

**THE WHEAT CURL MITE (*ACERIA TOSICHELLA*, PROSTIGMATA:
ERIOPHYIDAE) COULD ESTABLISH IN SOUTH AFRICA**

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Abstract

Biological invasions by agricultural pests can have serious negative impacts, including decreases in crop yield and economic losses. The MT-1 and MT-8 genotypes of the wheat curl mite (*Aceria tosichella*) ('WCM' refers to just these two genotypes) are globally distributed pests of wheat and maize that have not been recorded in South Africa. This study examined whether WCM could be introduced to, and establish in, South Africa. Trade data were used to determine if viable pathways of introduction are present. A species distribution model and data on wheat and maize production were used to determine if WCM could establish where its hosts are grown. WCM is most likely to be introduced to South Africa as a contaminant of maize from Argentina, Brazil, Uruguay, and USA; live plant imports from China and Germany; and on seed imports from Brazil and Australia. Some of these pathways are not currently prominent but could increase in the future. Parts of South Africa were predicted by the species distribution model to be climatically suitable for WCM, and within some of these areas the host crops are grown. Therefore, if WCM is introduced it is likely to establish and cause extensive damage to agriculture. We recommend that WCM be considered for inclusion in South Africa's import conditions as a quarantine pest.

Keywords: Agricultural pests, alien species, biosecurity, biological invasions, pathways of introduction, species distribution modelling

Introduction

The amount and frequency at which commodities are transported around the world has escalated dramatically with innovations in technology and has facilitated countless introductions of alien species (Meyerson and Mooney 2007, Faulkner et al. 2017a). The introduction of some alien species has had positive agricultural impacts, for example several introduced crop and livestock species account for the majority of the world's food supply (Pimentel et al. 2001). However, along with trade in agricultural commodities comes the risk of inadvertent introduction of contaminant pests and diseases. Alien agricultural pest species can decrease crop yields and food security (Bebber et al. 2014), and their post-introduction management is extremely costly (Simberloff et al. 2013). For example, in South Africa, alien arthropod pests and plant pathogens were estimated to cause 2.8 billion US dollars of damage per year to crops (Pimentel et al. 2001), a figure which may have increased in the intervening years. It is usually more efficient and cost-effective to prevent the introduction of alien species than to manage a subsequent invasion (Simberloff et al. 2013). For this reason, South Africa has enacted legislation and developed protocols to minimise the introduction of plant pests and pathogens with international trade. These protocols include lists of prohibited organisms for agricultural (Agricultural Pests Act, South Africa 1983) or environmental (National Environmental Management: Biodiversity Act, South Africa 2004) imports.

The wheat curl mite (*Aceria tosichella* Keifer, Prostigmata: Eriophyidae) is an agricultural pest of cereal crops (Poaceae), causing serious damage in many countries. It is believed to be native to Europe and southwest Asia and comprises a number of distinct genotypes which differ in pest status (Skoracka et al. 2014a). These genotypes are molecularly and physiologically distinct but are difficult (and in some cases impossible) to distinguish morphologically, leading to difficulties in accurately assessing their historic and current geographic distribution. Wheat curl mite has been reported on over 100 grass species (Poaceae family) (Brey et al. 1998, Navia et al. 2013a), with different genotypes being associated with different hosts (see Skoracka et al. (2017) for more detail). Two genotypes, MT-1 and MT-8, are wide-spread, have the largest host range, and are considered the most pestiferous (Skoracka et al. 2014a, 2018). They are closely associated with cereal crops, most notably wheat (*Triticum* L. species) and, to a lesser extent, maize (*Zea mays* L.) (Skoracka et al. 2014a, 2017). However, both MT-1 and MT-8 genotypes can colonise a number of

plants in the Poaceae family (Skoracka et al. 2014a, 2018) and the MT-1 genotype can successfully colonise garlic, onions and tulips (Skoracka et al. 2014a).

In wheat growing areas where wheat curl mite has been introduced, it has caused extensive damage to crops (Navia et al. 2010). Wheat curl mite itself can cause damage, which in some parts of the world has resulted in yield losses of up to 30% (Harvey et al. 2002), but the majority of the damage caused is by the viruses it transmits. These include the wheat streak mosaic virus (Slykhuis 1955 in Brey et al. 1998), which has caused wheat yield in the United States of America (USA) to be reduced by 32% to 99%, depending on the state and the variety of wheat (Navia et al. 2013a, 2013b).

Wheat curl mite, like all other phytophagous mites, relies on its host for survival and, in the ideal environment [i.e. warm and humid conditions (Schiffer et al. 2009)], genotypes MT-1 and MT-8 [which correspond to genotypes Type 1/WCM1 and Type 2/WCM2 in Schiffer et al. (2009) and Wosula et al. (2015)] can survive up to 276 hours off their live host plant (Wosula et al. 2015).

