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Multiple Categories of Resistance to Wheat Curl Mite (Acari: Eriophyidae) Expressed in Accessions of *Aegilops tauschii*

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ABSTRACT The wheat curl mite, *Aceria tosichella* Keifer, is an important pest in the western plains of the United States as well as in most major wheat-growing regions of the world. This mite is a vector of the economically important diseases wheat streak mosaic virus (WSMV), Triticum mosaic virus (TriMV), and High Plains virus (HPV). This study looked at seven accessions of *Aegilops tauschii* (Coss) Schmal to determine if they exhibit antibiosis, tolerance, and/or antixenosis to the wheat curl mite using ‘Jagger’, a known wheat curl mite-susceptible variety, and OK05312, a known wheat curl mite-resistant variety, as controls. Four of the seven tested accessions showed antibiotic effects on the population growth of wheat curl mite, as demonstrated by low number of wheat curl mite adults and nymphs at the end of the experiment. Three accessions and the commercial wheat variety Jagger showed some level of tolerance to wheat curl mite infestations, as demonstrated by a significantly reduced percentage proportional tissue dry weight and by tolerance index values. Four accessions demonstrated a strong antixenotic effect on the wheat curl mite, as demonstrated by significantly reduced numbers of mite adults at the end of the experiment. This study also established an effective method for determining antixenosis to the wheat curl mite in wheat that can be used for future experiments. All accessions demonstrated at least one type of plant resistance that could provide a genetic source for control of the wheat curl mite that may have the potential to be transferred into commercial wheat varieties.

KEY WORDS wheat, wheat curl mite, antibiosis, antixenosis, tolerance

The wheat curl mite, *Aceria tosichella* Keifer, is an important pest of bread wheat, *Triticum aestivum* L., in the western plains of the United States as well as in most major wheat-growing regions of the world (Murugan et al. 2011). This mite is a vector of the economically important diseases wheat streak mosaic virus (WSMV), Triticum mosaic virus (TriMV), and High Plains virus (HPV) (Slykhuis 1955; Seifers et al. 1997, 1998). WSMV is the most prevalent of these viruses in the western plains, causing damage in forage and grain production and resulting in up to 100% yield losses in wheat (Tosic 1971, Slykhuis 1976, Sanchez-Sanchez et al. 2001, Velandia et al. 2010). Wheat curl mite nymphs acquire WSMV after feeding for as little as 30 min on infected plants and can transmit WSMV for at least 7 d postfeeding (Slykhuis 1955, Orlob 1966). In 2011, WSMV was the second most important disease in Kansas wheat, causing up to 7% yield loss in susceptible varieties in areas of central Kansas (Appel et al. 2011). Wheat curl mite damage may also result in yield losses in wheat as a result of leaf rolling,

trapping of the flag leaf, and reduced grain yields when populations infest spikes (Harvey et al. 2000, 2002).

Wheat curl mite control is difficult because the mites are microscopic ($\approx 200 \mu\text{m}$ long), which means they are not often observed or properly identified by growers until wheat is heavily infested or infected with WSMV, TriMV, or HPV. Avoiding yield loss is unlikely at this point. Wheat curl mite over summer in volunteer wheat and other grasses near wheat crops, then move into early planted wheat in the fall (Connin 1956, Harvey et al. 2001). Current management practices include controlling volunteer wheat, planting wheat late in the fall, and applying acaricide (Velandia et al. 2010). Late planting is not feasible for growers using wheat for winter forage, however, and few acaricides effectively control the wheat curl mite; furthermore, little information is available on proper timing and conditions for acaricide applications (Velandia et al. 2010). Plant resistance to the wheat curl mite and to WSMV is the most viable and economical means to control the wheat curl mite and the diseases it vectors. Wheat curl mite-resistant wheat has been shown to reduce the spread of WSMV by inhibiting the reproductive capacity of wheat curl mite (Harvey et al. 1990, 2005; Conner et al. 1991).

