Wheat curl mite, *Aceria tosichella*, and transmitted viruses: an expanding pest complex affecting cereal crops

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Abstract The wheat curl mite (WCM), *Aceria tosichella*, and the plant viruses it transmits represent an invasive mite-virus complex that has affected cereal crops worldwide. The main damage caused by WCM comes from its ability to transmit and spread multiple damaging viruses to cereal crops, with *Wheat streak mosaic virus* (WSMV) and *Wheat mosaic virus* (WMoV) being the most important. Although WCM and transmitted viruses have been of concern to cereal growers and researchers for at least six decades, they continue to represent a challenge. In older affected areas, for example in North America, this mite-virus complex still has significant economic impact. In Australia and South America, where this problem has only emerged in the last decade, it represents a new threat to winter cereal production. The difficulties encountered in making progress towards managing WCM and its transmitted viruses stem from the complexity of the pathosystem. The most effective methods for minimizing losses from WCM transmitted viruses in cereal crops have previously focused on cultural and plant resistance methods. This paper brings

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together information on biological and ecological aspects of WCM, including its taxonomic status, occurrence, host plant range, damage symptoms and economic impact. Information about the main viruses transmitted by WCM is also included and the epidemiological relationships involved in this vectored complex of viruses are also addressed. Management strategies that have been directed at this mite-virus complex are presented, including plant resistance, its history, difficulties and advances. Current research perspectives to address this invasive mite-virus complex and minimize cereal crop losses worldwide are also discussed.

**Keywords** Eriophyidae · Plant virus · Mite vector · Cereal · Grasses · Poaceae · Invasive pest complex

Introduction

Aceria tosichella Keifer, commonly known as wheat curl mite (WCM), is tiny and wormlike (Fig. 1). It is less than 0.3 mm long and belongs to the superfamily Eriophyoidea (Keifer 1969). This mite can cause direct yield loss to wheat, *Triticum aestivum* L. (Poaceae) (Harvey et al. 2002). However, the main damage caused by WCM extends from its ability to transmit and spread multiple damaging viruses to a range of cereal crops (Oldfield and Proeseler 1996). At least four viruses have been reported as being transmitted by WCM: *Wheat streak mosaic virus* (WSMV) (Slykhuis 1955), *Wheat mosaic virus* (WMoV) (formerly known as *High plains virus* [HPV]) (Hadi et al. 2011; Jensen and Lane 1994; Jensen et al. 1996; Seifers et al. 1997; Skare et al. 2006), *Brome streak mosaic virus* (BrSMV) (Goetz and Maiss 1995) and *Triticum mosaic virus* (TriMV) (Seifers et al. 2008, 2009).

Wheat curl mite and the range of viruses it transmits, forms an invasive mite-virus complex affecting cereal crops throughout most of the world. Hence, this represents a significant threat to non-affected areas. Although this mite-virus complex has been of concern to cereal growers and studied by researchers for at least six decades, it continues to represent a challenge in terms of control measures. In North America, WCM and its associated viruses still have significant economic impact (e.g. Velandia et al. 2010). In Australia and South America, where these organisms have emerged in the last decade, they represent a new threat to cereal production (Coutts et al. 2008a, b; Dwyer et al. 2007; Ellis et al. 2003a; Truol and Sagadin 2008a; Truol et al. 2004). Although WSMV and WMoV are the most important and damaging viruses that are transmitted by WCM, a new virus, TriMV, has recently been confirmed to also be vectored by the mite (Seifers et al. 2008, 2009; Stephan et al. 2008). This has considerably increased the complexity and severity of the pathosystem as a result of the occurrence of mixed infections (de Wolf and Seifers 2008).

The exact origin of WCM is unknown and pathways that have facilitated its dissemination worldwide are uncertain. Additionally, there is little information about WCM colonization routes because first occurrence records of this mite in each country or continent are unreliable and do not allow for elaborate historical hypotheses. It is possible that WCM has been present in many areas for a long time but had remained undetected until one or more of the transmitted viruses were reported (e.g. Jeżewska and Wieczorek 1998; Navia et al. 2006).

This paper reviews biological and ecological aspects, including: taxonomic status, distribution, host range, damage symptoms and economic impact of WCM and its main
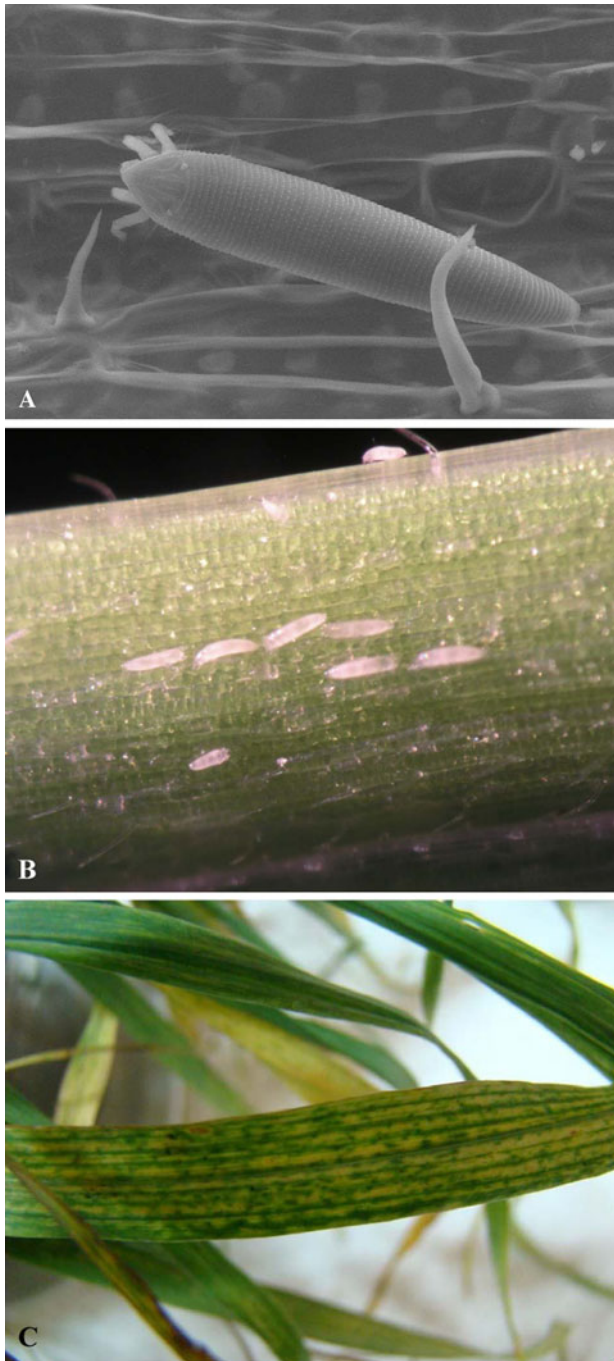
Fig. 1 Wheat curl mite (WCM), *Aceria tosichella*, and its main transmitted virus, *Wheat streak mosaic virus* (WSMV). (**A**) WCM dorsal view (SEM micrograph by Magdalena Gawlak, Institute of Plant Protection, Poznan, Poland); (**B**) WCM colony on leaves; (**C**) WSMV symptoms on wheat, Balcarce, Argentina

transmitted viruses. We also address the epidemiological relationships involved in this vectored complex of viruses. Management strategies are presented, including plant resistance and its history, difficulties and advances. Current research perspectives aimed at addressing this invasive mite-virus pest complex in order to minimize cereal crop losses and further spread worldwide are also discussed.

Aceria tosichella: taxonomic history and uncertainties

The identity of WCM has a long history of taxonomic uncertainties (Frost and Ridland 1996). This species was originally described by Keifer (1969) from wheat collected in the former Yugoslavia. It is morphologically very similar to *Aceria tulipae* (Keifer), which was first described from tulip bulbs originating from The Netherlands and collected during 1937 in California, USA (Keifer 1938, 1969). For many years, *A. tosichella* had often been misidentified as *A. tulipae*, the latter species supposedly also infesting wheat (in addition to the Liliaceae) and considered to be the vector of WSMV (e.g. Keifer 1953; Slykhuis 1955). Since most eriophyoid species are very host specific, the occurrence of the same mite on plants belonging to two completely different families, i.e. Poaceae and Liliaceae, prompted detailed biological and morphological studies. Shevtchenko et al. (1970) showed that the eriophyoid species found on Liliaceae was morphologically and biologically different from the species inhabiting wheat and described this grass-feeding mite as *Aceria tritici* Shevtchenko, occurring on four grass species in Uzbekistan. However, a few months before Shevtchenko's description was published in 1970, Keifer (1969) had already described *A. tosichella* to accommodate the wheat-feeding species that was associated with WSMV. Therefore, *A. tritici* was designated as a junior synonym of *A. tosichella* by Amrine and Stasny (1994). However, the name *A. tulipae* continued to be erroneously used for the eriophyoid species associated with wheat, especially by North American researchers until at least 1995 (Harvey and Livers 1975; Harvey et al. 1995a, b). The historical use of these names has been documented by Amrine and Stasny (1994), Frost and Ridland (1996), Halliday and Knihinicki (2004) and Kozlowski (2000).

Although the name of *A. tosichella* had already been widely accepted for the grass species instead of *A. tulipae*, uncertainties in the taxonomic status of this taxon still needed to be clarified. Hence, an important question arose—is *A. tosichella* a complex of species or a set of strains?

Most eriophyoid mite species are highly host-specific, being restricted to a single host plant or a few host plant species within a single plant genus (Oldfield and Proeseler 1996; Skoracka et al. 2010). *Aceria tosichella* is regarded as an exception among eriophyoid mites concerning the pattern of host-plant utilization since around 90 grass species have been reported as hosts (Amrine 2003). The worldwide distribution and air mode dispersal shown for WCM (Amrine 2003; Nault and Styer 1969) supports the finding that the mite is a plant host generalist which utilizes a wide range of hosts (Sabelis and Bruin 1996).

However, suggestions against the low plant host specificity of *A. tosichella* have been proposed since the early 1950s. Gibson (1957) and Slykhuis (1955) indicated the presence of host-adapted biological strains of WCM based on performance in transplants between plant hosts. Del Rosario and Sill (1965) demonstrated that there were various physiological strains of WCM which had different capabilities of surviving on wheat and *Agropyron smithii* Rydb. (western wheat grass), but could also adapt to new hosts. Specific strains of WCM that may have been different species were also noted by Connin (1956b).

Some evidence about the existence of strains of WCM had also been obtained during studies on wheat resistance to this mite and its ability to transmit viruses. Harvey et al. (1995a) found that WCM can develop a resistant strain, indicating the presence of a biotype. Harvey et al. (1995b, 1999) observed that collections of WCM (from the USA: Kansas, Nebraska, Montana, South Dakota and Texas; from Canada: Alberta) varied in their degree of virulence to different sources of resistant wheat, and according to the responses of these mite colonies, they were classified into three biotypes. Furthermore, studies by Malik et al. (2003a) showed the various responses of these three mite biotypes to numerous lines of *Aegilops tauschii* Coss. It has also been shown that strains of WCM varied in their ability to transmit WSMV and WMoV (Seifers et al. 2002). Harvey et al. (2001) suggested that strains of WCM may vary in their ability to survive or increase in number on potential hosts.

Morphological observations also have indicated the divergence within WCM. Sukhareva (1981) reported a wide variation in the morphological traits for *A. tosichella*. Frost (1995) suggested that two distinct forms of WCM on wheat in Australia could also correspond to two species. Follow-up work by Frost and Ridland (1996), Schicha (unpublished data, NSW Agriculture, 1985), Knihinicki (2007; unpublished data, NSW Agriculture 2003), Halliday and Knihinicki (2004) and Knihinicki and Halliday (2005) implied that *A. tosichella* is likely to be a complex of closely related species in Australia. Skoracka and Kuczyński (2006) described morphological variation among host-populations of WCM and suggested that these differences could be due to the presence of strains or species.

Because of the fast development of DNA-based techniques in recent years, molecular markers have become a powerful tool for helping to resolve many taxonomic issues. It has been shown that some mitochondrial and nuclear markers can serve as DNA barcodes for the identification of species in animals (Hebert et al. 2003; Sonnenberg et al. 2007), including eriophyoid mites (Carew et al. 2004; Kumar et al. 1999; Navajas and Navia 2010; Skoracka and Dabert 2010). This is also true for *A. tosichella.* Carew et al. (2009) used the mitochondrial 16S rRNA gene and two nuclear markers (internal transcribed spacer 1 and adenine nucleotide translocase) and showed that WCM from wheat and several other grass hosts in Australia consists of at least two lineages that may represent different but closely-related species. No evidence of genetic exchange between these lineages was seen. The average sequence divergence separating both WCM lineages for 16S rRNA (4.4 %) was only marginally lower than the sequence divergence distinguishing other *Aceria* species from WCM lineages (5.0–6.5 %) (Carew et al. 2009). The most recent studies presented in the XIII International Congress of Acarology in 2010 (Recife, Brazil) also supported indications that WCM may represent a species complex. They were based on experimental and molecular studies conducted on populations from different grass species in Poland (Skoracka and Kuczyński 2012) and on morphological and molecular analyses including different host populations from Europe, South America and Australia (Skoracka et al. 2012).

A deeper knowledge of the systematics of WCM is essential in order to advance the prevention and management of the WCM-virus complex. Evidence that WCM actually represents a complex of closely related species and/or a set of strains, and is not an extremely generalist feeder which infests numerous grass species, is very clear. However, it is necessary to delve into several aspects of each strain/species that comprises or has been identified as *A. tosichella*. This includes: its genetic and phenotypic traits, distribution, ability to transmit plant viruses, relationship with virus lineages, host range and populational growth rate on different hosts, and the resistance/susceptibility of cereal

varieties or germplasm lines to them. WCM strains/species can present different answers to cereals resistant genes/lineages as shown by Harvey et al. (1995b, 1999). It would be important to know the level of susceptibility of the various WCM strains/species to the cereals resistance genes used in breeding. The epidemiology of the diseases caused by WCM-transmitted viruses can be strongly influenced by the host range of the vector and its intrinsic rate of increase on each host (see section 'Ecological factors affecting wheat curl mite dispersal and virus epidemiology'). WCM strains/species probably present a different host range or population growth on each host. The presence of WCM strains/species with low efficiency in virus transmission could explain why in some areas WCM transmitted viruses are not of concern. Therefore, it is extremely important to be able to distinguish between WCM strains and to detect those that are the most effective virus vectors.

