populations by Carew et al. (2009) and later shown to match populations found in North America (Hein et al. 2012). These two genotypes differ in their response to different resistant genes in wheat (Harvey et al. 1999). They also differ in their ability to transmit two of the wheat viruses found in the Great Plains. The Type 2 genotype transmits TriMV and WoMV at significantly higher rates compared with the Type 1 genotype (Seifers et al. 2002, McMechan et al. 2014).

Under field conditions, wheat curl mite most often are found in the protected areas of the wheat plant, such as the whorls, trapped leaves, leaf sheaths, and glumes to avoid desiccation and predation (Nault and Styer 1969, Sabelis and Bruin 1996). Wheat curl mites have limited mobility owing to their small size; however, they are forced to move on the plant as the

plant grows and to new hosts when faced with host deterioration or maturation or competition owing to high populations (Nault and Styer 1969, Thomas and Hein 2003). When moving off their host, they move passively on air currents, and dispersal behavior has been observed only in adult mites (Nault and Styer 1969, Sabelis and Bruin 1996). After dispersing from the host, it is estimated that <10% of mites will reach an acceptable host (Jeppson et al. 1975).

Vector dispersal and survival is one of the most important components of the epidemiology of arthropod-borne pathogens. Increased survival of the vector increases the chances of dispersal, reproduction, and subsequent spread of the pathogen (Kovats et al. 2001). In poikilotherms, survival and movement are heavily influenced by temperature as this affects the rate of metabolic processes and by relative humidity as this influences their water balance (Hoffmann and Blows 1994, Chown et al. 2011, Melo et al. 2014). Temperature and relative humidity are reported to influence survival, development, and reproduction of mites (Perring et al. 1984, Courtin et al. 2000). Several authors have reported that wheat curl mite survive for a short period without a living host (Slykhuis 1955, Nault and Styer 1969, Jiang et al. 2005, Wegulo et al. 2008); however, no published studies have demonstrated the limits of these effects for the wheat curl mite. Survival of wheat curl mite is particularly important because the primary management strategy for this disease complex involves establishing a break in the "green bridge" of live hosts (volunteer wheat and other host plants) because they sustain mites and virus during the period between wheat harvest and emergence of new winter wheat in the fall.

The viruses in this wheat–mite–virus complex have been shown to alter the survival and reproductive rate of the wheat curl mite. Siriwetwivat (2006) observed increased wheat curl mite densities on WSMV-infected wheat plants compared with noninfected plants. Murugan et al. (2011) also observed significant wheat curl mite population increase on WSMV-infected susceptible cultivars compared with noninfected plants, but this increase was not observed for WSMV-resistant cultivars. However, TriMV-infected wheat plants had a 20–25% reduction in the number of plants with successful population establishment from single mite transfers compared with noninfected plants (McMechan et al. 2014). In addition, McMechan (2012) found slower mite population increases on TriMV-infected plants. This adverse effect of TriMV on mites could influence the mite's ability to survive off their host, and thus, influence virus spread and epidemiology.

Because wheat curl mite has limited movement and ability to find new host plants and its off-host survival characteristics are important in making management decisions, it is important to understand the factors that affect their survival after leaving its host. We hypothesize that temperature, relative humidity, mite genotype, and virus infection status affect off-host survival of wheat curl mite. The objectives of this study were to determine the degree to which temperature and relative humidity impact off-host survival of the different genotypes of wheat curl mite and to determine the

off-host survival of wheat curl mite after leaving WSMV- or TriMV-infected host plants.

Materials and Methods

Temperature and Relative Humidity Effect on Mite Survival. Three mite populations designated Type 1 (T1), Type 2 (T2), and ARDC were used in this study. T1 and T2 mite colonies were established from collections made in the summer of 2011 from various wheat fields in three counties (Box Butte, Scottsbluff, Chase) in the Nebraska Panhandle. Wheat tillers collected from the field were placed in contact with caged 14-d-old wheat plants to establish colonies. Eggs from these mite colonies then were transferred to new plants to establish nonviruliferous populations. Single clonal mite colonies were genetically identified as either Type 1 or Type 2 genotypes through polymerase chain reaction amplification and restriction digestion of the ribosomal internal transcribed spacer region (Hein et al. 2012). Several clonal colonies with matching genotypes were combined and used to establish T1 and T2 colonies. The ARDC colony was collected in the fall of 2013 from naturally infested wheat research plots at the University of Nebraska-Lincoln Agricultural Research Development Center (ARDC) in Mead, NE. The ARDC colony was found to include a mixture of T1 and T2 genotypes.

