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DETERMINATION OF FACTORS AFFECTING GRAIN APHID MOVEMENT WITH REFERENCE TO SPREAD OF BYDV IN THE AUTUMN AND WINTER AND FORECASTING DIRECT DAMAGE IN THE SUMMER

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DETERMINATION OF FACTORS AFFECTING GRAIN APHID MOVEMENT WITH REFERENCE TO SPREAD OF BYDV IN THE AUTUMN AND WINTER AND FORECASTING DIRECT DAMAGE IN THE SUMMER

by

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CONTENTS

1. SUMMARY

Grain Aphid Movement with Reference to Spread of BYDV in the Autumn and Winter

1. Movement of introduced aphids and spread of BYDV in barley during the winter were assessed on small plot field experiments. Results suggested that movement by the grain aphid under cold winter conditions was greater than that by the bird-cherry aphid, probably due to greater survival.

2. Laboratory studies to investigate abiotic factors which affect movement of wingless aphids showed that under conditions of constant wind, the distance moved by aphids increased with time; conditions of strongly gusting wind increased the proportion of aphids leaving a plant and the distance moved by them; aphid dispersal increased with rain intensity, droplet size and temperature.

3. Laboratory studies to investigate biotic factors which affect movement by wingless aphids showed that high aphid density was a strong stimulus for dispersal; at a plant spacing greater than 8 cm aphids were less likely to leave a plant; adult aphids were more likely to leave a plant and move further than nymphs; in glasshouse conditions a greater proportion of bird-cherry aphids moved than did grain aphids. When compared with field experiments above, the latter result suggests that environmental conditions may have a key role to play in the relative contribution to virus spread made by each species.

4. A comparison was made of the number of asexual grain aphids caught during the autumn in six types of trap at Starcross and Leeds. None of the trapping methods was an improvement on the 12.2 m or the 1.5 m suction traps.

5. Two synthetic aphid sex pheromones were assessed for their potential to monitor the sexual portion of the grain aphid population. The mixture of nepetalactol and nepetalactone was a strong attractant for male aphids.

Grain Aphid Movement with Reference to BYDV in the Spring and Direct Aphid Damage in the Summer

1. An investigation of the spread of virus by wingless aphids in spring-sown cereals showed that adults accounted for a greater proportion of virus spread than did nymphs, and that populations of wingless aphids on a crop may make a significant contribution to the spread of virus in the spring.

2. A field experiment showed that early-sown spring crops are at less risk of BYDV infection than late-sown crops and that the effectiveness of sprays aimed at controlling virus depends on the level of virus present in nearby overwintering crops, as well as the timing of aphid migration relative to crop development.

3. Overwintering aphids on winter wheat make a major contribution to the total size of aphid populations on the crop in the spring, particularly early in the season. A spray in March removes this problem. Sprays applied at the beginning of aphid immigration were

not effective. A spray at or just after growth stage (GS) 73 (Zadoks *et al.*, 1974) was effective in reducing peak numbers of aphids in the crop during the two years under study. The effectiveness of this spray may vary from year to year (Oakley and Walters, 1994).

2. OBJECTIVES

The overall objective of the project was to determine the role of movement of the grain aphid in relation to BYDV epidemiology in the autumn and winter, and to forecast aphid outbreaks in the summer. The main information required was:

- what is the potential for grain aphids that invade crops in the autumn to develop and spread virus in the autumn and spring
- whether the low number of grain aphids in samples from the Rothamsted Insect Survey's 12.2 m suction traps in autumn are due to an inappropriate sampling height, or whether low numbers of the grain aphid are having a greater significance for BYDV spread than the bird-cherry aphid.
- the potential of overwintered grain aphids to develop into damaging populations in the spring and summer.

3. INTRODUCTION

Barley yellow dwarf virus (BYDV) is the most serious viral disease of cereals in the UK and frequently causes severe yield losses. Because the incidence of the disease differs from year to year and region to region, most arable farmers ensure a healthy crop by applying insecticidal sprays prophylactically in the autumn. The cost of such spraying is estimated at approximately £10 million/year (Harrington *et al.*, 1994) and is of considerable detriment to the environment. The development of an accurate system for forecasting the risk of BYDV epidemics would avoid unnecessary spraying. To facilitate such a system considerable information concerning the epidemiology of the virus is needed, and much of the work collecting such information has been supported by levy-funded grants.

BYDV is a group of viruses vectored mainly by two aphids, the bird-cherry aphid and the grain aphid. PAV-like isolates of the virus are transmitted primarily by the former and by the latter to a lesser extent, MAV-like isolates are transmitted by the grain aphid and RPV-like isolates are transmitted by both. Healthy crops are infected in the autumn when infectious vectors migrate into the crop and feed on healthy plants, resulting in what is known as primary infection. A measure of the number of migrating aphids and the proportion which can transmit virus is needed to determine this initial infection in crops. This was the basis of the infectivity index developed at Rothamsted, which made a cumulative weekly measure of the total number of migrating aphids caught in the Rothamsted suction trap, multiplied by the proportion of these which were carrying virus (Plumb, 1976; Plumb, 1983; Plumb *et al.*, 1986). A high index provided good predictions of spring outbreaks on autumn-sown crops local to the trap from which aphid assessments were made, but there were serious regional discrepancies (Kendall and Chinn, 1990; McGrath and Bale, 1989; Foster *et al.*, 1993). This was due, in part, to inaccurate estimates of the number of infective aphids migrating into crops, as a large portion of the bird-cherry aphid population produce sexual forms in the autumn, which fly to bird-cherry trees and are therefore unlikely to introduce virus into autumn crops. Estimates for the number of bird-cherry aphids have now been improved greatly (Tatchell *et al.*, 1988) by disregarding this portion of the population and this has been made easy by the development of a simple technique to separate the two aphid forms, through work funded by the HGCA (Lowles, 1995). However, estimates of the number of aphids entering the crop are still thought to be inaccurate due to low absolute numbers in suction trap samples, with little variation between years. A method for increasing the sample size is needed.

The other major problem with the infectivity index is its failure to account for disease progression during winter months. This is of particular importance under mild conditions when aphids survive on the crop and spread virus through the winter by movement between plants. The consequent increase in the number of virus-infected plants within a crop is known as secondary infection or secondary spread. Because the grain aphid overwinters more successfully than the bird-cherry aphid (Dewar and Carter, 1984; Tatchell *et al.*, 1994) it is thought to be the prime contributor to this. Predictions of disease progression during the winter require an understanding of how vector movement and hence virus spread are determined by abiotic and biotic factors. A major part of the project was targeted at this problem.

Aphicide sprays applied to control BYDV vectors are intended to prevent secondary

spread within the crop. An understanding of the time interval between crop colonisation and the start of secondary spread will therefore allow a better timing of spray application. A knowledge of whether aphids have survived to this point in sufficient numbers to pose a threat to the crop will also improve identification of crops needing protection.

Control of BYDV in spring-sown cereals is particularly difficult. Winged aphids leaving their overwintering hosts migrate into crops and, if carrying BYDV, may infect healthy plants. Early sowing reduces aphid colonisation prior to stem elongation and hence increases protection from virus infection (Doodson and Saunders, 1970). However even this may not be adequate after mild winters when aphids begin to fly earlier, and once the migration has started they may colonise the crop over a prolonged period of time. As a result farmers often resort to frequent spraying during the growing period. Targeting these sprays more accurately for optimal control would be of both economic and environmental benefit.

In addition to their role as vectors of BYDV, aphids can cause direct damage to crops if their numbers are sufficiently high. Peak numbers of aphids in the summer, on crops sown in the autumn, are determined in part by the number of aphids which survive the winter on the crop, and in part by the number of aphids flying into crops in the spring. The relative importance of these aphids in determining both peak aphid abundance, and the timing of this in relation to crop growth stage, are key factors in determining the extent of direct crop damage by aphids.

This project aimed to provide data on the monitoring and prediction of movement of the grain aphid between and within crops, in order to develop more accurate predictions of the spread of BYDV in autumn and winter, and methods for the control of direct crop damage during the summer. Details of statistical analysis of the data have not been included in the report for simplicity, but are readily available on request.

4. GRAIN APHID MOVEMENT WITH REFERENCE TO SPREAD OF BYDV IN THE AUTUMN AND WINTER

4.1 Field Experiments Investigating Movement of Aphids and Spread of BYDV

Movement by aphids and spread of BYDV was assessed by releasing virus-infected aphids on small plot field experiments at Rothamsted during the autumn and winter of 1991/92 and 1992/93.

4.1.1 Materials and Methods

Aphid Cultures

Aphids to be introduced to the plots were reared under controlled conditions (18°C, 16 hours light, 8 hours dark) on barley and allowed to acclimatise at 10°C under the same photoperiod for one week prior to introduction to the field. Aphids were infected with virus by placing them on BYDV infected barley for 72 h prior to the release. According to their vector specificity, MAV-like isolates were used for the grain aphid, PAV-like isolates for the bird-cherry aphid.

Experimental Design

In 1991 3 x 3 m plots of winter barley were sown on 20th September and 10th October. For each sowing date five treatment plots were replicated four times for both the grain aphid and the bird-cherry aphid in a randomised block design. The five treatments were:

1) control plots to monitor background virus incidence;
2) control plots to monitor movement of introduced aphids;
3) virus infected aphids introduced at the beginning of November, cypermethrin sprayed at the beginning of March;
4) virus infected aphids introduced at the beginning of November, cypermethrin sprayed early January and March;
5) virus infected aphids introduced at the beginning of November, cypermethrin sprayed at the beginning of December, January and March.

Each plot was marked with two perpendicular transects running through the centre of the plot. Four aphids were confined in clip-cages to each of four plants approximately 12 cm from the centre of the plot along the transects. Aphids were allowed to establish for 72 h before clip-cages were removed. A subsample of these aphids was tested for BYDV transmission in the laboratory, to ensure that they were infective. Plots were sampled for aphids at 10 points, at intervals of 12.5 cm, along each transect just before each spray. Leaf samples were taken from 10 plants along each transect, again at intervals of 12.5 cm, and tested for BYDV using Triple Antibody Sandwich - Enzyme Linked Immunosorbent Assay (TAS-ELISA) (D'Arcy, 1992).

In 1992 winter barley (cv. Magie) was sown on 17th September. Viruliferous aphids were released on plots on 9th October and 5th November to simulate early and late colonisers (the methodology was the same as that described in the previous paragraph). To assess the timing of virus spread, plots were sprayed with an insecticide to prevent further infection, in December or in March. Further acclimated aphids were retained in clip-cages on leaves on the plots (12 clip-cages per aphid species) throughout the experiment to monitor overwintering survival. The number of dead aphids per clip-cage was calculated as a percentage of the number of aphids alive in that clip-cage the previous week, to calculate aphid mortality. The number of aphids per clip-cage was kept at a maximum of four nymphs and four adults per clip-cage. Any aphids in excess of this number were removed. Leaf samples were taken from transects across the plots in April for virus assessment using TAS-ELISA.

4.1.2 Results and Discussion

In 1991 numbers of aphids recovered during aphid sampling were low overall (Figures 1 and 2). Slightly more bird-cherry aphids than grain aphids were found prior to severe frosts in December, but in January both species dropped to very low numbers with very few aphids found on either early- or late- sown plots. In the final sample in February the number of grain aphids was higher than the previous sample on both sowings, suggesting that numbers were beginning to increase, while numbers of bird-cherry aphids remained very low. When all data were combined only four bird-cherry aphids were found more than 12 cm away from the point of release, while sixteen grain aphids were found at distances of 12-84 cm. Although numbers were too low to draw statistical conclusions, the results suggest that grain aphids were more mobile than bird-cherry aphids during the winter. This may be because low temperatures have less impact on grain aphids than on bird-cherry aphids (Dean, 1974; Williams, 1980).

Leaf samples showed a low percentage of the plants sampled to be virus positive, particularly those close to the point of release which one might expect to be 100% positive (Figures 3 and 4). This may have been because the numbers of aphids released on the plots were too low and sampling not sufficiently intense to detect the virus infection. Severe winter conditions, and the timing of aphid release relative to growth stage, may also have affected the ability of the aphid to transmit the virus or prevented the development of virus in the plant to detectable levels. Virus spread by both aphid species was greater on plots sown early than late.

In 1992 virus infected aphids were released in October and November. Very little virus was detected on plots infested with aphids in October. Problems experienced with virus sources at the time resulted in only a small proportion of the released aphids being virus infected. The release in November resulted in a greater percentage of plant infection, particularly on plots infested with the grain aphid, where up to 75% of plants sampled were virus infected on plots sprayed in March (Figure 5). BYDV infection by the bird-cherry aphid reached a maximum of 33% of plants on plots sprayed in December and March. Spread of virus by the grain aphid extended 50 cm from the centre of the plot, while that by the bird-cherry aphid extended 40 cm from the centre of the plot. Again leaf samples showed a low percentage of plants to be infected with virus. The greater amount of spread which occurred in 1992/93 than in 1991/92 may have been because twice the number of

aphids were released, or because of differences in the winter weather. More detailed experiments are needed to ascertain this.

Grain aphid survival overwinter in clip-cages was high with mean percentage mortality per clip-cage not exceeding 30%. Aphid populations resulting from both early (9.10.92) and late (5.11.92) release dates passed through two generations. Although clip-cages give some protection from external environmental conditions, this information provides an indication of the potential for grain aphids to survive and their generation time overwinter. Mortality of bird-cherry aphids released was too high to follow generation time during the winter.

4.2. Biotic Factors Influencing Movement by Wingless Aphids

The effects of aphid density, plant spacing, aphid species and aphid age on movement by wingless aphids were investigated under laboratory conditions.

4.2.1 Materials and Methods

Aphid Cultures

Grain aphids collected from fields at Rothamsted in January 1992, and bird-cherry aphids, collected from Amwell, Herts., in 1988, were reared on barley (cv. Magie) under controlled laboratory conditions (18° C, 16 hours light and 8 hours dark).

Aphid Density

In a preliminary experiment barley seedlings (cv. Magie) were planted at a spacing of 4 cm, in a 5 x 5 grid, in seed trays 22 x 36 cm. One week after plant emergence grain aphids were confined on the central plant in clip-cages at densities of 2, 4, 8, 16, and 24 aphids per plant and allowed to settle for 24 h before the clip-cage was removed. After a further 24, 48 and 72 h plants were searched and the positions of aphids were noted. Seed trays were maintained in a glasshouse at a temperature of 16°C and photoperiod of 16 h light and 8 h dark. Each experiment was replicated three times in randomised blocks.

Plant Spacing

As the size of trays used in the previous experiment was found to be too small to contain all aphids once movement had been initiated, it was increased to 54 x 54 cm. Pregerminated barley seedlings were planted in a grid at spacings of 2, 4, 6, 8 and 10 cm. One week after plant emergence 16 adult wingless grain aphids were confined on the central plants in clip-cages and allowed to settle for 24 h before the clip-cages were removed. After a further 48 h, all plants were searched and aphid positions noted. Each treatment was replicated four times. Seed trays were maintained in glasshouses and treatments arranged randomly within blocks

Aphid Species and Age

Pregerminated oat seedlings (cv. Dula) were planted in a 9 x 9 grid with a 6 cm spacing. Oat seedlings were used for consistency with other studies on BYDV, which use oats because virus symptoms produced are much clearer than in wheat or barley. (Personal observations indicated little difference between movement on oats and barley under these conditions). One week after plant emergence 16 wingless aphids were confined on the central plant of each tray using clip-cages. After 24 h the clip-cages were removed and aphids allowed to disperse for a further 48 h. All plants on the grid were then searched for aphids and their positions noted. Four treatments were designed to compare movement by a) the grain aphid I - III instar b) the grain aphid IV instar - adult c) the bird-cherry aphid I - III instar and d) the bird-cherry aphid IV instar - adult. Treatments were replicated four times. Seed trays were maintained in glasshouses and treatments arranged randomly within blocks.

