Weather factors in the prediction of western equine encephalitis epidemics in Manitoba

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SUMMARY

Cases of western equine encephalitis in horses in 1987 in western USA and Manitoba, Canada were examined by backward trajectory analysis of winds. Culex tarsalis mosquitoes infected with western equine encephalitis virus could have been carried on southerly winds from Texas and Oklahoma to northern USA and from there to Manitoba. The presence of the Polar front over North Dakota and Minnesota at the end of July would have led to the landing of Cx. tarsalis in Montana and Wisconsin and prevented further carriage into Manitoba. Temperatures in southern Texas during the winter months (average daily maximum temperatures 19.7 °C and higher) would have permitted continuous transmission of western equine encephalitis virus by Cx. tarsalis in this area.

Weather factors involved in outbreaks from 1975–88 were analysed to see if epidemics in Manitoba (23 or more cases in horses) could be predicted. The conditions for epidemics could be defined as follows: (a) the number of cases in horses in USA was 98 or more, (b) winds were southerly with speeds 45 kmh⁻¹ or higher, and (c) counts of Cx. tarsalis females/light trap per day were 3·2 or higher. There were 3 or fewer cases in Manitoba, when the number of cases in USA was 27 or less, even when Cx. tarsalis counts were higher than 3·2. With Cx. tarsalis counts below 3 and/or unsuitable winds, or the Polar front further south, the number of cases in Manitoba was between 0 and 17, even when the number of cases in USA was from 38–172. Without information on the extent of infection further south, the weather variables would probably be more useful in excluding the possibility of an epidemic in Manitoba than in predicting one.

INTRODUCTION

Western equine encephalitis (WEE) is a virus disease which causes encephalitis in horses and man [1]. It occurs in North, Central and South America with most cases in western USA and western Canada. The virus is transmitted by mosquitoes.

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The main vector in North America is *Culex tarsalis* and the virus circulates in mosquitoes and birds with horses and man as 'dead-end' hosts.

In the temperate regions of North America WEE virus may persist between outbreaks in mosquitoes or small vertebrate hosts in the affected areas or it may be reintroduced by birds or mosquitoes from outside the region [2]. In a previous paper [3] the possibility of the introduction of WEE virus to Minnesota, North Dakota and Manitoba was investigated. It was found that from 1980 to 1983 the time and place of WEE cases in horses and man, seroconversion in chickens, and isolation of WEE virus from Cx. tarsalis could all be correlated with trajectories of winds from states further south in USA. In most instances arrival of Cx. tarsalis coincided with the passage of cold fronts and rainfall. In 1981 there were WEE cases in horses in Oklahoma and the carriage on the wind of infected Cx. tarsalis from there could have led to infection with WEE virus further north. There were also suitable winds to carry infected Cx. tarsalis from southern Texas, on the Gulf of Mexico, to northern Texas and Oklahoma; but, although Cx. tarsalis is present in the Lower Rio Grande Valley during the winter months [4], there was no indication of WEE infection in southern Texas.

In 1987 there was an epidemic of WEE in Western USA with a northward progression of cases from southern Texas in April to northern Texas, Oklahoma, New Mexico, Colorado and Kansas in June and then to Nebraska, South and North Dakota and Minnesota in July [5]. It was therefore decided to investigate the sequence of outbreaks by backward trajectory analysis of winds to see if WEE virus could have been carried by infected Cx. tarsalis on the wind from southern Texas, on the Gulf of Mexico, to northern Texas and Oklahoma and from there to states further north. In 1987 there was only 1 case of WEE in horses in Manitoba in contrast to 123 cases in 1981 and 24 cases in 1983 and the effect of cold fronts and rainfall on this difference was also investigated.

Temperatures at places in Texas, Oklahoma, Kansas and Colorado during the winter and spring of 1986–7 were also examined to see if they were suitable for Cx. tarsalis to remain active and continue to transmit WEE in a bird-mosquito cycle during those seasons.

Analysis of outbreaks of WEE on the Great Plains in western USA and western Canada from 1975 to 1988 was carried out to see if weather factors could assist in the prediction of epidemics among horses in Manitoba (those with 20 or more cases). Such factors included temperatures at source, during flight and on arrival, rainfall at source and cold fronts and rainfall on arrival, wind direction and speed and high and low pressure areas. Such factors would be used for prediction in addition to the biometeorological model to predict mosquito numbers based on warmness and wetness [6] and surveillance of cases in horses, virus isolation from mosquitoes and seroconversion in sentinel chickens already developed or in use in Manitoba [7].

METHODS

Background data

Hosts

The incubation period for WEE in horses lies between 4 and 15 days. In birds virus is present in the blood between the first and fifth day after infection at titres

which can lead to transmission by Cx. tarsalis. In sentinel chickens haemag-glutination-inhibition antibodies are found between the sixth and fourteenth day [3].

