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Distance and Direction of Trivial Flights of Aphids in a Potato Field

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SUMMARY

Aphid flight behaviour in a potato field was observed to estimate parameters for virus epidemic models. The flight direction was strongly correlated with the wind direction, because most aphids were flying at heights, where the wind speed exceeded the active flight speed of aphids. Wind directions during periods suitable for aphid flight were different from the main wind directions during the growing season. No correlation between the flight direction and the sun position was found. The frequency distribution of the minimal and probable flight distances was estimated with the aid of a simulation model, based on observations. The probable mean flight distance was 13 m, 48 % of the flight distances were below 5 m. The frequency distribution of the flight distances was approximated by a Weibull distribution.

Keywords: epidemiology, simulation models, virus, wind

INTRODUCTION

Most epidemic models of plant diseases assume the spatial pattern of the diseased plants to be random, e.g. the paralogistic model of Vanderplank (1963), the PVY-epidemic model in potatoes (Sigvald 1986) or the citrus tristeza virus epidemic model of Marcus, Talpaz & Bar-Joseph (1989). For many virus diseases this assumption is questionable, since it has been shown that the spatial pattern of virus infected plants is often nonrandom (Scott 1985; Madden, Louie & Knoke 1987). This might be caused by irregularities in the field (Madden 1989) or, more frequently, by the spatial processes involved in the epidemics. Spatial spread of aphid-borne viruses depends on the behaviour (particularly movement) of the vectors, which is influenced by environmental factors. To take the nonrandom spatial pattern of the diseases into account in epidemic models, knowledge of dispersal behaviour is required. This study focuses on the nonpersistently transmitted potato virus Y (PVY), the major virus problem in potatoes.

Winged aphids, flying from plant to plant, are believed to be responsible for most non-persistent virus transmissions (e.g. Broadbent & Tinsley 1951; Carter & Harrington 1991). For simulation studies of the spatial virus spread, parameters describing trivial flight behaviour are required, which are not available in the literature. Parameters describing flight distance and direction for usage in virus epidemic models were estimated by observations in a potato field. Aphids in the post-migratory phase were used to obtain individuals performing trivial flights. As most of the flights could not be observed until landing, the minimal and probable flight distances were estimated by simple simulation models, based on the observations. The dependence of the flight direction on the wind direction and the sun position was studied.

Wind can inhibit or delay aphid flight (Dixon 1985) and influence the direction of flight and consequently of virus spread by winged vectors (Hampton 1967; Irwin 1981). The wind directions were analyzed for the whole growth season and for time periods, when aphid flight was supposed to be possible, to detect prevailing directions.

MATERIAL AND METHODS

Analysis of the Wind Directions

Experiments and analyses were performed at the Swiss Federal Agricultural Research Station of Changins, located between the lake of Geneva (south-east) and the Jura mountains (north-west). The mean hourly wind directions, measured at the height of 12 m above soil during the months May to July of the years 1983 to 1989 were used for the following comparison: from the set of all hourly values those values were extracted that fulfilled the following conditions: daylight and mean wind speed 2.5 m/s. It was assumed that these conditions were suitable for aphid flight, because aphids rarely fly in the dark and under high wind speeds (Johnson 1969; Walters & Dixon 1984; Robert 1987).

Aphid Material

The alatae originated from primary hosts or rearings on secondary hosts. They had passed the teneral-period (Robert 1987) and a hunger period of two hours. According to Klingauf (1976), a fasting period has similar effects on aphid behaviour as a distance flight. The conditioning procedure was described by Nemecek *et al*. (in press). Other alatae were collected on the upper leaf side of potato plants in the field. Only aphids that did not penetrate were used, which should ensure that these aphids were unsettled.

Flight Observations and Analysis

A single person carried out the observations in a field plot of 15 × 15 m, surrounded by potatoes on two sides. Each plant within the plot was labelled, to allow the calculation of the flight distances. Groups of five to ten alatae were placed on a detached potato leaf fixed with a wire in a water-filled petri dish, which was positioned on a post of 80 cm height (measured from the bottom of the furrow). The water prevented the aphids from walking off the leaf. The observations were performed during optimal flight conditions (no strong wind, no rain). If one of the aphids took off, the observer tried to follow it until landing. The flight direction (between the release and the landing site or the site, where the aphid was lost), the wind direction (measured simultaneously by a turnable fisherline trap, Labonne & Quiot 1988) and the time were recorded. The directions were determined by a compass. In case of a landing, the number of the plant was noted for later calculation of the flight distance and direction. In case of landings outside the plot, the distance was estimated. In case the aphid was lost during flight, the distance (d_l, **d**istance of **l**oss) and the height (h_l, **h**eight of **l**oss) of the location, where the aphid was lost, was estimated. The flight direction was compared with the wind direction and with the solar azimuth by circular-circular rank correlation (Batschelet 1981).

