HDC Project FV 162e

FINAL REPORT

Outdoor lettuce: Refinement and field validation of forecasts for the aphid pests of lettuce foliage

Rosemary Collier & Richard Harrington

Horticulture Research International
Wellesbourne
Warwick CV35 9EF

June 2001

Project Title:	Outdoor lettuce: Refinement and field validation of forecasts for the aphid pests of lettuce foliage
Project Number:	FV 162e
Project Leader:	Dr Rosemary Collier
Final Report:	1999-2001
Annual Report:	June 2000
Key workers:	Richard Harrington (analysis of suction trap data), Sally Minns (data collection, collation and analysis)
Location of Project:	HRI Wellesbourne, HRI Kirton, IACR Rothamsted, commercial crops
Project Co-ordinator:	Mr D Norman Fresh Produce Consultancy 115 Knights End Road March Cambs PE15 9QD
Date project commenced:	1 May 1999
Date project to be completed:	30 April 2001
Key words:	Lettuce, aphids, forecasts, peach-potato aphid (*Myzus persicae*), currant-lettuce aphid (*Nasonovia euphorbiae*), potato aphid (*Macrosiphum euphorbiae*)

CONTENTS OF REPORT

Page

PRACTICAL SECTION FOR GROWERS

COMMERCIAL BENEFITS OF THE PROJECT

Cost-benefit analysis

The outdoor lettuce crop is worth about £80M annually (MAFF Basic Horticultural Statistics for the UK, 1989/90-1999/00). The presence of even small numbers of aphids in salad crops can lead to supermarket rejections.

Sprays to outdoor lettuce crops cost about £290/ha (Nix, 1998) and approximately half of these will be for aphid control (about £145/ha). Thus a 5% reduction in the number of treatments applied for aphid control to the 6,000 ha lettuce grown in the UK could be worth about £44,000 per year, depending on the costs of insecticide and treatment. This would give a cost-benefit relationship of 1:3 for a period of five years.

More importantly, if higher levels of insecticide resistance were to develop due to intensive use of a small number of insecticide compounds, some crops would be totally unmarketable. A loss of 5% of the marketable crop would be worth about £4M per year. This would give a cost-benefit relationship of 1:250 over a period of five years.

BACKGROUND AND OBJECTIVES

Aphids are the major pests of outdoor lettuce crops. There are three important species that colonise the foliage, the currant-lettuce aphid (*Nasonovia ribisnigri*), the peach-potato aphid (*Myzus persicae*) and the potato aphid (*Macrosiphum euphorbiae*). The purpose of this project is to refine and validate forecasts of the timing of key events in crop colonisation by these species, so that these can form part of an integrated approach to aphid control.

SUMMARY OF RESULTS AND CONCLUSIONS

- Data collected by the Rothamsted Insect Survey were used to determine relationships between the timing of aphid flight and weather variables, using linear regression.
- Three aphid variables (date of first capture, mean date of first five captures, Log_{10} numbers caught to 1 July) for each of the three aphid species (peach-potato aphid, potato aphid, currant-lettuce aphid) were regressed on each of two weather variables (mean air temperature for January-February, mean air temperature for January-March), for each of 19 suction trap sites.
- The mean air temperature for January - February gave a stronger relationship than the mean air temperature for January - March on 61% occasions. The mean date of the first five captures gave a stronger relationship than the date of first capture on

69% occasions. Relationships with winter temperature were generally much stronger for peach-potato aphid and potato aphid than for currant-lettuce aphid.

- For each species, the relationship between winter temperature and the start of aphid flight differed between sites. However, any change in temperature had the same effect at all sites.
- The three aphid variables (first record, mean of first five, Log_{10} numbers to July 1st) for two aphid species (peach-potato aphid, potato aphid) were regressed on rainfall for each of seven periods (Jan-Feb, Jan-Mar, Jan-Apr, Jan-May, Oct-May, Nov-May, Dec-May) for eight trap sites. Rainfall alone showed very few significant relationships with aphid flight. Out of 336 regressions, 47, 30 and 5 were significant respectively at the $P<0.05$, $P<0.01$ and $P<0.001$ level, higher numbers than would be expected by chance. There was a tendency for relationships to be strongest with the inclusion of later months. The most consistent feature of the relationships was the slope of the lines. Where significant relationships were found, flights were delayed by higher rainfall and numbers caught were reduced. Even where relationships were not significant, the slopes usually followed this pattern.
- The effects of site latitude and longitude were determined. At any given temperature there was a strong tendency for aphids to fly earlier and in greater numbers further south and east.
- Multiple regression models with first aphid record explained in terms of the meteorological (Jan-Feb temperature, Jan-Mar temperature, Jan-Feb rainfall, Nov-Feb rainfall) and geographical variables (latitude, longitude and altitude) were fitted for each of the three aphid species. Terms were added to the model sequentially until no significant improvement was made. In all cases the best fit was obtained with a model using Jan-Feb temperature, log_e Jan-Feb rainfall, latitude (grid ref/1000), latitude squared, longitude (grid ref/1000), longitude squared, latitude x longitude, altitude.
- The observed and predicted values of first record in suction trap captures of peach-potato aphid, potato aphid and currant-lettuce aphid, respectively were compared for 1986, a year chosen at random. On average, the predictions for peach-potato aphid, potato aphid and currant-lettuce aphid were 18, 10 and 20 days out, respectively. All predicted values for peach-potato aphid and potato aphid and all but two for currant-lettuce aphid fell within the 95% confidence limits, but these are very broad. Since the 1986 records are included in the data set used to construct the model, a stricter test of the model will come when it is used to predict data not included in its construction.
- During 1999 and 2000, plots of lettuce for monitoring aphids were located at sites in Sussex, Kent, Warwickshire (HRI Wellesbourne), Lincolnshire, Norfolk and Yorkshire (HRI Stockbridge House). In general, five plots of approximately 300 plants were planted sequentially to cover the growing season.

- Sampling started in early May at most sites. Individual plots were sampled for several weeks, depending on the time of year and hence the rate of growth of plants. Each week, samples of 20 plants were cut and sent to HRI Kirton. Two plots at each location were sampled for much of the time (10 plants/plot), to ensure continuity. The aphids were removed from the plants, identified and counted. Currant-lettuce aphid was the predominant species at many sites, particularly in late summer.
- Estimates were made for each species, at each site, of the dates of key infestation events (the first adult aphid, peak numbers of adult aphids, the mid-season 'crash'). This included the three sites monitored in each of four years (1994-97) as part of LINK Project FV 162 and the six sites monitored in 1999 and 2000 during the current project.
- The dates when the first potato aphid and peach-potato aphid was captured in suction traps were compared with each other and were not correlated. In contrast, the dates when the first aphids were found on plants were highly correlated for potato aphid vs peach-potato aphid and currant-lettuce aphid vs potato aphid, but not for currant-lettuce aphid vs peach-potato aphid.
- The dates when peak numbers of each species were found on plants were correlated with one another. The mean dates when peak numbers of peach-potato aphid, potato aphid and currant-lettuce aphid were found on plants were 2 July, 1 July and 7 July respectively.
- Predictions made using the multiple regression models derived from suction trap data were compared with field sampling data, including the data collected in LINK Project FV 162. For both peach-potato aphid and potato aphid, the date by which the first aphid was found on plants was correlated with the model prediction, but was not correlated with the date by which the first aphid was captured in the nearest suction trap. On average, the first peach-potato aphid and the first potato aphid were found on plants 22 and 12 days respectively after the model predicted that the first aphid would be captured in a suction trap (if one were present at that site).
- Conversely, the dates when peak numbers of aphids were found on plants were correlated with the dates of first capture in the nearest suction trap. However, neither the dates when peak numbers of aphids were found on plants nor the dates when aphid infestations 'crashed' were correlated with regression model predictions.
- For the currant-lettuce aphid, dates of key colonisation events (first aphid, peak aphids, crash) were plotted against the numbers of day-degrees (above either 0 or 4.4°C) accumulated from either 1 January or 1 February to either 30 May (the mean date when the first aphid was found) or 7 July (the mean date when peak numbers of aphids were found).

- The date when the first aphid was found was most strongly correlated with accumulated day-degrees (base 4.4ºC) from 1 February-30 May and the date when peak numbers of aphid were found on plants was correlated with all accumulations above both bases.
- Using a base of 4.4ºC, the mean numbers of day-degrees accumulated until the first aphid was found and until peak numbers of aphids were found, were 507 $\pm$ 111 (SD) and 935$\pm$165 respectively. Comparisons between observed and predicted dates showed that there was a mean absolute difference of 9 days for the first aphid and 12 days for peak numbers of aphids.

ACTION POINTS FOR GROWERS

- In the UK, peaks of aphid abundance on lettuce foliage occur in mid-summer and in the autumn, with a distinct period of low abundance in the intervening period. Whilst all three species contribute to the first peak, currant-lettuce aphid dominates in the autumn. However, the precise timing of the periods of high and low aphid abundance varies from region to region and year to year.
- Infestations of peach-potato aphid and potato aphid on lettuce occur earlier following a mild winter. Infestations by currant-lettuce aphid are not correlated with winter temperature, but are related to spring temperatures (accumulated day-degrees).
- Site location also affects the timing of colonisation. Analysis of data collected by the Rothamsted Insect Survey has shown that at any given temperature, there is a tendency for aphids to fly earlier, and in greater numbers, further south and east.
- Multiple regression models have been fitted which predict the time of the first capture of an aphid in a suction trap based on Jan-Feb temperature, Jan-Feb rainfall, latitude, longitude and altitude. On average, the first peach-potato and potato aphids were found on plants 22 and 12 days respectively after the forecast dates. Thus provided appropriate weather data are available, it should be possible to indicate in March when peak colonisation by the peach-potato aphid and potato aphid is likely to occur at any location.
- Real time information on captures of peach-potato and potato aphids in suction traps may also provide useful information to growers, even though the closest suction trap is often more than 50 miles away from their farm. Such information is being provided weekly to HDC members by e-mail and through the IACR Insect Survey website. However, this study showed that the timing of suction trap captures were correlated only with the time when peak numbers of aphids were found on lettuce plants and not with the time that the first aphids were found. On average, peak numbers of peach-potato and potato aphids were found 60 and 58 days respectively after the first aphid was captured in the nearest suction trap.

- The forecast for the currant-lettuce aphid is based on accumulated day-degrees from 1 February, so the accuracy of predictions will increase during the spring and early summer. Using a base of 4.4°C, the mean numbers of day-degrees accumulated until the first aphid was found and until peak numbers of aphids were found were found were 507 and 935 respectively. Comparisons between observed and predicted dates showed that this forecast is likely to be accurate to within a 2-3 week period.
- Suction trap captures are unlikely to provide useful information to growers about the currant-lettuce aphid because, in general, very low numbers are captured in suction traps.
- Peak numbers of all three species of aphid occur usually at the same time. The timing of the peak is obviously determined by the timing of the subsequent mid-season crash. As yet we do not understand the cause of the crash. It may be due to natural enemies, including entomopathogenic fungi. It is unlikely to be caused by the changing physiological state of the host crop, as the crash occurs at the same time in sequentially planted plots of lettuce.
- None of the forecasts are likely to be accurate to within a week and may only be accurate to within a few weeks. This is due to the considerable variability in the data on which they are based, which includes a large amount of random sampling error.
- It should be possible to write routines in EXCEL (or similar packages) for growers to use with their own temperature and rainfall data, to run the prediction models for the peach-potato and potato aphids and to calculate accumulated day-degrees for the currant-lettuce aphid.

ANTICIPATED PRACTICAL AND FINANCIAL BENEFITS

- The project will increase lettuce growers' knowledge of aphid life cycles and help them to anticipate periods of aphid colonisation.
- Advanced warning of periods of aphid colonisation should lead to better use of crop monitoring resources and to improved targeting of insecticide treatments. This should lead in turn to a reduced number of supermarket rejections due to the presence of aphids in produce.
- The project will provide the industry with forecasts of the timing of aphid attacks. These could be made available as regional forecasts or could be generated locally using growers' own weather stations.
- Preliminary forecasts could be made available immediately to growers for initial assessment and validation and they could be supplied with refined forecasts, as they become available.
- Management systems which lead to targeted applications of lower numbers of sprays would be favoured highly by consumers and would have considerable benefits for the environment.

SCIENCE SECTION

INTRODUCTION

Aphids are the major pests of outdoor lettuce crops, which cover an area of about 6,000 ha each year (MAFF Basic Horticultural Statistics for the UK, 1989/90-199-00). There are four important pest aphid species. These are the lettuce root aphid (*Pemphigus bursarius*), and three species that colonise the foliage, the currant-lettuce aphid (*Nasonovia ribisnigri*), the peach-potato aphid (*Myzus persicae*) and the potato aphid (*Macrosiphum euphorbiae*).

The Pesticide Usage Survey Report for 1995 (Garthwaite *et al.*, 1995) indicates that each lettuce crop receives an average of 5.2 sprays for insect control. In 1995, a total area of 49,000 ha crop was treated with insecticide, of which only 3,500 ha were treated for specifically non-aphid pests. However this information was collected prior to the introduction of imidacloprid seed treatment.

Aphid control presents a number of problems for lettuce growers. Particular difficulties include:

- A limited choice of effective active ingredients.
- Insecticide resistance to several insecticide groups in *M. persicae*, *M. euphorbiae* and *N. ribisnigri.*
- The potential for development of resistance to other insecticide groups.
- Increasing pressure from processors, multiple retailers and consumers to justify and to reduce insecticide use.

However, there are future opportunities for more specific non-insecticidal methods of aphid control, including the development of lettuce varieties resistant to aphids and the use of entomopathogenic fungi incorporated into module compost for control of *P. bursarius*. There is, therefore, a requirement for a more integrated approach to aphid control, where specific control measures are targeted at particular species at certain stages in their life cycle. Early warning of the timing of aphid infestations would expedite this approach.

The phenology of the three main aphid species infesting lettuce foliage (*Myzus persicae*, *Macrosiphum euphorbiae*, *Nasonovia ribisnigri*) was investigated in MAFF LINK project P 131, FV 162 which was funded by MAFF, the HDC and Elsoms seeds. In this project, preliminary forecasts of aphid colonisation were developed, by establishing relationships between the timing of key infestation events and air temperatures. Key events considered included the start and peak of colonisation in early and late summer and the timing of the mid-season decline in aphid numbers (aphid ‘crash’).

For the two predominantly anholocyclic species (overwinter as nymphs or adults), *M. persicae* and *M. euphorbiae,* relationships were established between colonisation of lettuce crops and forecasts of aphid immigration developed by the Rothamsted Insect Survey. These forecasts use the relationship between the mean air temperature for January - February and the date when the first alate aphid is captured in suction traps each year (Harrington *et al.*, 1990). Richard Harrington and colleagues at IACR Rothamsted have shown that for *M. persicae,* the relationship with winter temperature changes with latitude (Harrington *et al.*, 1993). This may be true for *M. euphorbiae* also.

For the holocyclic species (overwinter as eggs), *N. ribisnigri,* a relationship was established between key infestation events and day-degrees above 0^{o} accumulated from 1 February each year. The forecast for *N. ribisnigri* was developed solely from field data collected during LINK project P 131, FV 162.

Analysis of monitoring data collected during the LINK project showed also that each year, the timing of the mid-season decline in aphid numbers (aphid 'crash'), was similar in all three species of foliage-feeding aphid (*M. persicae, M. euphorbiae, N. ribisnigri*). The aphid 'crash' appeared to occur at about the same time in all lettuce plots at a single location, regardless of the development stage of the crop.

Forecasts of the timing of peak populations of *M. persicae* and *M. euphorbiae* on ware potato crops have been developed using mean air temperatures for January to March. The forecast models were improved by the inclusion of mean May air temperatures (MAFF Project HP0103; Parker, 1998).

EXPERIMENTAL

OBJECTIVE 1

Use data from the Rothamsted Insect Survey to refine forecasts for aphid pests (*M. persicae, M. euphorbiae, N. ribisnigri*) of lettuce foliage.

Extract data on *M. persicae*, *M. euphorbiae* and *N. ribisnigri* from historical data sets.

The date of the first capture, mean date of the first five captures and numbers caught up to July 1st (Log $_{10}$) were extracted for each species for the following sites (Figure 1) and years: Rothamsted (1965-1998); Wye (1967-1997); Broom's Barn (1965-1998); Newcastle (1967-1997, not 1991); Dundee (1967-1997); East Craigs (1969-1997); Starcross (1970-1997); Elgin (1971-1997); Hereford (1973-1997); Preston (1975-1998, not 1983); Ayr (1975-1997, not 1993); Writtle (1976-1997); Kirton (1981-1997); Long Ashton (1970-1997, not 1989-1992); High Mowthorpe (1967-1988); Silwood (1968-

1988); Rosewarne (1969-1988); Aberystwyth (1969-1988, not 1970) and Shardlow (1971-1988). The years reflect availability of both aphid and weather data. Mean temperatures for the periods January to February and January to March each year were extracted for each site, or the nearest available weather station if not at the trap site, from the BBSRC 'ARCMET' database.

Determine relationships between the timing of aphid flight, aphid abundance and appropriate weather variables using regression and other statistical techniques.

Temperature alone

Three aphid variables (date of first capture, mean date of first five captures, Log $_{10}$ numbers caught to 1 July) for each of the three aphid species (*M. persicae*, *M. euphorbiae*, *N. ribisnigri*) were regressed on each of the two weather variables (mean air temperature for January-February, mean air temperature for January-March), for each of 19 suction trap sites (3 x 3 x 2 x 19 = 342 regressions). For each aphid versus weather combination, an analysis was done to see whether the relationship was best described by separate lines for each site, a single line combining all sites, or parallel lines (i.e. with the same slope for each site but with a different intercept on the aphid axis).

The percent variance accounted for in each individual regression is shown in **Table 1a** (*Myzus persicae*), **Table 1b** (*Macrosiphum euphorbiae*) and **Table 1c** *(Nasonovia ribisnigri*). The mean air temperature for January - February gave a stronger relationship than the mean temperature for January - March on 105 out of 171 occasions. The mean date of the first five captures gave a stronger relationship than the date of first capture on 79 out of 114 occasions.

Relationships were generally very much stronger for *M. persicae* and *M. euphorbiae* than for *N. ribisnigri*. This is probably due mainly to *N. ribisnigri* overwintering in the egg stage and the other two overwintering in the active parthenogenetic stage. Although the egg is much more cold tolerant than the active stages, the active stages are able to take advantage of warmer conditions with bursts of development and reproduction, whereas the eggs are in diapause and cannot. Numbers of *N. ribisnigri* in samples were generally very much smaller than of the other two species.

The percentage variance accounted for by single line, parallel line and separate line models is shown in **Table 1d**. A single line was never the best description. A parallel line accounted for more variance than separate lines on 9 out of 18 occasions, but the results were always very similar, differing by a maximum of 2.1% and a mean of 0.4%. It is therefore sensible to adopt the more parsimonious parallel line models, meaning that, for a given aphid species, any given *change* in temperature has the same effect at all sites, but that at any given temperature, the aphid variable is site-specific.

For *M. persicae* and *M. euphorbiae*, determine whether the relationships between key infestation events and winter temperature can be improved by including other weather variables.

Rainfall alone

The three aphid variables (first record, mean of first five, Log $_{10}$ numbers to July 1st) for two aphid species (*M. persicae*, *M. euphorbiae*) were regressed on rainfall for each of seven periods (Jan-Feb, Jan-Mar, Jan-Apr, Jan-May, Oct-May, Nov-May, Dec-May) for eight trap sites (Broom's Barn, Dundee, Long Ashton, Newcastle, Preston, Rothamsted, Starcross, Wye) (3 x 2 x 7 x 8 = 336 regressions). These rainfall periods and trap sites are sufficient to show whether rainfall alone can make a useful contribution to forecasting aphids. *Nasonovia ribisnigri* was not included because there was no biological reason to expect rainfall to influence egg survival. To cover all trap sites, aphid species and consecutive monthly rainfall combinations from October to May would have involved 4788 regressions. This was not possible within the allocated time.

Rainfall alone showed very few significant relationships with aphid flight **(Table 2)**. Out of 336 regressions, 47, 30 and 5 were significant respectively at the $P<0.05$, $P<0.01$ and $P<0.001$ level, higher numbers than would be expected by chance. There was a tendency for relationships to be strongest with the inclusion of later months. The most consistent feature of the relationships was the slope of the lines. Where significant relationships were found, flights were delayed by higher rainfall and numbers caught were reduced. Even where relationships were not significant, the slopes usually followed this pattern. The sites where rainfall was most strongly related to aphid activity were the two most northerly sites, Dundee and Newcastle, with 53 of the 82 significant correlations. On their own, these relationships would not have adequate predictive value. However, the possibility that rainfall could account for some of the residual variance in relationships between aphid activity and other variables was investigated.

Determine the effect of latitude on these relationships (this was extended to include longitude and altitude).

Temperature, Rainfall, Latitude, Longitude and Altitude

Latitudes, longitudes and altitudes of each site are shown in **Table 3**.

Multiple regression models with first aphid record explained in terms of the meteorological (Jan-Feb temperature, Jan-Mar temperature, Jan-Feb rainfall, Nov-Feb rainfall) and geographical variables (latitude, longitude and altitude) were fitted for each of the three aphid species. An interaction between rainfall and site was found. This was removed by taking the $\log_e$ of the rainfall. Terms were added to the model sequentially until no significant improvement was made. In all cases the best fit was obtained with a model using Jan-Feb temperature, $\log_e$ Jan-Feb rainfall, latitude (grid ref/1000), latitude squared, longitude (grid ref/1000), longitude squared, latitude x longitude, altitude. Resulting equations and the percent variances accounted for are shown in **Table 4**. 95% confidence were calculated as 1.96 times the standard error of the prediction. A computer programme for calculating the predictions and their standard errors has been produced for use in future years. A similar programme will be developed to forecast the means of the first five aphids trapped, and the numbers trapped by 1st July for future years.

Tables 5b – 5d show the observed and predicted values of first record of *M. persicae*, *M. euphorbiae* and *N. ribisnigri*, respectively for 1986, a year chosen at random from those in which all traps listed were operating. The original data are shown in **Table 5a**. On average, the predictions for *M. persicae*, *M. euphorbiae* and *N. ribisnigri* were 18, 10 and 20 days out, respectively. All predicted values for *M. persicae* and *M. euphorbiae* and all but two for *N. ribisnigri* fell within the 95% confidence limits but, as can be seen, these are very broad. It should be noted that the 1986 data are included in the data used to construct the model. A stricter test of the model will come when it is used to predict data not included in its construction.

Determine whether forecasts of the timing of key infestation events in lettuce can be improved by taking account of aphid abundance.

No account was taken of aphid abundance in these analyses, as it was decided to concentrate effort on the additional effects of longitude and latitude on timing instead.

For *N. ribisnigri* determine whether data from the Rothamsted Insect Survey can be used to refine forecasts of key infestation events.

The model fitted for *N. ribisnigri* accounted for only 27% of the variance (**Table 4**) and was obviously not as good a description of the phenology of this species as the models for *M. persicae* and *M. euphorbiae*.

OBJECTIVE 2

Obtain field-monitoring data from geographically separate areas of outdoor lettuce production to validate refined forecasts.

Locate sites in Sussex, Kent, Warwickshire (HRI Wellesbourne), Lincolnshire, Norfolk and Lancashire.

David Langmead (Sussex), Intercrop (Kent), Jarrow Produce (Essex), J. E. Piccaver & Co. (Lincolnshire) and County Crops (Lancashire) agreed to participate in the project. Subsequently, County Crops were unable to participate and plots were planted at HRI Stockbridge House (Yorkshire) instead. As a consequence, sampling was delayed at Stockbridge House in 1999. The same growers (and Stockbridge House) participated in the project during 2000.

Set up plots to monitor aphid pests of lettuce by making five sequential plantings of iceberg lettuce (cv Saladin, insecticide-free) at each site. Plot size to be approximately 300 plants. Plot dimensions will depend on individual growers.

Most growers made five sequential plantings of lettuce; Intercrop made 11 plantings in 1999. In general, the lettuce varieties were chosen, and the plants raised, by individual growers. All the plants were raised from insecticide free seed. The plants grown at HRI Wellesbourne and David Langmead were cv Saladin and were propagated at HRI (Wellesbourne or Kirton).

Arrange for a sample of plants (10-20) to be cut each week by HRI staff or by the grower. Samples cut by growers will be sent in a box (next day delivery) to HRI.

Sampling started by early May at most sites and finished usually in October.