Goat grass, *Aegilops tauschii* (Coss) Schmal, is the donor of many arthropod-resistance genes in bread

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wheat, because the D-genome of *Ae. tauschii* is completely homologous to the D-genome of bread wheat (Thomas and Whelan 1991). *Ae. tauschii* genes for wheat curl mite antibiosis resistance have been transferred to common wheat (Thomas and Conner 1986, Cox et al. 1999, Malik et al. 2003a), and *Ae. tauschii* is thought to contain at least five different genes for wheat curl mite resistance (Malik et al. 2003b). However, virulent wheat curl mite populations may quickly overcome antibiosis resistance (Harvey et al. 1995, 1999), and new sources of wheat curl mite resistance must be used in wheat breeding programs to manage wheat curl mite populations effectively (Harvey et al. 1999).

Ae. tauschii is composed of the subspecies *strangulata*, in Transcaucasia and southeastern Iran; and the subspecies *tauschii*, in north central Iran and southwestern Iran (Dvorak et al. 1998). Subspecies *tauschii* also contains the varieties *anathera* and *typica* (van Slageren 1994). The results of Malik et al. (2003b) and of preliminary experiments (M. Murugan, unpublished data) indicated that some accessions of subspecies *strangulata* and *tauschii* contain tolerance resistance. Further, no sources of wheat curl mite antixenosis exist and no published methods are available to determine antixenosis. In the current study, we developed methods to measure antixenosis and tolerance resistance to wheat curl mite in wheat and *Ae. tauschii*, and identified different antibiosis, antixenosis, or tolerance resistance to wheat curl mite resistance in accessions of *Ae. tauschii*.

Materials and Methods

Plants, Arthropods, and Environmental Conditions.

Based on results of Malik et al. 2003b and unpublished preliminary results of co-author Murugan, we evaluated seven *Ae. tauschii* accessions to determine their category of resistance to wheat curl mite. Accessions and associated origins included *Ae. tauschii* accessions TA1582, 1583, 1597, and 1578 from Turkey; *Ae. tauschii* subspecies *tauschii* variety *anathera* accession 2556 from Afghanistan; *Ae. tauschii* subspecies *tauschii* variety *typica* accession 2394 from Afghanistan; and *Ae. tauschii* subspecies *strangulata* accession 1695 from Japan.

The wheat curl mite-susceptible wheat variety 'Jagger' and the wheat curl mite-resistant variety OK05312 (provided by Dr. Brett Carver, Department of Plant and Soil Sciences, Oklahoma State University, Stillwater, OK) were used as controls (Murugan et al. 2011). Seeds of the seven accessions were obtained from the Kansas State University Wheat Genetic and Genomic Resource Center. Mites were obtained from a mass-reared colony held in the Kansas State University Department of Entomology that originated from virus-free mites collected in Hays, KS. The colony and had been reared on Jagger plants for multiple generations and a sample used to prepare voucher specimen No. 215 in the Kansas State University Museum of Entomological and Prairie Arthropod Research. Experiments were conducted in greenhouses

at Kansas State University in Manhattan, KS, from February through May 2011, maintained at 24/20°C day/night and a photoperiod of 14:10 (L:D) h.

Tolerance and Antibiosis Experiments. *Ae. tauschii* accessions were evaluated for antibiosis and tolerance to wheat curl mite in a no-choice test and compared them with susceptible variety Jagger and resistant OK05312. A single seed of each accession, Jagger, and OK05312 was sown in a 1-oz plastic cup containing Pro-Mix 'BX' soil (Hummert International, Earth City, MO) and slow-release fertilizer (Osmocote Classic, Scotts Company, Marysville, OH). For each accession, 10 pairs of equal-sized two-leaf stage plants were selected ≈ 7 d after sowing, and in each pair, one plant served as a noninfested control and the other was infested with a piece of leaf containing 30–35 wheat curl mite adults. Adults were counted using a 10 \times stereoscope (StereoZoom7, Bausch + Lomb, Rochester, NY). Plants were placed inside mite-proof cages (28 \times 28 \times 51.5 cm), and care was taken so leaves did not touch those of different plants. Experiments were arranged in a completely random design with 10 replicates.