The colonies were maintained on wheat variety "Settler CL" grown in 15-cm-diameter plastic pots and isolated with cages. Cages were assembled from plastic sheeting molded into 15-cm-diameter cylinder and 60 cm in height. Two 8-cm-diameter holes were cut on opposite side of cages approximately one-third of the way up the cage. The top of the cage and the side vents were covered with Nitex screen (mesh opening 80 mm; BioQuip Products Inc. Compton, CA). The three mite populations were kept in separate growth chambers held at 24–27°C, a photoperiod of 14:10 (L:D) h, and 30–40% relative humidity. Mite populations were maintained by transferring 50 mites per pot to 14-d-old wheat plants every ~3 wk.

The experimental design was a Latin square with five temperature (10, 15, 20, 25, and 30°C) levels and five replications, each consisting of temperatures randomly assigned to one of five growth chambers (Percival Scientific Inc., Perry, IA). Within the main plot temperature treatments, split-plot treatments of two relative humidity levels were included and three mite populations made up the split-split-plot treatments. Two levels of relative humidity were established within each temperature using 1.4-liter sealable plastic containers. High relative humidity containers were lined with damp paper towel (~95% relative humidity), and low relative humidity containers contained Drierite (~2% relative humidity; W. A. Hammond Drierite Co. Ltd., Xenia, OH). Growth chamber conditions were at 30–40% relative humidity and a photoperiod of 14:10 (L:D) h. In the growth chambers, mites were sheltered from exposure to direct light by placing a styrofoam sheet on top of the plastic containers. HOBO data loggers (MicroDAQ.com, Ltd. Con-toocook, NH) were placed in each of the plastic containers to record temperature and relative humidity every 15 min.

Mites from the three populations were collected from 3-wk-old colonies. Because the sex of wheat curl mite cannot be distinguished quickly and accurately with a stereomicroscope, the mites used for this study were not sorted by sex. For each split-split-plot treatment, large active adult mites from each population were transferred individually into two sets of paired mini-chambers using an eyelash tool (an eyelash attached to a wooden dowel) with the aid of a stereomicroscope. The paired mini chambers consisted of two-well sections cut from plastic Terasaki plates (Greiner Bio-One, Monroe, NC) and glued to an aluminum bar (5 by 2.5 by 0.5 cm). The individual mini-chambers were inverted cones that were 3mm in diameter at the top and 2mm in depth. The mini-chambers were tightly sealed using a thin layer of Parafilm (Pechiney Plastics, Neenah, WI) so that mites could be observed without opening the mini-chamber or disturbing the mites.

After isolation in the mini-chambers, mites were placed at the appropriate temperature and relative humidity treatments and monitored every 4 for 48 h and then every 8–12 h until all mites were dead. A stereomicroscope set at 15–25 \times magnification was used to inspect the mites within the mini-chambers. When mites remained inactive with no body or leg movement, the Parafilm covers were opened to probe mites with an eyelash. Mites were considered dead when no body or leg movement occurred after they were probed. Mini-chambers were resealed for mites showing any movement. The experiment was conducted five times with a total of 20 mites (two mini-chamber pairs per rep) per population–temperature–relative humidity combination. Paper towels were kept damp (<98% relative humidity), but not wet, to avoid 100% relative humidity. In a preliminary study, mites held at 100% relative humidity had impaired movement due to condensation and reduced survival time, although this was not consistently observed.

Virus Effect on Mite Survival. Settler CL was sown in 4-cm-diameter cone-tainers (Stuewe & Sons Inc., Tangent, OR) filled with standard greenhouse soil. The cone-tainers were covered with plastic cylindrical cages (5 cm in diameter and 50 cm in height) with two or three vents that were covered with Nitex screen. After 10 d, wheat plants were thinned to one seedling per cone-tainer, and this plant was mechanically inoculated with either WSMV (Sidney 81 strain) or TriMV (three plants per virus). The Sidney 81 isolate was obtained from an infectious cDNA clone whose *in vitro*-generated RNA transcripts were inoculated into wheat seedlings at the single-leaf stage (Choi et al. 1999). The TriMV isolate originally was obtained from wheat plants collected from Red Willow County, NE, and confirmed to be TriMV by immunology and polymerase chain reaction (Tatineni et al. 2009). The virus inoculum was prepared by grinding infected wheat tissue in sterile distilled water (1:10 wt/vol) using a mortar and pestle. The plant leaves were lightly dusted with carborundum and inoculated by gently rubbing the inoculum onto leaves using the pestle. An equal number of plants were inoculated with sterile distilled water to act as noninfected controls. Four days after inoculation, 10 aviruliferous mites (ARDC popula-

tion) were transferred onto each of the three source plants inoculated with WSMV, TriMV, or sterile water (mock). After 24 h to allow mites to establish on the plants, they were transferred to a growth chamber (a photoperiod of 14:10 [L:D] h and 26°C). Mites were allowed to build up on source plants for a period of 3 wk.