For all experiments the proportion of aphids leaving the plants on which they were released was determined, and the average distance moved by these aphids from the point of release was calculated. As no record of their path of movement was made, it was assumed that each recovered aphid had moved directly from the point of release, and this distance was calculated using Pythagoras' Theorem. The proportion of aphids lost was also determined. These aphids may have died, been on the soil or have left the arena.

4.2.2 Results and Discussion

All the factors investigated influenced aphid dispersal. High aphid density was shown to be a strong stimulus for dispersal. For aphids released at densities of 4-24 per plant there was little difference in the distance moved. However, at the lowest aphid density of 2 per plant, aphids moved a significantly shorter distance than for the other densities (Figure 6).

With increased plant spacing, the mean distance moved by aphids increased. However, when plants were spaced 10 cm apart, significantly less aphids left the release plant (Figure 7). It was not possible to assess whether more aphids were found on the release plant when plant spacing was greater because they could not detect neighbouring plants, or because they left the plant but returned to it. (Preliminary work suggests the latter). At the closest plant spacing (2 cm) no aphids were lost and the proportion lost at all other spacings was similar (approximately 10%).

Experiments comparing the movement by the bird-cherry aphid with that by the grain aphid clearly showed that in both species the nymphs were much less likely to move than adults, and that after they left the plant on which they were released the distance moved was less (Figure 8). Both stages of the bird-cherry aphid were more likely to leave the plant on which they were released than the grain aphid, but the mean distances moved by the two species were similar. The greater number of the bird-cherry aphid lost than the grain aphid, is probably due to difficulty in seeing them as they are smaller in size and often feed on the stem slightly below the soil surface.

4.3. Abiotic Factors Influencing Movement by Wingless Aphids

The effects of wind, rain, and the interaction between temperature and aphid density on the movement of wingless grain aphids, were investigated.

4.3.1 Materials and Methods

Aphid Cultures

See 4.2.1 above.

Equipment

The effects of wind and rain were simulated using the rain tower and wind tunnel at Rothamsted as described in detail in Mann *et al.* (1995).

Experiments investigating the effects of constant temperature on aphid movement were done in four controlled environment cabinets. Temperatures of 5, 12, 18 and 25°C ± 2 °C, and aphid densities of 2, 8, 16 and 24 aphids per plant were used with a daily light regime of 16 h light, 8 h dark.

Experimental Design

Wind and Rain

Pregerminated oat seedlings (cv. Coast Black) were planted in a 9 x 9 grid with 6 cm spacing, in plastic seed trays (54 x 54 x 5 cm). One week after plant emergence eight adult wingless grain aphids were confined on each of four central plants, using clip-cages. After 24 h the clip-cages were removed and the aphids exposed to wind or rain. Five experiments were designed to investigate the influence of wind and rain on the proportion of aphids dislodged from their release plant and the distances moved by them:

1) Aphids were exposed to a constant mean wind speed of 2 m s^{-1} (roughly equivalent to Force 5 over an open field) for 0.5, 1, 2 and 4 h.

2) Aphids were exposed for one hour to: a) wind at a constant speed of 2 m s^{-1}, b) wind with an average speed of 2 m s^{-1} and gusts ranging from 1.0 m s^{-1} to 2.5 m s^{-1}, or c) wind with an average speed of 2.5 m s^{-1} and gusts ranging from 0.5 m s^{-1} to 5 m s^{-1}

3) Aphids were exposed to rain of drop diameter 0.35 cm and intensity 0.31 mm min^{-1} for 0.5, 1, 2 and 4 h.

4) Aphids were exposed for one hour to three 'types' of rain: a) drizzle (0.03 mm min^{-1}, drop diameter 0.1 - 0.2 mm), b) light rain (0.16 mm min^{-1}, droplet diameter 1 mm), or c) heavy rain (0.3 mm min^{-1} drop diameter 3.5 mm).

5) Aphids were exposed to: a) gusting wind with an average speed of 2.6 m s^{-1} and

range from 1.0 m s^{-1} to 5.5 m s^{-1}, b) heavy rain (0.3 mm min^{-1}, drop diameter 0.35 mm), or c) a simultaneous combination of treatments a) and b).

In experiments 1 and 3 four trays of plants were exposed simultaneously in the target area and one was removed after each period of time had elapsed. A control tray was placed adjacent to the rain tower complex, and each experiment was replicated four times. In experiments 2, 4, and 5 the four replicates for each treatment were run simultaneously as only one treatment could be simulated at any time. One untreated control tray per treatment was placed adjacent to the complex giving three control trays per experiment.

All plants were searched and aphid positions noted immediately after treatment. From these positions the number of aphids leaving the plants on which they were released was determined, and the average distance moved by these aphids from the point of release was calculated (see Section 4.2.1).

Temperature

Pregerminated oat seedlings (cv. Dula) were planted in seed trays in a 9 x 9 grid as described above. Aphids were acclimatised for one week prior to the experiment. Those to be released at 25°C were acclimatised at 20°C, and those to be released at 5°C were acclimatised at 10°C. Those to be used at temperatures of 12°C and 18°C were reared at 15°C. One week after plant emergence, wingless adult grain aphids were confined in clip cages on the central plant of each of four seed trays, at each aphid density at each temperature and replicated five times. After 24 h, clip cages were removed and the aphids allowed to disperse. After a further 48 h all plants were searched and the aphid positions noted. As before the number of aphids leaving the plants on which they had been released, the average distance moved by these aphids, and the number of aphids lost were determined.

Data were analysed using analysis of variance, and weighted by aphid density (total number of replicates multiplied by aphid density). No movement occurred at an aphid density of 2 per plant, therefore all observations for this treatment were excluded from the analyses.

4.3.2 Results and Discussion

Sudden leaf disturbances caused by wind gusts and rain droplets affected the dispersal of wingless grain aphids. Under conditions of constant wind flow, the number of aphids leaving their release plant was not affected, but once dislodged the distance moved by aphids increased with treatment time (Figure 9A). In contrast, wind type had a considerable effect on both the proportion of aphids which had moved off the central plant and on the proportion of aphids lost, with both being significantly greater when aphids were exposed to strong wind gusts than to any other treatment (Figure 9B). Under such conditions leaves were subject to extreme agitation causing aphids to be dislodged and probably making it difficult for them to re-settle. The effect of wind gusting on the average distance moved by aphids was less simple: aphids dispersed further when exposed to conditions of constant wind or strong gusts than to gentle gusts or in untreated controls.

The length of time aphids were exposed to rain had no effect on the proportion leaving a release plant or on the average distance moved by dispersing aphids, but did increase the proportion of aphids lost (Figure 10A). When aphids were exposed to increasing rain intensities there was also an increase in the proportion of aphids that were not found (Figure 10B). This was demonstrated further in the experiment in which the effects of wind and rain were compared (Figure 11). However, as movement of aphids in the control treatments for different experiments varied, absolute values cannot be compared directly. Although lost aphids may have died, been on the soil and not visible or escaped from the trays, heavy rain appeared to make it difficult for aphids to re-settle on the plants. If the proportion of aphids lost is an indirect measure of mortality, then the data suggest that mortality increases with the duration and intensity of rain.

The proportion of aphids leaving their release plant and the distance moved by them both increased significantly when rain intensity and droplet size were increased. Drizzle, causing only wetting of the plants and aphids, had very little impact on dislodging, movement or recovery rate of aphids. Leaf disturbance, caused by large and frequent rain droplets, had a considerable impact on aphid dispersal.

When the effects of temperature and density were studied there was no movement at the lowest aphid density (2 aphids per release plant) and significant increases in both the proportion of aphids leaving their release plant and the distances moved by them as densities increased from 8 to 24 aphids (Figure 12). Temperature also had a very clear effect. At 5°C there was movement only at the higher aphid densities (16 and 24 aphids per plant), but between 12 and 18°C the proportion of aphids leaving their release plant and the distance moved by them increased at all aphid densities. At 25°C, however, there was no increase in the proportion of aphids leaving their release plant for any aphid density, and the mean distance moved increased only at aphid densities of 8 and 16 per plant. As a number were found dead on the plants or the soil, it appeared that high temperature was limiting their survival.

4.4 Methods For Monitoring Crop Colonisation in the Autumn

In order to improve the efficiency of monitoring grain aphid migration in autumn, 6 types of trap for monitoring the asexual portion of the aphid population were compared at Starcross and Leeds in 1992.

In 1991 two synthetic aphid sex pheromones - nepetalactone and nepetalactol, were assessed for their potential to lure the sexual portion of the grain aphid population into traps at Rothamsted, Starcross (Devon) and Leeds in 1991. These synthetic pheromones may be a useful tool in monitoring sexual clones of the grain aphid, and may also have applied applications for aphid control through parasitoid manipulation (Powell *et al.*, 1993).

4.4.1 Materials and Methods

Comparison of Trap Types

A comparison was made of the number of grain aphids collected from the 12.2 m suction traps (Macaulay *et al.*, 1988), with numbers from four other traps at Starcross and Leeds during the autumn of 1992. The four traps used were as follows:

1) a sticky trap cylinder 6.8 cm in diameter, 30 cm long, painted fluorescent yellow; detachable acetate wrap-around sheets coated in polythene adhesive were secured on the cylinder by clips for easy removal at each service;
2) a yellow water trap dish 17 cm in diameter, 6 cm deep, filled with soapy water;
3) a fishing wire trap, based on that described by Labonne *et al.* (1983); fishing wire was stretched across a 30 x 30 cm wooden frame around nails on opposite ends of the frame; the wooden frame was attached to a revolving vane which ensured that the trap pointed into the direction of the wind; the wire was sprayed with polybutene to provide a sticky surface;
4) a low level suction trap placed 5 cm above soil surface; this comprised a plastic box 90 x 30 x 22 cm fitted with a fan at one end which drew in a sample of 15 litres of air per minute; an opening at the other end of the box was covered with nylon netting (nylon tights) to trap the aphids.

Traps were positioned on barley plots close to the 12.2 m suction trap, a minimum of 15 m apart, with all except the low-level suction trap placed on a free-standing base just above the soil surface. The traps were emptied and their positions re-randomised twice weekly between mid-September and mid-November. In addition to these traps, a 1.5 m high suction trap sampling a similar volume of air to the 12.2 m suction trap was operated at Starcross. Catches were compared with those of the 12.2 m suction trap.

In order to compare the trap catches with the density of winged grain aphids within the crop, the crop was searched manually twice in the autumn at Rothamsted, Starcross and Leeds. Dates for these searches were targeted to coincide with the appearance of the first winged grain aphids on plots of barley planted on 15.9.92 and 28.9.92 being sampled at regular intervals for another experiment (HGCA Project 0003/3/89). Crops were searched for four hours or until 100 winged aphids had been collected and the area of search was noted. All aphids were frozen and subsequently tested for virus content using TAS-ELISA.

Pheromone Lures for Monitoring Male Aphids

Pheromone lures were used to make a comparison of the sexual portion of the population at Rothamsted and Starcross as outlined in detail by Powell et al., (1993) and Hardie *et al.* (1994). Traps were made using a Petri dish (14 cm diam.) with a length of plastic tubing fixed to the lower side, to allow the trap to be secured on a metal pole placed in the ground (Figure 13). A short length of tubing was fixed to the upper side of the Petri dish to support the phials containing pheromones. Two types of phials were used - a polythene cylinder allowing slow release of the pheromone through plastic, and a pair of glass phials with plastic lids through which the pheromone was released. Petri dishes were half-filled with soapy water to catch the aphids. The seven treatments used were as

follows:

1) Polythene (solvent control)
2) Glass blank (solvent control)
3) Yellow water trap
4) Nepetalactone in glass
5) Nepetalactol in glass
6) Glass mixture (nepetalactone and nepetalactol)
7) Polythene mixture (nepetalactone and nepetalactol)

Yellow traps were included as yellow is attractive for many aphid species, and such traps are often used in aphid monitoring (Moericke, 1969). Treatments 1-5 were replicated four times on separate plots at Rothamsted, Starcross and Leeds. Treatments 6-7 were used only at Rothamsted. At all sites traps were positioned in barley plots sown on 12th September. For two of the replicates traps were positioned 12 cm above the ground (ie. just above the crop surface) while the other two were at a height of 1.1 m.

4.4.2 Results and Discussion

In both years few aphids were caught in the traps.

Comparison of Trap Types

None of the trapping methods compared in 1992 for monitoring crop colonisation by the asexual portion of the population gave larger samples of winged aphids than did the 12.2 m and 1.5 m suction traps (Table 1) and more grain aphids were caught in the 1.5 m suction trap than in the 12.2 m. The fishing line trap, the yellow water trap, the yellow sticky trap and the 30 cm suction trap were unsuccessful in increasing the sample size of the grain aphid. The 1.5 m trap may be a method of increasing the sample size in the autumn, however further testing in different regions would be required to validate this suggestion. Alternatively, some form of attractant trap would increase the sample number. Although the grain aphid has been reported to be colour sensitive (A'Brook, 1973) the yellow traps used in this trial were not sufficiently attractive to the grain aphid to serve as a practical alternative.

At Starcross a manual crop search was carried out on 13.10.92, and at Rothamsted on 12.10.9 and 22.10.92 but none at Leeds as no aphids were were found on the sites despite regular sampling (Table 2). At Starcross 15 winged grain aphids were collected from 32 m^2 giving a density of 0.46 aphids m^{-2}, and of these 7% were carrying BYDV. At Rothamsted there was a higher density of grain aphids than at Starcross, with 1.6 aphids m^{-2} on 12.10.92 and 0.74 aphids m^{-2} on 22.10.92, and a higher percentage were carrying virus than at Starcross (33 and 26% respectively). No bird-cherry aphids were found at Starcross, and at Rothamsted densities were lower than those of the grain aphid. On 12.10.92 there were 0.62 aphids m^{-2} with 2.5% carrying virus, and on 22.10.92 0.05 aphids m^{-2} but none contained BYDV. Although this is a method of estimating the density of winged aphids in the crop at a given point in time, it is not a practical sampling alternative on a regular basis due to the many hours involved.

Pheromone Lures

Pheromones were very successful in increasing the sample size of the male proportion of the population. The mixture of nepetalactol and nepetalactone was the strongest male attractant with more caught when chemicals were released from glass phials (11 aphids) than from the polythene phials (2 aphids) (Table 3).

5. GRAIN APHID MOVEMENT WITH REFERENCE TO BYDV IN THE SPRING AND DIRECT APHID DAMAGE IN THE SUMMER

5.1 Contribution of Wingless Aphids to the Spread of Virus on Spring-Sown Cereals

Two experiments were designed to investigate the spread of virus on spring-sown cereals. First, in a controlled field experiment, spread of virus by nymphs of a winged coloniser was compared with spread by a mixed population of wingless adults and nymphs. The aims of the experiment were to assess any differences in the proportion of infected plants surrounding a point of initial infection, and to determine whether the probability of a plant being infected is based on the proportion of neighbouring plants which are infected.

Second, in an uncontrolled field experiment, the pattern of naturally occurring infection was described over time. The aims were to determine the distribution of infection caused by colonising aphids and how this pattern changes with time.

5.1.1 Materials and Methods

Spread of BYDV in a Controlled Field Experiment

Aphids were cultured as described in 4.1.1.

Experimental Design

The experiment was done in a field of barley (cv. Alexis) sown at a row spacing of 12 cm on 29 March 1993 at Rothamsted. Twelve plots 84 x 70 cm were each divided into a 7 x 7 grid, marked out using canes and baling twine perpendicular to the direction of drilling, such that seven rows of barley ran through it. Each box in the grid contained a 10 cm length of a single row of barley (Figure 14). The plots were arranged in four blocks each with two treatments and an untreated control. In the first treatment eight virus-infected wingless grain aphids were placed in clip-cages on each of four plants in the central grid-box of each plot. After three days clip cages were removed and the adult

aphids and their nymphs released. In the second treatment eight adult virus infected wingless grain aphids were confined in clip-cage at the centre of each plot as above, and after three days clip cages were removed, the wingless aphids killed and the nymphs released.

