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ABSTRACT. Since the introduction of *Aedes albopictus* into North and South America, 18 viruses in 3 families have been used in vector competence studies involving 10 North American and 4 South American geographic strains of *Ae. albopictus*. This review summarizes the results of these studies and discusses the potential of *Ae. albopictus* to become a vector of arboviruses of public health importance in areas of the Western Hemisphere where it has recently become established.

INTRODUCTION

Aedes albopictus (Skuse) was an abundant and common pest in Hawaii by the late 1890s, where it presumably was introduced from the western Pacific by sailing vessels (Perkins 1913, Joyce 1961). It was discovered in Houston, TX, in 1985 (Sprenger and Wuithiranyagool 1986) and currently is established in the Western Hemisphere in 18 of the contiguous United States, Hawaii and 4 states in Brazil (Centers for Disease Control 1989, Ferreira Neto et al. 1987; C. Moore, personal communication). It seems remarkable that almost a century passed following the establishment of Ae. albopictus in Hawaii before the species gained a foothold in other parts of the Western Hemisphere. Undoubtedly, this can be attributed to increased traffic in the used tire trade (Reiter and Sprenger 1987).

Public health officials are concerned about the current rapid spread of *Ae. albopictus* in the Western Hemisphere because of its known and potential vector relationship with several arboviruses of public health importance. Shroyer (1986) provided a useful review of experimental and natural associations of *Ae. albopictus* with arboviruses up to the time of the discovery of this mosquito in Houston, TX. Since then, much experimental work has been done to define the vector competence of geographic strains of *Ae. albopictus* from North and South America. The purpose of this review is to summarize these studies.

Direct comparison of data on virus infection and transmission rates from different laboratories is complicated by several variables, e.g., virus strain and passage history, titer of infectious meal, whether the infectious meal is from a viremic host or a virus suspension, incubation period and temperature, whether the transmission assay is *in vivo* or *in vitro*, and method of calculating transmission rates. An argument can be made for including uninfected as well as infected mosquitoes that refeed during the virus

transmission trial when calculating the transmission rate, thereby deriving the "population" transmission rate. However, I have chosen to present, whenever possible, transmission rates that are based only on the number of infected mosquitoes that refed. Uninfected mosquitoes cannot transmit virus, and eliminating them from the calculation removes some of the bias introduced when comparing transmission rates between groups of mosquitoes with widely disparate infection rates. This disparity, in turn, often is a result of differences in the titer of the infectious meal and whether the mosquitoes fed on a viremic host or a virus suspension. The "population" transmission rate can be derived by multiplying the infection rate by the transmission rate of infected females that refed.

DISCUSSION

Eleven publications have dealt with the vector competence of North and South American strains of Ae. albopictus (Beaman and Turell 1991, Boromisa et al. 1987, Grimstad et al. 1989, Miller and Ballinger 1988, Miller et al. 1989, Mitchell and Miller 1990, Mitchell et al. 1987, 1990; Scott et al. 1990, Smith and Francy 1991, Turell et al. 1988). Another article is in press (Heard et al. 1991). In addition, studies have been conducted with western equine encephalitis (WEE) virus (L. Kramer, S. Presser and J. Hardy, personal communication) and chikungunya (CHIK) virus (M. Turell and J. Beaman, personal communication). Eighteen viruses in 3 families have been used in vector competence studies with North and South American strains of Ae. albopictus as follows:

Flaviviridae

Genus *Flavivirus*: Dengue (DEN) 1,2,3,4 Yellow fever (YF)

Togaviridae

Genus Alphavirus:

Eastern equine encephalitis (EEE)

Western equine encephalitis (WEE)	Potosi (POT)
Venezuelan equine encephalitis (VEE)	Oropouche (ORO)
Ross River (RR)	Genus Phlebovirus:
Mayaro (MAY)	Rift Valley fever (RVF)
Chikungunya (CHIK)	These studies have included 10 North Amer-
Bunyaviridae	ican and 4 South American geographic strains
Genus Bunyavirus:	of Ae. albopictus. The North American strains
La Crosse (LAC)	are from Polk County, FL; Alsace, Evansville
Jamestown Canyon (JC)	and Indianapolis, IN; Lexington, KY; Gentilly
Keystone (KEY)	and New Orleans, LA; Potosi, MO; Memphis,
Trivittatus (TVT)	TN; and Houston, TX. The South American

Table 1. Vector competence of North and South American strains of Aedes albopictus for certain flaviviruses.