High and low relative humidity treatments were established as described above. Mites from the WSMV-infected, TriMV-infected, and noninfected plants were used from the 3-wk-old colonies. Adult mites of unknown age and sex from each treatment population were transferred individually into paired mini-chambers using an eyelash brush with the aid of a stereomicroscope. Five paired mini-chambers (10 mites) were divided between two plastic containers (3 + 2) for each relative humidity level. Mites were held in a growth chamber set at 20°C. The mini-chambers were handled and inspected for mite survival, as previously described. The experiment was conducted two times with a total of 20 mites (10 paired minichambers) per virus–relative humidity combination.

Data Analysis

Data analyses were performed by using SAS software version 9.4 (SAS Institute Inc., Cary, NC). The duration of mite survival in hours was analyzed by using PROC GLIMMIX with a gamma distribution, as the original data were not normally distributed. Generalized linear mixed model analysis was used to separate treatment combination means and generate least square means. In the first experiment, fixed factors were temperature, relative humidity, and mite population, and random factors were replication, and repetition of mini-chamber pairs within the treatment combinations. In the second experiment, fixed factors were relative humidity and virus status, and random factors were replication and repetition of mini-chambers within the treatment combinations. Means and SEs were obtained by using the PROC MEANS statement. The survival times at each temperature for low and high relative humidity were subjected to regression analysis with temperature as the independent variable and survival time as the dependent variable by using PROC REG (SAS Institute Inc. Cary, NC).

Results

Temperature and Relative Humidity Effect on Mite Survival. Temperature and relative humidity monitoring revealed that the desired environmental conditions were well maintained. Temperatures varied within 61°C degrees of the target temperature and relative humidity ranged within 61% of the 2% and 63% of the 95% targets. Temperature was affected during the process of checking for survival, but conditions returned to the desired levels within 5–10 min after being returned to the growth chamber.

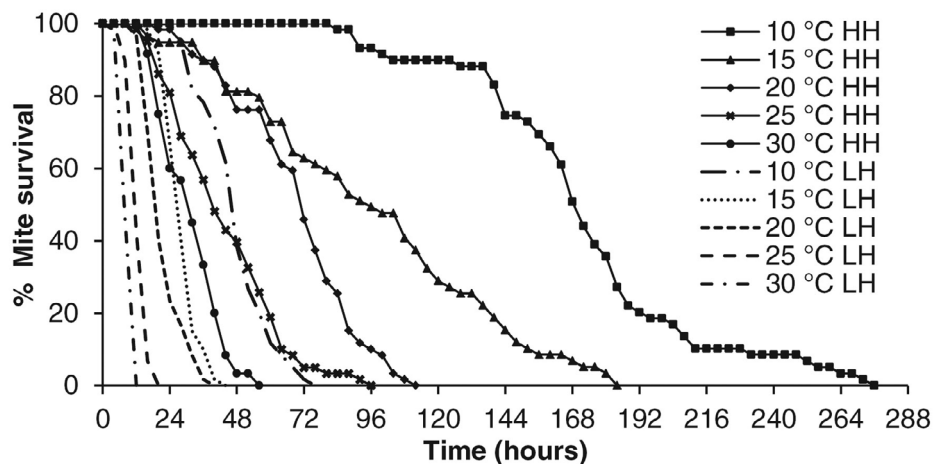


Figure 1. Survivorship curves of *A. tosicella* off-host as affected by temperature and relative humidity. HH, high relative humidity (95%); LH, low relative humidity (2%).

Mites held at the lowest temperature (10°C) for both low and high relative humidity were inactive and only moved when exposed to warmer temperatures during observation under the microscope. Mites held at the other four temperature levels walked constantly around the chamber, and mites were observed to be more active at higher temperatures. In addition, mites held at low relative humidity gradually shriveled and were reduced in size by more than half their original size before they died, but this change in size was not apparent for the high relative humidity treatments.

The survivorship response generated from mean survival hours of the three populations (Figure 1) indicate mites held at high relative humidity and low temperatures survived the longest, while those held at low relative humidity and high temperatures died rapidly. There were no significant interactions on wheat curl mite off-host survival between temperature and relative humidity ($F = 1.6$; $df = 4, 20$; $P = 0.219$), temperature and population ($F = 1.0$; $df = 8, 229$; $P = 0.425$), population and relative humidity ($F = 2.4$; $df = 2, 229$; $P = 0.093$), or temperature, relative humidity and population ($F = 1.22$; $df = 8, 229$; $P = 0.287$). Wheat curl mite off-host survival was significantly reduced by increases in temperature ($F = 143.7$; $df = 4, 12$; $P < 0.0001$). Average survival times across the five temperatures were 106.2, 59.8, 42.8, 24.7, and 17.0 h at 10, 15, 20, 25, and 30°C, respectively (Table 1). Low relative humidity also decreased survival time ($F = 562.4$; $df = 1, 20$; $P < 0.0001$) from 78.9 h for high relative humidity down to 21.3 h across all the five temperatures levels. Differences also were seen across temperature and relative humidity for population source (genotype; $F = 4.6$; $df = 2, 229$; $P = 0.011$), but these differences were much smaller than the survival differences between the temperature and humidity treatments (ARDC = 52.3 h, T1 = 51.8 h, T2 = 46.6 h).

