HGCA

PROJECT REPORT No. 129

KEY FACTORS FOR MODELLING SECONDARY SPREAD OF BARLEY YELLOW DWARF VIRUS

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KEY FACTORS FOR MODELLING SECONDARY SPREAD OF BARLEY YELLOW DWARF VIRUS

by

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SUMMARY

Data for constructing and testing a simulation model of movement by aphids during the late autumn, winter and early spring period were obtained from an outdoor experiment. Adult wingless grain aphids (*Sitobion avenae* (Fabricius)) and bird cherry aphids (*Rhopalosiphum padi* (Linnaeus)) were released on trays of barley seedlings, planted at field density, placed under three levels of sheltering: protection from wind and rain, protection from wind alone, and unprotected. After one week all plants were destructively sampled and the positions of all aphids on the tray were noted. The experiment was repeated monthly from November to March.

More aphids were retrieved from fully protected plots than from those protected only from wind, or unprotected, suggesting that rain may increase levels of mortality. Consistently more *S. avenae* were retrieved than *R. padi*, supporting previous suggestions that *S. avenae* are more winter hardy. Fewer aphids moved away from the plants on which they were released when protected from wind and rain, than when protected only from wind, or unprotected. Rain had a greater impact on whether or not aphids moved away from a plant than did wind, and more *R. padi* moved than *S. avenae*. The distance moved by both species was less when protected from rain than when protected from only wind or unprotected, and for all months except December the mean distance travelled by *R. padi* was greater than by *S. avenae*.

There is a need for thorough validation of the model using viruliferous aphids.

KEY FINDINGS

1. Rain increased both the amount of aphid movement and the distance travelled more than did wind. However, rain also increased mortality, which may offset the effect of increased aphid dispersal on virus spread.
2. *R. padi* were more mobile and moved further than did *S. avenae*, but consistently more *S. avenae* were retrieved than *R. padi* suggesting their greater survival.

INTRODUCTION

Barley yellow dwarf (BYDV) is a widespread, aphid-vectored, viral disease of cereals with a broad host range on grases (Slykhuis *et al.*, 1959). The disease has a complex epidemiology and characteristically causes sporadic epidemics which can be devastating, and result in considerable economic loss (Oerke *et al.*, 1994; D'Arcy and Burnett, 1995). This has been estimated to cost the industry £10 million per annum in the UK (Harrington *et al.*, 1994). The disease is controlled by eliminating vectors through insecticide use. However, correct timing of applications is difficult (Plumb, 1995), and as a result many British farmers resort to frequent prophylactic spraying, which is often unnecessary because winter conditions and/or activities of natural enemies prevent spread of the disease. There is, therefore, a need to target insecticidal applications more accurately but this requires detailed information on the behaviour of the aphid vectors and how this relates to disease spread during critical periods in the disease cycle.

The causal agent of BYDV is a complex of viruses which can be transmitted by more than 20 species of aphid (A'Brook, 1973) although generally only two or three are of relevance in a particular region. There are two primary aphid vectors of BYDV in Britain, the bird cherry aphid, *Rhopalosiphum padi* and the grain aphid, *Sitobion avenae*, and three isolates of the virus, termed MAV-like, PAV-like and RPV-like, according to the classification by Rochow (1970). MAV is mainly transmitted by *S.avenae*, RPV by *R. padi*, and PAV by both *S. avenae* and *R. padi*, although *R. padi* transmits the latter more efficiently. However, transmission specificity by vectors is not always definitive, and has been shown to alter according to the sequence in which different aphid species feed on a plant (Rochow *et al.*, 1983) and the geographic region of occurrence. The severity of an outbreak differs according to the strain(s) of BYDV involved.

As BYDV is not a seedborne disease, it is only introduced into crops by infective aphids. Both vector species display two types of life-cycle: those which have a sexual phase and pass the winter as eggs, and those which have no sexual phase and remain as wingless aphids on cereals and grasses during the winter. The majority of the *R. padi* populations display the former, with eggs overwintering on the bird cherry tree, *Prunus padus*, while the majority of the *S. avenae* populations display the latter. Virus epidemics are caused in part by infected winged aphids flying into a crop (primary infection) and in part by the wingless offspring of these colonizers, that is, those aphids which overwinter on the crop in the wingless form, moving through the crop and spreading virus (secondary spread). In winter cereals, primary infection occurs mainly early in the autumn, while secondary spread is of importance later in the autumn and winter, particularly during mild winters when better conditions allow aphid survival and movement.

Methods of predicting risk of BYDV outbreaks have been developed in the past (Plumb *et al.*, 1986; Gillet *et al.*, 1990; Dedryver *et al.*, 1991; Kendall *et al.*, 1992) but none has been sufficiently robust and practicable to gain widespread use (Kendall and Chinn, 1990; McGrath and Bale, 1989; Foster *et al.*, 1993; Harrington *et al.*, 1994). Methods of assessing risk require information in two main areas: firstly, accurate measures of the number of viruliferous aphids entering the crop and the level of primary infection which will result from them; and, secondly, the amount of secondary spread occurring during the autumn and winter months by wingless aphids in the crops. An understanding of how both of these factors are affected by field characteristics is also necessary for the development of forecasts which will be field specific and accurate nationwide.