Neither wheat curl mite nor its main associated virus, wheat streak mosaic virus, have been reported in South Africa (Smith Meyer and Craemer, 1999; CABI 2020a). Wheat curl mite has not been reported anywhere in Africa, but the virus is present in Zambia, Algeria, and Kenya, and therefore the mite is presumably present there (Kapooria and Ndunguru 2004, Benmokhtar and Yahia 2009, CABI 2020b). As wheat and maize are major food crops for South Africa (Statistics South Africa 2010), the introduction of the MT-1 and MT-8 genotypes of wheat curl mite and their associated viruses could result in major crop losses and other socio-economic impacts. We aimed to use trade data, a species distribution model, and maize and wheat production data to determine whether these two wheat curl mite genotypes (MT-1 and MT-8) are likely to be introduced to South Africa, and establish in areas of the country where hosts (wheat and maize) are grown. Hereafter 'wheat curl mite' will refer to all genotypes of wheat curl mite and 'WCM' will only refer to the two genotypes of wheat curl mite (MT-1 and MT-8) that were assessed in this study.

Methods

Pathways of introduction

In order to determine if WCM are likely to be introduced to South Africa, we performed a literature search to identify pathways that have facilitated the introduction

of WCM to other parts of the world. The pathways of introduction for WCM are not well known (Navia et al. 2013b), however, it could be transported to South Africa as a contaminant on three types of commodities: (1) on grasses growing in imported pot plants (Navia et al. 2006), (2) on the imported seeds of hosts (Navia and Fletchmann 2008, Navia et al. 2013b), and (3) on live tissues of host plants (Navia et al. 2013b).

Import data for South Africa that are related to the three potential pathways of introduction were obtained from the UN Comtrade database (<https://comtrade.un.org/>, accessed 7 August 2019, see supplementary material for more details). These data were used to determine if the potential pathways of introduction for WCM link South Africa to parts of the world where the mite occurs. As genotype information is not available for all records, it is difficult to identify the countries in which the MT-1 and MT-8 genotypes occur. However, according to Skoracka et al. (2014a) only the MT-1, MT-7 (which occurs only on barley) and MT-8 genotypes are found outside of Europe, and so records from other regions are likely to be of the two genotypes of interest. Therefore, we followed the precautionary approach and included all countries that have reported wheat curl mite in the pathway analysis.

As WCM can survive 11.5 days (276 hours) off their live host (Wosula et al. 2015), the length of time it takes seed imports to reach South Africa will play an important role in determining whether WCM could survive the journey to South Africa if it is transported as a contaminant of seed imports. We assumed that seed imports are transported by ship (Wilson et al. 2016). We used data recorded by The Automatic Identification System on the identity and location of ships travelling around the globe to calculate the minimum voyage duration from countries where wheat curl mite occurs to South Africa, and compared this to the maximum WCM off-host survival time. These shipping data were obtained through the Sea-Web Movements database provided by IHS Inc. (http://www.sea-web.com/seaweb_movements_module.html, accessed 1 March 2015), for further details see Faulkner et al. (2017b).

Climate suitability

Species distribution modelling was used to determine if the climate in South Africa is suitable for WCM to establish. The potential distribution of these genotypes was modelled using Maxent software version 3.4.0 (Phillips et al. 2006), which uses the maximum entropy principle to model the potential geographic distribution of a

species (Phillips et al. 2006). In order to produce a model in Maxent, species occurrence data, background data and environmental predictors are required.

Occurrence records for WCM were obtained from published papers (Pereira et al. 2009, Castiglioni and Navia 2010, Miller et al. 2013, Skoracka et al. 2012, 2013, 2014a, 2014b, 2018, Kuczyński et al. 2016, Ranabhat et al. 2018). Where genotype was recorded, only records for MT-1 and MT-8 genotypes were included. Records with no genotype information were only included if the host plant was wheat or triticale (genotype information was available for all records for which maize was the host). Triticale was included as it is a hybrid of wheat and rye and as WCM have previously been reported on this cereal. A total of 285 records were obtained, their quality was assessed using the Biogeo package (Robertson et al. 2016) in R version 3.5.2 (R Core Team 2019), and records with errors were removed. Two records, which did not have coordinates, and 153 records, which were duplicates within a 10-minute grid cell, were removed. A further 50 records from Poland were removed to reduce sample bias, as 76% of the records were from Poland. A subset of 80 occurrence records were thus available for modelling.

The Köppen-Geiger climate zones (Kottek et al. 2006) and the occurrence records in the native range were used to identify the climates that the WCM occupies in the native range. Ten thousand background points were randomly selected from areas in the native range where these climates occur, but where there were no occurrence records.

Bioclimatic variables from the Worldclim dataset (<http://worldclim.org/version2>, downloaded 18 June 2019) at a 10 minute spatial resolution were used for modelling (Fick and Hijmans 2017). The predictor variables used for modelling were: maximum temperature of the warmest month, minimum temperature of the coldest month, and annual precipitation. These variables were selected as temperature and humidity are important factors for WCM survival (Schiffer et al. 2009) and as a correlation analysis showed, these variables are not highly correlated.