Plant samples were taken at the time of aphid release on control plots (GS 12) and three times subsequently on all plots at intervals of approximately one week (GS 20-21, 22-23, 31-32). The upper 3 cm of the most recently emerged leaf was cut from plants within each 12 x 10 cm grid-box. All leaves from each box were pooled to give a single sample. These samples were assayed for BYDV using monoclonal antibodies in a TAS-ELISA.

Spread of BYDV under natural conditions

A field of barley (cv. Alexis) was sown on 28 April 1993. Plant samples were taken as described for the previous experiment, along three transects, in order to identify foci of infection around which secondary spread might occur. Four plots each 84 x 70 cm were divided into a grid of 7 x 7 marked out as above, with a focus of infection at their centre. Four further plots were marked as paired control plots having no such centre of infection. Plant samples were taken from all boxes within the plot three times, at intervals of approximately one week and growth stages similar to the previous experiment. Samples were assayed using TAS-ELISA.

For both experiments the proportion of boxes which had become infected since the previous sample was calculated. These proportions were analyzed using a logistic regression model. The means have been back-transformed for presentation.

Second, the probability of plants within a box becoming infected between two time points t_i an t_{i+1} (i = 1,2) was calculated based on the number of neighbours which were infected at time t_i. This was calculated as n/r where r = the number of boxes infected between t_i and t_{i+1} which were surrounded by N infected neighbours at time t_i and n = total number of boxes surrounded by N infected neighbours at time t_i. The probability of infection was tested for its dependence on the number of infected neighbours for each of the treatments.

5.1.2 Results and Discussion

Results from the first experiment showed that over a given period of time a greater proportion of plants were infected by populations of wingless adults and nymphs, than by nymphs alone (Figure 15). Under natural conditions, control and treatment plots were infected rapidly with an intense primary infection of virus, and as a result it was not possible to follow the spread of virus from an individual focus over time. Spread of virus in the plots was shown to increase with time, at a rate that would indicate that there were large populations of aphids already in the crop.

Data showed that the probability of a plant being infected is dependent on the total amount of virus surrounding it, and did not show a greater probability of infection from neighbours within a row than from an adjacent row.

Primary infection is thought to account for most BYDV in the crop during the spring with a relatively small contribution being made by wingless aphids already on the crop. This is in contrast to the situation in the autumn when secondary spread by wingless aphids is of critical importance. Results from this experiment show that in situations where large numbers of aphids are present in the crop in the spring, they make a significant contribution to the spread of virus through the crop, and should therefore be accounted for when making predictions of BYDV epidemics.

5.2 Control of Aphids and BYDV in Spring-Sown Cereals

This section describes a field experiment at Rothamsted, designed to examine the effects of sowing date and insecticidal spray date on aphid colonization and the incidence of BYDV in spring-sown barley. During the experiment the numbers of bird-cherry aphids found were negligible and have not been presented.

5.2.1 Materials and Methods

Barley (cv. Alexis) was sown in mid-March and mid-April in plots 3 x 10 m. Treatment plots were sprayed with pirimicarb at 140g AI ha^{-1} in 300 l water, approximately 10, 20 or 30 days after crop emergence for each sowing date, in order to protect the crop from viruliferous aphids prior to GS 30. Sprays were applied using a gantry fitted with Lurmark 04-F110 Jets at a pressure of 2.0 bar driven at 5 km h^{-1}. Treatments consisted of single sprays and each possible combination of these sprays, making 7 treatment plots for each sowing date and 1 control plot per block. Three replicate blocks were used. Throughout crop development aphid populations were assessed at intervals of seven to ten days, weather permitting, recording aphid species, morph and developmental stage. Prior to GS 30, samples were taken of aphids on all plants on ten randomly selected 0.5 m lengths of row, and after GS 30, 100 randomly selected shoots were examined. When populations exceeded two aphids per shoot on control plots, the number of shoots examined was reduced to 50. The number of aphids per plant or the number of aphids per shoot, was then calculated.

The aerial density of migrating aphids was measured using the Rothamsted 12.2 m suction trap situated approximately 1 km from the experimental site. Weekly samples from this trap were counted and identified to species (Woiwod *et al.*, 1984) as a measure of potential crop colonization.

Virus levels in the crop were assessed every second week following GS 30 by noting the area of each plot showing BYDV symptoms. Plots were harvested separately by combine and grain yield measured.

5.2.2 Results and Discussion

Aphid population development on the crop followed closely the timing and patterns of aerial aphid immigration and emmigration (Figure 16). Migration was late both in time and in relation to crop emergence and development, and a large proportion of the migration

and crop colonisation occurred after GS 30, and hence after sprays had been applied. As a result there were no significant differences in aphid number among treatments.

1992 was preceded by a harsh winter and no infective aphids were caught in suction traps prior to the end of June. This was reflected in the negligible levels of virus seen in the plots.

In early-sown plots yield was significantly greater than in late-sown plots due to the longer growing season available (Table 4).

5.3 Contribution of Overwintering Aphids to Population Development in the Spring

The following experiments were designed to compare the relative importance of overwintered aphid populations present in winter wheat, with aphids colonising during the spring, in the development of peak summer aphid populations. The experiment was done in a comparable way at Rothamsted and Kirton.

5.3.1 Materials and Methods

Winter wheat (cv. Mercia) was sown on 16th October 1991 and 9th October 1992, in plots 9 x 9 m at Rothamsted. There were three treatment plots and an unsprayed control plot, replicated four times and arranged randomly in each of four blocks. To avoid edge effects, there was an additional dummy plot at each end of the block randomly assigned a treatment but not assessed. Plots were kept free of insecticide during the winter to allow survival of resident overwintering populations. In the spring pirimicarb sprays (Aphox: 140 g AI / 100 l) were applied to treatment plots as follows:

1) single spray in late March to remove overwintered aphid populations (M);
2) spray in March, at the beginning of immigration (after the first winged aphid was caught in the Rothamsted 12.2 m suction trap) and at 10 days intervals until GS 61 (MI1);
3) spray in March, at the beginning of immigration, and at 10 day intervals until GS 73 (MI2).

Aphid populations were assessed in March prior to the first spray to measure the numbers of the overwintered grain aphid, rose-grain aphid and bird-cherry aphid, 10 days after the first spray and then after the time of the first grain aphid catch in the suction trap (10th May 1992, 24th April 1993) at intervals of a week to 10 days until the aphid populations crashed. Prior to stem elongation six 0.5 m row lengths were searched and after stem elongation 100 shoots were searched per plot. The number of each species and developmental stage were noted. In samples of 0.5 m row lengths the number of plants was also counted. When aphid numbers exceeded 10 per shoot in control plots the sample size was reduced to 50 shoots per plot. At harvest combine yield measurements were taken. Weekly counts of aphids from suction traps were used as a measure of aphid migration. Measurements of average daily windspeed and rainfall were obtained from a meteorological site at Rothamsted.

The number of aphids per plant (prior to stem elongation) and the number of aphids per shoot (after stem elongation) were calculated. Analysis of variance was done on numbers of aphids per 10 shoots ($\log_{10}(n+1)$) to evaluate the effects of insecticide treatment on aphid population development. As numbers of the bird-cherry aphid throughout the season in both 1992 and 1993 were minimal, this species was not included in the analysis.

5.3.2 Results and Discussion

Pirimicarb has a persistence of approximately 10-14 days. Differences in the number of aphids between treatments as a result of pirimicarb sprays were the result of direct pest kill and the subsequent delay in population development.

At Rothamsted the spray late in March significantly decreased populations of the grain aphid in both years (Figure 17 and 18) although the difference between populations on control and treated plots did not persist through the whole season in 1993. No rose-grain aphids were present in the crop prior to this spray, and it therefore had no impact on this species (Figure 19 and 20). The contribution of overwintering aphids to the total size of the population was greatest early in the season. At this time the potential for aphids to damage the crop directly is small, but in their capacity as vectors of barley yellow dwarf virus they are of great significance because the crop is most susceptible to infection at this time. Later in the season the contribution of overwintered aphids to total numbers varies. In 1993 the contribution made by overwintered aphids was surpassed by the migration of aphids into the crop, whereas in 1992 they made a significant contribution to peak abundance.

At Kirton lodging of the crop early in June 1992 prevented samples being taken throughout the season making interpretation of results in this year difficult as peak populations were not sampled. Despite this there was evidence that plots treated with a spray prior to the beginning of migration had smaller populations of both grain aphids (Figure 21 and 22) and rose-grain aphids (Figure 23 and 24) than in control plots in both years early in the season. In 1993 peak populations on control plots were significantly greater than on plots sprayed prior to immigration.

A spray applied at the beginning of immigration was not effective in reducing populations of either species in either year for any length of time, at Rothamsted or Kirton.

Sprays after the onset of immigration and prior to growth stage 61, were effective in controlling aphid populations in both years for both species, for the 10 day period required between sprays. These sprays only reduced peak populations of the grain aphid significantly in 1992 at Rothamsted, but were effective for both species at Kirton where three sprays were applied over a three week period. This strategy of spraying would probably only be useful in reducing damage if particularly large populations were developing in the crop early in the season.

The final spray treatments were very effective in reducing peak abundance during the two years under study. This is largely because older crops are less attractive to colonising aphids and thus despite the large numbers of winged aphids in the suction trap samples, they make a much smaller contribution to numbers in the crop. In cases where

the peak abundance is reached while the grains are still being formed, these sprays could be vitally important. It should be noted, however, that the efficacy of such sprays will depend on other factors including the number of aphids present in the crop, (Oakley and Walters, 1994) and any spraying decisions should be made with this in mind.

In both years aphid populations did not reach thresholds for economic damage and this was reflected in a lack of significant difference between combine yields at both sites.

6. DISCUSSION

This project has provided data on various aspects of movement by grain aphids which will facilitate the development of more accurate forecasts for BYDV epidemics and for direct crop damage by aphids.

Field experiments assessing movement by aphids and spread of BYDV during the winter indicated that movement and virus spread by the grain aphid is greater than that by the bird-cherry aphid, probably due to its greater survival under winter conditions. The interaction between winter conditions and crop growth stage on successful virus transmission and virus development in the plant also appear to be of crucial importance in disease progression during the winter.

Experiments to examine the relative importance of abiotic and biotic factors in determining movement by aphids produced clear results. Aphid dispersal increases with increasing aphid density, such that high densities are a strong stimulus for dispersal. At low aphid densities (2 per plant) as might occur on crops during the winter months, aphid density is not likely to be an important dispersal factor. Plant spacing influenced both the distance moved by aphids and the proportion of aphids dispersing. This may be of considerable importance in assessing movement along rows as opposed to across rows, particularly during the early stages of crop growth before leaves from plants in different rows are touching. Aphid movement by adults and IV instars is greater than I -III instar nymphs, emphasizing the importance of accounting for population structure as well as population size in estimating dispersal. The considerable difference in movement by the bird-cherry aphid and the grain aphid, suggests that data on movement by one species should not be directly extrapolated to another. Estimates of dispersal should however also account for the differential effects of environmental conditions on the 2 species.

The potential importance of weather in determining aphid dispersal was shown. Sudden leaf disturbances caused by wind gusts and rain droplets increased the proportion of aphids which moved and the distance travelled, although wetness alone did not. The experiments described were done under laboratory conditions, with treatments often being more extreme than might be expected in climates such as that experienced in the U.K. However, they have demonstrated that these are factors of potential importance and should be examined more closely under field conditions.

A comparison of trapping methods in the autumn showed that the number of grain aphids migrating during the autumn is small and the 1.5 m and 12.2 m suction traps are the best method to date for monitoring this colonisation. Differences in the relative number of the grain aphids and the bird-cherry aphids on crops during the winter appear to be due more to differential survival and reproduction than differences in crop colonisation (Tatchell *et al.*, 1994). The problem still remains, however, that the sample size of migrating aphids in the autumn is small with little variation between years, making estimates of crop colonisation difficult. The 1.5 m suction trap may improve on the sample size, although further sampling in different regions would be needed to ascertain this. Alternatively some form of attractant trap may solve the problem. The accuracy of estimates of crop colonisation and of primary BYDV infection in the autumn, is crucial to the development of accurate forecasts of BYDV epidemics.

Experiments investigating the contribution of wingless aphids to the spread of virus during the spring showed that in situations where large populations of wingless aphids are present on the crop they make a significant contribution to virus spread. It was also shown that wingless adults spread the virus more quickly and to a greater number of plants than nymphs.

Control of BYDV in the spring was shown to be difficult, supporting previous work in this area (Jenkyn and Plumb, 1983; Plumb *et al.*, 1990). Early-sown crops are at less risk from BYDV infection than those sown late and insecticidal sprays just prior to GS 30 may be effective in reducing aphid populations and decreasing the levels of virus. These effects are short-lived due to continued crop colonization, but after GS 30 this is of less significance. The effectiveness of these sprays, and correct timing of them, depends upon the level of the virus present in winter crops and the timing of aphid migration relative to crop development. The timing of the start of aphid migration can now be predicted accurately from winter temperatures (Harrington *et al.*, 1990). However, a detailed knowledge of virus levels during the winter is still needed to determine years in which insecticidal treatment just prior to GS 30 might be effective in reducing virus levels and hence crop loss.

The development of an accurate model on which to base forecasts of aphid movement and virus spread during the winter, based in part on data presented in this report, will be critical in providing estimates of BYDV risk to both autumn- and spring- sown crops. Such a model will also provide information on the most effective timing of spray applications in relation to the rate of aphid development on the crop. The most effective timing being when the first generation of wingless aphids on the crops reach the fourth instar and become more dispersive. On later sown crops the model will also provide useful information on aphid survival to this point and allow the omission of unnecessary sprays where survival is low as well as suggesting where a high survival rate has increased risk to the point where an aphicide spray is required.

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Table 1

The number of grain aphids caught in each trapping period in a comparison of trapping methods in 1992

Date (Week Ending)	1.5 m Suction Trap	12.2 m Suction Trap	Sticky Cylinder Trap	Fishing Line Trap	Yellow Water Trap	30 cm Suction Trap
11/9	0	1				
18/9	0	0				
25/9	1	8				
2/10	1	0	4	0	0	0
9/10	6	1	0	0	1	0
16/10	3	0	0	0	0	0
23/10	3	0	0	0	0	0
30/10	0	0	0	0	0	0
6/11	0	0	0	0	0	0
13/11	1	0	0	0	0	0
20/11	0	0	0	0	0	0
27/11	0		0	0	0	0
4/12	0					

Table 2
Winged aphids collected during the manual crop sample at Rothamsted and Starcross in 1992

Site	Date	Species	Number of Aphids	Density (aphids m^{-2})	% Carrying BYDV
Rothamsted	12.10.92	Grain aphid	104	1.6	33
Rothamsted	22.10.92	Grain aphid	55	0.74	26
Starcross	13.10.92	Grain aphid	15	0.46	7
Rothamsted	12.10.92	Bird-Cherry aphid	40	0.62	2.5
Rothamsted	22.10.92	Bird-Cherry aphid	4	0.05	0

Table 3

The number of grain aphids caught in each trapping period, in water traps with and without synthetic aphid sex pheromone lures at Rothamsted in autumn 1991.
L signifies aphids caught in traps placed just above crop height.