Much work has been done in these areas, including HGCA-funded work at Rothamsted (Project Report No. 110) which quantified some of the main factors influencing secondary spread within fields by wingless aphids during the winter. Data were collected on the frequency and distance of movement by aphids from laboratory experiments, and some of the principal factors involved were measured, but the behaviour in the laboratory may not adequately reflect that in the field. Field experiments are needed to validate these results and are the subject of this report. These data will be used in a model being developed with the Central Science Laboratory (MAFF) aimed at forecasting more accurately the incidence of BYDV. It is intended that this model could eventually be packaged for advisers in the form of a decision support system (DSS) within the DESSAC system.

OBJECTIVE

The objective of the project was to provide data for the development of the aphid component of a model of BYDV spread and to test the model under natural weather conditions.

METHODS

The model of BYDV spread being developed at CSL uses estimates of numbers of infected immigrant winged aphids per unit area, and their distribution to determine initial levels of infection in the field. Subsequent population levels of aphids, their age structure and movement are then simulated over the entire late autumn, winter and early spring period. Data for constructing and testing the latter component of the model were obtained from an outdoor experiment.

Aphid Cultures

S. avenae and *R. padi* cultures were reared on barley plants (cv Puffin) in a glasshouse. To keep conditions close to those experienced naturally, lighting and temperature were not controlled. Plants were replaced frequently (7 - 10 days) and aphid populations maintained at low densities to ensure that the majority of the population was wingless.

Plant Rearing

Pre-germinated barley seeds (cv Puffin) were planted in seed trays 54 x 54 cm, to approximate field density in rows separated by 12 cm, and seeds within rows separated by 2 cm. Plants were used at two growth stages. Seedlings to be used at Growth Stage (G.S.) 12 (Zadoks *et al.*, 1974) were grown at a temperature of 15 - 18 °C for

4 days before bringing the temperature down gradually to 10°C (approximately 1°C each day). Seedlings were then placed outside and protected from wind and frost by polythene sheeting for five days in order to acclimatise the plants. Seedlings to be used at G.S. 22 were grown at temperatures of 15 - 18 °C for 11 days before bringing the temperature gradually down to 10°C (approximately 1°C per day). They were then placed outside for 5 days as described above. All seedlings were placed in the experimental site just prior to aphid release.

Experimental Design

The experiment was designed such that four trays of seedlings were placed in each plot, with two trays at each growth stage, on which were released *S. avenae* or *R. padi*. Trays within each plot were separated by a low barrier coated with glue to ensure that no aphids moved between trays. The position of the tray within the plot was randomly assigned for each experiment in order to ensure that any effects of the glue-coated barrier were minimized. Each plot was randomly assigned to one of three levels of sheltering:

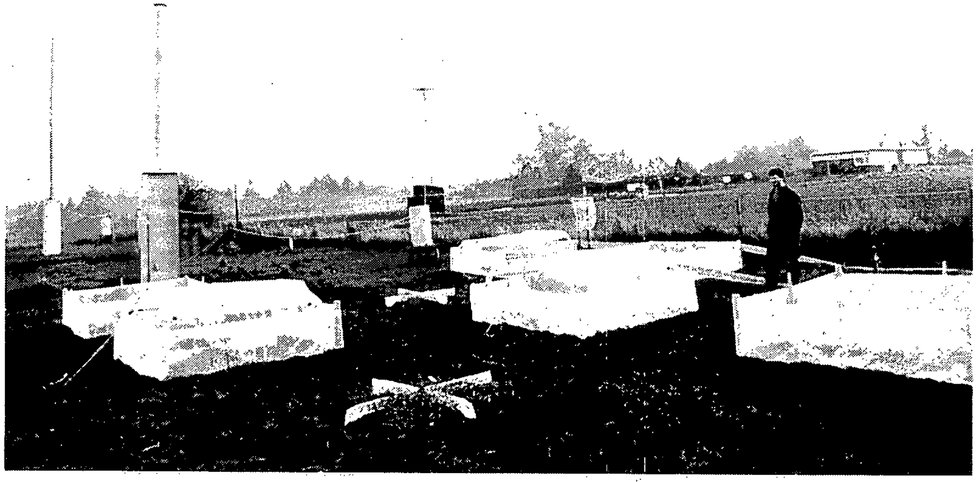
1) protection from wind and rain
2) protection from wind only
3) no protection

