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Project Leader: Dr. A. J. Biddle  
Processors & Growers Research Organisation  
Great North Road  
Thornhaugh  
Peterborough, PE8 6HJ

Co-operative Researchers: Dr. K. A. Walters (MAFF CSL Harpenden)  
Mr. J. Aegerter (MAFF CSL Harpenden)

Location of Project: Processors & Growers Research Organisation  
MAFF Central Science Laboratory, Harpenden

Project Co-ordinator: Mr. P. H. Shepherd

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The development of a pea aphid population model for vining peas

1995

**SUMMARY:** Using data of pea aphid growth, reproduction and mortality on two cultivars of vining peas of differing phenology in growth chambers, a core model, driven by temperature to predict the population changes, was developed.

The model was tested using data collected from a commercial crop of vining peas and the prediction correlated well with the actual infestation.

A spray trial also confirmed the optimum crop growth stage and economic action threshold for aphid control in vining peas.

**OBJECT:**

1. To convert the population model for pea aphid in combining peas to one suitable for vining peas.
2. To test the effectiveness of action thresholds in a timed spray application trial.

Background

The pea aphid (*Acyrthosiphon pisum* Harris) is a pest of vining peas (*Pisum sativum* L.). The aphid colonises the plants soon after crop emergence and the populations build rapidly in the spring and summer. Economic losses are caused by aphid attack during the pod setting and pod filling growth stages (Biddle, Blood Smyth and Talbot, 1994). It is therefore important to be able to predict whether aphid populations will rise above the economic threshold of 15% of plants infested that has been set for vining (PGRO) and 20% for combining peas (Lane & Walters, 1991; Walters *et al.*, 1994), in order to plan management action appropriately.

Currently no forecasting method is available and decisions are usually based on regular crop inspections coupled with an economic action threshold. This is both time consuming and expensive, and may be replaced by regular prophylactic spraying which if unnecessary is both expensive and environmentally damaging. This report describes the development of a simulation model designed to predict aphid population development during key crop growth stages and thus help refine management decision making processes.

Introduction

Aphid populations rise and fall in relation to a number of environmental and biological factors. Increased temperatures during the late spring and summer period coupled with the absence of drought effects on their host plant early in the year result in the aphids realising a high reproductive potential, and the predators, parasites and diseases which have been shown to affect aphid population dynamics do not significantly slow the rate of aphid population growth. Thus during the key periods of crop development, environmental factors are largely responsible for governing the rate of

aphid population growth, and determining whether the aphids in a crop will reach economically damaging levels during the vulnerable period. Of these, temperature has been shown to be the most important driving factor, -with rainfall as a more minor component.

The simulation model reported here takes as its basis the interaction between environmental temperature and important aspects of the pea aphid's biology, and structures them in order to forecast future aphid populations. Also reported is the laboratory based experimental work undertaken to quantify the specific relationships for the pea aphid on vining peas.

**METHODS:**

**Laboratory work**

**1. Culture methods**

Two varieties of pea were used to measure the effect of pea plant variety on aphid population growth. They were, Sancho a semi-leafless variety and Scout a fully leafed cultivar, both of which are widely grown commercially. Experimental plants were grown from seed in a glasshouse at approximately 20°C and under a 16h photoperiod. The plants were removed from experimentation at growth stage 102 to 105 (Knott, 1987) when the plants were approximately 5-10 cm high.

The aphids used were originally collected by PGRO in 1995 from fields in East Anglia and were maintained as a polyclonal culture of *A. pisum* representative of those clones likely to be found on crops in the east of England. The cultures were maintained on a mixture of pea varieties during the experimental period in order to avoid possible selection of individual aphid clones more or less suited to the individual experimental pea varieties. During experiments, plants were enclosed in a small ventilated plastic cloche along with an experimental aphid, and maintained at a constant temperature under 16h photoperiod. Nominal experimental temperatures of 12°C, 17°C, 20°C, 23°C and 26°C were programmed into the environmental cabinets used, and a datalogger was set to record the actual temperature in a minimum of two positions within the cabinets so that a true cabinet mean temperature could be calculated. This allowed variations of temperature within the cabinet to be reflected in the final analysis, and quality to be maintained by rejecting data where the cabinet has failed to maintain a sufficiently precise control on its internal environment.

**2. Experimental work on aphid development**

For the studies investigating the effects of temperature on the rate of aphid development, at least 20 first instar nymphs\* (known to be less than two hours old) were placed individually on whole plants and allowed to find their preferred feeding site. Aphids were checked daily for experiments at 12°C, twice daily for experiments at 17°C and 20°C and usually three times daily for experiments at 23°C and 26°C. Their survival and instar were recorded. Where mortality was high and insufficient individual aphids survived to the later instars and adulthood, fresh newly moulted aphids (less than two hours old) of the appropriate developmental age were taken from a temperature conditioned culture and placed individually on new plants, to ensure meaningful results.

