

Resistance to the wheat curl mite and mite-transmitted viruses: challenges and future directions

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Wheat curl mite (WCM) is the only known arthropod vector of four wheat viruses, the most important of which is *Wheat streak mosaic virus* (WSMV). Host resistance to WCM and WSMV is limited to a small number of loci, most of which are introgressed from wild relatives and are often associated with linkage drag and temperature sensitivity. Reports of virulent WCM populations and potential resistance-breaking WSMV isolates highlight the need for more diverse sources of resistance. Genome sequencing will be critical to fully characterize the genetic diversity in WCM and WSMV populations to better understand the incidence of WCM-transmitted viruses and to evaluate the potential stability of resistance genes. Characterizing host resistance genes will help build a mechanistic understanding of wheat-WCM-WSMV interactions and inform strategies to identify and engineer more durable resistance sources.

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Introduction

Globally, common wheat (*Triticum aestivum* L.) provides approximately 20% of the calories and proteins consumed in the human diet [1] and in the United States, ranks third among field crops in planted acreage, production, and gross farm receipts [2]. Among arthropod pests and phytopathogens that reduce wheat yields, one of the most important is the wheat curl mite, (WCM), *Aceria tosichella* Keifer (Acari: Eriophyidae) which affects wheat production in the Americas, Australia, Europe, and Asia [reviewed in Refs. [3,4,5]]. Eriophyid mites are microscopic arthropods

about 0.2 mm in length that usually infest young wheat leaves causing them to curl, hence the name wheat curl mite (Figure 1a). The mite causes direct physical damage by feeding, which can cause mild yield reductions [6]. More importantly, the WCM is the sole vector of four viruses, *Wheat streak mosaic virus* (family *Potyviridae*/genus *Tritimovirus*; WSMV) [7], *Triticum mosaic virus* (*Potyviridae*/*Poacevirus*; TriMV) [8], *High Plains wheat mosaic virus* (*Fimoviridae*/*Emaravirus*; HPWMoV) [9], and *Brome streak mosaic virus* (*Potyviridae*/*Tritimovirus*; BrSMV) [10]. Because of their common transmission and the difficulty in distinguishing symptoms, these diseases are commonly known as the wheat streak mosaic (WSM) complex. Of these viruses, WSMV is considered to have the greatest economic impact worldwide whereas BrSMV is only found in Europe and does not cause economic losses [11,12]. Plants infected with WSMV show yellow to light green streaks that coalesce to form a mosaic pattern (Figure 1b). Symptoms are more severe if plants are infected early in their development and can include stunting, poor fertility/sterility, and reduced grain set [reviewed in Refs. 3,13]. Although single infections of WSMV occur more frequently compared to TriMV and HPWMoV, co-infections by two or all three viruses are common, which can exacerbate yield losses [14]. Average yield losses range from 2 to 3%, but localized affected areas can have much more dramatic losses of up to 100% [15]. In Kansas, the statewide five-year average yield loss to the wheat crop is 1.74%, but in 2017, reached 5.6%, resulting in \$76.8 million lost revenue for Kansas wheat farmers [16].

The management of WCM and the disease complex has focused on an Integrated Pest Management (IPM) approach that combines host plant resistance to both mite and viruses with cultural practices such as controlling over-summering alternate hosts such as volunteer wheat, corn and wild grassy weeds [17]. These hosts serve as a ‘green bridge’ refuge for WCMs between harvesting of the mature wheat and the newly emerging winter wheat in fall. However, mites can infest over 90 other grass species and can travel distances of up to 3.3 km in wind currents during a single fall season [18], meaning that the effective control of secondary hosts is often impractical [11]. Delayed planting can also reduce fall infections by minimizing the overlap between the wheat crop and secondary hosts [19]. However, due to limited soil moisture in dryland production systems and time constraints associated with increasing farm size, it is often impractical to delay planting. Chemical control strategies are ineffective because WCM occupies secluded areas on the plant such as leaf sheaths and rolled and curled leaves [11] and there are no cost-effective miticides for use

Figure 1



Wheat curl mite (WCM) and *Wheat streak mosaic virus* (WSMV) symptoms. **(a)** Eggs, juveniles and adult WCMs on wheat leaf, **(b)** WSMV symptoms on wheat leaf, and **(c)** response of CSU varieties, Whistler (left) that harbors the *Cmc_{TAM112}* gene compared to Sunshine (center) and CO 13D1638 (right) that do not contain any resistance genes, to natural WSMV infection in an irrigated variety trial in Yuma, Colorado. Photos by T. Albrecht.

in wheat [20]. Moreover, there is accumulating evidence for apparent adaptation of mites to resistance genes [21,22] and novel resistance-breaking virus isolates [23,24,25]. Hence, there is an urgent need for alternative and effective control strategies for this complex pathosystem. In this review, we will highlight recent progress and future challenges for understanding host resistance to mites and viruses, with a focus on genetic diversity and its implications.

