



Genetic variation of the *Turnip mosaic virus* population of Vietnam: A case study of founder, regional and local influences

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ABSTRACT

Turnip mosaic virus (TuMV) is one of the most important viruses infecting a wide range of plant species, primarily from the family *Brassicaceae*. Thirty TuMV isolates were collected from *Brassica* and *Raphanus* plants in Vietnam during 2006–2008. Host reaction studies showed that many of the isolates belonged to *Brassica/Raphanus* (BR) host-infecting type. Sequence-based phylogenetic and population genetic analyses were made of the complete polyprotein gene sequences, and of four non-recombinogenic regions of those sequences (i.e. genes of the helper-component proteinase protein, protein 3, nuclear inclusion b protein and coat protein). These were used to assess the subpopulation differentiation and divergence between Vietnamese TuMV populations and those of nearby Asian countries. Nine inter- and intralinear recombination type patterns were identified in the genomes of the Vietnamese isolates, of which seven were novel. All the Vietnamese non-recombinant isolates fell into the world-B group of TuMV and clustered with Chinese isolates. The estimates of genetic differentiation and gene flow reveal that the TuMV populations of Vietnam, China and Japan are genetically linked but have clear local founder effects. This, the first population genetic study of a TuMV population in Southeast Asia, indicates the importance of such studies for providing the scientific basis of control strategies.

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1. Introduction

Studies of the genetic structure of populations of plant RNA viruses are important for understanding the evolution of virus/host interactions (García-Arenal et al., 2001; Gibbs et al., 2008; Gibbs and Ohshima, 2010), because plant RNA viruses are very variable enabling them to adapt rapidly to new or resistant hosts (Tsompana et al., 2005; Ohshima et al., 2010). There are several reports on the genetic structure of potyvirus populations, notably those on *Potato virus Y* (PVY) (Ogawa et al., 2008, 2012; Karasev et al., 2011), *Soybean mosaic virus* (SMV) (Seo et al., 2009), *Tobacco vein banding mosaic virus* (TVBMV) (Zhang et al., 2011), *Zucchini yellow mosaic virus* (ZYMV) (Lecoq et al., 2009) and *Turnip mosaic virus* (TuMV) (Ohshima et al., 2002; Tomimura et al., 2004; Tomitaka and Ohshima, 2006). These reports showed that virus populations have been shaped by selection, founder effects and genetic recombination.

TuMV infects a wide range of plant species, most from the family *Brassicaceae* (Walsh and Jenner, 2002). TuMV belongs to the genus *Potyvirus*. This is the largest genus of the largest family of plant RNA viruses, the *Potyviridae* (Gibbs and Ohshima, 2010; King et al., 2012). TuMV, like other potyviruses, is transmitted by aphids in the non-persistent manner. Potyviruses have flexuous filamentous particles 700–750 nm long, each of which contains a single copy of the genome, which is a single-stranded positive sense RNA molecule of about 9800 nucleotides. This is translated into one large polyprotein which hydrolyzes itself into at least 10 proteins (King et al., 2012). Furthermore, an overlapping pretty interesting *Potyviridae* ORF (PIPO) exists in the +2 reading frame within the protein 3 (P3 protein) encoding region (Chung et al., 2008).

Previous studies have shown that the different TuMV subpopulations have probably emerged from the more ancient Eurasian subpopulations, such as those found in the Mediterranean region, including Southeast Europe, Asia Minor and mid-Eurasia (Ohshima et al., 2002; Tomimura et al., 2004; Korkmaz et al., 2008; Farzadfar et al., 2009). In these regions, *Brassicaceae* crops are an important component of local agriculture; in Europe, the crops are mostly *Brassica* species; and in Asia Minor, both *Brassica* and *Raphanus* species are important. Furthermore, the studies (Ohshima et al., 2002; Tomimura et al., 2003, 2004; Tomitaka and Ohshima, 2006) have shown that TuMV isolates are of four host-infecting types;

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[(B)]-host type isolates infected *Brassica* plants latently and occasionally and did not infect *Raphanus* plants, [B]-host type isolates infected many of *Brassica* plants systemically causing mosaic of the systemically infected leaves but did not infect *Raphanus* plants, [B(R)]-host type isolates infected many *Brassica* plants systemically causing mosaic of systemically infected leaves but infected *Raphanus* plants occasionally, and [BR]-host type isolates infected both *Brassica* and *Raphanus* plants systemically causing mosaic of the uninoculated leaves. Moreover, phylogenetic analyses using gene sequences of different virus isolates collected from around the world revealed four main TuMV genogroups called basal-B (*Brassica*), basal-BR (*Brassica/Raphanus*), Asian-BR and world-B. The basal-B cluster of (B) or B-host type isolates was most variable, was paraphyletic, and was isolated from both non- and *Brassicaceae* plants.

Although TuMV was recently reported in Vietnam (Ha et al., 2008), little data on the incidence of TuMV and its biological and molecular characteristics are available in Southeast Asian countries. Recent studies of the genetic structures of TuMV populations in East Asia were made using partial genome sequences, and showed that recent Chinese and Japanese TuMV isolates are part of the same population but are a discrete lineage (Tan et al., 2004; Tomitaka and Ohshima, 2006). Here, we report the occurrence of TuMV in Vietnam of the Southeast Asian region from *Brassicaceae* hosts, all cultivated *Brassica* and *Raphanus* crops, together with the full genomic sequences of 30 of the isolates. Data from full genomic sequence and polyprotein encoding region was used for recombination and phylogenetic analyses, and for the estimation of subpopulation differentiation and divergence between Vietnamese populations and those in other East Asian countries. We have made these comparisons using the genomic sequences of c. 135 isolates of TuMV collected mostly from Eurasia, and discuss what they reveal

about the changes that have occurred during east Asia-wide evolution and migration of TuMV populations. Our analyses provide a preliminary definition of the geographical structure of TuMV populations in Vietnam, China and Japan, and indicate that it is strongly influenced by founder effects.