Plant height, number of tillers, number of leaves, presence of folded leaves (1 = no folding, 3 = folded), and percentage of rolling of the youngest fully developed leaf were recorded 20 d postinfestation. The 1–9 leaf rolling scale was: 1 = no rolling, 3 = 25% rolling, 5 = 50% rolling, 7 = 75% rolling, and 9 = 100% rolling). After collecting this data, noninfested and infested plants were cut at the soil level. Roots were carefully washed to remove soil and residues, and individual shoots and roots of noninfested plants were placed in preweighed aluminum bags and dried at 60°C for 5 d. Individual shoots of infested plants were placed on a sticky tape supported with a gridded blue paper (3.9 \times 7.5 cm) and stored in an uncapped 50-ml centrifuge tube for 5 d. As leaves dried, mites crawled off the vegetation and were trapped on the sticky tape. When dry, leaves were removed, placed in aluminum bags, and dried for an additional 3 d at 60°C. Roots of infested plants were also dried as previously described for noninfested roots. Nymphs and adults trapped on sticky tapes were counted using a 30 \times stereoscope (Nikon SMZ645, Nikon, Melville, NY). Shoot and root dry weights were measured with an XS-310D analytical balance with 1-mg sensitivity (Denver Instrument, Bohemia, NY) and used to estimate proportional weight change (DWT) and tolerance index (TI) (Reese et al. 1994). DWT and TI were calculated for shoots, roots, and total plant as $DWT = [(U-I)/U] * 100$; and $TI = \{[(U-I)/U] / WCM\} * 100$; where U is the weight of noninfested plant per accession, I is the weight of infested plant, and wheat curl mite is the total number of mites produced on the infested plant at end of the experiment. The degree of tolerance in each accession was determined from measurements of wheat curl mite damage symptoms, DWT, and TI. Tolerance resistance to wheat curl mite does not exist, so there are no known tolerant controls. Therefore, in this study we associated tolerance with a significant reduction in tolerance index values. Numbers of

wheat curl mite nymphs and adults present on each accession at the end of the experiment were used to evaluate antibiosis.

Antixenosis Experiments. We tested *Ae. tauschii* accessions TA1597, 1578, 2556, 1695, 2394, Jagger, and OK05312 for wheat curl mite antixenosis. All accessions and controls were planted together and arranged in a circle around the periphery of a 10-cm-diameter plastic pot. A single seed per accession was planted in each pot with ≈ 2 cm between each seed. Plants were sown with Pro-Mix 'BX' (Hummert International) and slow-release fertilizer (Osmocote Classic). At the two-leaf stage, 140 wheat curl mite adults (20 per plant) were released on a blue paper fixed on top of a plastic cup (2.5 cm in diameter \times 4 cm high) that was placed inside the circle of plants (Fig. 1). All seven plants were held together with a string noose, so that each touched the blue paper disc containing mites. We took care to avoid allowing stems to touch each other when plants touched the border of the cup. This experiment was arranged in a completely randomized block design with 16 replications where pots were the blocking factor. All pots were placed inside mite-proof cages (28 \times 28 \times 51.5 cm). At 7 d postinfestation, plants were cut at the soil level, and leaves from each plant were placed on sticky tape as previously described. The 7-d postinfestation interval was selected because in previous experiments, plants cut 2 and 5 d postinfestation were noninfested and had no wheat curl mite damage symptoms (unpublished data). According to Orlob (1966), adult mites move from 0.09 to 0.48 cm per day (0.63 cm to 3.36 cm in 7 d); therefore, we allowed 7 d for adults to reach and feed on test plants. After leaves were dried, mite adults and nymphs trapped on the tape were counted with a 30 \times stereoscope (Nikon SMZ645) as a measurement of antixenosis in each accession.

Statistical Analysis. Tolerance indexes and number of adults and nymphs data were transformed using the natural logarithm according to preliminary analysis of normal distribution of residuals and homogeneity of variances. Transformed and untransformed variables were analyzed by analysis of variance (ANOVA) using the SAS 9.2 (SAS Institute 2008). When the *F*-test was significant at $\alpha = 0.05$, means were separated using Tukey's studentized range (honestly significant difference [HSD]) test at $\alpha = 0.05$ level of significance. Data displayed in Tables 1 through 4 contain means and SEs of untransformed data.