	Maanita	Infection		Transmis- sion			
Virus and strain	Mosquito strain	n	%	n	%	Reference	
DEN-1							
PR-1620	Houston	292	23 - 100	24	88	Mitchell et al. 1987	
YARU 40130	Houston	21	71	8	38	Boromisa et al. 1987	
YARU 40130	Memphis	29	100	15	20	Boromisa et al. 1987	
YARU 40130	New Orleans	27	100	16	6	Boromisa et al. 1987	
PR-1620	Cariacica City	29	52	14	71	Miller and Ballinger 1988	
DEN-2							
PR-1615	Houston	333	3-92	23	74	Mitchell et al. 1987	
	Cariacica City	26	38	10	70	Miller and Ballinger 1988	
DEN-3	-						
MOZ-1557	Houston	241	22 - 64	15	53	Mitchell et al. 1987	
	Cariacica City	27	19	4	75	Miller and Ballinger 1988	
DEN-4	-						
PR-16 32	Houston	280	7-76	19	42	Mitchell et al. 1987	
	Cariacica City	26	35	8	25	Miller and Ballinger 1988	
YF	•						
TRIN-788379	Houston	146	30 - 70	67	0-55	Mitchell et al. 1987	
TRIN-788379	Cariacica City	35	57	20	15	Miller and Ballinger 1988	
PERU-1899/81	Cariacica City	33	36	8	38	Miller and Ballinger 1988	

Table 2. Vector competence of North and South American strains of Aedes albopictus for certain alphaviruses.