\* Only 15 aphids were used in work to quantify aphid development on Scout at 17°C

### 3. Experimental work on aphid reproduction

For the studies investigating the effects of temperature on the fecundity of adult aphids, at least 15 fourth instar aphids<sup>#</sup> were placed on plants and allowed to find their preferred feeding site. The aphid was observed daily for experiments at 12°C, 17°C, 20°C and 23°C and twice daily for experiments at 26°C. The duration of the adult pre-reproductive delay was noted as were the number of nymphs born between each observation. All new born nymphs were removed after counting. The experiment was continued until all of the adults had died or until their reproductive life exceeded 20 days.

### 4. Data analysis

The mean duration of each of the developmental stages was calculated in hours for the aphids at each of the experimental temperatures and for each of the pea cultivars. For each of the cultivars a linear regression of the duration of each developmental stage (in days) against the measured temperature was then calculated to describe the rate of development of each stage on each cultivar.

In calculating the regression line, the data of the rate of development at 26°C was omitted for two reasons; firstly the biological response to temperature is approximately linear from 12°C to 23°C whereas at the higher temperatures the trend changes. This implies that the simple physiological processes which governed development from 12 to 23°C and which produced a linear response to temperature become more complex, possibly by the addition of a new physiological factor. Understanding and modelling the changes in one part of a biological system is difficult but achievable with some accuracy. Modelling two interactive components in a system is very difficult and prone to errors. It is preferable therefore to treat temperature above 23°C differently (especially as they occur for a small percentage of the overall year) and restrict the main regressions to linear relationships between 12°C and 23°C. Secondly, the behaviour of mathematical models incorporating polynomial relationships is unpredictable and not suitable to a model to be used in economic decision making.

## Field work

### 1. Aphid population recording

Temperature recordings of air, soil and crop canopy were measured at 30 minute intervals by a Delta T automatic weather station in a commercial crop of vining peas cv. Nomad at Thorney, Cambs. Recording began on 6th June when aphids were first observed in the growing crop. Aphid numbers were counted on each of 60 randomly selected plants in an unsprayed area of the crop on eight occasions, noting the crop growth stage at each time. Recording ceased on 21st July when the crop was harvested at the optimum stage for freezing. No rainfall occurred throughout the monitoring period.

### 2. Spray trial

A spray trial was carried out in the same field as the monitoring exercise. Sprays of pirimicarb (Aphox) at 240 g/ha were applied to 5 m x 2 m plots using an Azo plot sprayer with Lurmark 02-F110 nozzles at 2.5 bar. Sprays were applied at specific crop growth stages as defined by Knott (1987) and each treatment was replicated four times. The treatment schedules and spray dates are shown in Table 1.

# Only 9 aphids were used to quantify aphid reproduction on Scout at 17°C

Table 1. Spray timings - Thorney

	Growth stage	Date
1. untreated	-	-
2. 1 spray	late vegetative (106)	9/6
3. 2 sprays	106 and enclosed bud (201)	9/6 and 3/7
4. 1 spray	201	3/7
5. 2 sprays	201 and first pod (204)	3/7 and 14/7
6. 1 spray	first flower (203)	6/7
7. 2 sprays	203 and 204	6/7 and 14/7

Pea aphid infestation was assessed prior to spraying by examining 15 shoots per plot and recording the presence or absence of aphid. At the freezing stage, the plots were cut and vined using the PGRO plot viner. The yield of the vined peas was recorded and maturity measured by tenderometer.

RESULTS:

Laboratory work

1. Rate of development

Both the overall rate of development (Fig. 1) and development rates for individual instars of the aphid (Tables 2a and 2b) increased with temperature on both pea cultivars until an upper threshold was reached near to 23°C.

