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Genetics and mechanisms underlying transmission of *Wheat streak mosaic virus* by the wheat curl mite

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Wheat streak mosaic virus (WSMV, genus *Tritimovirus*; family *Potyviridae*) is the most economically important virus of wheat in the Great Plains region of the USA. WSMV is transmitted by the eriophyid wheat curl mite (WCM), *Aceria tosichella* Keifer. In contrast to Hemipteran-borne plant viruses, the mode and mechanism of eriophyid mite transmission of viruses have remained poorly understood, mostly due to difficulty of working with these ~200 μm long microscopic creatures. Among eriophyid-transmitted plant viruses, relatively extensive work has been performed on population genetics of WCMs, WSMV determinants involved in WCM transmission, and localization of WSMV virions and inclusion bodies in WCMs. The main focus of this review is to appraise readers on WCM, WSMV encoded proteins required for WCM transmission and further details and questions on the mode of WSMV transmission by WCMs, and potential advances in management strategies for WCMs and WSMV with increased understanding of transmission.

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Introduction

Transmission by arthropod vectors is the most effective means of disseminating plant viruses. Viruses have evolved precise vector-specific transmission interactions between viral and vector proteins that determine the nature and efficiency of transmission. Arthropod transmission of plant viruses is divided into three broad categories based on the interactions between the virus and vector. These categories are nonpersistent, semipersistent, and persistent transmission [1••,2••]. In nonpersistent transmission or stylet-borne transmission, the virus can be transmitted only for a few minutes after a relatively brief period of acquisition (<5 min). In semipersistent or foregut-borne transmission, vectors acquire viruses after minutes to hours of feeding and transmission is retained for hours to days. The site of virus interaction with the vector in these methods is the stylet or the foregut. Because the lining of the stylet and foregut are lost in the molting process, retention of these viruses is limited, and viruses are not retained through the molt. Persistent transmission is defined as transmission with the most intimate interactions between virus and vector and is subdivided into circulative and propagative [3,4••]. In circulative transmission, viruses move through the vector, from the gut lumen into the hemolymph or other tissues and finally into the salivary glands, where they are introduced back into the plant during vector feeding. In propagative transmission, viruses also circulate through the vector, but they are able to replicate in various tissues within the vector. Because of their prevalence within the vector, they often can be transmitted to progeny of the vector via transovarial transmission.

Hemipteran insects (e.g. aphids, leafhoppers and whiteflies) are the most common vectors of plant viruses, but the family Eriophyidae (Subclass Acari) includes eleven species of mites that serve as vectors of several plant viruses [5•]. Wheat curl mite (WCM; *Aceria tosichella* Keifer) belongs to the family Eriophyidae in the superfamily Eriophyoidea [6]. Approximately 4000 species of eriophyoid mites have been reported [7,8]; however, all known eriophyoid species that serve as vectors of plant viruses belong to the family Eriophyidae [5•,6]. Recently, Stenger *et al.* [5•] presented a review of eriophyid mites and the viruses transmitted by these mites. In this review, we will focus specifically on the WCM and its transmitted viruses, with special emphasis on *Wheat streak mosaic virus* (WSMV).

Wheat viral diseases

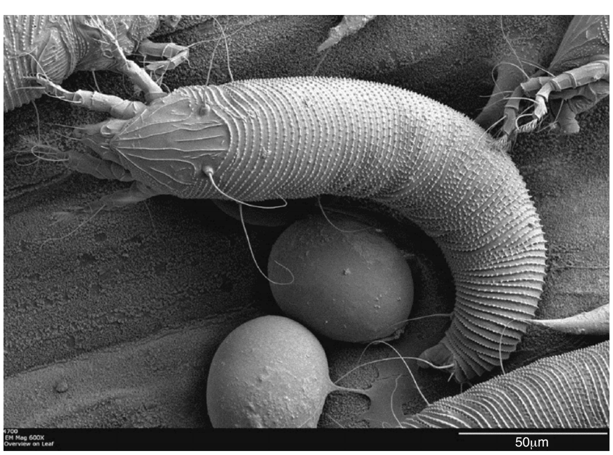
Wheat viral diseases in the Great Plains region of North America can cause 3–5% annual yield loss [9,10]. Viruses infecting wheat in the Great Plains include *Agropyron mosaic virus* (AgMV), *Barley yellow dwarf virus*, *High Plains wheat mosaic virus* (HPWMoV), *Soil-borne wheat mosaic virus*, *Triticum mosaic virus* (TriMV), *Wheat American striate mosaic virus*, and WSMV [10–12]. Among these viruses, HPWMoV, TriMV, and WSMV are transmitted by the WCM [13–15]. It appears that the transmission capabilities of HPWMoV and TriMV by WCM are similar to those of