The mean maximum survival hours of the three mite populations ARDC (178.6 h), Type 1 (169.4 h), and Type 2 (157.2 h) occurred at the lowest temperature (10°C) and high relative humidity, and were significantly longer compared to the other

temperature and relative humidity combinations. The mean minimum survival duration (5.6–6 h) occurred at the highest temperature (30°C) and low relative humidity (Table 1). Mite survival durations for all three populations at high relative humidity were significantly different at all five temperature levels except at 15 and 20°C for Type 1 and Type 2. At low relative humidity, survival durations for all three populations at the five temperature levels were significantly different (Table 1).

The limits of survival for wheat curl mite under high and low relative humidity were established from these data by regressing survival in hours on temperature at each relative humidity level (Figure 2). Regression analysis revealed no significant temperature by colony interactions at either high ($F = 0.2$; $df = 2, 9$; $P = 0.814$) or low relative humidity ($F = 0.3$; $df = 2, 9$; $P = 0.756$). Therefore, data for mite populations were pooled for each relative humidity level and regression analysis on these data resulted in significantly different equations for mite survival at low and high relative humidity ($F = 45.5$; $df = 1, 26$; $P < 0.0001$). Regression of mite survival on temperature for both relative humidity levels was improved with the inclusion of the quadratic (temperature squared) term and resulted in R^2 of 0.99 and 0.98 for the low and high relative humidity relationships, respectively (Figure 2).

Virus Effect on Mite Survival. The study was conducted two times. Initial analysis indicated no significant run by relative humidity interaction for survival, so a pooled analysis was run with four (two per run) replications. Low relative humidity was again found to significantly reduce off-host survival ($F = 1888.7$; $df = 1, 3$; $P < 0.0001$) from 97.6 to 22.5 h. Survival was significantly affected by virus treatment ($F = 8.4$; $df = 2, 48$; $P = 0.0007$). The interaction between virus host-infection status and relative humidity was marginally significant ($F = 3.14$; $df = 2, 48$; $P = 0.052$). Survival for the low relative humidity virus treatments did not differ at 23.0, 22.8, and 21.6 h for the non-infected, WSMV-, and TriMV-infected plants, respectively. However, at high relative humidity, off-host survival for TriMV was lower than the noninfected and WSMV treatments, 82.7 ± 4.8 h

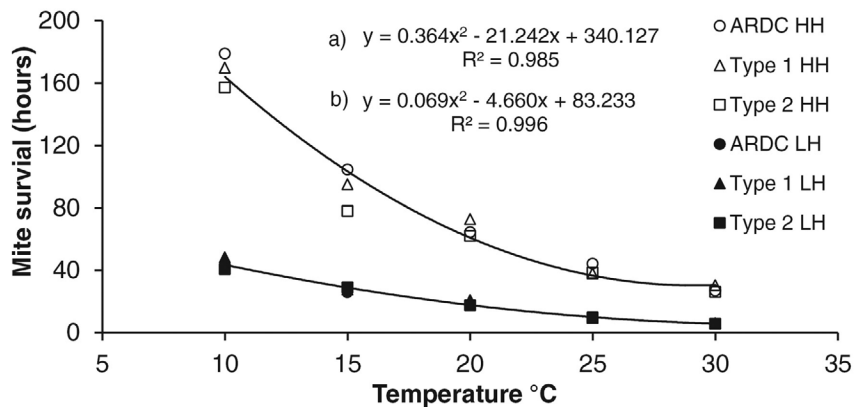


Figure 2. Regression plot of relationship between mite survival in hours and temperature. HH, high relative humidity (95%); LH, low relative humidity (2%). (a) and (b), Regression equations for high and low relative humidity, respectively.

h versus $101.8 \pm 3.4a$ and $108.2 \pm 3.6a$ h for noninfected and WSMV-infected plants, respectively (means were separated using Tukey–Kramer test, $P < 0.05$).

Discussion

The limits of wheat curl mite off-host survival under diverse environmental conditions that could allow mite movement were established in this study. Mites survived 5d longer at 10°C when held at 95% relative humidity compared with 2% relative humidity, but at 30°C, the difference was <1 d for mites held at the two relative humidity levels. This indicates that higher temperature during mite dispersal will greatly reduce off-host survival regardless of humidity. The increased survival under high relative humidity also could explain why the wheat curl mite predominately inhabits leaf whorls or induces leaf curling and rolling to provide more humid micro-environmental conditions, as opposed to inhabiting open leaves that would expose them to lower relative humidity and increased dehydration potential. Mites within the leaf whorls and leaf curl likely would experience higher relative humidity levels as a result of evapotranspiration.