In Maxent, we produced a conservative model [regularization multiplier 0.001] which predicts areas that are very similar climatically to the areas where the occurrence records were found (Phillips et al. 2006). A more lenient model may predict a larger potential distribution. However, as the prediction of our species distribution model is conservative, if any areas of South Africa are predicted as climatically suitable then it is highly likely that WCM would establish if introduced. The performance of the

model was evaluated using cross validation (with the data split five times) and by calculating the area under the receiver operating curve (AUC) statistic. A model is considered useful if the value of the AUC statistic is between 0.7 and 1 (Swets 1988).

Suitability of biotic environment

Wheat, the main host plant of WCM, is present in South Africa. Maize is also a host for these genotypes and was included in the analysis because it is an important crop for South Africa, having the highest production (du Plessis 2003). Data on the production of wheat and maize per magisterial district for the nine provinces of South Africa were obtained from Stats SA (Statistics South Africa 2010).

Establishment in areas where hosts are grown

The wheat and maize production data were mapped and a binary map (1 and 0) was produced using a threshold of 20000 metric tons, where areas with wheat and/or maize production above this threshold had a value of 1. The output of the species distribution model was reclassified into a binary map (1 and 0) using a threshold of 0.5, where areas with a climate suitability greater than 0.5 had a value of 1. The two maps were superimposed to identify parts of the country that are climatically suitable for WCM and where wheat and/or maize production is high.

Results

The value of imports that could facilitate the introduction of WCM to South Africa varies among the countries where wheat curl mite occurs (Figure 1). Maize imports (unprocessed maize and excluding seeds) are notably more prominent in comparison to the other types of imports through which the WCM could be introduced (Figure 1B). These imports are mostly from Argentina, followed by Brazil, Uruguay, and USA, while wheat imports (unprocessed wheat and excluding seeds) are mostly from Russia and Canada. Maize seed was the second highest import category, the majority of which comes from the USA, followed by Argentina and Brazil (Figure 1A). Live plant imports, which includes trees, ornamental foliage and cut flowers (thus including tulips), were fairly high and mostly imported from China followed by Germany (Figure 1C). In comparison, onion imports (mostly from the UK) and garlic imports (mostly from China and Argentina) were low. Live plant imports from China and Germany increased in relative terms between 2014 and 2018, such that China increased from being the

seventh highest exporter to South Africa to become the highest exporter, and Germany increased from being the 23rd highest exporter to become the fourth highest exporter to South Africa (UN-Comtrade 2019).