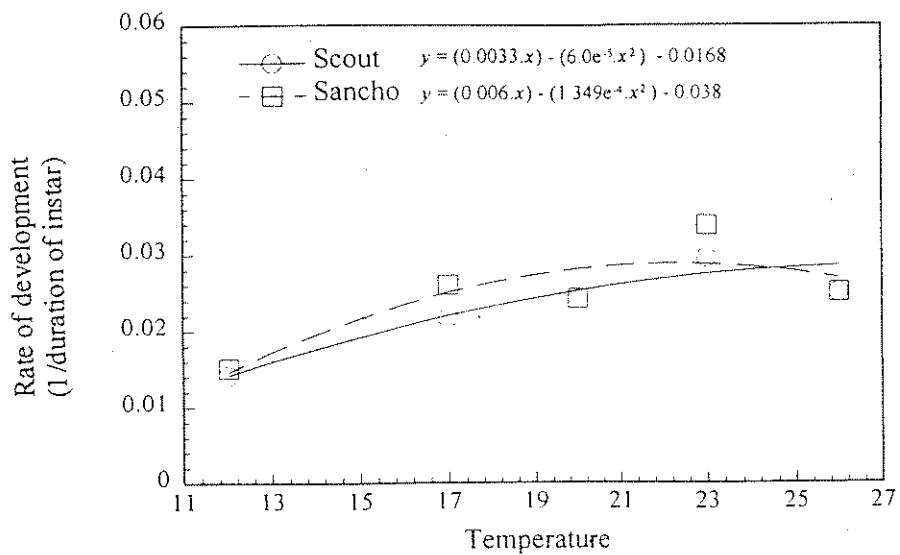
Table 2. The mean duration (days/instar( $\pm$ standard error)) of each of the developmental stages of the pea aphid on vining peas for (a) cv. Scout and (b) cv. Sancho

a)

Nominal temperature	Number of observations	Developmental stage of aphids on <u>Scout</u>					
		I	II	III	IV	Adult pre-reproduction	Total
12	20	3.78 (0.226)	3.43 (0.298)	2.92 (0.285)	3.45 (0.302)	3.00 (0.302)	16.58
17	15	3.40 (0.273)	2.42 (0.241)	1.64 (0.345)	3.40 (0.247)	1.72 (0.307)	12.58
20	25	1.83 (0.117)	2.45 (0.139)	1.89 (0.115)	2.33 (0.173)	1.52 (0.230)	10.02
23	45	2.00 (0.142)	1.46 (0.215)	1.58 (0.154)	1.79 (0.149)	1.69 (0.180)	8.53
26	30	1.73 (0.094)	2.80 (0.358)	2.30 (0.375)	0.99 (0.206)	0.68 (0.254)	8.50

b)

Nominal temperature	Number of observations	Developmental stage of aphids on <u>Sancho</u>					
		I	II	III	IV	Adult Pre-reproduction	Total
12	20	4.09 (0.241)	3.13 (0.218)	2.87 (0.238)	3.02 (0.275)	3.11 (0.223)	16.21
17	15	2.99 (0.039)	0.96 (0.106)	1.81 (0.133)	2.27 (0.145)	1.89 (0.283)	9.92
20	25	1.93 (0.087)	1.62 (0.167)	2.87 (0.084)	1.44 (0.164)	1.33 (0.245)	9.20
23	45	2.13 (0.127)	1.05 (0.171)	2.44 (0.302)	1.79 (0.232)	1.14 (0.17)	8.54
26	30	2.80 (0.071)	1.16 (0.196)	1.85 (0.196)	1.82 (0.143)	1.075 (0.192)	8.70



**Figure 1: The rate of development of *A. pisum* on vining peas (cv. Scout and Sancho) at a range of temperatures.**

The duration of each instar was regressed against measured temperatures in order to determine the response of each aphid's developmental stages to temperature (Tables 3a and 3b) and the resultant equations used to parameterise the subroutines of the development model.

Table 3. Regression parameter of the equation  $y = a + (bx)$ ; where  $y$  is the duration of the instar (in days) at temperature  $x$

a)

Developmental stage on <u>Scout</u>	Slope $b$	Intercept $a$	Number of observations	$r^2$
I	-0.183	5.964	83	0.457
II	-0.157	5.295	55	0.412
III	-0.108	4.000	66	0.286
IV	-0.159	5.495	63	0.474
Pre-reproductive adult	-0.149	4.691	49	0.348

b)

Developmental stage on <u>Sancho</u>	Slope $b$	Intercept $a$	Number of observations	$r^2$
I	-0.192	6.218	80	0.582
II	-0.163	4.503	78	0.379
III	-0.013	2.664	70	0.003
IV	-0.128	4.490	74	0.260
Pre-reproductive adult	-0.174	4.975	70	0.312

There was no significant difference between slopes of the regressions of overall development time against temperature for Scout and Sancho ( $F = 0.077$  on 1 and 6 df.), though this does not imply that the different model parameters will not interact over a long period to produce real differences in model estimations.

## 2. Mortality

The mortality of aphids within each developmental stage increased with temperature though under the laboratory conditions 80% of individuals survived until their next developmental stage (e.g. see figure 2). Details of regression equations relating mortality to temperature are given in table 4a and 4b for peas cv. Scout and Sancho respectively.