Distribution and host plants of the wheat curl mite

Wheat curl mite is widespread around the world (Table 2) being present in Europe (Oldfield and Proeseler 1996), North America (Amrine 2003; Hoffmann and Lopez-Campos 2000; Oldfield and Proeseler 1996), Asia (Oldfield 1970), Middle East (Denizhan et al. 2010; Makkouk and Kumari 1997; Oldfield 1970), Oceania (Halliday and Knihinicki 2004), and South America (Castiglioni and Navia 2010; Navia et al. 2006; Pereira et al. 2009). It is likely that WCM also occurs in both North (Algeria) and sub-Saharan Africa (Zambia) since the presence of some WCM transmitted viruses have been confirmed in these regions (Benmokhtar and Yahia 2009; Kapooria and Ndunguru 2004; Slykhuis 1961, 1962). However, WCM per se has not yet been collected from Africa (see Table 2). WCM occurs mainly on wheat, but populations can develop on other cereals, including *Avena sativa* L. (oats), *Hordeum vulgare* L. (barley), *Pennisetum glaucum* (L.) R.Br. (pearl millet), *Zea mays* L. (corn), and *Secale cereale* L. (rye). This mite has also been reported from various other grasses, including cultivated and uncultivated grasses including weeds of minor importance (Amrine 2003; Jeppson et al. 1975). Almost 90 grass species have been reported as host plants of WCM in various countries (Table 1).

Eurasia

Wheat curl mite was described by Keifer (1969) from specimens found on leaves of wheat in the former Yugoslavia (presently Serbia and Montenegro) in southern Europe. Despite *A. tosichella* having been reported officially in Eurasian countries since 1969, this mite actually was noted even earlier, for example, on wheat in the UK (del Rosario and Sill 1965). However, at the time it had been referred to as *A. tulipae*. Other early reports about the occurrence of *A. tosichella* in wheat production areas in Europe were from Bulgaria, Germany, Moldova, Romania and Russia (Brakke 1971; Juretič 1979; Lapierre 1980; Oldfield 1970; Oldfield and Proeseler 1996; Proeseler 1972; Shevtchenko et al. 1970; Slykhuis 1953). Wheat infested with WCM has also been found in Krasnoyarsk Krai in Russia, in Uzbekistan and the Middle East including Jordan and Syria (Makkouk and Kumari 1997; Oldfield 1970; Shevtchenko et al. 1970). In Asia, WCM has been reported from Mongolia (Skoracka et al. 2001), Xinjiang and Tibet in China (Hong and Zhang 1996; Lin et al. 1987 in Oldfield and Proeseler 1996) and India (Oldfield 1970).

Information about the occurrence of WCM has largely been obtained from surveys of wheat crops. Faunistic and ecological studies on other grass host species, apart from wheat, as potential hosts for WCM have been conducted only in the UK, Hungary, Poland and

Table 1 Grasses reported as host plants for wheat curl mite, *Aceria tosichella*, in different countries (not including the two most commonly cultivated cereals–wheat and corn)

Host plant–scientific name	Host plant–common name	Country	References
Aegilops cylindrica Host.	Goat grass	USA	Connin (1956b)[a,b], Somsen and Sill (1970)[a]
Agropyron cristatum (L.) Beauv.	Crested wheat grass	Mongolia	Skoracka et al. (2001)
Agropyron smithii Rydb.	Western wheat grass	USA	Connin (1956a, b)[a], Keifer (1953)[a]
Agropyron sp.	Wheat grass	Brazil, USA	Keifer (1953)[a], Pereira et al. (2010)
Agrostis capillaris L.	Common bentgrass	Poland	Skoracka (2004)[c]
Alopecurus pratensis L.	Meadow foxtail grass	Poland	Skoracka and Kozlowski (2002)
Andropogon bicornis L.	West India foxtail grass	Brazil	Pereira et al. (2010)
Arrhenatherum elatius (L.) Beauv. ex J. & C. Presl	Oat grass	Hungary, Poland, USA	Connin (1956b)[a,b], Golya et al. (2002), Skoracka (2004)
Avena fatua L.	Common wild oat	Australia	GRDC (2001), Halliday (2006)
Avena pubescens Huds.	Downy oat grass	Australia	GRDC (2001), Halliday (2006)
Avena sativa L.	Oat	Brazil, USA	Pereira et al. (2010), Somsen and Sill (1970)[a]
Avena sterilis L.	Animated oat	Australia	GRDC (2001), Halliday (2006)
Avenula pratensis (L.) Dumort.	Meadow oat grass	Poland	Skoracka and Kozlowski (2002)
Avenula pubescens (Huds.) Dumort.	Hairy oat grass	Poland	Skoracka and Kozlowski (2002), Skoracka (2004)
Bothriochloa macra (Steud.) S.T. Blake	Red grass	Australia	GRDC (2001), Halliday (2006)
Bouteloua hirsuta Lag.	Hairy grama	USA	Connin (1956b)[a,b], Somsen and Sill (1970)[a]
Brachiaria decumbens Stapf	Surinam grass, decumbens	Brazil	Pereira et al. (2010)
Brachiaria plantaginea (Link) Hitchc.	Alexander grass	Brazil	Pereira et al. (2010)
Bromus catharticus Vahl	Australian oat	Australia	GRDC (2001), Halliday (2006)
Bromus diandrus Roth	Great brome grass	Australia	GRDC (2001), Halliday (2006)
Bromus erectus Huds.	Erect brome	Poland	Skoracka and Kozlowski (2002)
Bromus hordeaceus L. (cited as *B. mollis* L.)	Soft brome	Australia, Poland	GRDC (2001), Halliday (2006), Skoracka and Kozlowski (2002)

Table 1 continued

Host plant—scientific name	Host plant—common name	Country	References
Bromus inermis Leyss.	Smooth brome	Poland, USA	Connin (1956b)[a,b], Skoracka (2004)
Bromus japonicus Thunb. ex Murray	Japanese brome	USA	Somsen and Sill (1970)[a]
Bromus racemosus L.	Smooth brome	Poland	Skoracka and Kozlowski (2002)
Bromus secalinus L.	Cheat grass	USA	Somsen and Sill (1970)[a]
Bromus sp.	Brome	Brazil	Pereira et al. (2010)
Bromus sterilis L.	Sterile brome	Poland	Skoracka and Kozlowski (2002)
Bromus tectorum L.	Downy brome	USA	Somsen and Sill (1970)[a]
Bromus unioloides (Kunth)	Rescue grass	Brazil, Uruguay	Castiglioni and Navia (2010), Pereira et al. (2010)
Buchloe dactyloides (Nutt.) Engelm.	Buffalo grass	USA	Somsen and Sill (1970)[a]
Calamagrostis arundinacea (L.) Roth	Tall fescue	Poland	Skoracka (2004), Skoracka and Kozlowski (2002)
Calamagrostis epigeios (L.) Roth	Chee reed grass	Poland	Skoracka (2004)[c]
Cenchrus pauciflorus Benth.	Sandbur	USA	Connin (1956b)[a,b]
Chascolytrum subaristatum (Lam.) Desv.		Brazil	Pereira et al. (2010)
Chloris polydactyla (L.) Sw.	White grass	Brazil	Pereira et al. (2010)
Corynephorus canescens (L.) Beauv.	Grey hair grass	Poland	Skoracka (2004), Skoracka and Kozlowski (2002)
Cynodon dactylon (L.) Pers.	Bermuda grass	Australia[d], USA	GRDC (2001), Halliday (2006), Somsen and Sill (1970)[a]
Dactylis glomerata L.	Cocks foot, orchard grass	Australia, Canada, Poland	GRDC (2001), Halliday (2006), Peterson (1989), Skoracka and Kozlowski (2002)
Digitaria horizontalis Willd.	Jamaican crab grass	Brazil	Pereira et al. (2010)
Digitaria insularis (L.) Fedde.	Sour grass	Brazil	Pereira et al. (2010)
Digitaria ischaemum (Schreb.) Muhl.	Smooth crab grass	USA	Connin (1956a, b)[a]
Digitaria sanguinalis (L.) Scop.	Crab grass, hairy crab grass, summer grass	Australia, USA	Connin (1956b)[a,b], GRDC (2001), Halliday (2006)

Table 1 continued

Host plant—scientific name	Host plant—common name	Country	References
Echinochloa crus-galli (L.) Beauv.	Barnyard grass, cockspur grass	USA	Somsen and Sill (1970)[a]
Eleusine indica (L.) Gaertn.	Crowsfoot grass	Australia	GRDC (2001), Halliday (2006)
Elymus canadensis L.	Canada wild rye	USA	Connin (1956a, b)[a], Conley et al. (2003)
Elymus repens (L.) Gould	Quackgrass	Poland, USA	Keifer (1954)[a], Kozlowski (2000), Somsen and Sill (1970)[a]
Elymus virginicus L.	Virginia wildrye	USA	Somsen and Sill (1970)[a]
Eragrostis cilianensis (All.) Vignolo ex Janch	Love grass, stink grass	Australia, USA	Connin (1956b)[a,b], GRDC (2001), Halliday (2006)
Euchlaena mexicana Schrad.	Teosinte	USA	Connin (1956b)[a,b]
Festuca sp.	Fescue	USA	Flechtmann and Davis (1971)
Hordeum leporinum Link	Foxtail	USA	Keifer (1954)[a]
Hordeum murinum subsp. *leporinum* (Link) Arcang.	Barley grass	Australia	GRDC (2001), Halliday (2006)
Hordeum pusillum Nutt.	Little barley	USA	Somsen and Sill (1970)[a]
Hordeum vulgare L.	Barley	Australia, Brazil, Tibet, USA	Gillespie et al. (1997), GRDC (2001), Halliday (2006), Hong and Zhang (1996), Pereira et al. (2010), Somsen and Sill (1970)[a]
Lolium multiflorum Lam.	Annual ryegrass	Australia, Brazil, UK, Uruguay	Castiglioni and Navia (2010), Chamberlain and Evans (1980), Pereira et al. (2010), Slykhuis (1962)[a]
Lolium multiflorum var. *oldenburgicum*	Ryegrass	Australia	Slykhuis (1962)[a]
Lolium perenne L.	Perennial ryegrass	UK, Hungary	Chamberlain and Evans (1980), Golya et al. (2002)
Lolium rigidum Gaudin	Rigid ryegrass	Australia, UK	Chamberlain and Evans (1980), GRDC (2001), Halliday (2006)
Lolium sp.	Ryegrass	USA	Walsh and Ferguson (2008)
Muhlenbergia wrightii Vasey ex Coult	Spike muhly	USA	Watts and Bellotti (1967)[a]

Table 1 continued

Host plant–scientific name	Host plant–common name	Country	References
Muhlenbergia sp.	Muhly	USA	Walsh and Ferguson (2008)
Oryzopsis hymenoides (Roem. & Schult.) Ricker	Indian rice grass	Canada	Slykhuis (1955)[a,b]
Panicum capillare L.	Common witch grass	USA	Somsen and Sill (1970)[a]
Panicum effusum R.Br.	Hairy panic grass	Australia	GRDC (2001), Halliday (2006)
Panicum miliaceum L.	Common millet	USA	Conley et al. (2003)
Panicum sp.	Millet	USA	Somsen and Sill (1970)[a]
Paspalidium gracile (R. Br.) Hughes	Slender panic	Australia[d]	GRDC (2001), Halliday (2006)
Pennisetum americanum (L.) Leeke	Pearl millet	Brazil	Pereira et al. (2010)
Phalaris aquatica L.	Canary grass	Australia	GRDC (2001), Halliday (2006)
Phleum pratense L.	Timothy grass	Hungary, Poland, USA	Golya et al. (2002), Skoracka and Kozlowski (2002), Walsh and Ferguson (2008)
Poa compressa L.	Canada blue grass	Canada	Slykhuis (1955)[a,b]
Poa pratensis L.	Smooth meadow grass	Poland	Skoracka and Kozlowski (2002), Skoracka (2004)[c]
Puccinellia distans (Jacq.) Parl.	Weeping alkali grass	Poland	Skoracka and Kozlowski (2002), Skoracka (2004)[c]
Rhynchelytrum repens (Willd.) C.E. Hubb.	Red natal grass	Brazil	Pereira et al. (2010)
Secale cereale L.	Rye	Australia, USA	GRDC (2001), Halliday (2006), Somsen and Sill (1970)[a]
Setaria jubiflora (Trin.) R.D. Webster	Warrego grass	Australia[d]	GRDC (2001), Halliday (2006)
Setaria lutescens (Weigel ex Stuntz) Hubb.	Yellow bristle grass, foxtail	USA	Somsen and Sill (1970)[a]
Setaria verticillata (L.) Beauv.	Bristly foxtail, pigeon grass	Australia[d]	Carew et al. (2009), GRDC (2001), Halliday (2006)
Setaria viridis (L.) Beauv.	Green foxtail	USA	Connin (1956a)[a], Somsen and Sill (1970)[a]
Sorghum bicolor (L.) Moench	Sudan grass	USA	Connin (1956b)[a,b]
Sorghum halepense (L.) Pers.	Johnson grass	Brazil, USA	Connin (1956b)[a,b], Pereira et al. (2010)

Table 1 continued

Host plant–scientific name	Host plant–common name	Country	References
Sorghum vulgare Pers.	Sorghum	Australia, USA	GRDC (2001), Halliday (2006), Somsen and Sill (1970)[a]
Trisetum flavescens (L.) Beauv.	Yellow oat grass	Poland	Skoracka (2004)[c], Skoracka and Kozlowski (2002)
Triticum x *Secale*	Triticale	Australia	Halliday and Knihinicki 2004
Urochloa panicoides Beauv.	Liverseed	Australia	GRDC (2001), Halliday (2006)[d]
Vulpia bromoides (L.) Gray	Squirrel tail fescue	Australia	GRDC (2001), Halliday (2006)

[a] Referred to by authors as *Aceria tulipae*

[b] Based on laboratory rearing or greenhouse studies (not found in the field)

[c] Considered as an accidental host by the authors

[d] Needs confirmation, other eriophyoid mites were found (see Halliday 2006)

eastern Turkey. In Hungary, *A. tosichella* was first recorded from *Arrhenantherum elatius* (L.) Beauv. ex J. & C. Presl (oat grass), *Lolium perenne* L. (perennial ryegrass) and *Phleum pratense* L. (timothy grass) by Golya et al. (2002). The same authors also identified *A. tosichella* on many other grass hosts, demonstrating that the mite must have been common in Hungary at the time. Recently, Ripka (2010) found *A. tosichella* on corn in Hajdu-Bihar County in eastern Hungary but mistakenly reported this as *A. tulipae*. The occurrence of WCM on *L. perenne* and *Lolium rigidum* Gaudin (rigid ryegrass) was reported in the UK (Wales) by Chamberlain and Evans (1980).