Date	Poly-Blank	Glass Blank	Yellow Trap	Glass Nepeta-lactone	Glass Nepeta-lactol	Glass Mix	Poly-Mix	12.2m Suction Trap
4. 10								0
7. 10								0
9. 10						1♂ L		2
11. 10								2
14. 10	1♂ L					6♂ 5L		2
16. 10				1♂ L			2♂ L	0
18. 10								0
21. 10								0
23. 10								0
25. 10								0
28. 10						4♂ L		0
30. 10								0
1. 11								1
4. 11		1♀ L						0
6. 11								0

Table 4

Combine Yield (tonnes hectare^{-1} at 85% D.M.) for Spring Sown Barley in 1992

Treatment	1992	
	Early	Late
Control	7.93	5.50
S1	7.89	5.48
S2	8.23	5.51
S3	8.10	5.42
S1S2	7.89	5.78
S1S3	8.12	5.62
S2S3	8.13	5.62
S1S2S3	7.92	5.72

S1 = Pirimicarb spray approximately 10 days after crop emergence
S2 = Pirimicarb spray approximately 20 days after crop emergence
S3 = Pirimicarb spray approximately 30 days after crop emergence

FIGURE 1

Mean Number of Grain Aphids Along Transects 1991/92

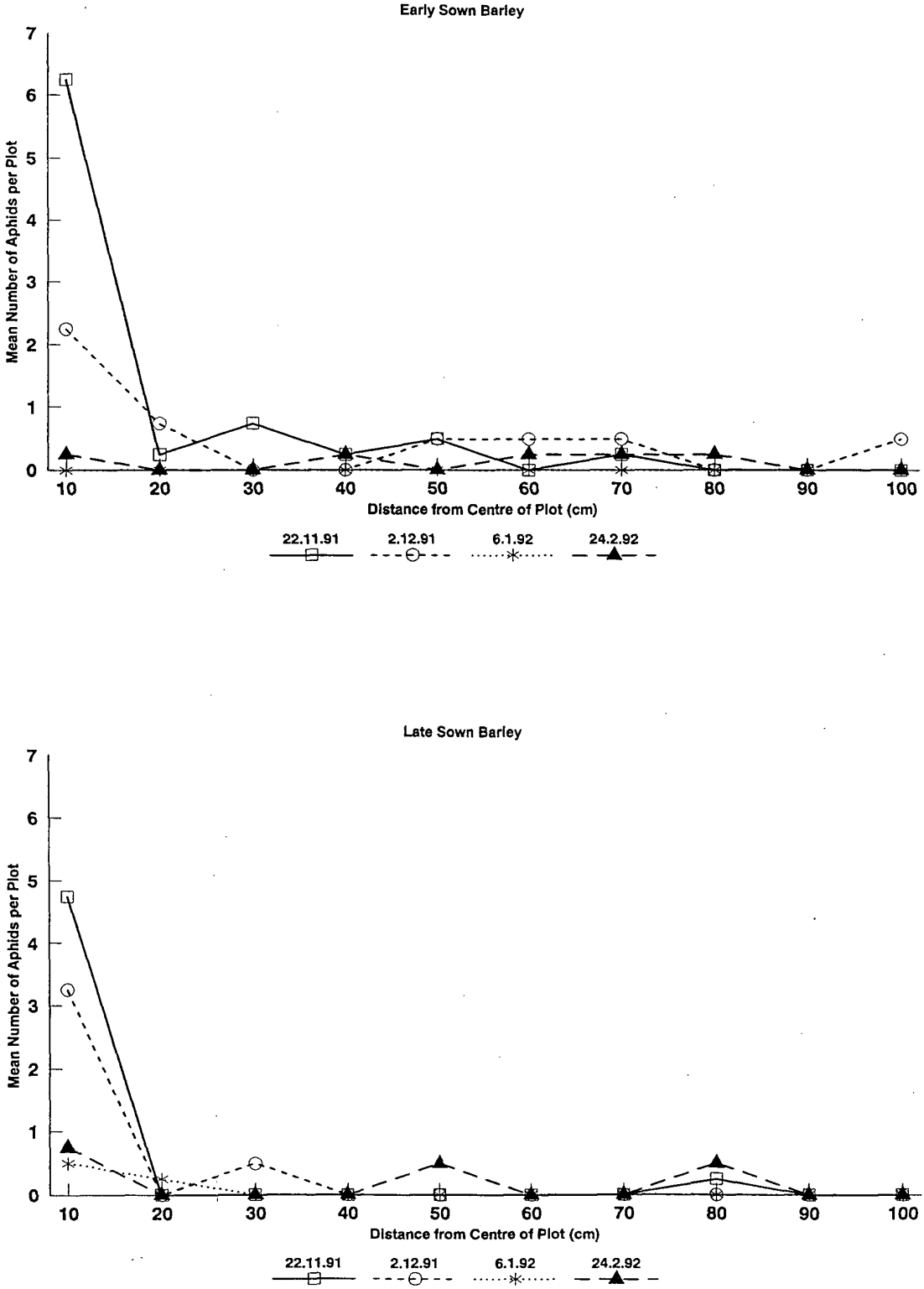
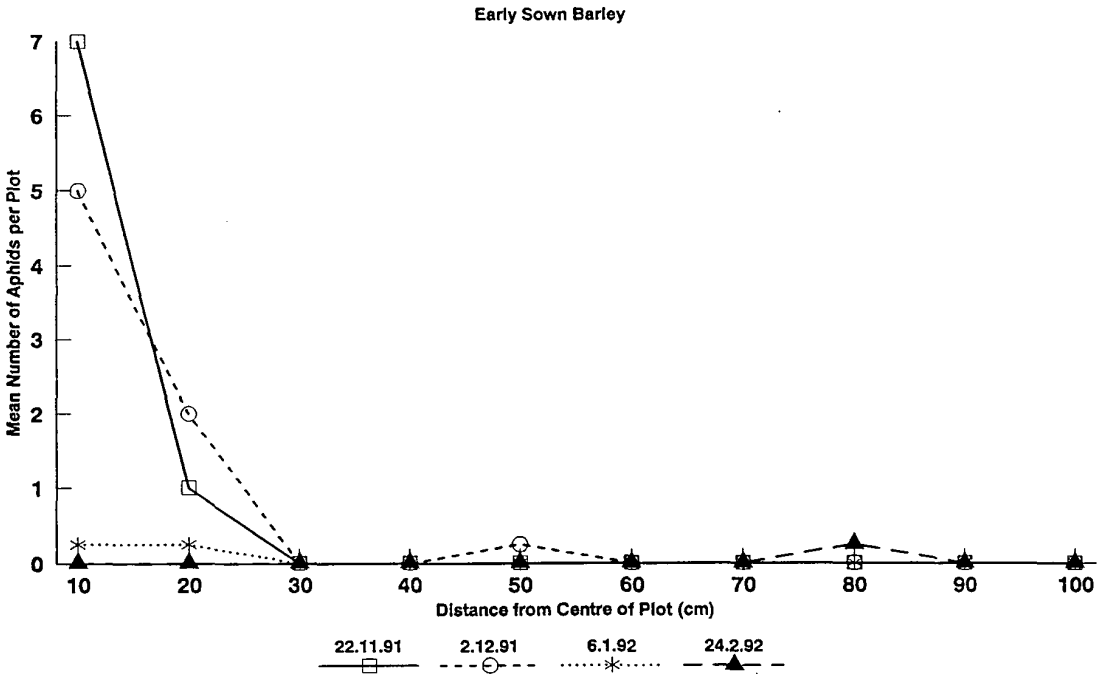


FIGURE 2

Mean Number of Bird-Cherry Aphids Along Transects 1991/92



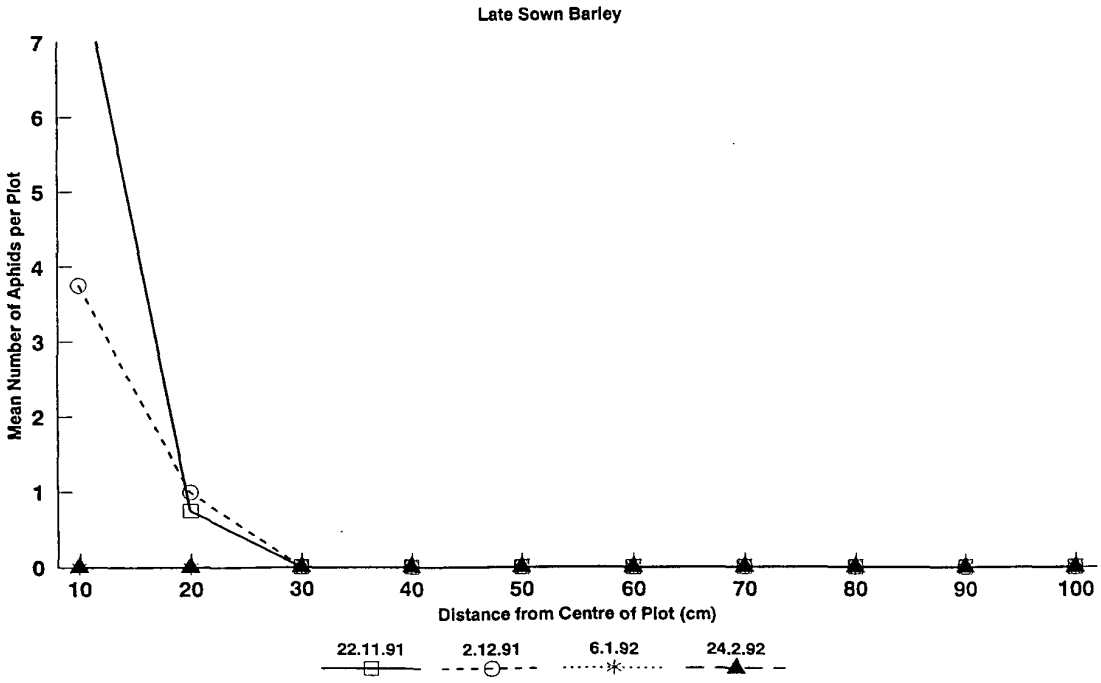
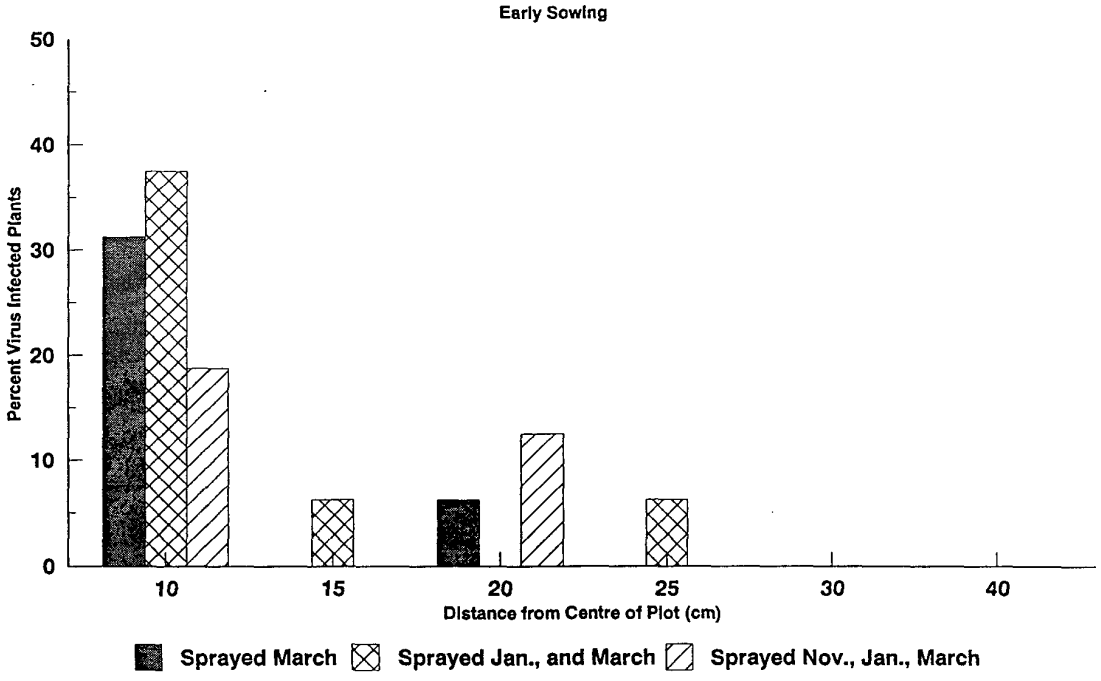


FIGURE 3

Percent Virus Infection by the Grain Aphid 1991/92



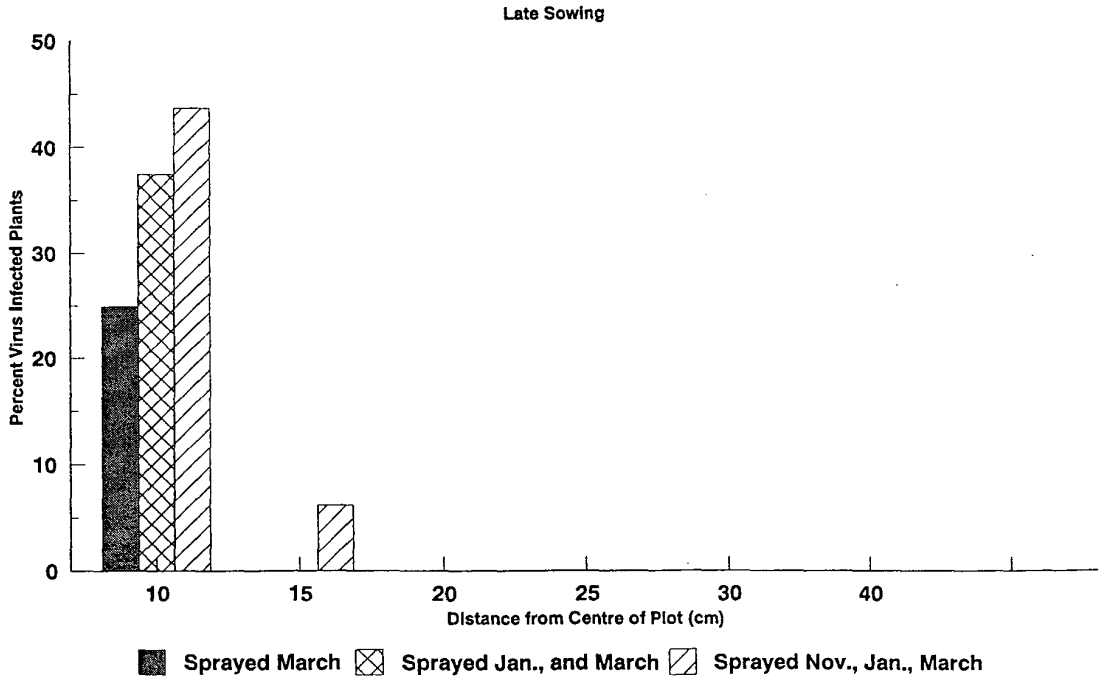
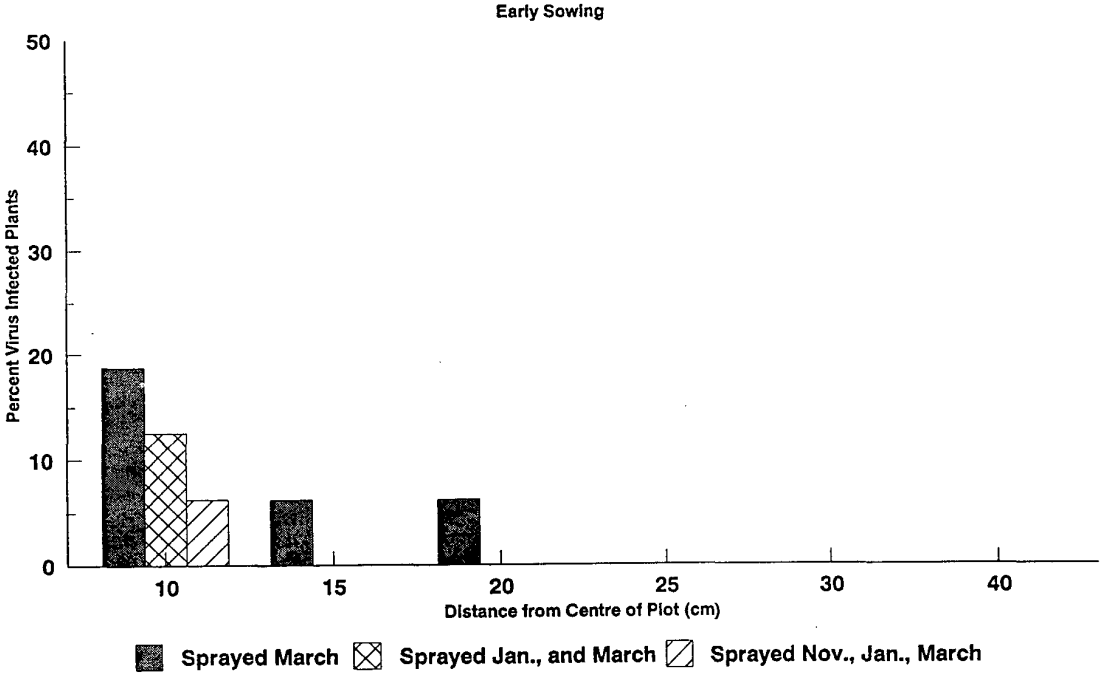


