



Discriminable roles of *Aedes aegypti* and *Aedes albopictus* in establishment of dengue outbreaks in Taiwan



Chao-Fu Yang^a, Jion-Nun Hou^a, Tien-Huang Chen^{a,1}, Wei-June Chen^{a,b,*}

^a Graduate Institute of Biomedical Sciences, Chang Gung University, Kwei-San, Tao-Yuan 33332, Taiwan

^b Department of Public Health and Parasitology, College of Medicine, Chang Gung University, Kwei-San, Tao-Yuan 33332, Taiwan

ARTICLE INFO

Article history:

Received 20 August 2013
Received in revised form 10 October 2013
Accepted 12 October 2013
Available online 23 October 2013

Keywords:

Aedes
Dengue outbreaks
Mosquito vectors
Taiwan

ABSTRACT

Aedes aegypti and *Aedes albopictus* were reported to be significant as vectors of dengue fever. In Taiwan, the latter is distributed throughout the island while the former appears only south of the Tropic of Cancer; i.e., 23.5° N. In the past decade, there were five outbreaks with over 1000 cases of dengue fever in Taiwan. Without exception, these outbreaks all occurred in the south where the two *Aedes* mosquitoes are sympatric. According to the Center for Disease Control of Taiwan, imported cases are thought to provide the seeds of dengue outbreaks every year. Mostly, the number of imported cases is greater in northern island, probably due to a larger population of travelers and imported workers from endemic countries. Looking at the example in 2002, northern, central, and southern parts of Taiwan reported 28, 11, and 13 imported cases, respectively. However, 54, 21, and 5309 total cases were confirmed in the corresponding regions over the entire year, indicating a significant skew of case distributions. A hypothesis is thus inspired that the existence of *Ae. aegypti* is a prerequisite to initiate a dengue outbreak, while participation of *Ae. albopictus* expands or maintains the scale until the *de novo* herd immunity reaches high level.

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* Corresponding author. Tel.: +886 3 218800/5139; fax: +886 3 2118408.

E-mail address: wjchen@mail.cgu.edu.tw (W.-J. Chen).

¹ Present address: Research and Diagnostic Center, Centers for Disease Control, Taiwan.

1. Introduction

Dengue fever (DF) is an important mosquito-borne viral infectious disease, mostly distributed in tropical regions of the world. Epidemics of DF were first recognized almost simultaneously in Asia, Africa, and North America in the 1780s (Armstrong, 1923). Afterward, dengue epidemics were mostly reported from Southeast Asia, particularly after the end of World War II (Rigau-Pérez et al., 1998). Unexpectedly, DF epidemics became more frequent and extended to Latin America in the early 1980s (Goh et al., 1987). The dengue virus (DENV) is the etiological agent of DF and dengue hemorrhagic fever (DHF)/dengue shock syndrome (DSS); it is naturally transmitted by mosquito vectors between humans to maintain its life cycle (Fig. 1). It is now known that there may be a sylvatic cycle that serves as an enzootic cycle involving monkeys and jungle mosquitoes (Rudnick et al., 1967). There is evidence showing that the currently circulating DENV-2 may have resulted from spillover of ancestral sylvatic strains (Teoh et al., 2010). The DENV is one of 70 members in the genus *Flavivirus* in the family *Flaviviridae*; which consists of four closely related but genetically distinct antigenic serotypes named DENV-1, -2, -3, and -4, originally classified based on their serological characteristics (Calisher et al., 1989). However, they can be clearly differentiated through amplification of specific gene fragments by a conventional reverse-transcriptase polymerase chain reaction (RT-PCR) or real-time RT-PCR (Kong et al., 2006). Any of the four serotypes may cause similar mild febrile illness or DF, although the disease can be subclinical or inapparent in most infections (Endy et al., 2011). Each serotype of DENV elicits neutralizing antibodies in infected humans, resulting in life-long immunity against the corresponding serotype of the virus (Rigau-Pérez et al., 1998). Within mosquito vectors, DENV can infect a variety of tissues especially the midgut and salivary glands (Salazar et al., 2007).

Clinical dengue cases have largely increased in number and become more widely distributed during the past few decades (WHO, 2009). One important reason is that vector populations, including the yellow fever mosquito *Aedes aegypti* and the Asian tiger mosquito *Aedes albopictus*, have substantially increased in density and/or distribution (Kalra et al., 1997). Of which, *Ae. aegypti* is considered the predominate vector of DF (Nelson, 1986) while *Ae. albopictus* is another mosquito species long noted for its potential role as a DF vector in Southeast Asia (Chow et al., 1998). However, in some areas like Taiwan, dengue outbreaks can easily occur in regions where *Ae. aegypti* and *Ae. albopictus* co-exist. Nevertheless, dengue outbreaks rarely appear in regions where only *Ae. albopictus* breeds with a few exceptions. It raises a question whether or not these two species of mosquitoes actually play different roles in initiating dengue outbreaks in nature.