	1999		**2000**	
	First sample	**Last sample**	**First sample**	**Last sample**
Sussex	05-May	14-Oct	08-May	18-Aug
Kent	04-May	04-Oct	27-Apr	05-Sep
Essex	31-May	11-Oct	12-Jun	10-Oct
Warwickshire	29-Apr	16-Nov	20-Apr	16-Oct
Lincolnshire	28-Apr	18-Oct	05-May	05-Oct
Yorkshire	06-Aug	18-Oct	03-May	03-Oct

Individual plots were sampled for several weeks, depending on the time of year and hence the rate of growth of plants. Two plots at each location were sampled for much of the time, to ensure continuity. Each week, samples of 20 plants were cut and sent to HRI Kirton (10 plants/plot when two plots were sampled). Samples were delivered by post or carrier.

Identify and count aphids from samples.

Aphids were removed from the lettuce foliage at HRI Kirton, counted (but not identified) and preserved in 70% alcohol for later identification at HRI Wellesbourne. Adult aphids were identified to species and the nymphs were counted. In addition, non-aphid species of invertebrate were counted and identified at least to Order and sometimes to species. Growers were informed (by return) of the numbers of aphids (and non-aphid pests) found on plants.

Collate monitoring data .

The monitoring data were collated at HRI and summarised graphically (**Appendices 1-4**). Scales differ considerably between individual graphs because there were such large differences in the numbers of aphids found. In general, there were two peaks of aphid abundance, separated by a period when numbers were low (the mid-season 'crash').

OBJECTIVE 3.

<u>Validate refined forecasts for the aphid pests of lettuce.</u>

Summarise monitoring data and identify key infestation events at each site in each year (start of colonisation, peak of colonisation, timing of aphid 'crash').

The timing of key infestation events (plots sampled once a week) and the maximum numbers of aphids/plant found at each site during each 'peak' are shown in **Tables 6-10**. Only adult aphids could be identified to species and the totals for alate (winged) and apterous (wingless) aphids of each species have been combined. Immature aphids (nymphs) were counted and shown in **Table 9** and their totals have been included in the table for 'total aphids' (**Table 10**). Not surprisingly, nymphs were more numerous than adult aphids. *Nasonovia ribisnigri* was the predominant species at most sites, particularly in late summer.

For all species, determine whether there are correlations between the three species in the timing of key infestation events, which could be used to improve the forecasts for any, or all, of the species.

The dates when the first aphid was captured in suction traps were compared for *M. euphorbiae* and *M. persicae* and were not correlated (**Figure 2**). The suction trap data for *N. ribisnigri* were not used, as such low numbers were caught overall. However, in contrast, the dates when the first aphids were found on plants were highly correlated for *M. euphorbiae vs M. persicae* ($p<0.01$) and *N. ribisnigri* vs *M.euphorbiae* ($p<0.001$), but not for *N. ribisnigri* vs *M. persicae* (**Figure 3**). This included data from the three sites monitored in each of four years (1994-97) as part of the LINK Project FV 162 (HRI Wellesbourne, HRI Kirton and commercial crop in Lancashire (ADAS)) and the six sites monitored in 1999 and 2000 during the current project.

Previous observations had shown that the dates when peak numbers of each species occurred in early summer appeared to be correlated with one another (as did the dates of the subsequent crash). The dates when peak numbers of each species were found on plants were correlated with one another and all species were highly correlated ($p<0.001$) (**Figure 4**). The mean dates when peak numbers of *M. persicae*, *M. euphorbiae* and *N. ribisnigri* respectively were found were 2 July, 1 July and 7 July.

Validate refined aphid forecasts by correlating forecast predictions with the timing of key infestation events.

Myzus persicae and *Macrosiphum euphorbiae*

The equations developed by IACR Rothamsted (**Table 4**) for *M. persicae* and *M. euphorbiae* were used to predict the timing of the first aphid capture for the year/site combinations where crop monitoring data were available. This was done in an EXCEL spreadsheet. The data included information from the three sites monitored in each of four years (1994-97) as part of the LINK Project FV 162 (HRI Wellesbourne, HRI Kirton and commercial crop in Lancashire (ADAS)) and the six sites monitored in 1999 and 2000 during the current project. The predicted dates of first capture derived from the equations were plotted against the:

1) date by which the first aphid was observed on plants (alate or aptera)
2) date on which peak numbers of aphids were observed (prior to the mid-season crash)
3) date of the mid-season crash.

All dates were plotted as days from 1 January. Sites where no crops had been planted by the predicted date, or where aphids were found as soon as sampling began, were excluded. The weather data to make the predictions were taken from the standard Met Office weather station nearest to each site and the latitude, longitude and altitude of the site were used also. In addition, the dates by which the first aphid was found on plants were plotted against the dates on which the first aphid was captured in the nearest suction trap to each site. The sources of weather data and suction trap data used for each group of monitoring sites are shown below:

Monitoring sites	Weather data	Suction trap data
Sussex	Thorney Island	Silwood Park
Kent	Manston	Wye
Essex	Wattisham	Writtle
Lincolnshire	Kirton	Kirton
HRI Wellesbourne	Wellesbourne	Hereford
Lancashire	Aughton	Preston
HRI Stockbridge House	Stockbridge House	Tadcaster

For both *M. persicae* and *M. euphorbiae*, the date by which the first aphid was found on plants was correlated with the model predictions ($p<0.01$), but was not correlated with the date by which the first aphid was captured in the nearest suction trap (**Figures 5-8**). On average, the first *M. persicae* and the first *M. euphorbiae* were found on plants 22 and 12 days respectively after the model prediction. In contrast, the dates when peak numbers of aphids were found on plants were correlated with the dates of first capture in the nearest suction trap ($p< 0.01$), but were not correlated with model predictions. On average, peak numbers of *M. persicae* and *M. euphorbiae* were found 60 and 58 days respectively after the first aphid was captured in the nearest suction trap. Neither the dates when peak numbers of aphids were found on plants, nor the dates when aphid infestations 'crashed', were correlated with the model predictions.

Nasonovia ribisnigri

For *N. ribisnigri,* a relationship had been established previously between key infestation events and day-degrees accumulated from 1 February each year (Tatchell *et al.*, 1998). Since the threshold temperature for development of *N. ribisnigri* is unknown, a base temperature of 0°C was used. However, this base temperature may be too low.

The data collected in 1999 and 2000 were added to the data set collected in the LINK project (1994-97) to validate relationships between key infestation events and accumulated day-degrees above base temperatures of 0 and 4.4°C, the threshold temperature for development of the lettuce root aphid (*Pemphigus bursarius*) (Dunn, 1959). Although the two species of aphid are not related closely, *P. bursarius* is another pest of lettuce and is also holocyclic, overwintering on poplar trees (*Populus* spp.).

The dates of key colonisation events (first aphid, peak aphids, crash) by adult *N. ribisnigri* were plotted against the numbers of day-degrees accumulated from either 1 January or 1 February to either 30 May (the mean date when the first aphid was found) or 7 July (the mean date when peak aphids were found). The correlation coefficients for the various relationships are shown in **Table 11**. The date when the first aphid were found was most strongly correlated with accumulated day-degrees (base 4.4ºC) from 1 February-30 May ($p<0.05$) (**Figure 9**) and the date when peak numbers of aphid were found on plants were correlated with all accumulations above both bases ($p<0.01$-0.02) (**Table 11, Figures 10-11**). The date of the mid-season crash was not correlated with any of the accumulations (e.g. **Figure 12**). Using a base of 4.4ºC, the mean numbers of day-degrees accumulated until the first aphid was found and peak numbers of aphids were found were 507 $\pm$ 111 (SD) and 935$\pm$165 respectively. Comparisons between observed and predicted dates showed that there was a mean absolute difference of 9 days for the first aphid and 12 days for peak aphids.

DISCUSSION

During 1999 and 2000, *N. ribisnigri* was the predominant species at many of the monitoring sites, confirming previous studies in north-west Europe (Aarts *et al.*, 1999; Reinink & Dieleman, 1993; Tatchell *et al.*, 1998). In general, there were two peaks of aphid abundance on lettuce foliage, with a distinct period of low abundance in the intervening period, again confirming previous studies (Aarts *et al.*, 1999; Tatchell *et al.*, 1998). However, the precise timing of the periods of high and low aphid abundance varied from site to site and from year to year (Tatchell *et al.*, 1998). Aphid abundance varied between sites and where numbers were low it was sometimes difficult to estimate when the 'peak' or the 'crash' occurred. To help with this, data were combined to estimate these parameters more accurately. For example, records of alates (winged aphids) and apterae (wingless aphids) were combined to estimate when infestations of each species 'peaked' or 'crashed'.

Previous analyses of long-term aphid monitoring data collected by the Rothamsted Insect Survey have shown that for species such as *M. persicae* and *M. euphorbiae*, which have predominantly anholocyclic life cycles in the UK, the time that the first alate is found in suction trap samples is negatively correlated with winter temperature (Harrington *et al.*, 1990). There is also a positive correlation between winter temperature and aphid abundance during the first half of the year. The analyses for the time of first capture have now been extended to include latitude, longitude and rainfall. Not surprisingly, the mean date of capture of the first five aphids is also negatively correlated with winter temperature and, in general, this relationship is stronger than that with the capture of the first aphid. In future, similar equations will be developed to relate the mean date of capture of the first five aphids to temperature, latitude, longitude and rainfall. Parker (1998) included site locations in linear regression analyses designed to develop forecasts for aphid populations (*M. persicae* and *M. euphorbiae*) on potatoes. However, the variates relating the peak infestation date to the geographical location of the site did not give significant t-statistics and the final model was based solely on temperature data (mean January-March air temperatures and mean May temperature).

Whilst the relationship with winter temperature is particularly pronounced for species such as *M. persicae* and *M. euphorbiae*, such relationships are much weaker for holocyclic species such as *N. ribisnigri* (Harrington *et al*., 1990). Early season activity is likely to be related more closely to spring temperatures (Thomas *et al*., 1983), through their effects on aphid development after egg hatch. Consequently, spring temperatures are more likely to predict the timing of infestation by *N. ribisnigri*, as shown by correlations between key infestation events and accumulated day-degrees. Similarly, it was unlikely that rainfall would have any direct effect on the rate of development of *N. ribisnigri*.

To date, almost nothing has been published on the developmental biology of *N. ribisnigri* and on its relationship with temperature and photoperiod and there is a need to quantify the temperature/daylength requirements for the production of diapausing eggs, completion of diapause, post-diapause development on the primary host, and development and reproduction on the secondary host. It may be valuable also to quantify intra-specific variation in the response of *N. ribisnigri* to daylength. Some aphids may survive the winter on Compositae and are then available to colonise lettuce much earlier that those that have overwintered as eggs on currant, which may affect the applicability of a forecast. There is anecdotal information to suggest that this does occur on occasions. For example, some of the data from the previous LINK project (FV 162) indicated that in some years, infestations occurred much earlier in Lancashire than might be expected.

The timings of the first peak in aphid numbers, and the mid-season 'crash', appeared to coincide for the three species. Indeed it is most likely that the timing of the 'crash' determined when peak numbers of each species occurred, since aphid numbers usually increased continuously up to that point. The mid-season 'crash' could be the result of one or more factors. Apart from nutritional factors mediated via the host crop, natural enemies have been considered as regulators of aphid populations on lettuce and other crops. In their studies in Germany, Nunnenmacher & Goldbach (1996) used cages to exclude predators from small plots of lettuce, once aphids had colonized the plants. They found that at harvest, there were many more aphids in the caged plots than in open plots, or in plots that were caged but still accessible to predators. Aphid numbers started to differ between the treatments from about three weeks before harvest. These results led the authors to propose that predators were the key factors reducing aphid populations one or two weeks before harvest. However, the plots were planted in early June in both years and harvested towards the end of July, at a time that probably coincided with mid-season 'crash'. Nunnenmacher & Goldbach (1996) might have obtained different results had the plots been planted earlier or later than this, since the present study indicates that aphid numbers do not decline prior to harvest on every planting.

Natural enemies have been considered as population regulators on other field crops infested by aphids. For example, Parker (1998) found that the inclusion of site-specific data on the level of aphid parasitism increased the robustness of weather-based forecasts of population size for *M. persicae* and *M. euphorbiae* on potatoes. Field populations of *Brevicoryne brassicae* on horticultural *Brassica* crops also 'crash' in mid summer and in some years fungal epizootics have been a major cause of the decline in the UK (Dunn & Kempton, 1971).

The direct or indirect effects of the weather may be important factors in determining the timing of the 'crash'. Whether this is mediated through direct effects on aphid physiology or indirectly through effects on the development of natural enemy populations is unknown. Different factors may be important in certain years and detailed biological studies, in conjunction with population modelling, are required to determine the key factors and their predictability. Whatever the factors are, they are not species-specific, since the numbers of all three species of foliage-feeding aphid decline on lettuce at the same time.

There is obviously a lot of variability in comparisons between model predictions and field observations and this must be due to a great extent to sampling error, both in the use of suction traps and in sampling lettuce plants. There is likely to be a good deal of random error associated with both types of sampling, and sample size and sampling frequency also provide limitations. In addition, weather data were taken from the 'nearest' weather station to each monitoring site, which was sometimes several miles away. Hence the predictions cannot be expected to give very precise guidance (for example to the nearest week), but it should be possible to develop them and present them in a way that provide growers with useful information about the likely risk of infestation within a period of 2-3 weeks.

<u>Future use of the models</u>

It should be possible to write routines in EXCEL (or similar packages) for growers to use their own temperature and rainfall data to run the prediction models for *M. persicae* and *M. euphorbiae* and to calculate accumulated day-degrees for *N. ribisnigri*.

Further validation and refinement of the models will take place over the next few years. Predictions of phenology and abundance of *M. persicae* and *M. euphorbiae* will be issued in early March each year. The success of the models in predicting phenology and abundance in suction traps and in crops will be compared to that of simpler models using just temperature data at specific suction trap sites.

CONCLUSIONS

The monitoring data collected in 1999 and 2000 confirmed that peaks of aphid abundance on lettuce foliage occur in mid-summer and in the autumn, with a distinct period of low abundance in the intervening period. Whilst all three species of aphid contribute to the first peak, *N. ribisnigri* dominates in the autumn. However, the precise timing of the periods of high and low aphid abundance varies from region to region and year to year.

Infestations of *M. persicae* and *M. euphorbiae* on lettuce occur earlier following a mild winter. Analyses of Rothamsted Insect Survey data showed that site location and rainfall also affects the timing of infestation. Infestations by *N. ribisnigri* are not correlated with winter temperature, but are related to spring temperatures (accumulated day-degrees).

It should be possible to indicate in March when peak colonisation by *M. persicae* and *M. euphorbiae* is likely to occur and by incorporating the effects of site location (latitude, longitude and altitude) into a temperature-based model.

The forecast for *N. ribisnigri* is based on accumulated day-degrees from 1 February, so the accuracy of predictions will increase during the spring and early summer.

ACKNOWLEDGEMENTS

We are especially grateful to the lettuce growers who provided lettuce plots and sampled the plants for the project, and to the HDC for funding this work. Thanks also to Sally Minns, Liz Vice, Sue Sime and Kelly Reynolds for technical assistance. The authors are extremely grateful to Suzanne Clark and Roger Payne (Rothamsted) for invaluable assistance with the modelling statistics. IACR receives grant aided support from the Biotechnology and Biological Sciences Research Council of the United Kingdom.

TECHNOLOGY TRANSFER

Date	Event	Title/topic
13-Jul-99	Leafy salads event HRI Stockbridge House	Pest control strategies
13-Jan-00	HRIA day HRI Wellesbourne	Casual intruders - understanding the problem
12-Jul-00	Salads seminar HRI Stockbridge House	Pest control in outdoor salad crops
3-Oct-00	HDC Outdoor Salads Panel ADAS Arthur Rickwood	Aphid forecasting project (FV 162e)

REFERENCES

Aarts, R., Schut, J.W., Driessen, R. & Reinink, K. (1999). Integrated control of aphids on lettuce varieties resistant to *Nasonovia ribisnigri*. *Mededelingen Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen* 64/3a, 11-15.

Dunn, J.A. (1959). The biology of lettuce root aphid. *Annals of Applied Biology* **47:** 475-491.

Dunn, J A. & Kempton, D.P.H. (1971). Seasonal changes in aphid populations on Brussels sprouts. *Annals of Applied Biology* **68**, 233-244.

Garthwaite, D.G., Thomas, M.R., Hart, M.J. & Wild, S. (1995). Pesticide Usage Survey Report 134, Outdoor Vegetable Crops in Great Britain 1995. *Ministry of Agriculture, Fisheries and Food & Scottish Office Agriculture, Environment & Fisheries Department.*

Harrington, R., Tatchell, G.M. & Bale, J.S. (1990). Weather, life-cycle strategy and spring populations of aphids. *Acta Phytopathologica et Entomologica Hungarica* **25**, 423-432.

Harrington, R., Bale, J.S. & Tatchell, G.M. (1993). Aphids in a changing climate. In: Insects in a changing environment. *R. Harrington & N.E. Stork (Editors). 17th Symposium of the Royal Entomological Society of London 7-10 September 1993, Academic Press, London.*

Nix, J. (1998). Farm Management Pocketbook. *Wye College, University of London. 29th edition (1999).*

Nunnenmacher, L. & Goldbach, H.E. (1996). Aphids on lettuce; the effects of excluding aphid predators. *Integrated Control in Field Vegetable Crops. IOBC/WPRS Bulletin* 1996, 19 (11), 38-47.

Parker, W.E. (1998). Forecasting the timing and size of aphid populations (*Myzus persicae* and *Macrosiphum euphorbiae*) on potato. *Aspects of Applied Biology* **52**, 31-38.

Tatchell, G.M., Ellis, P.R., Collier, R.H., Chandler, D., Mead, A., Wadhams, L.J, Parker, W.E., Blood Smyth, J. & Vice, E. W. (1998). Integrated pest management of aphids on outdoor lettuce crops. *Final Report 1994-98 MAFF LINK Project P 131, HDC Project FV 162. 77 pp.*

Thomas, G.G., Goldwin, G.K. & Tatchell, G.M. (1983). Associations between weather factors and the spring migration of the damson-hop aphid, *Phorodon humuli*. *Annals of Applied Biology* **102,** 7-17.

TABLES

Table 1a **The percent variance accounted for in each individual regression for *Myzus persicae*.**

SITES	Log_{10} Number to Week 26		1st Capture		Mean of First 5 Captures	
	Jan-Feb	Jan-Mar	Jan-Feb	Jan-Mar	Jan-Feb	Jan-Mar
Rothamsted	62.4	53.6	76.5	71.1	76.8	68.2
Wye	59.4	50.5	15.6	6.1	58.6	47.1
Brooms Barn	59.0	57.2	59.7	56.7	69.4	64.7
Newcastle	54.1	51.6	49.0	41.5	59.1	47.5
Dundee	34.9	34.3	28.6	35.2	48.2	52.5
East Craigs	57.1	51.9	64.5	62.8	64.8	58.7
Starcross	49.7	34.0	32.8	20.1	41.3	27.9
Elgin	19.4	18.5	8.9	13.8	21.0	13.7
Hereford	61.1	51.7	63.7	59.6	66.5	55.5
Preston	52.2	45.4	0	0	45.0	44.8
Ayr	43.4	38.6	54.1	53.1	71.2	59.8
Writtle	67.7	49.5	56.1	50.4	74.2	72.2
Kirton	68.4	57.1	55.8	58.0	67.0	62.7
Long Aston	64.9	44.2	60.4	53.2	66.2	60.4
High Mowthorpe	18.3	11.4	18.7	8.2	8.0	0
Silwood	52.6	40.0	17.8	20.7	48.4	48.1
Rosewarne	6.6	1.8	3.6	0	0	0
Aberystwyth	50.6	26.3	5.6	3.2	55.2	36.0
Shardlow	44.1	29.6	57.0	47.7	51.3	35.6

Table 1b The percent variance accounted for in each individual regression for *Macrosiphum eurphorbiae*.

SITES	Log_{10} Number to Week 26		1st Capture		Mean of First 5 Captures	
	Jan-Feb	Jan-Mar	Jan-Feb	Jan-Mar	Jan-Feb	Jan-Mar
Rothamsted	46.5	43.0	27.9	39.5	37.4	42.8
Wye	39.8	28.6	14.4	17.6	35.5	31.7
Brooms Barn	35.8	43.6	48.0	57.9	49.1	59.4
Newcastle	24.8	20.1	40.2	37.2	40.1	34.9
Dundee	30.6	29.3	25.9	33.2	35.5	37.3
East Craigs	51.0	55.5	39.0	48.5	45.1	55.4
Starcross	36.5	32.7	12.6	25.2	32.9	38.3
Elgin	27.2	18.0	24.1	15.2	26.9	16.0
Hereford	51.0	42.2	48.5	52.1	52.0	56.0
Preston	64.0	48.6	52.2	56.9	55.7	54.3
Ayr	34.1	31.1	33.2	34.5	54.3	57.8
Writtle	59.6	50.0	44.5	47.4	46.4	50.9
Kirton	59.3	55.2	50.4	57.3	58.8	64.6
Long Aston	32.8	14.6	12.6	2.7	18.8	6.3
High Mowthorpe	24.6	19.4	22.9	26.4	33.0	27.3
Silwood	67.1	51.9	38.0	28.1	49.3	41.9
Rosewarne	0	0	3.4	0.1	0	0
Aberystwyth	45.3	52.1	48.7	55.7	46.4	60.5
Shardlow	13.6	2.0	17.1	10.8	17.5	6.9

Table 1c **The percent variance accounted for in each individual regression for *Nasonovia ribisnigri*.**

SITES	Log_{10} Number to Week 26		1st Capture		Mean of First 5 Captures	
	Jan-Feb	Jan-Mar	Jan-Feb	Jan-Mar	Jan-Feb	Jan-Mar
Rothamsted	0	0	0	0	0	0
Wye	11.0	8.8	1.2	3.5	9.3	7.4
Brooms Barn	5.3	2.3	5.5	4.7	1.5	0
Newcastle	0	0	0	0	-	-
Dundee	2.3	1.2	7.1	7.0	6.3	14.8
East Craigs	0.3	0.2	0.7	6.0	29.3	30.6
Starcross	21.0	7.0	10.1	1.0	13.1	1.4
Elgin	16.9	16.4	3.8	3.9	35.1	23.9
Hereford	0	0	0	0	4.3	4.6
Preston	0	0	0	0	13.2	13.8
Ayr	5.0	1.8	22.6	10.1	-	-
Writtle	17.3	14.6	26.3	28.8	28.1	27.3
Kirton	27.5	33.5	58.7	61.9	30.7	39.6
Long Aston	0	0	0	0	24.1	9.3
High Mowthorpe	17.7	6.3	12.5	1.7	0	0
Silwood	34.3	20.1	18.2	2.4	29.4	16.4
Rosewarne	0	0	0	0	0	0
Aberystwyth	8.9	0.3	13.0	6.1	50.4	42.1
Shardlow	0	0	9.4	11.7	0	0

Table 1d **The percent variance accounted for by single line, parallel line and separate line models.**

	Log_{10} Number to Week 26		1st Capture		Mean of First 5 Captures	
	Jan-Feb	**Jan-Mar**	**Jan-Feb**	**Jan-Mar**	**Jan-Feb**	**Jan-Mar**
M. persicae						
Single Line	31.3	29.8	26.2	26.2	31.2	29.9
Parallel	67.2	61.9	52.9	50.4	68.7	64.1
Separate Lines	69.3	63.0	53.2	50.3	68.8	63.8
M. euphorbiae						
Single Line	30.8	30.4	30.1	35.3	32.0	35.5
Parallel	59.5	56.2	53.5	55.5	61.9	62.3
Separate Lines	59.4	56.4	53.1	55.5	61.9	62.8
N. ribisnigri						
Single Line	5.2	4.4	4.7	4.8	10.9	9.0
Parallel	40.4	38.5	29.6	28.5	32.3	28.9
Separate Lines	40.6	38.2	29.3	28.1	31.9	28.5

Table 2. Significance of relationships between aphid flights and rainfall. - or + P<0.05 (negative or positive slope respectively), -- or ++ P<0.01, --- or +++ P<0.001, NS not significant.