FIGURE 4

Percent Virus Infection by the Bird-Cherry Aphid 1991/92



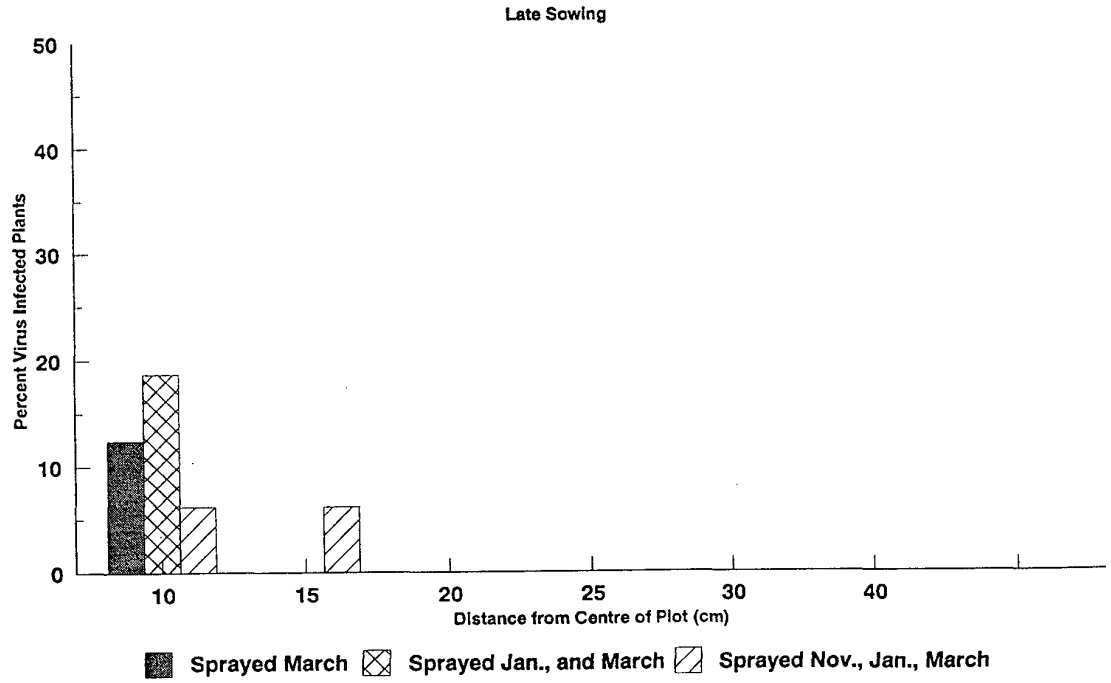
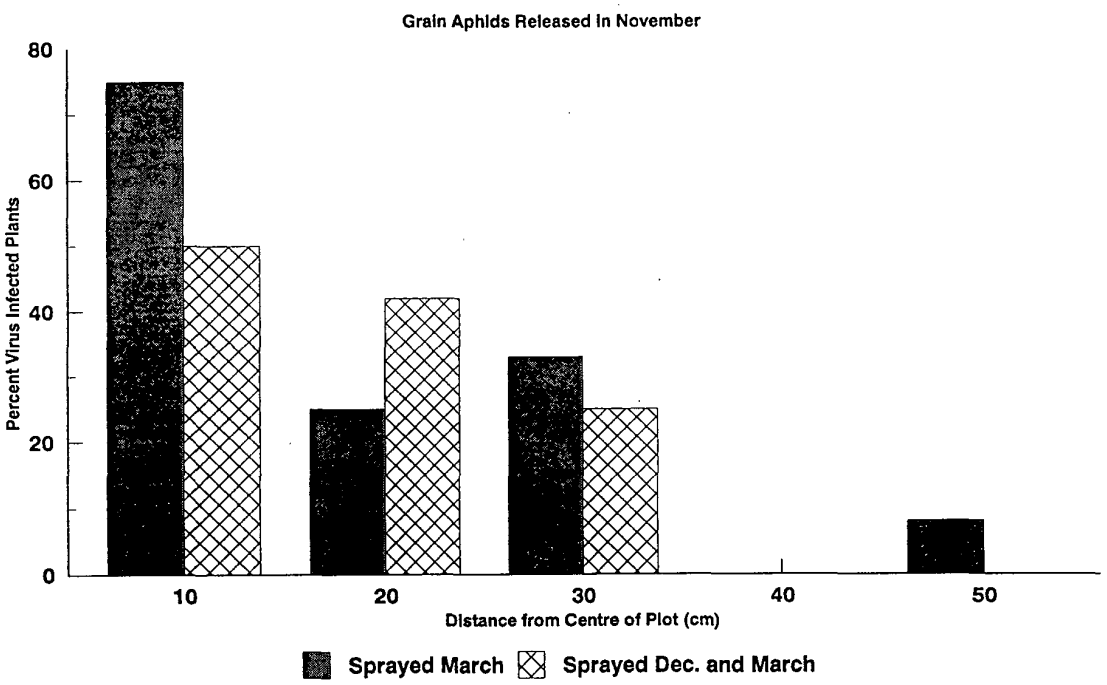


FIGURE 5

Percent Virus Infection by Aphids 1992/93



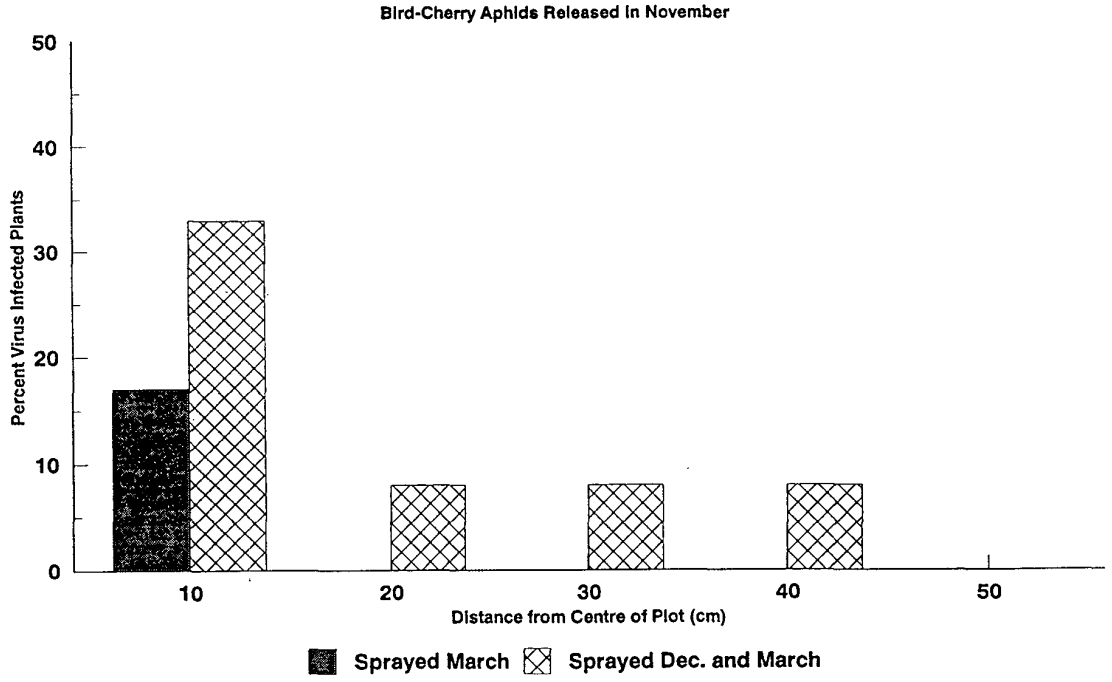


FIGURE 6

Effects of Aphid Density on Movement by Grain Aphids

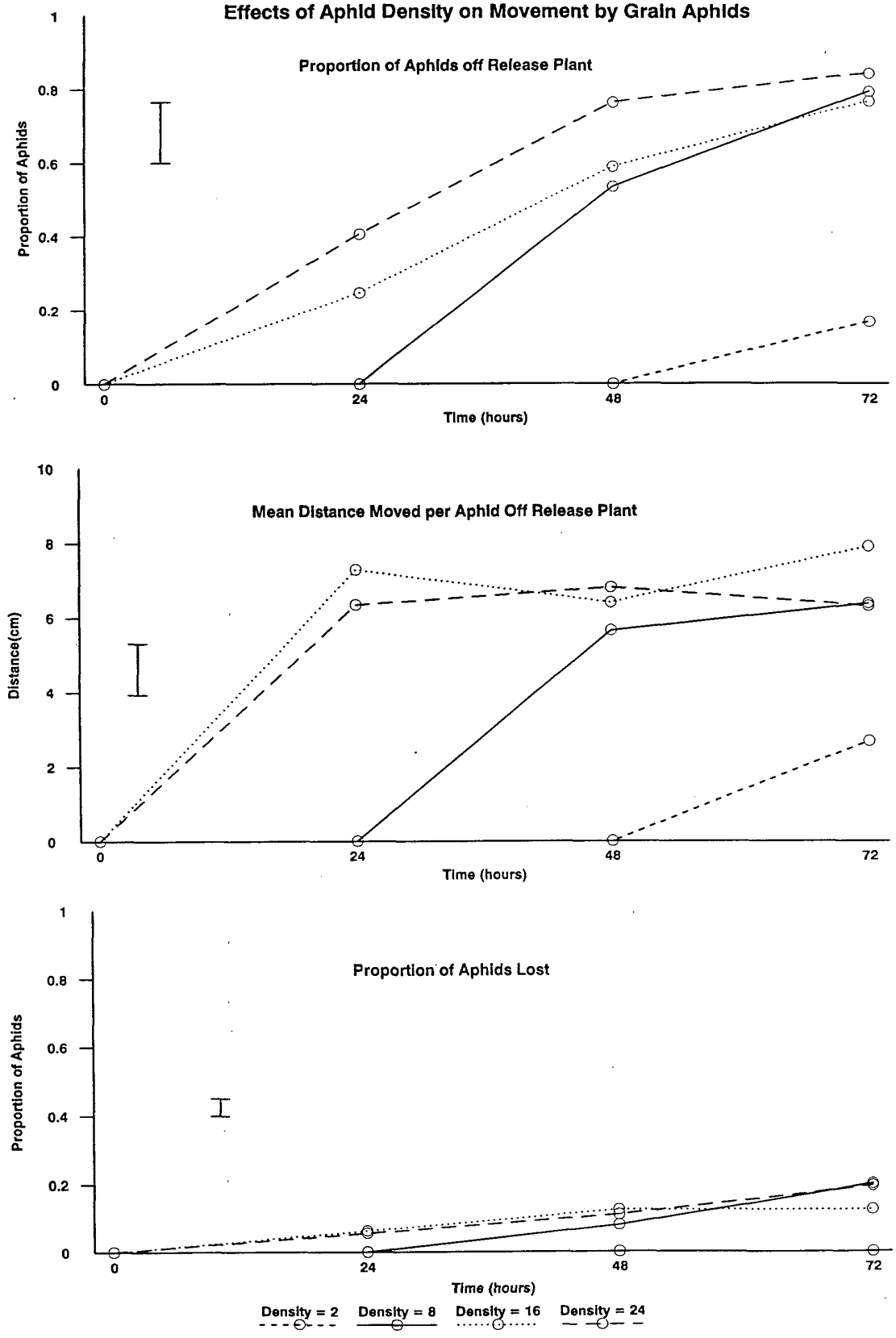


FIGURE 7

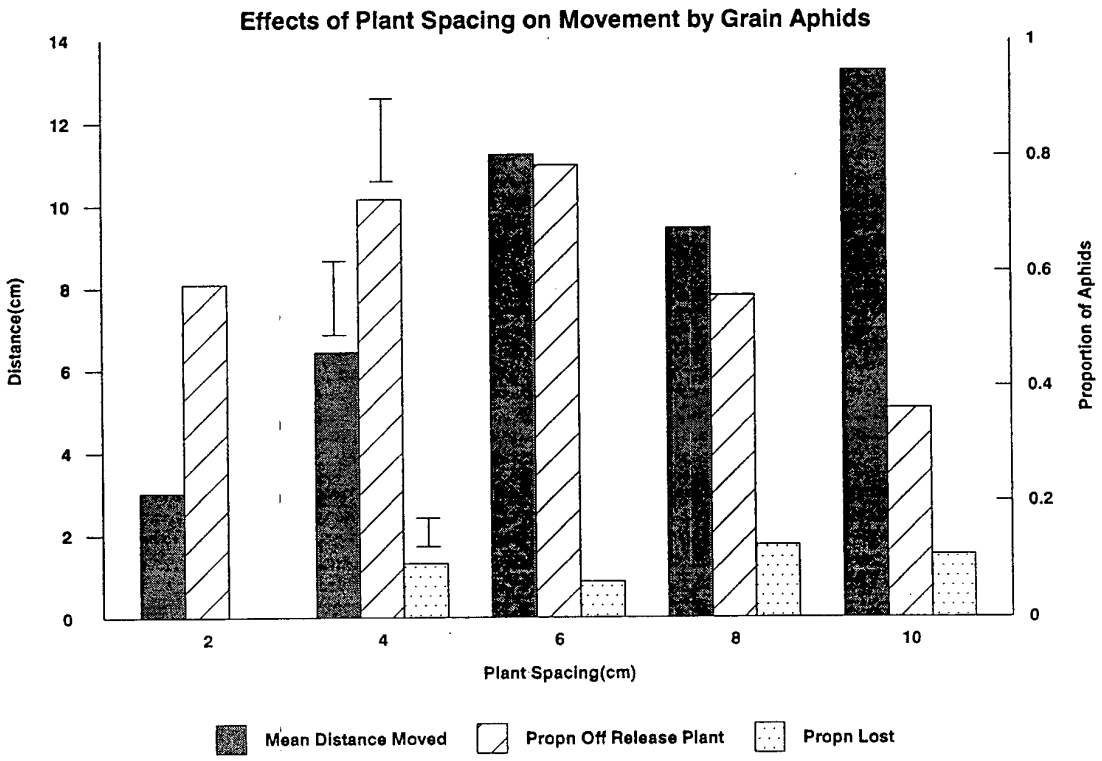

Effects of Plant Spacing on Movement by Grain Aphids
Distance(cm)
Proportion of Aphids
Plant Spacing(cm)
Mean Distance Moved
Propn Off Release Plant
Propn Lost