Wind Profile

The following wind profile above the potato canopy was assumed (after Zadoks & Schein 1979):

$$v_w(z) \quad = \quad a_v \ ln \ \frac{z\text{-}D_o}{z_o} \qquad\qquad (1)$$

where $v_w(z)$ is the wind speed at the height z above ground, a_v is a scaling factor (proportional to the wind speed at a certain time), D_o and z_o are parameters describing the effect of the crop canopy on the wind profile (Table 1). Eq. 1 was used in the simulation model and to determine the proportion of alatae that had left the boundary layer. The boundary layer (Taylor 1960) is the air layer, where the wind speed is lower than the maximum flight speed, i.e. the air layer, where aphids can fully control their movement relative to the soil. The maximum flight speed was assumed as 0.5 m/s (Robert 1987). a_v was calculated by Eq. 1, setting $v_w(z)$ to the measured wind speed and z to the anemometer height of 12 m. The wind speed was measured in intervals of 10 min. The recorded flight times were rounded to obtain the next measurement of wind speed.

Table 1: Parameters of the wind profile and the flight simulation model.

Parameter	Meaning	Unit	Value	Source
	Effect of crop on wind profile	m	0.3	Zadoks & Schein (1979), canopy height assumed as 0.5 m
	"	m	0.05	"
	sinking speed	m/s	-0.367	mean maximum speed of flying actively downwards, Thomas (1977)
	rate of climb	m/s	0.25	mean rate of climb of L. after take-off from potato plants, Wiktelius (1982)
Δ	difference between active flight speed and wind speed	m/s	0.1	Kennedy & Thomas (1974)
	maximum flight speed	m/s	0.5	Robert (1987)

Estimation of the Flight Distance Distribution with Simulation Models

Two simulation models were constructed to estimate a range of possible flight distances: A) the minimal and B) the probable flight distances of those aphids that were lost during flight. The movements in the three-dimensional space were reduced to movements in a vertical plane parallel to the wind direction. The way each aphid had travelled from the site of loss was simulated. The models are based on the following assumptions:

Model A: the aphids are actively flying downwards with the sinking speed v_s, but make no active horizontal movement, i.e. they are carried away with the wind.

Model B: the aphids are actively flying upwind with a flight speed slightly faster than the wind speed, whenever possible (Kennedy & Thomas 1974), but cannot exceed a maximum flight speed. The vertical movement of an aphid is a stochastic process, which can be described by the uniformly distributed random variable $U[v_s, v_c]$ between the sinking speed v_s and the rate of climb v_c (Table 1).

The movement of the aphids was described by two differential equations:

Model A

$$\frac{dz}{dt} = v_s \tag{2a}$$

$$\frac{d\,d_f}{dt} = v_w(z) \tag{3a}$$

where z is the height above ground, d_f is the flight distance travelled from the site of release ($d_f > 0$ means downwind, $d_f < 0$ means upwind). The wind speed $v_w(z)$ is given by Eq. 1.

Model B

$$\frac{dz}{dt} = U[v_s, v_c] \tag{2b}$$

$$\frac{d\,d_f}{dt} = v_w(z) + v_f \tag{3b}$$

where v_f is the flight speed of the aphid relative to the air masses ($v_f < 0$, since the aphid is flying upwind) and t is the time in seconds.