Vector

In northern USA and Canada Cx. tarsalis overwinter as non-blood fed adults (facultative diapause) [8]. In the Lower Rio Grande Valley in southern Texas adult Cx. tarsalis were caught from September to April but not during the summer months [3, 4]. The average daily maximum temperature of the coldest month (January) for the 30-year period, 1931–60, at Brownsville, Texas (25·54 N, 97·26 W) was 21·4 °C [9]. Adult Cx. tarsalis were also caught every month of the year in southeastern California [10] and WEE virus was isolated from Cx. tarsalis in January and February 1987 [2], months in which the average daily maximum temperatures were 21·1 °C and 23·8 °C respectively. In 1953 and 1954 WEE virus was isolated every month from July 1953 to July 1954 except December from Cx. tarsalis caught in Kern County, California [11]. The average maximum daily temperature at Bakersfield, California, (35·25 N, 119·05 W) for the coldest month, January 1954, was 15·3 °C.

In laboratory experiments Cx. tarsalis took blood at 15 °C (12) and WEE virus could be transmitted after 6–15 days by Cx. tarsalis kept at temperatures between 18° and 32 °C [13, 14]. After the initial virus replication Cx. tarsalis can transmit virus every 3–4 days on feeding until the end of their life.

Flight of Culex tarsalis

Cx. tarsalis flies unaided at speeds between 4·3 and 7·2 km h⁻¹, but unaided flight is inhibited at higher wind speeds. At speeds greater than 10·8 km h⁻¹ the track of Cx. tarsalis would be that of the air in which it is flying. Dispersal of 16 km per night was recorded for Cx. tarsalis and this species was caught by day and night at heights up to 615 m [15].

There is circumstantial evidence that Cx. tarsalis infected with WEE virus can be carried on the wind for distances of 1250–1350 km at heights up to 1.5 km. Once the mosquitoes were airborne flight continued at temperatures of 13 °C and higher [3].

Sources of information

WEE cases in horses

The numbers of WEE cases in horses and man reported in 1987, their dates and locations were obtained from the Centers for Disease Control, Fort Collins, Colorado, USA, from published reports [5, 16], and from Dr S. E. Ives, Minnesota and Dr G. P. S. Nayar, Manitoba (personal communications, 1987–92). Details of the outbreaks of WEE in 1980–3 have already been given [3]. Data on outbreaks in other years came from references 17 and 18 (USA), 19 (North Dakota and Minnesota) and 7 and 20–23 (Manitoba) and from Dr S. E. Ives and Dr G. P. S. Nayar. Only laboratory confirmed cases were included and the dates are those reported (i.e. onset of disease or collection of the first sample) [24].

Culex tarsalis populations in Manitoba

The number of female Cx. tarsalis in daily, weekly and monthly catches in Manitoba came from Brust and Ellis [25] for 1975, Brust [26] for 1976, Raddatz

[6, 27] for 1977-84 and Ellis [28] for 1985-8. For comparison between years, the daily counts from the week with the highest catch of female *Cx. tarsalis* were averaged to give the count/day/light trap for each year from 1975 to 1988.

Surveillance system

The surveillance system in Manitoba used the following criteria for determining the risk of an epidemic [7]. (i) Weekly average of mean temperature above normal during the last 2 weeks of June and at least 2 °C above normal in July. (ii) More than six confirmed cases of WEE in horses per week in July or August, (iii) > 20 Cx. tarsalis females/trap/week during late June and in early July. (iv) Four mosquito pools positive for WEE virus. (v) More than 20 % of sentinel chickens seroconverted.

In addition a biometeorological model, developed by Raddatz could be used to provide forecasts of Cx. tarsalis numbers [6].

Weather data

Tables. Temperatures and rainfall (precipitation) for individual weather stations were obtained from the Monthly Climatological Summary (USA and California) and from the monthly climatic data for the world. Average temperatures from 1931 to 1960 came from the tables of temperature, relative humidity, precipitation and sunshine for the world, part I, North America and Greenland [9].

Maps. The 6-hourly surface and 12-hourly 850 mb northern hemisphere maps of the Canadian Climate Centre and the daily surface northern hemisphere maps of the National Weather Center, USA were consulted for temperature, high and low pressure areas, wind direction and speed, position of fronts and rainfall.

Trajectory analysis. Backward trajectories of winds were computed every 6 h up to 120 h (5 days) starting at three levels: 1000, 900 and 850 mb at approximate heights of 0·1, 1·0 and 1·5 km above sea level respectively. These heights vary along the trajectory depending on the air parcel. A three-dimensional trajectory model [29] was applied. The model uses objectively analysed winds at four standard pressure levels (1000, 850, 700 and 500 mb) on the Canadian Meteorological Centre grid of 381 km. Cubic interpolation is used to obtain winds at intermediate level in the vertical, and bilinear interpolation between grid points in the horizontal. Heights and temperature fields are used to compute vertical motion in the upper levels. Mountain and friction-induced vertical motion are computed at the lowest level. Trajectory 6 h segments are determined using an iterative scheme on the three-dimensional wind field until horizontal and vertical convergence criteria are reached.

Analysis

Temperature

Based on the temperatures for Cx. tarsalis activity and replication of WEE virus in Cx. tarsalis already given (background data), an average daily maximum temperature of 18 °C or higher in the coldest month was chosen as the lowest temperature, at which overwintering of WEE virus by continuous transmission between Cx. tarsalis and birds could occur. This means that on about half the number of days temperatures would reach 18 °C and higher and be suitable for

mosquito activity and virus replication (30]. Temperatures on 850 mb maps for long distance flight had to be 13 °C or higher.

