A SIMULATION STUDY OF THE POPULATION, DAMAGE AND CONTROL OF THE ROSE GRAIN APHID, *METOPOLOPHIUM DIRHODUM*

by

Zhou Xilong

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Dept. of Entomology & Nematology
AFRC Inst. of Arable Crops Research
Rothamsted Experimental Station
Harpenden
Herts

Dept. of Pure & Applied Biology
Imperial College at Silwood Park
Ascot
Berks

Abstract

The rose grain aphid, *Metopolophium dirhodum*, overwinters mainly as eggs on Rosacea in England and migrates to cereals in spring. It feeds predominately on cereal leaves where it occasionally causes serious yield loss, as in 1979.

A field study was done to study effects of the aphid population development on yields under different nitrogen and fungicide levels. The aphid populations in the three years were low. Aphicide did not affect yield in 1987 and 1989 but significantly increased the yield in 1988. Input of nitrogen increased the yield in 1987 and 1888 but not in 1989. Fungicide reduced disease infection significantly but did not affect yield in the three years.

Aphid development time was longer and reproductive rate was lower on winter wheat in the laboratory study than that on barley reported in literature. Crop growth stages significantly affected the aphid development time and reproductive rate, which were similar when the aphids fed on flag and lower leaves. The results were compared with other studies.

A systems analysis approach was used to investigate relationships between crops, the aphid and weather. A simulation model was developed to study the population dynamics and damage potential of the aphid. The model was used to analyze the profit of different control strategies.

The model was validated using data from four contrasting years. It accurately predicted the aphid population and yield loss in 1979, but not in other years. The reasons for these results were presented. The model indicates that crop growth stage, temperature, reproduction and survival are the important factors in the aphid population growth.

The model indicates that one spray was necessary to achieve the maximum profit during late flowering and early milky ripe stage in 1979. The profitability of no-control, prophylactic and control based on a forecast was investigated with different outbreak probabilities and forecast accuracies.

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Preface

Cereal aphids were not regarded as being of economic importance until the 1950's in Europe (Dean, 1974a; Vickerman & Wratten, 1979). Following the outbreaks of *Sitobion avenae* in 1968, many studies have been done on this aphid (see reviews by Vickerman & Wratten, 1979; Carter *et al.*, 1980 and also see Chapter one). In 1979, an outbreak of *Metopolophium dirhodum* occurred and a lot of attention was centred on it (Cannon, 1981 and Thornback, 1983). However, simulation studies have not been done to investigate the population dynamics and damage potential of this species.

The objective of this study was to develop a computer model which simulated the population dynamics of *M. dirhodum* and its damage potential on winter wheat. The model was used to study aphid population dynamics and to analyze control strategies.

The first chapter is a review of studies on aphid biology, ecology and damage. The second is a field study on effects of different production levels on damage caused by aphid infestations. The third chapter describes biological studies of the aphid on winter wheat in the laboratory and field. The fourth chapter describes the development of a simulation model. The fifth chapter presents the results from the model and the final chapter is a general discussion.

CHAPTER ONE: REVIEW OF APHID STUDIES

1.1 Aphid biology

1.1.1 Life cycle

M. dirhodum overwinters holocyclically as eggs on Rosacea (Hille Ris Lambers, 1947) (Fig. 1.1) although it can also overwinter viviparously on cereals and grasses (George, 1974). Apterous fundatrices hatch from eggs on Rosacea at budburst during the spring. These fundatrices produce alate and apterous fundatrigeniae. The third generation is always alate (Hille Ris Lambers, 1947). These alates migrate to cereals and grasses in mid-May and early June and produce apterous exules which stay on Gramineae for several generations during the summer. Populations can develop rapidly from June to August, depending on the size of spring migration, weather and natural enemies (Dewar & Carter, 1984). Alatiform exules develop, dependent on aphid density and crop development stage (Carter *et al.*, 1982), and as the cereals ripen they emigrate to grasses. From August onwards, shortening daylength and lower temperatures induce first the appearance of gynoparae, and then males. These return to roses, favouring bushes in dense woodland and tall hedgerows rather than those in open woodland (Hand and Williams, 1980). The gynoparae produce oviparae which mature in time to mate with the males. These oviparae then lay the overwintering eggs.

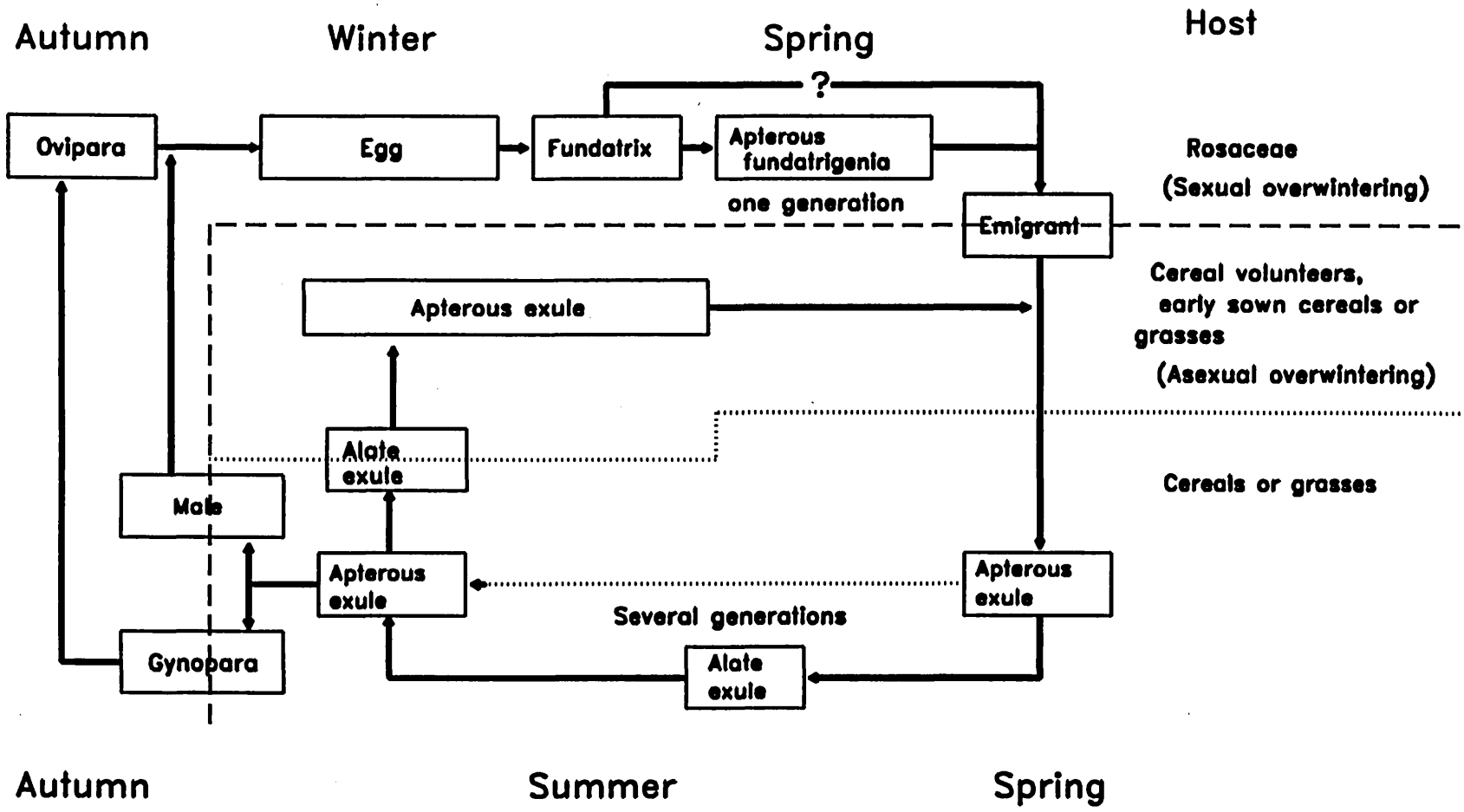


Fig. 1.1 Life cycle of the rose grain aphid, *Metopolophium dirhodum*

Anholocylic populations migrate to emerging cereals in September and October. Their survival is influenced by the severity of winter (Hand & Williams, 1980; Smith, 1981).