FIGURE 8

Effects of Aphid Age and Species on Aphid Movement

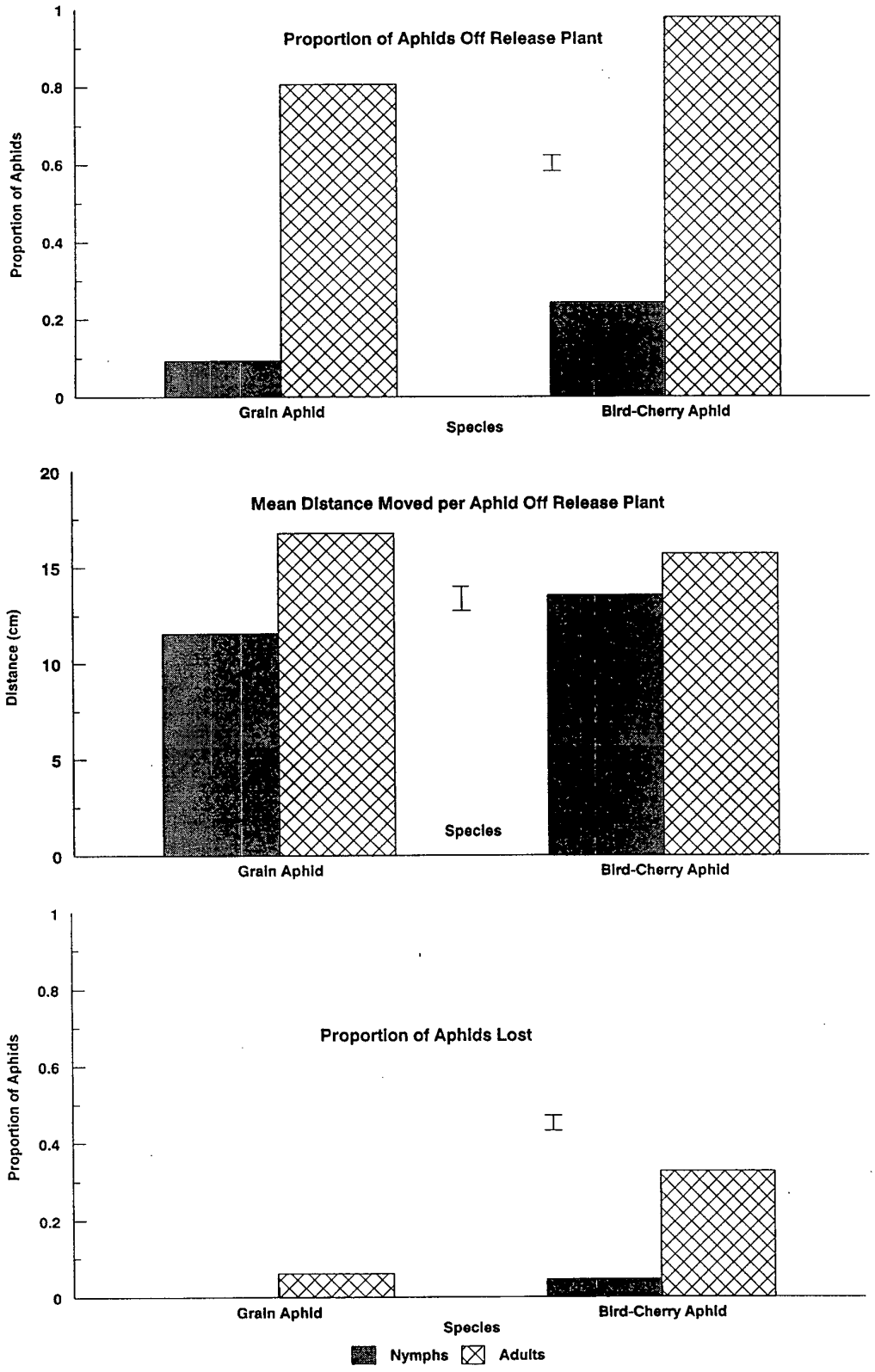


FIGURE 9

Effects of Wind on Movement by Grain Aphids

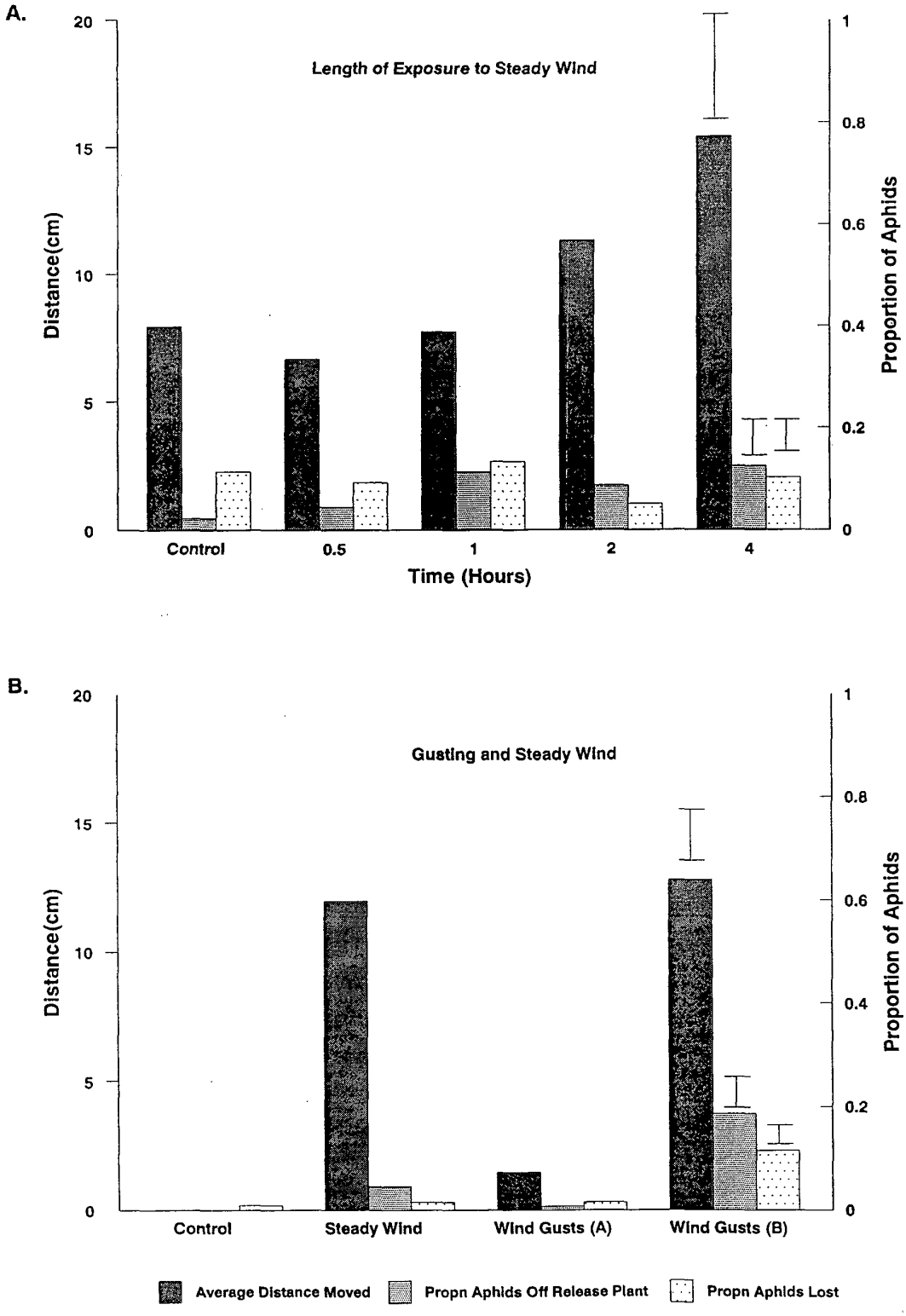


FIGURE 10

Effects of Rain on Movement by Grain Aphids

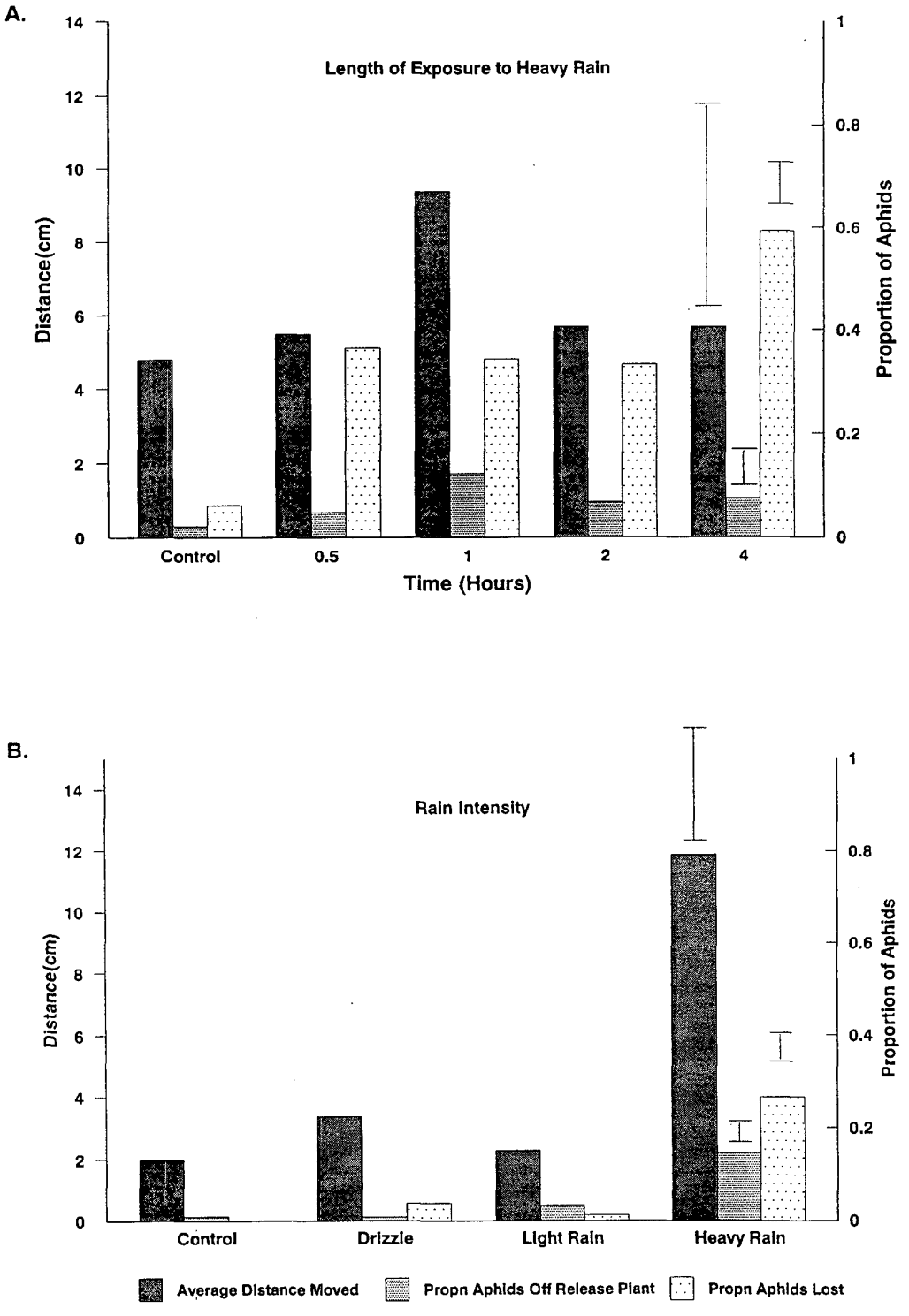


FIGURE 11

Effects of Wind and Rain on Movement by Grain Aphids

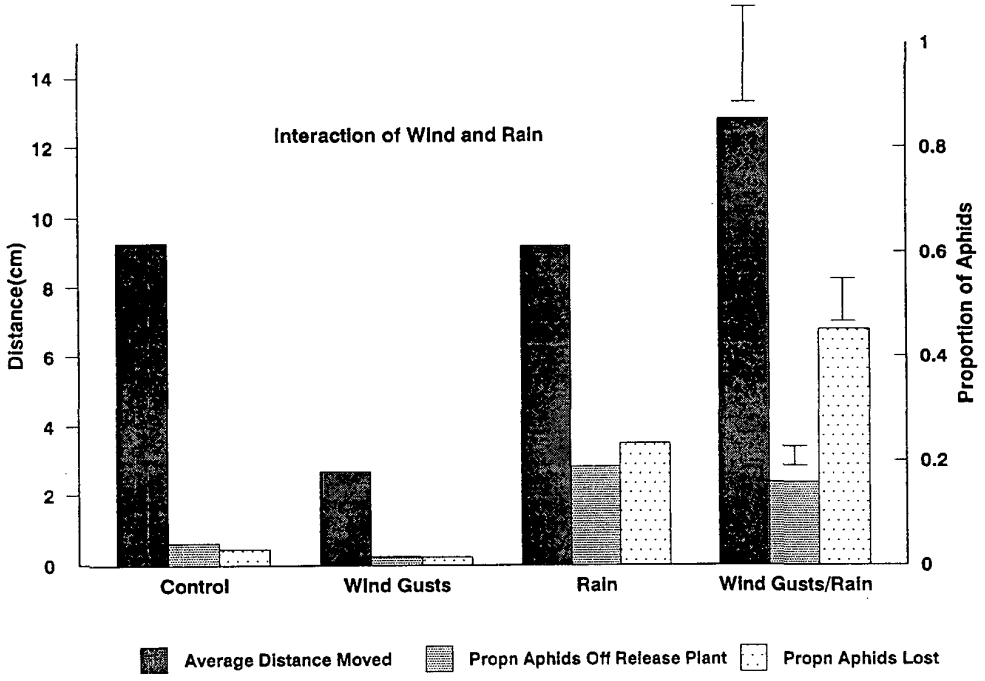


FIGURE 12

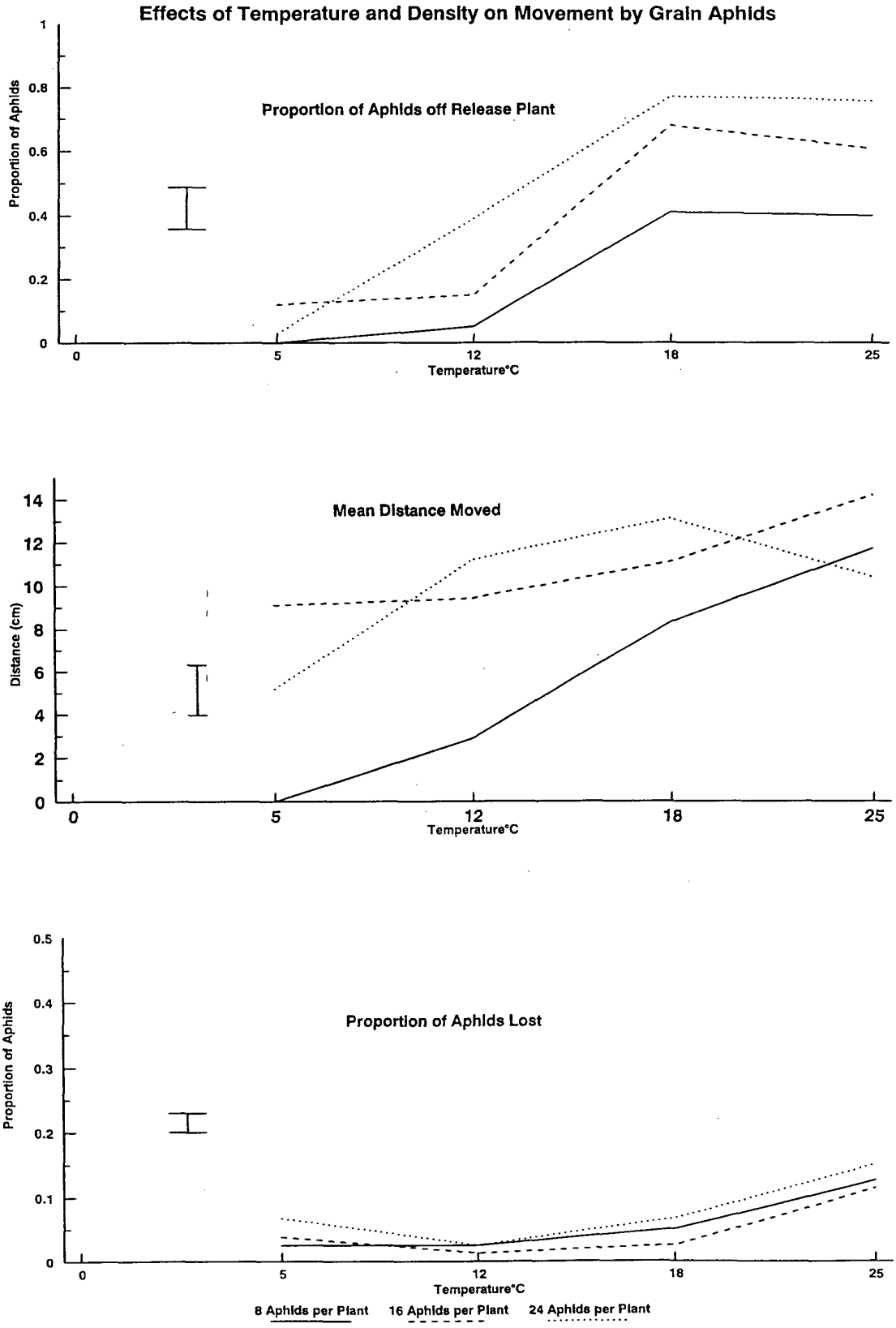

Effects of Temperature and Density on Movement by Grain Aphids
Proportion of Aphids off Release Plant
Proportion of Aphids
1
0.8
0.6
0.4
0.2
0
0
5
12
18
25
Temperature°C