Trajectories

Backward trajectories from the location of an outbreak were computed for each day starting at 18.00 h Greenwich Mean Time (GMT) (12.00 h Central Standard Time (CST)) over a period of 3-16 days before the outbreak, to cover the incubation period in horses and one day on either side. With some of the horse cases backward trajectories starting at midnight, 06.00 and 18.00 h CST around the likely date of arrival (see below) as shown by the 12.00 h CST trajectory were also determined. Cx. tarsalis may fly by day or night and, with backward trajectories starting at 12.00 h CST, this would give start times of flight from 06.00, 12.00, 18.00 h and midnight the previous day and 06.00 the same day to correspond with flight times of 30, 24, 18, 12 and 6 h respectively. Flight times of up to 30 h were chosen by analogy with the flight duration of the brown planthopper, whose unaided flight speed $(3.6-7.2 \text{ km h}^{-1})$ is similar to that of Cx. tarsalis [3, 31]. The trajectory for each day was examined to see on which day or days there was a likely source of WEE virus between 6 and 30 h beforehand. Weather maps on that day (date of arrival) and the day before and after were consulted for the presence of a front and/or rain.

Wind direction and speed, high and low pressure areas, cold fronts and rainfall

Three principal airflows, cool Polar air from the north, maritime Pacific air from the west and warm Tropical air from the south, meet over United States between April and October. 850 mb and surface weather maps were examined to determine areas of low pressure to the west and areas of high pressure to the east of the Great Plains and to see if warm southerly winds (Tropical airflow), which occur in such conditions, were present and if their speed was equal to or greater than 45 km h⁻¹ (25 knots). A speed of 45 km h⁻¹ or more is required for carriage of infected Cx. tarsalis from northern Texas and Oklahoma to Minnesota and North Dakota in 24–30 h. The positions and movement of cold fronts and rainfall, where southerly winds met Polar or Pacific airflows were also determined. Unfavourable conditions at this meeting would have led to convergence and subsequent landing and concentration of infected Cx. tarsalis followed by outbreaks of WEE. (For background and further information on weather and movement of insects, see References 32–34).

RESULTS

Western equine encephalitis, 1987

The numbers of cases in horses during 1987 by month and by state (USA) or province (Canada) are shown in Table 1. The first case of WEE in horses was reported in Hidalgo County, Texas, on 30 April 1987. Subsequently cases were reported from 2 June 1987 onwards in the states listed in Table 1. Cases occurring in Texas, Colorado, Minnesota, Kansas, Nebraska, North Dakota, Montana, Wisconsin and Manitoba were chosen for backward trajectory analysis as being representative of the first outbreak in a particular state, area of a state, or a province (Fig. 1).

	\mathbf{Month}							
State/Province	A	M	J	`	A	\overline{s}	O	Total
Manitoba				1				1
Montana			•	•	21	2		23
North Dakota			•	3	7	1	•	11
Minnesota			1	5	2	1		9
Oregon				•		1		1
Wisconsin			•		2			2
South Dakota			•	1	1	1		3
Idaho			•		1	•		1
Wyoming				•	3	1	•	4
Nebraska		•	•	3	3			6
Iowa			•		1	3		4
Illinois		•	•	٠		2		2
Kansas			1	5	1	3	1	11
Colorado			1	27	14	2		44
New Mexico			2	5	9	1		17
Oklahoma	•	•	6	6	3	1	•	16
Texas	1		5	12				18

Table 1. Numbers of cases of WEE in horses in USA and Canada in 1987*.

The places and dates of the outbreaks examined by trajectory analysis, the dates of arrival and the possible sources are given in Table 2. As these cases were the first outbreaks in a particular area, their locations were often at the extremes of the southerly airflow. Thus in most cases only one date was suitable for the arrival of the infected Cx. tarsalis; less suitable dates for five cases are given in Table 2. In the instances examined (cases 2–13) dates were found, on which backward trajectories showed as source, an area of a state where WEE was present in horses (case 2 at 30 h, cases 3, 5, 6, 8, 10–13) or where WEE virus could have been circulating in Cx. tarsalis and birds (case 2 at 18 h, cases 4, 7, 9) [1]. The backward trajectories for the cases were at 850 and 900 mb i.e. flight of Cx. tarsalis would have been at heights up to 1.5 km. Temperatures at such heights were 13 °C or higher. The arrival was accompanied by a front and rain on ten occasions and rain alone on two occasions. Fronts and rain could have led to the landing of Cx. tarsalis. The interval between date of arrival and disease in horses varied from 6–10 days, which was within the incubation period.

The sequence of the movement northward is shown in Figure 2. The first case in Hidalgo County, Texas, in April was followed by an outbreak in horses at the beginning of June in Minnesota with a source in southern Texas, on the Gulf Coast, 30 h earlier or in southwest Oklahoma 18 h earlier (Fig. 3). The initial outbreak in southeastern Colorado (case 4–27 June) could have resulted from the introduction of infected Cx. tarsalis on winds from eastern New Mexico and that in northern Texas (case 3–15 June) from the Gulf Coast.