Time of first *M. persicae*

	Rainfall period						
Trap	J-Feb	J-Mar	J-Apr	J-My	O-My	N-My	D-My
Broom's Barn	NS	NS	NS	NS	NS	NS	NS
Dundee	+	NS	+	++	+	++	+++
Long Ashton	NS	NS	NS	NS	NS	NS	NS
Newcastle	++	+	NS	NS	NS	NS	+
Preston	NS	NS	NS	NS	NS	NS	NS
Rothamsted	NS	NS	NS	NS	NS	NS	NS
Starcross	NS	NS	NS	NS	NS	NS	NS
Wye	NS	NS	NS	NS	NS	NS	NS

Mean of first 5 *M. persicae*

	Rainfall period						
Trap	J-Feb	J-Mar	J-Apr	J-My	O-My	N-My	D-My
Broom's Barn	NS	NS	NS	NS	NS	NS	NS
Dundee	NS	NS	NS	++	NS	+	+
Long Ashton	NS	NS	NS	NS	NS	NS	NS
Newcastle	++	++	NS	+	++	+	++
Preston	NS	NS	NS	NS	NS	NS	NS
Rothamsted	NS	NS	NS	NS	NS	+	+
Starcross	NS	NS	NS	+	NS	+	+
Wye	NS	NS	NS	NS	NS	NS	NS

Number of *M. persicae*

	Rainfall period						
	J-Feb	J-Mar	J-Apr	J-My	O-My	N-My	D-My
Trap							
Broom's Barn	NS	NS	NS	NS	NS	NS	NS
Dundee	NS	-	-	-	NS	-	-
Long Ashton	NS	NS	NS	NS	NS	NS	NS
Newcastle	-	-	NS	NS	NS	-	NS
Preston	NS	NS	NS	NS	NS	NS	NS
Rothamsted	NS	NS	NS	NS	NS	-	-
Starcross	NS	NS	NS	-	NS	-	-
Wye	NS	NS	NS	NS	NS	NS	NS

Time of first *M. euphorbiae*

	Rainfall period						
	J-Feb	J-Mar	J-Apr	J-My	O-My	N-My	D-My
Trap							
Broom's Barn	NS	NS	NS	NS	NS	NS	NS
Dundee	NS	NS	NS	NS	+	++	+
Long Ashton	NS	NS	-	NS	NS	NS	NS
Newcastle	+++	++	+++	++	+++	+++	++
Preston	NS	NS	NS	NS	NS	NS	NS
Rothamsted	NS	NS	NS	++	NS	+	++
Starcross	NS	NS	NS	NS	NS	NS	+
Wye	NS	NS	NS	+	+	+	+

Mean of first 5 *M. euphorbiae*

	Rainfall period						
	J-Feb	J-Mar	J-Apr	J-My	O-My	N-My	D-My
Trap							
Broom's Barn	NS	NS	NS	NS	NS	NS	NS
Dundee	NS	NS	NS	NS	+	++	+
Long Ashton	NS	NS	NS	NS	NS	NS	NS
Newcastle	+	NS	+	++	++	++	++
Preston	NS	NS	NS	NS	NS	NS	NS
Rothamsted	NS	NS	NS	++	NS	+	++
Starcross	NS	NS	NS	+	NS	++	++
Wye	NS	NS	NS	NS	NS	NS	NS

Number of *M. euphorbiae*

	Rainfall period						
	J-Feb	J-Mar	J-Apr	J-My	O-My	N-My	D-My
Trap							
Broom's Barn	NS	NS	NS	NS	NS	NS	NS
Dundee	NS	NS	NS	NS	-	--	--
Long Ashton	NS	NS	NS	NS	NS	NS	NS
Newcastle	-	NS	NS	-	--	--	-
Preston	NS	NS	NS	NS	NS	NS	NS
Rothamsted	NS	NS	NS	NS	NS	NS	NS
Starcross	NS	NS	NS	--	-	--	--
Wye	NS	NS	NS	NS	NS	NS	NS

Table 3. Latitude, longitude and altitude of suction trap locations

Site	Latitude Grid ref.		Longitude Grid ref.		Altitude
Rothamsted	51°48'	2134	0°21'W	5133	119m
Wye	51°11'	1470	0°56'E	6054	043m
Broom's Barn	52°15'	2656	0°34'E	5754	070m
Newcastle	55°12'	5911	1°40'W	4202	093m
Dundee	56°27'	7300	3°40'W	3341	029m
East Craigs	55°56'	6737	3°18'W	3181	060m
Starcross	50 °37'	0821	3°27'W	2972	012m
Elgin	57°38'	8625	3°21'W	3185	030m
Hereford	52 °70'	2476	2°38'W	3564	084m
Preston	53°51'	4401	2°45'W	3498	015m
Ayr	55°28'	6233	4°34'W	2378	046m
Writtle	51°44'	2067	0°25'E	5676	038m
Kirton	52°56'	3395	0°40'W	5297	003m
Long Ashton	51°25'	1698	2°40'W	3536	046m
High Mowthorpe	54°60'	4686	0°38'W	4888	171m
Silwood	51°24'	1687	0°38'W	4945	064m
Rosewarne	50°13'	0411	5°18'W	1642	075m
Aberystwyth	52°26'	2837	4°00'W	2632	040m
Shardlow	52°52'	3304	1°20'W	4438	038m

Table 4. Equations and variance accounted for by models of first aphid record

D = date of first record (Julian date)
JFT = mean temperature in January and February (ºC)
JFR = total rainfall in January and February ($\log_e$ mm)
X = longitude (as a four figure grid reference / 1000)
Y = latitude (as a four figure grid reference / 1000)
Z = altitude

Myzus persicae
$D = 256.6 - 11.616\ JFT + 4.44\ JFR - 44.78\ X - 9.65\ Y + 4.304\ X^2 + 0.947\ Y^2 + 2.308\ XY + 0.1353\ Z$
50.1% variance accounted for.
(74.03% of the site variance is accounted for by X, Y, X^2, Y^2, XY, Z)

Macrosiphum euphorbiae
$D = 207.9 - 8.536\ JFT + 5.31\ JFR - 36.22\ X - 5.25\ Y + 3.719\ X^2 + 0.348\ Y^2 + 2.054\ XY + 0.1279\ Z$
51.4 % variance accounted for.
(77.54% of the site variance is accounted for by X, Y, X^2, Y^2, XY, Z)

Nasonovia ribisnigri
$D = 262.6 - 4.246\ JFT - 1.68\ JFR - 48.56\ X + 5.75\ Y + 5.36\ X^2 + 0.058\ Y^2 - 0.279\ XY + 0.1209\ Z$
25.2 % variance accounted for.
(66.83% of the site variance is accounted for by X, Y, X^2, Y^2, XY, Z)

Table 5. Observed and predicted Julian dates of first record for 1986

a) Data (D = observed date of first flight in 1986):

Site	……..D ……			JFtemp	lgJFrain	X	Y	Z
	Mp	*Me*	*Nr*					
1 Rothamsted	193	175	165	0.350	4.710	5.133	2.134	119
2 Wye	182	160	168	1.100	4.763	6.054	1.470	43
3 Broom's Barn	175	167	189	0.800	4.225	5.754	2.656	70
4 Newcastle	213	181	269	1.750	4.530	4.202	5.911	93
5 Dundee	172	170	215	1.250	4.719	3.341	7.300	20
6 East Craigs	219	177	157	0.950	4.863	3.181	6.737	60
7 Starcross	189	151	179	2.100	4.612	2.972	0.821	12
8 Elgin	179	176	165	1.200	4.534	3.185	8.625	30
9 Hereford	205	176	163	1.150	4.521	3.564	2.476	84
10 Preston	196	173	167	0.450	5.449	3.498	4.401	15
11 Ayr	192	178	266	1.600	4.799	2.378	6.233	46
12 Writtle	177	153	164	1.150	4.748	5.676	2.067	38
13 Kirton	194	175	153	0.850	4.498	5.297	3.395	3
14 Long Ashton	191	162	162	.850	4.854	3.536	1.698	46
15 High Mowthorpe	207	181	216	-0.250	4.828	4.888	4.686	171
16 Silwood	167	167	162	1.200	4.695	4.945	1.687	64
17 Rosewarne	178	140	181	3.850	5.198	1.642	0.411	75
18 Aberystwyth	195	165	160	1.900	5.101	2.632	2.837	40
19 Shardlow	196	137	163	0.800	4.371	4.438	3.304	38

b) *Myzus persicae*

Site	Predicted D	upper 95%	lower 95%	Observed D
1	182	233	132	193
2	166	216	115	182
3	177	228	126	175
4	190	240	140	213
5	200	251	150	172
6	204	254	154	219
7	158	208	107	189
8	218	269	168	179
9	172	222	122	205
10	185	236	134	196
11	194	245	143	192
12	165	215	115	177
13	170	221	120	194
14	159	209	109	191
15	216	267	166	207
16	162	212	111	167
17	181	232	130	178
18	172	222	122	195
19	170	220	120	196

c) *Macrosiphum euphorbiae*

Site	Predicted D	upper 95%	lower 95%	Observed D
1	170	206	135	175
2	158	193	122	160
3	167	203	132	167
4	175	210	139	181
5	176	211	140	170
6	180	215	145	177
7	142	178	107	151
8	185	221	149	176
9	158	194	123	176
10	169	205	133	173
11	172	207	136	178
12	157	193	122	153
13	161	196	125	175
14	147	182	111	162
15	199	235	164	181
16	152	187	117	167
17	162	198	126	140
18	158	193	122	165
19	158	194	123	137

d) *Nasonovia ribisnigri*

Site	Predicted D	upper 95%	lower 95%	Observed D
1	169	223	115	165
2	164	218	110	168
3	170	224	116	189
4	178	232	125	269
5	188	241	134	215
6	193	246	139	157
7	155	208	101	179
8	199	253	145	165
9	167	221	114	163
10	171	225	117	167
11	202	256	148	266
12	160	214	106	164
13	160	214	106	153
14	156	209	102	162
15	189	243	134	216
16	156	209	102	162
17	183	238	129	181
18	175	229	121	160
19	162	216	108	163

Table 6. Summary of monitoring data collected in 1999-2000 (*Myzus persicae*).

Myzus persicae	Date of first sample	Date of first aphid	Date of peak aphids pre-crash	No. aphids at peak (20 plants)	Date of crash	Min no. aphids after crash (20 plants)	Date of first aphid post-crash	Date of peak aphids post-crash	No. aphids at peak (20 plants)	Date of last sample
1999										
Sussex	05-May	10-May	15-Jun	114	02-Aug	0	06-Sep	14-Oct	88	14-Oct
Kent	04-May	11-May	11-May	14	24-May	0	07-Jun	21-Jun	83	04-Oct
Essex	31-May	31-May	15-Jun	44	19-Jul	0	27-Jul	01-Sep	28	11-Oct
Warwickshire	29-Apr	05-May	02-Jul	79	27-Jul	0	30-Sep	14-Oct	40	16-Nov
Lincolnshire	28-Apr	02-Jun	30-Jun	50	13-Jul	0	07-Sep	14-Sep	3	18-Oct
Yorkshire	06-Aug						31-Aug	06-Sep	10	18-Oct
2000										
Sussex	08-May	08-May	27-Jun	78	04-Jul	0				18-Aug
Kent	27-Apr	17-May	21-Jun	18	13-Jul	0	19-Jul	02-Aug	6	05-Sep
Essex	12-Jun	20-Jun	26-Jun	92	14-Aug	0	28-Aug	05-Oct	40	10-Oct
Warwickshire	20-Apr	09-May	19-Jun	38	04-Jul	0	09-Aug	13-Oct	8	16-Oct
Lincolnshire	05-May	24-May	05-Jul	29	19-Jul	1	26-Jul	02-Aug	18	05-Oct
Yorkshire	03-May	17-May	21-Jun	22	02-Aug	0				03-Oct

Table 7. Summary of monitoring data collected in 1999-2000 (*Macrosiphum euphorbiae*).

Macrosiphum euphorbiae	**Date of first sample**	**Date of first aphid**	**Date of peak aphids pre-crash**	**No. aphids at peak (20 plants)**	**Date of crash**	**Min no. aphids after crash (20 plants)**	**Date of first aphid post-crash**	**Date of peak aphids post-crash**	**No. aphids at peak (20 plants)**	**Date of last sample**
1999										
Sussex	05-May	10-May	22-Jun	8	26-Jul	0	06-Sep	13-Sep	4	14-Oct
Kent	04-May	04-May	01-Jun	24	07-Jun	2	14-Jun	05-Jul	22	04-Oct
Essex	31-May	31-May	08-Jun	42	15-Jul	0	19-Jul	24-Aug	32	11-Oct
Warwickshire	29-Apr	05-May	01-Jun	294	19-Aug	0				16-Nov
Lincolnshire	28-Apr	05-May	30-Jun	70	09-Aug	0	14-Sep	14-Sep	4	18-Oct
Yorkshire	06-Aug						31-Aug	20-Sep	6	18-Oct
2000										
Sussex	08-May	08-May	05-Jun	26	04-Jul	0				18-Aug
Kent	27-Apr	10-May	10-Jul	12	26-Jul	0				05-Sep
Essex	12-Jun	20-Jun	10-Jul	174	31-Jul	2	08-Aug	10-Oct	316	10-Oct
Warwickshire	20-Apr	02-May	19-Jun	88	18-Aug	0	13-Sep	4-Oct	6	16-Oct
Lincolnshire	05-May	17-May	21-Jun	36	12-Jul	6	19-Jul	16-Aug	30	05-Oct
Yorkshire	03-May	03-May	21-Jun	412	02-Aug	0				03-Oct

Table 8. **Summary of monitoring data collected in 1999-2000 (*Nasonovia ribisnigri*)**

Nasonovia ribisnigri	Date of first sample	Date of first aphid	Date of peak aphids pre-crash	No. aphids at peak (20 plants)	Date of crash	Min no. aphids after crash (20 plants)	Date of first aphid post-crash	Date of peak aphids post-crash	No. aphids at peak (20 plants)	Date of last sample
1999										
Sussex	05-May	08-Jun	12-Jul	292	09-Aug	0	14-Oct	14-Oct	21	14-Oct
Kent	04-May	07-Jun	07-Jun	26	28-Jun	6	05-Jul	02-Aug	350	04-Oct
Essex	31-May	31-May	01-Jul	582	19-Jul	0	10-Aug	24-Aug	210	11-Oct
Warwickshire	29-Apr						10-Sep	02-Nov	50	16-Nov
Lincolnshire	28-Apr	05-May	23-Jun	70	20-Jul	0	27-Jul	09-Aug	238	18-Oct
Yorkshire	06-Aug						16-Aug	06-Sep	136	18-Oct
2000										
Sussex	08-May	15-May	21-Jun	244	04-Jul	28	11-Jul	20-Jul	59	18-Aug
Kent	27-Apr	31-May	13-Jul	144	16-Aug	2				05-Sep
Essex	12-Jun	20-Jun	10-Jul	28	21-Aug	0	28-Aug	10-Oct	90	10-Oct
Warwickshire	20-Apr	09-May	11-Jul	4	09-Aug	0	13-Sep	13-Sep	2	16-Oct
Lincolnshire	05-May	31-May	21-Jun	6	28-Jun	0	17-Aug	30-Aug	32	05-Oct
Yorkshire	03-May	07-Jun	28-Jun	12	04-Jul	0	12-Jul	29-Aug	31	03-Oct

Table 9. Summary of monitoring data collected in 1999-2000 (nymphs).

Nymphs	Date of first sample	Date of first aphid	Date of peak aphids pre-crash	No. aphids at peak (20 plants)	Date of crash	Min no. aphids after crash (20 plants)	Date of first aphid post-crash	Date of peak aphids post-crash	No. aphids at peak (20 plants)	Date of last sample
1999										
Sussex	05-May	10-May	12-Jul	1620	26-Jul	0	06-Sep	14-Oct	169	14-Oct
Kent	04-May	04-May	02-Aug	2176	23-Aug	8	06-Sep	04-Oct	1012	04-Oct
Essex	31-May	31-May	21-Jun	6406	19-Jul	0	27-Jul	24-Aug	2224	11-Oct
Warwickshire	29-Apr	29-Apr	09-Jun	3350	03-Aug	4	13-Aug	26-Oct	444	16-Nov
Lincolnshire	28-Apr	05-May	23-Jun	496	20-Jul	4	27-Jul	09-Aug	418	18-Oct
Yorkshire	06-Aug						16-Aug	06-Sep	918	18-Oct
2000										
Sussex	08-May	08-May	21-Jun	2194	04-Jul	112	11-Jul	2-Aug	520	18-Aug
Kent	27-Apr	03-May	13-Jul	1904	16-Aug	16				05-Sep
Essex	12-Jun	20-Jun	10-Jul	1204	14-Aug	12	21-Aug	10-Oct	2290	10-Oct
Warwickshire	20-Apr	02-May	05-Jun	494	22-Aug	0	05-Sep	10-Oct	64	16-Oct
Lincolnshire	05-May	17-May	21-Jun	274	12-Jul	23	19-Jul	02-Aug	220	05-Oct
Yorkshire	03-May	03-May	21-Jun	2608	09-Aug	0	16-Aug	29-Aug	157	03-Oct

Table 10. Summary of monitoring data collected in 1999-2000 (all aphids).

All aphids	Date of first sample	Date of first aphid	Date of peak aphids pre-crash	No. aphids at peak (20 plants)	Date of crash	Min no. aphids after crash (20 plants)	Date of first aphid post-crash	Date of peak aphids post-crash	No. aphids at peak (20 plants)	Date of last sample
1999										
Sussex	05-May	10-May	12-Jul	1914	16-Aug	0	31-Aug	14-Oct	278	14-Oct
Kent	04-May	04-May	02-Aug	2530	23-Aug	12	31-Aug	04-Oct	1212	04-Oct
Essex	31-May	31-May	21-Jun	7082	19-Jul	4	27-Jul	24-Aug	2630	11-Oct
Warwickshire	29-Apr	29-Apr	09-Jun	3600	25-Aug	0	03-Sep	26-Oct	508	16-Nov
Lincolnshire	28-Apr	05-May	23-Jun	632	20-Jul	5	27-Jul	09-Aug	656	18-Oct
Yorkshire	06-Aug						16-Aug	06-Sep	1066	18-Oct
2000										
Sussex	08-May	08-May	21-Jun	2444	04-Jul	140	11-Jul	2-Aug	572	18-Aug
Kent	27-Apr	03-May	13-Jul	2088	16-Aug	22				05-Sep
Essex	12-Jun	20-Jun	10-Jul	1448	14-Aug	22	21-Aug	10-Oct	2723	10-Oct
Warwickshire	20-Apr	02-May	05-Jun	560	22-Aug	0	05-Sep	10-Oct	78	16-Oct
Lincolnshire	05-May	17-May	21-Jun	344	12-Jul	34	19-Jul	02-Aug	268	05-Oct
Yorkshire	03-May	03-May	21-Jun	3032	09-Aug	16	16-Aug	29-Aug	190	03-Oct

Table 11. ***Nasonovia ribisnigri*** **- correlations between the timing of key colonisation events (first aphid, peak aphids, crash) and accumulated day-degrees.**

	Day-degrees base 4.4°C				**Day-degrees base 0°C**			
	1 Jan-30 May	**I Jan-7 Jul**	**1 Feb-30 May**	**1 Feb-7 Jul**	**1 Jan-30 May**	**I Jan-7 Jul**	**1 Feb-30 May**	**1 Feb-7 Jul**
First aphid								
R^2	0.1451		0.2021		0.102		0.1813	
R	0.381		0.450		0.319		0.426	
p (19 df)	NS		<0.05		NS		NS	
Peak aphids								
R^2	0.2984	0.2534	0.3118	0.2681	0.3725	0.3227	0.3585	0.319
R	0.546	0.503	0.558	0.518	0.610	0.568	0.599	0.565
p (19 df)	<0.02	<0.02	<0.01	<0.02	<0.01	<0.01	<0.01	<0.01
Crash								
R^2		0.0435		0.0349		0.0849		0.0571
R		0.209		0.187		0.291		0.239
p (19 df)		NS		NS		NS		NS

FIGURES

Figure 1. Map showing locations of Rothamsted Insect Survey suction traps.

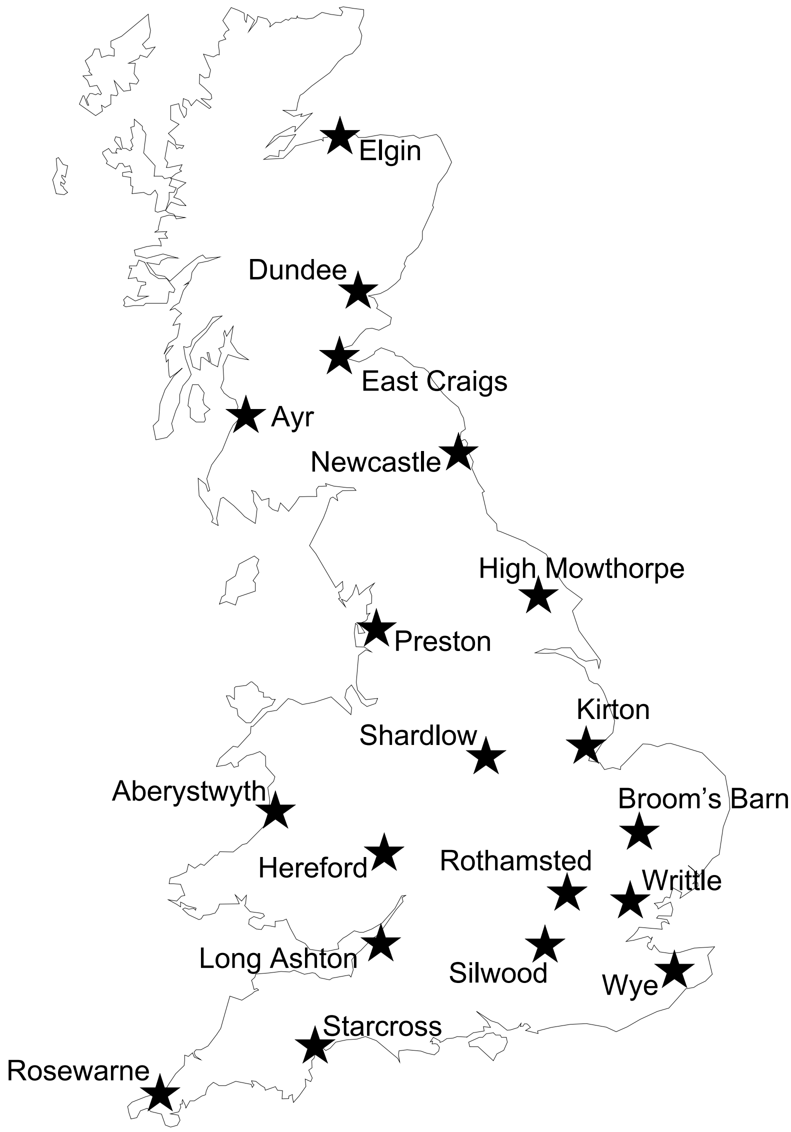


Figure 2. Correlations between *M. persicae* and *M. euphorbiae* for the date (no. days from 1 January) when the first aphid was captured in suction traps.

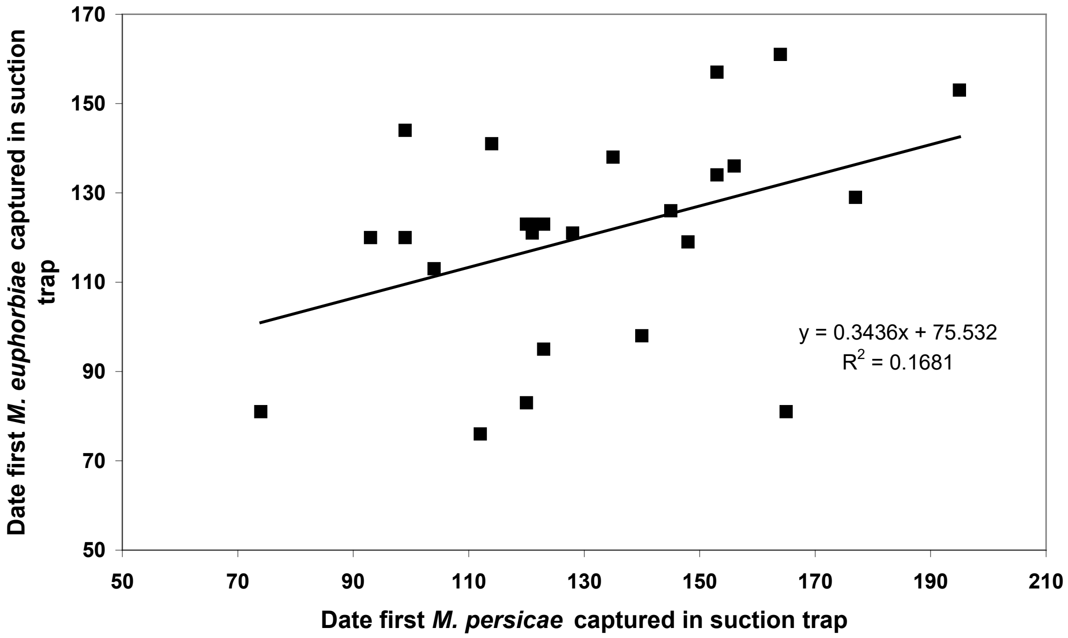


Figure 3. Correlations between *M. persicae* and *M. euphorbiae* and *N. ribisnigri* in the date (no. days from 1 January) that the first aphid was found on plants.