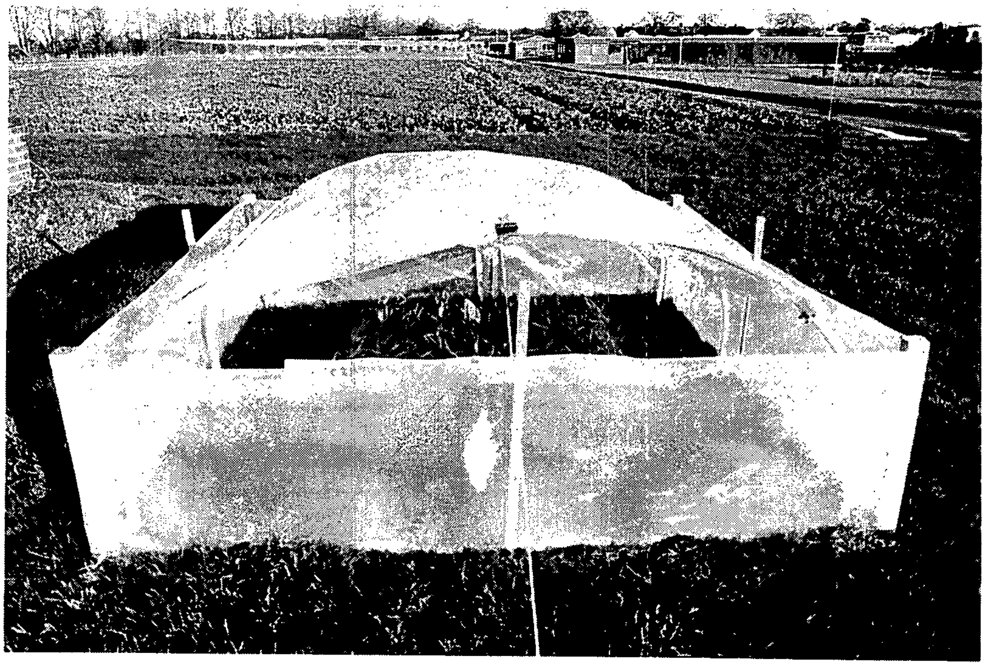
Each treatment was replicated three times (giving 9 plots), and treatments were randomly arranged within the three replication blocks. Plots were arranged in a staggered design to minimize the possibility of one set of barriers sheltering another plot from the wind.

Wind barriers around plots were constructed to surround a 2 x 2 m area, giving a border around the trays of approximately 0.5 m (Plate 1). Wooden stakes were placed at each corner, and a double layer of polythene sheeting attached around the circumference of the plot up to a height of 0.5 m. The polythene was further supported by wire along the top edge and a stake at the midpoint of each side. The

Plate 1

Experimental site showing plots with protection from wind and rain, those with protection from wind alone and those unprotected.





bottom of the plastic was buried to ensure rigidity.

An adaptation of a polytunnel was used to protect the plots from rain (Plate 1). Plastic tubing was arched over the plots and fitted onto metal rods placed in the ground just inside two opposite sides of the wind barrier. Aluminium grip-strip was secured to the plastic tubing slightly above and parallel to the top of the wind barrier. A double layer of 500 nm polythene sheeting was placed over the tubing and secured in the grip-strip using polythene filler. This provided a gap for the passage of air between the top of the the wind barrier and the roof, to minimize the build-up of temperature inside the enclosure.

Hourly temperatures, wind-speed and rainfall were measured during the experiment. Temperatures were measured using thermocouples attached to leaf surfaces at each level of protection; windspeed was measured using two A100R switching anemometers (Campbell Scientific Ltd.) placed at crop height; and rainfall was measured using two ARG100 Tipping Bucket Raingauges (Campbell Scientific Ltd.). During the experiment, wind and rain recorders were placed in plots protected from wind only and protected from both wind and rain. These were calibrated to give a measure of rain and windspeed in the unprotected plots.

Aphid Release

Five adult wingless *S. avenae* or *R. padi*, were confined on each of five of the central plants on the central row of the seed trays using clip-cages, and allowed to establish for two days. On removing the clip-cages, aphid survival and the number of nymphs produced were noted. Nymphs were killed before allowing the aphids to disperse. Seed-trays were left undisturbed for one week. All plants on the seed trays were then carefully searched by destructive sampling and the plants noted from which aphids were retrieved. The experiment was repeated monthly from November to March. However, due to unbalanced data in November only data from December, January, February and March were analyzed statistically.

RESULTS

Weather

Amounts of wind and rain, and mean, maximum and minimum weekly temperatures are displayed in Tables 1-3. December had the highest rainfall, and March considerably less than the other three months. Mean windspeed was high in February, but there was little difference in the mean windspeed during the other three months. Mean temperatures were lowest in January, but the greatest fluctuations were seen in March which had both the highest maximum temperature and the lowest minimum temperature.

Table 1 Total rainfall (mm) for the week during which aphids were released in December, January, February and March.

December	January	February	March
40.6	17.57	24.6	5.05

Table 2 Average windspeed (m s^{-1}) for the week during which aphids were released in December, January, February and March.

	December	January	February	March
Protected from Wind and Rain	0.42	0.41	0.58	0.41
Protected from Wind	0.65	0.63	1.04	0.68
Unprotected	1.11	1.08	1.87	1.17

Table 3 Weekly mean, maximum and minimum temperatures (°C) for the week during which aphids were released in December, January, February and March.

