Virus Research 186 (2014) 104–113

Contents lists available at ScienceDirect

Virus Research

journal homepage: www.elsevier.com/locate/virusres

Emergence and diversity of begomoviruses infecting solanaceous crops in East and Southeast Asia

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ARTICLE INFO

Article history:
Available online 15 January 2014

Keywords:
Geminiviridae
Solanum lycopersicum
Capsicum annuum
Solanum melongena
ssDNA virus
Recombination

ABSTRACT

Over the past three decades diseases caused by whitefly-transmitted geminiviruses (begomoviruses) have emerged to be important constraints to the production of solanaceous crops, particularly tomato (*Solanum lycopersicum*) and peppers (*Capsicum* spp.), in many tropical and subtropical regions of the world. The most studied of these is *Tomato yellow leaf curl virus* (TYLCV), which has spread to many other areas from its likely origin in the Mediterranean basin region. The virus is usually associated with the polyphagous and virus-vectoring-efficient B-biotype of its vector whitefly (*Bemisia tabaci*). However, in Southeast and East Asia, a wide variety of distinct local begomovirus species have been identified from tomato and pepper crops over this period, and TYLCV was detected in Japan only in about 1996, China in 2006 and Korea in 2008, despite B-biotype whiteflies being present in several of the countries of the region since at least the early 1990s. Continental Southeast Asia appears to be a major center of diversity for begomoviruses and some species may have spread across the region; *Tomato yellow leaf curl Thailand virus* (TYLCTHV) appears to have spread from the Thailand–Myanmar region into southern China and is now displacing the local tomato-infecting species in Taiwan, and *Tomato yellow leaf curl Kanchanaburi virus* (TYLCKaV) appears to have spread from the Thailand–Vietnam region to Java, Indonesia. Since many of the native tomato- or pepper-infecting begomoviruses and associated satellite DNAs have also been detected in local weed species, it seems likely that their ancestors originated in these weed hosts, but with the expansion and intensification of tomato and pepper production in the region, there was selection for recombinant or mutant forms with greater virulence on tomato and/or pepper. Expansion and intensification of these crops may also have resulted in increased populations of local, and if present, B- or Q-biotype whiteflies, aiding the increase and spread of local begomovirus species.

1. Introduction

The *Geminiviridae* is a family of plant-infecting viruses that have a circular single-stranded DNA genomes and twinned icosahedral (geminate) particles. The family comprises four genera: *Mastrevirus*, *Curtovirus*, *Topocuvirus* and *Begomovirus* (Brown et al., 2012). Members of the genus *Begomovirus* infect dicotyledonous plants, are transmitted in a persistent manner by the whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) and can have either a mono- or bipartite genome. The monopartite begomoviruses previously were found only in the Old World, while the bipartite begomoviruses were predominantly located in the New World. However, there is evidence that some bipartite begomoviruses were present in Asia (Vietnam) prior to continental separation (Ha et al., 2008), and that monopartite viruses are emerging in Latin America through convergent evolution of bipartite viruses (Melgarejo et al., 2013). The International Committee on Taxonomy of Viruses (ICTV) species demarcation criteria is an 89% nucleotide identity threshold between full-length DNA-A component nucleotide sequences for begomovirus species (Brown et al., 2012), and strains of a species are defined by a 93% nucleotide identity threshold (Fauquet et al., 2008).

The emergence of begomoviruses over the last 20–30 years as one of the most important groups of plant viruses affecting production of a variety of vegetable crops, particularly in the tropics and subtropics, has generally been associated with increases of populations of the vector whitefly, *B. tabaci*. Tomato leaf curl or tomato yellow leaf curl has become the most devastating viral disease of tomato worldwide (Hanssen et al., 2010). The disease is caused by a complex of mainly monopartite begomovirus species; of the begomovirus species recognized by the ICTV, over 40 have 'tomato leaf curl' as part of their name (Brown et al., 2012). The disease was first reported from the Jordan valley (now Israel) in the late 1930s and the causal agent there was identified as *Tomato yellow leaf curl virus* (TYLCV) in 1961. From the 1970s TYLCV spread from its origin in the Mediterranean basin region, first to neighboring countries and then starting in the 1980s, much more widely across tropical and subtropical regions of the world. Two different strains of the virus from

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0168-1702/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.virusres.2013.12.026

Israel were identified, the Israel (IL) and the Mild (Mld) strain. Also, a related species, *Tomato yellow leaf curl Sardinia virus* (TYLCSV) became important in Italy in the late 1980s and subsequently in Spain. The spread of the two forms of TYLCV and of TYLCSV around the world has been well documented and analyzed (Lefeuvre et al., 2010; Navas-Castillo et al., 2011).

The global emergence and spread of many begomoviruses, including TYLCV and TYLCSV, has been associated with the spread and increase of a more fecund and polyphagous whitefly biotype, referred to as the B-biotype (Seal et al., 2006). There has long been debate as to whether *B. tabaci* is a complex species or a species complex. Morphologically indistinguishable *B. tabaci* populations can have different host plant feeding preferences and virus transmission properties; this resulted in distinct populations being described as biotypes. By the early 2000s biotypes A to T had been described (Perring, 2001). The invasive Q-biotype, which was characterized by its increased resistance to many pesticides and tolerance to higher temperatures, was also associated with some of the spread and increase in begomoviruses such as TYLCV (Horowitz et al., 2007). The current approach to assessing the taxonomy of *B. tabaci* is to determine the degree of similarity between mitochondrial *cytochrome oxidase subunit I* (*COI*) gene sequences. Based on comparing 454 *COI* sequences, and with a threshold of 3.5% difference, Dinsdale et al. (2010) identified 24 constituent species within the *B. tabaci* complex. More recently, the number of constituent species identified increased to 31 and with this it was suggested that the threshold for difference in *COI* sequence should be increased to 4% (Lee et al., 2013). Based on this molecular phylogeny, the B-biotype and the Q-biotype are now often referred to as the Middle East-Asia Minor 1 (MEAM1) and Mediterranean (Med) cryptic species or haplotypes of *B. tabaci*, respectively. A further level of complexity in the virus–vector–host relationship is that the persistent transmission of TYLCV, and probably some other begomoviruses by *B. tabaci* depends on chaperonin GroEL homologs produced by endosymbiotic bacteria in the whiteflies (Diaz-Pendon et al., 2010).