Subsequent spread from northern Texas (Panhandle) and Oklahoma would have been to northeastern Colorado, Kansas and Minnesota on 22–23 June. Later spread would have been on 1 and 9 July to Minnesota and to North Dakota, on 22 July to Manitoba and on 28 and 29 July to Montana and Wisconsin.

^{*} No cases were reported in Alberta and Saskatchewan in 1987.

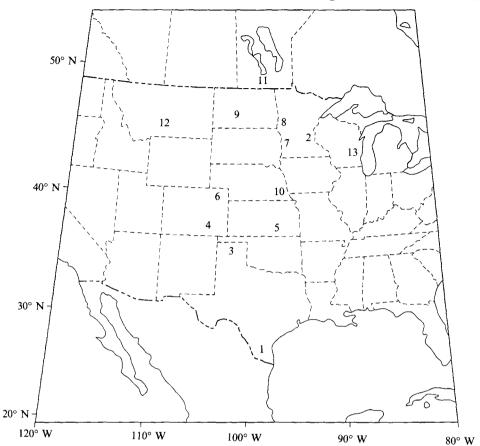


Fig. 1. Location map showing the first WEE case in Texas and the subsequent cases selected for trajectory analysis: 1, Hidalgo County, Texas; 2, McLeod County, Minnesota; 3, Moore County, Texas; 4, Fremont County, Colorado; 5, Reno County, Kansas; 6, Sedgwick County, Colorado; 7, Lyon County, Minnesota; 8, Ottertail County, Minnesota; 9, Ward County, North Dakota; 10, Otoe County, Nebraska; 11, Glenboro, Manitoba; 12, Meager County, Montana; 13, Sauk County, Wisconsin.

The number of cases of WEE in horses in 1987 in Manitoba, North Dakota and Minnesota (1, 11 and 9 respectively) was lower than in 1981 (123, 58 and 40) and in 1983 (24, 16 and 13). Examination of the backward trajectories and weather maps for 23–31 July 1987 showed that the positions of cold fronts between Polar air and Tropical air lay west to east over North Dakota and Minnesota. This could have led to the carriage of infected Cx. tarsalis into Montana (case 12) and Wisconsin (case 13) and inhibited further spread into Manitoba.

Temperatures in Texas, Oklahoma, Kansas and Colorado in the winter and spring of 1986-7

The average daily maximum temperature for each month from November 1986 to June 1987 for stations in Texas, Oklahoma, Kansas and Colorado is shown in Table 3. Brownsville, Texas was the only station, where the average daily

Location*	Date of disease	Date of arrival†	Source
1. Hidalgo Co, TX‡	30 April		
2. McLeod Co, MN	$2 \stackrel{1}{ m June}$	27 May	18 SW Okl§
		v	30 S Texas
3. Moore Co, TX	15 June	8 June	$30 \mathrm{~S~Texas}$
4. Fremont Co, CO	$27 \mathrm{June}$	21 June	18 E New Mex
5. Reno Co, KS	$29 \; \mathrm{June}$	22 June	12 SW Okl
6. Sedgwick Co, CO	$2 \mathrm{July}$	22 June	18 Texas PH
7. Lyon Co, MN	$2 \mathrm{July}$	23 June	24 N Kansas
8. Ottertail Co, MN	10 July	1 July	18 S Nebr
9. Ward Co, ND	19 July	9 July	24 S S Dak
10. Otoe Co, NE	28 July	18 July	6 S Kansas
11. Glenboro, Manitoba	31 July	22 July	18 SE N Dak
12. Meager Co, MT	4 Aug	29 July	24 NW S Dak
13. Sauk Co, WI	6 Aug	28 July	24 SE Nebr

Table 2. Source of backward trajectories up to 30 h previously for WEE cases in horses in 1987

- * See Fig. 1 for location of cases.
- † Date of arrival the date of arrival is that which best satisfies a source of virus, trajectory and front and/or rain. With locations 2, 3, 5, 10 and 12 the following dates were less suitable: 2–28 May, 24 Texas Panhandle, 3–9 June, 30 SSE Texas, 5–23 June, 12 C Okl, 10–19 July, 6 C Kansas, 12–28 July, NW S. Dakota. On the other dates examined the trajectories were not from known or likely sources or the flight times would have been over 30 h.
- ‡ CO, Colorado; KS, Kansas; MN, Minnesota; MT, Montana; ND, North Dakota; NE, Nebraska; TX, Texas; WI, Wisconsin.
- § 18 h previously; N, north; NE, northeast; SE, southeast; S, south; SW, southwest: NW, northwest; C, central; N Dak, North Dakota; Nebr, Nebraska; New Mex, New Mexico; Okl, Oklahoma; S Dak, South Dakota.

maximum temperature for the coldest month (December) exceeded 18 °C, and thus satisfied the chosen temperature criterion for continuous transmission of WEE virus in Cx. tarsalis and birds during the winter. In December 1986 at Brownsville there were 22 days when the maximum temperature was 18 °C or higher. Average daily maximum temperatures 18 °C or higher were reached in February in San Antonio and in April in Oklahoma City, Lubbock. Amarillo, Wichita and Denver, months when continuous transmission by Cx. tarsalis would have become possible after the winter.