1.1.2 Migration and colonization of cereals

Migration is a common feature in many aphid species. *M. dirhodum* starts migrating to cereals in spring. However low aerial densities of aphids in early spring are difficult to detect (Taylor, 1977). Aerial populations have been sampled using suction traps (Taylor, 1974), water traps (A'Brook, 1973a, b) and sticky traps (Heathcote, 1957, 1970; A'Brook, 1973a, b). These traps vary in efficiency for individual species and also with time. For instance, yellow water-traps are less attractive to cereal aphids than other species (Heathcote, 1957; Heathcote *et al.*, 1969). Suction traps sample numbers of aphids per unit volume of air and are non-selective among migrating species (Heathcote, 1957), presenting a reliable estimate of the aerial populations within a radius of 20-50 km around each trap (Taylor, 1979). Therefore, in Western Europe and North America, suction traps are now increasingly used to monitor aerial aphid populations.

Taylor (1965) and Dry and Taylor (1970) noted that temperature below 14°C inhibited aphid take-off and Cockbain (1961) reported that under a certain temperature, aphids (*Aphis fabae* Scop) were unable to fly. Walters and Dixon (1984), used suction trap catches and meteorological data together with laboratory experiments, to obtain a minimum take-off temperature

threshold for *M. dirhodum*. The threshold was 20.5°C which was higher than that for *S. avenae* (16°C estimated from the suction traps and 19°C from laboratory studies at constant temperature) (Walters and Dixon, 1984).

Some observations indicate that high winds delay but do not permanently inhibit aphid take-off (Walters & Dixon, 1984) while others suggest that they also inhibited aphid take-off (Malwyn, 1936; Thomas & Vevai, 1940). Wind direction directly affects flight direction when its speed is in excess of the flight speed of the insect (Taylor & Palmer, 1972).

The Rothamsted Suction Trap Insect Survey, operating since 1964, has provided useful information on the migrations of many aphid species (Taylor & Palmer, 1972). The traps sample large volumes of air per unit time and usually catch cereal aphids before they are sampled in cereal crops (Dean, 1973; Dean & Luuring, 1970, George, 1974; Taylor, 1974). Carter *et al* (1982) used suction trap and sticky trap samples from 1965 to 1971 to standardize the two trap types for *M. dirhodum*. That study indicates that the abundance of aerial populations of *M. dirhodum* has increased from 1942 to 1980.

Sources of migrant *M. dirhodum* on cereals are not clear. Leather and Walters (1984) argued that immigrants on cereals are not from primary hosts but from secondary hosts. Migrants, which fly from roses in mid-May (Dewar *et al.*, 1980) and settle on cereals and grasses (Dewar *et al.*, 1980), are often rare in suction trap samples (Taylor, 1972). Dewar *et al.* (1980) showed

that the date of the population peak of *M. dirhodum* caught at each site was correlated with latitude, being later at northerly sites in 1979. Furthermore, the timing and size of the spring migration are influenced by weather (Dewar *et al.*, 1980; Walters & Dixon, 1984). High winds and low temperature delay cereal aphid migration (Walters & Dixon, 1984). The size of previous autumn migration also affects the size of the next spring migration (Carter *et al.*, 1980).

M. dirhodum colonizes cereals over the whole field while *S. avenae* and *R. padi* occur initially at field edges (Dean, 1973, Dean & Luuring, 1970). However, Carter *et al.* (1980) and Latteur (1976) did not have this edge effect in their studies and Rautapää (1976) also did not observe any edge effects in fields. This probably results from the nature of surrounding habitats in the areas. The fields in the studies of Latteur and Carter *et al.* were not surrounded by hedgerows, therefore, edge effects may be absent while the fields in the other studies were surrounded by high hedgerows or woodland. Hedges affect insect deposition more than wind direction and more insects were caught in suction traps along high hedges than low ones (Bawden & Dean, 1977).

Dewar (1980) observed that 48% or more *M. dirhodum* occurred on plots with the high nitrogen input level later in the season in a multidisciplinary experiment although rates of population increase were the same in plots with different nitrogen levels. Kowalski and Visser (1983) suggested that aphids may prefer to settle on high nitrogen crops.

1.1.3 Population development on the secondary host

Population development of *M. dirhodum* varies on different secondary hosts. Dean (1973, 1974b) studied the survival, development and fecundity of *M. dirhodum*, *S. avenae* and *R. padi* on seedlings of oats, wheat and barley and on barley leaf discs at a range of constant temperatures. Populations of *M. dirhodum* develop faster on barley than on either wheat or oats as development, survival and fecundity rates are highest on barley. Oats is the least favourable host of the three cereals (Thornback, 1983).

There are also varietal differences within one type of cereal. Kolbe (1969) tested ten West German winter wheat varieties and found that there were seven times as many *M. dirhodum* on cv. Hanno as on cv. Heines. Winter wheat cv. Norda was resistant to *M.dirhodum* in Belgium (Latteur, 1976). Winter wheat, Anna Miglori and Master, were also partially resistant cultivars (Lowe, 1978). However, results from different trials were variable and more reliable and consistent assessment methods are required (Lowe, 1977, 1978). Spiller and Llewellyn (1986) used two wheats, *Triticum aestivum* (susceptible), and *T. monococcum* (resistant), to measure honeydew production of *M. dirhodum*. They found that more honeydew was excreted by the aphid which fed on the susceptible *T. aestivum*.

Crop growth stage also affects population development (Lowe, 1978). *M. dirhodum* is more fecund on wheat during flowering (G.S. 60-69) and milky ripe stage (G.S. 71-79) than on seedlings (G.S. 10-12). In contrast, on barley it is more fecund on seedlings than on plants at booting to inflorescence (G.S.

41-60) (Thornback, 1983). *M. dirhodum* has a higher survival rate and is more fecund before the milky ripe stage on winter wheat (Watt, 1979; Vereijken, 1979). Honek (1985) found that the annual variation in *M. dirhodum* was positively correlated with plant vigour measured by average leaf area per tiller.

1.1.4 Feeding sites and local dispersal

M. dirhodum is almost entirely a leaf feeder on all cereals. Its population initially begins on the lower leaves and it moves up the plants to occupy the higher leaves as the lower leaves senesce (Wratten, 1975; Cannon, 1982; 1985). Cannon (1982) observed 68.5% of the populations were on the flag leaves on winter wheat later in the season (from 4 June to 2 August). But Dean (1973) found that 84.6% of all individuals were on the lower leaves, with only 15% on the flag leaves on barley. Latteur (1976) recorded 70% of *M.dirhodum* on the upper two leaves at the beginning of flowering (G.S. 61) and the whole population was on these leaves, with 90% on the flag leaves at the milky ripe stage (G.S. 71). This suggests that *M. dirhodum* prefers to feed on lower leaves on barley.