Since durations of trivial flights are short, the wind profile, resp. a_v was assumed to be constant during this time. The active flight speed v_f is:

$$v_f = \begin{cases} -(v_w(z) + \Delta v_f) & \text{if } v_w(z) + \Delta v_f \leq v_{fmax} \\ -v_{fmax} & \text{otherwise} \end{cases} \tag{4}$$

v_{fmax} is the maximum flight speed and Δv_f the difference between active flight speed and wind speed. The initial values for z and d_f were the coordinates of the point, where the aphid was lost:

$$z(0) \quad = \quad h_l \tag{5}$$

$$d_f(0) \quad = \quad \begin{cases} d_l & \text{for } |\text{flight direction-wind direction}| \geq \dfrac{\pi}{2} \text{ (downwind)} \\ -d_l & \text{for } |\text{flight direction-wind direction}| < \dfrac{\pi}{2} \text{ (upwind)} \end{cases} \tag{6}$$

Landing occurred if z 0.5 m (crop height). The total flight distance was d_f at the moment of landing. The models were integrated with Heun's method using an integration step of 0.05.

The absolute values of the observed and simulated flight distances of colonizing and non-colonizing species were compared by a Mann-Whitney-U test. It was assumed that all aphids collected in the field were noncolonizing aphids. Most of the aphids caught during this period in fisherline traps in the field were *Brevicoryne brassicae* L., a noncolonizing species.

$$F(x) \quad = \quad 1-e^{-(x/\beta)^{\alpha}} \tag{7}$$

A Weibull function with two parameters was fitted to the frequency distribution of the probable flight distances after adding a constant of 0.00001 to all values. The Weibull distribution function with the shape parameter α and the scale parameter β is given in Eq. 7.