Wheat curl mite was first found in Poland in 1997 during a study on virus-infected wheat (Jeżewska and Wieczorek 1998). Since then, the infestation of wheat and other grasses by WCM has been thoroughly studied in this country. Kozłowski (2000) found *A. tosichella* on several winter wheat cultivars, namely Almari, Kamila, Kobra, Rosa, Jawa, Kaja, Rysa, Sakwa and Mikon. The highest density of WCM was noted on the cultivar Mikon. *Elymus repens* (L.) Gould (quackgrass), growing near cultivated wheat, has also been shown to host high densities of *A. tosichella*, but it was not found on *Apera spica-venti* (L.) Beauv. (wind bentgrass) or *Echinochloa crus-galli* (L.) Beauv. (cockspur grass) (Skoracka and Magowski 2002). In addition to *E. repens*, 16 other wild grass species have been recorded as hosts of WCM in Poland (Table 1). Six of these, namely *Avenula pratensis* (L.) Dumort. (meadow oat-grass), *Avenula pubescens* (Huds.) Dum. (hairy oat grass), *Bromus inermis* L. (smooth brome), *Corynephorus canescens* (L.) Beauv. (grey hair grass), *Dactylis glomerata* L. (cocks foot or orchard grass) and *Poa pratensis* L. (smooth meadow grass), were infested the most frequently and intensively by *A. tosichella*. This mite was found to mostly inhabit the leaf sheaths, young leaves or spaces under the leaf ligules. Sometimes, *A. tosichella* occurred together with *Aculodes mckenziei* (Keifer) (Kozłowski 2001; Skoracka 2004). The observations on WCM population dynamics in Poland showed that the highest and most frequent peaks of population densities occurred in summer and autumn (Skoracka and Kuczyński 2003).

Surveys of eriophyoid mites inhabiting wild grasses in Turkey were initiated in 2009. So far, eight grass host species have been carefully inspected and WCM has been recorded as the most common eriophyoid mite infesting at least six grass hosts. Further surveys for WCM on wheat and other potential cereal hosts in Turkey are still in process (Denizhan et al. 2010).

Apart from *A. tosichella*, several other eriophyoid mite species are also known to occur on grass hosts (including cereals and other economically important grass species) in Europe. However, *A. tosichella* is considered to be the most significant pest (Golya et al. 2002; Kozłowski 2001; Oldfield 1970; Proeseler 1972). Some authors such as Makkouk and Kumari (1997) and Oldfield (1970), that have reported on the occurrence of WCM in European and Middle East countries have indicated the presence of severe symptoms, for example, shoot stunting, leaf rolling and curling, yellow spotting, leaf discoloration and the abnormal development of leaves. Other authors do not report such significant injuries (e.g. Kozłowski 2001).

In summary, *A. tosichella* has been recorded from the following Eurasian countries: Bulgaria, China, Germany, Hungary, India, Jordan, Moldova, Poland, Romania, Russia, Syria, Turkey, UK, Uzbekistan and former Yugoslavia. However, it should be stated that the known viruses transmitted by this mite species have also been found in several additional countries such as Italy (Credi et al. 1997), France (Gadiou et al. 2009; Goetz and Maiss 1995), Slovakia and the Czech Republic (Gadiou et al. 2009; Kúdela et al. 2008), Croatia (Milicic et al. 1982), Ukraine (Reshetnik et al. 1996) and Iran (Foulad and Izadpanah 1986) (Table 2). See section 'Taxonomy, host range, symptoms, affected areas

and impact of wheat curl mite transmitted viruses' for further details about the viruses, inferring that WCM is probably also present in those areas. Considering the high potential of WCM to be dispersed by air currents (Nault and Styer 1969) or human activity, it is likely that the mite is much more widespread throughout Europe and the Middle Eastern regions.

North America

Wheat curl mite is widespread in North America. The first records were from the early 1950s in the USA and Canada when authors referred to WCM as *A. tulipae*. Keifer (1954) identified such specimens collected on *Hordeum leporinum* Link (foxtail) in 1948 from Davis, CA, USA. Earlier, Keifer (1953) reported extensive WCM infestations on wheat in Alberta (Canada) and Nebraska and Kansas (USA). This author also mentioned that the WCM infestation in Kansas and Nebraska on perennial grasses also occurred on the genus *Agropyron*. At that time, WCM was also collected in the USA on *E. repens* at Logan, UT (Keifer 1954).

In Canada, WCM was reported as occurring in widely scattered locations in Alberta and Saskatchewan where it was found infesting wheat and grasses throughout the Canadian spring wheat belt (Slykhuis 1955). Also, it was observed on wheat in Ontario before the first records of WSMV became apparent in this province (Slykhuis 1961). In 1966 and 1967, WCM was also found in southwestern Ontario under the immature husks of some ears of corn that had been affected with kernel red streak (Nault et al. 1967; Slykhuis et al. 1968). A few symptomatic *D. glomerata* leaves collected in Sainte Anne de Bellevue, Quebec, were also found to be infested with eriophyoid mites, which were later identified as *A. tosichella* by the Agriculture Canada Biosystematics Research Centre. The association of WCM with some symptomatic *D. glomerata* was highlighted as a potentially hazardous virus-vector association since this mite had also been suspected to be the vector of *Orchard grass mosaic virus* (OGMV) (Peterson 1989). However, this virus-vector relationship has never been confirmed. Recently, *A. tosichella* was listed among the pests reported in Manitoba (Gavloski 2008, Gavloski and Elliot 2010). Hence, this species is widely distributed in the wheat growing areas of Canada primarily because of the overlapping occurrence of winter and spring wheat and wild and cultivated grasses which provide available hosts for the survival of WCM throughout the year.

Wheat curl mite is more or less distributed throughout the USA. It is present everywhere that wheat is grown, especially winter wheat. In the USA, since WSMV was considered to be a serious disease of wheat and WCM was confirmed as its vector (Slykhuis 1955), studies have been performed on virus transmission, alternate grass hosts, plant resistance, management and surveys in areas adjacent to wheat crops. Such studies have provided extensive information about the occurrence of *A. tosichella* in this country.

Wheat curl mite is a common mite infesting wheat fields in the Central Plains of the USA. In Kansas, it was reported from samples collected in Ellis, Barton, Dickinson, Ellsworth, Finney, Geary, Greeley, Saline (Harvey et al. 1999; Seifers et al. 2002) and Manhattan counties (Connin 1956b) where specimens were obtained from the tillers of volunteer wheat, wheat's spikes and wild grasses. WCM was also randomly collected from the maturing heads of wheat (soft to hard dough stage) in counties throughout Nebraska: Grant, Oshkosh, Big Springs, Kimball, Crawford, Scottsbluff, Sideny, Lincoln, Clay Center (Mahmood et al. 1998; Seifers et al. 2002). In Texas, High Plains WCM has been known to occur on wheat for several years (Daniels et al. 1956) and has been reported in the Texas Panhandle at Hartley, Hutchinson, Sherman and Castro counties (Daniels 1963)

Table 2 Worldwide distribution reported for wheat curl mite (WCM), *Aceria tosichella*, and/or WCM-transmitted virus and its respective host plants (WSMV *Wheat streak mosaic virus*, BrSMV *Brome streak mosaic virus*, WMoV *Wheat mosaic virus*, TriMV *Triticum mosaic virus*)

Geographic region	Country	WCM host plants	WCM-transmitted virus & host plants	References
Africa	Algeria		WSMV on *T. aestivum*	Benmokhtar and Yahia (2009)
	Zambia		WSMV on *T. aestivum*	Kapooria and Ndunguru (2004)
Eurasia	Bulgaria	*Triticum aestivum*	WSMV on *T. aestivum*	Markov et al. (1975)
	Czech Republic		WSMV on *T. aestivum*	Gadiou et al. (2009), Rabenstein et al. (2002)
	China	*T. aestivum*		Hong and Zhang (1996), Lin et al. (1987) in Oldfield and Proeseler (1996)[a]
	Croatia		WSMV on *T. aestivum*	Juretić (1979), Miličić et al. (1982)
	France		WSMV on *T. aestivum*; BrSMV on *Hordeum vulgare*	Gadiou et al. (2009), Huth et al. (1995), Rabenstein et al. (2008)
	Germany	*T. aestivum*	BrSMV on *Bromus sterilis*, *Hordeum murinum*	Rabenstein and Stanarius (1981), Rabenstein et al. (1982), Schubert and Rabenstein (1995)
	Hungary	*Arrhenatherum elatius*, *Lolium perenne*, *Phleum pratense*, *Zea mays*	WSMV on *T. aestivum*; BrSMV on *Cyperus esculentus*	Golya et al. (2002), Nyitrai and Gaborjanyi (1988), Ripka (2010)[a], Takacs et al. (2008)
	India	*T. aestivum*		Oldfield (1970)[a]
	Italy		WSMV on *T. aestivum, T. durum, H. vulgare*	Credi et al. (1997)
	Iran		WSMV on *Digitaria sanguinalis, Echinochloa colonum, T. aestivum*	Foulad and Izadpanah (1986), Khadivar and Nasrolahnejad (2009)
	Jordan	*T. aestivum*	WSMV on *T. aestivum*	Slykhuis and Bell (1963)[a]
	Kazakhstan		WSMV on *T. aestivum*	Rabenstein et al. (2002)

Table 2 continued

Geographic region	Country	WCM host plants	WCM-transmitted virus & host plants	References
	Moldova	T. aestivum	WSMV on T. aestivum	Juretič (1979)
	Mongolia	T. aestivum		Skoracka et al. (2001)
	Poland	Agrostis capillaris[c], Alopecurus pratensis, Avenula pratensis, A. pubescens, Bromus erectus, B. hordeaceus (cited as B. mollis), B. inermis, B. racemosus, B. sterilis, Calamagrostis arundinacea, C. epigeios[c], Dactylis glomerata, Elymus repens, Phleum pratense, Poa pratensis, Puccinellia distans, Trisetum flavescens[c], T. aestivum	WSMV on T. aestivum	Jeżewska and Wieczorek (1998), Kozłowski (2000), Skoracka (2004), Skoracka and Kozłowski (2002), Skoracka and Magowski (2002), Trzmiel and Jeżewska (2006)
	Romania	T. aestivum	WSMV on T. aestivum	Slykhuis and Bell (1963)[a]
	Russia	T. aestivum	WSMV on T. aestivum	Gerasimov et al. (1970), Razyyazkina et al. (1963)
	Slovakia		WSMV on T. aestivum	Kúdela et al. (2008)
	Syria	T. aestivum	WSMV on T. aestivum	Makkouk and Kumari (1997), Oldfield (1970)[a], Shevtchenko et al. (1970)
	Turkey	T. aestivum	WSMV on Avena sativa L., H. vulgare, T. aestivum, Triticum x Secale	Denizhan et al. (2010), Ilbaggi et al. (2005)
	Ukraine		WSMV on T. aestivum	Reshetnik et al. (1996)
	UK	L. perenne, L. rigidum, T. aestivum	WSMV on T. aestivum	Chamberlain and Evans (1980), del Rosario and Sill (1965)[a], Brakke (1971)
	Uzbekistan	T. aestivum		Shevtchenko et al. (1970)[a]

Table 2 continued

Geographic region	Country	WCM host plants	WCM-transmitted virus & host plants	References
	Former Yugoslavia (Serbia and Montenegro)	T. aestivum	WSMV on T. aestivum; BrSMV on Bromus mollis L., Hordeum murinum	Juretić (1979), Keifer (1969), Milicic et al. (1980, 1982), Sutič (1974), Tosišč (1971)
North America	USA	Aegilops cylindrica[b], Agropyron smithii, Arrhenatherum elatius[b], Avena sativa, Bouteloua hirsuta[b], Bromus inermis[b], B. japonicus, B. secalinus, B. tectorum, Buchloe dactyloides, Cenchrus pauciflorus[b], Cynodon dactylon, Digitaria ischaemum, D. sanguinalis[b], Echinochloa crus-galli, Elymus canadensis, E. repens, E. virginicus, Eragrostis cilianensis[b], Euchlaena mexicana[b], Festuca sp., Hordeum leporinum, H. vulgare, Lolium sp., Muhlenbergia sp., Panicum sp., P. capillare, P. miliaceum, Phleum pratense, Secale cereale, Setaria lutescens, S. viridis, Sorghum bicolor[b], S. halepense[b], S. vulgare, T. aestivum, Zea mays	WSMV on T. aestivum, Z. mays; WMoV on A. sativa, B. secalinus, H. vulgare, S. cereale, S. glauca, S. viridis, T. aestivum, Z. mays; TriMV on T. aestivum	Conley et al. (2003), Connin (1956b)[a], Flechtmann and Davis (1971), Jensen and Lane (1994), Jensen et al. (1996), Keifer (1953, 1954)[a], McKinney (1937), Nault et al. (1970)[a], Seifers et al. (1998, 2008), Somsen and Sill (1970)[a], Walsh and Ferguson (2008)
	Canada	Dactylis glomerata, Oryzopsis hymenoides[b], Poa compressa, T. aestivum, Z. mays	WSMV on T. aestivum, Z. mays	Atkinson and Grant (1967), Keifer (1953)[a], Nault et al. (1967)[a], Peterson (1989), Slykhuis (1955)[a], Slykhuis et al. (1968)[a]
	Mexico	T. aestivum	WSMV on T. aestivum	Sánchez-Sánchez et al. (2001)

Table 2 continued

Geographic region	Country	WCM host plants	WCM-transmitted virus & host plants	References
Oceania	Australia	*Avena fatua, A. pubescens, A. sterilis, Bothriochloa macra, Bromus catharticus, B. diandrus, B. hordeaceus* (cited as *B. mollis*), *Cynodon dactylon*[d]*, Dactylis glomerata, Digitaria sanguinalis, Eleusine indica, Eragrostis ciliamensis, Hordeum murinum* subsp. *leporinum, H. vulgare, Lolium multiflorum, L. m. var. oldenburgicum, L. rigidum, Panicum effusum, Paspalidium gracile*[d]*, Phalaris aquatica, Secale cereale, Setaria jubiflora*[d]*, S. verticillata*[d]*, Sorghum vulgare, Triticum aestivum, Triticum* x *Secale, Urochloa panicoides*[d]*, Vulpia bromoides*	WSMV on *A. fatua, E. tristachya, E. curvula, H. murinum, L. multiflorum, Panicum* sp.*, S. verticillata, T. aestivum*	Coutts et al. (2008a, b), Dwyer et al. (2007), Ellis et al. (2003a, b, 2004), Edwards et al. (2006), Halliday (2006), Halliday and Knihinicki (2004)
	New Zealand		WSMV on *T. aestivum*	Lebas et al. (2009)
South America	Argentina	*Avena sativa*[b]*, T. aestivum*	WSMV on *Avena fatua, A. sativa, Brachiaria* sp.*, Cynodon dactylon, Digitaria sanguinalis, Echinochloa crus-galli, Grama* sp.*, H. vulgare, Panicum* sp.*, Setaria italica, Setaria* sp.*, Sorghum halepense, T. aestivum, Z. mays, Triticum* x *Secale*; WMoV on *S. glauca, T. aestivum, Z. mays*	Navia et al (2006), Sagadin and Truol (2008), Truol (2009), Truol and Sagadin (2007, 2008b), Truol et al. (2004, 2010)