Results

Antibiosis. Mean number of wheat curl mite adults, nymphs, leaf folding, and leaf rolling produced after 20 d of infestation were statistically different among all accessions ($F = 144.99$, $df = 8, 74$, $P < 0.0001$; $F = 333.61$, $df = 8, 74$, $P < 0.0001$; $F = 61.00$, $df = 8, 74$, $P < 0.0001$; and $F = 102.62$, $df = 8, 74$, $P < 0.0001$, respectively). Accessions TA1582, 1583, and 1597 produced significantly higher numbers of wheat curl mite adults and nymphs than resistant variety OK05312 (Table 1). The average numbers of nymphs produced on acces-

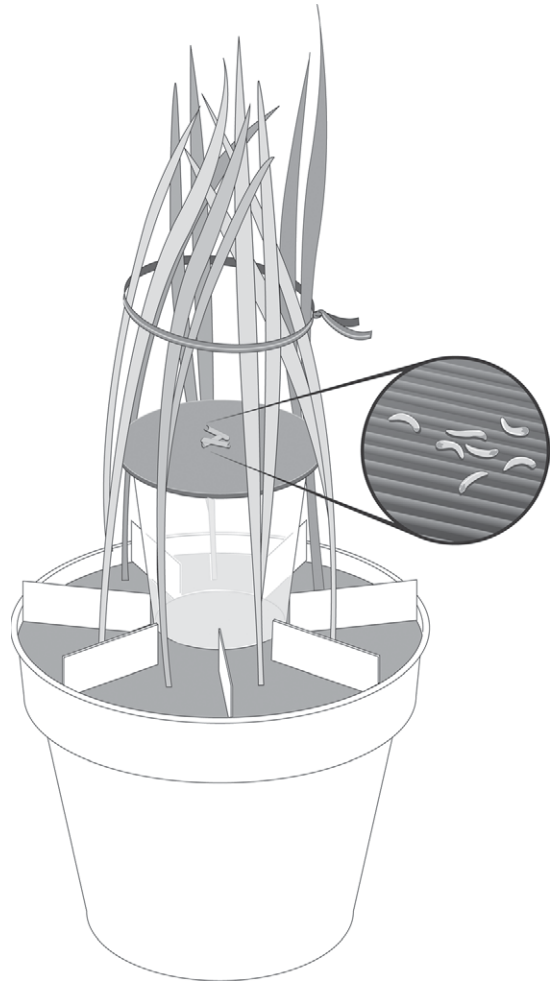


Fig. 1. Antixenosis experiment. A single seed per accession was planted in each pot with ≈ 2 cm between each seed. At the two-leaf stage, 140 wheat curl mite adults (20 per plant) on a piece of wheat leaf were placed on a blue germination paper disc on top of a plastic cup (2.5 cm diameter \times 4 cm high) placed inside a circle of test plants. All plants were held together with a string noose, so that each touched the blue paper containing mites. (Illustration by Robert Holcombe, Kansas State University Research & Extension.)

sions TA1578, 2556, 1695, and 2394 were lower than the susceptible variety Jagger, and were not significantly different from OK05312. Jagger plants produced the highest mean numbers of wheat curl mite adults and nymphs. The low numbers of wheat curl mite adults and nymphs indicates a strong antibiotic effect of these accessions on wheat curl mite population growth. Mean leaf folding and leaf rolling were significantly greater on plants of accessions TA1582, 1583, 1597, and Jagger than on plants of accessions TA1578, 2556, 1695, 2394, and OK05312 (Table 1).

Tolerance. We found no significant differences among the seven accessions or either control in their ability to compensate for damage resulting from wheat curl mite feeding, as measured by shoot, root, or total

Table 1. Mean \pm SE no. of *A. tosichella* adults and nymphs developing on plants of seven *Aegilops* spp. accessions, the *A. tosichella*-susceptible wheat variety 'Jagger', and the resistant variety OK05312 at 20 d after infestation in no-choice tests, and leaf folding and rolling scores of infested plants