Observations by Dewar *et al.* (1982) and Cannon (1984) showed that adult and fourth instar nymphs of *M. dirhodum* were more likely to disperse than younger nymphs. Sopp *et al.* (1987) observed that *M. dirhodum* was more prone to fall from plants than *S. avenae*. Using sticky traps to intercept the falling aphids, Sunderland *et al.* (1986) showed that about 20-50% of the shoot population fell to the ground each day and this could increase to 100% late in the season. Griffiths *et al.* (1985) observed that between 4% to 71% of the aphid population was on

the soil surface during inspection. Sopp *et al.* (1987) obtained a negative correlation between the percentage of aphids falling on ground and the density on plants, but a positive relationship between the absolute number of aphids on the ground and the density. The fate of these aphids has rarely been studied. Sopp *et al.* (1987) found, from a visual examination of the ground area, that about 30% of the aphids on the ground were dead due to a unknown reason. Ground predators may consume a proportion of the aphids, which is suggested to be important in preventing aphid outbreaks (Sunderland & Vickerman, 1980; Chiverton, 1986; Scheller, 1984). Finally, a proportion of the aphids climb back to plants, which may act as a means of local redistribution of the aphid population on cereals (Winder, 1990).

1.1.5 Weather factors

Temperature is the most important factor influencing aphid population development. *M. dirhodum* has a lower optimum temperature than *S. avenae* and *R. padi* (Dean, 1974b). The optimum temperature for development, survival and reproduction is 20°C. It survives better between 10-15°C than between 20-25°C and nymphs die before completing their development at 27.5°C (Dean, 1974b; Hand and Williams, 1980). Warm conditions from mid-May to the end of June are positively correlated, and very high temperature (> 27°C) over the same period are negatively correlated, with peak abundance of *M. dirhodum* (Honêk, 1985).

Low temperatures in winter can delay crop development and allow the cereal aphids more time to feed on the crops the

following summer (Dewar, Woiwod & Janvry, 1980) and *M. dirhodum* growth is faster in cooler and more humid microclimates (Honek, 1987). However, the effects of temperatures below 10°C have not been studied.

Low temperature, heavy rainfall and lack of sunshine adversely affect cereal aphid populations on crops, especially during May and June when immigration of alates and their subsequent reproduction lead to the establishment of colonies (Dean & Luuring, 1970; Dean, 1973; 1974a, b; Jones, 1972). High rainfall encourages the development of fungal diseases of aphids as it provides sufficient humidity for their growth. In Brittainy, the rainfall is negatively associated with peak aphid numbers (Pierre & Dedryver, 1984, 1985).

1.1.6 Natural enemies

There are three groups of natural enemies of cereal aphids: predators, parasitoids and pathogens. They may sometimes prevent aphid population outbreaks (Carter, 1989). However, difficulties in quantifying the effectiveness of these natural enemies in reducing cereal aphid population growth in the field still remain (Carter *et al.*, 1980; Dixon, 1989; Carter, 1989).

Aphid predators are divided into two categories; (i) aphid-specific and (ii) polyphagous predators. Aphid-specific predators are coccinellids and syrphids. In some years, coccinellids may prevent aphid populations reaching the economic threshold when the cereals are favourable for aphid development (Chambers *et al.*, 1983, 1986). The number of coccinellids is positively

correlated with the number of aphids in the previous summer (Carter, Dixon & Rabbinge, 1982). Field cage studies also suggest that coccinellids could be important in reducing aphid abundance (Rautapaa, 1972, 1975; Chambers *et al.*, 1983). Simulation studies also reveal that effects of these predators are sensitive to the aphid population dynamics (Carter *et al.*, 1982). There are many polyphagous predator species including beetles, mites and spiders. Some species consume aphids at low densities and are usually present in crops when aphids arrive. Therefore they can be effective in reducing the size of aphid populations early in the season (Carter, 1989).

Three species of fungal pathogen belonging to the same order of *Emtomophthorales* were recorded to attack cereal aphids in Britain (Dean & Wilding, 1971, 1973; Jones & Dean, 1975). Their importance in reducing field aphid populations varies from year to year and from locality to locality (Dean & Wilding, 1973; Jones & Dean, 1975). When conditions are humid and diseased aphids appear early in the season, these pathogens are important in reducing aphid abundance (Latteur, 1973).

Parasitoids belong to two families of Hymenoptera; Aphelinidae and Aphidiidae. The latter is more common (Carter, 1989). They can be active early in the season and very numerous (Powell, 1983). Their role in reducing aphid abundance is often underestimated in the field (Carter, 1989). For instance, a simulation study indicates that the population of *S. avenae* could be seven times higher at flowering in the absence of parasitism (Vorley & Wratten, 1985). However, hyperparasitsm may be important in suppressing the increase of parasitoids

especially towards the end of the season (Carter *et al.*, 1989), and it reduces their effectiveness in reducing aphid population growth.

1.2 Aphid population models

Aphids are major pests in the world and their successful control using pest management principles requires an understanding of their population dynamics. However, aphid populations pass through several generations in a year, these generations overlap, and populations rarely reach a stable age structure (Carter *et al.*, 1978; Barlow & Dixon, 1980) making analysis of their population dynamics complicated.

Attempts at using statistical models to describe relationships between aphid population and other factors have been made. For instance; in a study of lime aphid, *Eucallipterus tiliae* (L.) populations, Barlow & Dixon (1980) showed that the peak density of oviparae in autumn was related to the maximum population of fundatrices in the preceding spring; Walters (1983), in developing a method for long-term predictions of outbreaks of the grain aphid, *S. avenae*, showed that the timing and size of the population peak could be predicted from the mean temperature in January. Entwistle & Dixon (1986) found that the peak aphid density in a wheat field was positively correlated with the population density at the end of anthesis. The advantage of this type of model is that it is easy to use in forecasting. However, as these models are usually derived with a lack of biological background, they may fail when applied in new circumstances and cannot be used to explain the reasons for the breakdown in the relationship (Ward, Rabbinge & Dixon, 1988).

Simulation models are ideal in studying aphid population as age structure and overlapping generations are easily incorporated. They are constructed using biological information although they may require many parameters. Values for these are obtained from laboratory experiments and field work, which is very time-consuming.

Hughes & Gilbert (1968), and Gilbert and Hughes (1971), developed one of the first simulation models for aphids (the cabbage aphid, *Brevicoryne brassicae* (L.)) which concentrated on the effects of natural enemies on aphid population development. The model used a physiological time scale with aphid instar-periods as units (the average number of daydegrees of the four instars above the development threshold). It was used to investigate stochastic variation of population dynamics, parasitism strategies and the application of the model in biological control. The model suggested that the parasitoids maximised its reproduction, without endangering their host population and more detailed information of parasitoid behaviour was required on the effects on aphid populations.

In the Netherlands, a simulation model of the population development of *S. avenae* in winter wheat was developed (Rabbinge *et al.*, 1979). It was used to study populations of *S. avenae* and its natural enemies over three years. The model was initialized with an aphid density already on the crop. However, as knowledge of the relationship between aphid density and the effects of their natural enemies and wing formation were unknown, the model did not predict accurately the population collapse.