Table 2 continued

Geographic region	Country	WCM host plants	WCM-transmitted virus & host plants	References
	Brazil	Agropyron sp., Andropogon bicornis, Avena sativa, Brachiaria decumbens, B. plantaginea, Bromus sp., B. unioloides, Chascolytrum subaristatum, Chloris polydactyla, Digitaria horizontalis, D. insularis, Hordeum vulgare, Lolium multiflorum, Pennisetum americanum, Rhynchelytrum repens, Sorghum halepense, T. aestivum, Z. mays		Pereira et al. (2009, 2010)
	Uruguay	Bromus unioloides, Lolium multiflorum, T. aestivum		Castiglioni and Navia (2010)

[a] Referred to by authors as Aceria tulipae or A. tritici

[b] Based on laboratory rearing or greenhouses studies

[c] Considered as an accidental host by the authors

[d] Needs confirmation, other eriophyoid mites were found (see Halliday 2006)

and at the community of Bushland in Potter county (Velandia et al. 2010). In the drier areas of Oklahoma, i.e., primarily the panhandle and western Oklahoma, WCM and the transmitted virus have been observed on wheat, corn and many other grasses (Hunger et al. 2004). WCM has been of great economic significance in the wheat-producing areas of Wyoming (Ferrell 2001), Colorado (Peairs 2010) and North Dakota, where management recommendations to reduce the sources of this mite and virus in wheat fields have been set up by McMullen and Waldstein (2010).

In the western USA, following the first detections in California and Utah (Keifer 1938, 1954), the presence of WCM was confirmed from Idaho in 1993, Washington in 1998 (Rondon 2006) and Oregon (Cooperative Extension Washington State University 2003). The first outbreak of WCM and WSMV in northcentral Washington was observed in 1997 which was then exacerbated by a set of favorable environmental conditions including a cool moist summer, hailstorm and a warm winter. The largest concentration of mites was always found on the youngest leaf of wheat or barley tiller (Gillespie et al. 1997). In Oregon, the pest has been found there since the early 1990s although it was not of major significance until 2003 (Cooperative Extension Washington State University 2003).

In the eastern USA, WCM has been reported in Ohio, Michigan, Arkansas, Georgia, Kentucky and Missouri. Ohio registered the first collection of WCM from corn in 1965. However, the mite had been present there as early as 1963 when WSMV and Kernel red streak (KRS) were first recorded (Nault 1970; Nault et al. 1967). Those authors suggested that a strain of WCM adapted to corn had become widespread in Ohio, southern Michigan and adjacent areas and was the primary cause of KRS. Corn was considered to be an important host for the mite in Ohio and Iowa (McKinney et al. 1966). Nault and Styer (1969) found WCM at Hoytville, Wooster, Marietta and Portsmouth indicating its presence throughout Ohio. In Arkansas, WCM was included among pests that had invaded the state (Boyer 1964). In the southeastern USA, in Georgia, WCM was collected in Clarke county on corn and *Festuca* sp. (fescue) (Flechtmann and Davis 1971). WSMV and WCM were later noticed in Kentucky in 1987 with widespread infestations recorded in 1988 (Townsend and Johnson 1996). In Missouri, WCM has been found to be an occasional and statewide pest of wheat and cereal grains. Its main host crop is wheat, but to a lesser degree it also occurs on corn, *Elymus canadensis* L. (Canada wild rye), *Panicum miliaceum* L. (common millet) and a few species of weedy grasses (Conley et al. 2003).

Sánchez-Sánchez et al. (2001) found WSMV and its vector WCM for the first time in wheat fields in the state of Texacoco, Mexico. This was the first report of the virus and its vector so far south in North America.

Wheat curl mite has been reported from a wide range of grass hosts in North America. Slykhuis (1955) reared this mite on wheat, *Oryzopsis hymenoides* (Roem. & Schult.) Ricker (Indian rice grass) and *Poa compressa* L. (Canada blue grass). Connin (1956a) found WCM naturally infesting *A. smithii*, *Digitaria ischaemum* (Schreb.) Schreb. ex Muhl. (smooth crab grass), *E. canadensis*, *Setaria viridis* (L.) Beauv. (green foxtail) and oversummering volunteer wheat. In greenhouse studies, Connin (1956b) reproduced WCM on 27 varieties of wheat, six barley varieties, 10 corn varieties, five *Sorghum bicolor* (L.) Moench (Sudan grass) varieties and 12 of 24 wild grass species that had also been tested (Table 1). Somsen and Sill (1970) presented extensive data on grass hosts of WCM and its infestation symptoms and seasonal development on volunteers and planted wheat, corn, rye, barley, oats, *Panicum* sp. (millet), *Sorghum vulgare* Pers. (sorghum) and other native grasses in Kansas (Table 1). Additionally, WCM was observed on *Lolium* sp. and *Muhlenbergia* sp. in Colorado and on *P. pratensis* grown in Washington State (Walsh and Ferguson 2008).

Oceania

The identification and confirmation of the occurrence of WCM in Australia has a confused history. As part of an international study for virus diseases of cereals and pasture grasses during the spring of 1960, a survey was undertaken in Queensland (Qld), New South Wales (NSW), Victoria (Vic) and South Australia (SA) by Slykhuis (1962). This author was the first to document that 'Eriophyid mites identical to *A. tulipae* K. in North America, except that they have eight- instead of seven-rayed featherclaws, were found on oversummered wheat in irrigated plots at Warwick, Queensland. Similar mites were found on annual ryegrass, *Lolium multiflorum* Lam., Armidale, NSW and Parafield, SA; and on *L. multiflorum* var *oldenburgicum*, CSIRO, Canberra.' It is likely that the eriophyoid species that Slykhuis (1962) had referred to was *A. tosichella*. However, it is not possible to validate those early records of WCM to find out exactly which species was involved because as far as can be determined, there are no reference specimens available for study that were collected by Slykhuis at the time (Halliday 2006; Halliday and Knihinicki 2004; Slykhuis unpublished report 1960). Of interest is that the unconfirmed detection of eriophyoid mites on wheat in Australia by Slykhuis (1962) had taken place several years before *A. tosichella* was described by Keifer (1969).

Confirmation of the presence of WCM in Australia was formally published by Halliday and Knihinicki (2004). This was based on the examination of slide-mounted specimens held at the reference collection of the Agricultural Scientific Collections Unit (ASCU), Orange, NSW, which showed that the earliest records were from Victoria in 1980 and 1981. In NSW, the earliest known specimens of *A. tosichella* damaging wheat plants were collected from glasshouses at the Agricultural Research Centre (ARC) at Tamworth during 1985 and 1987. At the time, the eriophyoid species involved was tentatively identified as being close to *A. tosichella* (previously known as *A. tulipae*). Because of the morphological variation that was observed between specimens, there was speculation that at least two species were involved, including a possibly native, undescribed species (E. Schicha, NSW Agriculture, unpublished data 1985). Much later, specimens collected from a survey for *A. tosichella* conducted during 2003, following the first serious outbreak of WSMV in Australia, indicated that this mite species was widespread (Halliday and Knihinicki 2004). The study of those specimens highlighted the need for further taxonomic research on eriophyoid mites (especially *Aceria* species) associated with cereals and grasses in Australia (Knihinicki and Halliday 2005).

While conducting a study on the cereal rust mite, *Abacarus hystrix* (Nalepa) (the vector of *Ryegrass mosaic virus*), Frost (1995) also reported that WCM (referring to it as *A. tulipae*) was widespread in wheat crops in South Australia and gave a brief summary of its behaviour and life cycle. Baker et al. (1996) also stated that *A. tosichella* occurs in Australia, on the basis of specimens collected near Adelaide (Amrine, pers. comm. to Halliday 2001, cited in Halliday and Knihinicki 2004). As far as can be determined from the literature and based on specimens in reference collections, WCM is found in all major wheat growing and breeding areas throughout Australia including NSW, Australian Capital Territory (ACT), Qld, SA, Western Australia (WA) and Tasmania (Tas) (Carew et al. 2009; Halliday and Knihinicki 2004; Schiffer et al. 2009).

Wheat curl mite has been reported on many plant hosts across several genera of grasses and cereals. Some of these hosts may act as a 'green bridge' between crop/pasture rotation when wheat is not grown (Carew et al. 2009; Murray et al. 2005). To date, *A. tosichella* has been found on several varieties of wheat (such as Marombi, Whistler, Wedgetail, Diamondbird, Whyla, H45, Ventura, McKellar and Tennant) and it has also been found

damaging *Triticum* × *Secale* (triticale) which is a wheat/rye hybrid (Carew et al. 2009; Halliday and Knihinicki 2004). Other cereal and grass hosts from Australia are listed in Table 1. It is important to note that further detailed study of these reported hosts of *A. tosichella* is recommended because some may be inaccurate. Those include records from *Cynodon dactylon* (L.) Pers. (Bermuda grass), *Paspalidium gracile* (R. Br.) Hughes (slender panic), *Setaria jubiflora* (Trin.) R.D. Webster (Warrego grass), *Setaria verticillata* (L.) Beauv. (bristly foxtail) and *Urochloa panicoides* Beauv. (liverseed) (Table 1) after Halliday (2006) found that these were occupied by eriophyoid species that were different from *A. tosichella*.

In 2009, the WSMV was formally reported for the first time from New Zealand by Lebas et al. (2009) after wheat seeds of a breeding line tested positive in 2005. Following this, an extensive survey of cereal experimental trials and commercial wheat crops was undertaken during the 2005–2006 summer season. The results indicated that WSMV was widely distributed in New Zealand on wheat. Despite targeted and repeated surveys at the time, *A. tosichella* has not yet been detected there. Hence, Lebas et al. (2009) suggested that the widespread occurrence of WSMV in New Zealand was the result of seed transmission. Further surveys could help to clarify the status of WCM in New Zealand.

South America

Reports of the presence of WCM in South America are fairly recent. *Aceria tosichella* was first found in Argentina in 2004 (Navia et al. 2006), 2 years after WSMV was first detected there (Truol et al. 2004). A few years later, WCM was also found in Brazil in 2006 and in Uruguay during 2007 (Castiglioni and Navia 2010; Pereira et al. 2009).

Since the detection of WSMV in Argentina, plant virologists have been looking unsuccessfully for its vector in the field. During 2004, in the locality of Azul, province of Buenos Aires, samples of wheat cv. Baguette 10 with symptoms of WSMV, were tested via ELISA. Simultaneously part of each sample was submitted for acarological inspection utilizing the washing and sieving extraction method as was described by Pereira et al. (2009). The presence of numerous eriophyoid mites was revealed which were later identified as *A. tosichella* by Navia et al. (2006). In Argentina, surveys for WCM were conducted from 2006 to 2010 in all wheat-producing areas. In addition to Buenos Aires, WCM and its associated viruses were detected in the provinces of Córdoba, Entre Ríos, La Pampa, Santiago del Estero, Santa Fe, Tucumán and Salta (Navia et al. 2010; Alemandri pers. comm. 2009). In addition to wheat, WSMV has also been detected in several other cultivated and volunteer grasses in Argentina including oats, barley, corn, triticale, *C. dactylon*, *Setaria italica* (L.) Beauv. (Italian foxtail millet), and *Sorghum halepense* (L.) Pers. (Johnson grass) (Table 1) (Sagadin and Truol 2008; Truol et al. 2010; Sagadin and Truol pers. comm. 2009). This indicates that the mite vector is also likely to be present on the above mentioned host plants in this country.

The occurrence of WCM and associated viruses in Argentina alerted other South American countries to the fact that this mite-virus complex was potentially present, especially in Argentina's neighbouring countries with contiguous cereal production areas. Thus, in 2006, a collaborative project was initiated among institutions from Argentina, Brazil, Paraguay and Uruguay with one of the major aims being to map the occurrence of this invasive mite-virus complex in the wheat production areas of those countries.

In Brazil, WCM was first detected during 2006 in the state of Rio Grande do Sul, which is located to the extreme south having its border with Argentina. In this state, WCM was initially found only in wheat samples from the municipalities of Passo Fundo, Palmeira das

Missões, São Luís Gonzaga and Santo Antonio das Missões, all of them in the northwest region of Rio Grande do Sul (Pereira et al. 2009). Since the first detection of WCM in Brazil, continuous surveys have been conducted there in order to monitor the occurrence of the mite vector and to determine its host range in the region. Such surveys have covered the main Brazilian wheat production areas along the states of Rio Grande do Sul, Santa Catarina, Paraná and Mato Grasso do Sul. Results of the surveys have indicated a wider distribution of *A. tosichella* in the northern and western municipalities of Rio Grande do Sul; however, this mite has not yet been found in the other Brazilian states. In addition to wheat, corn, oats and barley, WCM has also been detected on 14 grasses in Brazil (Table 1) (Navia et al. 2010; Pereira et al. 2010). Symptoms resulting from high WCM infestations consisting of curling or rolling of young leaves were observed only in greenhouses (Pereira et al. 2009). Field surveys suggest that high WCM populations are not present in the field in Brazil.

In addition to *A. tosichella*, two other *Aceria* species identified as being new to science were also found on grasses in Brazil. The first new species was collected only in the state of Parana and the second new species presented a wider distribution after it was found in the states of Rio Grande do Sul, Paraná and Mato Grosso do Sul. These two *Aceria* species are very similar to *A. tosichella*, but can be distinguished by the ornamentation on the prodorsal shield, the number of empodial rays, and the length of the scapular (*sc*) and lateral (*c₂*) setae (Navia et al. unpubl.). The descriptions of the new species are in preparation. This emphasizes the importance of undertaking a detailed taxonomic study of eriophyoid mites associated with grasses in order to accurately determine the occurrence and status of *A. tosichella*. It is important to determine whether these other *Aceria* species have a role in virus transmission.