Accession	Mean \pm SE			
	No. of adults ^a	No. of nymphs ^a	Leaf folding score ^b	% leaf rolling ^c
TA2394	1.1 \pm 0.4a	0.3 \pm 0.3a	1.0 \pm 0.0a	1.0 \pm 0.0a
OK05312	2.5 \pm 1.1a	0.0 \pm 0.0a	1.0 \pm 0.0a	1.0 \pm 0.0a
TA1695	3.9 \pm 0.9a	0.9 \pm 0.4a	1.0 \pm 0.0a	1.4 \pm 0.3a
TA2556	4.4 \pm 1.5a	0.5 \pm 0.2a	1.0 \pm 0.0a	1.0 \pm 0.0a
TA1578	5.7 \pm 2.9a	0.7 \pm 0.3a	1.0 \pm 0.0a	1.7 \pm 0.4a
TA1597	315.9 \pm 52.5b	430.6 \pm 92.5b	2.8 \pm 0.2b	5.2 \pm 0.2b
TA1583	343.0 \pm 49.4b	615.8 \pm 135.8bc	2.8 \pm 0.2b	5.6 \pm 0.3b
TA1582	449.0 \pm 57.9b	914.6 \pm 103.0c	3.0 \pm 0.0b	5.4 \pm 0.4b
Jagger	613.1 \pm 117.4b	983.2 \pm 220.3c	2.8 \pm 0.2b	7.4 \pm 0.3c

Means within a column followed by different letters are significantly different, separation by Tukey's studentized range test (HSD) ($\alpha = 0.05$).

^a Differences in the mean numbers of wheat curl mites adults and nymphs were based on log-transformed data.

^b 1 = no folding; 3 = leaf folded.

^c 1 = 0%; 3 = 25%; 5 = 50%; 7 = 75%; 9 = 100%.

plant percentage proportional dry weight (DWT) loss ($F = 1.30$, $df = 8, 70$, $P = 0.26$; $F = 1.23$, $df = 8, 74$, $P = 0.30$; and $F = 1.84$, $df = 8, 74$, $P = 0.08$, respectively). However, when DWT measurements were corrected for differences in numbers of wheat curl mite on plants; root, shoot and total plant TI values differed significantly ($F = 117.65$, $df = 8, 65$, $P < 0.0001$; $F = 106.70$, $df = 8, 60$, $P < 0.0001$; and $F = 88.04$, $df = 8, 65$, $P < 0.001$, respectively) among accessions and controls (Table 2). Mean root, shoot, and total plant TI values of accessions TA1582, 1583, 1597, and Jagger were significantly lower than those of accessions TA2394, 1695, 2556, and 1578 and the resistant control, suggesting that Jagger and TA1582, 1583, and 1597 tolerate wheat curl mite to a certain extent (Table 2).

The mean numbers of leaves and tillers differed among varieties ($F = 13.09$, $df = 8, 74$, $P < 0.0001$; $F = 12.17$, $df = 8, 74$, $P < 0.0001$), and there were significantly more leaves and tillers produced on plants of TA2556, 1695, 1583, and 1597 than on those of susceptible Jagger or resistant OK05312 plants. However, there were no statistically significant differences in mean percent proportional plant height loss among varieties ($F = 0.88$; $df = 8, 72$; $P = 0.54$) (Table 3).

Antixenosis. Differences in the mean number of wheat curl mite adults, leaf folding, and leaf rolling were highly significant ($F = 38.47$, $df = 8, 81$, $P < 0.0001$; $F = 6.76$, $df = 8, 81$, $P < 0.0001$; and $F = 84.81$, $df = 8, 79$, $P < 0.0001$, respectively) among varieties. Plants of TA2394, 2556, 1578, and 1695 were significantly less preferred and had significantly fewer mean numbers of wheat curl mite adults than TA1597 and Jagger (Table 4). These results indicate a strong antixenotic effect of these four varieties on the wheat curl mite. Results for mean leaf folding and leaf rolling ratings were similar to number of wheat curl mite adults, because plants of TA2394, 2556, 1578, and 1695 had significantly less folding and rolling than TA1597 and Jagger (Table 4).

Discussion

Antibiosis. The identification of new sources of wheat curl mite resistance is important for wheat curl mite management because wheat curl mite virulence has been shown to overcome antibiosis resistance quickly in commercial wheat varieties (Harvey et al. 1999). *Ae. tauschii* accessions TA1578, 1695, 2394, and

Table 2. Mean \pm SE percentage proportional dry weight loss and tolerance index values for shoots, roots, and total plants of seven *Aegilops* spp. accessions, the susceptible wheat variety 'Jagger', and the resistant variety OK05312 after 20 d of *A. tosichella* infestation