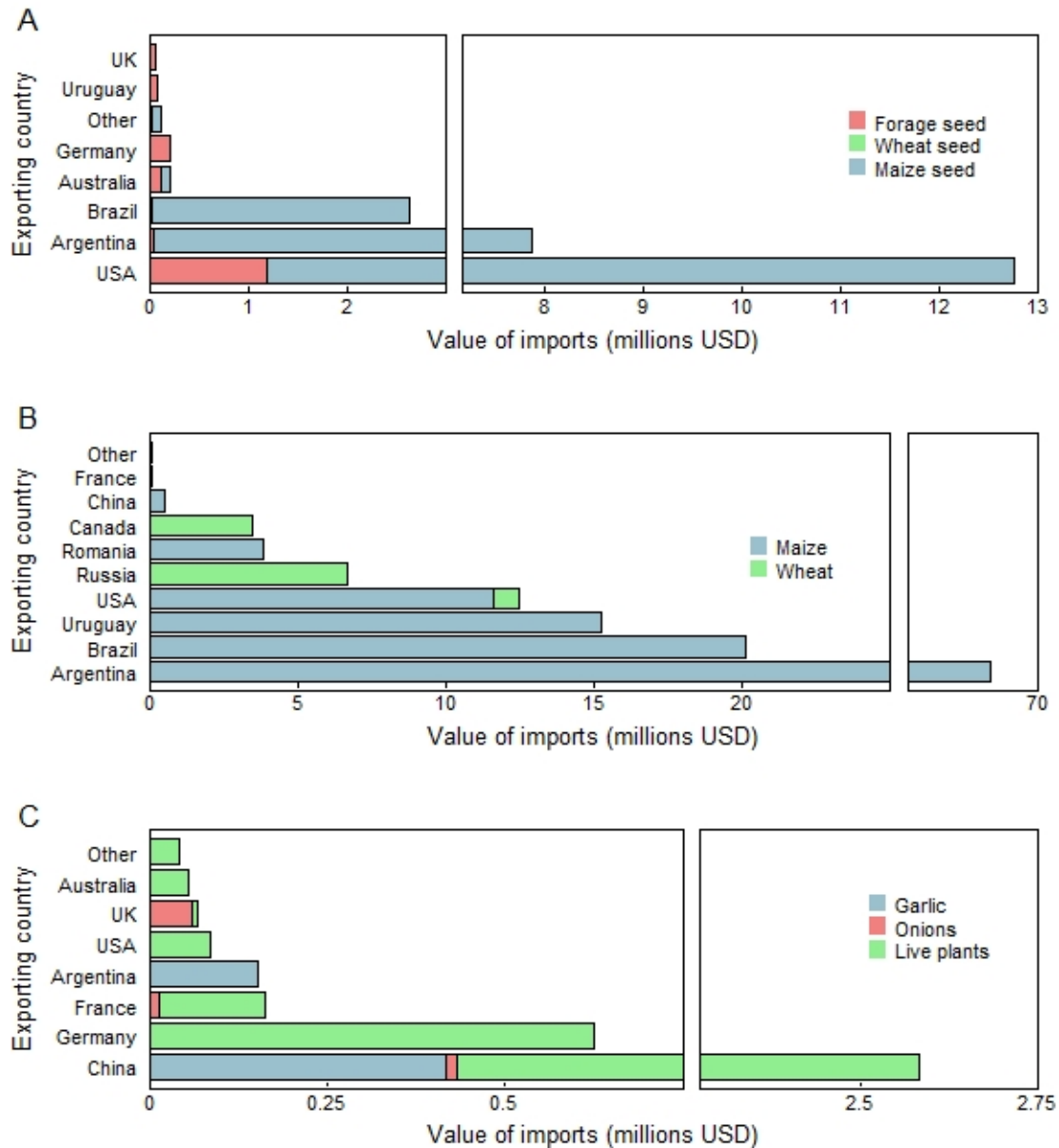


Figure 1: The value of (A) seed imports, (B) maize and wheat imports, and (C) garlic, onion, and live plant imports to South Africa from the countries where wheat curl mite occurs. The value of wheat seed imports (A) is small in comparison that for forage and maize seed imports. The x-axes are cut from (A) USD 3 to 7 million, (B) USD 25 to 65 million, and (C) USD 750000 to 2250000. Also note that the x-axes are different for each graph to accommodate the varying import values. The label “Other” includes all countries where import values are less than USD 60000 (A and B) and USD 40000 (C). The “Other” countries include in A: Canada, France, Turkey, China, Syria and Bulgaria; B: Turkey, Australia Germany, United Kingdom and Poland; C: Turkey, Poland, Bulgaria, Canada, Brazil, Romania, Syria, Iran and Russia.

For most countries from which South Africa imports host seed, voyages take longer than what WCM can survive off their host (Figure 2). There are only two countries, Australia and Brazil, from which ships can travel to South Africa in less than 11.5 days (Figure 2). Therefore, WCM could be introduced to South Africa as a contaminant of seed imports from Australia or Brazil. However, it is important to note that the values reported in Figure 2 are the minimum travel times, and that the average number of days it takes ships to reach South Africa from Australia and Brazil is actually longer (52.8 and 42.8 days, respectively). The USA and Argentina, which are the largest exporters of seed to South Africa, fall outside the off-host survival time of WCM, and thus WCM are unlikely to be introduced alive with seed imports from these countries (Figure 2).