In Uruguay, surveys were conducted from February 2007 until November 2008, in the main wheat production areas in 13 municipalities of six departments (Colonia, Flores, Paysandú, Rio Negro, San José, and Soriano). WCM was detected in the departments of Colonia (four municipalities), Rio Negro and Soriano (one municipality each), where it was found infesting wheat, *Bromus unioloides* (Kunth) (rescue grass) and *L. multiflorum* (annual ryegrass) (Castiglioni and Navia 2010). Symptoms of WCM infestation or its associated viruses were not observed in the field.

Surveys in Paraguay were conducted during August 2007 within 12 localities of four departments (Coaguaçu, Maria Auxiliadora, Naranjal and Pirapó) and included wheat and corn. WCM was not found in any of these areas at the time; however, complementary surveys should now be conducted to verify those results (Navia et al. 2010).

Surveys for the presence of WCM in wheat production areas in the southern countries of South America showed that this vector is widespread in Argentina but it appears to have a restricted distribution in Uruguay and Brazil. It is not possible to know how long WCM has been present in South America because extensive surveys of eriophyoid mites on grasses had not previously been conducted on this continent. It is very likely that WCM was present in Argentina long before its first official detection in 2004, at least since the first detection of WSMV in 2002 and perhaps even longer.

Biological aspects of wheat curl mite

The life cycle of WCM comprises the egg, larva, nymph and adult stages. Deuterogyny has not been reported for WCM (Oldfield and Proeseler 1996). In the north-central USA, all stages of WCM have been found to be present on their host plants during winter (Jeppson

et al. 1975). Individual females lay 3–25 eggs in 10 days, averaging one egg per day during their lifetime. Eggs are deposited in straight lines along parallel leaf veins and incubation lasts 3–5 days at 9 °C, but hatching stops at freezing temperatures. A complete life cycle takes 8–10 days under favourable conditions. The larva period takes about 2.25 days and the nymph 2.75 days. Adult females have a preoviposition period that varies from 1 to 3 days (del Rosario and Sill 1958, 1965; Jeppson et al. 1975). Boczek and Chyczewski (1975) in Sabelis and Bruin (1996) reported that WCM's period of development lasts 13 days at 20 °C and 7 days at 27 °C. Theoretically, under ideal conditions, one adult of WCM can produce 3 million offspring within 60 days (Townsend and Johnson 1996).

Wheat curl mite have been shown to survive without food or water for less than 8 h at 24 °C and 30–40 h at 3 °C. However, on sterile agar culture plates, the mites survived for longer periods. These survival times indicate that WCM cannot survive dry conditions for extended periods (del Rosario and Sill 1965; Jeppson et al. 1975). During an experiment in Texas, USA, WCM colonies were maintained for several months at 5 °C, although with low egg viability (Skare et al. 2002). All stages can survive for at least 3 months at near freezing temperatures including several days at around −18 °C (Townsend and Johnson 1996). Warm and humid conditions appear to be ideal for optimal growth in WCM development (Coutts et al. 2008b; Schiffer et al. 2009; Somsen and Sill 1970). CLIMEX© analysis of WCM distribution in Australia suggests that the species has an ability to persist in both semi-arid and temperate areas, with distribution limited by heat and dry stress (Schiffer et al. 2009).

Studies on the life cycle of WCM were conducted some decades ago. Despite the great economic importance of this mite, there are no recent publications available on this subject. Probably this is because of the difficulties found in conducting biological observations on eriophyoid mites. Thinking about strategies for the management of this mite-virus complex, it is important to have data available on the biological parameters for WCM under different environmental conditions including the various host plants, in particular grasses, that are known to provide the mite with a 'green bridge' (see more details in section 'Ecological factors affecting wheat curl mite dispersal and virus epidemiology').

Taxonomy, host range, symptoms, affected areas and impact of wheat curl mite transmitted viruses

The viruses transmitted by WCM are very diverse and belong to different taxonomic groups. Based on the physical virion characteristics and genome sequence, the WSMV, BrSMV and TriMV are classified as part of the family Potyviridae. WSMV and BrSMV belong to the genus *Tritimovirus*, whereas TriMV is proposed to belong to a new genus named *Susmovirus* (Fellers et al. 2009). HPV was named after the geographical location where the diseases it causes was first found (High plains) and probably is a newly emerged virus that resembles both tenuiviruses and tospoviruses. Two new names were proposed for HPV: *Maize red stripe virus* (MRStV) and *Wheat mosaic virus* (WMoV)—in this paper we use the latter because it was proposed most recently. There is reason to speculate that WMoV in fact represents a possible re-emergence of *Wheat spot mosaic* (WSpM) described and studied in the 1950s by Slykhuis (1956) (Skare et al. 2006).

Wheat streak mosaic virus (WSMV)

Wheat streak mosaic virus is the type species of the genus *Tritimovirus* of the family Potyviridae (Stenger et al. 1998). Tritimoviruses are transmitted by eriophyoid mites to

monocotyledonous hosts and are phylogenetically distinct from eriophyoid mite-transmitted viruses in the genus *Rymovirus* (Salm et al. 1996; Stenger et al. 1998). WSMV has a genome organization similar to that of other monopartite members of the family Potyviridae, encoding a polyprotein that is subsequently cleaved by viral-encoded proteinases into 8–10 mature proteins capable of complex protein–protein interactions (Choi et al. 2000).

The main cereals infected by WSMV are wheat, barley, oats, corn and *Panicum* sp. (Brakke 1971). The two main symptoms caused by WSMV in wheat are leaf mottling (mosaic pattern of green and chlorotic zones) and leaf streaking (Fig. 1) (Ellis et al. 2003a; Murray et al. 1998). Other grasses also presented these kinds of symptoms (Ellis et al. 2004). The symptoms may progress to chlorosis and severe stunting of the plant. In many cases the plants were sterile or produced shriveled seed (Ellis et al. 2003a). Seeds harvested from infected plants are smaller and reduced in weight (Truol 2009). At the microscopic level, WSMV infection includes the accumulation of cylindrical and amorphous inclusion bodies (Gao and Nassuth 1992), nuclei and chloroplast deformation (Gao and Nassuth 1993), membrane proliferation and deposition along the walls of mesophyll and bundle sheath cells (Gao and Nassuth 1994). At the field level, disease development often begins at the edges of fields facing nearby volunteer wheat fields or grasslands which harbour the vector (Thomas and Hein 2003). As the season progresses, a disease severity gradient develops and there are significant cross-correlations between yield and wheat streak intensity (Workneh et al. 2009). WSMV infections reduce root biomass and water use efficiency, making it a serious concern in regions with limited availability of water (Price et al. 2010). Losses due to WSMV infections are correlated with the time of infection; generally infections on early stages of the plant results in higher yield losses (Hunger et al. 1992). A review on the biology and management of WSMV was recently published by Hadi et al. (2011).

Wheat streak mosaic virus was first reported from the Central Great Plains of the USA in the 1920s (McKinney 1937). Nowadays it is widely distributed in wheat-growing regions of North America (Brakke 1987; Sánchez-Sánchez et al. 2001; Slykhuis and Bell 1963), Eurasia (Makkouk and Kumari 1997; Nyitrai and Gaborjanyi 1988; Reshetnik et al. 1996), Africa (Algeria and Zambia) (Benmokhtar and Yahia 2009; Kapooria and Ndunguru 2004), Oceania (Ellis et al. 2003a, b; Lebas et al. 2009) and South America (Truol et al. 2004) (Table 2).

North America

In North America, WSMV is widespread being present in the main wheat production areas of the USA (Arkansas, California, Georgia, Idaho, Kansas, Kentucky, Missouri, Montana, Nebraska, North Dakota, Ohio, South Dakota, Texas, Utah) (CABI International 2002; Forster et al. 2001; Harvey et al. 1995a, b; Townsend and Johnson 1996) and in Canada (Alberta, Ottawa and Ontario) (Harvey et al. 1995a, b; Seifers et al. 1998). It was also detected in Mexico during the last decade (Sánchez-Sánchez et al. 2001).

The USA is the country where WSMV has assumed the main economic importance, causing significant losses in important wheat production areas. Accordingly to Velandia et al. (2010), WSMV losses are associated with a reduction in water-use efficiency, indicating that the disease reduced the wheat plant's ability to uptake available soil moisture, resulting in grain and forage yield losses ranging from US\$ 60.1–US\$ 339.9 ha^{-1} in the Texas High Plains. In the Great Plains region, WSMV is responsible for average annual yield losses of approximately 5 % and complete yield loss in localized

areas. Annual economic losses have amounted to a total cost of US$ 80 million in Kansas alone (Christian and Willis 1993; French and Stenger 2003; University of Illinois 1989). Wheat yield reduction due to WSMV infections have also been estimated in other USA states, varying from 50.2 to 91.4 % in Colorado after the evaluation of 12 wheat cultivars for WSMV impact (Shahwan and Hill 1984), from 31.9 to 98.7 % in a two-year field study in North Dakota (Edwards and McMullen 1988), and a maximum reduction of 75 and 87 % in fertile tillers and grain yield, respectively, in a two-year field study in Oklahoma (Hunger et al. 1992). Even when the average regional loss in yield potential seemed to be moderate, it is possible to find individual fields that suffer total loss because of WSMV infection (Hadi et al. 2011). Differently from the USA, data on wheat yield losses in Canada are scarce; Atkinson and Grant (1967) reported losses of 18 % in Alberta, in 1963.

Eurasia

Wheat streak mosaic virus was reported for the first time in Europe and Middle East in 1963 from Russia (Gerasimov et al. 1970; Razvyazkina et al. 1963), Romania and Jordan (Slykhuis and Bell 1963). However, the virus could have been present in Europe much earlier but without a proper diagnosis since WSMV-like symptoms on crops were reported in 1949 in Kazakhstan (Dijemboev 1956; Rabenstein et al. 2002). Later on, this virus was reported from the Ukraine in 1966 and confirmed in 1996 (Moskovets and Oleĭnik 1966; Reshetnik et al. 1996). WSMV also occurs in the central region of the former Yugoslavia (Sutič and Tosišč 1964), with information on WSMV being widely distributed in Serbia (Sutič 1974; Tosišč 1971), Moldova and Croatia (Juretič 1979). It has also been found in Bulgaria (Markov et al. 1975) and Hungary (Nyitrai and Gaborjanyi 1988). In the Middle Eastern region, WSMV has been detected in Jordan, Turkey, Iran and Syria. Records from Turkey (Bremer 1971) were confirmed by recent studies in the Trakya region (Ilbaggi et al. 2005) where WSMV-infected wheat, barley, oats and triticale had been found. WSMV also occurs in Iran (Foulad and Izadpanah 1986); and lately in 2009, infection symptoms were also observed in crops in northern Iran. However, ELISA tests and RT-PCR reactions confirmed WSMV infections only for weeds, namely *Digitaria sanguinalis* (L.) Scop. (hairy crab grass) and *Echinochloa colonum* (L.) Link. (junglerice) which were found to be new hosts for WSMV (Khadivar and Nasrolahnejad 2009). WSMV was also reported from wheat in Syria (Makkouk and Kumari 1997), western Poland (Jeżewska and Wieczorek 1998), western Slovakia (Kúdela et al. 2008), the Burgundy region of France (Gadiou et al. 2009; Rabenstein et al. 2008), northern Italy and Tuscany (Credi et al. 1997; Gadiou et al. 2009; Rabenstein et al. 2008) and Czech Republic (Gadiou et al. 2009; Rabenstein et al. 2002). Rabenstein et al. (1982) reported WSMV infection of *Bromus sterilis* L. (sterile brome) and *Hordeum murinum* L. (false barley) in Germany, but later it had been designated to be a BrSMV infection (Schubert and Rabenstein 1995).

There is no report on yield losses caused by WSMV in Europe. Based on data from the 1960s to 1990s, Middle Asia is the region with the highest severity of WSMV reported for wheat (20–40 % of disease distribution) while the moderate severity zone (10–20 %) includes Moldova, Ukraine, Volga Basin Region and Voronezh Region of Russia (Tsyplenkov and Saulich 2008). The survey did not cover central and western Europe or Middle Eastern countries. The study in Trakya in Turkey showed an infection rate of 0–10 % in wheat, 0–14.3 % in barley, 0–6 % in oats and 50 % in triticale, although wheat was the most intensively sampled (Ilbaggi et al. 2005). A local preliminary study in western Poland revealed an infection rate of 39.1–81.5 % in corn (Trzmiel and Jeżewska 2006). More data are needed from a broader range of hosts and countries to determine the scope of infection

severity in Europe. Investigated crops and weeds should also be examined for the occurrence of WCM as the WSMV vector. In the majority of countries where WSMV infections have been reported, WCM has also been recorded. The exception where the mite has not yet been detected includes Croatia, Czech Republic, France, Italy, Iran, Kazakhstan, Slovakia and Ukraine (see Table 2 and section 'Distribution and host plants of the wheat curl mite').

Oceania

The discovery of an outbreak of WSMV in 2002 led to the definitive documentation of this serious disease in Australia by Ellis et al. (2003a, b) who suggested that it had arrived several years ago but remained undetected. In the literature, the occurrence of WSMV in the wheat-producing areas of Australia was reported much earlier by Jeppson et al. (1975) and Meyer (1981) who claimed that WSMV was very common in Australia (in reference to its mite vector, *A. tosichella*) but the source of information contained in these reports could not be verified. Certainly, anecdotal evidence exists which implies that WSMV may have been present in Australia for much earlier than the first official record as reported by Ellis et al. (2003a, b), possibly since the 1980s. A newsletter published by the Crop Science Society of South Australia (June 2003, August 2003) outlined the historical perspective of WSMV in Australia where it was noted that during the mid-1980s, viral symptoms were observed at the Waite Institute, SA, in young (wheat?) plants growing next to mature plants, both in the paddock and glasshouse situation. Plant samples, collected in 1995, were positively identified overseas as being infected with WSMV. Although formal notification of the presence of WSMV in Australia was apparently given at the time, the damage caused by the virus during the period of 1992 and 2002 was only minimal and it seemed that Australian wheat varieties were quite tolerant to the disease. This proved to be a different scenario during 2003.

Following the discovery of WSMV on wheat plants in breeding facilities and field sites in Canberra, ACT, as reported by Ellis et al. (2003a, b), additional surveys also detected this disease in many areas of NSW, SA, Qld, Vic and WA (Coutts et al. 2008b; Dwyer et al. 2007), and Tas (Schiffer et al. 2009). Schiffer et al. (2009) explained that WA had experienced fewer detections and outbreaks of WSMV compared to eastern Australia, particularly in NSW. The same authors surmised that this may have been because the climate in WA is much hotter and drier or due to the ability of the dominant WCM lineage as WSMV vector (see section 'Relationship between wheat curl mite and transmitted viruses').