The length of adult life was longer at the lower temperatures than at 23°C and 26°C. However, regressions lines similar to those calculated for the aphid pre-reproductive development ignore the important effects of adult aphid age on its chances of surviving (i.e. the older an adult aphid the greater its chances of dying that day at any given temperature) and are therefore not adequate for incorporation into a simulation model. The solution adopted was to produce a multiple regression describing the change in adult aphid mortality with temperature and adult age. A non-linear approach was used as the data showed distinct non-linear trends in both independent variables (e.g. see figure 3), but the analysis was limited to no more than the cubic partition to reduce the possibility of unpredictable regression behaviour. The regression was fitted according to the equation:

$$y = (a.a) + (\beta.b) + (a^2.c) + (\beta^2.d) + (a^3.e) + (\beta^3.f) + g \quad \text{Eq.1}$$

The adult mortality ( $100 - y$ ) is expressed as function of the age of the adult aphid in days ( $a$ ) and the temperature ( $\beta$ ). The coefficients  $a$  through  $g$  are shown in table 5.

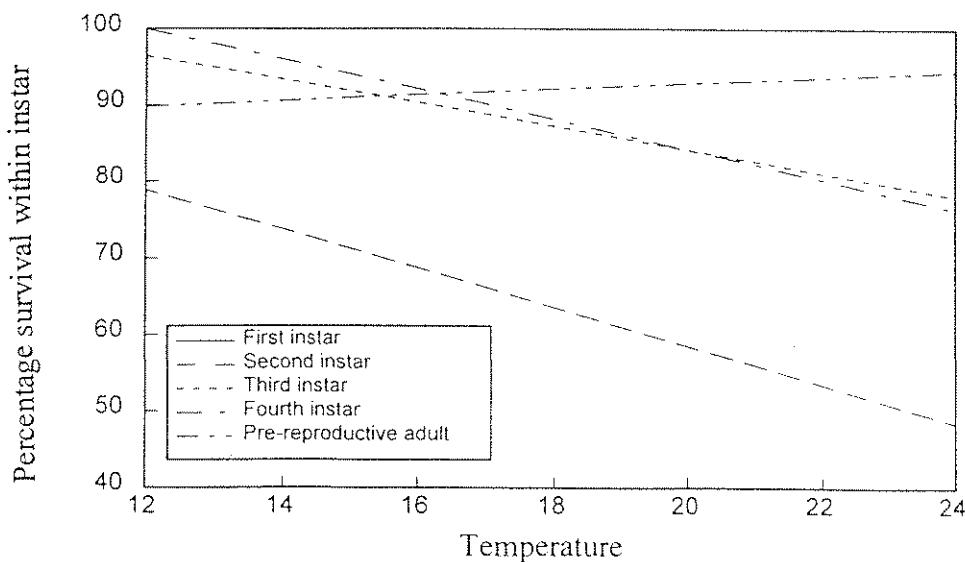


Figure 2 : The within stage survival of each pre-reproductive developmental stage of *A. pisum* across a range of temperatures.

Table 4. The linear regression coefficients used to estimate the mortality of pre-reproductive aphids at a range of temperatures. The percentage mortality (100-y) is a function of temperature (x) according to  $a + -(bx)$ . Data from *A. pisum* on peas for (a) cv. Scout and (b) cv. Sancho.

a)

Aphid life stage	Slope <i>b</i>	Intercept <i>a</i>	Number of observations	<i>r</i> <sup>2</sup>
I	0	100	5	1
II	-2.537	109.3	5	0.54
III	-1.541	114.96	5	0.287
IV	-1.971	123.59	5	0.283
Pre-reproductive adult	0.384	85.185	5	0.192

b)

Aphid life stage	Slope <i>b</i>	Intercept <i>a</i>	Number of observations	<i>r</i> <sup>2</sup>
I	-1.911	130.46	5	0.437
II	-1.097	114.77	5	0.389
III	-1.535	119.51	5	0.123
IV	0.319	89.12	5	0.076
Pre-reproductive adult	100	0	5	1

Table 5. The regression coefficients for the multiple non-linear equation (eq. 1).