Prediction of WEE epidemics in Manitoba

The epidemic years in Manitoba (≥ 20 cases a year [23]) in 1975, 1977, 1981 and 1983 were characterized by an epidemic curve, which started in July (1975, 1977, 1981) or August (1983) and reached a peak 17–21 days later [3, 20–23]. Similar epidemic curves were found in these years in Minnesota and North Dakota with onsets 7–23 days earlier than in Manitoba and with peaks 12–24 days after the onset [3, 19] (Table 4). In Manitoba the start of the epidemic curve was preceded by cases in horses in early June in 1975 and in mid-June in 1983, but in 1981 the first cases in horses coincided with the start of the epidemic curve. In 1980 (a non-epidemic year) there were cases in horses in late May but none later in the year [3] and in 1976 there were cases in horses by 14 June [22]. Hence cases in horses before July do not necessarily presage an epidemic in Manitoba. In Saskatchewan from 1963 to 1966 WEE virus was isolated from amphibians, reptiles, birds and small

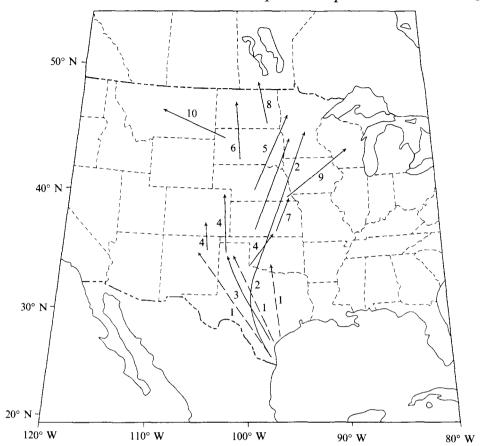


Fig. 2. Suggested spread of WEE from Gulf Coast of Texas to northern USA and western Canada in 1987. ← —, spread based on trajectory analysis; ← — —, hypothetical spread. 1. April to May. Gulf Coast to eastern New Mexico, southeastern Colorado, Texas Panhandle and Oklahoma; 2. 27 May, Gulf Coast of Texas through Oklahoma to Minnesota; 3. 8 June, Gulf Coast to Texas Panhandle and Oklahoma; 4, 21–23 June, from latitude 36–37 N to Colorado, Kansas and Minnesota; 5, 1 July, Nebraska to Minnesota; 6, 9 July, South Dakota to North Dakota; 7, 18 July, Kansas to eastern Nebraska: 8, 22 July, North Dakota to Manitoba; 9, 28 July, eastern Nebraska to Wisconsin; 10, 29 July, South Dakota to Montana.

mammals before July, but more isolations were made in non-epidemic years than in epidemic years [35]. Thus early detection of infection cannot be used to predict an epidemic.

The important part of the year to monitor would therefore be the latter part of June and all July to cover the incubation period before the start of the epidemic curve.

Conditions for epidemic to develop in Manitoba

In a previous paper [3] we suggested that a number of conditions must be satisfied for an epidemic to occur in Manitoba, given that WEE virus could be introduced by infected Cx. tarsalis carried on the wind. There must be (i) a source

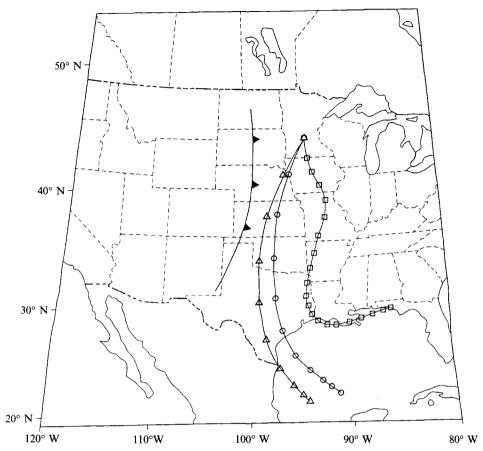


Fig. 3. Six-hourly segments of backward trajectories at three levels (\triangle , 850 mb; \bigcirc , 900 mb; \square , 1000 mb) terminating at McLeod County, MN on 27 May 1987 at 18.00 GMT (12.00 CST). Position of cold front at 12.00 GMT (06.00 CST) on 27 May 1987 also shown.

Table 3. Average daily maximum temperatures (°C) at US weather stations, November 1986–June 1987

	Month							
Station	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Denver CO* 39.45 N, 104.52 W	10.8	6.4	7.2	8.4	10.5	19.4	22.1	28.5
Wichita KS 37.39 N, 97.25 W	10.7	6.9	3.7	11.0	14.7	21.8	26.9	31.2
Oklahoma City OK 35.24 N, 97.36 W	12.5	9.2	6.4	12.6	16.1	23.9	28.2	30.6
Amarillo TX 35.14 N, 101.42 W	13.2	8.9	7.5	11.6	14.5	21.6	24.6	29.0
Lubbock TX 33.39 N, 101.49 W	15.2	10.3	10.4	13.4	16.9	23.7	27.3	31.4
San Antonio TX 29.32 N, 98.28 W	20.6	15.4	16.9	18.4	21.3	26.8	29.4	31.6
Brownsville TX 25.54 N, 97·26 W	24.3	19.7	20.7	22.8	23.9	26.6	30.5	32.3

^{*} CO, Colorado; KS, Kansas; OK, Oklahoma; TX, Texas.