These findings are consistent with some studies on eriophyid mites that have observed reduced off-host survival when mites are exposed to increasing temperatures and decreasing relative humidity levels. The regression equations determined from this study were used to estimate potential

wheat curl mite survival times at different temperatures and compare them to previous eriophyid mite survival studies (Table 2). Frost (1997) reported cereal rust mites held at 94–97% relative humidity had a survival duration that was slightly lower at 30°C (18 vs. 30 h), and slightly higher at 20°C (73 h vs. 62 h) compared with wheat curl mite survival in our study (Table 2). However, survival of cereal rust mite at 32% relative humidity at these two temperatures was similar to wheat curl mite survival in our study at 2% relative humidity. The off-host survival of coconut mites was comparable with wheat curl mite survival at 27°C and 95% relative humidity (34 h vs. 32 h; Melo et al. 2014). At 27°C and 10% relative humidity coconut mites survived for 10 h compared with 8 h for wheat curl mite held at 2% relative humidity (Table 2). However, coconut mites held at 18 and 33°C and 75% relative humidity survived only about a third as long as wheat curl mite held at 95% relative humidity (Table 2). A study by Bergh (2001) reported much shorter off-host survival of citrus rust mites (8 h at 23°C and 99% relative humidity; 4 h at 32°C and 56% relative humidity) compared with wheat curl mite survival estimates at 95% relative humidity from our study. However, the citrus rust mite values were comparable to the wheat curl mite survival times at 2% relative humidity (Table 2). It is perhaps a bit surprising that off-host survival of the cereal rust mite and the citrus rust mite is not greater than that for wheat curl mite as these species are thought to have more vagrant lifestyles (Sabelis and Bruin 1996) and thus be more exposed on their host than wheat curl mite.

Table 1. Effect of temperature and relative humidity on off-host survival for *A. tosichella* (means ± SE in hours)

Temperature °C	High relative humidity (95%)			Low relative humidity (2%)			Average ^a
	ARDC	Type 1	Type 2	ARDC	Type 1	Type 2	
10	178.6±10.2a	169.4±10.9a	157.2±.3a	43.0±2.9f	48.2±2.6ef	40.8±3.7f	106.2
15	104.6±8.8b	93.5±.7bc	78.0±.9cd	26.2±1.6hi	27.6±0.9gh	29.0±1.2gh	59.8
20	60.4±6.4de	72.8±3.2cd	62.0±6.6de	19.0±1.9j	20.8±1.9ij	17.7±1.7j	42.8
25	44.2±4.3f	37.4±3.9fg	38.4±6.4fg	9.4±0.9k	9.4±0.5k	9.8±0.8k	24.7
30	27.0±3.1hi	30.4±1.9gh	26.2±2.9hi	5.6±0.6l	6.0±0.7l	5.8±0.6l	17.0

Means with same letter within rows and columns are not significantly different ($P < 0.05$ Tukey–Kramer test).

a. Average survival hours at each temperature across relative humidity and population.

Table 2. Comparison of results calculated from regression equations in the current study (Figure 2) to off-host survival data presented in previous publications for eriophyid mites

Study	Results from cited studies	Survival (h)	Calculated results from this study	
	Temp °C (RH) ^a		Survival at 2% RH (h) ^a	Survival at 95% RH (h) ^a
Frost 1997 (cereal rust mite)	20 (95)	73	18	62
	30 (95)	18	6	30
	20 (32)	20	18	62
	30 (32)	5	6	30
Melo et al. 2014 (coconut mite)	18 (75)	28	22	76
	33 (75)	11	5 ^b	30 ^c
	27 (10)	10	8	32
	27 (95)	34	8	32
Bergh 2001 (citrus rust mite)	23 (99)	8	13	45
	32 (56)	4	5 ^b	30 ^c

a. RH, relative humidity.

b. Minimum of 2% relative humidity regression line (~5 h) occurred between 33 and 34°C.

c. Minimum of 95% relative humidity regression line (~30 h) occurred between 29 and 30°C.

Minor differences in off-host survival between laboratory populations were seen with Type 2 having ~10% reduction in survival time across the temperature–relative humidity combinations. This indicates that these mite populations likely have comparable microclimatic interactions and survival behaviors relative to temperature and relative humidity. This supports the coexistence of these two genotypes across the Great Plains, but also, in similar habitats on the same plant, as demonstrated by Siriwetwivat (2006).