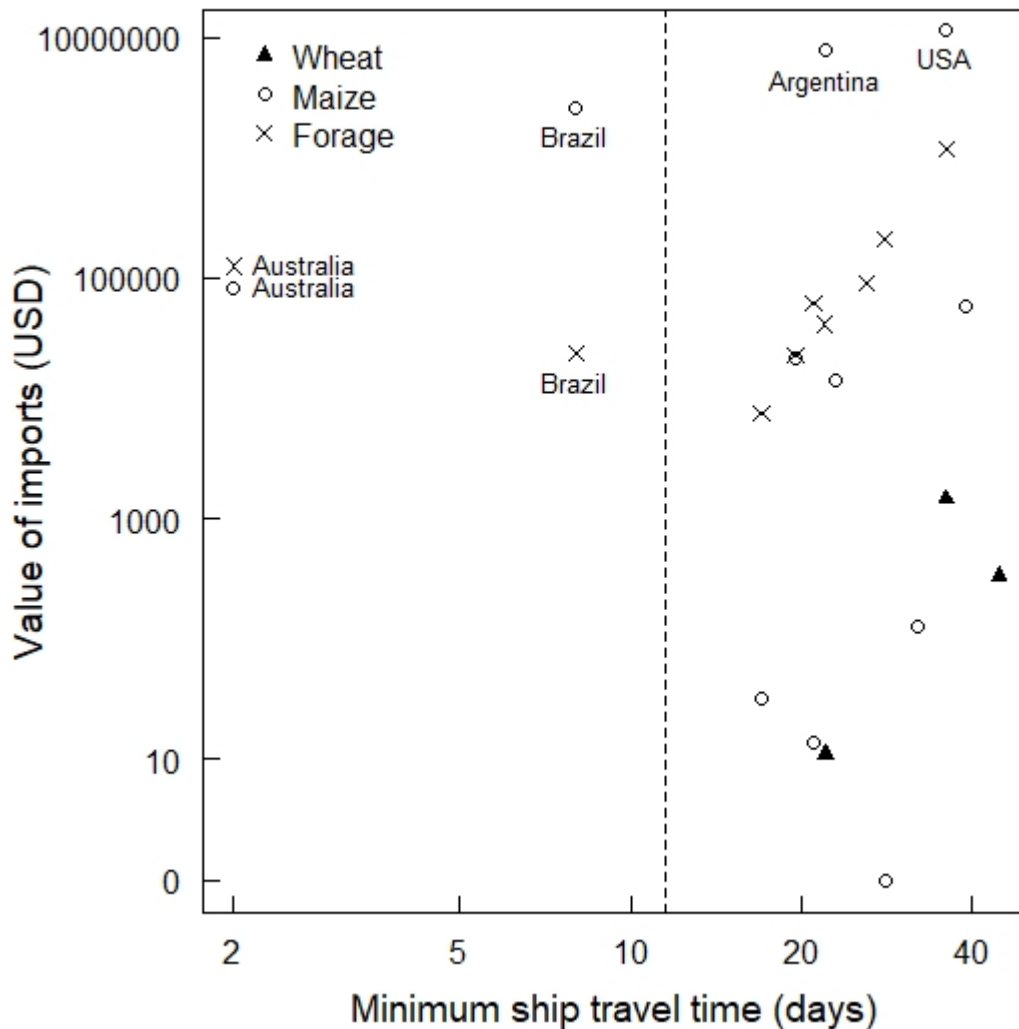


Figure 2: The value of seed imports and the minimum number of days it takes a ship to travel to South Africa from countries where the wheat curl mite occurs. The axes have been logged and the vertical dashed line represents the maximum off-host survival time (11.5 days) for MT-1 and MT-8 genotypes of wheat curl mite (WCM). Labelled on the figure are the countries from which South Africa imports a high quantity of seed (Argentina and USA) and those from which WCM could be introduced alive to South Africa with imported seed (Australia and Brazil).

The species distribution model predicted parts of South Africa as being climatically suitable for WCM, including areas along the south and east coasts and the interior of South Africa (Figure 3A). Based on the AUC statistic the model performed well (AUC value > 0.7).

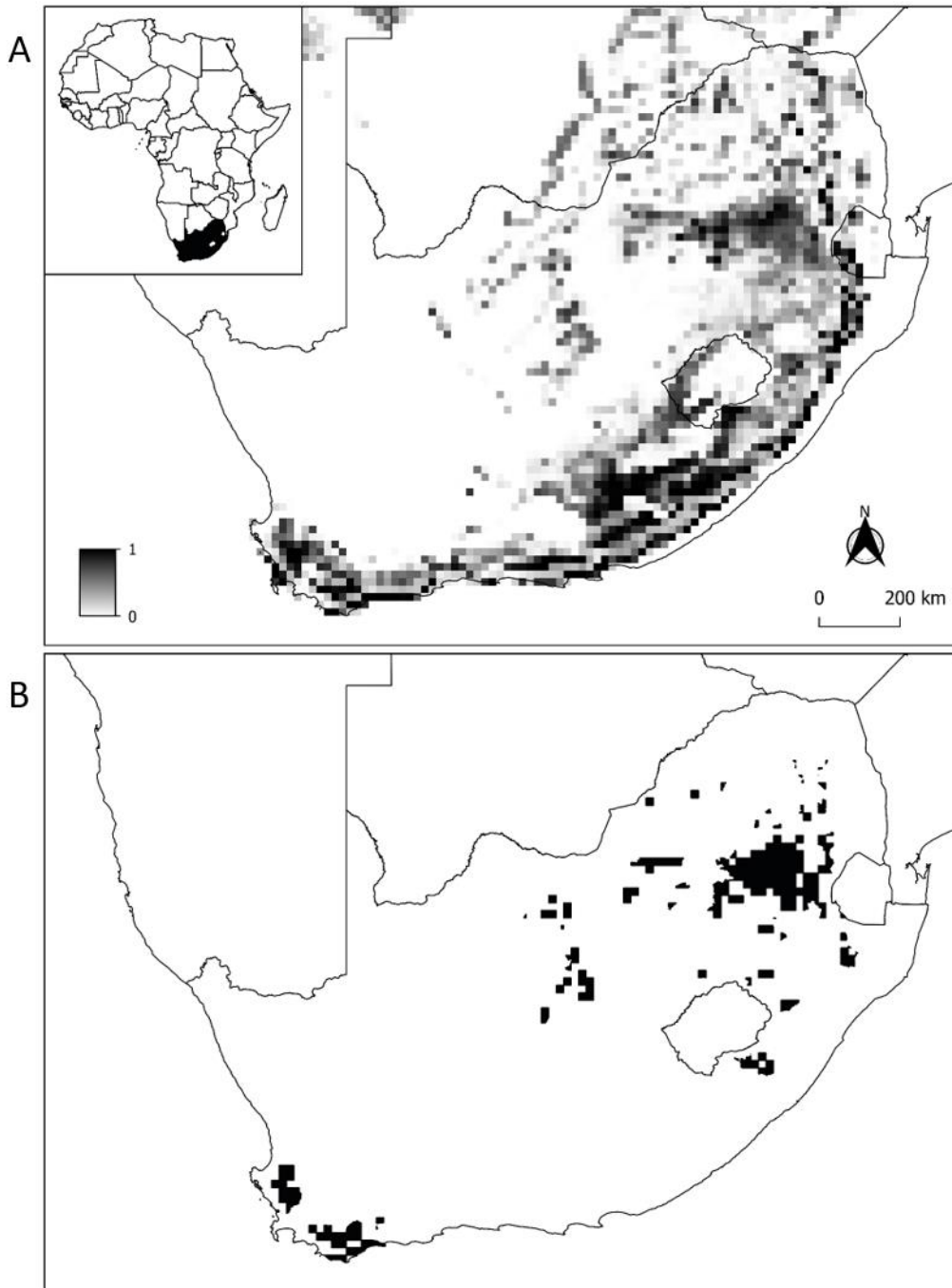


Figure 3: A) The potential distribution of wheat curl mite genotypes MT-1 and MT-8 in Southern Africa as predicted by the species distribution model (AUC = 0.886). B) Parts of South Africa where the climate is suitable for establishment of genotypes MT-1 and MT-8, and where production of wheat and/or maize is high.