	Mosquito	Infection		Transmission			
Virus and strain	strain	n	%	n	%	Reference	
EEE ME 77132	Houston	10	100	20	25-57	Scott et al. 1990	
WEE BFS 1703	Houston	74	83-100	24	75-83	Kramer et al. pers. comm	
VEE, 1A	Houston	127	54	26*	19	Beaman and Turell 1991	
(Trinidad Donkey)	Alsace, IN	91	74	31*	13	Beaman and Turell 1991	
	Sao Paulo	189	70	33*	58	Beaman and Turell 1991	
	Santa Teresa	168	62	32*	63	Beaman and Turell 1991	
MAY TR 4625	Sao Paulo	181	9–85	17	45–50	Smith and Francy 1991	
RR Rarotonga	Houston	317	13–100	168	33–78	Mitchell et al. 1987	
СНІК	Houston	218	20-76		Yes**	Turell, pers. comm.	
~~~~	Gentilly, LA	226	47-89		Yes**	Turell, pers. comm.	
	Polk Co., FL	120	22-92		Yes**	Turell, pers. comm.	
	Sao Paulo	189	32 - 72		Yes**	Turell, pers. comm.	

* Mosquitoes with disseminated infections.

** Transmission demonstrated but rates were not determined.

				j		
Virus and	Mosquito	In	fection	Trans	mission	
strain	strain	n	%	n	%	Reference
LAC GW-1978	Houston Evansville Indianapolis	80 9 10	93–98 89 80	75* 6* 6*	47 33 17	Grimstad et al. 1989 Grimstad et al. 1989 Grimstad et al. 1989
JC 800245	Houston	30	97	26*	8	Grimstad et al. 1989
KEY B64-5587	Houston	37	92	31*	0	Grimstad et al. 1989
TVT CMWA	Houston	50	28	12*	0	Grimstad et al. 1989
POT 89-3380	Lexington	140	11-45	14	21	Mitchell et al. 1990
POT 89-3364	Potosi	361	83-100	274	0–28	Heard et al. 1991, in press
ORO TR-9760	Sao Paulo	120	2-12	5	0	Smith and Francy 1991
RVF ZH-501	Houston	275	3-89	66*	15	Turell et al. 1988

l'able 3. Vector competence of North and South American strains of Aedes albopictus for California serogroup	,
viruses and other Bunyaviridae.	

* Mosquitoes with disseminated infections.

Table 4. Vertical transmission of certain arboviruses by North and South American strains of Aedes albopictus.

Virus and	Mosquito	Route	F ₁ ir	nfections	
strain	strain	mothers infected	n	Ratio	Reference
DEN-1	Anchieta	Inoc.	546	1:182	Mitchell and Miller 1990
PR-1620	Santa Teresa	Inoc.	1,558	1:390	Mitchell and Miller 1990
	Sao Paulo	Inoc.	408	<1:408	Mitchell and Miller 1990
DEN-4	Anchieta	Inoc.	1,884	<1:1,884	Mitchell and Miller 1990
PR-1632	Santa Teresa	Inoc.	1,906	1:1,906	Mitchell and Miller 1990
	Sao Paulo	Inoc.	1,819	<1:1,819	Mitchell and Miller 1990
YF, TRIN 788379	Houston	Inoc.	6,180	<1:6,180	Miller et al. 1989
EEE ME-77132	Houston	Oral	1,657	<1:1,657	Scott et al. 1990
РОТ	Lexington	Inoc.	6,635	<1:6.635	Mitchell et al. 1990
89-3380	2	Oral	1,196	<1:1,196	Mitchell et al. 1990
POT 89-3364	Potosi	Oral	5,145	<1:5,145	Heard et al. 1991, in press

strains are from Anchieta, Cariacica City and Santa Teresa, Espirito Santo State, Brazil; and São Paulo State, Brazil.

Flaviviridae: Because of concern that Ae. albopictus might become involved in the transmission cycle of dengue (DEN) viruses in the Americas, vector competence studies with these viruses have received high priority (Table 1). Per os infection rates and transmission rates indicate that a North American strain (Houston) and a South American strain (Cariacica City) of *Ae. albopictus* are competent experimental vectors of each DEN serotype. The DEN-1 virus transmission rates reported for Houston *Ae. albopictus* ranged from 38% (Boromisa et al. 1987) to 88% (Mitchell et al. 1987). This difference

	Ae. albopictus strains from					
	outsi	and areas de W. sphere ¹	North and South America			
Viruses	Infect.	Trans.	Infect.	Trans.		
Chikungunya	+	+	+	+		
Dengue 1, 2, 3, 4	+	+	+	+		
Eastern equine encephalitis	+	+	+	+		
Jamestown Canyon			+	+		
Japanese encephalitis	+	+				
Keystone			+	-		
La Crosse			+	+		
Mayaro			+	+		
Nodamura	+	?				
Oropouche			+	_		
Orungo	+	+				
Potosi			+	+		
Rift Valley fever			+	+		
Ross River	+	+	+	+		
San Angelo	+	+				
St. Louis encephalitis	+	+				
Trivittatus			+	-		
West Nile	+	+				
Western equine encephalitis	+	+	+	+		
Venezuelan equine encephalitis			+	+		
Yellow fever	+	+	+	+		

Table 5. Susceptibility of Aedes albopictus to oral infection with arboviruses and ability to transmit by bite.