2. Materials and methods

2.1. Virus isolates

The *Brassicaceae* crop-producing areas of Vietnam, including Northwest, Northeast, Red river delta, North central coast, South central coast and Central highlands regions, were surveyed during the growing seasons of 2006–2008. All collected samples were tested by direct double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) (Clark and Adams, 1977).

Details of the Vietnamese TuMV isolates, their place of origin, original host plant, symptom on collected plant, year of isolation, and host type are shown in Table 1, together with details of the isolates used in the analyses and for which complete genomic sequences have already been reported (Table S1). The Northeast region in Vietnam is one of major areas of *Brassicaceae* crop production.

All the isolates were inoculated to *Chenopodium quinoa* and serially cloned through single lesions at least three times. This procedure is essential as field collected isolates are often mixtures. They were propagated in *Brassica rapa* cv. Hakatasuwari or *Nicotiana benthamiana* plants. Plants infected systemically with each of the TuMV isolates were homogenized in 0.01 M potassium phosphate buffer (pH 7.0), and the isolates were mechanically inoculated to young plants of *Brassica chinensis* cv. Choyo, *Brassica juncea* cv. Hakarashina, *Brassica napus* cv. Otsubu, *Brassica rapa* cv.

Table 1
Turnip mosaic virus isolates collected in Vietnam.

Isolate	Original host	Location (city, province/district)	Symptom on collected plant ^a	Year of collection	Host type ^b	Accession No.
VIET15	<i>Raphanus sativus</i>	Van Giang, Hung Yen	M	2006	B(R)	AB747286
VIET56	<i>Brassica juncea</i>	Moc Chau, Son La	M	2007	B	AB747287
VIET58	<i>B. juncea</i>	Moc Chau, Son La	M	2007	BR	AB747288
VIET65	<i>R. sativus</i>	Gia Lam, Ha Noi	M	2007	BR	AB747289
VIET66	<i>R. sativus</i>	Gia Lam, Ha Noi	M	2007	B	AB747290
VIET73	<i>R. sativus</i>	Van Giang, Hung Yen	M	2007	BR	AB747291
VIET79	<i>R. sativus</i>	Cam Giang, Hai Duong	M	2007	BR	AB747292
VIET80	<i>R. sativus</i>	Cam Giang, Hai Duong	M	2007	B	AB747293
VIET82	<i>R. sativus</i>	Ban Me Thuot, Dak Lak	M	2007	B(R)	AB747294
VIET83	<i>R. sativus</i>	Ban Me Thuot, Dak Lak	M	2007	B	AB747295
VIET89	<i>R. sativus</i>	Ban Me Thuot, Dak Lak	M	2007	BR	AB747296
VIET138	<i>B. juncea</i>	Thanh Long, Thua Thien Hue	M, S	2007	B(R)	AB747297
VIET153	<i>B. juncea</i>	Hoi An, Quang Nam	M	2007	B(R)	AB747298
VIET158	<i>B. juncea</i>	Gia Lam, Ha Noi	M	2007	B(R)	AB747299
VIET159	<i>B. juncea</i>	–, Lang Son	M	2007	B	AB747300
VIET160	<i>B. juncea</i>	Huu Lung, Lang Son	M	2007	B	AB747301
VIET164	<i>B. juncea</i>	Thuong Tin, Ha Tay	M, S	2007	B	AB747302
VIET166	<i>B. juncea</i>	Thuong Tin, Ha Tay	M	2007	B	AB747303
VIET167	<i>B. juncea</i>	Gia Lam, Ha Noi	M	2007	B	AB747304
VIET169	<i>B. juncea</i>	Vo Cuong, Bac Ninh	M	2007	B	AB747305
VIET170	<i>B. juncea</i>	Vo Cuong, Bac Ninh	M	2007	B(R)	AB747306
VIET172	<i>B. juncea</i>	Gia Lam, Ha Noi	M	2007	B	AB747307
VIET173	<i>B. juncea</i>	Viet Yen, Bac Giang	M	2007	B	AB747308
VIET174	<i>B. juncea</i>	Viet Yen, Bac Giang	M	2007	B	AB747309
VIET175	<i>B. juncea</i>	Viet Yen, Bac Giang	M	2007	B(R)	AB747310
VIET176	<i>B. juncea</i>	Vu Thu, Thai Binh	M	2007	B(R)	AB747311
VIET177	<i>B. juncea</i>	Vu Thu, Thai Binh	M, S	2008	B	AB747312
VIET178	<i>B. juncea</i>	Nam Truc, Nam Dinh	M, S	2008	B(R)	AB747313
VIET179	<i>B. juncea</i>	Nam Truc, Nam Dinh	M	2008	B(R)	AB747314
VIET180	<i>B. juncea</i>	Viet Yen, Bac Giang	M	2008	B(R)	AB747315

^a M, mosaic; S, stunting.

^b Host type B; *Brassica*, isolates infected *B. rapa* cv. Hakatasuwari systemically giving mosaic symptoms. Host type BR; these isolates infected both *B. rapa* and *R. sativus* cvs. Akimazari and Taibyosobutori (Japanese radish) systemically giving mosaic symptoms. Host type B(R); isolates infected *B. rapa* systemically giving mosaic symptoms and infected *R. sativus* cvs. Akimazari and Taibyosobutori only occasionally.

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