In Australia, WSMV has been found in several important cereal and grass hosts (Coutts et al. 2008a, b; Ellis et al. 2004) especially wheat, *Avena fatua* L. (wild oats), *H. murinum* and *L. multiflorum*. Other reported hosts include *Eleusine tristachya* (Lam.) Lam. (spike goose-grass), *Eragrostis curvula* (Schrad.) Nees (African lovegrass), *Panicum* sp. and *S. verticillata* (Edwards et al. 2006). WSMV has been detected in 14 cultivars of wheat in Australia (Coutts et al. 2008a).

Prior to 2005, WSMV did not cause any very serious crop losses in Australia when symptoms of this disease were noticed in only a few paddocks (Coutts et al. 2008a, b; Dwyer et al. 2007). According to those authors, WSMV was responsible for only minimal crop losses during 2003 and 2004, with the Murrumbidgee Irrigation Area (MIA) in NSW being the area that was most affected. Unfortunately, the situation of only minimal crop damage was reversed in 2005 when early-sown 'graze-and-grain' wheat crops in the MIA were severely affected. More than 5,000 ha of wheat paddocks in the high rainfall zone of

the NSW grain belt were devastated. During 2006, wheat crop losses had expanded to 20 000 ha even though the season was not very favourable for the development of WSMV. As this situation unfolded, future economic losses as a result of WSMV were estimated to be in the order of $AUD 21 million by the NSW Department of Primary Industries, especially if farmers opted not to grow high quality 'graze-and-grain' wheat crops but instead planted lower value crops such as oats and triticale (Dwyer et al. 2007; Jones and Burges 2006; Jones et al. 2005; Murray 2006).

In 2009, WSMV was reported for the first time from New Zealand by Lebas et al. (2009). Of interest is that the sequence tested was 99 % identical with WSMV isolates from Turkey and the USA and 96–97 % identical to isolates from Australia. Following this, an extensive survey of cereal experimental trials and commercial wheat crops was undertaken during the 2005–2006 summer season. Symptoms of wheat leaf samples taken from different cultivars ranged from being mild to symptomless. Nonetheless, the results indicated that WSMV is widely distributed in New Zealand on a range of wheat cultivars.

South America

In South America the presence of WSMV has been reported only in Argentina, although its mite vector, *A. tosichella*, has also been found in Brazil and Uruguay. In 2002, WSMV was detected in Argentina, in the central province of Cordoba (localities Jesús María, Marcos Juárez) (Truol et al. 2004). Within a few years the virus disseminated to the main wheat production areas of the country. Currently, in addition to Cordoba, the WSMV has been detected in the provinces of Buenos Aires, Entre Ríos, La Pampa, Santiago del Estero, Santa Fe, Tucumán, and Salta (Truol 2009). WSMV is considered to be a regulated, non-quarantine pest in Argentina (SENASA Resolución 248/2003), which implies permanent surveillance. In the provinces of Cordoba and Buenos Aires, in addition to wheat, other WSMV-infected Poaceae species during summer or winter (including cereals and voluntary weeds) are: corn, barley, triticale, *A. fatua*, *Brachiaria* sp., *C. dactylon*, *D. sanguinalis*, *E. crus-galli*, *Grama* sp., *Panicum* sp., *S. italica*, *Setaria* sp., and *S. halepense* (Sagadin and Truol 2008, pers. comm. 2009; Truol et al. 2010).

In 2007, a serious WSMV epidemic was observed in wheat in the province of Buenos Aires. Given its severity, it was suspected that a possible mixed infection of WSMV and WMoV was present. On this occasion, the diagnosis of WMoV in the localities of Necochea, Balcarce, Colonia de La Galia and Azul was confirmed (Truol and Sagadin 2008b). In 2007, severe WSMV outbreaks in wheat crops with 100 % incidence caused total losses on several farms in the zone of Mar y Sierras, Buenos Aires (Truol 2009; Truol and Sagadin 2008b).

In 2008, in different localities of the province of Cordoba (Jesús Maria, Marcos Juárez, Río Cuarto and Las Acequias), were also detected outbreaks associated with WSMV/WMoV mixed infections, but with a smaller incidence of disease than in Buenos Aires. In this province, it was observed that there was a WMoV incidence of about 13 % and a WMoV/WSMV mixed infection incidence of 17 % (Truol and Sagadin 2008c). It was also determined that in the locality of Jesús Maria, 24 % of spontaneous corn plants were infected with WSMV and only 3.4 % with WMoV (Truol 2009).

Wheat mosaic virus (WMoV)

High Plains disease (HPD), a severe disease of corn and wheat caused by WMoV, was first reported in the USA in 1993–1994 from Texas and Kansas and later from Colorado,

Nebraska, Idaho and New Mexico (Jensen and Lane 1994; Jensen et al. 1996). In addition to North America, WMoV has also been detected in South America, in Argentina (Truol and Sagadin 2007); however, it is not present in Europe or Asia and its presence in Australia has not been confirmed (Coutts et al. 2008a; Dwyer et al. 2007; Murray 2006) (Table 2).

Wheat mosaic virus is an RNA virus and infected plants have shown the accumulation of RNAs of three size classes: RNA-l (8 kb), RNA-m (2–2.5 kb) and RNA-s (1.4 kb) (Skare et al. 2006). The host range of WMoV includes wheat, barley, oats, rye, corn, *Bromus secalinus* L. (cheat grass) and some weeds such as *Setaria glauca* (L.) Beauv. (yellow foxtail) and *S. viridis* (Seifers et al. 1998).

Wheat mosaic virus infections of field-grown corn and wheat were associated with leaf symptoms including mosaic and curling. A generalized chlorosis was common on wheat, whereas corn exhibited red and yellow striping (Skare et al. 2006). On corn, symptoms included red striping (Jensen et al. 1996). WMoV symptoms may be confused with those caused by WSMV but WMoV symptoms can be much more severe than WSMV. WMoV symptoms range from mottling, chlorosis, necrosis and severe stunting to rapid death of the plant depending on environmental conditions, plant genotypes and time of infection (Mahmood et al. 1998). Highly susceptible host genotypes often die within 2 weeks of infection (Marcon et al. 1997a, b).

In Argentina, WMoV was detected for the first time in 2006, in the locality of Corral de Busto, province of Córdoba (Truol and Sagadin 2007). After that, WMoV was also detected in the provinces of Buenos Aires and Corrientes (Truol and Sagadin 2008d; Truol et al. 2010). In this country, corn and *S. glauca* were also found to be infected with WMoV on the edges of wheat crops (Sagadin and Truol 2008). Mixed infections have been observed causing severe symptoms in wheat with WSMV [see above, '*Wheat streak mosaic virus* (WSMV)'].

Coutts et al. (2008a) reported that WMoV was not found in any plant samples from Australia that had been tested for this virus. Despite this evidence, there have been conflicting reports about the occurrence of WMoV on that continent. Murray et al. (2005) noted that this disease had been detected in eastern Australia but this finding required further study. Dwyer et al. (2007) stated that WMoV was detected in stored wheat samples collected in 2003 from ACT, SA, NSW, Qld and Vic, usually in conjunction with WSMV (Geering pers. comm.). It was later reported by Murray (2006) that WMoV was detected in a small proportion of wheat samples from NSW that displayed WSMV-like symptoms during 2006. Schiffer et al. (2009) stated that WMoV was unofficially known to occur in eastern Australia (NSW) and that further research was pending. Hence, the occurrence of WMoV in Australia is yet to be confirmed.

Triticum mosaic virus (TriMV)

Triticum mosaic virus was isolated from wheat in Kansas (USA High Plains) in the spring of 2006. It was discovered when wheat plants of the cv RonL and other lines with WSMV resistance developed systemic virus-like symptoms in the field (Seifers et al. 2008). TriMV is transmitted by *A. tosichella* (Seifers et al. 2009). TriMV like other Potyviridae has flexuous filamentous particles and a single-stranded positive-sense RNA genome which is translated into one large polyprotein. The RNA strand has 10,266 nucleotides and the predicted polyprotein consists of 3,112 peptides. Altough TriMV is mite-transmitted like the *Tritimovirus* WSMV and *Brome streak mosaic virus*, it is significantly divergent and has more in common with *Sugarcane streak mosaic virus*, a member of the newly proposed genus *Susmovirus* (Fellers et al. 2009).

Double infections in wheat of WSMV and TriMV may induce disease synergism with severe leaf deformation, bleaching and stunting. Symptoms depend on cultivar and temperature (Tatineni et al. 2010). This virus has not been reported in any other country than the USA (Table 2).

Brome streak mosaic virus (BrSMV)

Brome streak mosaic virus was first isolated in the former Yugoslavia in 1977 from *Bromus mollis* L. (soft brome) and *H. murinum* (Milicic et al. 1980, 1982). Since then, BrSMV has been reported from *B. sterilis* and *H. murinum* in Germany (although originally misidentified as WSMV) (Rabenstein and Stanarius 1981; Rabenstein et al. 1982; Schubert and Rabenstein 1995) and from barley crops in France (Huth et al. 1995). In 2008, BrSMV was detected in Hungary, infecting an invasive weed species *Cyperus esculentus* L. (yellow nutsedge) (Takacs et al. 2008). No yield losses attributed to BrSMV have been officially reported in Europe. The presence of this virus was not reported in other continents (Table 2).

Brome streak mosaic virus like other Potyviridae has flexuous filamentous particles which are about 700 nm long and a single-stranded positive-sense RNA genome which is translated into one large polyprotein (Goetz and Maiss 1995). Originally classified in the genus *Rymovirus* that included the mite-transmitted Potyvirus, BrSMV together with WSMV was repositioned in the genus *Tritimovirus* (Stenger et al. 1998). The host range of BrSMV is restricted to plant species of the family Poaceae and Cyperaceae, in which it causes chlorotic leaf streaks. Evidence that WCM is the vector of BrSMV was obtained in 2007 (Stephan et al. 2008).

Relationship between wheat curl mite and transmitted viruses

Some eriophyoid mites, including WCM, have been recognized as vectors of several viruses. The relationships between such mites and transmitted viruses are highly specific. However, the mechanisms of transmission of most eriophyoid-borne diseases are not well understood, mainly because of the minute size of eriophyoid mites (Oldfield and Proeseler 1996).

Wheat curl mite was identified as a vector of WSMV by Slykhuis (1955). This virus is acquired by WCM during feeding and the mites remain infective for up to 9 days at 20–25 °C after removal from an infected plant, even after molting (Orlob 1966; Siriwetwiwat 2006; Slykhuis 1955). Although all stages (except eggs) are infective, adult mites can transmit the virus only if they acquired this at an immature stage (del Rosario and Sill 1965; Orlob 1966; Siriwetwiwat 2006; Slykhuis 1955). Although the adult stage is able to acquire the virus, it is probably unable to inoculate the plant (Orlob 1966). WSMV transmission efficiency varies among growth stages of WCM (Orlob 1966; Siriwetwiwat 2006; Slykhuis 1955). Immature stages exhibit a higher ability to transmit WSMV than do adult mites. Orlob (1966) had shown that the virus can be acquired after only a short feeding period, i.e., after a minimum stay of 15 min on an infected plant. The longer the time period, the higher the number of mites that can become infective. It is not certain whether WSMV transmission by WCM is due to regurgitation or via saliva. WSMV antigens have been detected in body fluids of WCM (Sinha and Paliwal 1976). WSMV particles have also been found in the mite gut by several investigators (Paliwal 1980; Paliwal and Slykhuis 1967; Stein-Margolina et al. 1969; Takahashi and Orlob 1969).

Paliwal (1980) reported that WSMV particles accumulated in the midgut persisted for at least 5 days. He had succeeded to find WSMV particles also in the salivary glands, suggesting that WSMV is circulative in its vector body but with no evidence for multiplication. Virus-specific immunofluorescent microscopy detected WSMV antigens near the anterior and posterior ends of bodies of viruliferous mites (Mahmood et al. 1997).

It has been confirmed that different WCM lineages present different abilities in vectoring WSMV. Schiffer et al. (2009) studied the occurrence of WCM lineages and WSMV infections in wheat fields in WA, Australia, between 2005 and 2006. The authors suggested that fewer WSMV detections and outbreaks observed in the studied areas could be because of the ability of WCM lineage present to transmit the virus. Despite extremely high populations of WCM being found in many locations in WA by Schiffer et al. (2009) as part of their molecular study, WSMV was not detected at each collection site. Based on the molecular results obtained by those authors, the mites present at the sites where WSMV was absent were found to belong to a single lineage of WCM that may not be a (efficient) vector of the virus. Seifers et al. (2002) found that populations of WCMs from five geographical regions in the USA all transmit multiple isolates of WSMV (see section 'Control strategies for wheat curl mite and transmitted viruses'). Further research in relation to this issue is still being undertaken (Schiffer et al. 2009).

The ability of WCM to vector WMoV was demonstrated by Seifers et al. (1997). Mites transmitted WMoV alone, or both WMoV and WSMV, to wheat and barley. A single mite specimen was able to propagate the virus. However, in experimental assay this transfer ability decreased over time and more mite specimens were needed for successful plant inoculation. Furthermore, the ability of WCM to transmit a virus varies among mite populations from different geographical sources. Hence, the epidemiology of High Plains disease may be influenced by inter- and intra-population variation of WCM (Seifers et al. 2002).

Wheat curl mite had been proposed for a long time to be a natural vector of BrSMV (Goetz and Maiss 1995; Goetz et al. 1995; Huth et al. 1995; Milicic et al. 1980). The first experimental evidence was given by Stephan et al. (2008). Mites raised on infected wheat were able to transmit the virus to healthy plants, with 80 % efficiency (four of five test plants) in transmission of a full-length cDNA clone of BrSMV and 33.3 % efficiency (two of six test plants) for the wild type BrSMV. No specific information is available on the mites' virus acquisition time, inoculation feeding time, the ability of instars to transmit the virus and temperature requirements for virus transmission.

Seifers et al. (2009) had experimentally shown that WCM transmits the TriMV to wheat. Transmission assays using bird cherry oat aphids, *Rhopalosiphum padi* (L.), did not succeed in infecting test plants, therefore WCM was considered to be the only TriMV vector. TriMV can be transmitted by WCM together with WSMV, or alone. The percentage of infected plants that were infested experimentally by WCM appears to depend on the source of mites suggesting that transmission abilities differ among mite populations. More research is needed to estimate the effect of WCM growth stage, acquisition time, inoculation feeding time and temperature during acquisition feeding, as well as inoculation feeding on TriMV transmission.