Carter *et al.* (1982) developed a simulation model to describe the population dynamics of the grain aphid, *S. avenae*. The model was also initialized with immigration estimated from suction trap samples and the first field count of aphid density if field populations existed at the start of the simulation. Temperature, expressed in physiological time was the main driving variable. The model included effects of crop development and some natural enemies on the aphid population. It generally predicted field observations accurately but was less reliable when natural enemies were important in regulating aphid populations. The model revealed that the roles of natural enemies in preventing aphid increase were poorly understood and more work is needed. This simulation approach has also been used to study plant resistance on population growth of *Rhopalosiphum padi* (Wiktelius & Petterson, 1985) and resistant plant breeding for insects (Carter & Dixon, 1981).

1.3 Cereal aphid damage and its control

In Britain, there are three economically important cereal aphid species: *S. avenae*, *M. dirhodum* and *R. padi*. *R. padi* causes crop damage primarily by transmitting barley yellow dwarf virus (BYDV) to all types of cereals, especially barley. *S. avenae* is important as a virus vector and through the damage it does directly and *M. dirhodum* is only important in the latter category. The effect of honeydew excreted by aphids is thought to be more important than the damage caused by feeding (Rabbinge *et al.*, 1981; Rabbinge & Carter, 1984; Roermond *et al.*, 1986). A number of studies on its damage potential have been carried out (for instance, Wratten, 1979; Lee *et al.*, 1981; Holt *et al.*, 1984) and several control schemes and strategies have been

studied and developed (Mann *et al.*, 1986; Wratten & Mann, 1986; Zadoks *et al.*, 1984).

1.3.1 Yield loss studies

The number of grains per ear is determined before anthesis (Thorne, 1973). Aphids reduce grain number before anthesis and alter the translocation of nutrients to the grains during milky ripe stage, and may therefore affect grain quality and thousand grain weight (Wratten, 1978). Fungal diseases, which may be stimulated by honeydew, can change plant physiology and reduce yield and quality (Lee *et al.*, 1981; Wratten, 1975).

A heavy infestation can result in a significant yield loss (Wratten, 1978; George & Gair, 1979). However, yield loss by *M. dirhodum* was not reported before the 1960s (Kolbe, 1969). Lowe (1974) demonstrated the effect of *M. dirhodum* on spring wheat in a glasshouse. High and low infestations of 2200 and 340 aphid units (A.U.D., calculated as one aphid unit equal to one adult, or 1.5 fourth instar, or 2 third instar, or 3.5 second instar or 5 first instar nymphs) during the period from stem elongation to ripening, caused 36.9% and 11% yield loss, respectively, compared with the control. An infestation (110 A.U.D. from 29 January to 9 February) did not affect yield. A similar yield loss - aphid density relationship was reported in field cage experiments (Wratten, 1975; 1978).

A significant yield loss occurred in winter wheat (15%) when aphids were present from the start of booting (G.S. 41) to the end of anthesis (G.S. 69). A similar accumulated aphid index (503) (one aphid unit is equal to one adult or two 4th and/or

three other instar nymphs, the same as in following experiments) did not cause a significant yield loss from mid-anthesis (G.S. 65) to early milk (G.S. 73) (Holt *et al.*, 1984). However, the initial number of aphids in both trials was low and aphid populations only builted up towards the end of the treatment. Therefore, the significant yield loss for the early treatment may have been because the peak population occurred during flowering which is a particularly susceptible stage (Basedow *et al.*, 1985). In an experiment using three narrow crop growth periods, total grain weight per ear and mean thousand grain weight were significantly affected by the timing of aphid infestations of similar sizes (Holt *et al.*, 1984). An early infestation from the start of stem elongation (G.S. 31) to the start of booting (G.S. 41) did not cause yield reduction, but infestations from the start of booting (G.S. 41) to mid-flowering (G.S. 65) and mid-flowering to late milk (G.S. 77) did result in significant yield reductions (8%, 27% respectively).

On barley, damage has been studied over three periods of crop growth stage: (i) from the start of stem elongation (G.S. 31) to the beginning of anthesis (G.S. 61), (ii) mid-inflorescence (G.S. 55) to mid-milk (G.S. 75) and (iii) watery ripe (G.S. 71) to early dough (G.S. 80) (Lee *et al.*, 1981). Yields were reduced significantly in the first two treatments (by 16% and 11% respectively), but not in the third. However, the sizes of the infestations were different, as the first two treatments had similar aphid indices, 376 and 394 respectively, but the third one had a smaller index of 194.

M. dirhodum was first recorded in New Zealand in 1982 when

heavy infestations occurred (Stufkens & Farrell, 1984; 1985a) and was first recorded in Australia in 1984 (Carver, 1984). Stufkens and Farrell (1985b) found that control of *M. dirhodum* on barley at flag leaf extension (G.S. 41), and in the fields at both flag leaf extension and mid-inflorescence (G.S. 55) showed significant yield increases with 310 and 230 accumulated aphid days (AAD) respectively, compared with 2350 AAD in unsprayed fields. However, in spring oats sprayed at mid-inflorescence, no significant yield increase occurred compared with control plots infested with 2200 AAD. Sprays at both flag leaf extension and mid-inflorescence showed a significant yield increase with 150 AAD, compared with 1350 AAD in control fields on barley. They found no significant yield increase to the treatments on winter wheat which may be due to the low infestations (420 AAD in unsprayed fields and 30 to 310 AAD in the sprayed fields).

Results from these experiments indicate that flowering is the most susceptible crop growth stage to aphid damage. Other yield loss studies show a similar conclusion. Spraying against *M. dirhodum* and *S. avenae* with 20 to 200 aphids per shoot resulted in 42% yield increase at the beginning (G.S. 61) to end (G.S. 69) of anthesis, compared with unsprayed fields (Kolbe, 1969) and 14% increase at the end of flowering (G.S. 69) (Kolbe, 1970). Spraying at the end of anthesis (G.S. 69) had the highest yield increase (Basedow *et al.*, 1985).

Roermond *et al.* (1986) constructed a simulation model to study the damage potential of *S. avenae*, incorporating the influence of *S. avenae* on several physiological parameters: carbohydrate and nitrogen content in the grain. In the model,

two types of damage were included. Primary damage is caused by withdrawal of carbohydrate and nitrogen which leads to less carbohydrate taken up by grains and an increase of nitrogen translocation from leaves. This leads to a reduction in photosynthesis of the leaves and an increase in leaf senescence. Secondary damage is caused by a reduction in maximum gross photosynthesis and light use efficiency by coverage of ears and leaves with honeydew. The model accurately predicted the yield reduction in field observations and it was concluded that more damage is caused by excretion of honeydew, which interferes with leaf photosynthesis, than damage from direct feeding.

Cereal aphids can reduce grain protein content which is important for bread baking (Rautapaä, 1968; Wratten, 1975). Quantitative yield loss only occurred when *M. dirhodum* was confined on flag leaves, but aphids confined on the second and third leaves reduced grain protein content (Wratten, 1978). Furthermore the nitrogen content in lower leaves which were infested was higher at senescence compared with uninfested leaves. Such changes are due directly to aphid feeding which senesces leaves and intercepts nitrogen translocation from leaves (Wratten, 1978). However, the indirect effects of aphid feeding damage, honeydew excretion and disease growth, also reduce protein content in grains (Wratten, 1975). Finally, flour colour was darkened by *M. dirhodum* infestations (Wratten, 1978)

1.3.2 Forecasting and control

The main aim of a forecasting scheme is to predict when and how much yield loss caused by aphids is likely to occur. This

prevents the overuse of insecticides and should result in the maximum profit. Without an accurate forecasting system, farmers are likely to apply aphicides prophylacticly (Watt, 1983). With the increase in concern over environmental contamination by insecticides, accurate forecasting systems are more necessary. A forecasting system, however, should not need labour-consuming crop inspections but must be simple and accurate (Dixon, 1987).