Areas where wheat and maize production are high overlap with the parts of South Africa that were predicted to be climatically suitable for WCM (Figure 3B). Areas of South Africa where the WCM could establish and have an impact on wheat and maize production include the interior and along the south-west coast.

Discussion

Wheat curl mite genotypes MT-1 and MT-8 (WCM) are major agricultural pests that have caused economic loss in regions where they have established. Despite having a wide global distribution they have not yet been reported in South Africa. To inform preventative interventions, it is important to determine whether these two genotypes could be introduced and establish in South Africa.

WCM are most likely to be introduced as a contaminant of maize imports from Argentina, Brazil, Uruguay and USA; as a contaminant of live potted plant imports from China and Germany; and as a contaminant of host seed imports from Brazil and Australia. Some of these pathways are currently not very prominent, and this may be the reason why WCM has not yet been introduced to South Africa. However, live plant imports from China and Germany to South Africa have increased over time and may continue to do so in the future. Furthermore, as China, Brazil and South Africa are members of BRICS, trade between these countries could increase further in the future. Increased trade in these products would increase the probability of transport of WCM, and hence its introduction to South Africa. Conversely, due to the low amount of wheat, onion, and garlic imports, these are unlikely to be an introduction pathway.

There are areas in South Africa that are climatically suitable for WCM and within some of these areas the main hosts (wheat and maize) are grown. While our conservative species distribution model may not accurately predict the global distribution of WCM, it does predict areas that are very climatically similar to where occurrence records are found. Therefore, as there is overlap between the areas that are predicted as climatically suitable and the areas where wheat and maize production is high, it is highly likely that WCM could establish and have negative impacts in South Africa if introduced. Furthermore, genotype MT-1, in particular, has a wide host range and can survive on many grass species (Skoracka et al. 2013). This genotype could also establish in climatically suitable areas where wheat and maize are not produced (but where their other host plants are found), and from these areas it could spread onto these grain crops. Since a conservative model was used, it is also possible that other areas in South Africa, beyond what was predicted by the model, are suitable for WCM establishment.

Therefore, it may only be a matter of time before WCM is introduced, and if introduced it is likely that it will establish, spread and impact agriculture, especially if any of its associated viruses are introduced along with the organism. Currently, neither

WCM nor its associated viruses are recorded in South Africa. Since these wheat viruses typically cause noticeable crop losses (Navia et al. 2013a, 2013b), if it were present in South Africa it would likely have been reported. WCM is often detected in a new area after the wheat viruses it transmits are identified and associated damage necessitates surveys to detect the vector (Navia et al. 2013a). However, no intensive surveys have been conducted for this mite and there is a possibility that populations are established but are small or are not carrying the associated viruses and are therefore not causing a noticeable amount of damage. Nevertheless, even if WCM is present in South Africa, preventing the introduction of more WCM is important. New additional introductions could be carrying one of the associated viruses or could increase the size of the population to the point where the mites themselves start causing noticeable damage.

We recommend that WCM be considered for inclusion in South Africa's import conditions as a quarantine pest for the specified imports. Imported consignments are regularly inspected for pests of quarantine concern. By including WCM as a quarantine pest, adequate preventative measures could be taken to minimise the risk of its transport and entry. If WCM were to be found during import inspections, then South Africa would also have the correct protocol in place to manage this pest (e.g. detain, destroy, treat, or send back that import) and would have the legal right to follow through on said protocol.

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References

- BEBBER, D. P., HOLMES, T., SMITH, D. & GURR, S. J. 2014. Economic and physical determinants of the global distributions of crop pests and pathogens. *New Phytologist* 202:901–910.
- BENMOKHTAR, K., YAHIA, A.A. 2009. Contribution to the study of cereal viruses by the biological characterization of wheat and barley mosaic viruses: WSMV, WSSMV and BMSV in the central zone of Algeria. In: *Association Française de*

Protection Des Plantes, 9ème Conférence Internationale Sur Les Maladies Des Plantes, 8–9 Décembre, Tours, France. pp 48–57.