	December	January	February	March
Protected from Wind and Rain (Mean)	6.5	4.8	5.9	6.0
Protected from Wind (Mean)	6.4	5.0	5.8	6.0
Unprotected (Mean)	6.27	5.1	6.4	6.4
Protected from Wind and Rain (Maximum)	12.71	13.4	13.8	25.1
Protected from Wind (Maximum)	11.86	12.4	10.7	26.9
Unprotected (Maximum)	13.78	16.62	14.4	33.7
Protected from Wind and Rain (Minimum)	-2.4	-3.6	-3.4	-6.0
Protected from Wind (Minimum)	-4.2	-3.3	-1.6	-5.0
Unprotected (Minimum)	-4.4	-2.5	-1.0	-2.8

Survival of Aphids

More aphids were retrieved from plots which were protected from both wind and rain ($F_{2,92} = 30.26$; $P < 0.005$) than from plots protected only from wind, or plots which were totally unprotected (Figure 1A). In addition, the difference between the number of aphids retrieved from fully protected plots and plots protected from wind only was greater than the difference between plots protected from wind only and those unprotected. This suggested that rain was having more effect on retrieval than was wind. Although there is no direct evidence to indicate what had happened to aphids which were not retrieved, almost no aphids were found on the sticky barriers bordering trays, suggesting that aphids were not moving off the trays. The proportion of aphids which was lost may therefore represent mortality, and based on this assumption, rain appears to cause increased aphid mortality (Table 4).

The proportion of *S. avenae* retrieved was consistently greater ($F_{1,92} = 31.34$, $P < 0.005$) than the proportion of *R. padi* (Figure 1B). In searching plants for aphids, *R. padi* are more difficult to find than *S. avenae*, sometimes remaining on the stem of the plant at or beneath the soil surface. However this is a marginal difference and unlikely to explain fully the species difference displayed in these data. It has been suggested that *R. padi* may be less winter hardy than *S. avenae* particularly in its response to low temperatures (Knight and Bale, 1986; Dewar and Carter, 1984). This may also be true of a difference between the species ability to endure periods of wind and rain.

The proportion of aphids retrieved also differed significantly between months ($F_{3,92} = 7.64$; $P < 0.005$). Data collected in March showed a much greater proportion of aphids retrieved than for any other month (Figure 1C). Maximum temperatures in March were higher and the amount of rainfall lower than for the other months. Both of these climatic conditions probably allowed greater aphid survival during this period (Table 4).

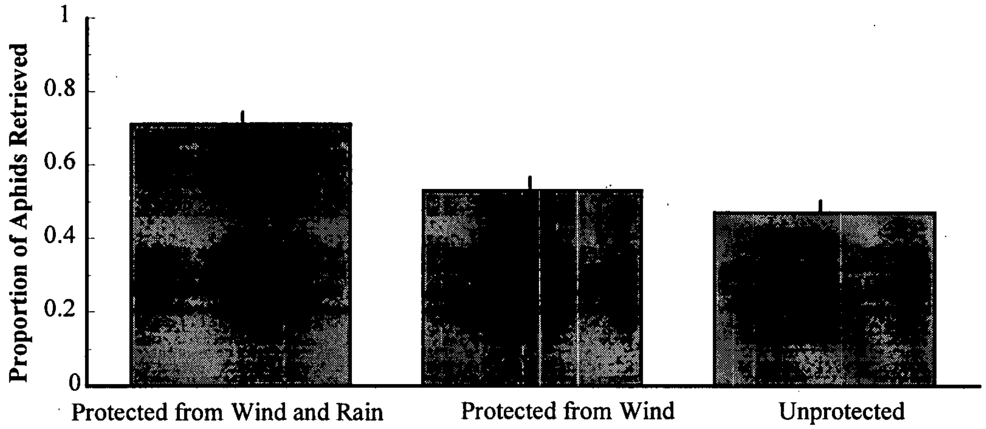


Figure 1A

Mean proportion of aphids retrieved one week after release under protection from wind and rain, protection from wind alone andunprotected. Error bars represent one standard error of the mean.

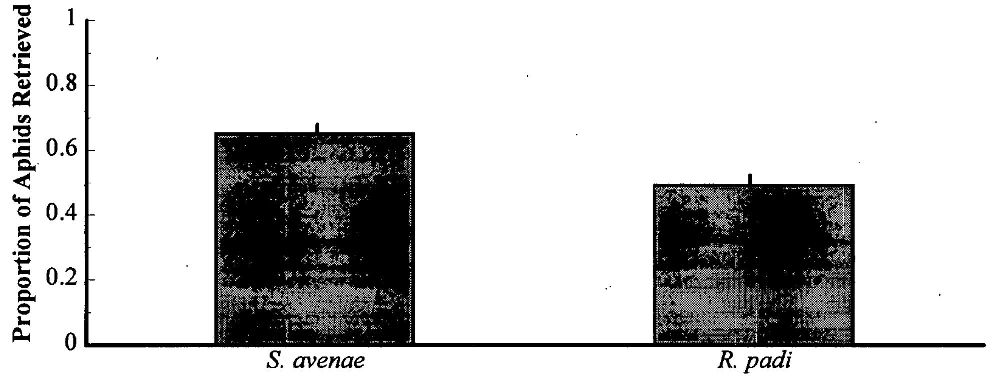


Figure 1B

Mean proportion of *S. avenae* and *R. padi* retrieved one week after release. Error bars represent one standard error of the mean.

