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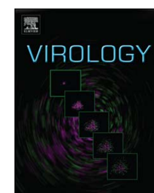

Ongoing geographical spread of *Tomato yellow leaf curl virus* ☆

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Tomato yellow leaf curl virus (TYLCV) seriously impacts tomato production throughout tropical and sub-tropical regions of the world. It has a broad geographical distribution and continues to spread to new regions in the Indian and Pacific Oceans including Australia, New Caledonia and Mauritius. We undertook a temporally-scaled, phylogeographic analysis of all publicly available, full genome sequences of TYLCV, together with 70 new genome sequences from Australia, Iran and Mauritius. This revealed that whereas epidemics in Australia and China likely originated through multiple independent viral introductions from the East-Asian region around Japan and Korea, the New Caledonian epidemic was seeded by a variant from the Western Mediterranean region and the Mauritian epidemic by a variant from the neighbouring island of Reunion. Finally, we show that inter-continental scale movements of TYLCV to East Asia have, at least temporarily, ceased, whereas long-distance movements to the Americas and Australia are probably still ongoing.

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1. Introduction

Tomato yellow leaf curl virus (TYLCV) is a monopartite begomovirus in the family *Geminiviridae* and is one of many closely related viruses that cause tomato yellow leaf curl disease (TYLCD) (Abhary et al., 2007; Navot et al., 1991). TYLCD was initially recognised in the Jordan Valley, Israel, in the 1930s, but it was not until the early 1960s that TYLCV was identified (Cohen and Nitzany, 1960, 1966). Subsequently, the virus has spread unabated into the Mediterranean basin and into most tropical and sub-tropical regions of the world and is recognised as one of the world's most devastating pathogens of tomato (Abhary et al., 2007; Delatte et al., 2007; Delatte et al., 2005; Diaz-Pendon et al., 2010; Duffy and Holmes, 2007; Kenyon et al., 2014; Lefeuvre et al., 2010; Moriones and Navas-Castillo, 2000; Péréfarres et al., 2012; Picó et al., 1996; Polston and Anderson, 1997; Stonor et al., 2003; Van Brunschot et al., 2010).

Although there are seven recognised strains of TYLCV (Brown et al., 2015), only two, the mild (Mld) and Israel (IL) strains, have ever been found outside of Iran. The global dissemination of TYLCV-Mld and TYLCV-IL from the Middle East or the Eastern Mediterranean (Duffy and Holmes, 2007; Lefeuvre et al., 2010) is attributed to the movement of infected planting material (Seal et al., 2006), together with spread of the Middle East-Asia Minor (MEAM1 formally referred to as the B biotype) and the Mediterranean (MED formally referred to as the Q biotype) cryptic species of its whitefly vector, *Bemisia tabaci* (Czosnek et al., 2002; Diaz-Pendon et al., 2010; Horowitz et al., 2007; Seal et al., 2006). Recent reports suggest that TYLCV is possibly unique amongst begomoviruses in that it is capable of both replicating within *B. tabaci* (Pakkianathan et al. (2015), as well as being seed

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transmitted in tomato (Kil et al., 2016). These characteristics may have contributed to it achieving a geographical range that is far broader than those of almost all other begomovirus species.

As with other begomoviruses, TYLCV is able to rapidly adapt to new environments as a consequence of its high rates of mutation and recombination (Delatte et al., 2005; Duffy and Holmes, 2007, 2008; Lefeuvre et al., 2010; Monci et al., 2002). For example, TYLCV-IL is a recombinant of TYLCV-Mld and *Tomato leaf curl Karnataka virus* (another tomato-infecting begomovirus), while other begomoviruses from the Mediterranean basin are recombinants of TYLCV-IL and TYLCV-Mld (Navas-Castillo et al., 2000).

The global spread of TYLCV began in the 1980s, after the emergence of the Mld and IL strains (Duffy and Holmes, 2008; Lefeuvre et al., 2010). The region centred on Iran harbours the highest diversity of TYLCV, although there has been little obvious movement of viruses out of this region since before the early 1980s (Lefeuvre et al., 2010). A previous phylogeographic study by Lefeuvre et al. (2010) included 91 coat protein and 82 full genome sequences of TYLCV, which had been generated over 22 years. However, this study was limited in geographical scope, as the virus isolates were primarily from the Mediterranean basin, the Middle East and the Americas, with Southeast Asia, the Pacific and Indian Ocean island nations/territories and Australia being greatly underrepresented. Furthermore, the analytical tools to account for the potentially confounding influences of recombination were not then available.