Table 4. The dates of the start of rise in the numbers of cases in horses in epidemic years in Minnesota, North Dakota and Manitoba

	Date of start of rise in epic	demic curve
Year	In Minnesota/North Dakota	In Manitoba
1975	4 July	27 July
$\frac{1977}{1981}$	Early July 4–8 July	16 July 14 July
1983	$22 ext{}27~ ext{ m July}$	$2~\mathrm{Aug}$

of WEE virus circulating between sufficient vertebrate hosts and Cx. tarsalis further south in USA, (ii) warm winds for the northward carriage of infected Cx. tarsalis and (iii) sufficient susceptible vertebrate hosts and local populations of Cx. tarsalis in Manitoba to transmit virus once it has been introduced. The numbers of susceptible small vertebrate hosts in USA and Manitoba are difficult to assess, but data on Cx. tarsalis numbers in Manitoba, weather and cases in horses in USA and Manitoba are available.

(i) (a) Culex tarsalis in southern USA. Numbers of Cx. tarsalis depend among other factors on warmth and moisture [8]. The mean temperatures and total rainfall at Brownsville, Texas, (where continuous transmission is possible through the winter) from November to April preceding the summers of 1975-88 were examined. No significant differences were found, when the mean temperatures and rainfall for epidemic years in USA (1974-5, 1976-7, 1980-1, 1982-3 and 1986-7) were compared with the other years (P > 0.05, t test). Nor were there any significant differences between years with > 70 cases (1975, 1977, 1979, 1981, 1983, 1987 and 1988) and other years (P > 0.05, t test). When mean temperatures and rainfall for individual months were compared, no significant difference was found between rainfall in epidemic years and rainfall in non-epidemic years or between rainfall in years with > 70 cases and years with < 70 cases (P > 0.05 in t test). However a significant difference in mean temperatures between epidemic and non-epidemic years was found for November at Brownsville (P < 0.05, > 0.01, t test), when the average mean temperature for the epidemic years was lower than in non epidemic years. An explanation for this association for November is not known.

A comparison was also carried out on mean temperature and precipitation at Oklahoma City from April to June for the same years to see if there could have been an effect on the spring rise in Cx. tarsalis populations. No significant differences were found for individual months or for the whole period (P > 0.05, t test).

(b) Extent of WEE infection in USA. The number of cases in horses in USA can provide a crude estimate of the weight of infection south of Manitoba. Table 5 shows the numbers of cases in the USA and in Manitoba. The years can be divided into four groups: (1) \geq 23 cases in Manitoba, \geq 98 cases in USA – 1975, 1977, 1981 and 1983. (2) 10 and 17 cases in Manitoba, 38 and 91 cases in USA – 1976, 1988. (3) 0–1 cases in Manitoba, 42–172 cases in USA – 1979, 1986, 1987. (4) 0–3 cases in Manitoba, 13–27 cases in USA – 1978, 1980, 1982, 1984, 1985.

Table 5. WEE cases in horses in Manitoba and USA, days with southerly winds and with southerly winds $\geq 45 \text{ km h}^{-1}$ and average daily count of Cx. tarsalis, 1975-88

	WEE cases in horses		Days wi	Cx. tarsalis	
Year	Manitoba	USA	From south	$\geq 45 \text{ km h}^{-1}$	count*
1 (Epidemic years)					
1975	135	703	21	12	7.9
1981	120	328	18	14	$3\cdot 2$
1977	53	584^{+}	19	11	10.5
1983	23	98†	21	15	$22 \cdot 1$
2					
1988	17	91†	12	5 F‡	4.1
1976	10	38	8	6	1.6
3					
1987	1	172†	13	7 F	$2\cdot 3$
1979	0	73	9	4 F	1.0
1986	1	42†	9	5 F	33.2
4					
1978	1	17	6	3 F	8.7
1980	0	27	11	7	0.3
1982	3	27	12	9	4.7
1984	1	18†	12	4	9.5
1985	0	13†	11	6	1.4

^{*} Average daily count of female Cx. tarsalis per light trap in City of Winnipeg (except 1976) in the week with the highest catch.

When there were few cases in USA, there were usually few in Manitoba (group 4). More than 90 cases in USA was associated with more than 20 cases in Manitoba in 1975, 1977, 1981 and 1983 but not in 1987 and 1988.

(ii) Winds. Weather maps (850 mb) and trajectories for the years 1975–88 were examined for the period 20 June to 31 July to determine the number of days, on which the winds were blowing from the south and the number of these days on which the wind speed was 45 km $\rm h^{-1}$ or higher. Such conditions are suitable for long distance wind carriage of infected Cx. tarsalis mosquitoes.