- BREY, C. W., JOHNSON, G. D. & BLODGETT, S. L. 1998. Survey of Montana grasses for wheat curl mite (Acari: Eriophyidae), the vector of wheat streak mosaic virus. *Journal of Agricultural Entomology* 15:173–181.
- CABI. 2020a. *Aceria tosichella* (wheat curl mite). In: *Invasive Species Compendium*. Wallingford, UK: CAB International. Available at: www.cabi.org/isc. [Accessed 05-Mar-2020]
- CABI. 2020b. Wheat streak mosaic virus (wheat streak) [original text by J. Price & C. Rush]. In: *Invasive Species Compendium*. Wallingford, UK: CAB International. Available at: www.cabi.org/isc. [Accessed 05-Mar-2020]
- CASTIGLIONI, E. & NAVIA, D. 2010. Presence of the wheat curl mite, *Aceria tosichella* Keifer (Prostigmata: Eriophyidae), in Uruguay. *Agrociencia* 14:19–26.
- DU PLESSIS, J. 2003. Maize Production. Department of Agriculture, Pretoria, South Africa. Available at: www.nda.agric.za/publications. [Accessed 3-Aug-2020]
- FAULKNER, K. T., HURLEY, B. P., ROBERTSON, M. P., ROUGET, M. & WILSON, J. R. U. 2017a. The balance of trade in alien species between South Africa and the rest of Africa. *Bothalia* 47:1–16.
- FAULKNER, K. T., ROBERTSON, M. P., ROUGET, M. & WILSON, J. R. U. 2017b. Prioritising surveillance for alien organisms transported as stowaways on ships travelling to South Africa. *PLoS ONE* 12:1–20.
- FICK, S. E. & HIJMANS, R. J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37:4302–4315.
- HARVEY, T. L., MARTIN, T. J. & SEIFERS, D. L. 2002. Wheat yield reduction due to wheat curl mite (Acari: Eriophyidae) infestations. *Journal of Agricultural and Urban Entomology* 19:9–13.
- KAPOORIA, R. G. & NDUNGURU, J. 2004. Occurrence of viruses in irrigated wheat in Zambia. *EPPO Bulletin* 34:413–419.
- KOTTEK, M., GRIESER, J., BECK, C., RUDOLF, B. & RUBEL, F. 2006. World Map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* 15:259–263.
- KUCZYŃSKI, L., RECTOR, B. G., KIEDROWICZ, A., LEWANDOWSKI, M., SZYDŁO, W. & SKORACKA, A. 2016. Thermal niches of two invasive genotypes of the

- wheat curl mite *Aceria tosichella*: congruence between physiological and geographical distribution data. *PLoS ONE* 11:1–18.
- MEYERSON, L. A. & MOONEY, H. A. 2007. Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment* 5:199–208.
- MILLER, A. D., SKORACKA, A., NAVIA, D., DE MENDONÇA, R. S., SZYDŁO, W., SCHULTZ, M. B., SMITH, C. M., TRUOL, G. & HOFFMANN, A. A. 2013. Phylogenetic analyses reveal extensive cryptic speciation and host specialization in an economically important mite taxon. *Molecular Phylogenetics and Evolution* 66:928–940.
- NAVIA, D., DE MENDONÇA, R. S., SKORACKA, A., SZYDŁO, W., KNIHINICKI, D., HEIN, G. L., DA SILVA PEREIRA, P. R. V., TRUOL, G. & LAU, D. 2013b. Wheat curl mite, *Aceria tosichella*, and transmitted viruses: an expanding pest complex affecting cereal crops. *Experimental and Applied Acarology* 59:95–143.
- NAVIA, D. & FLECHTMANN, C. H. W. 2008. Eriophyoid mites intercepted from plant germplasm in Brazil—addressing questions on new introduction pathways. In: *Sixth European Congress of Acarology. Abstracts, Montpellier*. European Association of Acarologists (EURAAC). pp 1–58.
- NAVIA, D., MARSARO JÚNIOR, A. L., GONDIM JÚNIOR, M. G. C., DE MENDONÇA, R. S. & PEREIRA, P. R. V. DA S. 2013a. Recent mite invasions in South America. In: Peña, J. (ed.), *Potential invasive pests of agricultural crops*. Brazil. CAB International. pp 251–287.
- NAVIA, D., OCHOA, R., WELBOURN, C. & FERRAGUT, F. 2010. Adventive eriophyoid mites: a global review of their impact, pathways, prevention and challenges. *Eriophyoid Mites: Progress and Prognoses* 51:225–255.
- NAVIA, D., TRUOL, G., MENDONÇA, R. S. & SAGADIN, M. 2006. *Aceria tosichella* Keifer (Acari: Eriophyidae) from wheat streak mosaic virus-infected wheat plants in Argentina. *International Journal of Acarology* 32:189–193.
- PEREIRA, P. R. V. DA S., NAVIA, D., SALVADORI, J. R. & LAU, D. 2009. Occurrence of *Aceria tosichella* in Brazil. *Pesquisa Agropecuária Brasileira* 44:539–542.
- PHILLIPS, S. J., ANDERSON, R. P. & SCHAPIRE, R. E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- PIMENTEL, D., MCNAIR, S., JANECKA, J., WIGHTMAN, J., SIMMONDS, C., O'CONNELL, C., WONG, E., RUSSEL, L., ZERN, J., AQUINO, T. & TSOMONDO, T. 2001. Economic and environmental threats of alien plant,