Accession	Mean \pm SE % proportional dry weight loss ^a			Mean \pm SE tolerance index ^b		
	Total plant	Shoots	Roots	Total plant	Shoots	Roots
Jagger	28.4 \pm 4.5a	26.6 \pm 5.2a	38.5 \pm 4.9a	0.03 \pm 0.00a	0.02 \pm 0.00a	0.03 \pm 0.00a
TA1582	42.7 \pm 4.0a	35.6 \pm 6.0a	53.3 \pm 6.7a	0.03 \pm 0.00a	0.03 \pm 0.00a	0.04 \pm 0.00a
TA1583	45.7 \pm 5.4a	45.6 \pm 5.1a	45.9 \pm 6.8a	0.06 \pm 0.01a	0.06 \pm 0.01a	0.06 \pm 0.01a
TA1597	40.4 \pm 2.8a	38.2 \pm 4.5a	44.2 \pm 6.6a	0.09 \pm 0.03a	0.09 \pm 0.03a	0.08 \pm 0.02a
OK05312	38.1 \pm 3.8a	35.6 \pm 3.9a	41.3 \pm 4.8a	6.62 \pm 3.09b	6.36 \pm 3.00bc	6.97 \pm 3.22b
TA1578	24.0 \pm 11.0a	26.9 \pm 9.2a	46.3 \pm 7.3a	6.72 \pm 3.20b	6.07 \pm 3.64b	10.70 \pm 2.46b
TA1695	32.0 \pm 5.2a	33.9 \pm 3.9a	29.4 \pm 11.6a	8.15 \pm 1.58b	11.92 \pm 3.36b	2.86 \pm 5.48b
TA2556	43.8 \pm 4.0a	39.6 \pm 3.0a	53.7 \pm 6.8a	15.30 \pm 4.39b	13.49 \pm 3.50bc	19.53 \pm 6.50b
TA2394	36.0 \pm 8.4a	37.8 \pm 7.8a	32.9 \pm 0.8a	26.04 \pm 9.98b	26.02 \pm 10.06c	26.07 \pm 10.03b

Differences in the mean tolerance indexes were based on log-transformed data.

Means within a column followed by different letters are significantly different, separation by Tukey's studentized range test (HSD) ($\alpha = 0.05$).

^a Percentage proportional dry weight loss = $[(U-I)/U] \times 100$; U = wt of noninfested plant, I = wt of infested plant.

^b Tolerance index = percentage proportional dry weight loss/no. of wheat curl mites produced on infested plants.

Table 3. Mean \pm SE no. of leaves, number of tillers, and percentage proportional plant ht loss on plants of seven *Aegilops* spp. accessions, the susceptible wheat variety 'Jagger', and the resistant variety OK05312 after 20 d of *A. tosicHELLa* infestation

Accession	No. of leaves (mean \pm SE)	No. of tillers (mean \pm SE)	% proportional plant ht loss ^a (mean \pm SE)
Jagger	4.1 \pm 0.1a	1.0 \pm 0.0a	14.2 \pm 3.5a
TA2394	4.1 \pm 0.1a	1.1 \pm 0.1ab	9.4 \pm 6.4a
OK05312	4.3 \pm 0.2a	1.0 \pm 0.0a	10.8 \pm 2.3a
TA1578	4.7 \pm 0.4ab	1.3 \pm 0.2abc	6.6 \pm 3.3a
TA1582	5.0 \pm 0.6ab	1.3 \pm 0.2ab	13.2 \pm 1.6a
TA1583	6.2 \pm 0.5bc	1.9 \pm 0.2bcd	13.3 \pm 3.5a
TA1597	6.2 \pm 0.4bc	2.2 \pm 0.2cd	18.7 \pm 1.7a
TA1695	7.3 \pm 0.5c	2.5 \pm 0.2d	11.2 \pm 3.7a
TA2556	7.4 \pm 0.2c	2.4 \pm 0.2d	12.2 \pm 2.7a

Means within a column followed by different letters are significantly different, separation by Tukey's studentized range test (HSD) ($\alpha = 0.05$).

^a Percentage proportional plant ht loss = (U-I)/U; U = mean of noninfested plants, I = infested plants.