Pea variety	Regression surface coefficients (see eq. 1)							<i>r</i> <sup>2</sup>
	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>f</i>	<i>g</i>	
Scout	-1.287	20925	-0.250	-1307	0.025	26.68	-108834	0.171
Sancho	-5.060	42.58	0.869	-2.261	-0.049	0.038	-144.8	0.495

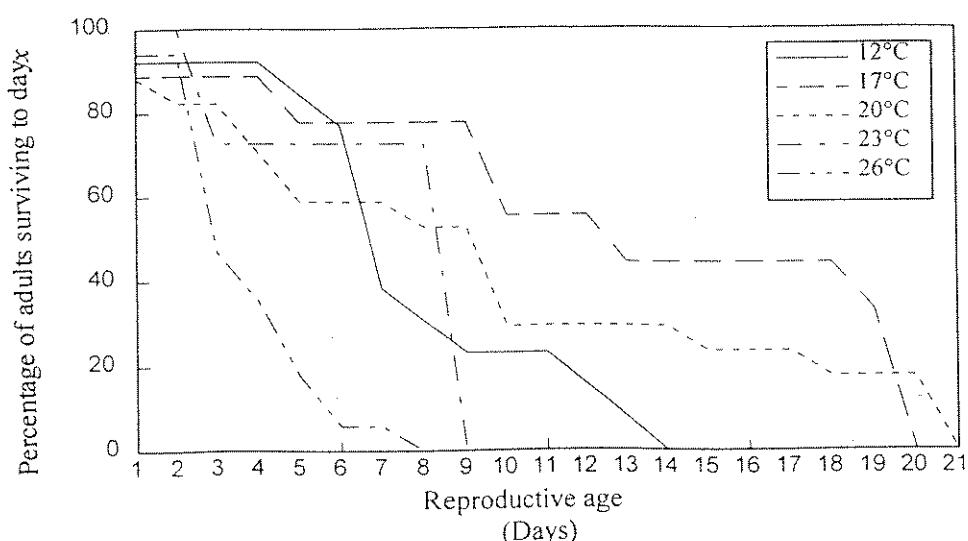


Figure 3 : Reproductive lifetimes of *A. pisum* at a range of temperatures on pea cv. Scout

### 3. Reproduction

The number of nymphs produced by each reproducing adult is a function of the length of its reproductive life (figure 3) and the mean number of nymphs produced per day of its reproductive life (figure 4).

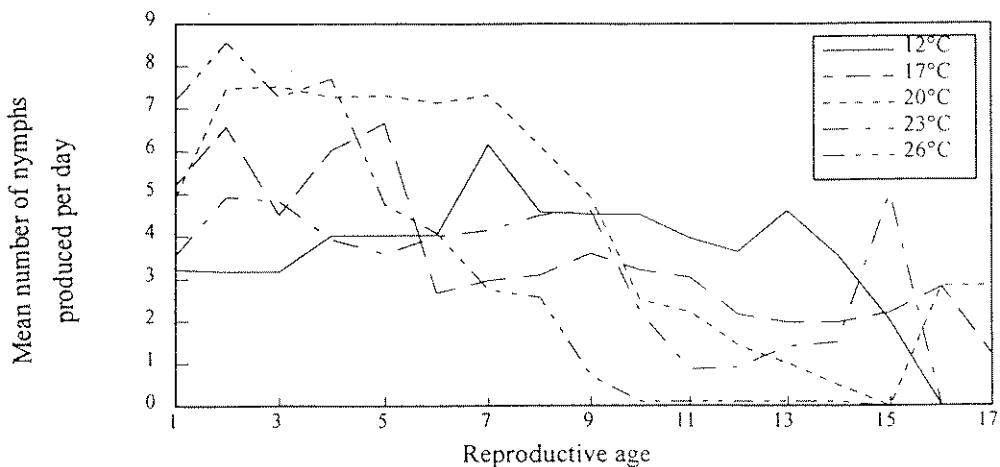


Figure 4 : Mean number of nymphs produced per day at a range of temperatures on pea cv. Sancho

The daily reproductive output of the aphids was highest around 20°C (figure 4) with nymph production apparently being inhibited at 26°C. However, a simple analysis was not suitable for use in the model, as it must also reflect the reproductive schedule of the aphids. A large proportion of the reproductive effort of the aphid occurred early in the reproductive life with characteristically lower rates of nymph production occurring later (figure 4). The death of a recently moulted adult will negate a proportionally greater reproductive potential than that of an elderly aphid. Thus the daily rate of adult mortality must be carefully modelled. The combined effects of adult mortality and daily reproductive rate is illustrated in figure 5, where the difference in the aphids reproductive performance between aphids at 20°C and those at 23°C was most striking. The similarity in the results from Scout and Sancho indicate that this was not an artefact.