1.3.2.1 *Cereal aphid economic threshold*

If an economic threshold is exceeded, control is justified as the value of the potential loss of yield saved by control is greater than the control costs. A number of economic thresholds have been suggested on cereal aphids in different countries (Way & Cammell, 1979). In Britain spraying is justified economically when an increasing density of *S. avenae* reaches five per ear at the start of flowering (G.S. 61) (George, 1974; George & Gair, 1979) and 5 per flag leaf and increasing for *M. dirhodum* during flowering (George & Gair, 1979) (the current threshold is 5/shoot, Walters, per. comm.). In West Germany, the economic threshold is one aphid per ear or flag leaf at the end of flowering and six afterwards (Way & Cammell, 1979). Wetzel & Freier (1980) reported 2-5 aphid per ear at the beginning of ear filling for *S. avenae* and 15 per tiller at flowering for *M. dirhodum* as the cereal aphid economic thresholds. A similar threshold to that in Britain was reported in China for *S. avenae* (Liu, Stoltz & Ni, 1986). Wratten (1979) obtained a damage threshold, in terms of an aphid index (one unit is equal to one adult, or fourth instar and or three first to third instar nymphs), to be 21 to 25 on ear and flag leaf combined at watery ripe when significant yield loss occurred. This threshold was

not useful in control decision making, because the economic damage had already been done when the aphid population reached that level.

1.3.2.2 *Forecasting*

Rautupää (1976) suggested a method to forecast the peak number of *R. padi* 2-3 weeks before the peak was reached using the number observed 3 to 10 days after the first alate was found in the crop. As it is difficult to determine when the first aphid landed on crop, Wikletius (1982) suggested modifying the Rautupää's model by using suction traps to monitor the time of the initial colonization.

Dewar & Carter (1984) suggested that the Rothamsted Insect Survey suction trap system might be used directly in forecasting the peak density of cereal aphids. However, the suction trap samples are not always related to subsequent peaks on wheat crops, e.g. in 1980, 1981 and 1983 when high aphid number caught in suction traps were generally followed by low aphid peak densities in crops. More studies are needed before suction traps can be used in forecasts.

Direct counts of aphid numbers at heading (G.S. 50-59) or beginning of flowering (G.S. 61) are used in forecasting, taking into account rate of increase in the field obtained in the past (Freier & Wetzel, 1980; Carter *et al.*, 1982; Zadoks *et al.*, 1984; Reinink, 1985; Mann & Wratten, 1987). However, Entwistle & Dixon (1986, 1987) used multiple regressions to predict peak aphid populations and yield loss. They found that the peak population density in each field was positively correlated with

the population densities at the end of ear emergence (G.S. 59), mid-anthesis (G.S. 65) and the end of anthesis (G.S. 69), and the observed rates of increase of the aphids on the crop immediately before these stages. The accuracy of these forecasts, based on two field samples, increases from ear emergence to end of anthesis and they claimed that the forecast peak density at mid-anthesis was more accurate than other published methods.

A decision tree was constructed to aid the forecasting of *S. avenae* and *M. dirhodun* (Dewar & Carter, 1984). Factors such as crop sowing date, size of autumn migration, severity of previous winter, size of spring migration and incidence of natural enemies were considered. Each branch of the tree has several pathways until a final decision is reached. This technique is useful when the information for each branch can be estimated accurately.

1.3.2.3 *Computer packages developed in aphid forecasts*

A number of forecasting schemes, based on computer models, have been developed. In the Netherlands, EPIPRE (EPIdemics PREvention and PREdiction) is a system which advises farmers on the need to control diseases as well as aphids in cereals (Zadoks, Rijsdyk & Rabbinge, 1984). Farmer are expected to monitor their own crops and send information by post regarding pest and disease levels to a central database. This information, also including details of crop development, is integrated into a computer system. Based on dynamic decision rules developed in the system, a decision is made if a spray is necessary, i.e. when the yield gain will equal or exceed the cost of the

application. They are then advised on whether to spray or not and when to sample crops again (Rabbinge & Carter, 1984). In Great Britain, a viewdata system has been developed based on the crop loss relationships described by Watt *et al.* (1984), Wratten *et al.* (1981) and Holt *et al.* (1984) (Mann *et al.*, 1986; Wratten & Mann, 1986). The program predicts the damage that an aphid infestation may inflict on a specific field of winter wheat and advises the farmer on a rational control policy. It assumes the maximum aphid population growth rate at particular growth stages so it is likely to result in an overuse of aphicides

1.3.2.4 *Monitoring*

Field monitoring for forecasting is expensive and labour-intensive (Rabbinge & Mantel, 1981; Rabbinge & Carter, 1984). To avoid this, two simpler methods have been proposed (i) suction trap (12.2 m) samples can be used to determine the size and timing of immigration and so estimate the number of aphids landing on crops (Taylor, 1972, 1977; Dewar & Carter. 1984) which gives an indication to farmers when to inspect their crops, and (ii) a significant linear relationship was fitted between aphid density and percentage of infested shoots (Rabbinge & Carter, 1984). Such a relation is used in EPIPRE and has proved to be reliable in estimating aphid densities (Rabbinge & Carter, 1984).

1.3.2.5 *Development of control strategies*

There are three control strategies: no control, prophylactic control and control following a forecast. Six factors are important in making these strategies: (1) probability of an outbreak; (2) expected level of damage; (3) the accuracy of the

forecast; (4) the cost of control; (5) a farmer's attitude to risk and (6) market grain price.

A cost benefit analysis (Watt, 1983) of these three control strategies concluded that the optimal strategy varies depending on the accuracy of forecasting and control costs and the probability of an outbreak. Such analysis was based on the assumption that the aphid population will not resurge after aphicide is applied, which leads to a false conclusion: it is more profitable if the aphicide is applied as early as possible.

CHAPTER TWO: FIELD STUDIES

2.1 Introduction

Some forecasting schemes of cereal aphid damage (Entwistle & Dixon, 1986; Mann *et al.*, 1986) assume that aphids cause the same amount of damage regardless of expected yield. It has been suggested, however, that the damage potential of cereal aphids is a function of production level (Rabbinge *et al.*, 1983). Indirect effects of the aphids, such as honeydew reducing photosynthesis and accelerating leaf senescence, cause more yield loss at high production levels. Furthermore, high nitrogen input may result in high aphid populations because of increases in reproduction, survival and development rates and these populations are more likely to reach the economic threshold (Vereijken, 1979). if percentage damage is constant then the amount of damage (kg/ha) increases as yield expectation increases. Therefore, high production systems should have lower economic thresholds. This field trial was designed to investigate the effects of aphid populations on winter wheat receiving different nitrogen and fungicide inputs.

2.2 Methods

2.2.1 Experiment design

The experiment consists of three blocks, each of 12 plots (3x12m) randomised for three treatments: aphicide or none, fungicide or none and three levels of nitrogen. The plots were separated by 3m sown spray paths and blocks separated by 6m.

Winter wheat, cv. Avalon, was sown on 6 Nov at 197kg/ha, on 6 Oct. at 160kg/ha and 30 Sept. at 180kg/ha in 1986, 1987 and 1988 respectively. Herbicides and growth regulators were applied according to standard practice (Table 2.1). Nitrogen was applied at one of three levels to each plot. The standard input level of the nitrogen fertilizer was varied in the two years dependent on the previous crop and the expected soil residues. The upper and lower levels were 25% more or less of the standard respectively (Table 2.1). Aphicide was applied 3 to 5 times to half of the plots to ensure aphid populations remained below damage levels. Fungicide was applied three times to half of the plots with the other plots receiving no fungicide (Table 2.1).