In Table 5 the number of days with southerly winds and the number of those days on which the windspeed was ≥ 45 km h⁻¹ are shown. There were more days in the epidemic years in Manitoba (1975, 1977, 1981 and 1983) than in the non-epidemic years (P < 0.01 in χ^2 test), although in some of the non-epidemic years 11–13 days with southerly winds were found.

(iii) Fronts. Passage of cold fronts and/or rain results in the termination of the flight of infected Cx. tarsalis on warm southerly winds, followed by landing and infection of local hosts. This effect is shown in the following examples.

In 1981 a cold front lying over North Dakota and South Dakota on 27 June moved eastwards to lie over Minnesota and South Dakota on 28 June. There were subsequently WEE outbreaks in North Dakota and Minnesota 6–11 days later [3]. Similarly in 1987 a cold front, which lay over North Dakota, Wyoming and Utah

[†] Horses cases in Washington. Idaho, Oregon, Nevada, Utah, California and Arizona excluded. Cases in horses in June or earlier excluded from the Manitoba figures.

[‡] F, year in which fronts were found further south.

on 22 June moved eastwards to lie over Minnesota, Nebraska, Kansas, Oklahoma, Texas (Panhandle) and New Mexico on 23 June. This was followed by outbreaks in Colorado, Kansas and Minnesota 7–10 days later (Table 2, cases 5–7).

In 1975 strong southerly winds on 25 and 26 June meeting a cold front were followed by heavy rainfall in the Red River Valley in Minnesota and North Dakota. Subsequently a deep trough extending southward from Canada transported Polar air from the north between 7 and 13 July thus inhibiting the northward flow of warm southerly air and infected Cx. tarsalis. Later warm southerly winds blew from the 15 to 17 July meeting a cold front over Manitoba. The southerly winds on 25–26 June preceded the start of the epidemic curve in the Red River Valley on 4 July and the return of southerly winds on 15–17 July was followed by the start of the epidemic curve in Manitoba on 27 July [3] (Table 4). Thus Polar air between 7 and 13 July resulted in infected Cx. tarsalis being introduced to Manitoba later in 1975 than in 1977 and 1981 (Table 4).

In 1987 the position of the cold front was further south at the end of July (see earlier), which would have affected the northward movement of Cx. tarsalis. In 1988 at the end of July cold fronts were in a similar position. However infected Cx. tarsalis could have been introduced earlier on southerly winds on 7 and 15 July and in addition the Cx. tarsalis daily eatch was higher in 1988 than in 1987 (Table 5). Cold fronts were also further south in 1978, 1979 and 1986, years in which the days with southerly winds were fewest (Table 5).

(iv) Culex tarsalis population in Manitoba. The average daily count per light trap of female Cx. tarsalis during the week of the highest catch is shown in Table 5. In the epidemic years (1975, 1977, 1981 and 1983) the lowest average daily count per trap was 3·2 in 1981 and, based on the suggestion by Raddatz [26], this figure was taken as the minimum count for an epidemic to develop. In 5 of the 9 years in which the count was 3·2 or greater, the number of cases of WEE in horses was 17 and higher, but in the other 4 years the number of WEE cases ranged from 1 to 3. In the years when the count was below 3·2, the number of WEE cases in horses was 10 or less.

Raddatz [6] developed a biometeorological model to predict the average daily counts of Cx. tarsalis. A correlation coefficient of 0.91 was obtained between the model and the actual counts for the years 1977–84.

In 1978, 1982, 1984, 1986 and 1988 the Cx. tarsalis counts indicated that an epidemic was possible but none occurred. There were southerly winds on 6–12 days during these years compared with 18–21 days in epidemic years, and windspeeds > 45 km h⁻¹ on 3–9 days compared with 11–15 days in epidemic years. In addition in 1978, 1986 and 1988 the positions of the fronts were on occasions further south.

Conclusions on prediction of epidemics in Manitoba

Mean temperature and rainfall in southern Texas would not provide a guide to predict epidemics further north; investigations need to be carried out on daily counts and infection rates of Cx. tarsalis in that area as is being done in Manitoba [6, 7].

The number of cases in horses in US could indicate the weight of infection and if cases are few an epidemic is unlikely to develop in the north. Cases in Texas and Oklahoma in the second half of June could be taken as an indicator, but due to the preference of Cx. tarsalis for feeding on birds the extent of infection could be

greater in some years than the number of cases in horses suggests. Reports of cases in Minnesota and North Dakota in early July would also be a positive indicator. However, delays in reporting and confirmation may hinder the availability of information.

The biometeorological model gives a 3-week lead time on the Cx. tarsalis population in Winnipeg [6]. It could therefore predict when a count of $3\cdot 2$ or higher would be reached. In the past such counts were reached from the last week of June to the last week of July, so the model would be in operation 3 weeks earlier from the second week of June onwards.

Examination of wind direction and speed at 850 mb and the analysis of backward trajectories would predict an outbreak 4–15 days later (incubation period in the horse). Examination of wind direction and speed during the last 11 days in June could enable prediction of cases in Minnesota and North Dakota and examination in July could predict cases in Manitoba, Minnesota and North Dakota. Although there were more days with southerly winds and with windspeeds \geq 45 km h⁻¹ in epidemic than in non-epidemic years, this was apparent only after the last week of July in the year concerned. Therefore all days from 20 June to the end of July, when winds are favourable, should be regarded as days when infected Cx. tarsalis could be introduced.