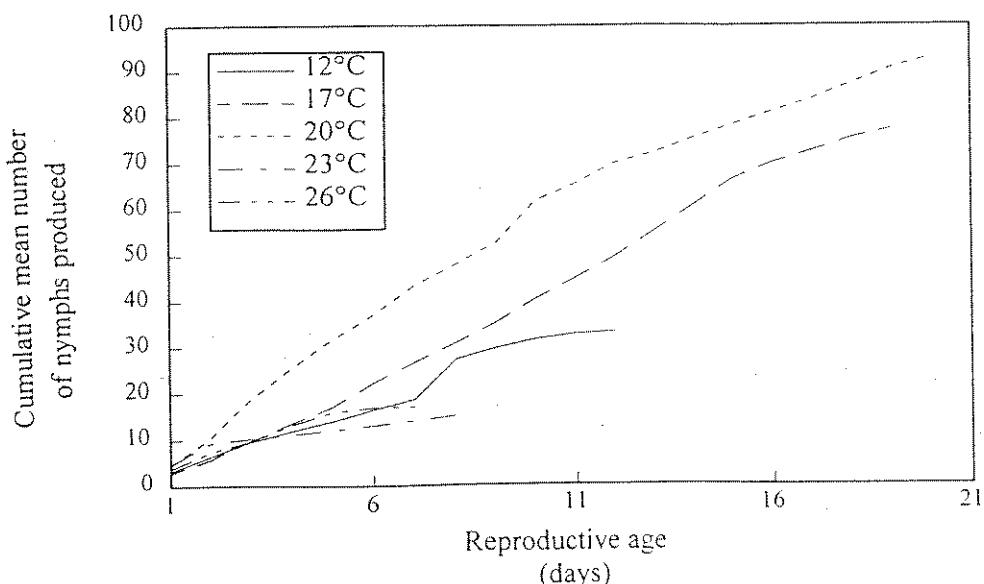


Figure 5 : Cumulative reproductive effort of *A. pisum* on pea cv. Scout at a range of temperatures.

To address the observation a regression surface was fitted describing the non-linear changes in the mean number of nymphs produced per day with respect to both temperature and adult age. An example of the regression surface produced from the experiments on pea cv. Scout calculated according to equation 1 (above) where  $a$  is the age of the adult in days and  $\delta$  is the temperature given in figure 6. The coefficients  $a$  to  $g$  are give in table 6.

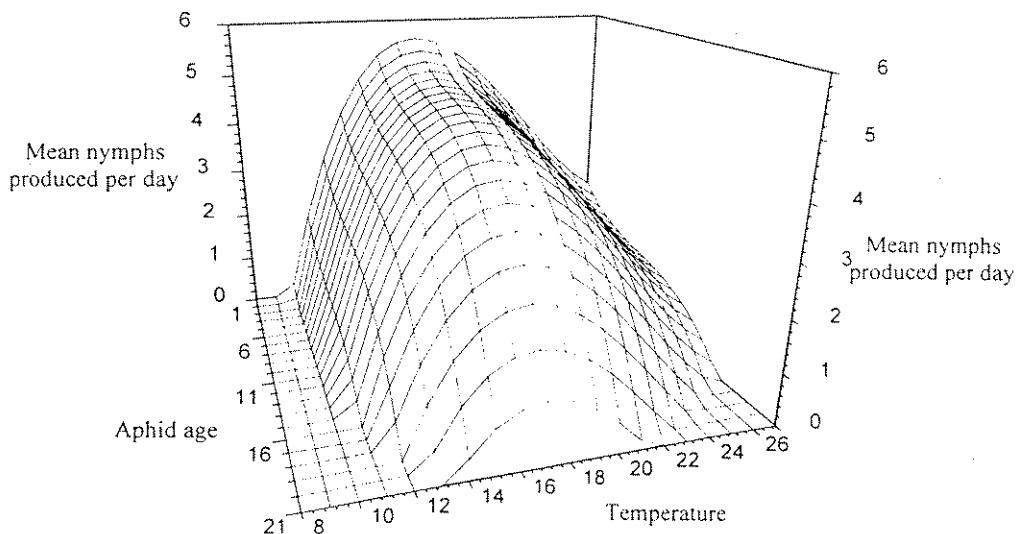


Figure 6 : A non-linear surface representing the change in mean nymph production with adult aphid age and temperature on pea cv. Scout

Table 6. The regression coefficients for the multiple non-linear regression equation (eq. 1), relating mean daily nymph production with temperatures and adult age.

Pea variety	Regression surface coefficients (see eq. 1)							
	$a$	$b$	$c$	$d$	$e$	$f$	$g$	$r^2$
Scout	-0.3258	6.643	0.03592	-0.3121	-1.50e <sup>-3</sup>	0.00456	-39.21	0.344
Sancho	0.702	-0.325	-0.143	0.026	0.005	-0.001	6.116	0.533

#### Model construction

The model framework utilises on the "box car" method (Carter *et al.*, 1982), where a structure is established that mirrors the biological development of the insect. In this case four structures for each of the development instars, one for the adult pre-productive delay and one for the adult life were constructed. The aphids are moved sequentially through the structures as they age; their rate of ageing being dependant upon the temperature experienced by the aphid. Regression equations derived from experimentation are used to determine the rate of ageing at any temperature. The model is divided into time steps, in this case of 30 minutes duration for most of the operations, and cohorts of aphids are examined at every time step and age. Other operations are also applied to the cohorts at the appropriate times, e.g. mortality, alate production and reproduction in the adults, each of which is modelled in its own subroutine which are activated when cohorts reach the appropriate stages. Each of these sub-processes are also made temperature sensitive where applicable.