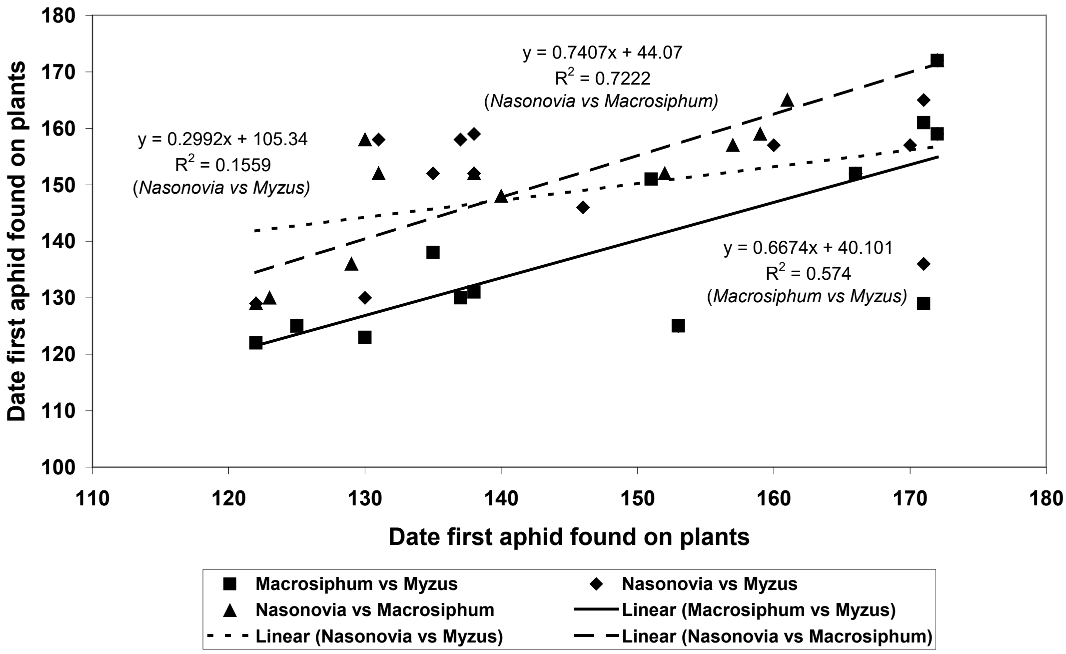


Figure 4. Correlations between *M. persicae* and either *M. euphorbiae* and *N. ribisnigri* in the date (no. days from 1 January) when peak numbers of aphids were found.

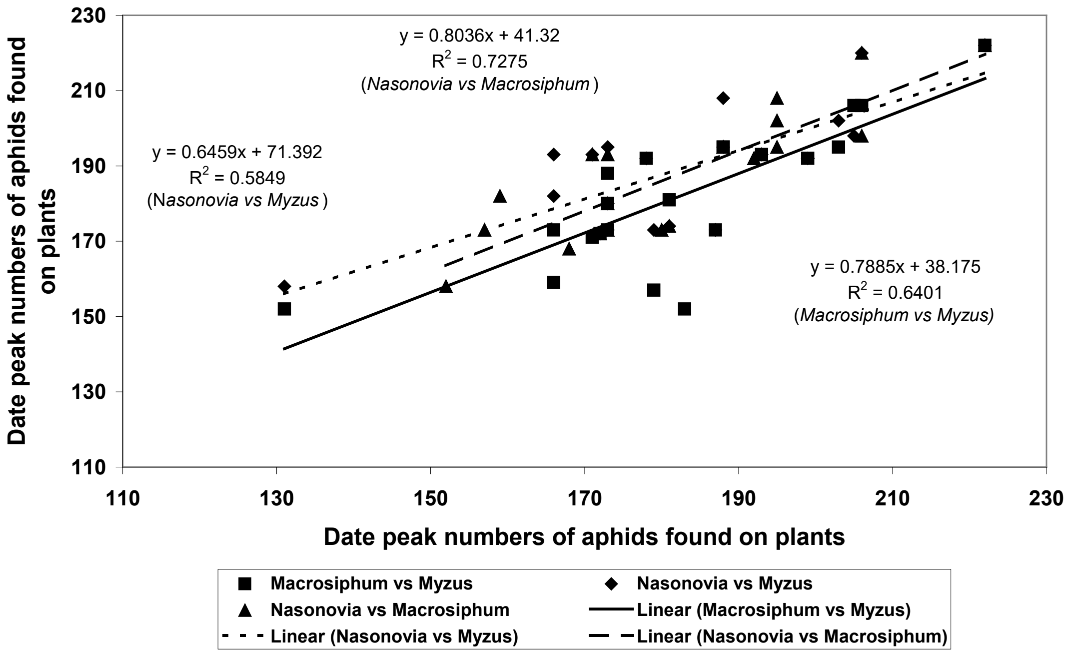


Figure 5. Comparison of plant sampling records with the forecast of first capture of *Myzus persicae* in suction traps (dates shown as no. days from 1 January).

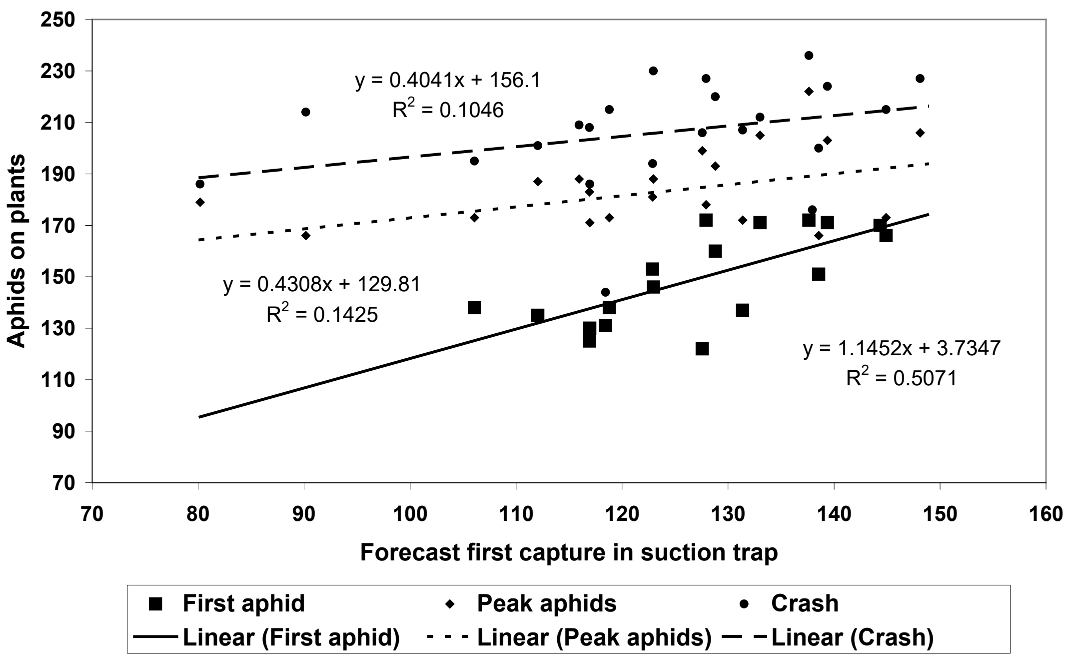


Figure 6. Comparison of plant sampling records with the forecast of first capture of *Macrosiphum euphorbiae* in suction traps (Dates shown as no. days from 1 January).

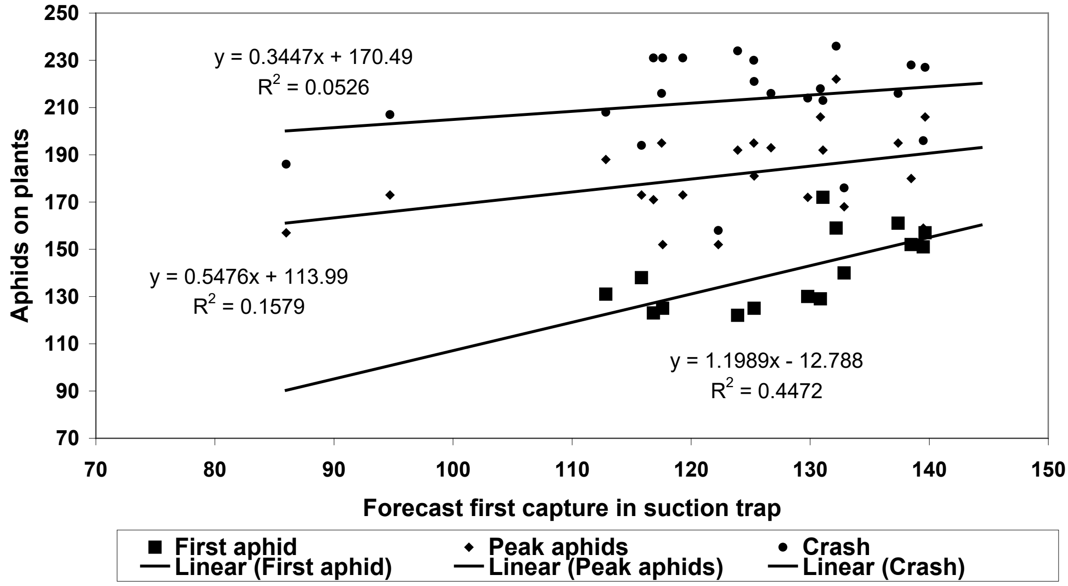


Figure 7. Dates of key colonisation events on plants plotted against the dates on which the first aphid was captured in the nearest suction trap to each site (*Myzus persicae*) (dates shown as no. days from 1 January).

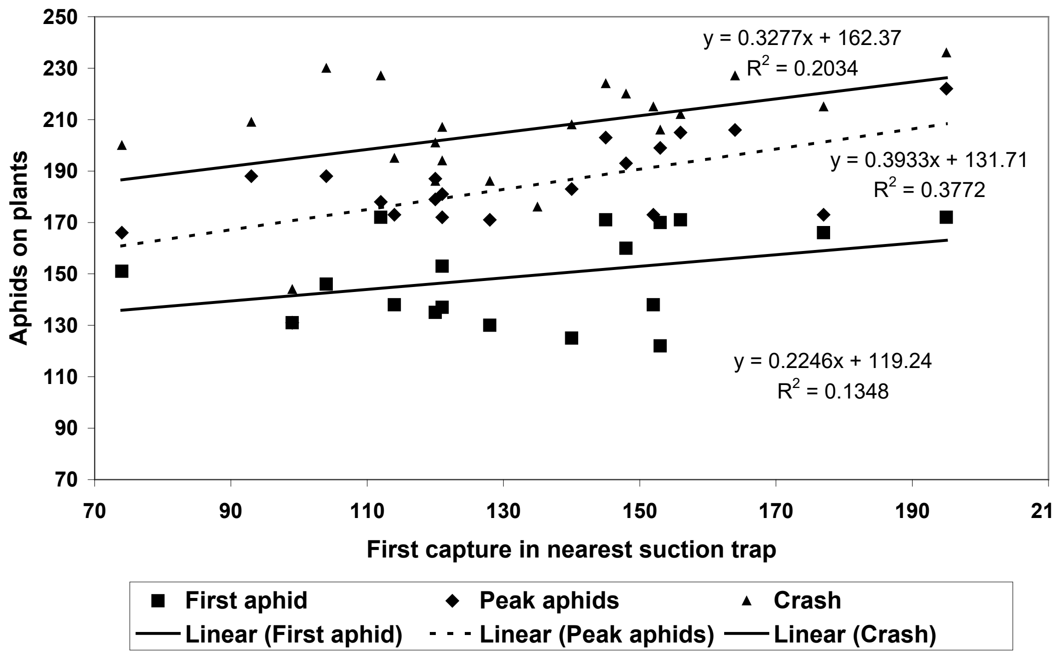


Figure 8. **Dates of key colonisation events on plants plotted against the dates on which the first aphid was captured in the nearest suction trap to each site (*Macrosiphum euphorbiae*). (dates shown as no. days from 1 January)**

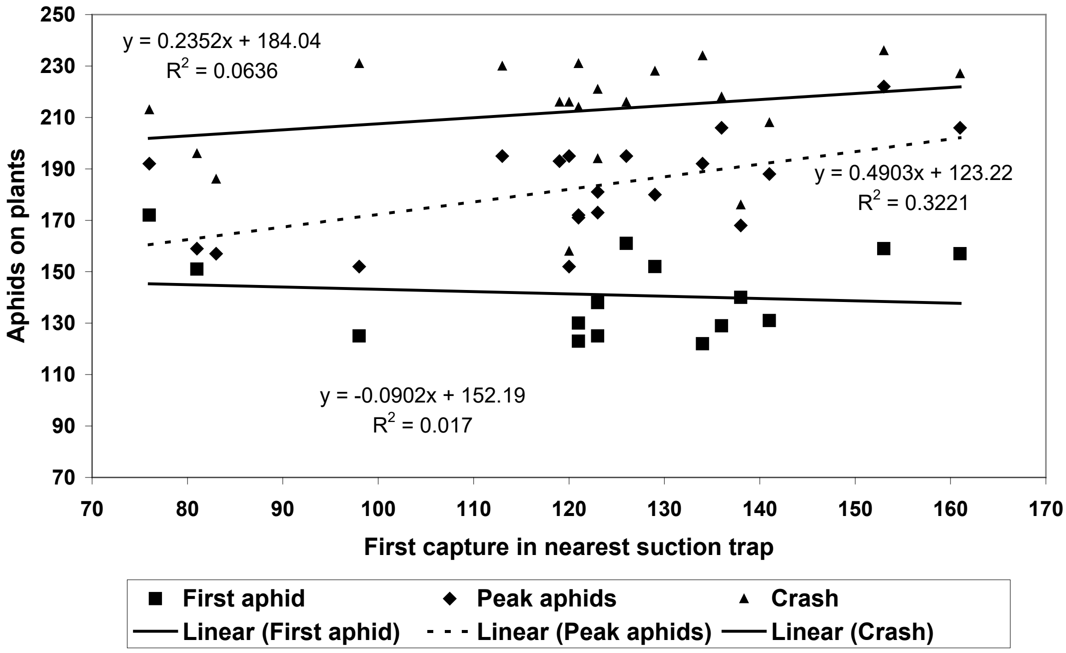


Figure 9. **The dates (shown as no. days from 1 January) when the first adult *N. ribisnigri* were found on plants plotted against the numbers of day-degrees (base 4.4°C) accumulated from 1 February to 30 May (the mean date when the first aphid was found).**

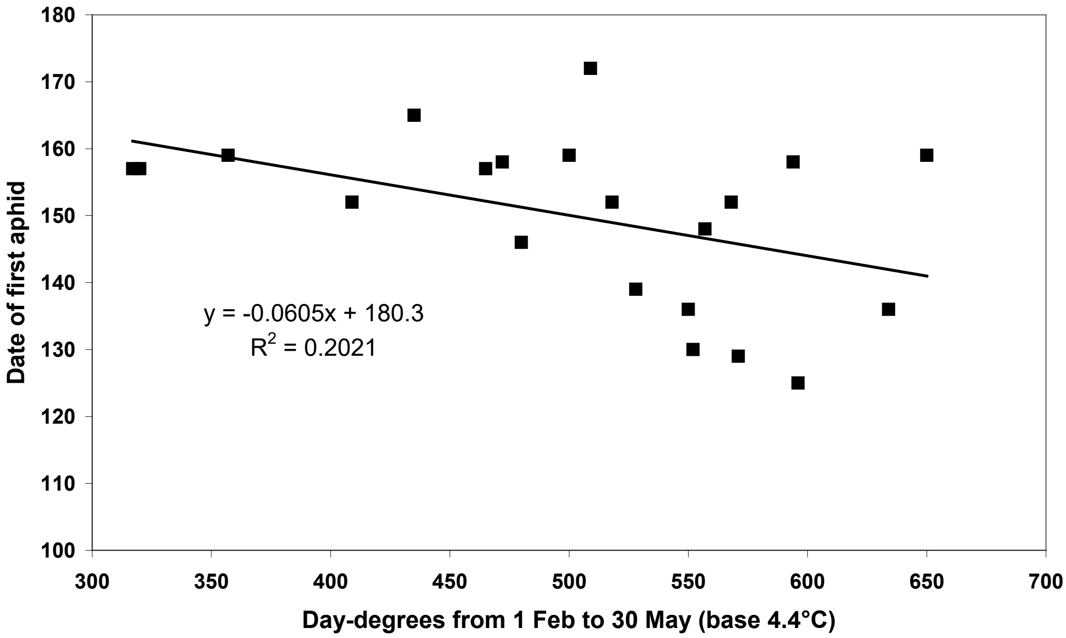


Figure 10. **The dates (shown as no. days from 1 January) when peak numbers of adult *N. ribisnigri* were found on plants plotted against the numbers of day-degrees (base 4.4°C) accumulated from 1 February to 30 May (the mean date when the first aphid was found).**

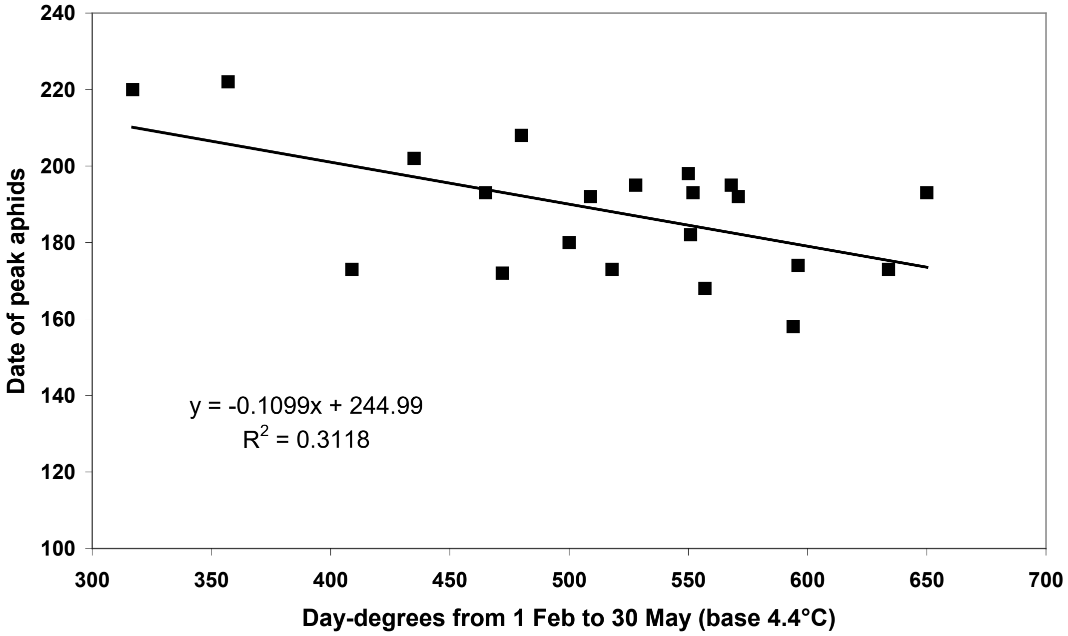


Figure 11. **The dates (shown as no. days from 1 January)when peak numbers of adult *N. ribisnigri* were found on plants plotted against the numbers of day-degrees (base 4.4°C) accumulated from 1 February to 7 July (the mean date when peak numbers of aphids were found).**

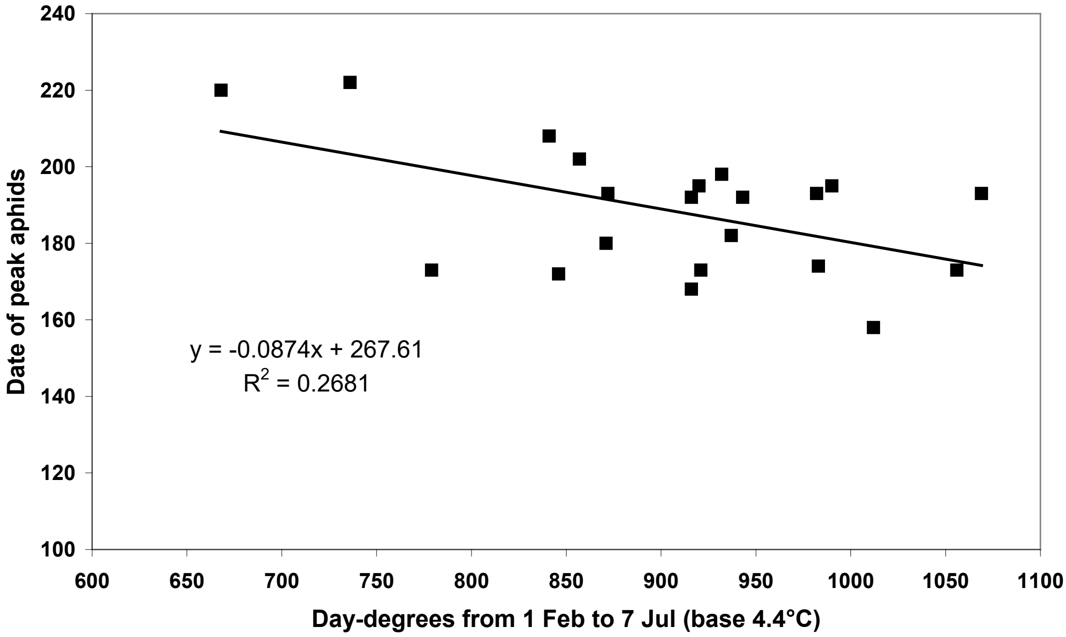
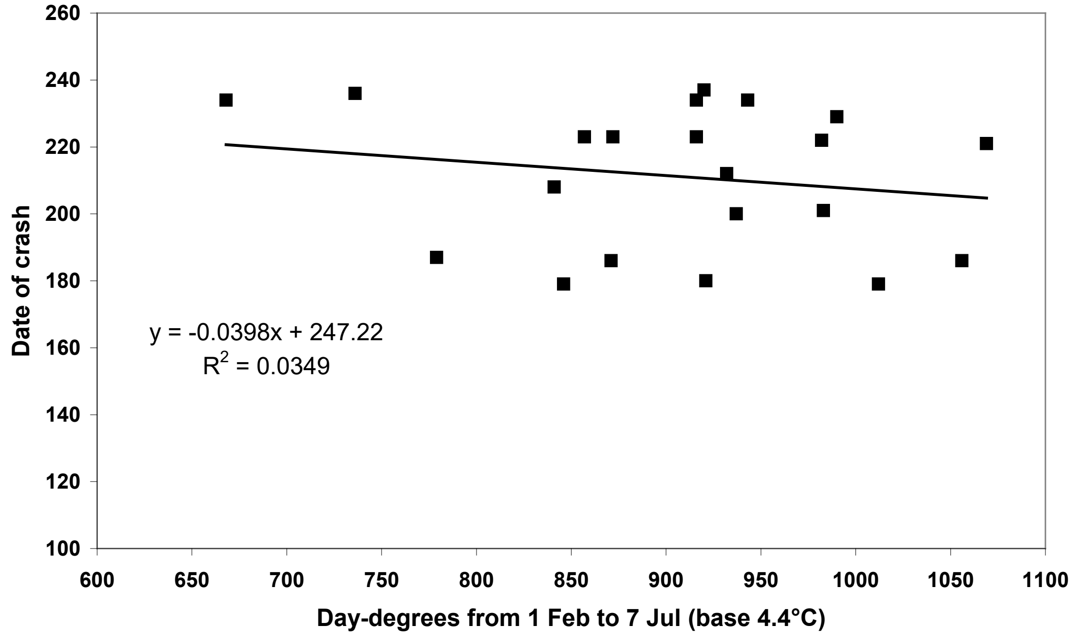
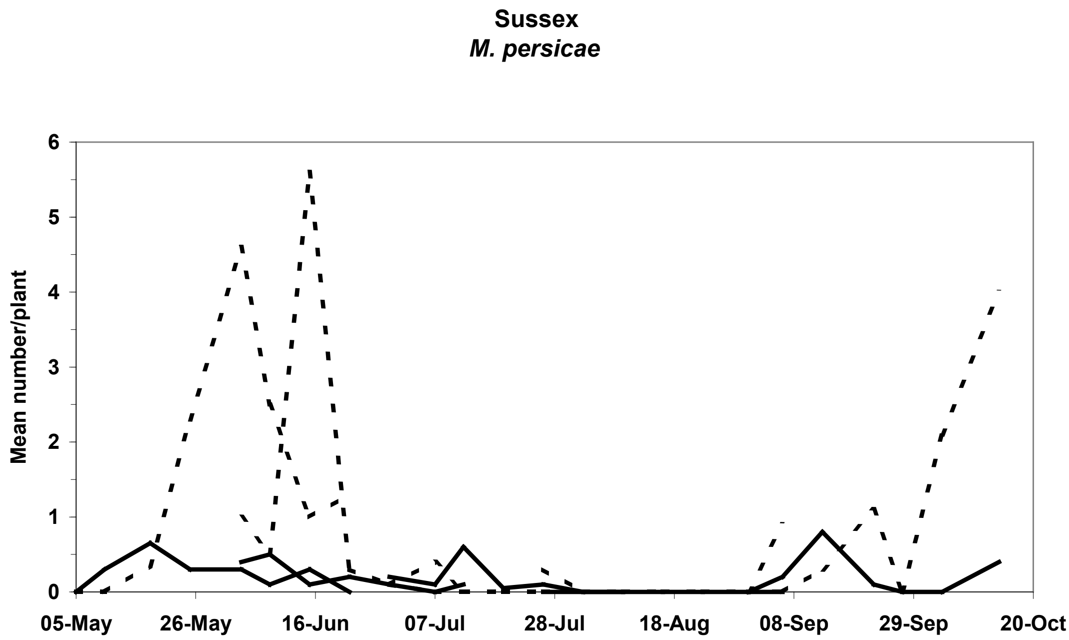