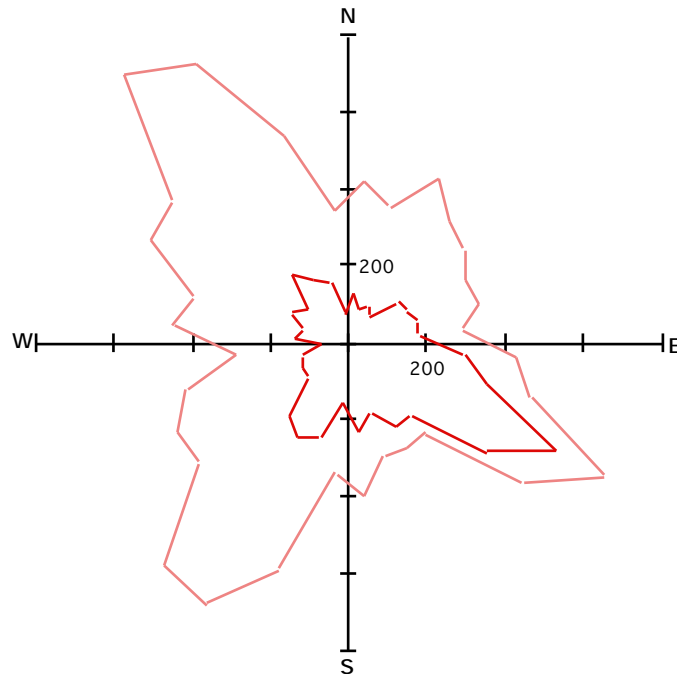## RESULTS

Flight and Wind Directions

Fig. 1: Frequency distribution of the mean hourly wind directions measured at 12 m height at the research station in Changins from May to July of the years 1983 to 1989 of all winds (broken line) and winds suitable for aphid flight (unbroken line, hourly measurements during the day with wind speeds 2.5 m/s).
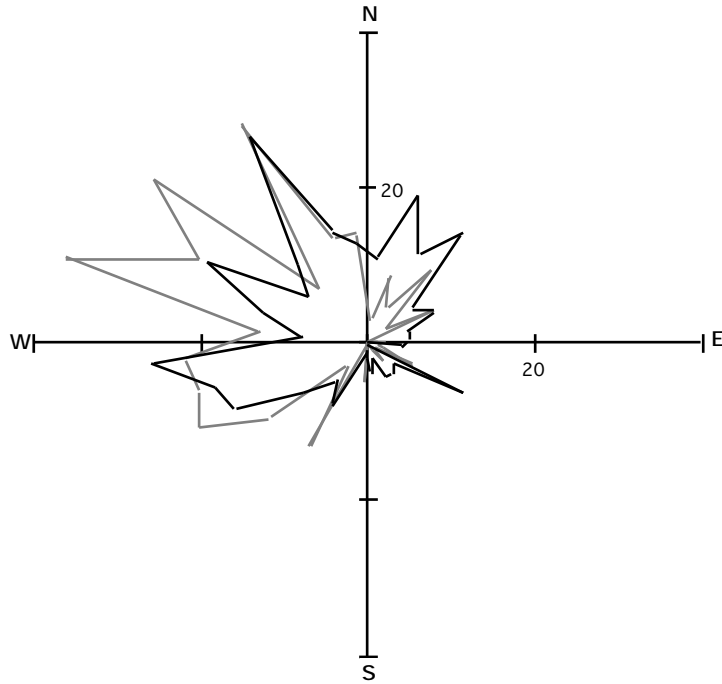
Fig. 2: Frequency distribution of the flight directions (solid line) of the aphids and the simultaneously measured wind directions (broken line) rotated by   (for better comparison). The distance from the origin shows the number of observations per class.
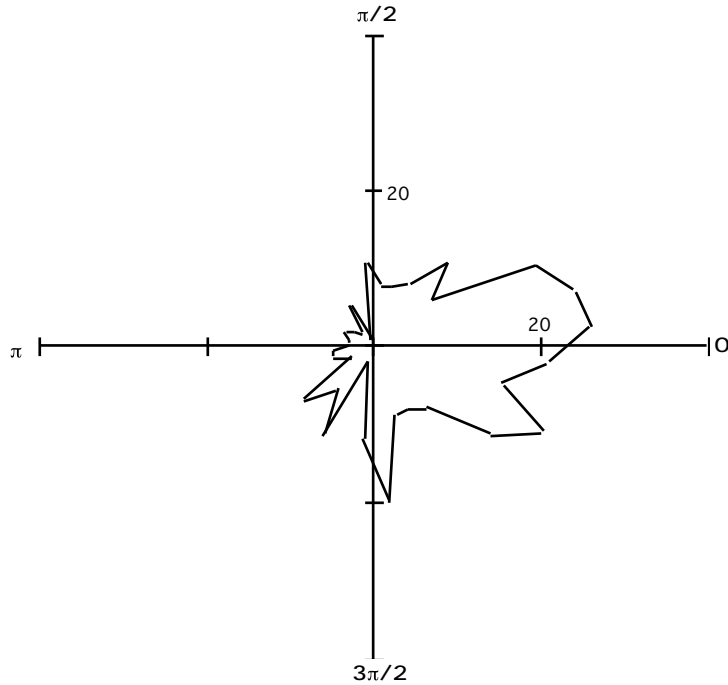

Fig. 3: Frequency distribution of the difference angles between the flight directions of the aphids and the simultaneously measured wind directions (rotated by   ). Correlation: r = 0.17, P = 8*10^{-5}, N = 341. The distance from the origin shows the number of observations per class.

The main direction of winds suitable for aphid flight (south-east) differed markedly from the overall wind directions (north-west, south-west and south-east, Fig. 1 see also Fig. 2).

Most of the aphids were flying downwind, i.e. mainly from south-east to north-west (Fig. 2). The differences between the flight and the simultaneous wind direction were grouped around 0 (Fig. 3), which means that downwind flight were the most common. Although the correlation was highly significant, the correlation coefficient was small. A comparison showed no dependence of the differences between flight direction and simultaneous wind direction (Fig. 3) on the wind speed measured at the Swiss Federal Agricultural Research Station of Changins.

No correlation existed between the flight directions and the azimuth of the sun (direction in the horizontal plane, r = 0.03, P = 0.91, N = 354).