Host plant resistance to WSMV and WCM

Because of the difficulties of WCM management, developing crop varieties carrying genetic factors that either confer virus resistance and/or reduce WCM reproductive success are likely to be the most effective strategies to reduce yield losses from this disease complex. However, only two significant loci for WSMV resistance were detected in a winter wheat association mapping panel [26], highlighting the

limited number of resistance loci in common wheat cultivars. Currently, there are just four identified sources of genetic resistance to the virus complex; *Wsm1*, *Wsm2*, *Wsm3* and *c2652*. Both *Wsm1* and *Wsm3* were transferred into common wheat by Robertsonian translocations from *Thinopyrum intermedium* [27–30]. *Wsm2* was identified in Colorado State University breeding line CO960293-2 [31] and, most recently, resistance locus *c2652* was isolated from a hard red spring wheat population selected in Canada [32]. In field trials, all four loci provide strong resistance to WSMV, while *Wsm1* and *Wsm3* also confer resistance to TriMV [33–36]. There has been less attention paid to identifying resistance alleles for HPWMoV or BrSMV, likely due to their relatively lesser impact on wheat production. One drawback of these resistance loci is their temperature sensitivity. All four loci are more effective at 18°C than at 24°C or above, although the resistance conferred by *Wsm3*

and *c2652* is more resilient at higher temperatures than either *Wsm1* or *Wsm2* [35]. Since the discovery of these resistance genes, *Wsm1* has been introgressed into the commercial common wheat variety Mace, and *Wsm2* has been introgressed into several common wheat varieties, including RonL [PI 648020], Clara CL [PI 665948], Oakley CL [PI 670170], Joe [PI 676270], Snowmass [41], and Snowmass 2.0 [PI 691605]. One reason *Wsm1* is not more widespread in elite cultivars may be the linkage drag often associated with alien introgressions, though efforts have been undertaken to reduce the size of the introgressed segment [37]. In the absence of viral pressure, *Wsm1* confers a yield penalty in some environments [36,38], although not others [34]. *Wsm2* exhibited no yield drag in Australian national field trials [35], possibly because it most likely originated in a common wheat background. Germplasm carrying *Wsm3* has only very recently been made available, and it is not known if linkage drag will be an issue.

There are four characterized Curl Mite Colonization (CMC) loci that confer resistance to WCM, all derived from alien introgressions. The mite-resistant varieties inhibit the reproductive potential of mites, thereby reducing the spread of WSMV [22]. Two independent dominant resistance loci, *Cmc1* and *Cmc4*, were transferred from *Aegilops tauschii*, onto wheat chromosome arm 6DS [39,40]. It remains unclear whether a resistance locus mapped to chromosome arm 6DS in the variety ‘TAM112’ (*Cmc_{TAM112}*) is allelic to *Cmc4* or an independent *Cmc* locus [26*]. *Cmc2* is derived from an alien introgression from *Thinopyrum ponticum* to chromosome arm 6DL [41] and *Cmc3* was introgressed to common wheat as part of the 1AL:1RS wheat-rye translocation [42,43], and later transferred to the variety ‘TAM107’ [44]. A distinct 1AL:1RS wheat-rye translocation line ‘Salmon’ also contains a segment of rye DNA that confers WCM resistance [45,46]. The deployment of these alleles in elite varieties has been facilitated by the development of closely linked, inexpensive KASP markers specific for the alien introgression [26*,47*]. Although WCM resistance varies by host genotype, these alleles are effective in reducing symptoms of mite damage under field conditions (Figure 1c [33,48,49]). However, because each locus is derived from an alien introgression, it will be important to test the performance of varieties carrying these resistance genes in replicated field trials.

Genetic diversity and its implications

The effectiveness of host genetic resistance also varies according to genetic diversity in both WCMs and the viruses. There is great genetic variation among WCM populations including cryptic diversity (i.e., morphologically similar but genetically different individuals) as determined by analysis of mtDNA and nuclear markers [50]. For instance, Skoracka *et al.* [51*] identified at least 16 different genotypes with numerous host associations and specificity in Poland. In North America, only two genetically distinct types of WCM have been characterized: Type 1, initially

identified from South Dakota, Kansas, Montana, Nebraska and Texas, and Type 2, from Nebraska [52]. These two genotypes have also been found in South America, Europe and Australia [reviewed in Refs. [4*,11]]. Both genotypes occur in mixed populations in wheat-producing areas of the U.S. Great Plains [52,53**] and Australia [54], but there is no evidence of genetic exchange between the two genotypes, even when both were found co-existing on the same plant [54]. Indeed, WCM is thought to reproduce by arrhenotokous parthenogenesis, where unfertilized eggs develop into males and fertilized eggs develop into females resulting in a female-biased sex ratio and inbreeding within mite populations [55]. These findings highlight the importance of understanding mite species diversity in each area and the implications for pest management. The genetic diversity in WCM corresponds to differential virus transmission abilities and responses of mites to different host resistance genes. The Type 2 mites have a higher reproductive capacity when infected with WSMV and transmit WSMV and TriMV more efficiently than Type 1 mites [56,57]. The Type 1 mites are avirulent to *Cmc3* whereas Type 2 mites are virulent to *Cmc3* [21]. More recently, additional WCM genotypes have been identified in the Great Plains and the variation in their spatio-temporal distribution was found to be influenced by precipitation and landscape composition [53**]. One factor contributing to the increase in WCM diversity may be the growing number of wheat varieties containing resistance genes and WCM adapting to this resistance [58]. Hence, the characterization of WCM diversity will be critical to monitor the emergence of resistant populations and understand their ability to overcome host resistance.