Here we analyse a much larger TYLCV sequence dataset comprising 414 full-genome sequences (70 of which are published here for the first time) sampled over 26 years from 33 countries to infer the historic global movement dynamics of TYLCV. Using fully probabilistic Bayesian modelling methods and accounting for recombination, we specifically focus on the contributions of south-western Pacific (Australia and New Caledonia) and south-eastern Indian Ocean (Mauritius and Reunion) states to the spread of TYLCV. Also, because of the intensified sampling for TYLCV over the past five years in various other parts of the world, we are also able to provide much more clarity on TYLCV movements into and across Asia, the Americas and the Caribbean.

2. Methods and materials

2.1. Sampling, TYLCV genome recovery and sequencing

Total DNA was extracted from tomato samples displaying leaf curl symptoms from Australia (n=52), Iran (n=12) and Mauritius (n=6). Circular DNA was enriched by rolling circle amplification (RCA) using Templiphi (GE Healthcare, USA). Unit length TYLCV genomes were recovered from the RCA concatemers using *Xmn*I, *Nco*I, *Bam*HI or *Sal*I restriction enzymes, and cloned into pJET 1.2 plasmid vector (ThermoFisher, USA) for *Xmn*I digested genomes and into pBluescript SK (Stratagen, USA) for *Nco*I, *Bam*HI or *Sal*I digested genomes. The recombinant plasmids were Sanger sequenced by primer walking at Macrogen Inc. (South Korea). Complete genome sequences were assembled using DNA Baser V4 (Heracle Biosoft S.R.L., Romania).

2.2. Construction of a recombination free dataset

A dataset of 435 full TYLCV genomes was assembled, which contained sequences of isolates sampled from 33 countries between 1988 and 2014 (Supplementary Table 1) including 356 full genome sequences retrieved from GenBank.

A preliminary multiple sequence alignment was generated using the slow, iterative refinement method (FFT-NS-I) implemented in MAFFT version 7 (Katoh and Standley, 2014). This alignment was then manually edited using IMPALE (available from http://web.cbio.uct.ac.za/~arjun/).

The resulting alignment was used for recombination analyses using the seven detection methods implemented in RDP version 4.36 (Martin et al., 2015) with default settings and a Bonferroni corrected *p*-value cut-off of 0.05. Events detected with three or more methods coupled with significant phylogenetic support were considered credible evidence of recombination. The breakpoint positions and recombinant sequence(s) inferred for every detected potential recombination event were manually checked and adjusted where necessary using the extensive phylogenetic and recombination signal analysis features available in RDP4.56 (Martin et al., 2015).

The final TYLCV recombination-free dataset (RF-dataset) comprised 414 TYLCV sequences, all generated following recombination analysis and the removal of (i) all tracts of sequence from the alignment that were detected to have been acquired through recombination (replaced in the alignment with gap characters), and (ii) 21 sequences from the TYLCV dataset that were inferred to have acquired >30% (or >810 nucleotides) of their genomes via recombination with non-TYLCV parental viruses.

2.3. Geographical clustering

Geographical clustering was done as described by Lefeuvre et al. (2010), using the centroid hierarchical clustering method (Rokach and Maimon, 2005) implemented in R (R Core Team, 2013) to determine the most appropriate regional grouping scheme for the phylogeographic analyses.

2.4. Identification of best-fit evolutionary models

The best-fit nucleotide substitution model was inferred using jModelTest (Posada, 2008) implemented in MEGA6 (Tamura et al., 2013) and the best-fit molecular clock, and demographic models were inferred using Path Sampling and Stepping stone methods with 100 path steps and a chain length of one million (Baele et al., 2012; Baele et al., 2013) using BEAST v1.8.1. (Drummond and Rambaut, 2007) and the BEAGLE high-performance library v2.1.2 (Ayres et al., 2012).

We used linear regression techniques available in TempEst (Rambaut et al., 2016) to visually examine the degree of divergence accumulation that had occurred over the sampling time interval as a proxy for temporal signal. This method explores the root-to-tip distances of the branches in the maximum likelihood tree as a function of sampling time. In this analysis, TempEst outputs the correlation coefficient and the coefficient of determination, for which higher values indicate strong temporal signal in the data, and improved fit of the data to the strict clock nucleotide substitution model, respectively.

2.5. Phylogeographic analyses

A discrete reversible diffusion model with the Bayesian stochastic search variable selection (BSSVS) procedure (Lemey et al., 2009), implemented in BEAST v1.8.1. (Drummond and Rambaut, 2007), was used to conduct Bayes factor (BF) tests that identified the statistically supported epidemiological links between the geographical regions considered (Lemey et al., 2009). Statistically supported links between locations were identified as those with an associated BF test statistic >5: where BF scores >100 were taken as representing decisive support for one or more movements between locations, BF scores >10 were taken as indicating strong support for movement(s), and BF scores <5 were taken as indicating negligible support (Kass and Raftery, 1995).

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