Relating the height of loss h_l to the current wind profile showed that 97 % of those aphids that have been lost during flight, had left the boundary layer. These aphids were unable to fly upwind, because the wind speed exceeded their active flight speed, assumed as 0.5 m/s.
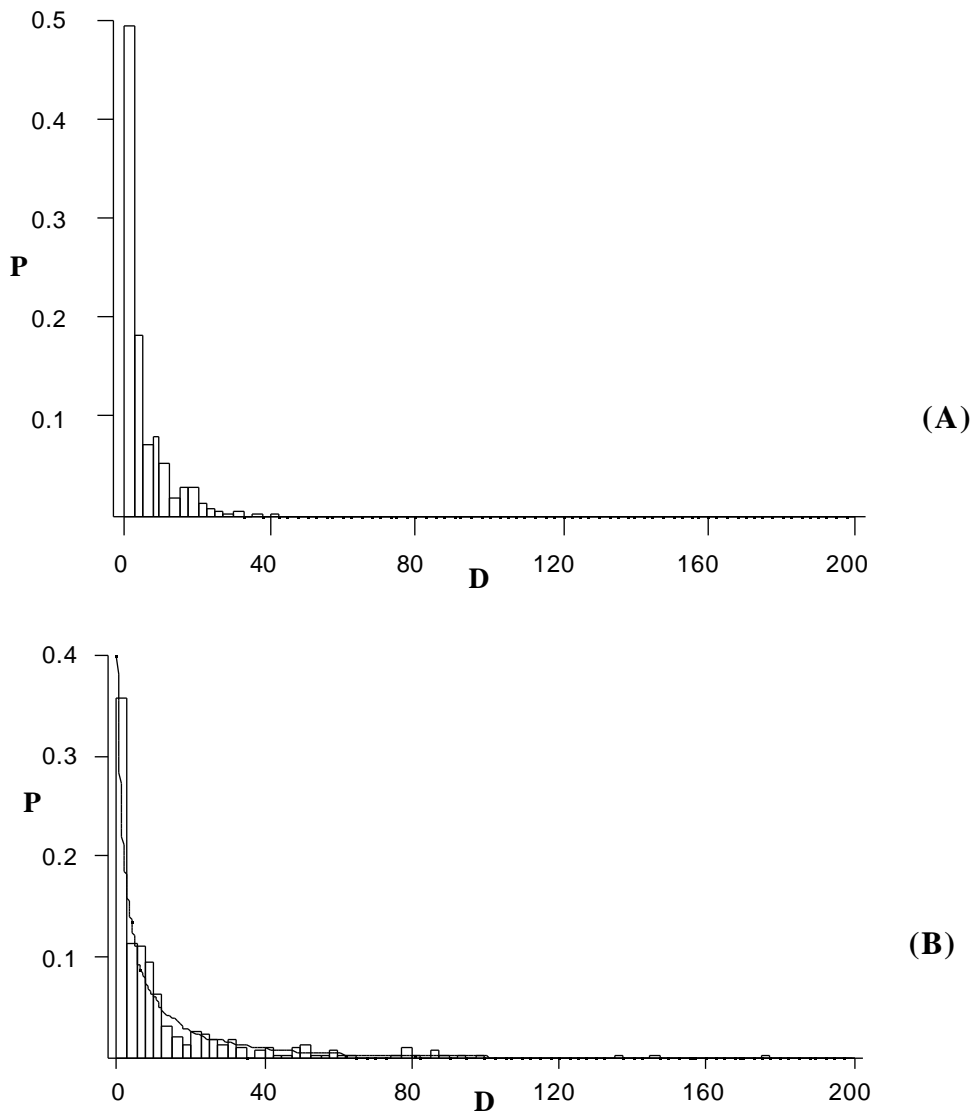
Flight Distance

Fig. 4: Frequency distribution of observed and simulated flight distances of aphids (bars). *A* = minimal flight distances, *B* = probable flight distances. Fitted Weibull distribution shown by curve. *D* = flight distance in m, *P* = proportion of observations in the respective class.

386 flights were observed. In 32 cases (8.3 %) the landing could be observed in other 31 cases (8.0 %) the probable flight distance could be estimated, because the aphid was lost very near the plants during downward flight. 349 observations with complete data were retained for statistical analysis.

To estimate the minimal and probable flight distances (Fig. 4), the effectively observed distances were used for the observations, where aphids could be followed until landing and the results of the deterministic simulations (model A) or the averages of 20 stochastic simulation runs (model B) were taken for all other observations.

The minimum flight distances, estimated by model A, had an average of 5.2 m. The estimated probable flight distances (model B) were longer (average 13.2 m). Nevertheless, short flights were prevailing: 20 % of the probable flight distances were within 1 m from the take-off site and 48 % within 5 m. Only in 13 % of the cases, the estimated landing site lied upwind of the take-off site. The comparison of the probable flight distances of colonizing and noncolonizing aphids with the Mann-Whitney-U-test yielded no significant difference. Hence all observations were pooled for further analysis. A Weibull distribution with the parameters $\alpha = 0.657$ and $\beta = 9.61$ was fitted to the results (Fig. 4). The Kolmogorov-Smirnov goodness of fit test indicated that the fit was satisfactory (test value $T = 0.054$, $P = 0.256$).