¹ Information from Shroyer (1986).

probably is due, in part, to differences in the *in vitro* transmission assay used in the 2 laboratories. Boromisa et al. (1987) diluted their feeding suspensions containing mosquito salivary secretions and froze them before injecting them into uninfected mosquitoes for virus amplification, whereas Mitchell et al. (1987) injected fresh suspensions containing salivary secretions shortly after collection and without further dilution. Also, the DEN-1 virus strains used in the two laboratories were different, and this may have affected transmission rates.

Dutch investigators (Dinger et al. 1929) reported that *Ae. albopictus* could transmit yellow fever (YF) virus under experimental conditions; however, infection and transmission rates were not determined. It is clear from studies conducted at the Centers for Disease Control (CDC) that *Ae. albopictus* strains from North and South America are competent vectors of YF virus (Table 1). Therefore, in view of the adaptation of *Ae. albopictus* to peridomestic habitats, this mosquito has the potential to bridge the gap between jungle and urban YF cycles in the Western Hemisphere (Mitchell et al. 1987).

Alphaviridae: The vector competence of North and South American strains of *Ae. albopictus* has been assessed for 6 alphaviruses (Table 2). *Aedes albopictus* is a competent vector for each of these viruses under experimental conditions. Fortunately, 2 of the viruses, Ross River (RR) and chikungunya (CHIK), are not found in North or South America. Recently, *Ae. albopictus* has been found in Fiji (Laird 1990) where a large epidemic caused by RR virus occurred in 1979 (Aaskov et al. 1981). Results of vector competence studies with *Ae. albopictus* and RR virus (Mitchell et al. 1987, Mitchell and Gubler 1987) provide a basis for estimating the likelihood that *Ae. albopictus* may become involved in the transmission cycle in Fiji.

Since birds are the principal amplification hosts for eastern equine encephalitis (EEE) and western equine encephalitis (WEE) viruses, it seems unlikely that Ae. albopictus will become a major vector of these viruses unless a significant degree of feeding on birds is found to occur. Also, WEE virus activity generally occurs in dry and semi-arid areas of the Great Plains and western United States, areas that are unfavorable to a mosquito that requires humid environments. Estimating the chances of Ae. albopictus becoming involved in the transmission cycles of Venezuelan equine encephalitis (VEE) and Mayaro (MAY) viruses is more problematic. Currently, the distribution of Ae. albopictus in Texas overlaps with areas that experienced epizootic VEE activity during 1971. Aedes albopictus is not present in areas where MAY epidemics have occurred.

Bunyaviridae: A major concern regarding the establishment of Ae. albopictus in the United States has been the possibility that this mosquito may become involved in the transmission cycle of La Crosse (LAC) virus. Grimstad et al. (1989) showed that 3 geographic strains of Ae. albopictus from the United States are competent vectors for LAC virus (Table 3), and the mosquito occurs within the range of LAC virus activity (Wesson et al. 1990). Three other California sereogroup viruses, Jamestown Canyon (JC), Kevstone (KEY) and trivittatus (TVT), were included in the studies of Grimstad et al. (1989). Jamestown Canyon virus was transmitted inefficiently (8%), and none of 12 Ae. albopictus with disseminated TVT virus infections or 31 with disseminated KEY virus infections transmitted virus (Table 3).