Zeidan et al. (1998) wrote that "Geminiviruses infecting tomatoes are rapidly spreading to regions where they were unknown before, threatening tomato production", but then showed with the molecular sequence data available at the time that the isolates then present in Southeast and East Asia were distinct local begomovirus species and not the TYLCV or TYLCSV that were starting to appear in other parts of the world. Seven years later, Green et al. (2005) in an updated assessment of what was known of the diversity of begomoviruses of tomato and weeds in Asia, cataloged many more distinct begomovirus species having been identified in the region, and also the first identification of TYLCV in the region in Japan. Now, eight more years on, we here collate the recent and older information to provide an updated account of the emergence of begomoviruses infecting tomato, capsicum peppers and eggplant in East and Southeast Asia. We also use the available information to speculate as to what the main drivers for the emergence and diversity of these viruses across the region are.

2. Begomoviruses infecting solanaceous crops in Southeast Asia

The first detection, identification and distribution of different begomovirus species from tomato, pepper and eggplant across the different countries of East and Southeast Asia is presented below for each country of the region and is summarized in Table 1. Based mainly on Zeidan et al. (1998) and Green et al. (2005), the earliest record of observing a disease of tomato, pepper and egg plant likely to be caused by begomovirus is also presented. To assess the diversity of the begomovirus species described below, nucleic acid sequences of DNA-A components representative all the species were retrieved from GenBank (http://www.ncbi.nlm.nih.gov/), then aligned using the ClustalW facility, and a phylogenetic tree was constructed using the neighbor-joining method with 1000 bootstrap replications, using the MEGA5 package of programs (Tamura et al., 2011) (Fig. 1).

2.1. Cambodia (KHM)

Tomato with leaf curl symptoms were observed in Cambodia pre-1989, but it was not until 2004 that a distinct monopartite virus was identified and named Tomato leaf curl Cambodia virus (ToLCKHV) with highest similarity to *Tomato leaf curl Malaysia virus* (ToLCMYV) (Green et al., 2005). Despite reports of severe leaf curl in tomato crops in some parts of Cambodia in recent years, there remain no published sequences of begomovirus from tomato in Cambodia.

2.2. China (CHA)

A tomato disease probably caused by a begomovirus was first reported (though at low incidence) in China in 1965 in the tomato-producing areas of the south, and later the virus causing disease in tomatoes in Guangxi province was identified as *Tomato yellow leaf curl China virus* (TYLCCNV) (Yin et al., 2001). Several other tomato-infecting begomoviruses were identified in the early 2000s. In Yunnan province, as well as TYLCCNV, Li et al. (2004) identified *Tobacco curly shoot virus* (TbCSV), *Tobacco leaf curl Yunnan virus* (TbLCYnV) and *Tomato yellow leaf curl Thailand virus* (TYLCTHV) infecting tomato. Although the isolates of TYLCTHV first identified in Thailand were bipartite, no DNA-B was detected associated with any of the tomato-infecting begomoviruses in China. Zhou et al. (2003) showed that TYLCCNV and begomovirus isolates from tobacco and some weeds in Yunnan were associated with three specific clades of betasatellites with which they had co-evolved. Isolates collected from Guangzhou were identified as *Tomato leaf curl Taiwan virus* (ToLCTV), and a distinct novel monopartite begomovirus, *Tomato leaf curl Guangxi virus* (ToLCGxV) was identified from tomato in Guanxi province in 2003 (Xu et al., 2007).

In March 2006, a yellow mosaic disease was observed on tomato with disease incidence up 90% in fields of Sunqiao, Shanghai Province. This was subsequently identified as a strain of TYLCV with very high nucleic acid sequence homology to the Japanese "Tosa" strain, and the first incursion of TYLCV into China (Wu et al., 2006). The following year, an isolate of TYLCV was sequenced from the weedy "Dutch Eggplant" (*Solanum aculeatissimum*) in Shanghai province and found to be more closely related to TYLCV isolates from Africa and the Americas, suggesting a second distinct route into China (Yongping et al., 2008). By 2010 TYLCV had spread to be prevalent in at least six provinces of China, and by 2012 it had been detected in 11 provinces. The B-biotype of *B. tabaci* had been known in China since the mid 1990s, but the rapid spread of TYLCV after 2006 coincided with the arrival of the Q-biotype and was aided differentially by whitefly B- and Q-biotypes (Pan et al., 2012). Sequences of TYLCV from pepper and eggplant in Xinjiang province in 2011 have been deposited in GenBank as accessions JX456642 and JX456643 respectively, and TYLCV appears to be becoming more widespread in pepper production systems in southern provinces of China (Group R in Fig. 1).

Zhang et al. (2010) identified a novel monopartite begomovirus from Hainan Island, Tomato leaf curl Hainan virus (ToLCHaV), and observed that it may have arisen by recombination between viruses related to *Papaya leaf curl China virus* (PaLCuCNV), *Ageratum leaf curl virus* (ALCuV) and *Tomato leaf curl Vietnam virus* (ToLCVV). Recently, several sequences labeled Pepper yellow leaf curl china virus (PYLCCNV) collected from peppers in China in 2010 were deposited in