One of the main features of the model design is that it is both "open", allowing the easy integration of additional components, and biologically realistic, so that the action of individual processes operating on the aphids can be targeted most accurately to the appropriate place in the aphids life cycle. For example, the action of rain may be later found to act mainly on the youngest aphid nymphs rather than the adult aphids. This model framework allows this to be simulated accurately, and will then be more able to make realistic forecasts.

As with any mathematical modelling exercise a number of assumptions have been made. Some of these relate to very basic aspects of the pea aphid biology for which accurate data are not available, some relate to information about *A. pisum* obtained from other sources (and which were outside the remit of the current experimental work), and some result from the need to simplify extremely complex biology into a logical form that can be simulated. The two major assumptions made for this model are detailed below:

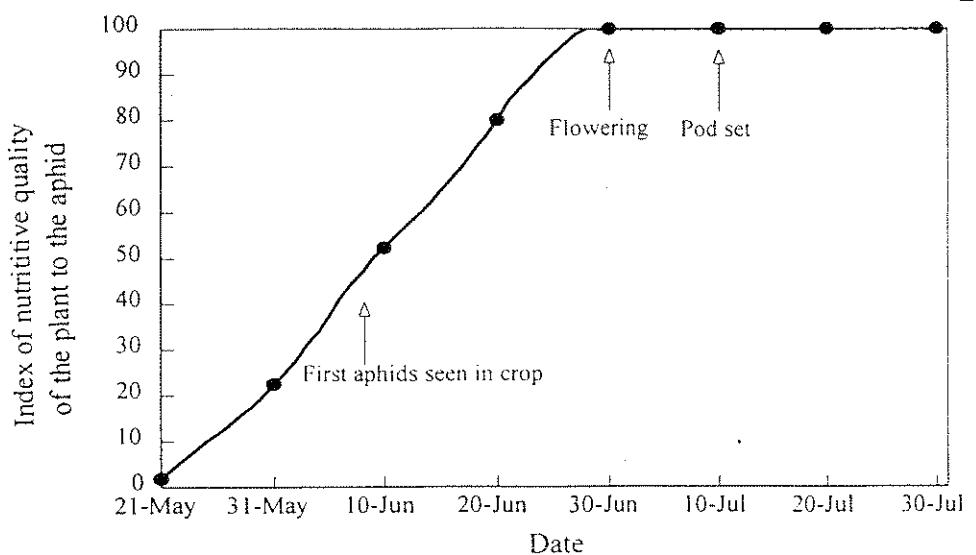
#### 1. Timing of reproduction

The model assumes that reproduction occurs constantly over the 24 hour period. Previous studies suggest that there may be slight peaks and troughs in reproductive effort with fewer nymphs produced over the dark hours and more immediately after dawn. This will cause the model to slightly overestimate the reproductive efforts of the aphid population just before dawn, and should comparative field counts be made at this time of day a slight discrepancy will be expected. In practise however, it is unlikely to affect forecasts made for decision making, as any slight error is corrected within the 24 hour time period, and it was concluded that the longer run-time required enable the model to reflect such diurnal reproductive rhythms was not justified.

#### 2. The nutritional status of the plant

The model assumes that the quality of nutrition that the vining pea plant provides to the aphid changes over time. A small seedling does not provide the same quality of nutrition as a flowering plant or a pea plant swelling its pods. As no definitive work quantifying this change in plant nutritional quality (defined in terms of the aphid) exists in the literature, and its collection was beyond the scope of the experimental component of this project, the way in which plant age affects the rate of aphid population growth was assumed to be similar to that presented in figure 7. An arbitrary index was constructed with 100 representing a high quality nutritive resource (with respect to the aphid) and lower numbers representing a lower quality resource which limits aphid population dynamics. The plant is available to aphid colonisation immediately after it emerges from germination, but is of a lower nutritive quality. As it grows its photosynthetic area increases making it a better source of nutrition to aphids. At the point that it flowers the plant sap becomes a high quality resource for the aphids. The quality of the resources is reflected in a high index of nutritive quality (a maximum) 100. This continues through the period when the pods swell. In vining peas the season ends with harvest at this point.