The WSMV populations are also complex with over 78 known isolates, although different genotypes rarely occur in the same plant [59–61]. Based on whole genome sequencing, these genotypes can be separated into three clades, A, B and D [60]. Clade A represents isolates from Mexico, known as El Batán and clade B contains isolates from Europe, Russia, Turkey and Iran [62]. Within clade B isolates, there was sequence diversity between crop (wheat) and non-crop (other grass) hosts, hence a subtype of grass-associated isolates, B1 was proposed [63]. Clade D includes isolates from North and South America, Australia, and Turkey [59,64]. Recently, shotgun metagenomic sequencing revealed novel WSMV isolates from Colorado [23]. One of these isolates was collected from ‘Snowmass 2.0’, a variety carrying *Wsm2*, and another isolate had 100% sequence similarity to a potentially resistance-breaking strain reported from Kansas [24*]. However, in both studies the presence of other pathogens including viruses could not be ruled out and may have contributed to the breakdown of the resistance. A *Wsm2*-breaking WSMV variant was also isolated from *Setaria viridis* [25]. The discovery of these novel WSMV isolates highlights the challenges of breeding for durable resistance and the limitations of current options for genetic resistance. The risk of resistance breakdown may be

reduced by pyramiding multiple WCM and WSMV resistance loci into a single wheat variety, or by combining genetic resistance with broader cultural practices such as managing ‘green bridge’ hosts and delaying planting date as part of a multi-faceted IPM strategy to control this disease complex. There is also genetic diversity in HPWMoV populations across the U.S., with two distinct groups of isolates [65], while a third group with two new HPWMoV variants was recently identified in Colorado [23]. This suggests greater diversity in HPWMoV populations across the U.S. In contrast, there is limited sequence variability in field isolates of TriMV from the Great Plains suggesting that the populations are highly homogenous [66].

Future research directions

A priority for future research will be to characterize *Cmc* and *Wsm* resistance genes, providing opportunities to identify and engineer novel resistance alleles acting in the same genetic and metabolic pathways. The identification of these genes will be invaluable for researchers to understand the mechanisms by which *Cmc* alleles impact WCM behavior and reproduction, and how *Wsm* alleles reduce viral replication. This knowledge will also help us evaluate the impact of genetic variation in WCM populations and WSMV isolates. High-resolution genotypic screens of both mite and virus populations will be a powerful approach to reveal the full extent of genetic diversity in worldwide mite and virus populations and to be better able to respond to the emergence of virulent WCM populations and novel virus isolates. To date, no resistance gene has been cloned, although characterization of the *Wsm1* and *Wsm2* loci reveal that they both prevent the long distance transport of WSMV [67] and are ineffective at field temperatures above 24°C [38,68], providing clues to the identity of the causative gene. A set of characterized resistance alleles will also help breeders make more informed decisions when stacking alleles. For example, the Colorado State University common wheat variety ‘Guardian’ carries both *Wsm2* and *CmcTAM112* loci, and exhibits stronger WSMV resistance than Snowmass 2.0, which only carries *Wsm2* [23]. The combination of resistance alleles acting in complementary pathways could be a powerful approach to confer more durable resistance in elite wheat varieties. In addition, cloning resistance genes will facilitate searches for novel genetic variation. In cases where resistance genes are present in the common wheat gene pool, targeted searches across broader germplasm collections may reveal previously unidentified genetic variation that can be directly utilized in wheat breeding programs. Alternatively, CRISPR-based genome editing provides the means to induce a specific functional variant directly in elite wheat genetic backgrounds [69], although it is important to note that current regulatory restrictions limit the application of this technology for plant breeding in some parts of the world.

Novel molecular tools offer the opportunity to engineer allelic variation for WSMV and WCM resistance that may

not exist in common wheat or its wild relatives. In other plant systems, natural variation in genes encoding the eIF4E protein complex confer resistance to potyviruses [70]. In wheat, using RNAi to suppress eIF4E homologs [71*], as well as to directly target viral RNA for degradation [72], confers WSMV and TriMV resistance, although restrictions on the use of transgenic wheat in agriculture and the potential yield penalties of these lines may restrict their use. A more effective approach may be to use base editing [73] or prime editing [74] to engineer targeted recessive resistance alleles on all three homoeologous copies of *eIF4E* family genes, informed by characterized natural resistance alleles in other plant species. Finally, CRISPR-Cas13-derived RNA editors have recently shown their potential to confer *Potyvirus* resistance by targeting and degrading viral RNA *in planta* [75*]. Comprehensive characterization of the genetic diversity in viral populations will facilitate the design of Cas13 constructs to target all known viral strains in a target environment. Furthermore, multiplexing constructs to target multiple sites in a single virus genome, or to target multiple viruses, provides an exciting opportunity to confer broad and durable resistance to the WSM disease complex.

Conflict of interest statement

Nothing declared.

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