WSMV (see below) ([14–17]; G. Hein, unpublished]. However, further studies are needed to unravel the transmission characteristics of TriMV and HPWMoV. Wheat infections by WSMV, TriMV and HPWMoV are widespread across the Great Plains, and co-infection of wheat by two or all three viruses is common in growers' fields with exacerbated yield loss [18–20]. WCM-transmitted viruses are the most economically important viral pathogens of wheat in the Great Plains region with an estimated annual yield loss of ~5.44 million quintals valued at $120 million (at $6/27.2 kg) [9,10], and these losses are often expressed as severe infections with up to 100% yield loss in localized areas.

Biology and genetics of wheat curl mites

WCMs, like other eriophyid mites, are much smaller in size than other arthropod vectors with an average length of ~200 μm (Figure 1) [21,22]. The short stylets of WCMs limit the depth of penetration of the plant to about 5 μm; thus, they can penetrate only the epidermis of the plant [23,24]. Besides their size, the most distinctive feature of WCMs is that they possess only two pair of well-developed legs located near the front end of their elongated body (Figure 1). WCMs have a relatively simple life cycle. After hatching from the egg, they undergo two immature stages (larval and nymphal), each lasting about 2–3 days, before becoming adults. Between each of these stages, the mites spend a short quiescent period (<1 day) before molting to the next stage. The time period from egg to adult requires 7–9 days. Eriophyid mites undergo arrhenotokous reproduction with the males being haploid and a single female capable of establishing a colony [8]. The rapid developmental rate coupled with this reproductive strategy results in tremendous reproductive potential. The WCM relies primarily on wind currents for movement, and the spread of mite-transmitted viruses benefits from the mite's extreme reproductive capabilities.

Figure 1



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Scanning electron micrograph of an adult wheat curl mite (*Aceria tosichella* Keifer) feeding on a wheat leaf. Note that two pairs of legs attached to the front end of the elongate mite and also see a pair of eggs located next to the mite.

Analyses of portions of ribosomal ITS1 and mitochondrial DNA sequences of WCM populations from Australia and the Great Plains demonstrated the presence of two comparable genotypes, each present in both Australia and North America [25,26]. Hein *et al.* [26] identified the two genotypes of WCMs from five populations collected across the Great Plains: Type 1 (collected from Kansas, Texas, Montana and South Dakota) and Type 2 (collected from Nebraska). Additional work has shown that these genotypes are both commonly present across the Great Plains [27], and little evidence has been found in either North America or Australia to suggest extensive interbreeding of these two genotypes even though they commonly occur together [25–27]. These two genotypes have also commonly been found in Europe and other global regions [28]; however, Skoracka *et al.* [29] and Szydło *et al.* [30] have revealed even greater genetic diversity in WCMs from Poland and Turkey and identified the wheat curl mite as a cryptic species complex.

The genetic differences in WCM populations correspond to variable transmission efficiencies of different wheat viruses. For example, the same five WCM populations identified by Hein *et al.* [26] from the Great Plains areas differentially transmitted HPWMoV isolates, but not WSMV [31]. However, Wosula *et al.* [32] found both Type 1 and Type 2 mites from the Great Plains to be effective at transmitting WSMV, but Type 2 mites consistently transmitted WSMV at higher rates. Alternatively, Schiffer *et al.* [33] found that Type 2 mites in Australia transmitted WSMV well, but Type 1 mites were not able to transmit WSMV. McMechan *et al.* [17] showed that Type 2 but not the Type 1 WCM effectively transmitted TriMV. WCMs exhibited mutualistic (Type 2 only) and antagonistic (both Type 1 and 2) effects on WCM reproduction with WSMV and TriMV, respectively, in infected wheat [17,27,34]. The observed negative effects of TriMV infection on WCM population might explain the lower incidence of TriMV most often found in growers' fields [35]. Additional work on comparison of transmission capabilities of various genotypes of wheat curl mites across world regions or continents would be ideal, especially if they could be tested with the same virus isolates for best comparison.

WSMV and its transmission characteristics by WCM

WSMV is the type species of the genus *Tritimovirus* within the family *Potyviridae* [36]. WSMV virions are flexuous filaments (690–700 nm × 11–15 nm) (Figure 2a) encapsidating a single positive-strand genomic RNA of 9384 nucleotides. The genomic RNA is polyadenylated at the 3′ end and probably with a VPg (virus protein linked