Mean Distance Moved
Distance (cm)
14
12
10
8
6
4
2
0
0
5
12
18
25
Temperature°C
Proportion of Aphids Lost
Proportion of Aphids
0.5
0.4
0.3
0.2
0.1
0
0
5
12
18
25
Temperature°C
8 Aphids per Plant
16 Aphids per Plant
24 Aphids per Plant

FIGURE 13

Assembled Pheromone Trap

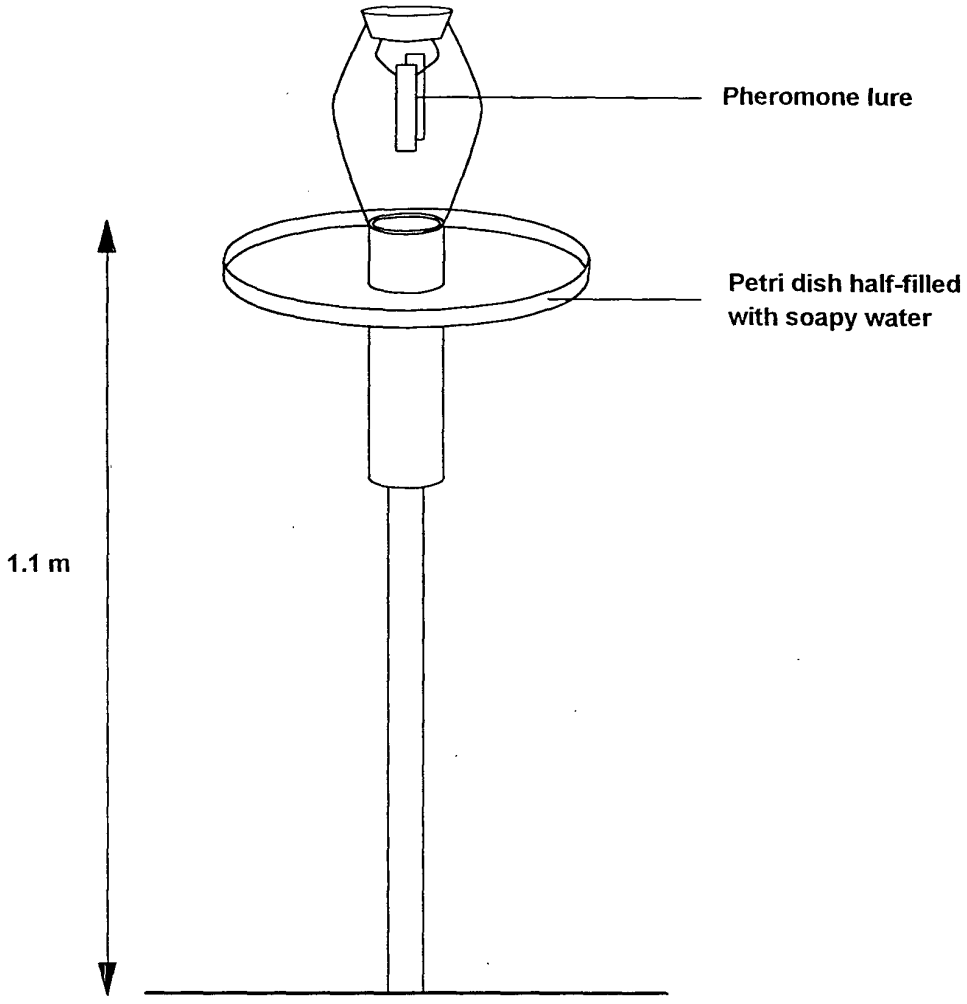


FIGURE 14

7 × 7 Grid of Barley to
Measure Secondary Spread

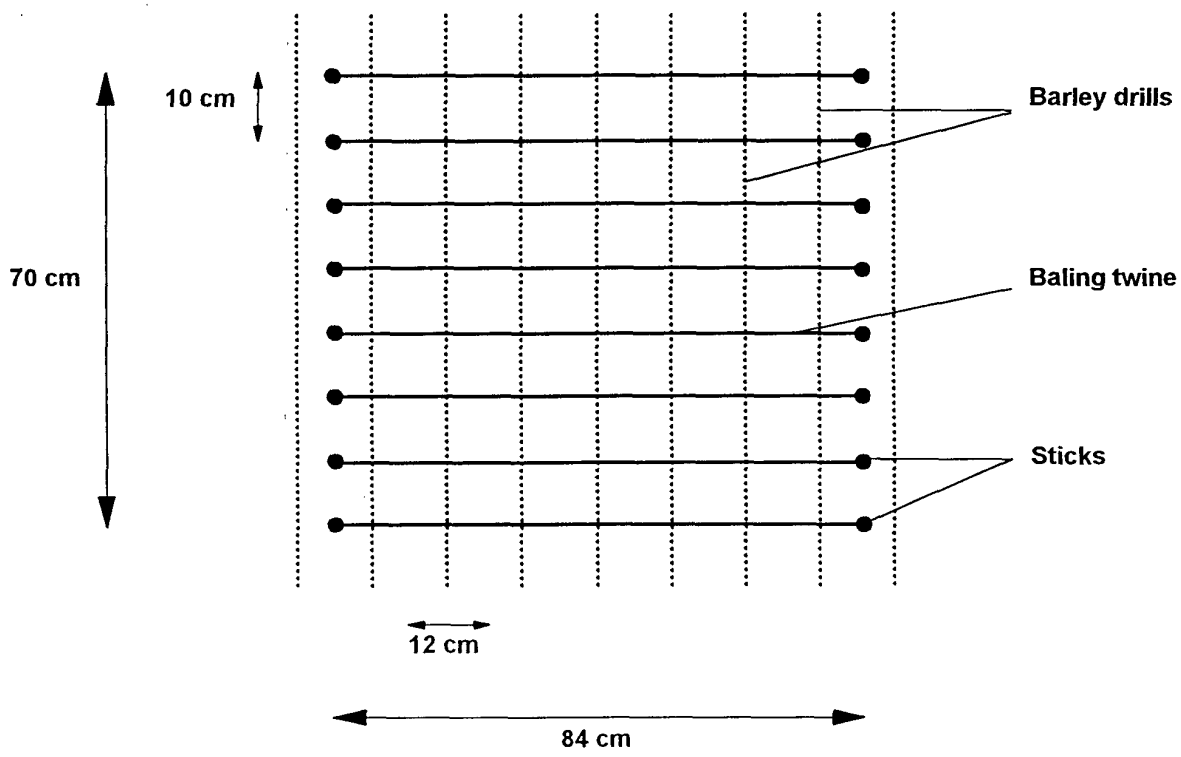


FIGURE 15

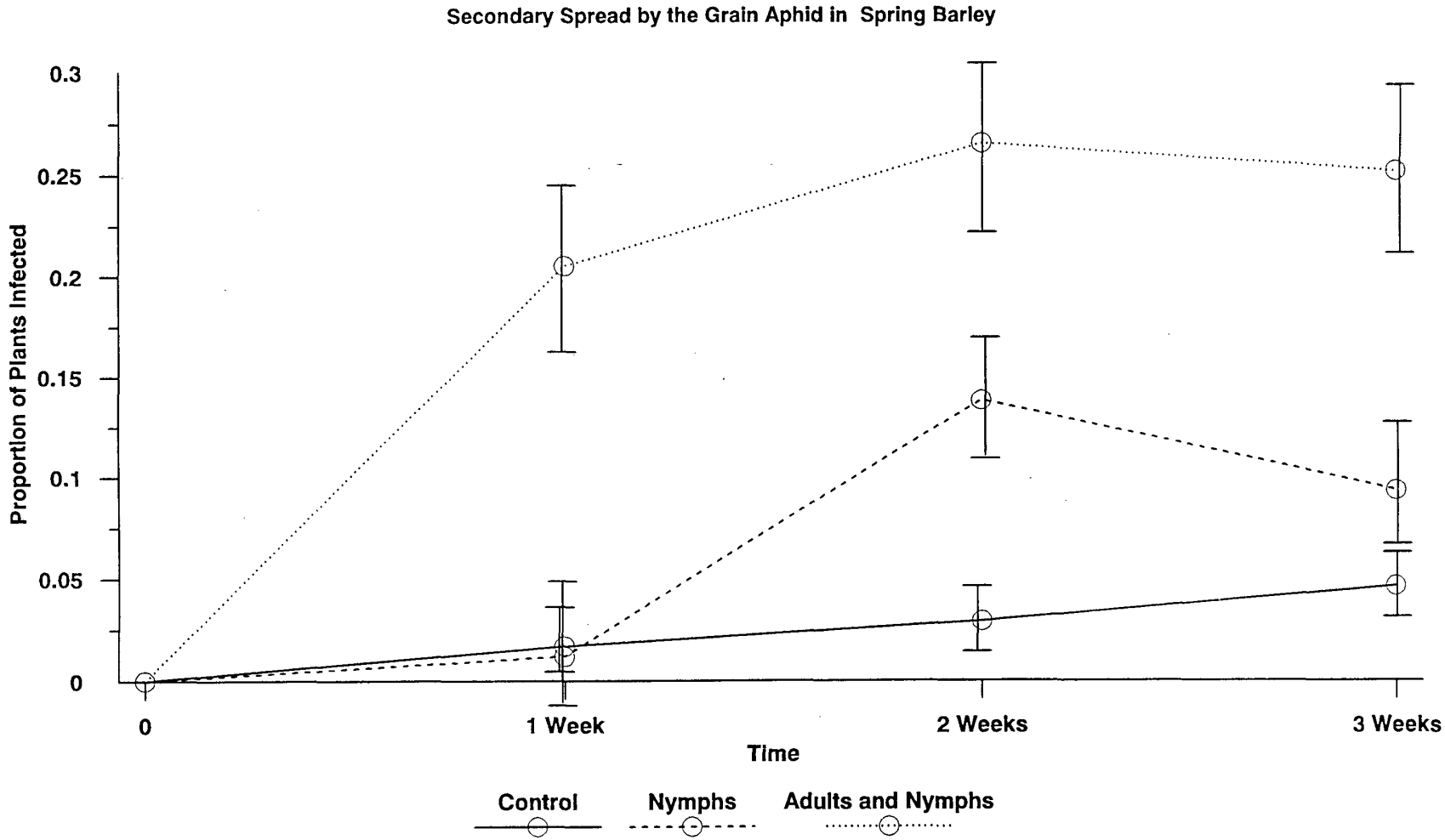

Secondary Spread by the Grain Aphid in Spring Barley
Proportion of Plants Infected
0.3
0.25
0.2
0.15
0.1
0.05
0
0
1 Week
2 Weeks
3 Weeks
Time
Control
Nymphs
Adults and Nymphs