The limits of off-host survival for the wheat curl mite provide perspective on the potential that these mites have for invasive movement. McNeil et al. (1996) noted widespread diversity of WSMV isolates across the Great Plains, and Siriwetwivat (2006) provided evidence that the two mite genotypes occur across Kansas, Nebraska, and Montana. These findings suggest that extensive mixing of wheat curl mite and its vectored virus populations is occurring throughout the Great Plains. The off-host survival times shown in this study would seem to be sufficient to enable this type of regional movement. Skoracka et al. (2013, 2014) indicate that wheat curl mite is a complex of lineages some of which have spread across multiple continents. The limits of off-host survival shown here demonstrate that intercontinental movement of mites will be very unlikely unless living plant material is transferred. Skoracka et al. (2014) indicates that those wheat curl mite lineages that have the largest worldwide spread are also polyphagous, including multiple grass species and Amaryllidaceae and Liliaceae bulbs. Considering wheat curl mite off-host survival limits, the potential for this type of movement seems more plausible, if associated with the transfer of these host bulbs.

Plant viruses can have negative, neutral or positive impact on vector behavior and biology (Mauck et al. 2012). WSMV-

infected wheat has been shown to enhance the reproductive capability of wheat curl mite (Siriwetwivat 2006, Murugan et al. 2011). In the current study, WSMV infection did not affect off-host survival. In another eriophyid mite, the fecundity of *A. cajani* was enhanced on pigeon pea plants infected with pea sterility mosaic disease compared with noninfected plants (Kulkarni et al. 2002). In this study, mites from TriMV-infected plants had a 19–24% reduction in off-host survival compared with those from noninfected or WSMV-infected plants. This negative effect for TriMV demonstrates that infection will likely reduce vector survival during dispersal, and subsequently, impact the extent of virus spread. Additional negative effects on wheat curl mite from TriMV infection have been shown. McMechan et al. (2014) and McMechan (2012) observed reduced population establishment and reproduction on TriMV-infected plants compared to noninfected plants. The negative effects on wheat curl mite from TriMV-infected plants raise questions about the long-term ability of this virus to sustain itself at a significant level. In addition, the negative effects reinforce the need for studies focusing on potential pathogen effects on off-host survival of arthropod vectors.

In this study, we used moderately damp instead of saturated paper towels in the holding containers to maintain ~95% relative humidity and avoid constant saturated conditions. In preliminary observations, humidity saturation impaired mite movement and reduced survival. Other authors also avoided 100% relative humidity, and have reported a negative impact on egg hatchability or mite survival due to condensation (Per-ring et al. 1984, Frost 1997, Courtin et al. 2000). The limitations of a saturated microenvironment may influence the wheat curl mite survival and could be a factor in the mites increased prevalence throughout the more arid western Great Plains. Wheat curl mites are predominately found in the protected areas of the wheat plant (e.g., leaf whorl, curled leaves, and recesses within the head) where evapotranspiration is likely to keep the relative humidity elevated. Extensive rainfall and dew formation in wetter climates would likely increase the prevalence of saturated conditions within these secluded areas and potentially have a negative impact on survival.

In the central Great Plains, winter wheat matures in late June or early July and its senescence usually triggers movement of mites to volunteer wheat and other alternate hosts that act as green bridge hosts for both the mites and viruses (Nault and Styer 1969; Thomas and Hein 2003; Wegulo et al. 2008). In the fall, mites move from the green bridge to infest newly emerged winter wheat and cause severe virus infections (Thomas and Hein 2003; Wegulo et al. 2008). Wheat curl mite movement just prior to wheat harvest (summer) and after wheat planting (fall) is a critical determinant to the epidemiology of its vectored viruses. Complete destruction of volunteer wheat either mechanically or chemically before planting winter wheat is the primary management strategy for management of these wheat viruses (Wegulo et al. 2008). The limits of off-host survival of the wheat curl mite presented here will provide a more precise time frame necessary for breaking this green bridge and effectively reducing potential for mite survival and virus spread.

Acknowledgments — This project was supported by funds provided through the U.S. Department of Agriculture, USDA-NIFA grant 2013-68004-20358 and the Nebraska Wheat Board. We thank Dr. W. W. Stroup and C. Stock for assistance with statistical analysis.