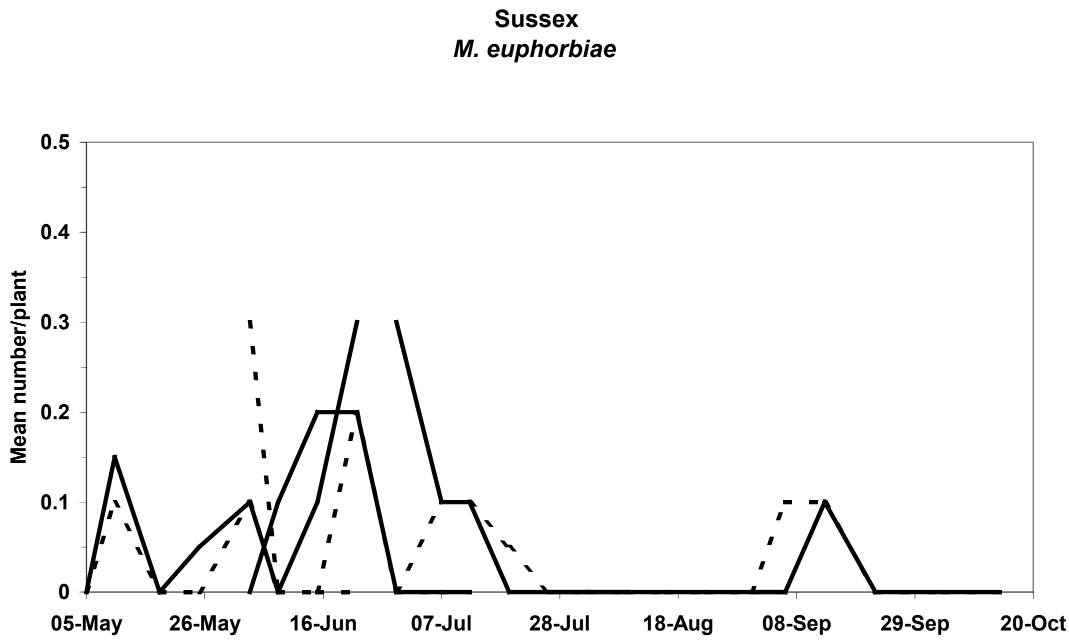
Figure 12. The dates (shown as no. days from 1 January) when adult *N. ribisnigri* infestations crashed plotted against the numbers of day-degrees (base 4.4°C) accumulated from 1 February to 7 July (the mean date when peak numbers of aphids were found).



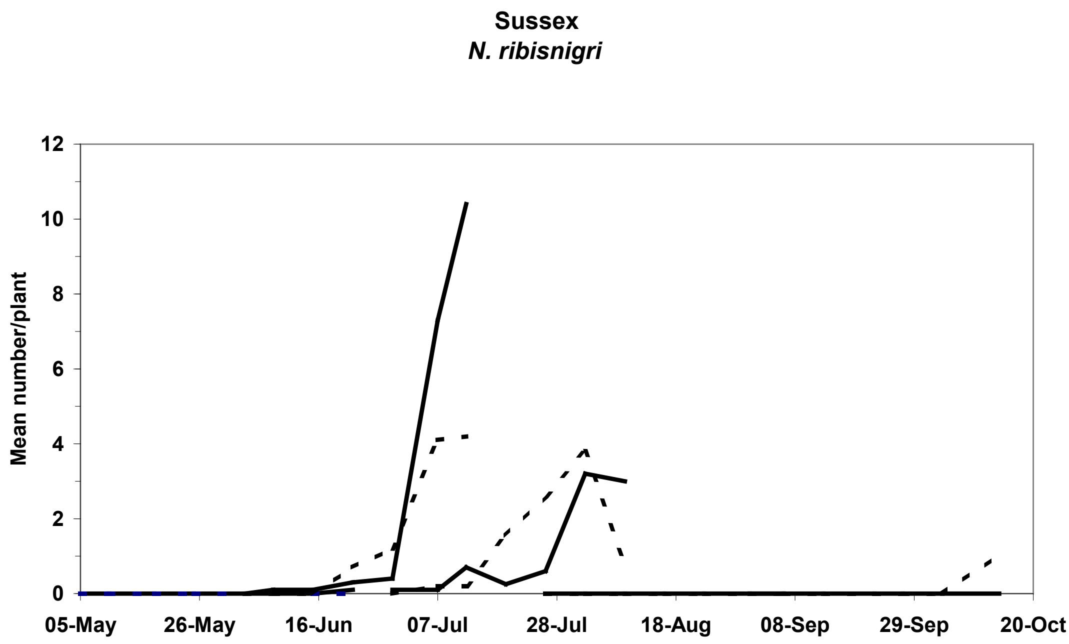
APPENDIX

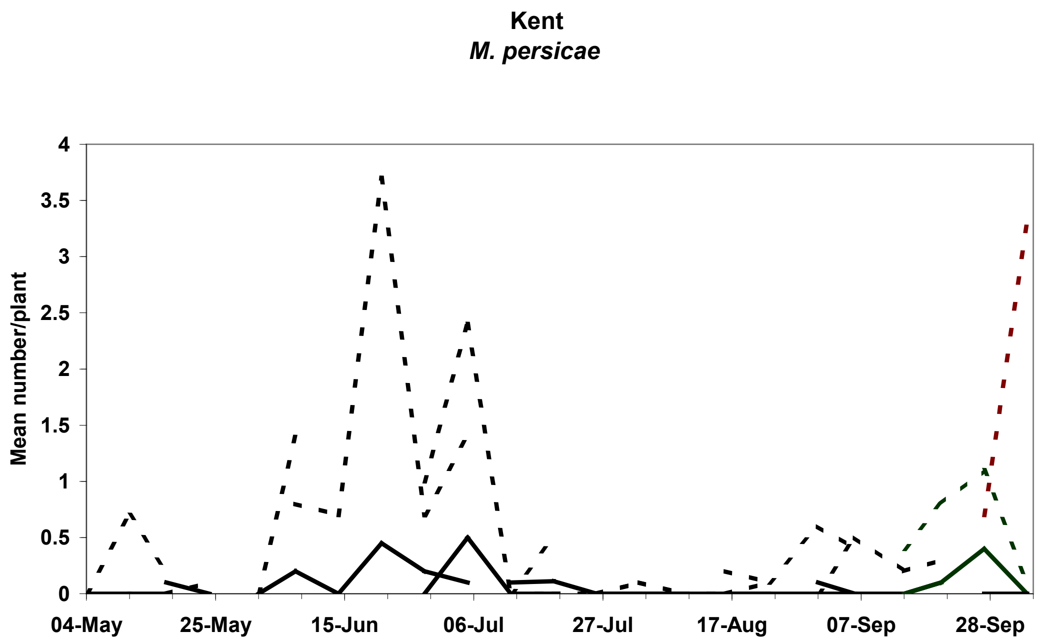
Appendix 1. The numbers of aphids found on untreated lettuce plants in 1999. (Solid lines = alates, dashed lines = apterae).





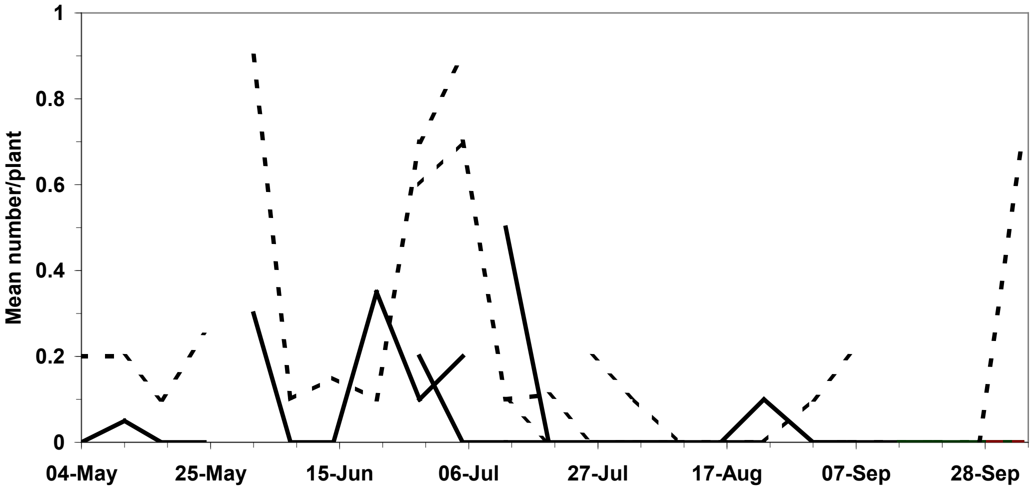
Appendix 1. The numbers of aphids found on untreated lettuce plants in 1999. (Solid lines = alates, dashed lines = apterae).



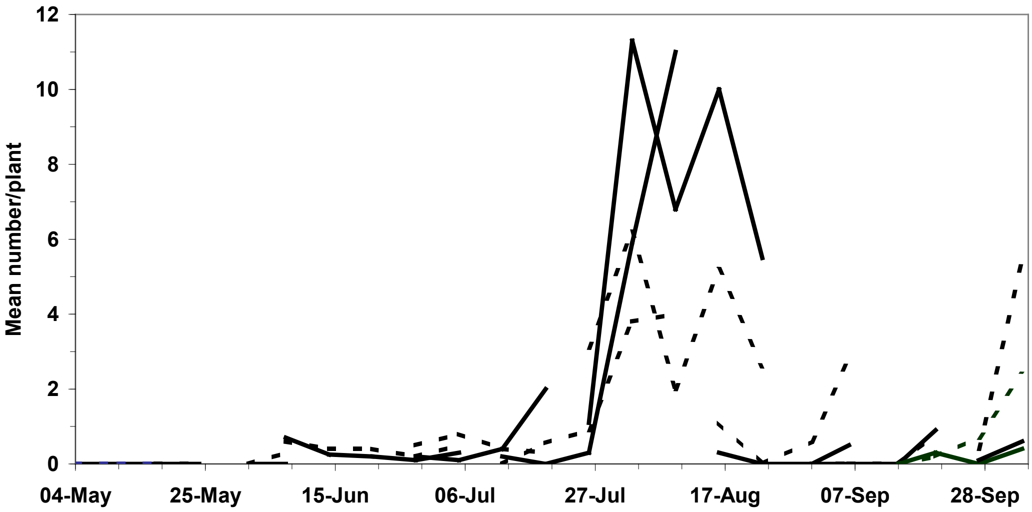


Appendix 1. The numbers of aphids found on untreated lettuce plants in 1999. (Solid lines = alates, dashed lines = apterae).

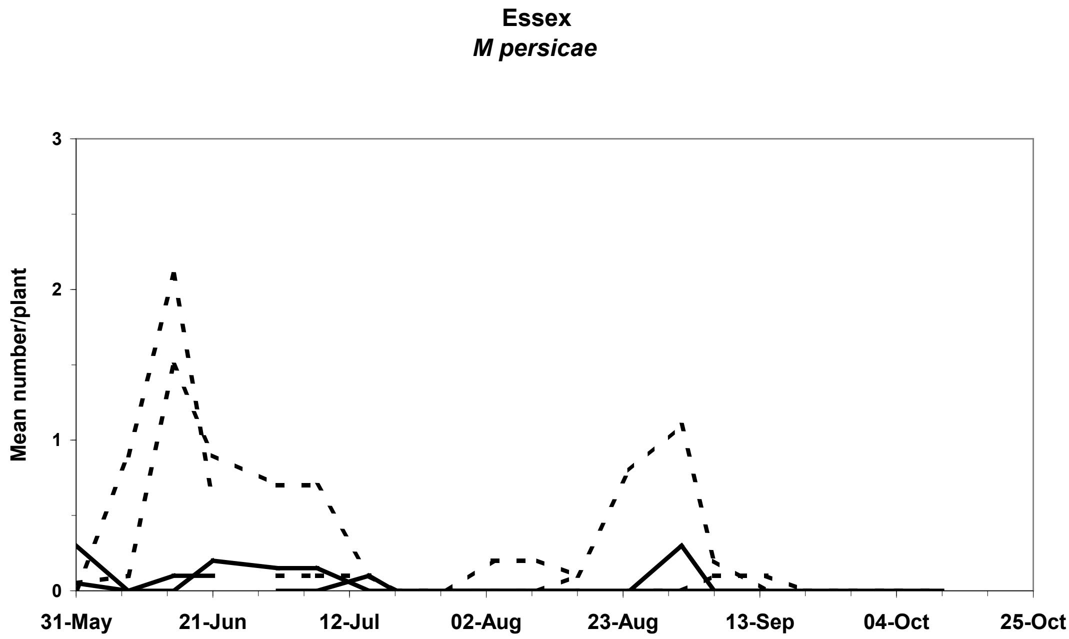
Kent
M. euphorbiae

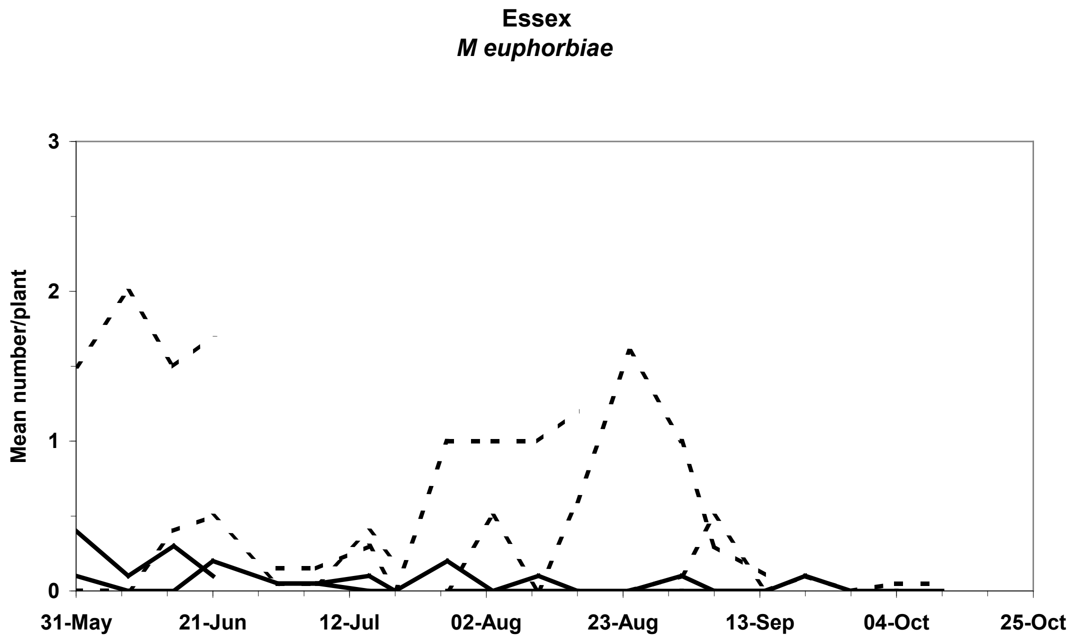


Kent
N. ribisnigri

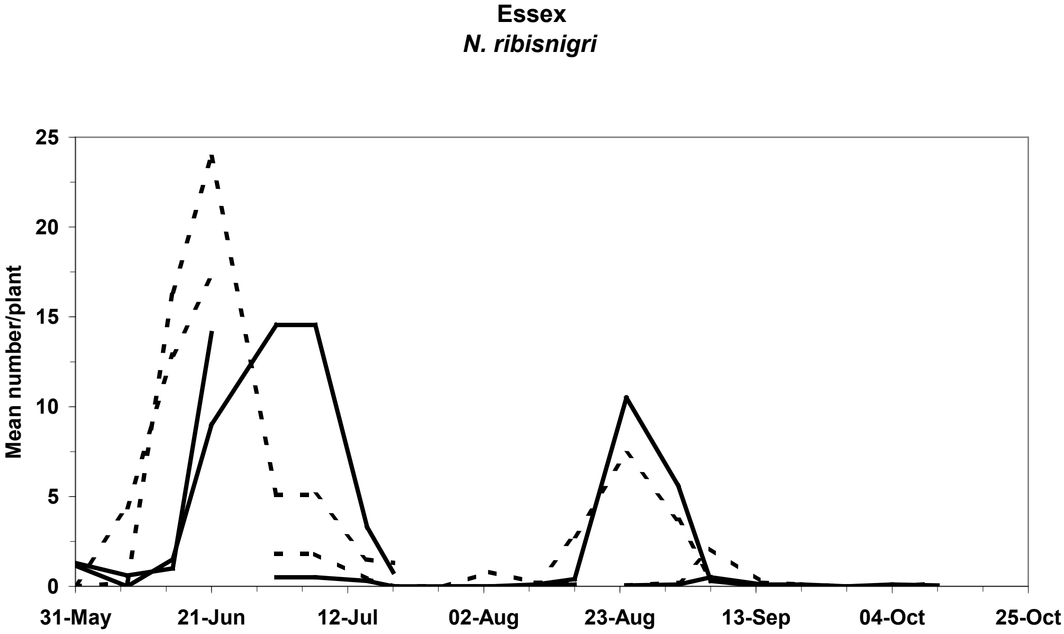


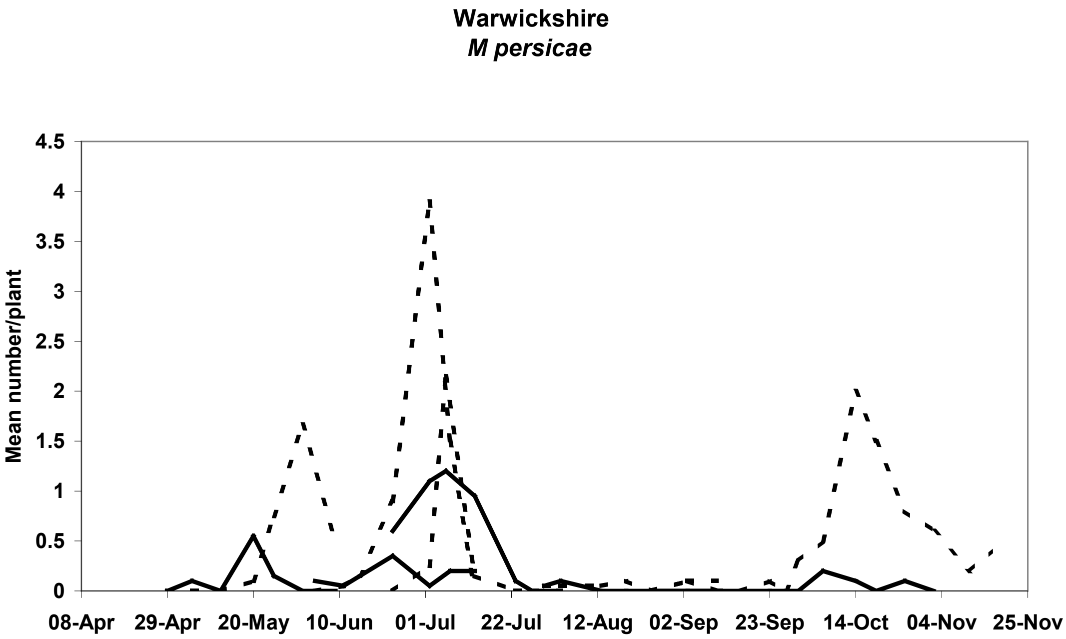
Appendix 1. The numbers of aphids found on untreated lettuce plants in 1999. (Solid lines = alates, dashed lines = apterae).



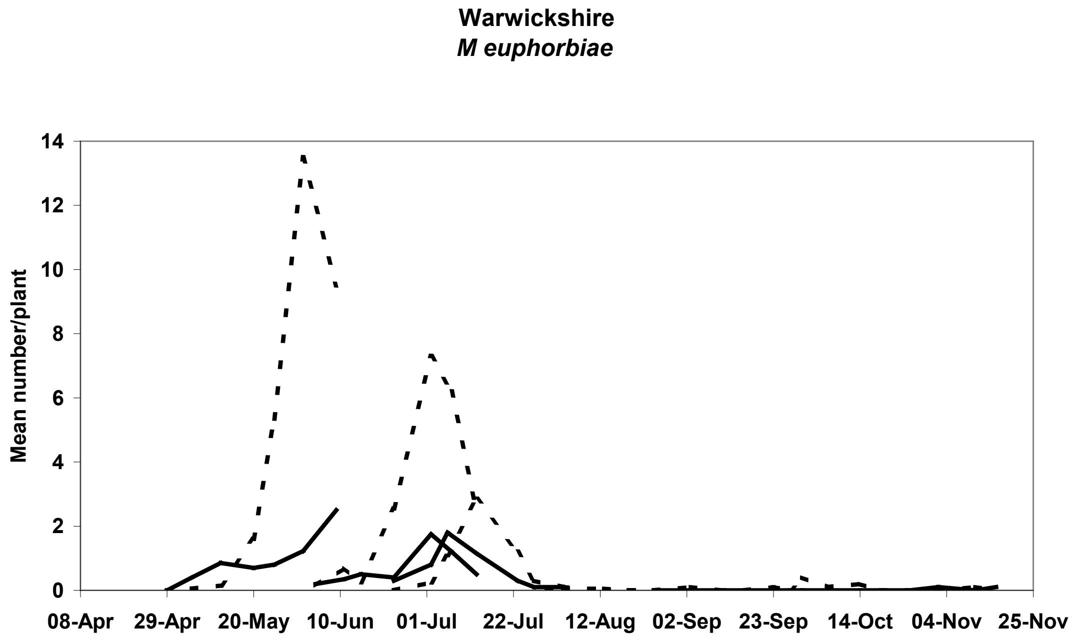


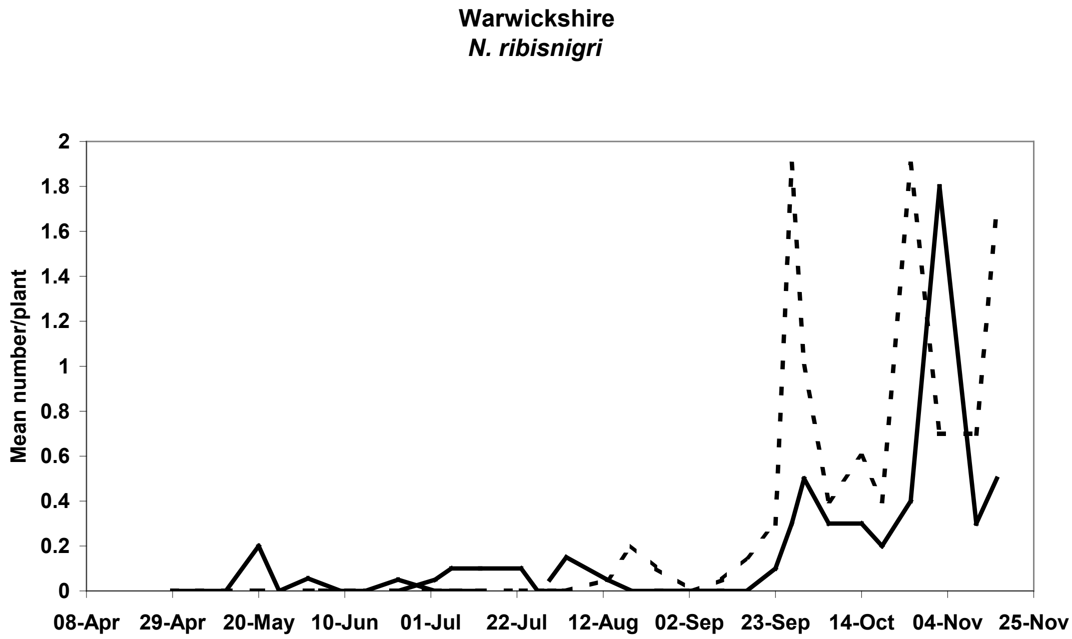
Appendix 1. The numbers of aphids found on untreated lettuce plants in 1999. (Solid lines = alates, dashed lines = apterae).