FIGURE 16

Effects of Insecticidal Sprays on Number of Aphids in Spring Barley

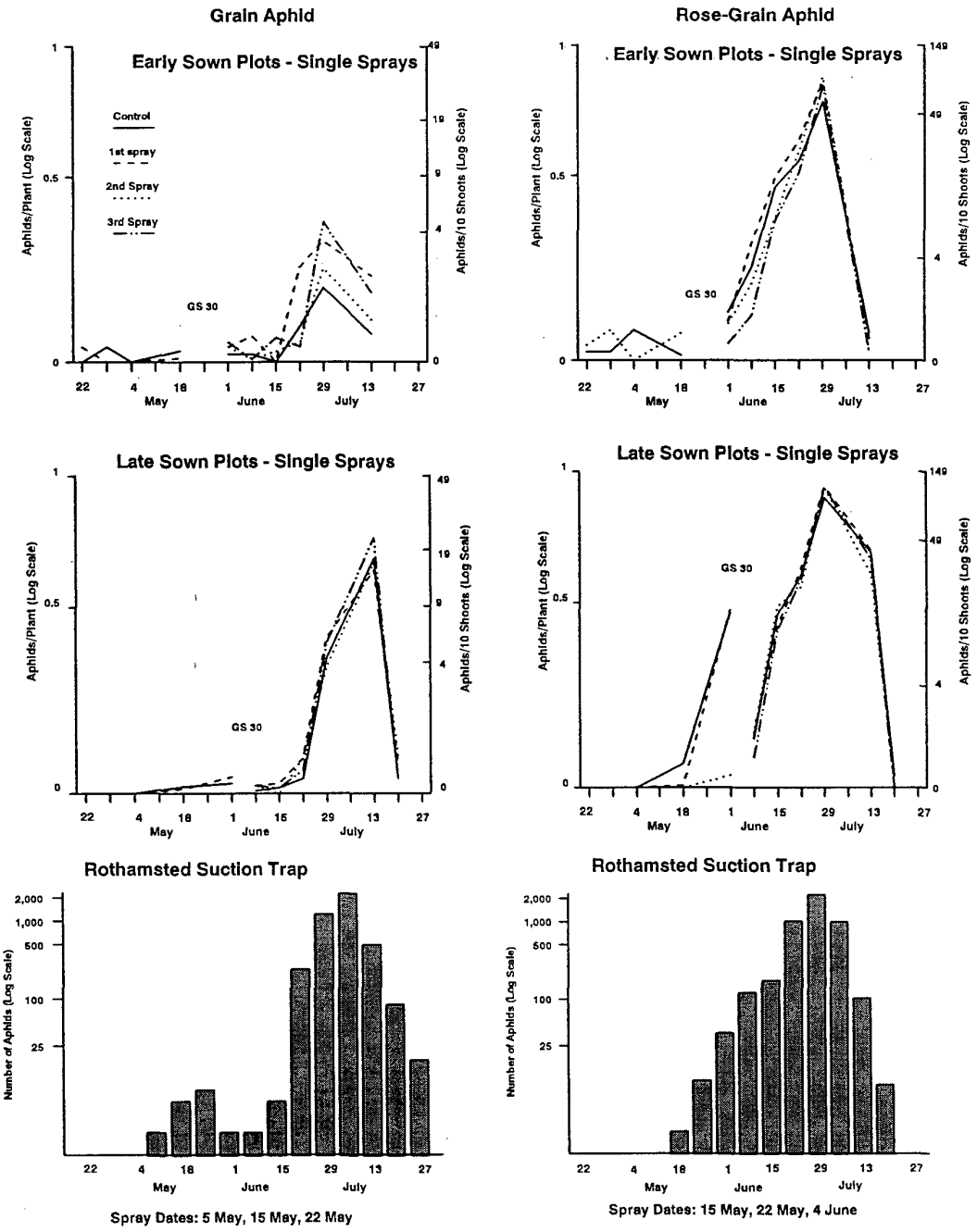


FIGURE 17

Rothamsted

A. Number of Grain Aphids on Winter Wheat during the Spring 1992

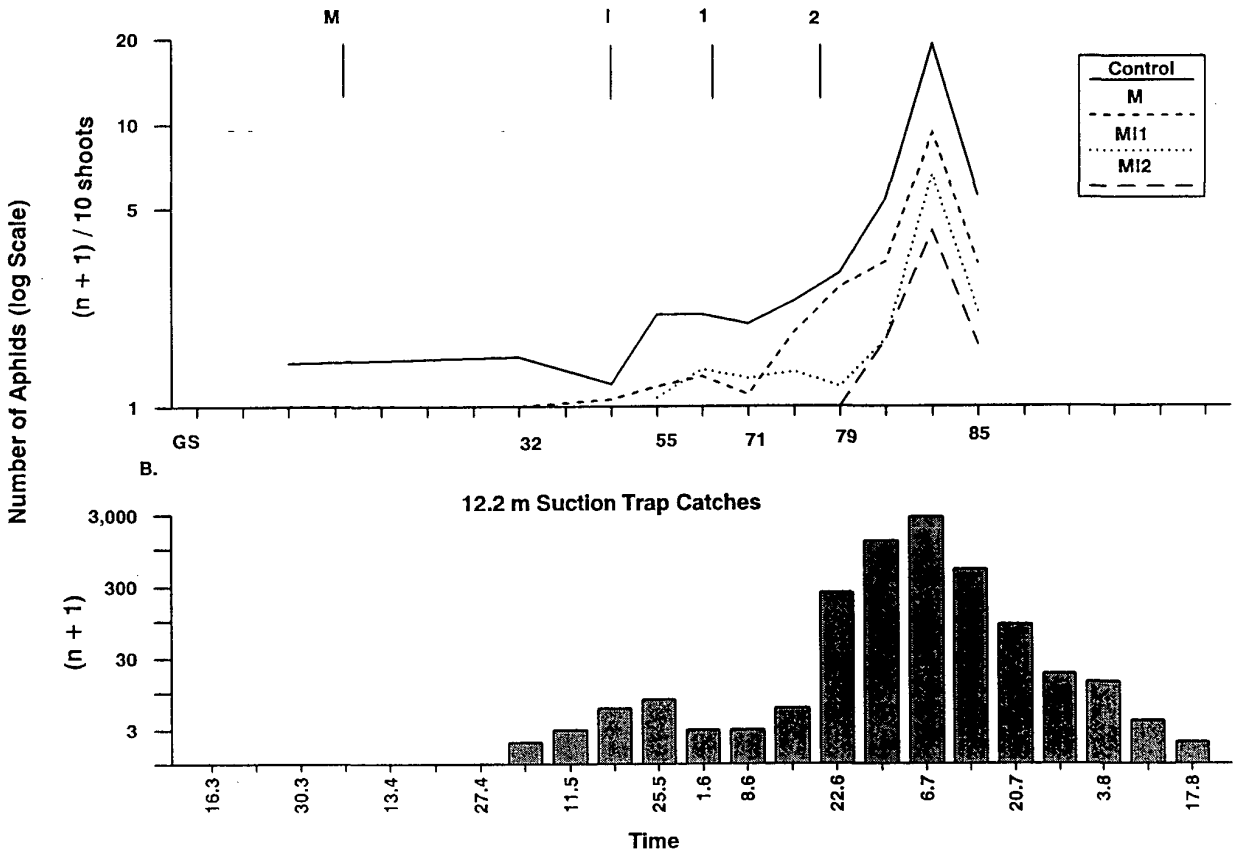


FIGURE 18
Rothamsted
Number of Grain Aphids in Winter Wheat during the Spring 1993

FIGURE 19
Rothamsted
Number of Rose-Grain Aphids in Winter Wheat during the Spring 1992

FIGURE 20
Rothamsted
Number of Rose-Grain Aphids in Winter Wheat during the Spring 1993

FIGURE 21

Kirton

Number of Grain Aphids in Winter Wheat during the Spring 1992

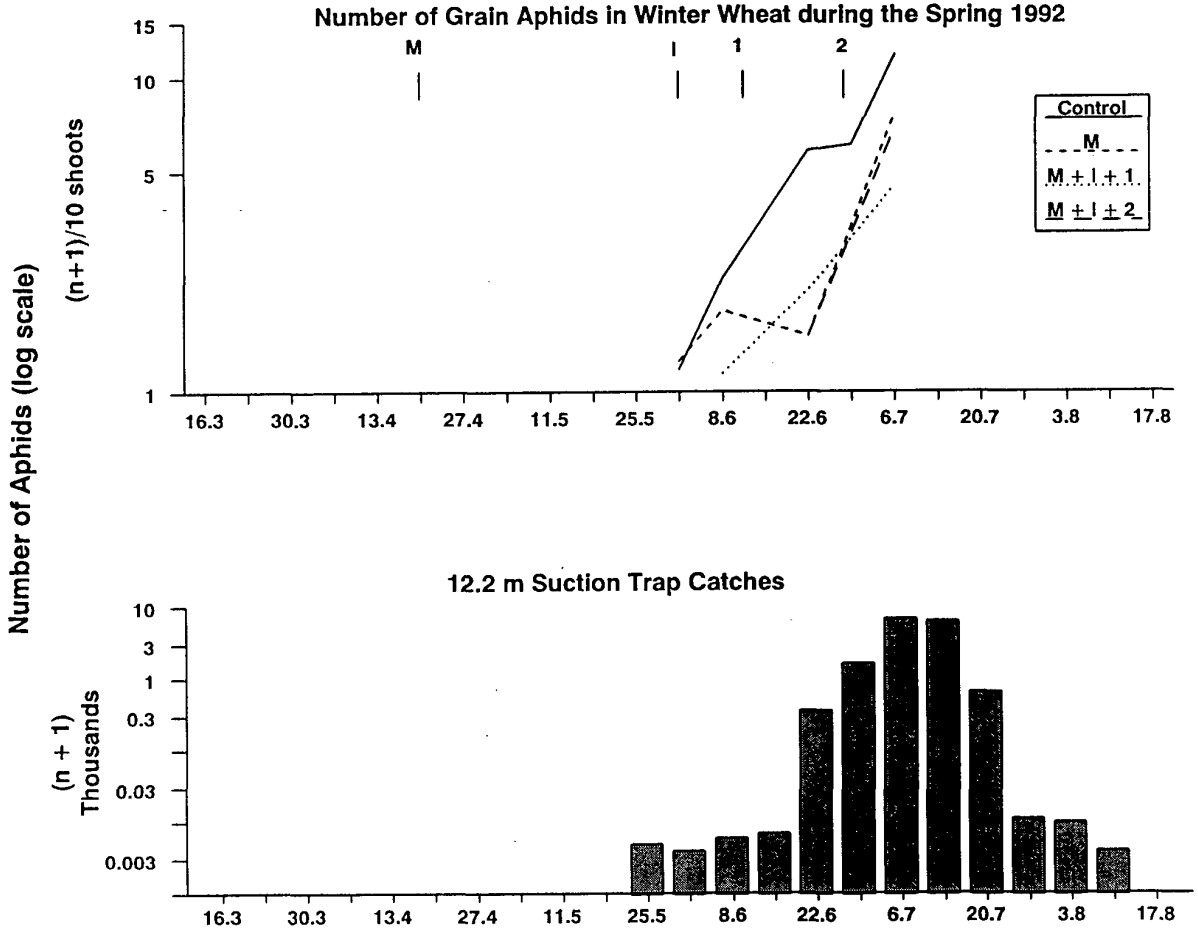


FIGURE 22

Kirton

Number of Grain Aphids in Winter Wheat during the Spring 1993

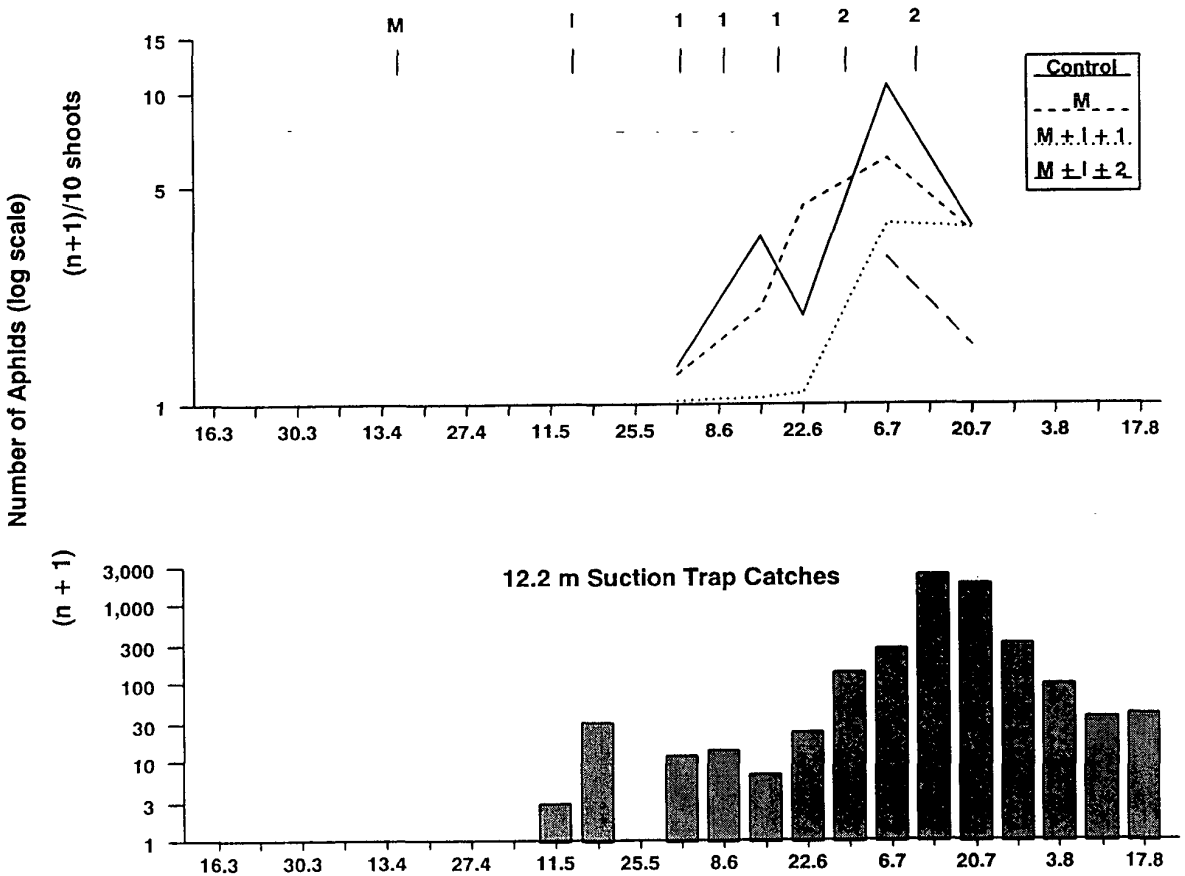


FIGURE 23
Kirton
Number of Rose-Grain Aphids in Winter Wheat during the Spring 1992

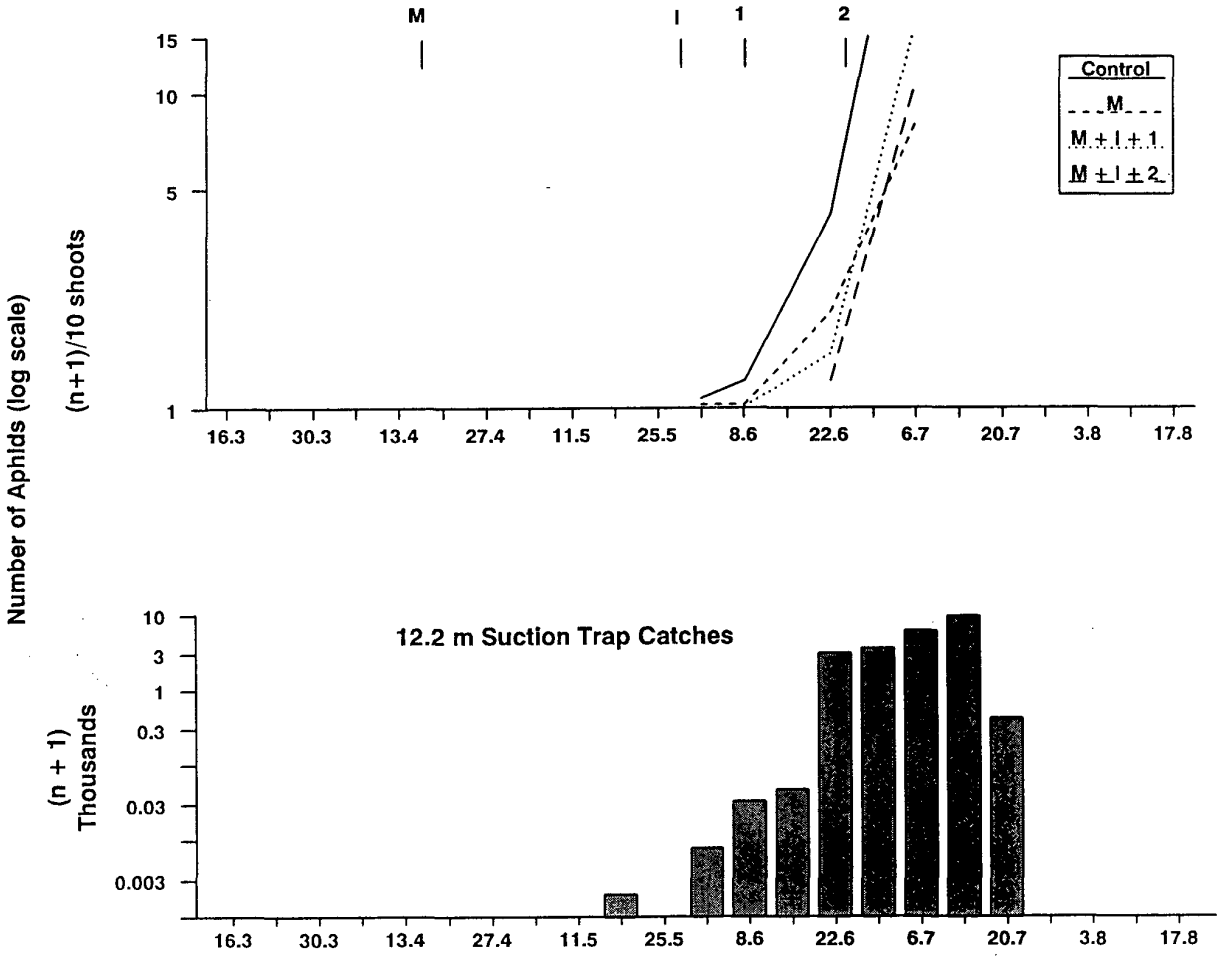


FIGURE 24

Kirton

Number of Rose-Grain Aphids in Winter Wheat during the Spring 1993