Pathways for wheat curl mite, its transmitted viruses and regulatory measures

The pathways through which WCM has been disseminated throughout the world are unknown. Eriophyoid mites are typically disseminated through the green tissues of

propagation material of their host plants or through fresh fruits or flowers and are not usually capable of disseminating by seed dispersion. These mites are usually very susceptible to dry conditions (Jeppson et al. 1975). Exchange and/or trade of wheat, other cereals and grasses that host WCM usually occur through seeds, except for the grass carpets that are commonly used for lawns. Some researchers have discussed the hypothesis that WCM could disseminate through infested seedlings of grasses that could be growing as contaminants in pots of flowers or ornamental plants being transported in international trade. Another hypothesis would be that WCM is able to survive for a short period of time as a contaminant with seeds of its host plants. If seeds were to originate from highly infested areas, numerous WCM could be harvested and transported as contaminants accompanying them. Even if a reduced number of mites could survive during transport and the seeds are quickly sown, they could then colonize the new seedlings. It is necessary to conduct experiments to evaluate how long WCM can survive when transported with seeds under different conditions. Another fact that should be taken into account is that WCM has often been found in greenhouses/glasshouses at experimental stations (e.g. Halliday and Knihinicki 2004) and sometimes high infestations are detected inside those areas (e.g. Pereira et al. 2009). It is possible that mites were originally infesting fields around the greenhouses and have then found favourable conditions indoors, allowing for the build-up of high populations. Another possibility is that mites could have been associated with seeds sown inside the greenhouses which were originally obtained through domestic or international germplasm exchange or breeding programs; next they may have colonized emergent seedlings and potentially reached high population levels.

In contrast to the possible pathways for WCM, those for WCM transmitted viruses are known. It has been demonstrated that the main WCM transmitted viruses—WSMV and WMoV—are seed borne, although only a low percentage of their transmission is by seeds. Studies by Jones et al. (2005) and Lanoiselet et al. (2008) showed that WSMV can be transmitted by seed and that this is likely to be an important source of inoculum especially when the mite vector is also present. In Australia, Jones et al. (2005) showed that the WSMV transmission rate by wheat seeds is around 1.5 %, which is similar to the highest rate obtained in Argentina by Sagadin et al. (2008). Transmission of WMoV has been reported for sweet corn under greenhouse conditions in the USA with a rate of 0.008 % (Forster et al. 2001). Although seed transmission is unlikely to be important in areas where WSMV already occurs, it plays an important role for introducing this virus into new areas. The risk of introducing more virulent forms of virus into areas that have a milder form of the virus through the exchange or trade of seed should also be considered.

Pathways for the introduction of WSMV into Australia and Argentina have been discussed. It was concluded by Dwyer et al. (2007) that the Australian outbreak of WSMV resulted from a single incursion taking place 10–20 years ago from the Pacific Northwest of the USA. Dwyer et al. (2007) stated that this had occurred as a result of imported wheat seeds that had passed through the principal post-entry quarantine facility at Tamworth in NSW where from infected seed had been distributed around Australia via the wheat breeding centres at Adelaide (SA), Canberra (ACT), Horsham (Vic) and Toowoomba (Qld). In contrast to Dwyer et al. (2007), Lanoiselet et al. (2008) suggested that WSMV may have entered Australia through a number of channels. Firstly, wheat seeds directly imported into Australia must be grown in a quarantine facility glasshouse and inspected for pest and disease symptoms at four stages of growth after which harvested seed from the screened disease-free plants may be released from quarantine. Secondly, wheat seeds are grown for a single generation in New Zealand. If found to be disease-free, harvested seed from those plants can then be sown under open field quarantine in Australia after

which the plants are inspected by a plant pathologist. These authors considered that this second approach presents a higher risk for the introduction of a disease such as WSMV because symptoms that are readily seen in greenhouses/glasshouses are much more difficult to observe in the field. Of importance is the fact that WSMV is also a seed-borne disease of corn and therefore most likely of other grass hosts including *C. dactylon*, *L. rigidum*, and *Phalaris aquatica L.* (canary grass). Seeds of corn and sweet corn are imported into Australia for direct sowing in the field and are not subject to the same quarantine measures as for wheat (Lanoiselet et al. 2008). Based on molecular data, Stenger and French (2009) found that WSMV isolates from Australia are closely related to isolates from the American Pacific Northwest and Argentina. Altogether, the results indicated that the same WSMV lineage established simultaneously in both Argentina and Australia. Of interest is that Truol et al. (2004) documented the first occurrence of WSMV from Argentina which was not long after the disease had been formally reported from Australia by Ellis et al. (2003a, b).

It is necessary to adopt strict regulatory measures to avoid the wider dissemination of WCM and its associated viruses. In addition, it is important to monitor the presence of this mite-virus complex in cereal production areas that have not yet been affected. Protocols for seed certification should consider that WCM-associated viruses only present a very low transmission rate through seeds and that their symptoms are not expressed under specific environmental conditions. A higher biosecurity level could be obtained through the maintenance of plants under quarantine conditions for several stages of growth that are away from commercial production areas.

Ecological factors affecting wheat curl mite dispersal and virus epidemiology

The hosts for WCM are mostly annual grasses, which means that it requires extensive dispersal from host to host in order to survive throughout the entire year. During its life cycle, both walking and aerial dispersal are important elements in the survival of a mite. Phoresy has been observed and proposed as another dispersal mechanism (Gibson and Painter 1957; Michalska et al. 2010; Sabelis and Bruin 1996). When insects and mites are both present in high numbers, the potential for successful phoresy may be good. However, extensive movement is not likely to take place, and reliance on the vagaries of potentially sporadic insect populations would be a poor survival strategy.

The presence of WCM in the field is closely tied to the growth patterns of its host plants. In North America, the most important host for WCM is winter wheat because this provides a live host for the mite to survive on for about three quarters of the year. On winter wheat, the mites go through a predictable cycle of population buildup (Wegulo et al. 2008). Mite populations that establish on winter wheat in autumn will likely survive through the winter and build up in the spring and early summer. Serious mite and virus problems can also impact on spring wheat, but this will only occur in areas where mite populations have developed and moved from winter wheat or volunteer winter wheat as noted by Gillespie et al. (1997).

After arriving on a host plant, WCMs always crawl to the most secluded places, thus they are almost always found deep within the whorl of vegetative wheat. Mites constantly move from one expanding leaf to the next developing leaf. This movement can expose mites to potential predation, desiccation and dislodgement from the plant; however, such exposure is limited as much of this movement occurs within the whorl of the plant. This cycle of movement on the plant is continued until the head emerges from the boot. Once

the wheat head emerges, the number of secluded sites among the developing kernels that are suitable for mite feeding and reproduction dramatically increases. One result of the increase in feeding sites and the reduced need to move on the plant is a dramatic increase in the mite population as the wheat is approaching maturity (Gillespie et al. 1997).

Mite population densities on wheat as it is maturing will be greater than in any other time of the year. Mahmood et al. (1998) measured WCM populations in the heads of maturing wheat in Nebraska, and by using these values and the average density of wheat tillers, the estimated potential densities of mites can range from 5–12 billion mites per hectare. This population increase contributes to the mites' successful dispersal strategy.

The small size of WCM enables it to be effective in aerial dispersal on air currents. The presence of the caudal lobe on the mite enables it to stand erect with legs in the air and when it senses air movement it can rapidly release the grip of the caudal lobe and become airborne (Lindquist and Oldfield 1996; Nault and Styer 1969). Under conditions conducive for movement, WCMs move to the top of the plant, some stand erect on their caudal lobes and others climb over these mites to provide themselves an elevated advantage for escape through the surface boundary layer and into the wind. Numerous studies have noted the strong relationship between wind and mite movement (Coutts et al. 2008b; Nault and Styer 1969; Staples and Allington 1956). Stilwell (2009) in using remote sensing to track virus symptoms in wheat, and thus, mite movement, found that tracking the direction of wind speeds over 9 m/s provided the best relationship with eventual spatial spread of the virus.

Because WCMs can be found in large numbers moving off maturing wheat plants, it is often assumed that such movement is initiated when plant condition begins to deteriorate. However, Thomas and Hein (2003) demonstrated that a more important component in determining the extent of mite movement may be the size of the mite population itself. Plants in good condition produce more dispersing mites than plants in poor condition. This idea was also supported by the work of Jiang et al. (2005) who found that 'total green leaf area' was the best predictor of mite dispersal. This demonstrates perhaps the most important factor in mite movement. Mites are r-strategists and rely on their tremendous reproductive capacity to enhance their dispersal success. Maximizing the numbers of mites available to move will maximize the success of dispersal and, thus, virus spread.

The importance of reproductive success to mite dispersal is often not considered when evaluating hosts for their potential to contribute to mite movement or virus spread. Other plant hosts can be important green bridge hosts, such as corn as demonstrated by Nault and Styer (1969) and many of other host grasses (Brey et al. 1998; Christian and Willis 1993; Connin 1956b; Coutts et al. 2008b; del Rosario and Sill 1965). However, these studies mostly demonstrate the qualitative ability of grass species to host WCMs, primarily at a single growth stage. But, there is little quantitative data on the mites' ability to reproduce on most of these grass hosts, especially considering more than one growth stage under the stressed conditions that often occur for such hosts in the field. The limited quantitative data on WCM hosts indicate that there are few hosts for the mite that allow the reproductive success that wheat offers, and hence the potential success in dispersal. The ecology of the mite and epidemiology of the viruses will vary in different growing areas worldwide depending on the presence, seasonality and suitability of hosts for mite reproduction and maintenance of the viruses.

There are two periods of WCM aerial dispersal that are critically important to mite ecology and virus epidemiology in wheat. Successful dispersal from maturing wheat to acceptable summer hosts allows for both mites and virus to survive the 'green bridge' period between wheat maturity and emergence of the new wheat crop. Even though there are several hosts that the mite can use during this period, it has been demonstrated

repeatedly that the most important host in the epidemiology of wheat viruses is volunteer wheat that arises before wheat harvest (Somsen and Sill 1970; Staples and Allington 1956; Wegulo et al. 2008). Historically, in the Great Plains of North America where WSMV problems have been the most prevalent, volunteer wheat that arises after a pre-harvest hail storm has a very high chance of supporting serious populations of mites and virus. This results because there is no break in the 'green bridge' as mites move directly from the maturing wheat to the seedling volunteer and later to the new crop wheat in the fall. One interesting factor that has arisen in recent years with the presence of both WMoV and TriMV, is that volunteer wheat infested with mites and infected with multiple viruses has a more difficult time surviving throughout the summer. It is uncertain how significant this impact may be on virus epidemiology.

The second critical period of aerial dispersal for WCM is the movement from the 'green bridge' host back to the new wheat crop. Virus infections that are initiated during the early stages of wheat growth will have the greatest impact on the ultimate yield of the plant (Wegulo et al. 2008). Severity of infection in a field will depend on the number of mites present in the source or 'green bridge' host and the distance that source is from the field. Sources with lower mite density and, thus, lower movement will be characterized by virus spread only into the borders of the field (Coutts et al. 2008b; Somsen and Sill 1970; Staples and Allington 1956; Wegulo et al. 2008). Greater mite density in the source results in greater dispersal that will expand this border effect to perhaps include an entire field or beyond. Stilwell (2009) through remote monitoring of spatial virus spread around small field plots has made estimates that significant spread could extend up to three or more kilometers with the greatest spread in the direction of the prevailing winds.

Dispersal beyond a local growing area is an important consideration in developing management options for newly infested/infected growing regions, but this is extremely difficult to measure directly. Indirect evidence exists that implies considerably longer range movement for the mite than has been considered previously. Erayman et al. (2003) and McNeil et al. (1996) characterized the genetic variability of WSMV across Nebraska and found as much virus variability within a field as was seen between counties across Nebraska. Seed transmission of WSMV (Jones et al. 2005) could contribute to this variability, but the extent of this variability suggests that extensive mite dispersal and subsequent virus transmission across this growing region seems a more likely major contributor. The presence of TriMV was quickly found across much of the Great Plains region in North America (Burrows et al. 2009), indicating that the virus spread across a wide region may be quite efficient. Siriwetwiwat (2006) also saw the distribution of A. tosichella haplotypes to be well mixed across parts of Nebraska, Kansas and Montana, also indicating these mites are mixing regionally.

The greatest impact of mite dispersal is in the effect on the spread and redistribution of viruses; however, our knowledge of mite dispersal and virus spread is limited. Recent occurrences of these wheat viruses worldwide have raised questions about intercontinental movement of the mite and virus. Because of the mites very limited ability to survive off green plants it is unlikely that the mites themselves are responsible for this spread. Genetic comparisons of mites across these world regions may be able to address this question. Perhaps the best answer lies in a greater understanding of virus transmission through seed wheat and associated cereal crops (Dwyer et al. 2007; Jones et al. 2005). If WCMs capable of transmitting virus are present in a region, the introduction of the virus, even at low levels thus far demonstrated for seed transmission, could be very important.

The introduction of one or more of these viruses into new production areas will require an improved understanding of how WCM fits into the areas cropping system. Management

in these areas will require a better understanding of the major hosts for both the mite and the virus and how they survive through the season both on the wheat, but especially during the time period between wheat crops. As in North America, effective management of this problem will need to focus on what happens during the 'green bridge' period.

Control strategies for wheat curl mite and transmitted viruses

Management of WCM-transmitted viruses must be tied to the management of the mite vector. Chemical control of WCM is not effective and has been shown to be difficult because of the secluded nature of the mites on plants (Harvey et al. 1979; Skare et al. 2003; Kozlowski 2000; Wegulo et al. 2008). The most effective methods to minimize losses from WCM-transmitted viruses in cereal crops have focused on cultural and plant resistance methods.

Cultural methods

The most important management practices have proven to be those that target the control of 'green bridge' hosts of the mite. It is extremely important to disrupt the lifecycle of WCM to reduce the potential for virus spread by destroying all cereal volunteers (particularly wheat) and grass hosts, which act as a green bridge at least 3 weeks prior to sewing wheat. In the Great Plains of North America where this virus complex has caused the most serious and consistent damage through the years, the primary host of concern is volunteer wheat that arises after a preharvest hail, providing a direct link for the mites to move from host to host (Wegulo et al. 2008). Other potential green bridge hosts include corn and grass weeds in surrounding paddocks, borders and grain storage areas. Another important cultural practice that limits virus infection is to avoid planting cereals in early autumn to help provide a host-free period for the mite and virus between green summer hosts. This helps to reduce the period that wheat seedlings are exposed to favourable temperatures in autumn that allow for the rapid build-up of mite populations and virus infection. Sowing oats, triticale and possibly barley rather than longer-season wheat varieties in high-risk situations will reduce damage potential (de Wolf and Seifers 2008; Simfendorfer and Nehl 2010). Other management options include using seeds from virus free crops as much as possible (bulk seed testing is commercially available), and monitoring of their crops to determine whether symptoms of WSMV/WMoV or feeding by WCM are present.