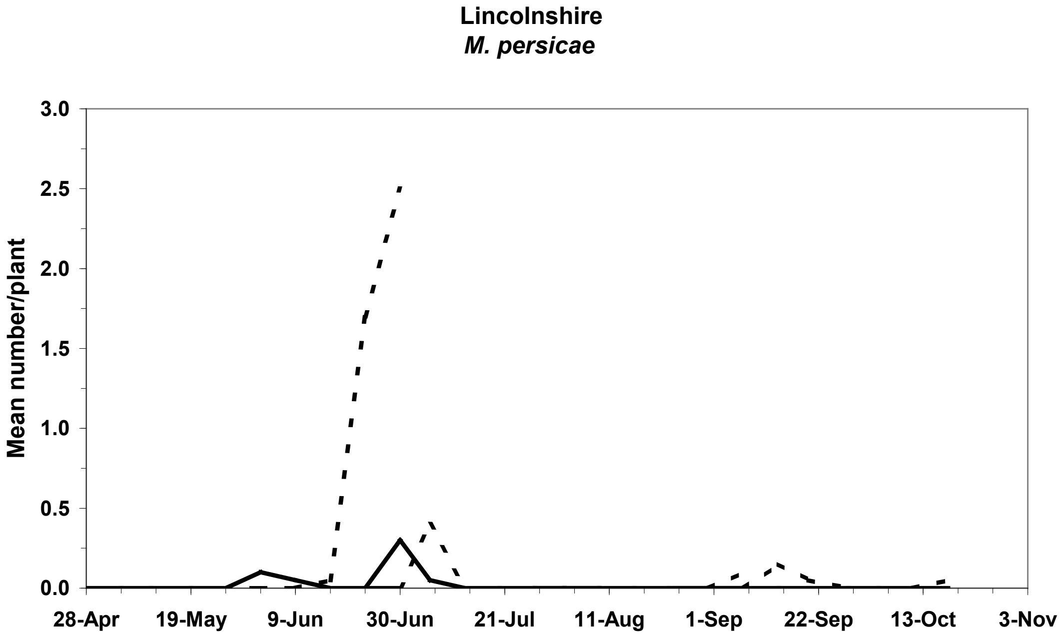


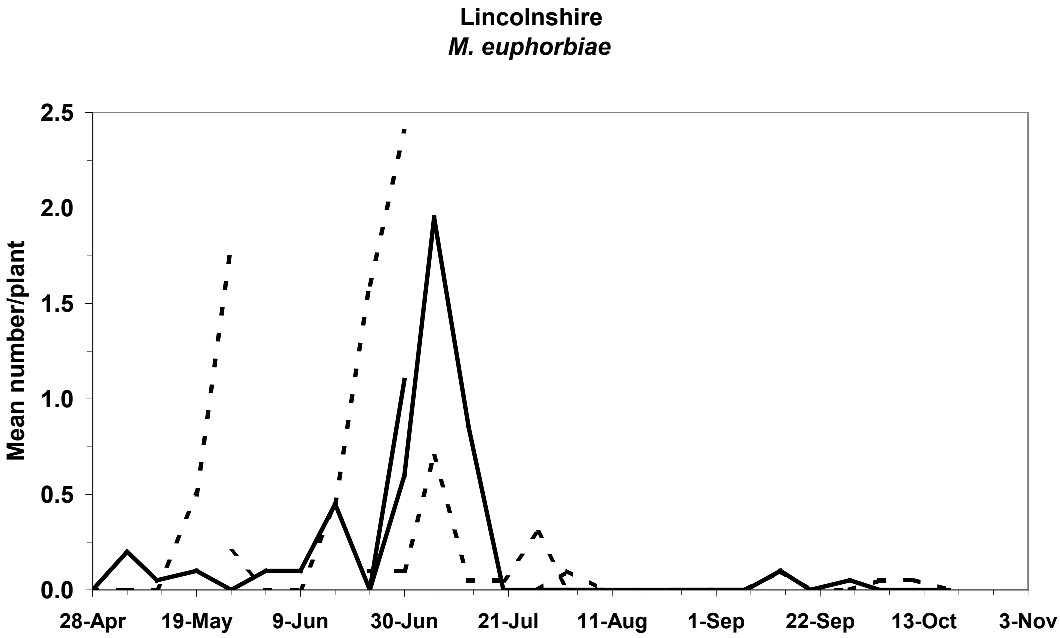
Appendix 1. The numbers of aphids found on untreated lettuce plants in 1999. (Solid lines = alates, dashed lines = apterae).



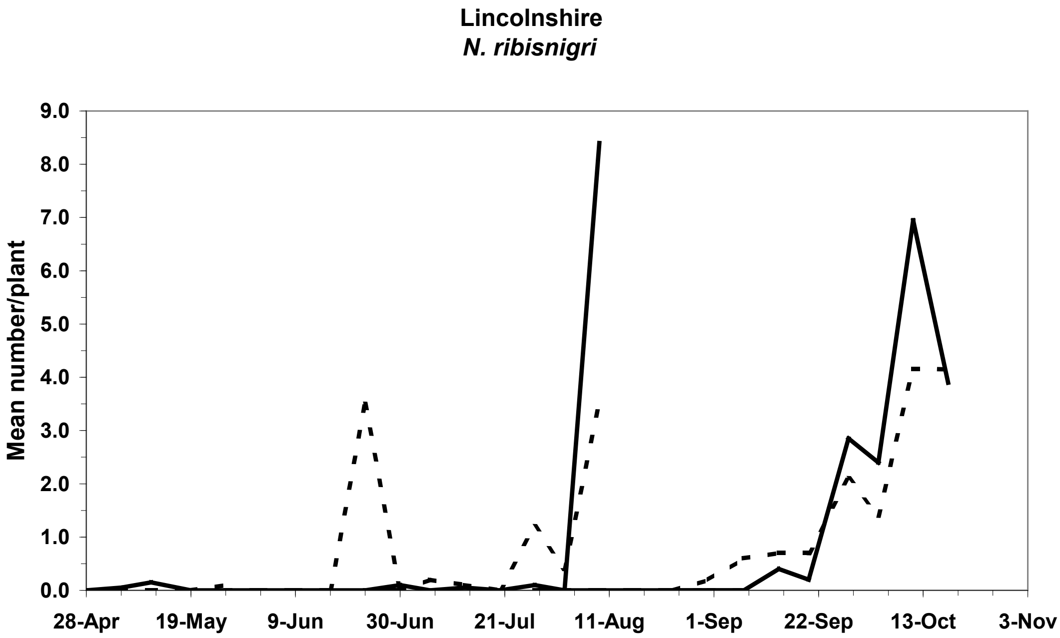


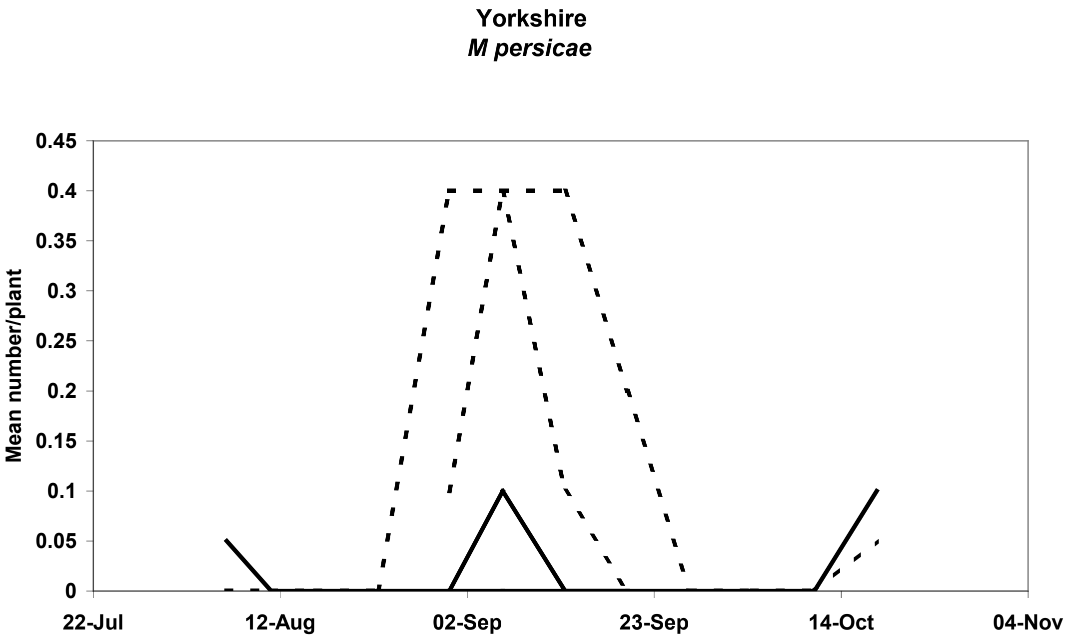
Appendix 1. The numbers of aphids found on untreated lettuce plants in 1999. (Solid lines = alates, dashed lines = apterae).



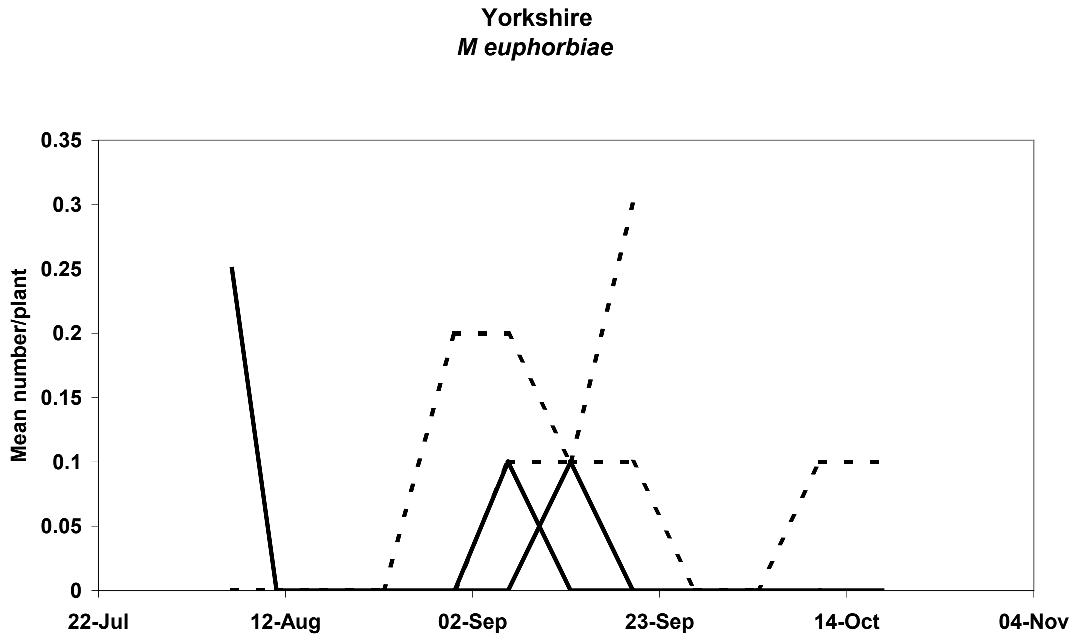


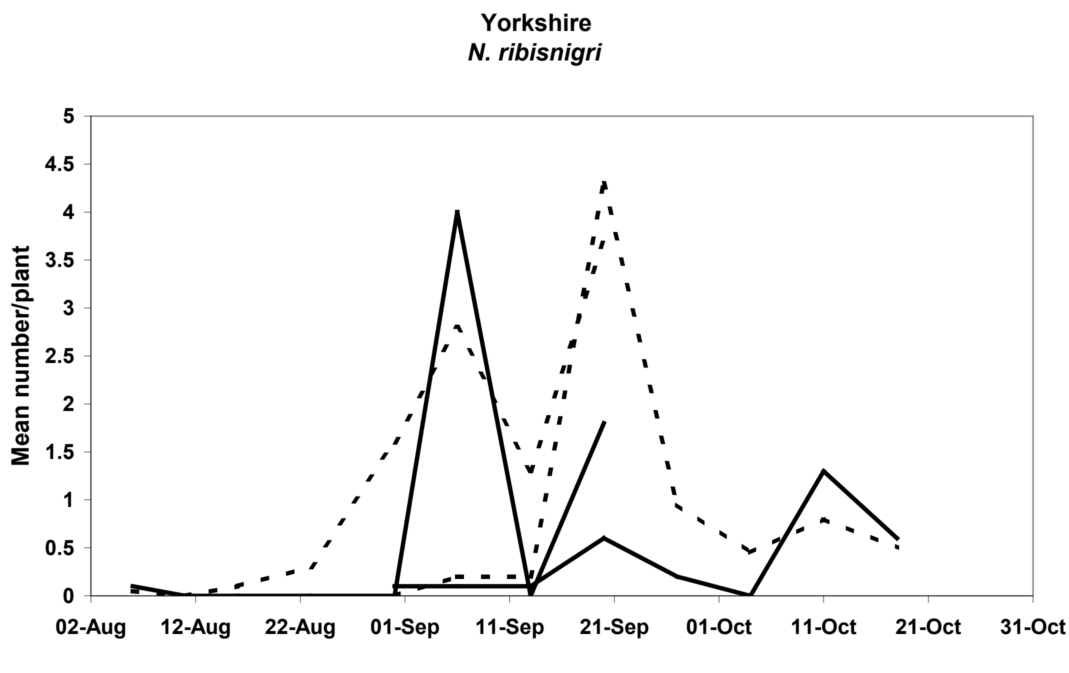
Appendix 1. The numbers of aphids found on untreated lettuce plants in 1999. (Solid lines = alates, dashed lines = apterae).



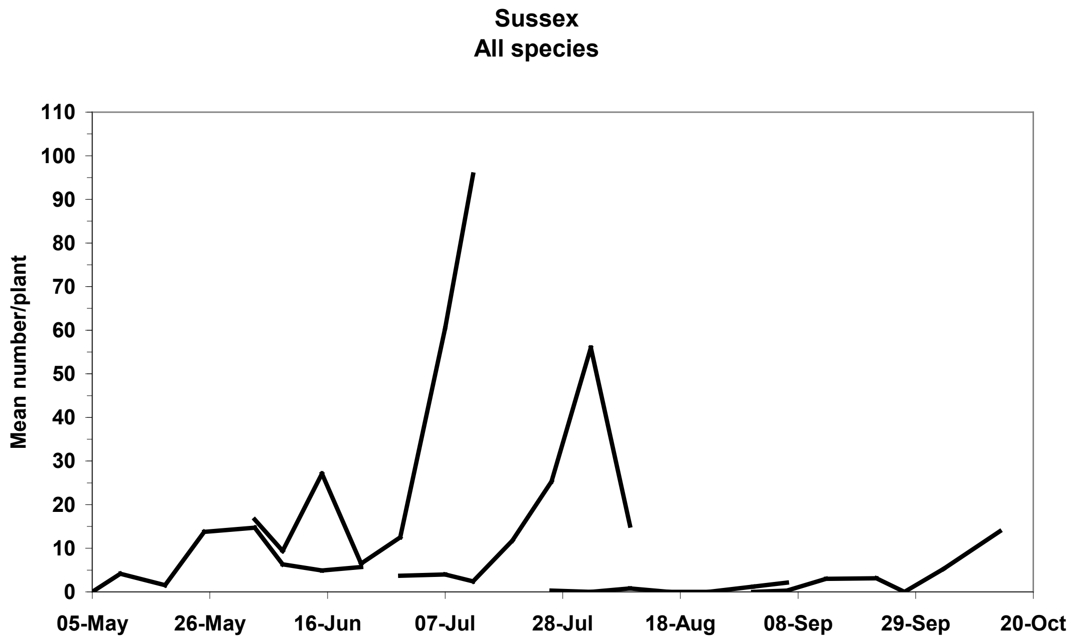


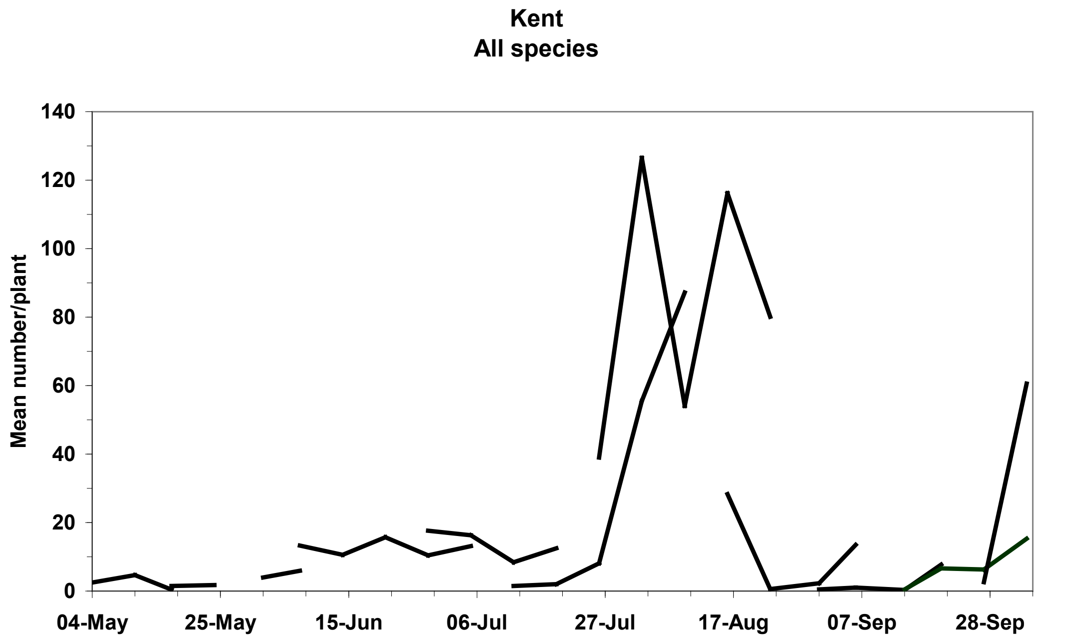
Appendix 1. The numbers of aphids found on untreated lettuce plants in 1999. (Solid lines = alates, dashed lines = apterae).



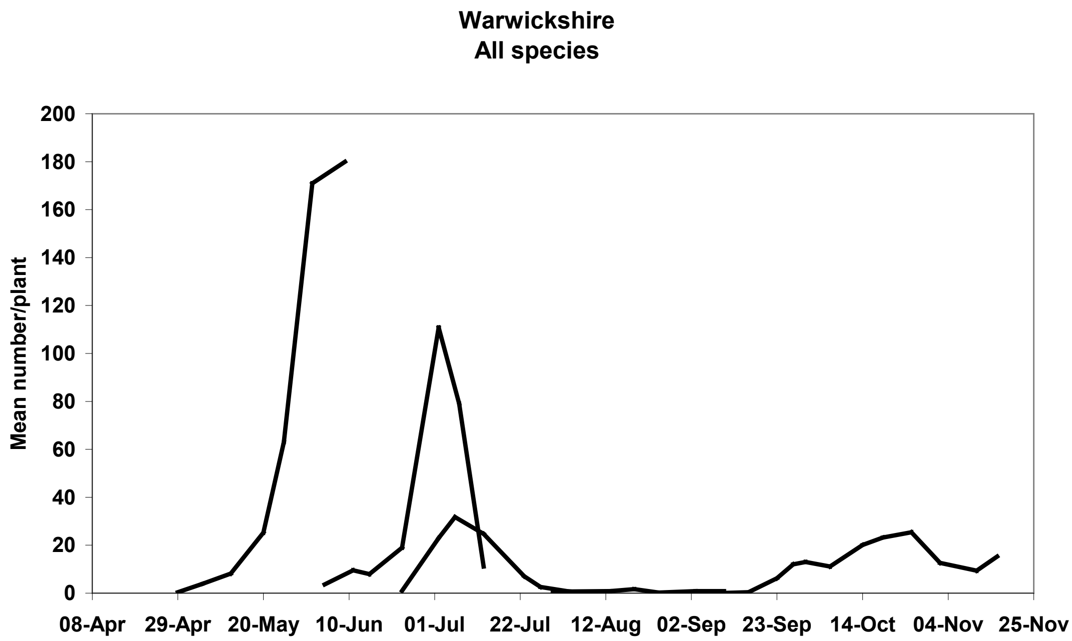


Appendix 2. The numbers of aphids (all species) found on untreated lettuce plants in 1999.

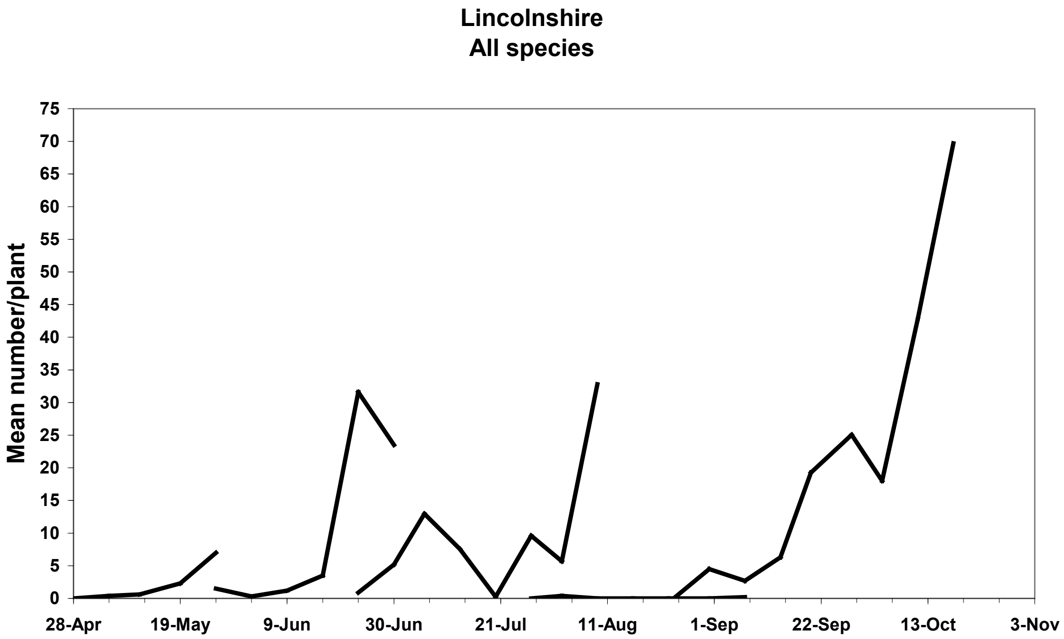


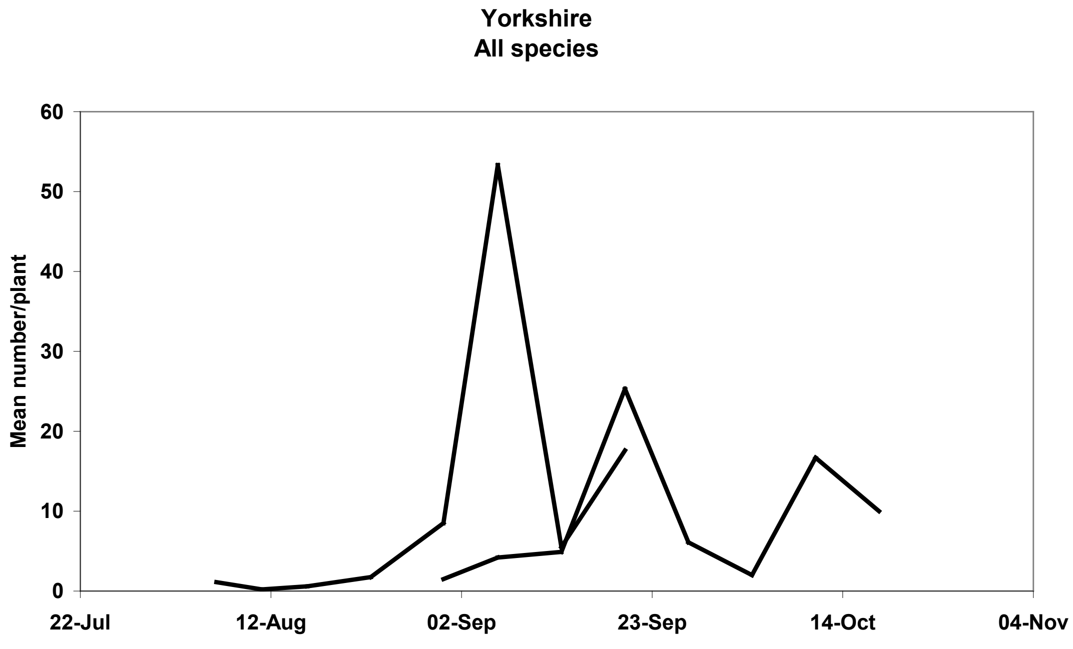


Appendix 2. The numbers of aphids (all species) found on untreated lettuce plants in 1999.