2.2.2 Sampling

Aphid sampling was started on 2 June, 1987, on 12 May, 1988 and 14 April, 1989 on the plots receiving no aphicide and continued at approximately one week intervals. Twenty to twenty five shoots were selected at random dependent on the abundance of the aphid population in 1987 while in 1988 and 1989 fifty shoots were always inspected. Ears, stems and leaves were inspected for aphids and the species and their numbers were recorded. The numbers of each aphid species was separated into five components; 1-3 instar nymphs, apteriform and alatiform fourth and apterous and alate adults. Mummified and diseased aphids, and eggs and larvae of lacewing, syrphid and ladybird were also counted. Plots treated with aphicide were inspected during each observation to ensure aphid populations on these plots were below damaging levels.

Table 2.1 Crop agronomy of experiments in 1987, 1988 and 1989.

1987	1988	1989
Weedkiller (/ha)		
Clopyralid at 0.07 kg and bromoxynil at 0.34 kg with mecoprop at 2.5 kg in 200 l Glyphosate at 1.4 kg in 200 l	Chlortolurn at 3.5kg in 200l Mecoprop at 3.0kg in 200l	Chlortolurn at 3.5kg in 200l Metsulfuron-methyl at 0.0062kg in 400l
Growth regulator (/ha)		
Chlormequat at 1.6kg in 200l	Chlormequat at 1.3kg in 260l	Chlormequat at 1.3kg in 200l
Previous crops		
Winter Wheat in 1985 Potatoes in 1986	Winter barley in 1986 Potatoes in 1987	Winter barley in 1987 Winter oilseed rape in 1988
Nitrogen fertilizer		
'Nitram': kg/ha on 14 April 80 120 160	'Nitram': kg/ha on 22 April 105 140 175	'Nitram': kg/ha on 14 April 80 120 160
Aphicide: Pirimicarb (/ha)		
Applied at 0.14 kg on 23 June, 3 and 16 July or none	Applied at 0.14 kg in 260 l on 6 May, in 200 l on 20 May and in 260l on 6, 20 June and 12 July or none	Applied at 0.14 kg on 31 May, 13 and 28 July or none
Fungicide (/ha)		
G.S. 31: Prochloraz at 0.4 kg and carbendazim at 0.15 kg in 380l on 6 May G.S. 39: Propiconazole at 0.12kg in 200 l on 28 May G.S. 59: Propiconazole at 0.12kg with carbendazimat 0.25kg and maneb at 1.5 kg in 200 l on 23 June or none	G.S. 31: Prochloraz at 0.4 kg and carbendazim at 0.15 kg in 200l on 21 April G.S. 39: Propiconazole at 0.12kg and Tridemmorph in 200 l on 20 May G.S. 65: Fenpropimorph at 0.75kg with chlorothalonil at 1.0kg in 260 l on 20 June or none	G.S. 31: Prochloraz at 0.4 kg and carbendazim at 0.15 kg in 200l on 15 April G.S. 39: Propiconazole at 0.12kg in 200 l on 17 May G.S. 65: Propiconazole at 0.12kg with chlorothanlonil at 1.0kg in 200 l on 13 June or none

Two plant samples were taken during the summer. The first one was at the end of anthesis (G.S. 69) on 29 June in 1987 and at the middle anthesis (G.S. 65) on 14 June in 1988 and 1989. Ten rows x 0.5 m of above-ground material per plot were harvested, starting 0.5 m from one end and one row from one side of each plot. samples were stored in a cold room (10°C). Total fresh weights were measured, and a subsample (approximately 500g) was taken, chopped and oven-dried at 80°C overnight and then weighed. Another subsample of twenty earring shoots, of known fresh weight, from the fresh material was selected at random and stored at 10°C. Then, the green leaf areas of flag, stem and other leaves were measured separately using a Delta-t area measurement system in 1987 and a Paton industries leaf area meter in 1988 and 1989. These flag, stem and other leaves, and ears and dead leaves then were oven-dried overnight at 80°C and weighed separately. Also, ten shoots from the total sample were taken for disease assessment. The incidence levels of any fungal pathogens found were recorded, according to Cereal Disease Keys (CIBA-GEIGY, 1982).

The second sample was taken immediately prior to harvest on 23 July, 1987, on 26 July, 1988 and on 27 July, 1989. The same area of above ground material was taken, adjacent to the earlier sample, and weighed. About 500 g of the material were taken, chopped and oven-dried overnight at 80°C, and then weighed. Ten shoots were also taken for disease assessment. Yellow areas were visually assessed in 1987 and 1988.

The plots were harvested with a combine on 1 September in 1987, on 23 August in 1988 and on 3 August in 1989 and the yield of each plot was obtained. Thousand grain weights were measured after drying overnight at 80°C.

The number of shoots per m^2 was counted directly before harvest in 1988 from four randomly placed quadrates (0.1 m^2) in each plot. There were four counts in each plot. The percentages of leaf area which had turned yellow were also assessed at pre-harvest (G.S. 95) on 26 July in 1988.

2.2.3 Data analysis

i) The leaf areas in mm^2 were used to calculate the LAI:

$$LAI_i = (Xa_i * A/B/C/10000) * Scal$$

where i is flag, other leaves and stems, Xa is areas in mm^2, A is the total fresh weight of the samples, B is fresh weight of the 20 shoots, C is the sampling area (m^2), Scal is 3.1415 when i is for stem otherwise it is 1 because the stem area obtained is the area of the stem diameter profile and was multiplied by 3.1415 to obtain the surface area of the stem.

ii) Aphid density was analyzed per 10 shoots on a $\log_{10}$ scale.

iii) Disease assessment data were normalized due to their skewed distribution by the function:

$$y = 0.5\log_e\{(10x + 0.5)/1001/[1 - (10x + 0.5)/1001]\}$$

Where x is the percentage of leaf area infected by pathogens (Todd, pers comm.).

iv) Ear number/m^2 (E_n) was estimated from the sample by the function:

$E_n = 20A/B/C$

Where A, B and C are as in the above functions.

All data were analyzed using Genstat 5 (Payne *et al.*, 1987).

2.3 Results in 1987

2.3.1 Yields

The applications of fungicide and increases in the amount of applied nitrogen resulted in significant yield increases individually (both $p<0.001$) and as an interaction component ($p<0.05$) (Table 2.2). The highest yield increase (15.8%) occurred in plots sprayed with fungicides compared with those not receiving fungicide, regardless of the nitrogen treatment. Yields of the plots receiving the higher and standard nitrogen fertilizer were similar, but they were both significantly higher than the yield of plots receiving the lower nitrogen level (>6.6%) ($p < 0.001$) (Table 2.3). Aphicide did not significantly increase yields, although the average yield from treated plots was slightly higher (3.3%).

The application of fungicides significantly increased thousand grain weight (11.1%, $p < 0.001$), whereas increasing the amount of nitrogen resulted in a reduction in thousand grain weight (4.5%, $p < 0.001$) (Table 2.4). Aphicide did not affect the thousand grain weight. Numbers of ears per m^2 were higher as

Table 2.2 Effects of aphicide, fungicide and nitrogen on yields (t/ha) in 1987.