Host plant resistance to wheat curl mite and transmitted viruses

The significant impact and persistence of this mite-virus complex in winter wheat in North America has made it an important target for the development of host plant resistance to WCM and/or WSMV. Since the identification of the mite-virus relationship in the 1950s, numerous efforts have been made to find resistance in wheat and related species to aid in the management of this complex of viruses. These efforts have increased through the decades and have provided considerable benefits; however, limitations in the diversity of the resistance that has been identified and complications resulting from vector-virus-plant relationships have limited its success.

An early effort in evaluating wheat varieties for resistance to WCM focused on the trichome density of wheat. Studies found that varieties with increased trichome density

and/or length were more heavily infested with WCMs and likely to be more heavily infected with WSMV (Harvey and Martin 1980; Harvey et al. 1990). Such studies proposed that landing efficiency was improved for WCM on those varieties with higher trichome density and this characteristic would benefit varieties that had been developed for high-risk regions. However, there have been limited efforts in identifying and breeding for trichome density, because of the difficulties involved in breeding for this characteristic and the limited perceived benefit of the partial resistance provided.

A great deal more effort has gone into identifying and selecting for resistance to WCM. No mite resistance in common wheat had been reported until Harvey and Martin (1992) found several wheat accessions with strong resistance. Prior to this, several sources of resistance had been transferred into wheat from related species. The first of these was the 1B–1R chromosome from rye (Harvey and Livers 1975; Martin et al. 1984). These findings documented the value of the rye gene and lead to the development of the cultivar 'TAM 107', which became widely used in the Great Plains region of the USA. This gene was later mapped and named *Cmc3* by Malik et al. (2003b). Additional sources of resistance to mite colonization have been identified from partial amphiploids of wheat and related species. The mite resistant gene *Cmc1* originated from *A. tauschii* and was found on the 6DS chromosome (Thomas and Conner 1986; Whelan and Thomas 1989; Thomas and Whelan 1991). The *Cmc2* gene originated from *Thinopyrum ponticum* (Podp.) Barkworth & DR Dewey (tall wheat grass) and is also found on chromosome 6 (Chen et al. 1998; Martin et al. 1976; Whelan and Hart 1988). A fourth named gene, *Cmc4*, was found to also originate from *A. tauschii*, and it was found to segregate independently from *Cmc1* (Malik et al. 2003b). Another mite-resistant gene originated from *Haynaldia villosa* (L.) Schur. and is also found on chromosome 6 (Chen et al. 1996). Other resistant sources have been identified as well, e.g. wheat-*Thinopyrum intermedium* (Podp.) Barkworth & DR Dewey partial amphiploids (Chen et al. 1998, 2003).

Evaluations of the effectiveness of mite resistance for controlling WSMV have demonstrated that the tactic has been successful, but these studies primarily relied on the resistance derived from rye (Conner et al. 1991; Harvey et al. 1994). However, Harvey et al. (1999) and Thomas et al. (2004) demonstrated that effectiveness may vary depending on the genes that are deployed. Harvey et al. (2003) in a greenhouse study also showed that even in the absence of virus, mite resistance did provide some yield protection from the mites.

None of these genes have been deployed as widely as the rye translocation gene in 'TAM 107'; however, many have been incorporated into varietal development. A major drawback to widespread deployment of most of these genes is that the reaction to these genes varies depending on the source of mites that are used. Harvey et al. (1995b) first identified WCM strains with differential responses to various sources of resistance (i.e., biotypes). Harvey et al. (1999) found a varied response to seven WCM-resistant sources by five geographically distinct mite collections (USA: Nebraska, South Dakota, Montana, Texas; Canada: Alberta). They also found a varied response when comparing eight mite collections from across Kansas. These differences between mite populations, in response to resistance genes, have serious implications to gene deployment and managing these genes to avoid biotype development. This is demonstrated by findings in the mid 1990's, that WCM populations in the region were found to have overcome the resistance gene in TAM 107 (Harvey et al. 1995b, 1997).

The search for resistance to WSMV began in the early 1950s (Fellows and Schmidt 1953; McKinney and Fellows 1951), and these efforts continue today with increasing hope for success. However, through all these efforts, only very modest improvements have resulted

from selections within the primary gene pool of wheat (Friebe et al. 2009; Graybosch et al. 2009). Considerable resistance has been found in wild relatives of wheat. Multiple sources for WSMV resistance have been transferred into wheat via translocation or amphiploid generation from *Thinopyrum* species (Chen et al. 1998, 2003; Friebe et al. 1991, 1996). Through all these efforts only one WSMV resistant gene, *Wsm1*, has been named. *Wsm1* traces back to transfers from *T. intermedium* in the 1970's (Wells et al. 1973). Considerable effort has been made through the years both to identify and improve transferred genetic material from numerous gene transfers to wheat; however, recent developments provide perhaps the greatest hope for important progress since this effort began nearly 60 years ago.

The first release of a cultivar with dramatically improved resistance to WSMV was made in 2006 with the release of the cultivar 'RonL' (Martin et al. 2007). The source of the resistance in RonL is not known, but it traces back to the germplasm CO960293 (Haley et al. 2002). The resistance in RonL has been shown under controlled conditions to be temperature sensitive with very strong levels of resistance at 18 °C, but complete breakdown of resistance at 24 °C (Seifers et al. 2006, 2007). Temperature sensitivity in the field has proven to be an issue with RonL, but its success has also been compromised by the appearance of TriMV (see discussion below).

A second major advance in WSMV resistance development has occurred in the recent release of the cultivar 'Mace', the first cultivar to carry the *Wsm1* gene (Divas et al. 2006; Graybosch et al. 2009). The resistance level in this cultivar is a major leap in the level of resistance to WSMV, and it has been demonstrated to hold up well in the field. However, recent trials indicate that even this level of resistance can be overcome under very heavy infection pressures (Hein unpubl. data).

Another area of WSMV resistance in wheat that has been investigated is the potential of resistance in perennial wheat. Investigations into WSMV resistance in perennial wheat germplasm have identified several sources that are resistant (Cox et al. 2002, 2005). WSMV resistance would be critical to perennial wheat, but the utility of moving this resistance to regular wheat has yet to be proven.

In addition to genes found in wild wheat relatives, attempts are underway to develop transgenic sources of resistance. Sivamani et al. (2000) used a viral replicase NIb gene to confer resistance to wheat, but the resulting plants did not show effective resistance. Later, the WSMV viral coat protein gene was used to confer resistance, but no coat protein was detected (Sivamani et al. 2002). Sharp et al. (2002) tested transgenics developed with both the replicase gene and coat protein with success in the greenhouse, but they found no effective field resistance. Transgenic improvements may hold great promise for the availability of virus resistant commercial lines in the future, but there has been limited success in developing transgenic improvements in wheat.

The association of WCM and WSMV with corn was recognized in the 1950s (Sill and del Rosario 1959; Staples and Allington 1956). Most corn hybrids were found to be resistant but some inbreds are highly susceptible (How 1963). The majority of this resistance is expressed as tolerance as corn remains a symptomless carrier of the virus. Movement away from the use of these inbreeds as parent crossing lines resulted after severe symptomology limited their performance in hybrid production. Later work has identified three major resistance genes (*Wsm1*, *Wsm2* and *Wsm3*) in corn (McMullan et al. 1994). Perhaps the most obvious aspect of the relationship between corn and WCM is the presence of kernel red streak (KRS). This reddening of the pericarp tissue can be dramatic and varies with corn lines, but KRS is considered to be due to a reaction of corn to the feeding of the mites on the kernels as they are developing, rather than a relationship with

transmitted viruses (Nault et al. 1967). In addition, there is little economic impact of the presence of KRS, except associated with food-grade corn (Liu et al. 2005).

One major factor in the deployment of WSMV resistance is the occurrence of two other wheat viruses known to be transmitted by WCM: WMoV and TriMV. WMoV shares some similarities with two other diseases found in association with WCM and wheat, WSpM (Slykhuis 1956) and wheat spot chlorosis pathogen (Bradfute et al. 1970; Nault et al. 1970). However, like WMoV, these viruses could not be manually inoculated and antisera were not developed, so no direct comparisons can be made. Because WMoV cannot be manually inoculated to wheat, little is known of the interaction between WSMV and WMoV. However, Seifers et al. (2002) demonstrated the possibility of enhanced transmission of WMoV in the presence of WSMV. Because of the difficulties in studying the two viruses together, it is difficult to predict the impact of WMoV presence on WSMV resistance expression in the field. No resistance to WMoV has been found in wheat, but strong resistance has been found and is widely deployed in corn (Marcon et al. 1997a, b, 1999). The resistance found in corn results from tolerance to the virus presence and, thus, corn also serves as a symptomless carrier of WMoV.

Another complication of studying WMoV and WSMV is the virus' relationship to WCM. Seifers et al. (2002) found that populations of WCM from five geographical regions (Kansas, Montana, Nebraska, South Dakota, Texas) all transmitted multiple isolates of WSMV; however, they differentially transmitted WMoV. These were the same populations that Harvey et al. (1999) separated into various biotypic categories in response to different mite resistant genes in wheat. Only the Nebraska population transmitted WMoV effectively, but under some conditions the Montana populations did transmit as well. Siriwetwiwat (2006) was able to separate these five groups into two genetically distinct groups and found that these mite populations could be found in different proportions in mite samples from Nebraska, Kansas and Montana. This demonstrates the robustness of the mite populations for adapting to selection pressure through the deployment of resistant genes.

A third virus has recently added complications to this mite-virus complex. Seifers et al. (2008) identified TriMV as a new virus present in wheat in the Great Plains of North America, and also it was determined that corn is not a host for this virus (Seifers et al. 2010). The presence of this new virus illustrates the difficulties encountered with this multi-virus complex. RonL, a wheat cultivar recently released with very strong WSMV resistance has been found to be quite susceptible to TriMV (Friebe et al. 2009); however, Mace, also a recently released wheat cultivar with strong resistance to WSMV has been found to be resistant to TriMV in both greenhouse studies (Tatineni et al. 2010) and in field trials (Hein unpubl. data).

Final remarks

Wheat curl mite and the viruses it transmits can cause serious impact on cereal crops, particularly wheat, in important production areas throughout North America, Europe and Asia (Table 2). In the last decade, this mite-virus complex has expanded into Oceania and South America where it has become an emergent phytosanitary issue. Although efforts have been directed towards preventing or minimizing crop losses, the problem associated with declining yields still remains. The difficulty in making progress towards managing WCM and its transmitted viruses in areas that have been affected for decades is mainly because of the increasing complexity of the pathosystem as a result of the detection of several new WCM-transmitted viruses. The widespread presence of this mite-virus

complex and its recent emergence on specific continents partly relates to the uncertain pathways that have occurred for the movement of WCM. This also relates to the difficulty in detecting virus-infected seeds that have been mixed in with large amounts of exchanged or market seeds. Those aspects have complicated the tasks of plant protection organizations and facilitated introductions into new areas.

Basic knowledge of the systematics and biology of WCM is scanty. Such information is desperately needed for both the prediction of risks associated with the mite-virus complex and the establishment of management measures in the most diversely affected areas. An integrative approach utilising molecular tools and detailed morphological studies is necessary for characterizing biotypes and/or species composition within the WCM complex in order to map their occurrence. This should be possible through the joint efforts of researchers from various continents. The next step would be to study the ability of strains/species to transmit viruses. It would also be important to study the biological parameters of strains/species under different environmental conditions and the host plant range so that improved resistant varieties/genes can be developed. And it is necessary to gather information on the multigenerational host plants for WCM and to study its intrinsic rate of growth on those grasses which can be used as a 'green bridge' in different affected areas. Such information would be very useful for predicting virus epidemiology and working out the most effective control strategies.

Although the results from extensive efforts over the last 60 years in developing mite- and/or virus-resistant wheat cultivars have been somewhat disappointing, several important advances have been made. Tremendous benefits were obtained from the incorporation of mite resistance into some widely used lines, even though this resistance was not stable. A greater understanding about the identity and ecology of WCM is necessary in order to predict the long-term success of mite resistance in wheat. The recent release of varieties with much stronger resistance to WSMV provides renewed hope for even greater advances in the future. The increased use of molecular breeding techniques to improve and incorporate resistant genes into germplasm and commercial cultivars more efficiently is also valuable. In addition, an improved understanding of mite-virus-plant interactions may increase our ability to eventually target potential transgenes that may be incorporated into wheat to provide more robust resistance to this mite-virus complex.

A greater knowledge about virus transmission via seed and of the longer-range movement potential of WCM and its pathways, could be extremely useful for providing technical support for plant protection organizations as it would help to guide the adoption of more effective quarantine measures. The optimization of virus detection methods surely would also be beneficial. The adoption of quarantine measures should take into account the occurrence of WCM biotypes or species complexes that have not yet been mapped and also the fact that some WCM-transmitted viruses still present a restricted distribution. Avoiding the wider dissemination of members of this mite-virus complex is important for minimizing its impact on cereal crops worldwide.

Another challenge are the possible effects of climate change on this mite-virus complex and the impact this will have on cereal production areas. For instance, in North America, the trend towards a longer and warmer autumn season has resulted in an increased time period for WCM to spread and transmit viruses as populations build-up on wheat. Such conditions have given rise to more significant virus problems in situations that had previously been considered to be of low risk (Hein, unpubl. data). Better understanding of WCM ecology and the epidemiology of its transmitted viruses under the senario of climatic change is necessary, considering that future management will need to incorporate an

integrated approach that relies upon controlling 'green bridge' plant hosts but also on a more robust level of resistance in wheat cultivars.

In areas where WCM and the transmitted virus(es) have represented a recent or emerging problem, continuous monitoring should be conducted in order to detect and map the occurrence of both the mite vector and virus. Establishing the range of important host plant species, improving prediction capabilities and determining varietal impact under virus pressure is also vital. The evaluation of resistance and/or susceptibility of commercial wheat and corn varieties to this mite-virus complex in newly affected areas should be a priority. Equally important is that breeding for resistant varieties needs to take into account whether there are any selected varieties with resistance that are adapted to the growth conditions of those areas.

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