Potosi (POT) virus, a new Bunyavirus isolated from Ae. albopictus collected in Potosi, MO (Francy et al. 1990; C. J. Mitchell, G. C. Smith. T. F. Tsai, and C. Frazier, unpublished data), is of interest because it represents the first recognized involvement of Ae. albopictus in a virus transmission cycle in the United States. Potosi virus has not been shown to infect or cause disease in humans. A serosurvey of 243 people living within 1.6 km of the tire yard from which POT virus was isolated showed no evidence of human infection with the virus (T. Tsai, personal communication). Two strains of Ae. albopictus have been shown to be competent vectors of POT virus (Table 3). However, neither strain appears capable of transmitting POT virus vertically (Table 4). This suggests that the virus was not introduced into Missouri via infected Ae. albopictus eggs in imported used tires (Mitchell et al. 1990).

Although the sample tested in virus transmission trials was small, Ae. albopictus does not appear to be a competent vector of Oropouche (ORO) virus (Table 3). It seems unlikely that Ae. albopictus would become involved in the transmission of ORO virus since Culicoides paraensis (Goeldi) is believed to be the main vector (Roberts et al. 1981). Currently, the distributions of Ae. albopictus and Rift Valley Fever (RVF) virus do not overlap; however, Ae. albopictus has recently been reported from tires in South Africa (Cornel and Hunt 1991). If Ae. albopictus expands its range into RVF endemic areas it should be considered a potential vector (Turell et al. 1988).

Vertical transmission: Relatively few attempts have been made to assess the ability of North and South American strains of *Ae. albopictus* to transmit viruses vertically (Table 4). The results of studies with POT virus are discussed above. Both DEN-1 and DEN-4 viruses have been shown to be vertically transmitted by Brazilian strains of *Ae. albopictus* following parenteral injection of virus into females. Filial infection rates ranged from 1:182 to 1:1,906 (Table 4). Vertical transmission of YF virus was not demonstrated in 6,180 progeny of infected females.

Scott et al. (1990) tested a small sample (1,657) of *Ae. albopictus* for vertical transmission of EEE virus. The negative results are consistent with those for other alphaviruses that have been studied; none has been conclusively shown to be transmitted vertically.

# SUMMARY AND CONCLUSIONS

The vector competence of Ae. albopictus has been tested for 24 viruses (Table 5). Previous studies with Ae. albopictus from Hawaii and areas outside the Western Hemisphere included 15 viruses (Shroyer 1986). Studies conducted with North and South American strains of Ae. albopictus have confirmed results for 9 of these viruses and have added an additional 9 viruses to the list.

The greatest danger posed by Ae. albopictus in the Western Hemisphere, outside of Hawaii, is its potential to serve as a vector of DEN, LAC and YF viruses. However, at this time, the only virus isolated from Ae. albopictus collected in nature in the Western Hemisphere is the apparently innocuous POT virus. It should be emphasized that Ae. albopictus has yet to be implicated as the vector of any case of vector-borne disease in North or South America.

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## **REFERENCES CITED**

Aaskov, J. G., J. U. Mataika, G. W. Lawrence, V. Rabukawaqa, M. M. Tucker, J. A. R. Miles and D. A. Dalglish. 1981. An epidemic of Ross River virus infection in Fiji, 1979. Am. J. Trop. Med. Hyg. 30:1053-1059.

- Beaman, J. R. and M. J. Turell. 1991. Transmission of Venezuelan equine encephalomyelitis virus by strains of Aedes albopictus (Diptera:Culicidae) collected in North and South America. J. Med. Entomol. 28:161-164.
- Boromisa, R. D., K. S. Rai and P. R. Grimstad. 1987. Variation in the vector competence of geographic strains of *Aedes albopictus* for dengue 1 virus. J. Am. Mosq. Control Assoc. 3:378-386.
- Centers for Disease Control. 1989. Update: Aedes albopictus infestations—United States, Mexico. MMWR 38:440-446.
- Cornel, A. J. and R. H. Hunt. 1991. Aedes albopictus in Africa? First records of live specimens in imported tires in Cape Town. J. Am. Mosq. Control Assoc. 7:107-108.
- Dinger, J. E., W. A. P. Schuffner, E. P. Snijders and N. H. Swellengrebel. 1929. Onderzoek over Gele Koorts in Nederland (Dedre Medeeling). Nederl. Tijdschr. V. Geneesk. 73:5982-5991.