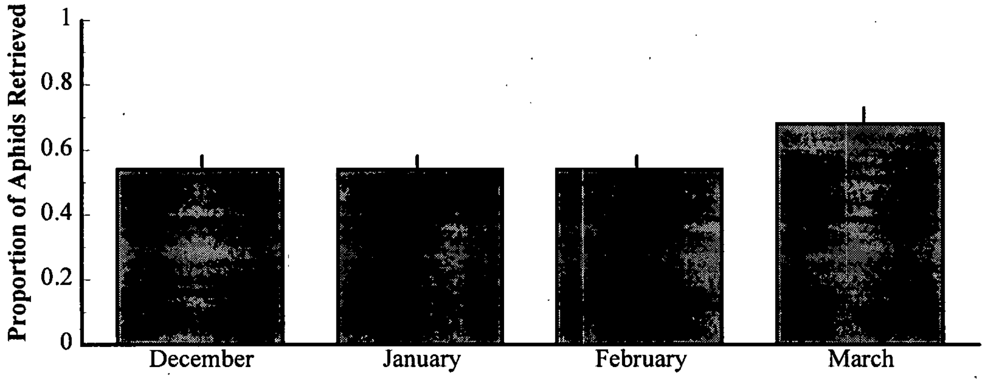


Figure 1C

Mean proportion of aphids retrieved one week after release in December, January, February and March. Error bars represent one standard error of the mean.

Table 4 Mean windspeeds and total rainfall during the period of the experiment and the resulting mean proportion of aphids off the plants on which they were released, mean distance moved by retrieved aphids and mean proportions lost.

Mean Windspeed (m s^{-1})	Total Rainfall (mm)	Proportion Off	Distance Moved A (cm)	Distance Moved B (cm)	Proportion Lost "Mortality"
December					
0.42	0	0.48	6.4	12.4	0.30
0.65	40.6	0.70	10.5	14.6	0.52
1.11	40.6	0.69	9.0	13.0	0.57
January					
0.41	0	0.41	6.2	13.2	0.32
0.63	17.6	0.73	11.6	15.1	0.51
1.08	17.6	0.65	9.2	14.1	0.58
February					
0.58	0	0.51	6.3	11.8	0.33
1.04	24.6	0.72	11.1	14.4	0.58
1.87	24.6	0.67	8.7	12.5	0.49
March					
0.41	0	0.15	1.6	9.3	0.22
0.68	5.1	0.28	3.6	11.5	0.26
1.17	5.1	0.34	5.0	10.7	0.49

Distance Moved A: An average of the distance moved by all retrieved aphids, including those which remained on the plants on which they were released.

Distance Moved B: An average of the distance moved by all aphids retrieved which had moved away from the plant on which they were released.

Movement by Aphids

Dispersal of aphids was measured in two ways: firstly, by whether or not the aphids moved away from the point at which they were released and secondly, by the distance subsequently moved by them.

As was seen in the retrieval of aphids, the proportion of aphids off the plant on which they had been released differed significantly among treatments ($F_{2,92} = 31.16$, $P < 0.005$) with the greatest effect being due to plots which were protected from both wind and rain (Figure 2A). The other two treatments, that is protected from wind only and unprotected, were similar. It seemed therefore that as well as increasing mortality rain had a greater impact on whether on not aphids moved away from a plant than did wind (Table 4).

Consistently more *R. padi* moved away from the plants on which they were released than did *S. avenae* ($F_{1,92} = 23.46$, $P < 0.005$), particularly in March (Figure 2B). As the main climatic differences in March were the high maximum temperatures and lack of rainfall, these data indicate that given better conditions *R. padi* are more mobile than *S. avenae*. The proportion of aphids leaving the plants on which they were released (Figure 2C) differed significantly among dates ($F_{3,92} = 31.41$, $P < 0.005$). This was largely due to a considerable drop in the dispersal in March when weather conditions were milder (Table 1 and Table 4).

Distance has been presented both as a measure of the distance moved by all retrieved aphids including those that remained on the release plants, and as a measure of the distance moved only by aphids which left the plants on which they were released (Figures 3 and 4). The former is effectively weighting the distance moved by the overall aphid dispersal, thus including aphids that moved but were subsequently not retrieved. The effect of treatment was significant both for the distance moved by all recovered aphids ($F_{2,16} = 20.61$, $P < 0.001$) and by only those aphids that left the release plants ($F_{2,16} = 7.57$, $P < 0.005$). The main difference between treatments was for plots protected from both wind and rain

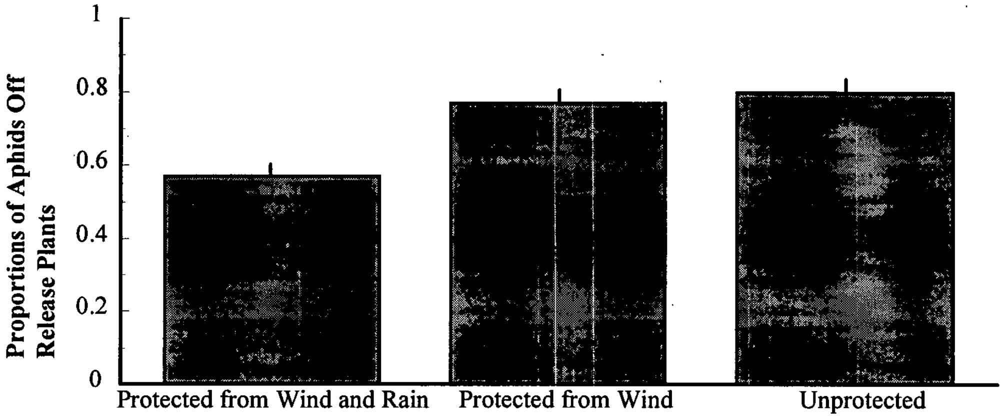


Figure 2A

Mean proportion of aphids off release plants one week after release under protection from wind and rain, protection from wind alone and unprotected. Error bars represent one standard error of the mean.