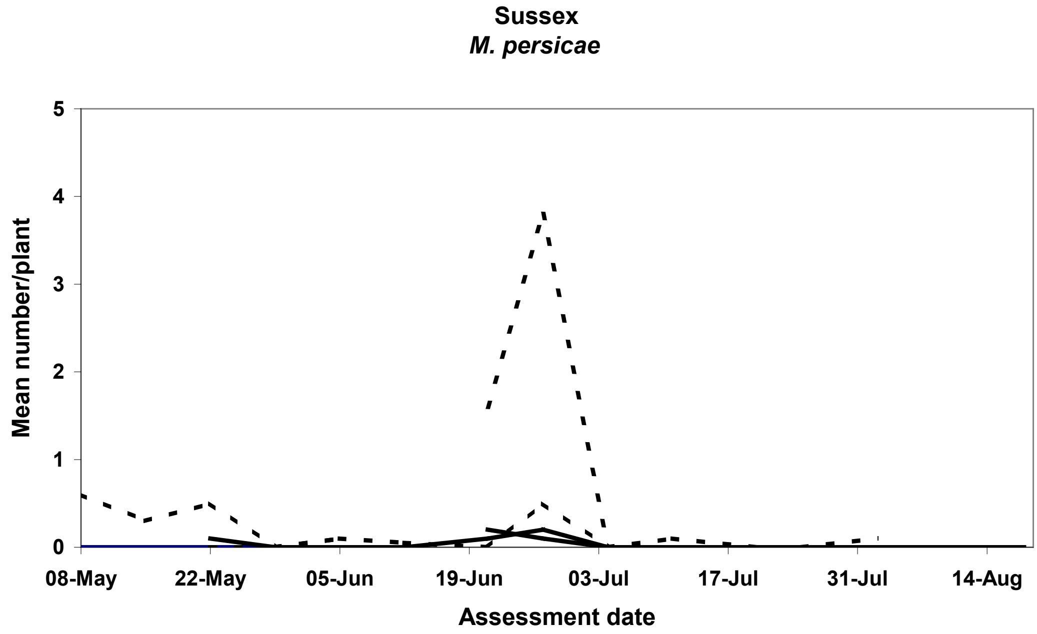


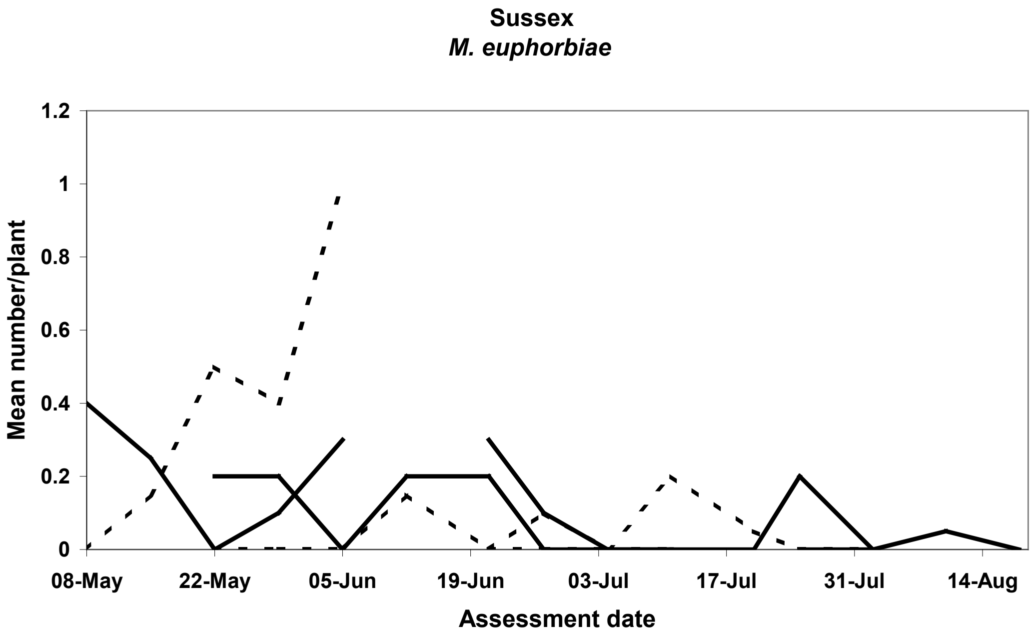
Appendix 2. The numbers of aphids (all species) found on untreated lettuce plants in 1999.



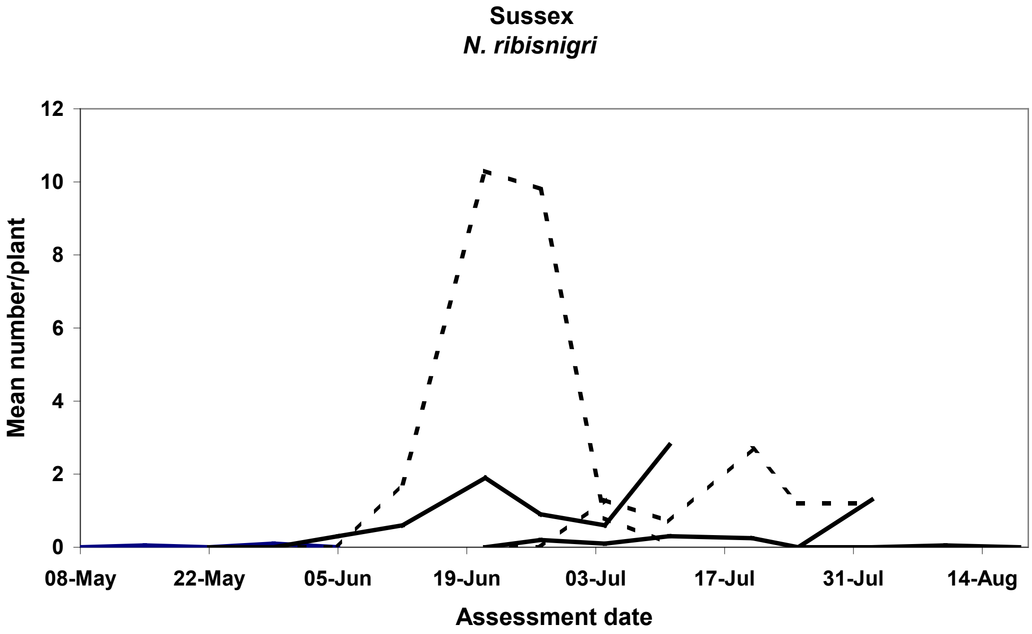


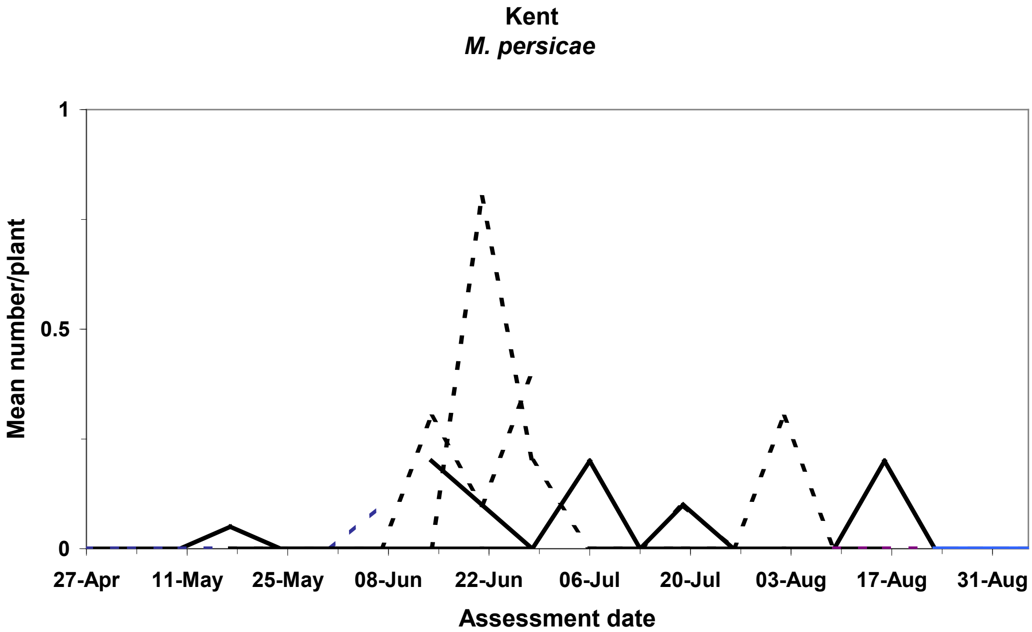
Appendix 3. The numbers of aphids found on untreated lettuce plants in 2000. (Solid lines = alates, dashed lines = apterae).



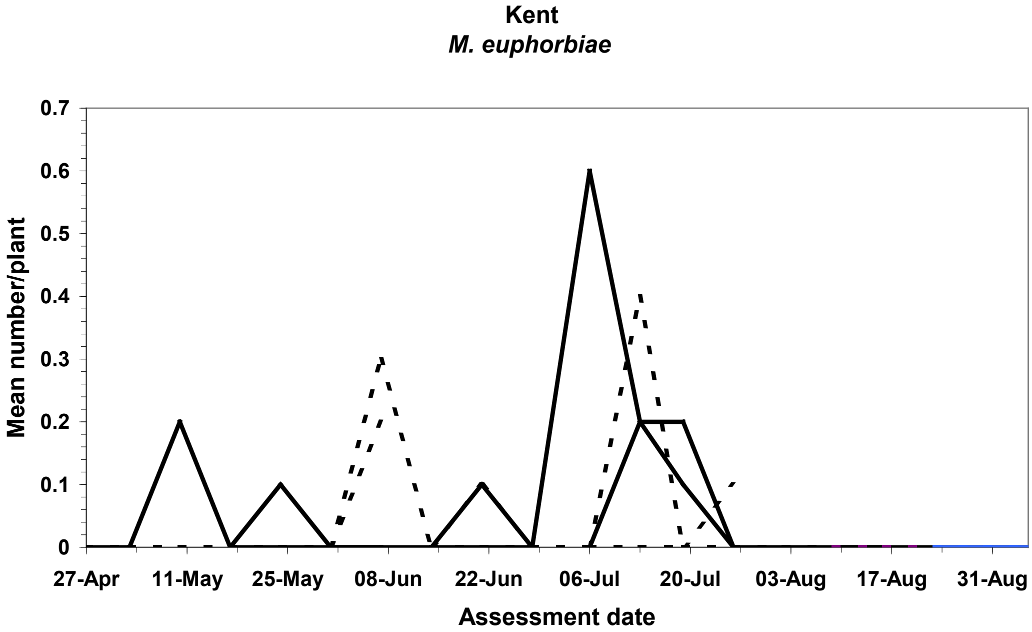


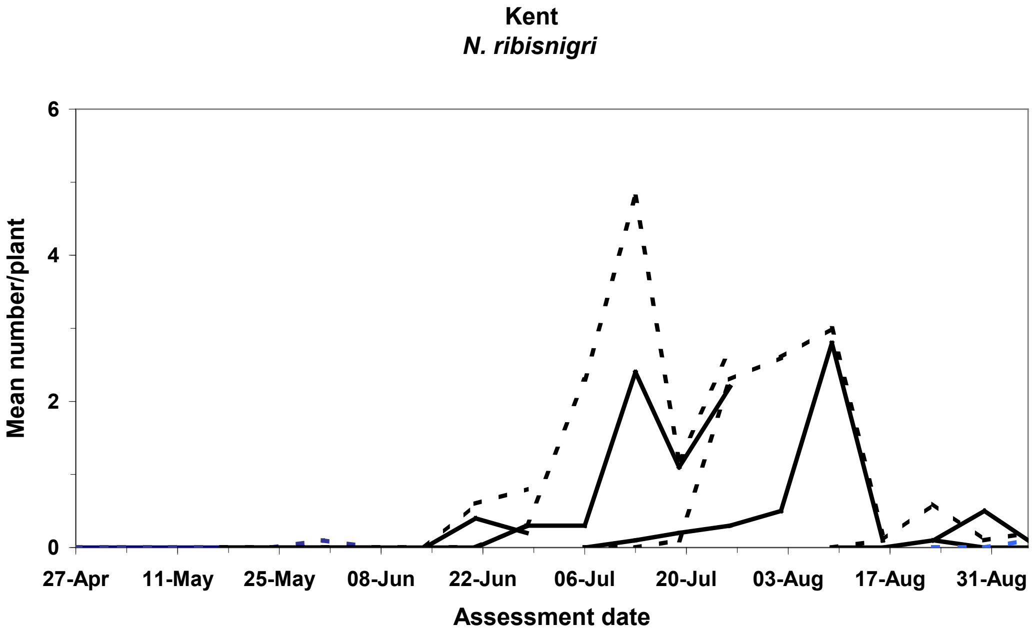
Appendix 3. The numbers of aphids found on untreated lettuce plants in 2000. (Solid lines = alates, dashed lines = apterae).



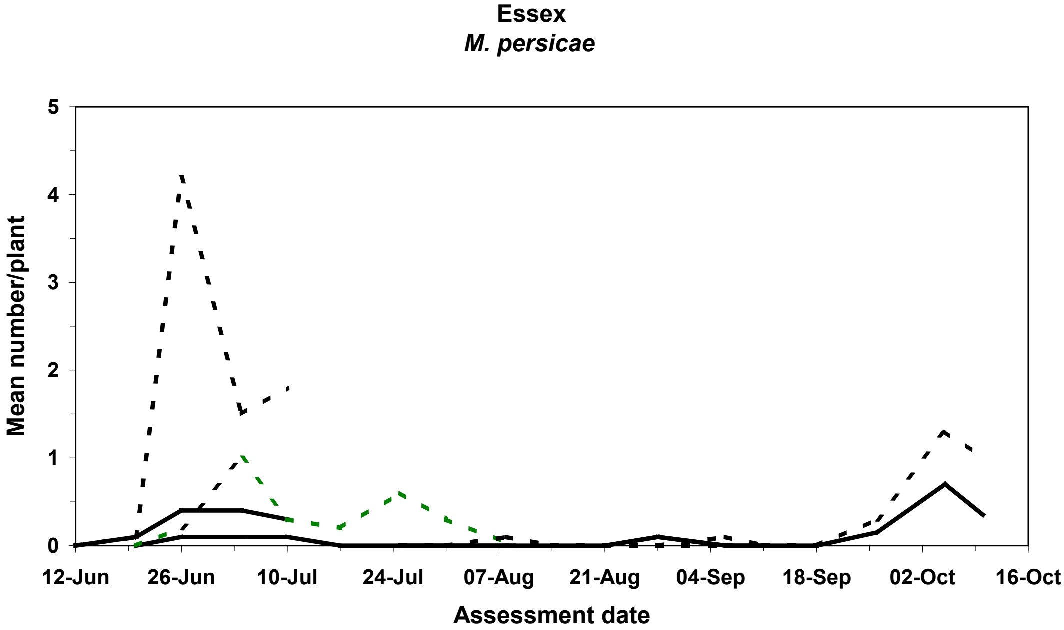


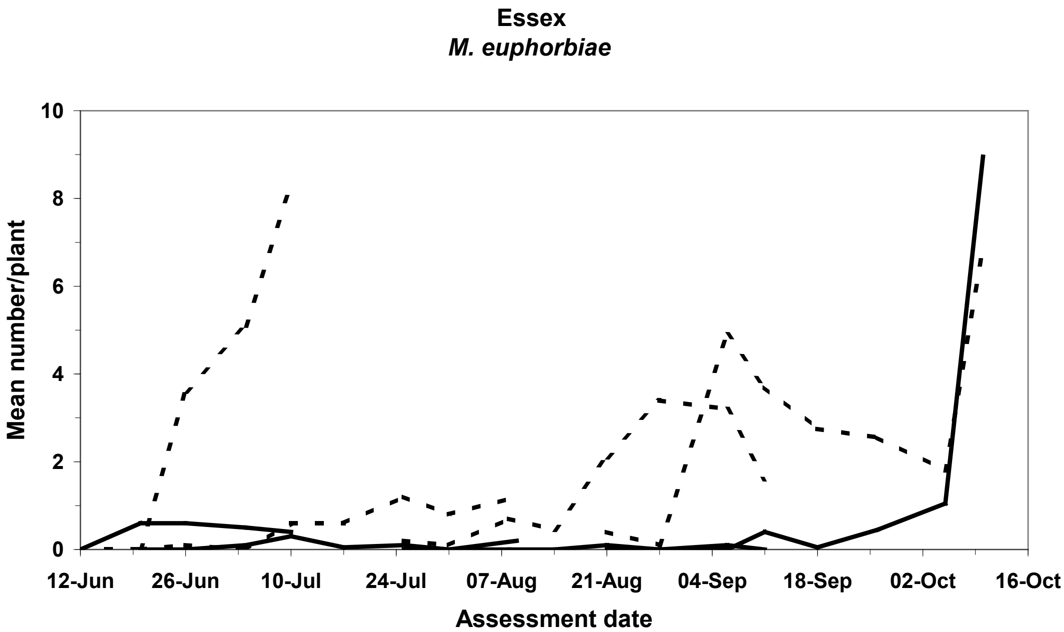
Appendix 3. The numbers of aphids found on untreated lettuce plants in 2000. (Solid lines = alates, dashed lines = apterae).



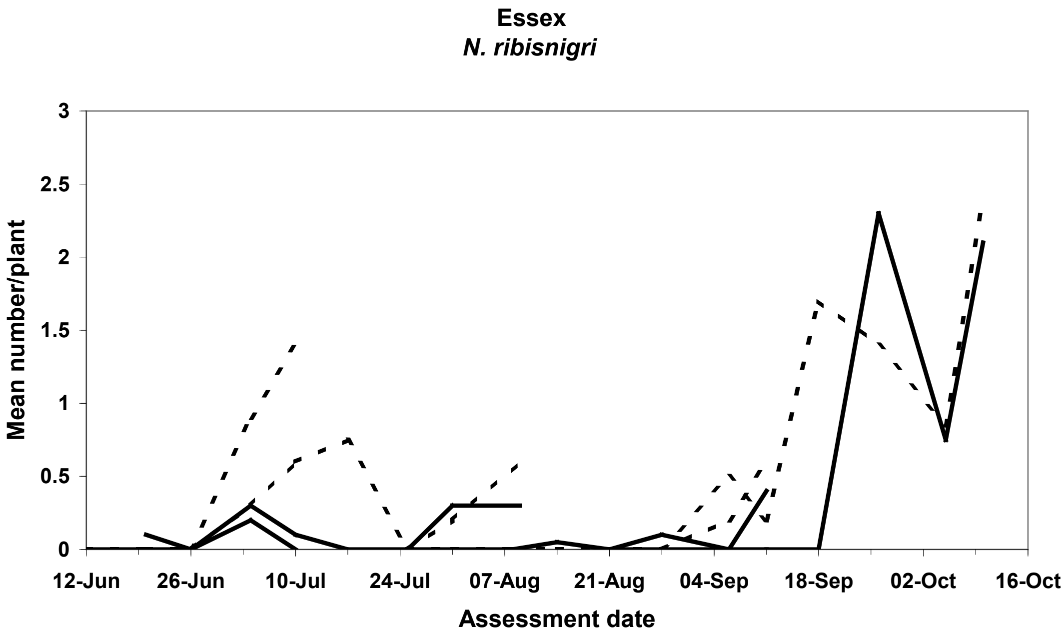


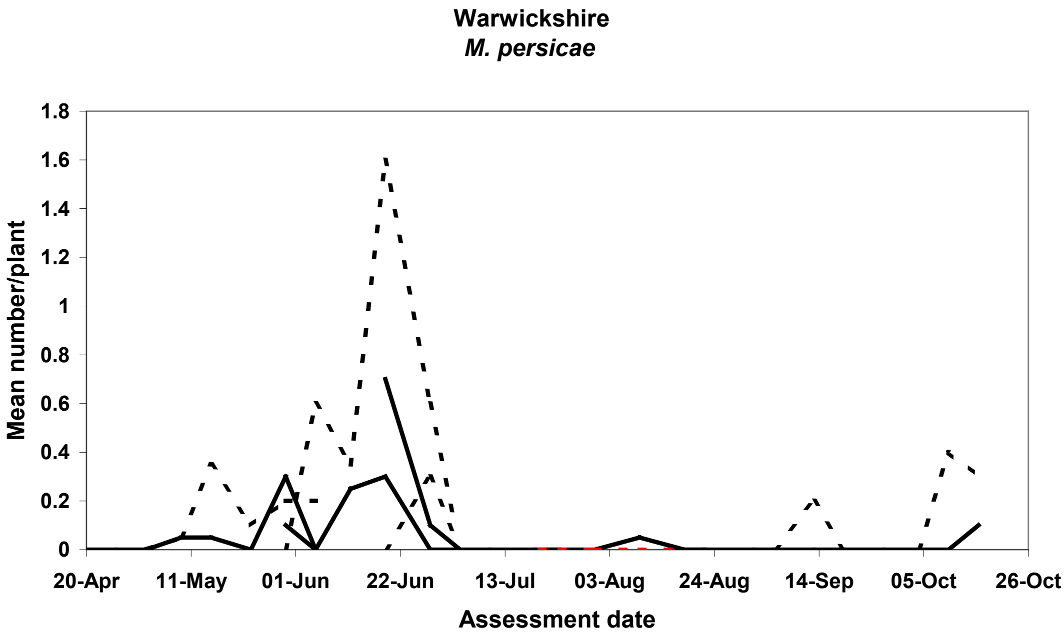
Appendix 3. The numbers of aphids found on untreated lettuce plants in 2000. (Solid lines = alates, dashed lines = apterae).