References

- Appel, J. A., E. DeWolf, W.W. Bockus, and R. L. Bowden. 2007.** Preliminary 2007 Kansas wheat disease loss estimates. Kansas Cooperative Plant Disease Survey Report.
- Amrine, J. W., and T. A. Stasny. 1994.** Catalog of the Eriophyoidea (Acarina: Prostigmata) of the World, p. 798. Indira Publishing House, Michigan.
- Bergh, J. C. 2001.** Ecology and aerobiology of dispersing citrus rust mites (Acari: Eriophyidae) in central Florida. *Environ. Entomol.* 30: 318–326.
- Carew, M., M. Schiffer, P. Umina, A. Weeks, and A. Hoffmann. 2009.** Molecular markers indicate that the wheat curl mite, *Aceria tosichella* Keifer, may represent a species complex in Australia. *Bull. Entomol. Res.* 99: 479–486.
- Choi, I. R., R. French, G.L. Hein, and D.C. Stenger. 1999.** Fully biologically active in vitro transcripts of the eriophyid mite-transmitted wheat streak mosaic tritrovirus. *Phytopathology* 89: 1182–1185.
- Chown, S. L., J. G. Sørensen, and J. S. Terblanche. 2011.** Water loss in insects: an environmental change perspective. *J. Insect Physiol.* 57: 1070–1084.
- Connin, R.V. 1956.** The host range of the wheat curl mite, vector of wheat streak-mosaic. *J. Econ. Entomol.* 49: 1–4.
- Courtin, O., G. Fauvel, and F. Leclant. 2000.** Temperature and humidity effects on egg and nymphal development of *Aceria tulipae* (K.) (Acari: Eriophyidae) on garlic leaves (*Allium sativum* L.). *Ann. Appl. Biol.* 137: 207–211.
- Del Rosario, M. S., and W. H. Sill Jr. 1958.** A method of rearing large colonies of *Aceria tulipae* (Keifer), in pure culture from a single egg or adult. *J. Econ. Entomol.* 51: 303–306.
- Frost, W. E. 1997.** Polyphenic wax production in *Abacarus hystrix* (Acari: Eriophyidae), and implications for migratory fitness. *Physiol. Entomol.* 22: 37–46.
- Frost, W. E., and P. M. Ridland. 1996.** Grasses, pp. 619–629. In E. E. Lindquist, M. W. Sabelis, and J. Bruin (eds.), *World crop pests*, Vol. 6. Eriophyid mites- Their Biology, Natural Enemies and Control. Elsevier Science B. V., Amsterdam, The Netherlands.
- Harvey, T. L., D.L. Seifers, and T. J. Martin. 1999.** Survival of wheat curl mites on different source of resistant in wheat. *Crop Sci.* 39: 1887–1889.
- Harvey, T. L., D. L. Seifers, and T. J. Martin. 2001.** Host range differences between two strains of wheat curl mites (Acari: Eriophyidae). *J. Agric. Urban Entomol.* 18: 35–41.
- Harvey, T. L., T. J. Martin, and D. L. Seifers. 2002.** Wheat yield reduction due to wheat curl mite (Acari: Eriophyidae) infestations. *J. Agric. Urban Entomol.* 19: 9–13.
- Hein, G. L., R. French, B. Siritiwat, and J. W. Amrine. 2012.** Genetic characterization of North American populations of wheat curl mite and dry bulb mite. *J. Econ. Entomol.* 105: 1801–1808.
- Hoffmann, A. A., and M. W. Blows. 1994.** Species borders: Ecological and evolutionary perspectives. *Trends Ecol. Evol.* 9: 223–227.
- Jeppson, L. R., H. H. Keifer, and E. W. Baker. 1975.** Mites injurious to economic plants, pp. 166, 171–173. University of California Press, Berkeley, CA.
- Jiang, W., K. A. Garrett, D.E. Peterson, T. L. Harvey, R.L. Bowden, and L. Fang. 2005.** The window of risk for emigration of *Wheat streak mosaic virus* varies with host eradication method. *Plant Dis.* 89: 853–858.
- Keifer, H.H. 1938.** Eriophyid Studies. Calif. Dept. Agric. Bull. 27: 182–206.
- Keifer, H. H. 1969.** Eriophyid Studies. ARS-USDA, C-3, 1-2, USDA, ARS. Special publication with the California Department of Agriculture, Sacramento, CA.
- Kovats, R. S., D. H. Campell-Lendrum, A. J. Michael, A. Woodward, and J. S. Cox. 2001.** Early effects of climate change: Do they include changes in vector-borne disease? *Philos. Trans. R. Soc. Lond. B.* 356: 1057–1068.
- Kulkarni, N. K., P. L. Kumar, V. Muniyappa, A. T. Jones, and D.V.R. Reddy. 2002.** Transmission of Pigeon pea sterility mosaic virus by the eriophyid mite, *Aceria cajani* (Acari: Arthropoda). *Plant Dis.* 86: 1297–1302.
- Mauck, K., N. A. Bosque-Pérez, S. D. Eigenbrode, C. M. De Moraes, and M. C. Mescher. 2012.** Transmission mechanisms shape pathogen effects on host-vector interactions: evidence from plant viruses. *Funct. Ecol.* 26: 1162–1175.
- McMechan, A. J. 2012.** Transmission of *Triticum mosaic virus* and its impact on the biology of the wheat curl mite *Aceria tosichella* Keifer (Eriophyidae), and an evaluation of management tactics for the wheat curl mite and the wheat-mite-virus complex. M. S. thesis. University of Nebraska, Lincoln.
- McMechan, A. J., S. Tatineni, R. French, and G. L. Hein. 2014.** Differential transmission of *Triticum mosaic virus* by wheat curl mite populations collected in the Great Plains. *Plant Dis.* 98: 806–810.
- McNeil, J. E., R. French, G. L. Hein, P. S. Baenziger, and K. M. Eskridge. 1996.** Characterization of genetic variability among natural populations of *Wheat streak mosaic virus*. *Phytopathology* 86:1222–1227.
- Melo, J. W. S., D. B. Lima, M. W. Sabelis, A. Pallini, and M.G.C. Gondim Jr. 2014.** Limits to ambulatory displacement of coconut mites in absence and presence of food-related cues. *Exp. Appl. Acarol.* 62: 449–461.
- Murugan, M., P. S. Cardona, P. Duraimurugan, A. E. Whitfield, D. Schneewis, S. Starkey, and C. M. Smith. 2011.** Wheat curl mite resistance: interactions of mite feeding with *Wheat streak mosaic virus* infection. *J. Econ. Entomol.* 104: 1406–1414.
- Nault, L. R., and W. E. Styer. 1969.** The dispersal of *Aceria tulipae* and three other grass-infesting eriophyid mites in Ohio. *Ann. Entomol. Soc. Am.* 62: 1446–1455.
- Perring, T. M., T. O. Holtzer, J. A. Kalisch, and J. M. Norman. 1984.** Temperature and humidity effects on oviposition rates, fecundity and longevity of adult female Banks grass mites (Acari: Tetranychidae). *Ann. Entomol. Soc. Am.* 77: 581–586.
- Sabelis, M. W., and J. Bruin. 1996.** Evolutionary ecology: life history patterns, food plant choice and dispersal, pp. 329–366. In E. E. Lindquist, M. W. Sabelis, and J. Bruin (eds.), *Eriophyid mites- their*