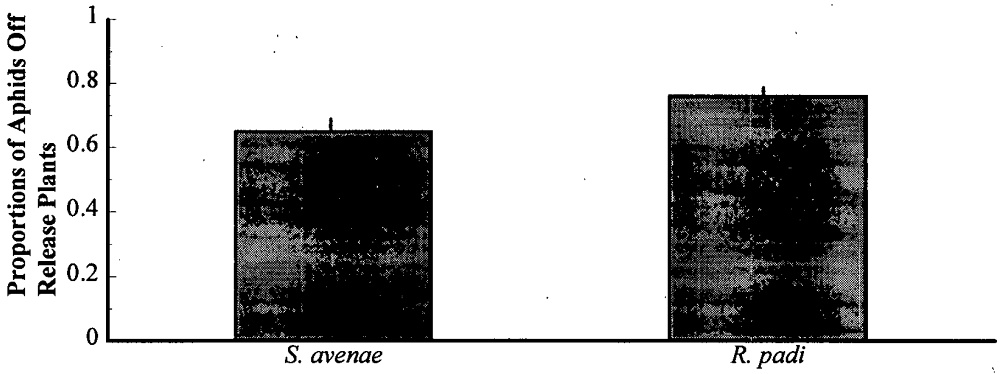


Figure 2B

Mean proportion of *S. avenae* and *R. padi* off release plants one week after release. Error bars represent one standard error of the mean.

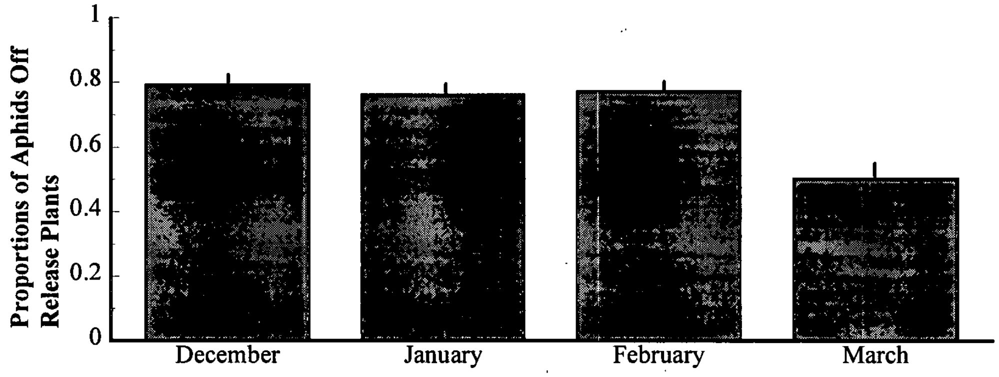


Figure 2C

Mean proportion of aphids off release plants one week after release in December, January, February and March. Error bars represent one standard error of the mean.

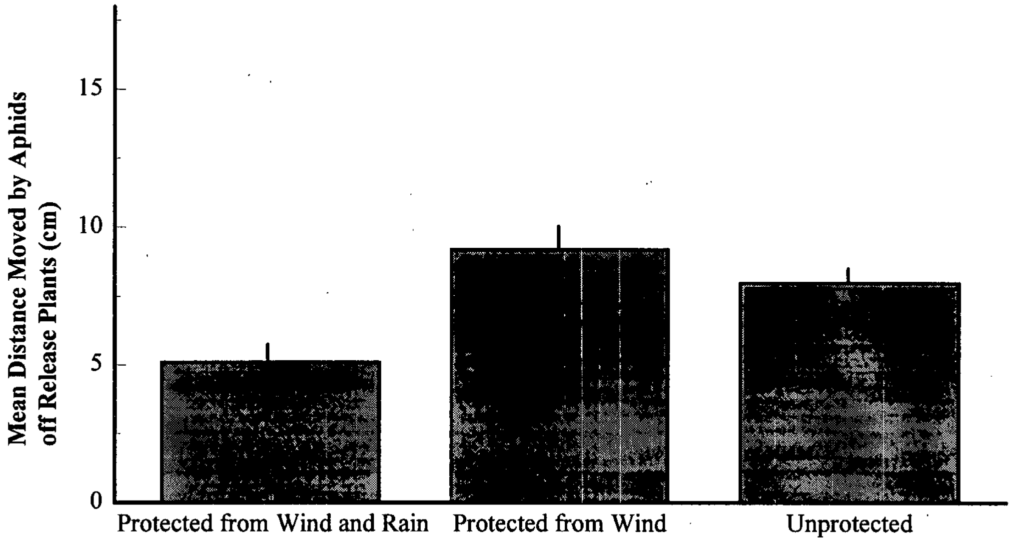


Figure 3A

Mean distance moved by all retrieved aphids one week after release under protection from wind and rain, protection from wind alone and unprotected. Error bars represent one standard error of the mean.