- animal, and microbe invasions. *Agriculture, Ecosystems and Environment* 84:1–20.
- R CORE TEAM. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org/>.
- RANABHAT, N. B., SEIPEL, T., LEHNHOFF, E. A., MILLER, Z. J., OWEN, K. E., MENALLED, F. D. & BURROWS, M. E. 2018. Temperature and alternative hosts influence *Aceria tosichella* infestation and wheat streak mosaic virus infection. *Plant Disease* 102:546–551.
- ROBERTSON, M. P., VISSER, V. & HUI, C. 2016. Biogeo: an R package for assessing and improving data quality of occurrence record datasets. *Ecography* 39:1–8.
- SCHIFFER, M., UMINA, P., CAREW, M., HOFFMANN, A., RODONI, B. & MILLER, A. 2009. The distribution of wheat curl mite (*Aceria tosichella*) lineages in Australia and their potential to transmit wheat streak mosaic virus. *Annals of Applied Biology* 155:371–379.
- SIMBERLOFF, D., MARTIN, J., GENOVESI, P., MARIS, V., WARDLE, D. A., ARONSON, J., COURCHAMP, F., GALIL, B., GARCÍA-BERTHOUS, E., PASCAL, M., PYŠEK, P., SOUSA, R., TABACCHI, E. & VILÀ, M. 2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution* 28:58–66.
- SKORACKA, A., KUCZYŃSKI, L., RECTOR, B. & AMRINE, J. W. 2014b. Wheat curl mite and dry bulb mite: untangling a taxonomic conundrum through a multidisciplinary approach. *Biological Journal of the Linnean Society* 111:421–436.
- SKORACKA, A., KUCZYŃSKI, L., SANTOS DE MENDONÇA, R., DABERT, M., SZYDŁO, W., KNIHINICKI, D., TRUOL, G. & NAVIA, D. 2012. Cryptic species within the wheat curl mite *Aceria tosichella* (Keifer) (Acari: Eriophyoidea), revealed by mitochondrial, nuclear and morphometric data. *Invertebrate Systematics* 26:417–433.
- SKORACKA, A., KUCZYŃSKI, L., SZYDŁO, W. & RECTOR, B. 2013. The wheat curl mite *Aceria tosichella* (Acari: Eriophyoidea) is a complex of cryptic lineages with divergent host ranges: Evidence from molecular and plant bioassay data. *Biological Journal of the Linnean Society* 109:165–180.
- SKORACKA, A., LEWANDOWSKI, M., RECTOR, B. G., SZYDŁO, W. & KUCZYŃSKI,

- L. 2017. Spatial and host-related variation in prevalence and population density of wheat curl mite (*Aceria tosichella*) cryptic genotypes in agricultural landscapes. *PLoS ONE* 12:1–17.
- SKORACKA, A., LOPES, L. F., ALVES, M. J., MILLER, A., LEWANDOWSKI, M., SZYDŁO, W., MAJER, A., RÓŻAŃSKA, E. & KUCZYŃSKI, L. 2018. Genetics of lineage diversification and the evolution of host usage in the economically important wheat curl mite, *Aceria tosichella* Keifer, 1969. *BMC Evolutionary Biology* 18:1–15.
- SKORACKA, A., RECTOR, B., KUCZYŃSKI, L., SZYDŁO, W., HEIN, G. & FRENCH, R. 2014a. Global spread of wheat curl mite by its most polyphagous and pestiferous lineages. *Annals of Applied Biology* 165:1–14.
- SLYKHUIS, J. T. 1955. *Aceria tulipae* Keifer (Acarina: Eriophyidae) in relation to the spread of wheat streak mosaic. *Phytopathology* 45:116–128.
- SMITH MEYER, M. K. P. & CRAEMER, C. 1999. Mites (Arachnida: Acari) as crop pests in southern Africa: an overview. *African Plant Protection* 5:37–51.
- SOUTH AFRICA. 1983. Agricultural Pests Act and amendments (Act No. 36 of 1983). Available at: <https://www.gov.za/documents/agricultural-pests-act-30-mar-2015-1202>. [Accessed 05-Mar-2020]
- SOUTH AFRICA. 2004. National Environmental Biodiversity Act and amendments (Act No. 10 of 2004). Available at: <https://www.gov.za/documents/national-environmental-management-biodiversity-act-0>. [Accessed 05-Mar-2020]
- STATISTICS SOUTH AFRICA. 2010. Census of commercial agriculture, 2007. Pretoria, South Africa. Available at: <http://www.statssa.gov.za/>. [Accessed 02-Oct-2019]
- SWETS, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240:1285–1293.
- UN-COMTRADE. 2019. Trade Data. Available at: <https://comtrade.un.org/>. [Accessed 07-Aug-2019]
- WILSON, C. E., CASTRO, K. L., THURSTON, G. B. & SISSONS, A. 2016. Pathway risk analysis of weed seeds in imported grain: a Canadian perspective. *NeoBiota* 30:49–74.
- WOSULA, E. N., MCMECHAN, A. J. & HEIN, G. L. 2015. The effect of temperature, relative humidity, and virus infection status on off-host survival of the wheat curl mite (Acari: Eriophyidae). *Journal of Economic Entomology* 108:1545–1552.