The rate at which the plant ages is temperature dependant in the model and has been matched to show approximately the same rate of plant development as that shown at the field site at Thorney in 1995.



**Figure 7: The estimated index of relative nutritional quality of vining peas to pea aphids adjusted to match a field of vining peas at Thorney in 1995.**

#### Model output

The model was run using the 40 days of detailed weather data collected at Thorney between the 6th of June and the 21st of July 1995, and compared with field counts taken by PGRO from the same field between those dates.

The results of separate simulations on data derived from experiments on peas cv. Scout and Sancho are given in figure 8. Although there are no statistically significant difference in the rates of aphid development between aphids reared on Scout and Sancho and the figures for their reproduction and mortality are also very similar, the model has taken the existing but small differences and produced strikingly different estimates of the aphid populations. In the context of an aide to decision making, the model has produced traces that are both quantitatively and qualitatively similar in field observations.

Further work in relating the output of the simulation models to the real field situation will be needed before the models may be safely used to refine economic decision making. With regard to the core population models, this will require additional independent data against which to test the model output. Such data needs to comprise both field counts of aphids and accurate and regular temperature recording.

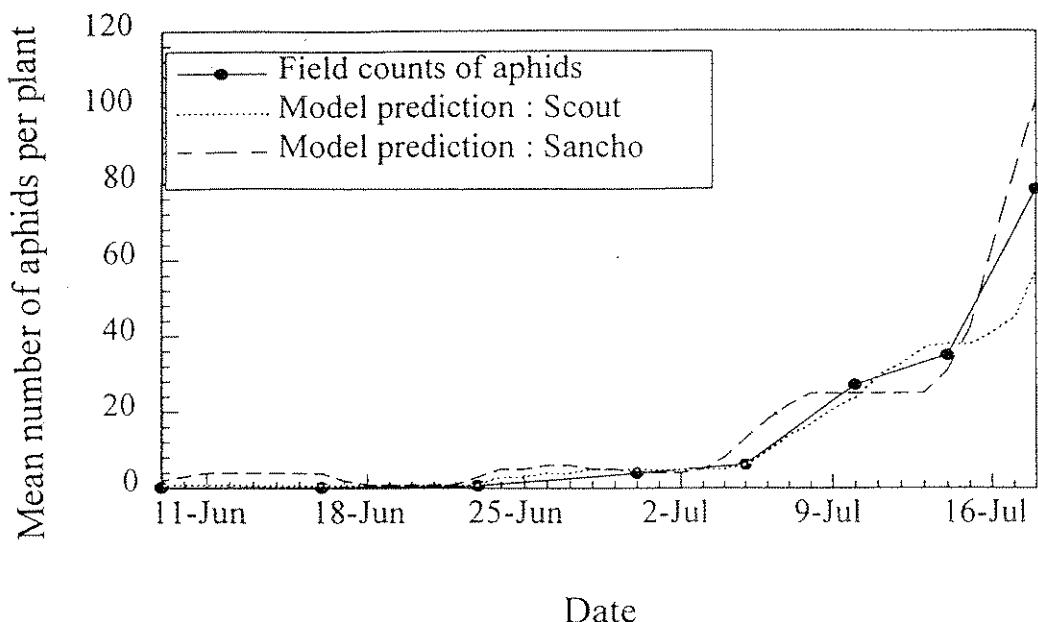


Figure 8 : A comparison of two model simulations using parameters taken from experiments on peas cv. Scout and Sancho with real population counts taken from Thorney in 1995.

#### Spray trial

Table 7 shows the number of infested shoots at each spray timing and on the untreated plots, together with the yield and maturity of the peas.

Table 7. Spray timing results.

growth stage	106	% infested shoots	201	203	204	yield t/ha	maturity (TR)
1. untreated	10.0	46.7	41.7	55.0	3.47	112	
2. 106	-	-	28.3	61.7	3.43	114	
3. 106 + 201	-	25.0	16.7	15.0	3.92	117	
4. 201	-	50.0	11.7	18.3	3.93	115	
5. 201 + 204	-	38.3	11.7	21.7	2.92	109	
6. 203	-	-	58.3	10.0	4.36	115	
7. 203 + 204	-	-	63.3	16.7	3.96	113	
SED @ p = 0.05		nsd	11.60	11.12	0.26	4.83	
cv*		58.8	49.6	55.5	9.7	6.0	

The highest yields were obtained from sprays applied at the first flower stage, but by then the aphid infestation level was well above the threshold of 15%. There was no economic response as a result of a second spray made at first pod, but the aphid infestation level had recovered to a level only just above the 15% guide-line indicated by earlier work.

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