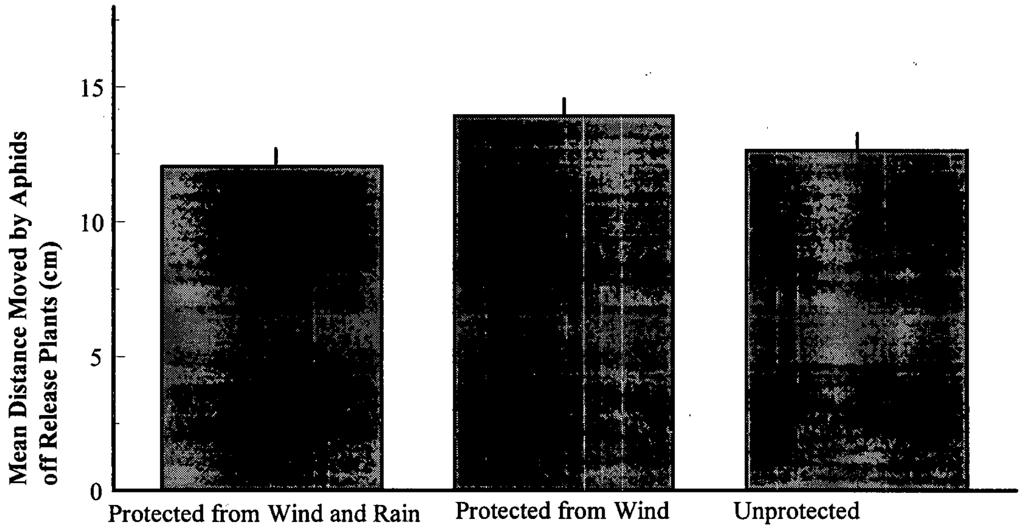


Figure 3B

Mean distance moved by all retrieved aphids excluding those on the central plants one week after release under protection from wind and rain, protection from wind alone and unprotected. Error bars represent one standard error of the mean.

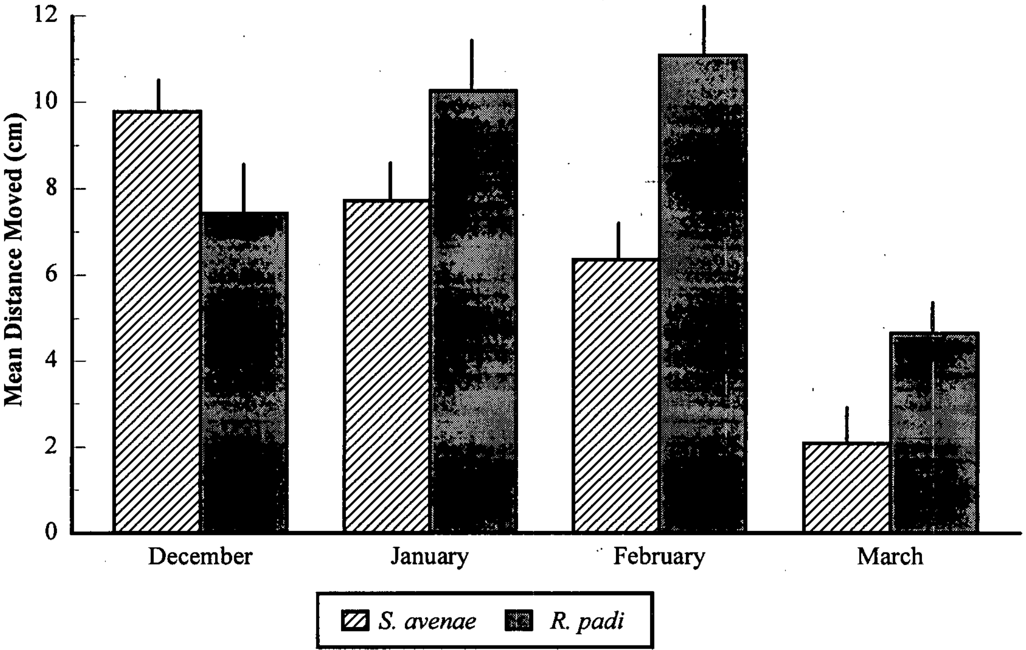


Figure 4A

Mean distance moved by all retrieved *S. avenae* and *R. padi* one week after release in December, January, February and March. Error bars represent one standard error of the mean