- Ferreira Neto, J. A., M. M. Lima and M. B. Aragao. 1987. First observations on *Aedes albopictus* in Brazil (in Portuguese). Cad. Saude Publica, R.J. 3:56– 61.
- Francy, D. B., N. Karabatsos, D. M. Wesson, C. G. Moore, Jr., J. S. Lazuick, M. L. Niebylski, T. F. Tsai and G. B. Craig, Jr. 1990. A new arbovirus from Aedes albopictus, an Asian mosquito established in the United States. Science 250:1738-1740.
- Grimstad, P. R., J. F. Kobayashi, M. Zhang and G. B. Craig, Jr. 1989. Recently introduced Aedes albopictus in the United States: potential vector of La Crosse virus (Bunyaviridae: California serogroup). J. Am. Mosq. Control Assoc. 5:422-427.
- Heard, P. B., M. L. Niebylski, D. B. Francy and G. B. Craig, Jr. 1991. Transmission of a newly recognized virus (Bunyaviridae, *Bunyavirus*) isolated from *Aedes albopictus* (Diptera: Culicidae) in Potosi, Missouri, U.S.A. J. Med. Entomol. 28: In press.
- Joyce, C. R. 1961. Potentialities for accidental establishment of exotic mosquitoes in Hawaii. Proc. Hawaii. Entomol. Soc. 17:403-413.
- Laird, M. 1990. New Zealand's northern mosquito survey, 1988–89. J. Am. Mosq. Control Assoc. 6:287– 299.
- Miller, B. R. and M. E. Ballinger. 1988. Aedes albopictus mosquitoes introduced into Brazil: vector competence for yellow fever and dengue viruses. Trans. R. Soc. Trop. Med. Hyg. 82:476-477.
- Miller, B. R., C. J. Mitchell and M. E. Ballinger. 1989. Replication, tissue tropisms and transmission of yellow fever virus in *Aedes albopictus*. Trans. R. Soc. Trop. Med. Hyg. 83:252–255.

- Mitchell, C. J. and D. J. Gubler. 1987. Vector competence of geographic strains of *Aedes albopictus* and *Aedes polynesiensis* and certain other *Aedes* (*Stegomyia*) mosquitoes for Ross River virus. J. Am. Mosq. Control Assoc. 3:142–147.
- Mitchell, C. J. and B. R. Miller. 1990. Vertical transmission of dengue viruses by strains of Aedes albopictus recently introduced into Brazil. J. Am. Mosq. Control Assoc. 6:251–253.
- Mitchell, C. J., B. R. Miller and D. J. Gubler. 1987. Vector competence of *Aedes albopictus* from Houston, Texas, for dengue serotypes 1 to 4, yellow fever and Ross River viruses. J. Am. Mosq. Control Assoc. 3:460-465.
- Mitchell, C. J., G. C. Smith and B. R. Miller. 1990. Vector competence of *Aedes albopictus* for a newly recognized *Bunyavirus* from mosquitoes collected in Potosi, Missouri. J. Am. Mosq. Control Assoc. 6:523-527.
- Perkins, R. C. L. 1913. Fauna Hawaiiensis, Introduction, 1(6) XV-CCXXVIII. Cambridge Univ. Press.
- Reiter, P. and D. Sprenger. 1987. The used tire trade: a mechanism for the worldwide dispersal of container breeding mosquitoes. J. Am. Mosq. Control Assoc. 3:494-501.
- Roberts, D. R., A. L. Hoch, K. E. Dixon and C. H. Llewellyn. 1981. Oropouche virus. III. Entomological observations from three epidemics in Para, Brazil, 1975. Am. J. Trop. Med. Hyg. 30:165–171.
- Scott, T. W., L. H. Lorenz and S. C. Weaver. 1990. Susceptibility of *Aedes albopictus* to infection with eastern equine encephalomyelitis virus. J. Am. Mosq. Control Assoc. 6:274-278.
- Shroyer, D. A. 1986. Aedes albopictus and arboviruses: a concise review of the literature. J. Am. Mosq. Control Assoc. 2:424–428.
- Smith, G. C. and D. B. Francy. 1991. Laboratory studies of a Brazilian strain of *Aedes albopictus* as a potential vector of Mayaro and Oropouche viruses. J. Am. Mosq. Control Assoc. 7:89–93.
- Sprenger, D. and T. Wuithiranyagool. 1986. The discovery and distribution of *Aedes albopictus* in Harris County, Texas. J. Am. Mosq. Control Assoc. 2:217– 219.
- Turell, M. J., C. L. Bailey and J. R. Beaman. 1988. Vector competence of a Houston, Texas, strain of Aedes albopictus for Rift Valley fever virus. J. Am. Mosq. Control Assoc. 4:94-96.
- Wesson, D., W. Hawley and G. B. Craig, Jr. 1990. Status of *Aedes albopictus* in the midwest La Crosse belt distribution, 1988. Proc. Ill. Mosq. Control Assoc. 1:11-15.