The position of cold fronts and rainfall could be used to determine where infected Cx. tarsalis are likely to land after being carried northwards on southerly winds. In addition the possibility that the infected Cx. tarsalis would or would not be carried into Manitoba can be determined.

Despite a prediction that there could be an epidemic, an epidemic is unlikely to take place if there is an insufficient amount of virus circulating. In 1982 and 1984 there was an adequate Cx. tarsalis population in Manitoba and there were southerly winds on 12 days. However, there were few cases in USA and the chances of introduction of infected Cx. tarsalis were less.

Thus if a low Cx. tarsalis count is predicted and/or winds are unsuitable, an epidemic is unlikely. If the Cx. tarsalis count is predicted to be above $3\cdot 2$ and the winds are suitable, there may or may not be an epidemic depending on the extent of infection further south.

DISCUSSION

Analysis of wind trajectories during the WEE epidemic of 1987 showed that infected Cx. tarsalis could have been carried on the wind progressively from southern Texas to Minnesota and North Dakota. However, in contrast to 1981 and 1983, the position of cold fronts further south at the end of July inhibited the carriage of infected Cx. tarsalis into Manitoba.

Analyses of temperatures from November 1986 until March 1987 showed that a continuous cycle of virus in birds and Cx. tarsalis was likely only in southern Texas. Further north, Cx. tarsalis would have entered diapause and persistence of WEE virus would have been unlikely [36]. Persistence further north is also unlikely through transovarial transmission as this has not been demonstrated with WEE virus in mosquitoes [37, 38].

North of southern Texas virus might persist in small vertebrates, but details of the amplification cycle during the spring remain to be demonstrated. A study of persistence of WEE in Kern County, California indicated that from 1986 to 1989, WEE virus did not overwinter in small vertebrates and mosquitoes but became extinct and required reintroduction [38].

Reintroduction could be by birds or mosquitoes. Migratory birds fly north in the spring [39] but there is an interval before the Cx. tarsalis population reaches a level sufficient to support transmission of virus leading to an epidemic. Birds could also introduce infection through flights on southerly winds in June and July. Birds usually fly at heights where the wind speed is 25 km h^{-1} (J. R. Riley, personal communication, 1992) and a distance of 1200 km would be covered in 48 h i.e. within the period of viraemia in birds. However, there is no evidence for introduction of virus by birds from further south at this time.

Southerly winds from 20 May onwards were found to be capable of introducing infected Cx. tarsalis from further south to Minnesota, North Dakota and Manitoba [3]. However, the data for Cx. tarsalis catches in Winnipeg indicate that an epidemic would not take place until the count had reached a certain level. This level was reached at the end of June at the earliest in Manitoba and so for earlier introductions Cx. tarsalis numbers would not have been sufficient at the time of arrival.

Introduction of infected Cx. tarsalis on the wind may account for the initial cases in Minnesota, North Dakota and Manitoba, but the problem remains of how WEE virus persists in the Lower Rio Grande Valley or further south from May to August, when Cx. tarsalis are absent or few in number (4). When temperatures suitable for the flight of Cx. tarsalis are present, WEE virus could be carried north by Cx. tarsalis on the wind from May to August, and back south again from August to October by Cx. tarsalis and by birds [3, 39]. There may be transfer of virus by birds and mosquitoes to and from Mexico and Central America, resembling the movement of waves of yellow fever and Venezuelan equine encephalitis in those areas [40, 41].

Evidence for long-range dispersal of plant and other viruses in North America has been presented by many authors [3, 15, 32–34, 42–47]. One example describes wind trajectories involved in the introduction of aster yellows 'virus' into Manitoba by the six-spotted leafhopper between 1954 and 1964 [42] and another the introduction of maize dwarf mosaic virus by aphids from Oklahoma into Minnesota on 2 July 1977 [45]. The same winds, that transported aphids, could also have introduced Cx. tarsalis infected with WEE virus into Minnesota on 2 July 1977, at the start of the epidemic in that state in early July (Table 4). Longrange dispersal of plant and animal viruses by insects associated with wind systems has been described for other parts of the world [43, 44].

Various methods of surveillance of clinical cases, wild vertebrates, vectors and sentinels have been carried out to predict the risk of WEE for man and animals [1, 48]. Sometimes disease has been successfully predicted, as in eastern Colorado in 1965, but at other times conditions were right but WEE virus remained at a low level of activity, as in California in 1969 [49, 50].

In Manitoba various indicators have been used or suggested for predicting an epidemic ([3, 7] and Methods). In addition, Cx. tarsalis counts can now be predicted ahead of time [6] and southerly winds and windspeeds at 850 mb, fronts and rainfall can be monitored. The weather data are available at the time of the

prediction. The occurrence of epidemics depends on the coincidence of factors involving host, vector, virus and environment. Prediction based on weather variables may exclude the possibility of an epidemic, but if the weather is favourable, an epidemic may or may not occur depending on whether all the other factors are in place.

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