Source of variation	d.f.	s.s.	.m.s.	v.r.	
Aphicide	1	0.4678	0.4678	3.37	
N-rate	2	2.7379	1.3690	9.85	***
Fungicide	1	9.4052	9.4052	67.68	***
Aphicide*N-rate	2	0.0703	0.0351	0.25	
Aphicide*Fungicide	1	0.0107	0.01007	0.08	
N-rate*Fungicide	2	1.0789	0.5399	3.87	*
Aphicide*N-rate*Fungicide	2	0.1915	0.0958	0.69	
Residual	22	3.0572	0.1390		

* —— $p<0.05$; *** —— $p<0.001$

Table 2.3 Effects of aphicide, fungicide and nitrogen on grain yield (t/ha) in 1987.

N-rates(kg/ha)	80		120		160		Mean
Fungicide / Aphicide	-F	+F	-F	+F	-F	+F	
-	6.25	7.00	6.50	7.42	6.46	7.95	6.93
+	6.54	6.92	6.65	7.90	6.81	8.13	7.16
Mean	6.39	6.96	6.57	7.66	6.64	8.04	7.04

Table 2.4 Effects of aphicide, fungicide and nitrogen on thousand grain weight (g).

N-rate(kg/ha)	80		120		160		Mean
Fungicide / Aphicide	-F	+F	-F	+F	-F	+F	
-	37.8	42.0	36.5	41.1	35.6	40.3	38.9
+	38.2	41.6	36.8	40.1	36.5	39.9	39.0
Mean	38.0	41.8	36.7	41.0	36.1	40.1	38.9

the amount of nitrogen applied increased although the effect was not statistically significant and the ear numbers were similar in plots with and without fungicide, and with and without aphicide (Table 2.5). The number of grains per ear was not significantly affected by any of the treatments.

Table 2.5 Effects of aphicide, fungicide and nitrogen on ear numbers/m^2 in 1987

N-rate(kg/ha)	80		120		160		Mean
Fungicide Aphicide	-F	+F	-F	+F	-F	+F	
-	399.7	416.0	416.2	453.1	487.9	473.3	444.1
+	437.3	416.1	420.2	455.9	500.0	466.3	449.3
Mean	418.5	416.1	418.2	454.5	493.9	469.8	445.2

2.3.2 Plant physiology

The average dry weight of the above ground material in the first sample was 886.9 g m^{-2}. Dry weights were increased significantly as the level of nitrogen input rose (Table 2.6). The percentage increase between higher and standard nitrogen levels (8.2%) was greater than that between standard and lower levels (5%). The average dry weight (1227.9 g m^{-2}) in the second sample was 38.5% higher than the first sample. There was a 10% increase in dry matter between the lowest and highest nitrogen levels and a 10% increase in the plots receiving fungicide in the second sample and no significant effects of fungicide on the dry matter in the first sample were found (Table 2.6).

Mean total LAI was 6.33 and mean flag, other leaves and stem area indices were 1.26, 1.58 and 3.50 respectively. Nitrogen treatment had significant effects on all components of the LAI's while fungicide only affected lower LAI (Table 2.7). There was

Table 2.6. Effects of aphicide, fungicide and nitrogen on total dry weight (g/m^2) in 1987.

		First sample			Second sample		
Source of variation	d.f.	s.s.	m.s.	v.r.	s.s.	m.s.	v.r.
Aphicide	1	1385.0	1385.0	0.17	24327.0	24327.0	2.07
N-rate	2	79127.0	39564.0	4.86 *	428038.0	204019.0	18.24 ***
Fungicide	1	2481.0	2481.0	0.30	113758.0	113758.0	9.70 **
Aphicide*n-rate	2	11279.0	5640.0	0.69	29226.0	14613.0	1.25
Aphicide*Fungicide	1	1973.0	1973.0	0.24	15854.0	15854.0	1.35
N-rate*Fungicide	2	12777.0	6389.0	0.78	8536.0	4268.0	0.36
N-rate*Aphicide*Fungicide	2	6493.0	3247.0	0.40	2625.0	1312.0	0.11
Residual	22	179228.0	8147.0		258068.0	11730.0	

* —— $p<0.05$; ** —— $p<0.01$; *** —— $p<0.001$

Table 2.7. Effects of aphicide, fungicide and nitrogen on Leaf Area Index (LAI) in 1987

Source of variation	d.f.	m.s.(+)	m.s.(++)	m.s.(+++)	v.r.(+)	v.r.(++)	v.r.(+++)
Aphicide(F1)	1	1.57	2.01	0.46	0.41	0.41	0.03
N-rate(F2)	2	44.08	105.14	207.41	11.60 ***	21.53 ***	13.18 ***
Fungicide(F3)	1	0.56	35.86	2.62	0.15	7.34 *	0.17
F1*F2	2	0.19	5.90	0.19	0.05	1.21	0.01
F1*F3	1	0.1	2.91	1.38	0.03	0.60	0.09
F2*F3	2	7.26	2.01	12.45	1.91	0.41	0.79
F1*F2*F3	2	0.33	2.86	1.96	0.09	0.59	0.12
Residual	22	3.80	4.88	15.73			

\+ —— flag leaf area; ++ —— rest green leaf area;

+++ —— stem area; * —— $p<0.05$; ** —— $p<0.01$;

*** —— $p<0.001$

an increase of 10.8% in LAI of lower leaves from plots treated with fungicides. Increases of LAI for flag, other leaves and stem were 14.8%, 16.0% and 10.9% between the lower and standard nitrogen levels and 17.7%, 23.5% and 13.9% between the standard and higher levels respectively.

Dry weights of flag and lower leaves were increased by each increase in the amount of nitrogen applied ($F_{2,22}$=14.33; $p<0.001$; $F_{2,22}$=19.96; $p<0.001$ respectively), but not that of stem or dead leaves. The dry weight of the lower leaves was also increased by 10% by the application of fungicide ($F_{1,22}$=4.45; $p<0.05$). The dry weight of dead leaves was significantly decreased by 33% ($F_{1,22}$=-10.66; $p<0.001$).

2.3.3 Aphid populations

Three aphid species were found during the summer; *M. dirhodum*, *S. avenae* and *Metopolophium festucae*. *M. dirhodum* was the predominate species and accounted for an average of 70% of the entire aphid population before middle milk stage (G.S. 75). *S. avenae* populations were small although its proportion increased slightly later in the season. Only a few *M. festucae* were found occasionally throughout the season (Fig. 2.1).

No aphids were found on 2 June and populations in the plots were also low on 10 June and increased gradually to a peak density of 6.6 per shoot on 8 July at middle milk stage (G.S. 75) (Table 2.8). The populations decreased rapidly to below 1 aphid per shoot one week later except on plots treated with fungicide and the standard rate of nitrogen. The highest density of 7.88 occurred in plots receiving the largest amount of

Table 2.8. Aphid densities per shoot in 1987

		Metopolophium dirhodum						*S. avenae*	Total
Date	G.S.	Instar I-III	Instar IV	Instar IV winged	Apt. adult	Alate adult	Total	Total	
10 June	47	0.073±0.039	0.004±0.00	0	0.011±0.004	0.002±0.002	0.091±0.04	0.009±0.005	0.1±0.067
16 June	53	0.106±0.029	0.018±0.01	0.004±0.003	0.034±0.013	0.002±0.002	0.163±0.048	0.107±0.045	0.287±0.048
24 June	65	0.400±0.067	0.080±0.031	0.011±0.006	0.045±0.012	0.005±0.005	0.54±0.068	0.186±0.038	0.753±0.064
3 July	71	1.78±0.174	0.325±0.047	0.042±0.014	0.227±0.023	0.063±0.01	2.44±0.22	0.66±0.065	3.13±0.23
8 July	75	3.66±0.36	0.337±0.03	0	0.778±0.129	0.094±0.02	4.85±0.477	1.72±0.24	6.59±0.53
15 July	83	0.2±0.041	0.018±0.008	0.02±0.006	0.018±0.007	0.002±0.002	0.258±0.055	0.511±0.063	0.769±0.087
28 July	85	0.02±0.015	0.002±0.002	0	0.002±0.002	0.004±0.003	0.029±0.016	0.058±0.016	0.096±0.02

nitrogen and lowest density of 5.29 in the plots receiving the lowest amount of nitrogen on 8 July when the nitrogen had a significant effect on the total population (Table 2.10).