- biology, natural enemies and control, Vol. 6. Elsevier Science B. V., New York, NY.
- Seifers, D. L., T. L. Harvey, T. J. Martin, and S. G. Jensen. 1997.** Identification of the wheat curl mite as the vector of the High Plains virus of corn and wheat. *Plant Dis.* 81: 1161–1166.
- Seifers, D.L., T. L. Harvey, R. Louie, D. T. Gordon, and T. J. Martin. 2002.** Differential transmission of isolates of the High Plains virus by different sources of wheat curl mites. *Plant Dis.* 86:138–142.
- Seifers, D. L., T. J. Martin, T. L. Harvey, J. P. Fellers, and J. P. Michaud. 2009.** Identification of the wheat curl mite as the vector of *Triticum mosaic virus*. *Plant Dis.* 93: 25–29.
- Siriwetwivat, B. 2006.** Interactions between the wheat curl mite, *Aceria tosichella* Keifer (Eriophyidae), and wheat streak mosaic virus, and distribution of wheat curl mite biotypes in the field. Ph.D. dissertation, University of Nebraska, Lincoln.
- Skoracka, A., L. Kuczyński, W. Szydło, and B. Rector. 2013.** The wheat curl mite *Aceria tosichella* (Acari: Eriophyoidea) is a complex of cryptic lineages with divergent host ranges: evidence from molecular and plant bioassay data. *Biol. J. Linn. Soc.* 109: 165–180.
- Skoracka, A., B. Rector, L. Kuczyński, W. Szydło, G. Hein, and R. French. 2014.** Global spread of wheat curl mite by its most polyphagous and pestiferous lineages. *Ann. Appl. Biol.* 165: 222–235.
- Slykhuis, J. T. 1955.** *Aceria tulipae* Keifer (Acarina: Eriophyidae) in relation to the spread of wheat streak mosaic. *Phytopathology* 45: 116–128.
- Somsen, H.W., and H. W. Sill Jr. 1970.** The wheat curl mite, *Aceria tulipae* Keifer, in relation to epidemiology and control of wheat streak mosaic. Kansas State University. Research Publication 162.
- Staples, R. and W. B. Allington. 1956.** Streak mosaic of wheat in Nebraska and its control, p. 40. University of Nebraska College of Agriculture Experimental Station, Research Bulletin 178.
- Tatineni, S., A. D. Ziems, S. N. Wegulo, and R. French. 2009.** *Triticum mosaic virus*: A distinct member of the family Potyviridae with an unusually long leader sequence. *Phytopathology* 99: 943–950.
- Thomas, J. A., and G. L. Hein. 2003.** Influence of volunteer wheat plant condition on movement of the wheat curl mite *Aceria tosichella*, in winter wheat. *Exp. Appl. Acarol.* 31:256–268.
- Wegulo, S. N., G. L. Hein, R. N. Klein, and R. C. French. 2008.** Managing wheat streak mosaic. University of Nebraska–Lincoln Extension. EC1871.