2556 expressed antibiosis by reducing numbers of wheat curl mite adults and nymphs, which were no different from those on the antibiosis control, OK05312. Malik et al. (2003b) reported that these accessions were resistant to wheat curl mite biotypes originally identified in Montana, Kansas, and Nebraska. However, more up-to-date evaluations of these accessions and related breeding material against different wheat curl mite populations are necessary for improved long-term wheat curl mite management (Harvey et al. 1999).

Tolerance. Although no previous studies have examined tolerance to wheat curl mite damage, our results indicate that the variety, Jagger, and *Ae. tauschii* accessions TA1582, 1583, and 1597 contain tolerance to wheat curl mite feeding, as exhibited by significantly reduced shoot-, root-, or whole plant tolerance indices (Table 2). The mean numbers of leaves and tillers per plant also varied significantly among accessions, which suggests that plant growth factors contribute to wheat curl mite tolerance (Table 3). However, when growth differences were proportionalized, there were no significant differences among accessions for mean percent proportional plant height loss.

While antibiosis resistance effectively reduces the incidence of WSMV, plant tolerance does not, suggesting that wheat curl mite tolerance may be less

important to producers than WSMV resistance (Harvey et al. 1990, Conner et al. 1991). Because WSMV can lead to severe yield loss, controlling the mite before it feeds is important to minimize wheat curl mite populations on wheat, or to grow WSMV-resistant wheat. Nevertheless, WSMV resistance transferred to wheat from rye, *Aegilops* spp., and several grass species (Harvey et al. 1994; Wood et al. 1995; Li et al. 2002, 2007; Malik et al. 2003b) could be combined with wheat curl mite tolerance to increase producer wheat yields.

Results of Table 2 illustrate the lack of a relationship between tolerance and antibiosis or antixenosis in the accessions evaluated (Tables 1 and 4, respectively). Accessions TA1582, 1583, and 1597 had significantly lower tolerance indices than accessions demonstrating antibiosis (TA1578, 1695, 2394, and 2556) (Table 2) but had significantly less antibiosis (higher wheat curl mite populations) (Table 1). TA1597 was also significantly more preferred by wheat curl mite than accessions TA1578, 1695, 2394, or 2556 (Table 4).

Our study inadvertently lacked a tolerant control for comparison, because Jagger the susceptible control chosen, demonstrated tolerance. Further research on wheat tolerance to the wheat curl mite is necessary to identify additional tolerant controls and to examine the potential reasons for tolerance.

Table 4. Mean \pm SE leaf folding and rolling scores on plants of five *Aegilops* spp. accessions, the *A. tosicHELLa*-susceptible wheat variety 'Jagger', and the resistant variety OK05312 7 d after mite release in choice tests, and mean \pm SE number of mites occurring on infested plants

Accession	No. of adults ^a (mean \pm SE)	Leaf folding score ^b (mean \pm SE)	% leaf rolling ^c (mean \pm SE)
TA2394	0.6 \pm 0.3a	1.0 \pm 0.0a	1.0 \pm 0.0a
TA2556	1.8 \pm 0.9a	1.0 \pm 0.0a	1.1 \pm 0.1a
TA1578	2.3 \pm 0.8a	1.0 \pm 0.0a	1.0 \pm 0.0a
TA1695	2.8 \pm 0.9ab	1.0 \pm 0.0a	1.0 \pm 0.0a
OK05312	10.5 \pm 2.8b	1.1 \pm 0.1ab	1.5 \pm 0.3a
TA1597	35.3 \pm 10.6c	1.6 \pm 0.2bc	3.5 \pm 0.4b
Jagger	50.1 \pm 18.4c	1.9 \pm 0.3c	6.5 \pm 0.2c

Means within a column followed by different letters are significantly different, separation by Tukey's studentized range test (HSD) ($\alpha = 0.05$).

^a Differences in the mean numbers of wheat curl mites adults and nymphs were based on natural log-transformed data.

^b 1 = no folding; 3 = leaf folded.

^c 1 = 0%; 3 = 25%; 5 = 50%; 7 = 75%; 9 = 100%.

Antixenosis. In the current study, we provide the first evidence of antixenosis (nonpreference) resistance to the wheat curl mite in *Ae. tauschii* accessions TA1578, 1695, 2394, and 2556. Antixenosis experiments were developed to determine if *Ae. tauschii* leaf differences were sufficient to result in differential wheat curl mite orientation, movement and feeding. The strong antixenotic effects evident in the four accessions may indicate the presence of chemical or morphological leaf factors that alter wheat curl mite behavior, resulting in mite nonpreference.