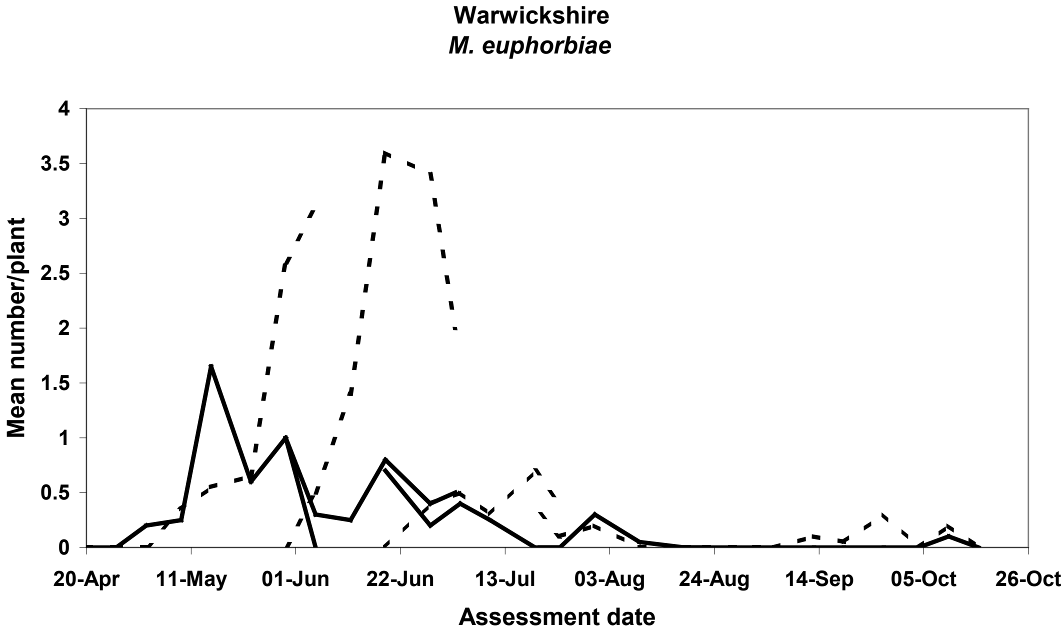


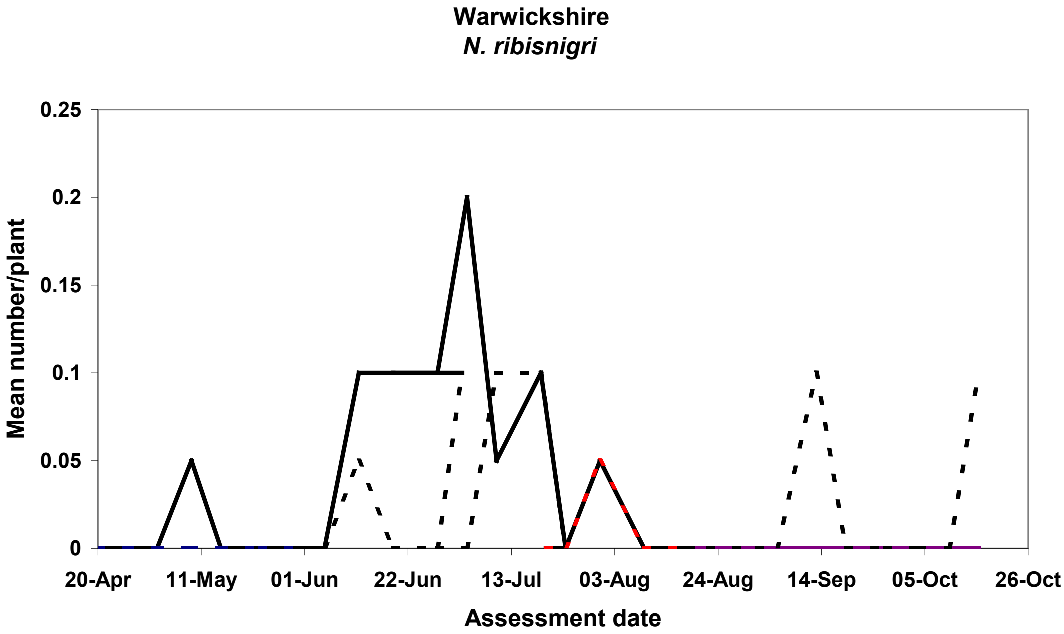
Appendix 3. The numbers of aphids found on untreated lettuce plants in 2000. (Solid lines = alates, dashed lines = apterae).



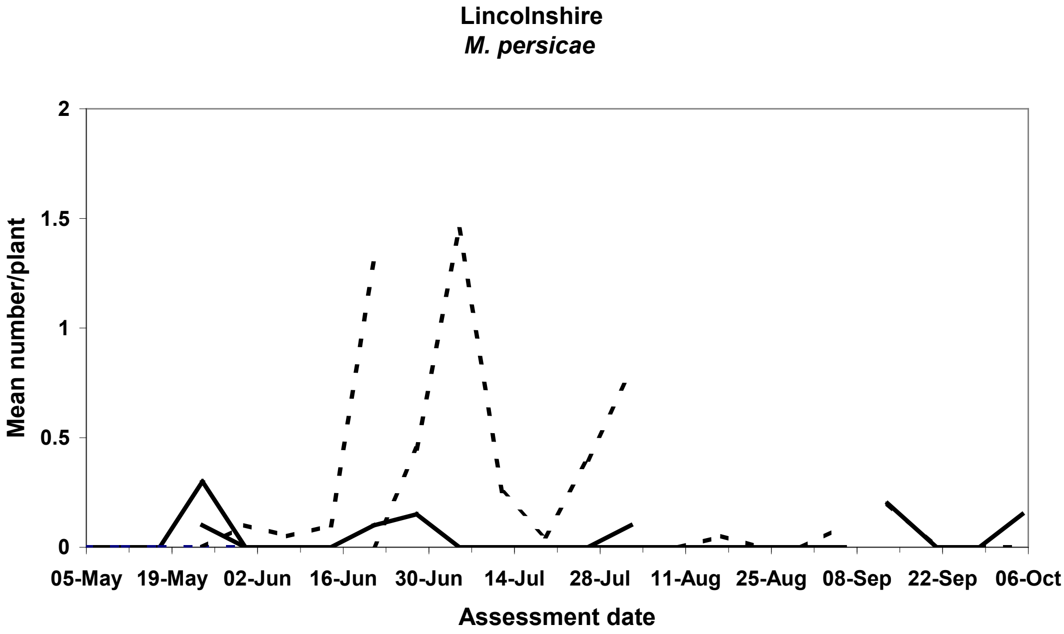


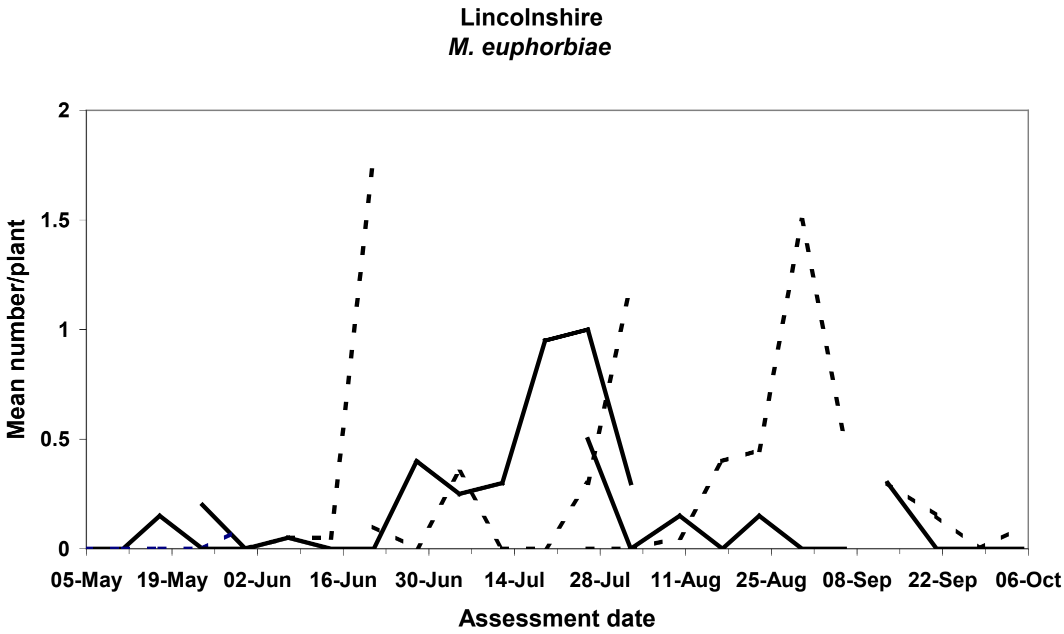
Appendix 3. The numbers of aphids found on untreated lettuce plants in 2000. (Solid lines = alates, dashed lines = apterae).



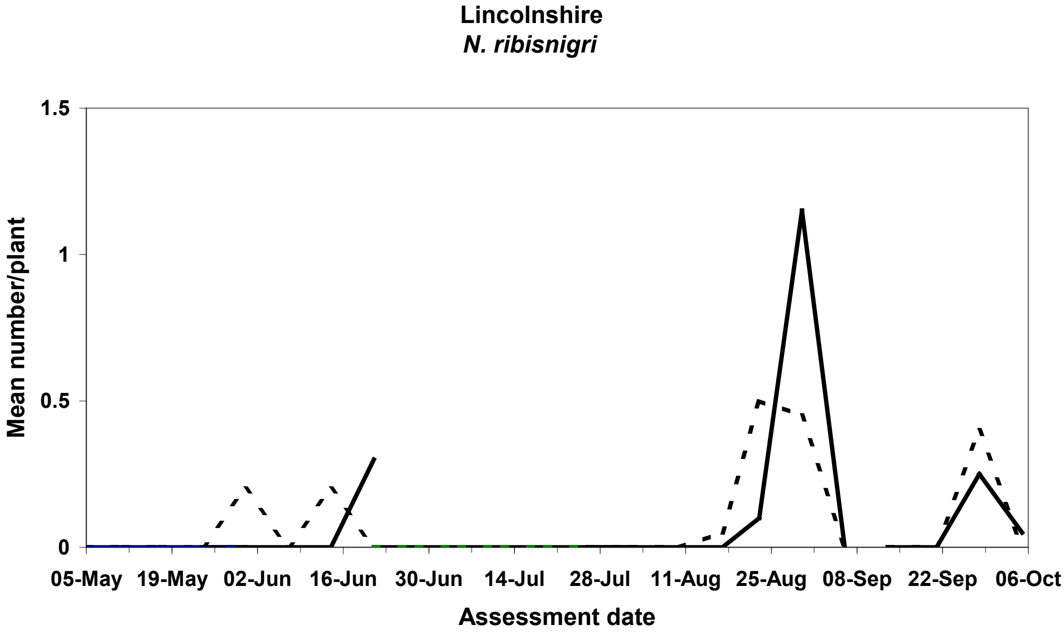


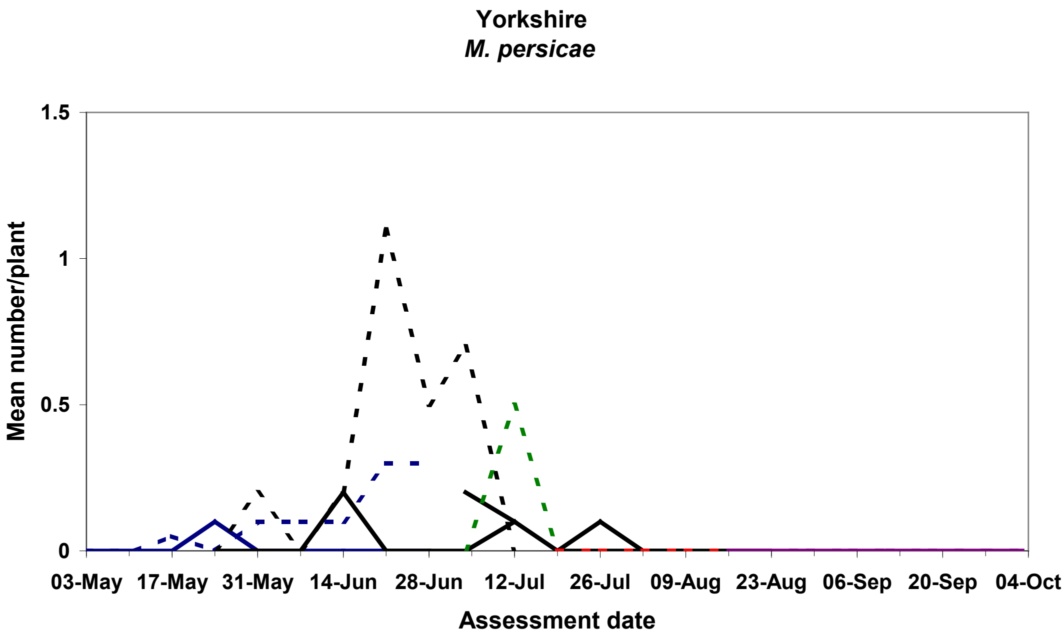
Appendix 3. The numbers of aphids found on untreated lettuce plants in 2000. (Solid lines = alates, dashed lines = apterae).



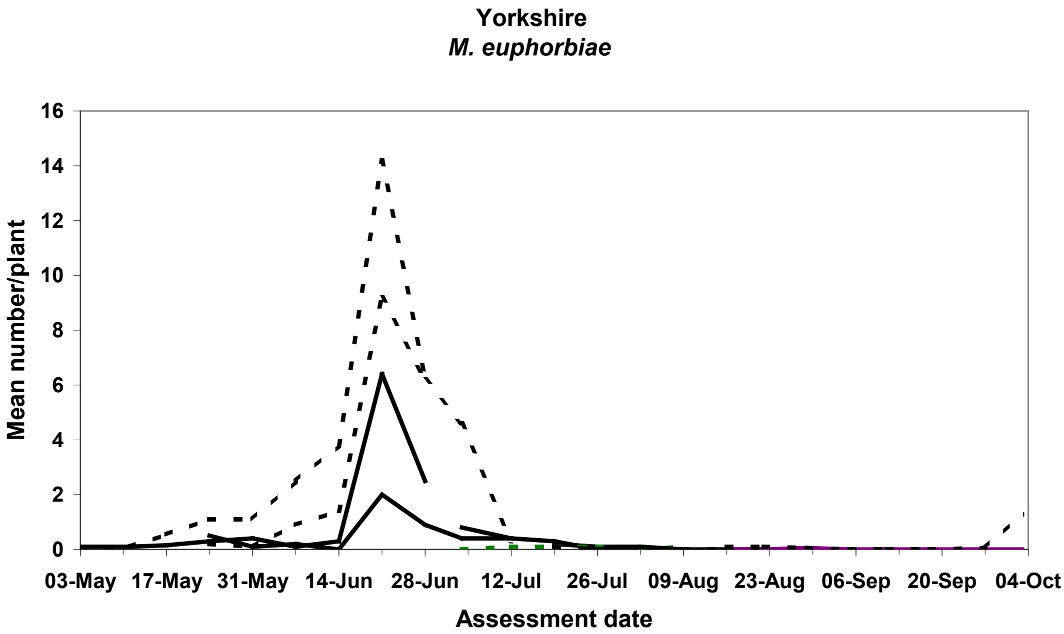


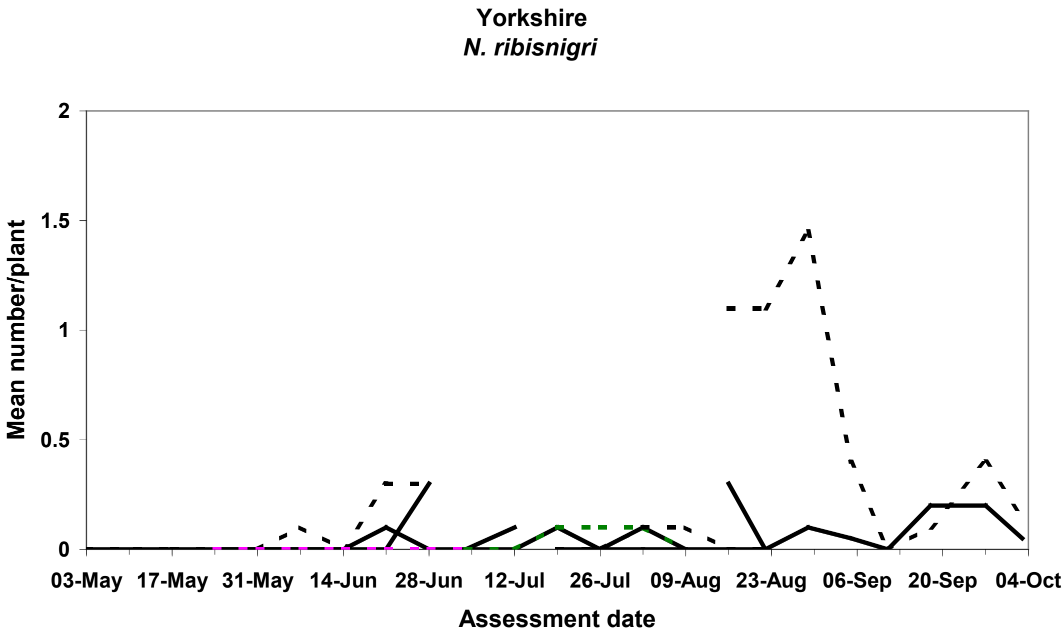
Appendix 3. The numbers of aphids found on untreated lettuce plants in 2000. (Solid lines = alates, dashed lines = apterae).



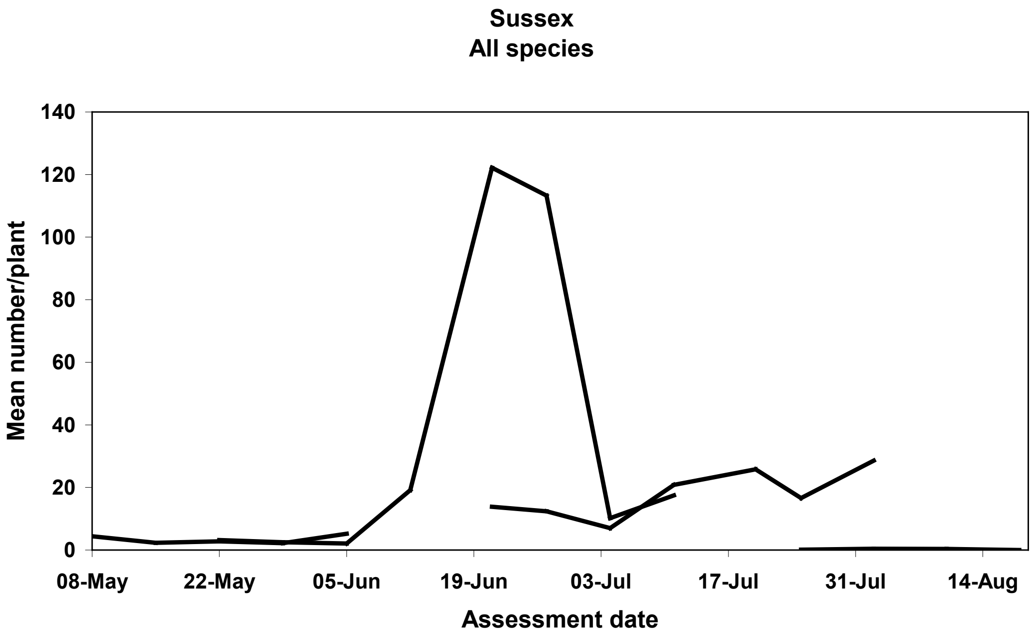


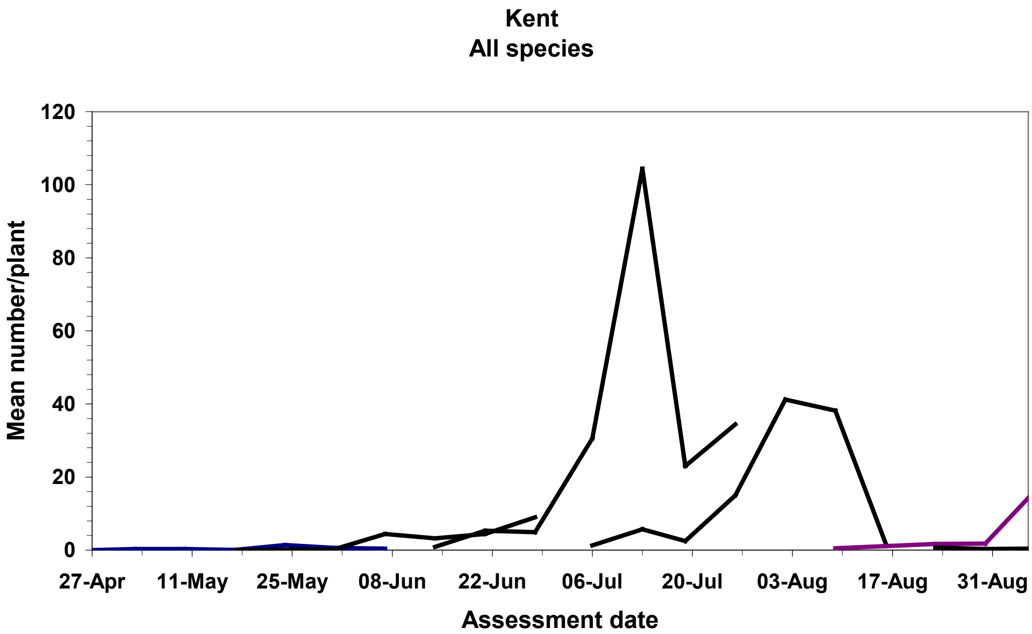
Appendix 3. The numbers of aphids found on untreated lettuce plants in 2000. (Solid lines = alates, dashed lines = apterae).



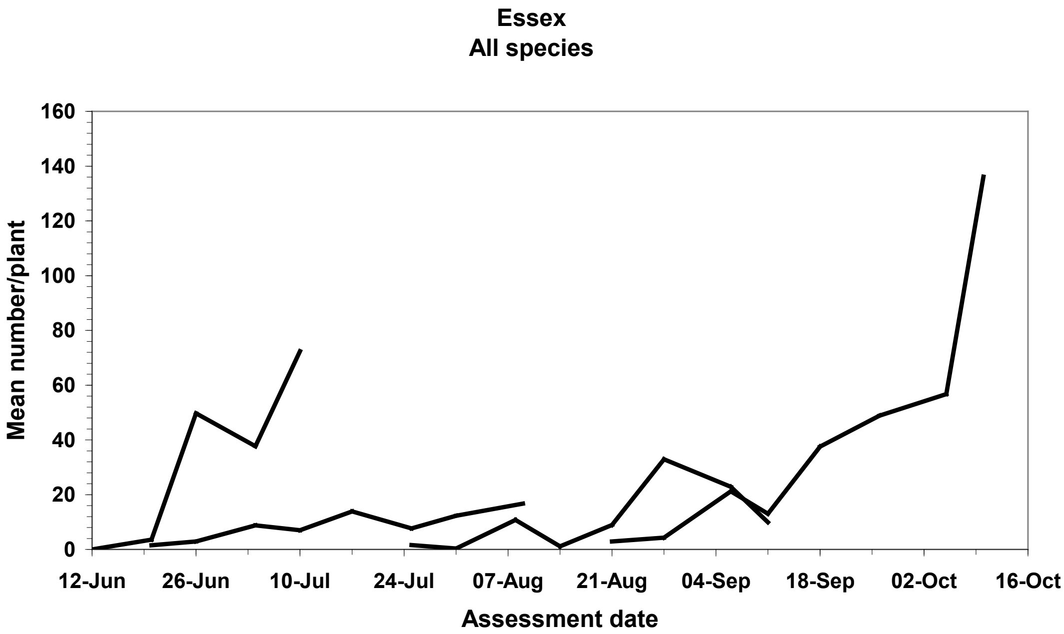


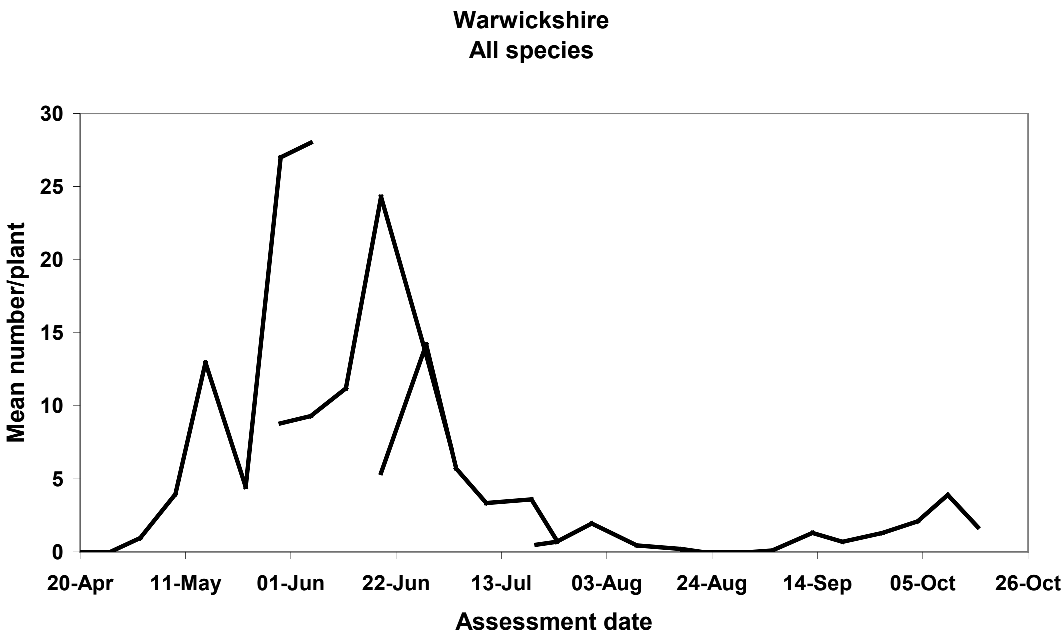
Appendix 4. The numbers of aphids (all species) found on untreated lettuce plants in 2000.





Appendix 4. The numbers of aphids (all species) found on untreated lettuce plants in 2000.





Appendix 4. The numbers of aphids (all species) found on untreated lettuce plants in 2000.