If only the observed flight distances had been used to determine the flight distance distribution, the distance would have been substantially underestimated (average distance 2.5 m), because shorter flights are more likely to be followed until landing than longer ones.

DISCUSSION

Flight and Wind Direction

An analysis of the wind directions showed that during the night winds were blowing mainly from north-west. North-eastern and south-western winds were usually strong and therefore unsuitable for aphid flight, whereas south-eastern winds were weak and the most frequent ones during summer days. This breeze, suitable for aphid flight, blows from the lake of Geneva towards the Jura mountain chain, due to different heating by sunshine. The results (Fig. 1) emphasize the necessity to consider only the wind directions during the phases, when aphids fly.

Kennedy & Thomas (1974) have observed that flying aphids orient upwind. If the wind speed exceeds their flight speed, they are carried with the wind, but their bodies are orienting upwind. The field observations showed that almost all aphids had left the boundary layer and therefore were carried downwind (Figs 2 and 3). The direction of the flight movement seemed not to be influenced by the position of the sun. Probably most aphids performed trivial flights and were not attracted by short wave light like during the distance flight.

Since a prevailing wind direction exists, a concentration of infections downwind of the infection sources might occur, as it has been found e.g. by Irwin (1981) for soybean mosaic virus in a soybean field. In another system (white-fly transmitted viruses in the cassava crop) a concentration of infections upwind within a short distance from the source has been observed (N'Guetta, Fargette & Fauquet 1986). The vectors of the cassava virus diseases used the boundary layer to fly upwind and therefore most infections occurred upwind of the sources. However, the boundary layer is much deeper in the cassava, due to the crop height of about 1.8 m. In the presented field observations only few aphids had travelled upwind. Although southeast was the prevailing wind direction in our experimental fields during aphid flight periods, neither in south-east nor in north-west direction of the infection sources the infections were more frequent than in the other directions in our virus epidemic experiments. This apparent contradiction could be explained by the distance at which wind direction plays an important role. The reports showing the influence of wind direction on virus spread (e.g. Hampton 1967; Thresh 1976; Irwin 1981) concern experiments with one focus of initial sources and have quantified virus spread over distances of tenths and hundreds of meters. In potato fields the mean distance between source plants does not exceed a few meters. It seems that over so short distances no clear directional tendency can be detected (see also Gregory & Read 1949). The in-

fluence of wind direction seems to be relevant over longer distances, e.g. transmission between fields, but negligible for shorter distances.

Flight Distance

It can be assumed that the aphids were in the post-migratory flight phase, because they had passed a hunger period or were collected in the field (most of these individuals had immigrated from outside the field). Hence the observed flights were probably trivial. Trivial flights are of highest interest for within-field epidemic studies.

Short flight distances were prevailing (Fig. 4). The estimated flight distances were much shorter than the post-migratory flight distances observed by Taimr & Kriz (1978) for *Phorodon humuli* SCHRANK in a hop garden. The authors found marked aphids in a distance of 49 to 149 m from the release site during the days after the release. However, from our results we conclude that most of these aphids had probably performed more than one trivial flight. A further indication that trivial flight distances are actually short, are the steep spatial disease gradients of many virus diseases (Thresh 1976 & 1978), including PVY and PLRV. These gradients can only partly be attributed to wingless aphids. It can be concluded that most aphids performing trivial flights will land again in the same field and can potentially transmit viruses.

The flight distances of colonizing and noncolonizing aphids might have been different, if different parameters had been assumed for the two aphid groups. The rates of climb of *A. fabae* can be higher or lower after landing on host than on non-host leaves Kennedy (1965 & 1966). Thus the assumption of the same parameters for both groups seems justified. Colonizing and noncolonizing aphids will have a similar chance to land again in the same field and both groups can potentially contribute to within-field virus spread.

The flight distance might be influenced by the wind speed, but no clear dependence could be found, probably because aphids flew only when the wind speed was low. The estimated Weibull distribution describes flight distances during conditions suitable for flight, i.e. when wind speed is low. The derived parameters were used to study the role of vector behaviour in the spatio-temporal spread of PVY in potato fields (Nemecek 1993).

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