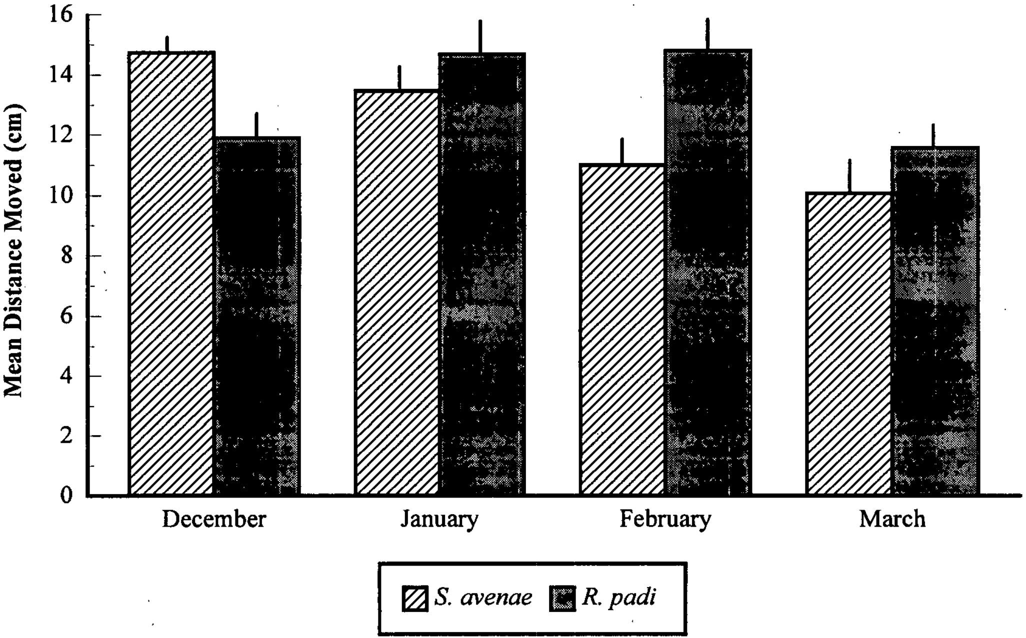


Figure 4B

Mean distance moved by all retrieved *S. avenae* and *R. padi* excluding those on the central plants one week after release in December,January, February and March. Error bars represent one standard error of the mean.

compared with the other two treatments (Figure 3), seen most clearly when all retrieved aphids were taken into account.

The effect of species on the distance moved varied with date (Figure 4), both when all aphids were included and when those on the release plants were excluded. For all months except December *R. padi* moved further than *S. avenae*. The most obvious climatic factor distinguishing December from the other three months was the high rainfall (Table 1). It may be that under conditions of heavy rainfall *R. padi* is less successful at reaching plants at a distance, possibly due to the direct effect of rain droplets, or due to indirect effects such as splash, or increased soil moisture.

DISCUSSION AND CONCLUSIONS

The amount of secondary spread which occurs during the autumn and winter months depends on both the survival of the wingless aphids in the crop, and on their levels of movement to new uninfected plants. Throughout the experiments more *S. avenae* were retrieved than *R. padi* suggesting greater survival. Aphids used in the tests had been reared on plants exposed to normal outside temperatures, and should therefore have been acclimatised. Despite this there was a species difference in survival which may not be solely due to a difference in temperature tolerance, but also a difference in tolerance to wind and rain. This suggestion is supported by data for March when there was very little rain and the relative number of *R. padi* retrieved was much greater.

Rain appeared to decrease survival, or at least reduce successful movement to a new plant, and acted as a strong stimulus for movement away from a plant, as well as increasing the subsequent distance moved. The effect of wind on movement by aphids was less clear and certainly in these experiments had a less dramatic effect than rain. In a recent study Bailey *et al.*, (1995) measured the effects of wind and rain on the spread of BYDV. Wind increased virus incidence whereas rain did not. This is in contrast to evidence presented by Zuniga (1991), Knaust (1994) and

Mann *et al.*, (1995) on *S. avenae*, and the present study suggesting that rain has a major effect on movement of aphids. Treatment times and the intensities of rain and wind used by Bailey *et al.*, (1995) were different to those used or experienced in this experiment and may have caused the differences in results observed. Alternatively, the explanation may be, as suggested by Bailey *et al.* (1995), that aphids displaced from plants may subsequently drown, return to the same plant or in some way be disabled thus preventing virus transmission. Therefore, rain may increase movement, but the increased mortality which it causes may counterbalance this movement to reduce overall virus spread. This question emphasises the need for thorough testing of the model of secondary virus spread being developed, which is based on aphid movement. This should be done under field conditions using viruliferous aphids. In addition, these data describe movement over a period of a week only during each winter month, and may not represent aphid movement over the entire winter period. They do not give information on the effects which prolonged exposure to low temperatures, wind and rain might have on aphid movement.

The data described have been collected in a quantitative way in order to allow movement by aphids to be related to temperature, rain and wind using mathematical functions. This is currently being done at CSL (MAFF). These will be used to adjust the model of aphid movement which has been developed, and is aimed at being part of a larger Decision Support System to predict virus incidence within the DESSAC system. It is intended that the details of the virus-vector-plant interaction which result in aphid transmission are incorporated in the model of movement, and this is clearly imperative for accurate predictions of spread. Conditions which determine the relative importance of primary infection and secondary spread in any particular year, and how this varies with field characteristics and among regions are important features of forecasts of BYDV which are also currently being investigated through HGCA funding.

ACKNOWLEDGEMENTS

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