Although we did not assess wheat curl mite wind dispersal, an important method of movement (Harvey et al. 1990), antibiosis experiments essentially tested whether a high level of antixenosis (alone or in combination with antibiosis) resulted in reduced wheat curl mite populations. Mite populations were no different on leaves of three of the four antibiotic and antixenotic accessions (TA2394, 2556, and 1578) than on leaves of the resistant control in antibiosis experiments and were significantly lower than on leaves of control plants in antixenosis experiments (Tables 1 and 4). However, these results should be viewed with caution. A large-field no-choice experiment was beyond the scope of the current study, and the potential value of nonpreference in wheat monoculture lacking plants of more preferred host species remains to be determined.

Harvey et al. (1990) determined that wheat curl mite infestation rate and WSMV infection incidence are increased in wheat cultivars with high densities of leaf trichomes. Large variation in spike and leaf trichome density occurs between *Ae. tauschii* subspecies *tauschii* and *strangulata* (Morihoro and Takumi 2010), between *Ae. tauschii* and other *Aegilops* species, and between *Ae. tauschii* bread wheat (Doroshkov et al. 2011, Kilian et al. 2011). The trichome density and length of *Ae. tauschii* accessions tested are not known, but if the antixenotic effects identified in TA1578, 1695, 2394, and 2556 can be attributed to reduced leaf pubescence, they may be highly beneficial in reducing WSMV transmission in wheat. Further research is necessary to determine if leaf trichome density and length; leaf color; and leaf volatiles affect wheat curl mite behavior and reproduction. Finally, it will also be necessary to replicate the experiments in the current study under field conditions to confirm the greenhouse results reported here.

The development of a method to analyze wheat curl mite antixenosis underscores the need to better understand wheat curl mite dispersal. As indicated previously, wind-driven dispersal is one of the most important methods of wheat curl mite population movement, but little is known about movement of individual mites on plants. Orlob (1966) observed wheat curl mite dispersal and movement during feeding on wheat leaves and determined that the rate of movement of individual mites ranged from 0.09 to 0.48 cm per day. Based on this range, we estimated that an individual wheat curl mite moves from 0.63 cm to 3.36 cm in 7 d. Thus, the 7-d antixenosis assay period allowed sufficient time for

mites to move 2.25 cm from the release point in the center of the paper disc to the disc edge and an additional 0.37 cm to reach leaf surfaces in sufficient numbers to cause feeding damage symptoms and infestation counts that differed significantly among test accessions.

Mites differ from other plant virus-vectors in that they feed only on the epidermis, specifically on epidermal bulliform cells, which contain primarily water (Orlob 1966). Bulliform cells are believed to function in the folding or rolling of grass leaves. Wheat curl mite feeding damage presumably creates changes in plant leaf water potential, causing leaves to roll and fold, creating a tubular refuge from biological and chemical control as well as a safe place for mites to reproduce. The reduced level of leaf folding and rolling of the four accessions exhibiting antibiosis and antixenosis should be advantageous in developing improved wheat curl mite integrated management, if mite virulence can be delayed or avoided. The antixenosis assay will be useful in future research to understand more about wheat curl mite movement, feeding, and the vectoring of WSMV infections.

Wheat curl mite management in the United States is currently based on volunteer wheat control, delayed fall wheat planting to delay availability of a new plants, and acaricide applications. However, delayed planting is often infeasible, as planting date is more normally determined by availability of soil moisture and many producers use wheat as a winter forage (Velandia et al. 2010). Acaricides for wheat curl mite are ineffective (Morgan et al. 2005). The *Ae. tauschii* accessions in this study that display both antibiosis and antixenosis resistance to wheat curl mite exhibit reduced incidence of wheat curl mite-induced leaf folding and rolling that aid plants by promoting improved photosynthesis and growth processes over that of wheat curl mite-susceptible plants. These benefits provide wheat plants an obvious advantage in maintaining or improving development and yield, and the antixenotic effects identified may be highly beneficial in reducing WSMV transmission in wheat.

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