2. Pathogenesis and epidemiology of dengue infections

Classic DF in human is the most common feature of an infection; it is characterized by a persistent high fever with nausea and vomiting, headaches, retro-orbital pain, muscle pain or myalgia, and joint pain or arthralgia, followed by white/red rashes or a maculopapular rash on the body (WHO, 2009). In consideration of clinical symptoms, DF is also known as “breakbone fever” (Powers, 1860). Cross-protection by elicited antibodies against any specific serotype of the DENV usually does not occur unless at the very early stage of infection (Nishiura, 2008). This renders human infection by a heterologous serotype of the DENV possible and potentially leads to the occurrence of DHF and/or DSS based on the concept of sequential infections or so-called “antibody-dependent enhancement” (Halstead, 1988). Hyperendemic dengue infection reflects continuously circulating multiple serotypes of the DENV, which

puts people at risk for severe outcomes in those areas (Barrera et al., 2002).

Alternatively, DHF/DSS was shown to be associated with the viral strain. Infections with more-virulent strains may result in severe outcomes (Rosen, 1986). Genetic diversity of the DENV, even of the same serotype, is frequently observed in nature (Chaudhry et al., 2006). Spontaneous mutations in the linear ssRNA of the dengue genome frequently occur due to the lack of a proofreading mechanism and the inability to repair errors during RNA synthesis (Holland, 1996). This contributes to the formation of genetically diverse populations or “quasispecies” of DENVs during the process of viral replication (Eigen, 1996; Holmes, 2004). Quasispecies of DENV may lead to some, if not all, phenotypic changes (Chen et al., 2003). It was estimated that approximately 5% of DHF/DSS patients die, predominantly children younger than 15 years (Noisakran and Perng, 2008). In addition to DHF/DSS, unusual neurological manifestations were reported in a small proportion of dengue infections (Chen et al., 1991); of these, reduced consciousness and convulsions are the most frequent signs (Solomon et al., 2000). Increasing evidence showed neurotropism in some dengue cases, implying that direct viral encephalitis may be possible in patients with DENV infection (Varatharaj, 2010).

DF has become an extremely significant public health problem threatening many lives in multiple tropical and subtropical countries (Gubler, 2002a,b). It is estimated that 2.5 billion people are at risk of dengue infections in areas where DENV circulates (Brady et al., 2012). Moreover, ca. 50–100 million clinical cases occur annually in over 100 countries in the world (Simmons et al., 2012). Of these, some 2.5% of dengue cases become more severe and progress into DHF and/or DSS. These severe forms of the disease are responsible for highly morbid and even fatal outcomes. However, it seems that severe dengue cases arise among adults in some areas in recent years (Cummings et al., 2009; Sam et al., 2013). The World Health Organization (WHO) has estimated that there are 0.5–1 million cases of DHF and 22,000 deaths each year worldwide (Guerdan, 2010).

Extensive and rapid urbanization without good planning may have directly resulted in large numbers of artificial containers that are suitable for breeding *Aedes* mosquitoes around households. Rapidly developing air transportation has accelerated virus translocation, allowing it to easily migrate from endemic to non-endemic areas (Gubler, 2002a,b). Therefore, the probability of virus introduction through imported cases has obviously increased, even in countries where dengue has never been reported. It is worth noting that travelers who catch the DENV are not only the victims of the infection but also serve as vehicles for its potential transmission (Jelinek, 2000). Other environmental factors such as global warming are also reported to be associated with the occurrence of dengue epidemics (Herrera-Martinez and Rodríguez-Morales, 2010), causing this disease to be more complicated and thus more difficult to deal with.

Aedes aegypti is believed to have originated in Africa; it is now present in a large part of the world, mainly tropical and subtropical regions (Tabachnick, 1991). *Aedes albopictus* is another mosquito species long noted for its potential role as a DF vector in Southeast Asia, its original range (Chow et al., 1998). *Aedes albopictus* is now extensively established in many parts of the world, being introduced into the United States in the early 1980s (Hawley, 1988), first found in Europe in 1979 (European Center for Disease Prevention and Control, 2009), and now widespread in many parts of Europe (Caminade et al., 2012). *Aedes albopictus* is also now prevalent in Africa (Gubler, 2003), and may be involved in the transmission of DENV and chikungunya virus (Paupy et al., 2010). Because *Ae. albopictus* was demonstrated to be susceptible to DENVs in the laboratory (Chen et al., 1993), and in the field (Gratz,

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