The density of aphids each day was calculated on the assumption that population development during the period between two observations was exponential. These daily densities were summed to give an accumulated aphid index (one aphid unit is equal to one adult, or fourth nymph or three first to third instar nymphs). The average accumulated aphid index was 32.2 per shoot. These indices were affected by nitrogen levels ($F_{2,22}=7.67$, $p < 0.01$, log10 transformed analysis), being higher in plots with the two higher nitrogen levels. Indices in plots with or without fungicides were similar (Fig. 2.2).

Taylor (1961, 1965) stated that there is an intrinsic relationship between the sample mean and variance from a study of a large number of species;

$$S^2=am^b$$

The parameter a is dependent on the sampling method and environmental factors whereas b is a constant for a population species and is a measure of the type of distribution. As b approaches 0, the population is regularly distributed; with b close to 1, it is randomly distributed and greater than 1, it is aggregated. There was a significant relationship found between log *M. dirhodum* population density and variance in this experiment (Fig. 2.3);

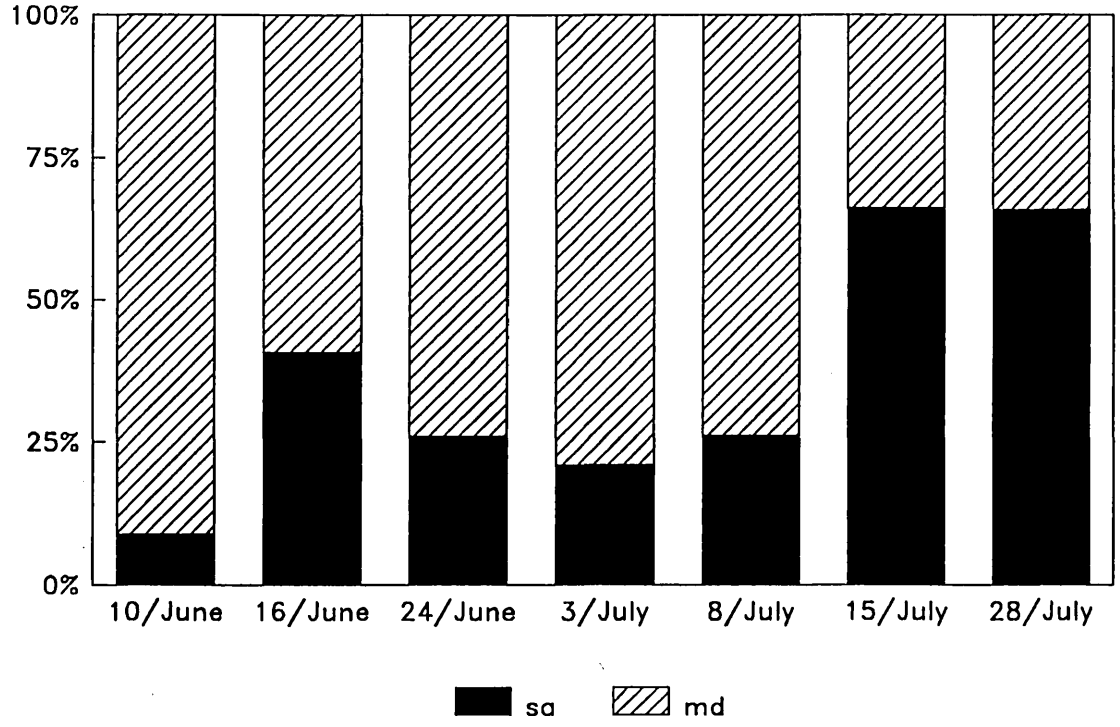


Fig. 2.1 Percentage of each aphid species in the total aphid population observed in 1987 (sa - *S. avenae*; md - *M. dirhodum*).

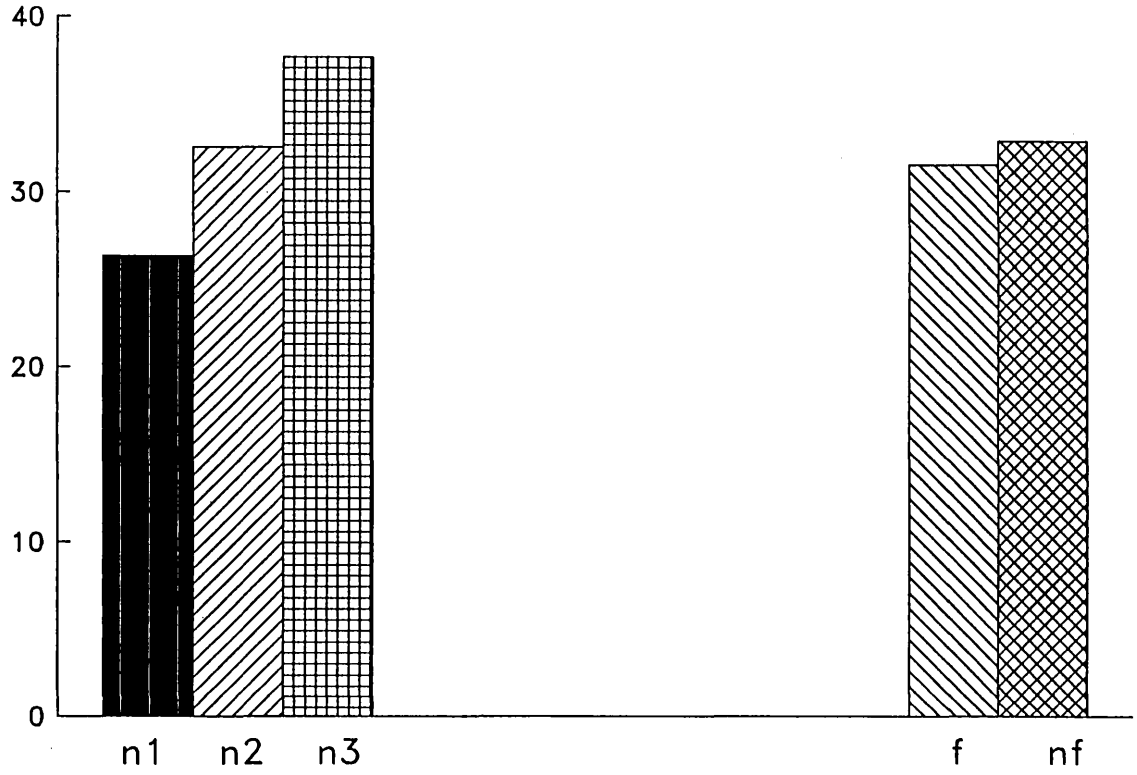


Fig. 2.2 Effects of nitrogen (n1 - 80kg, n2 - 120kg and n3 - 160kg/ha) and fungicide (f - fungicide and nf - no fungicide) on accumulated aphid indices in 1987.

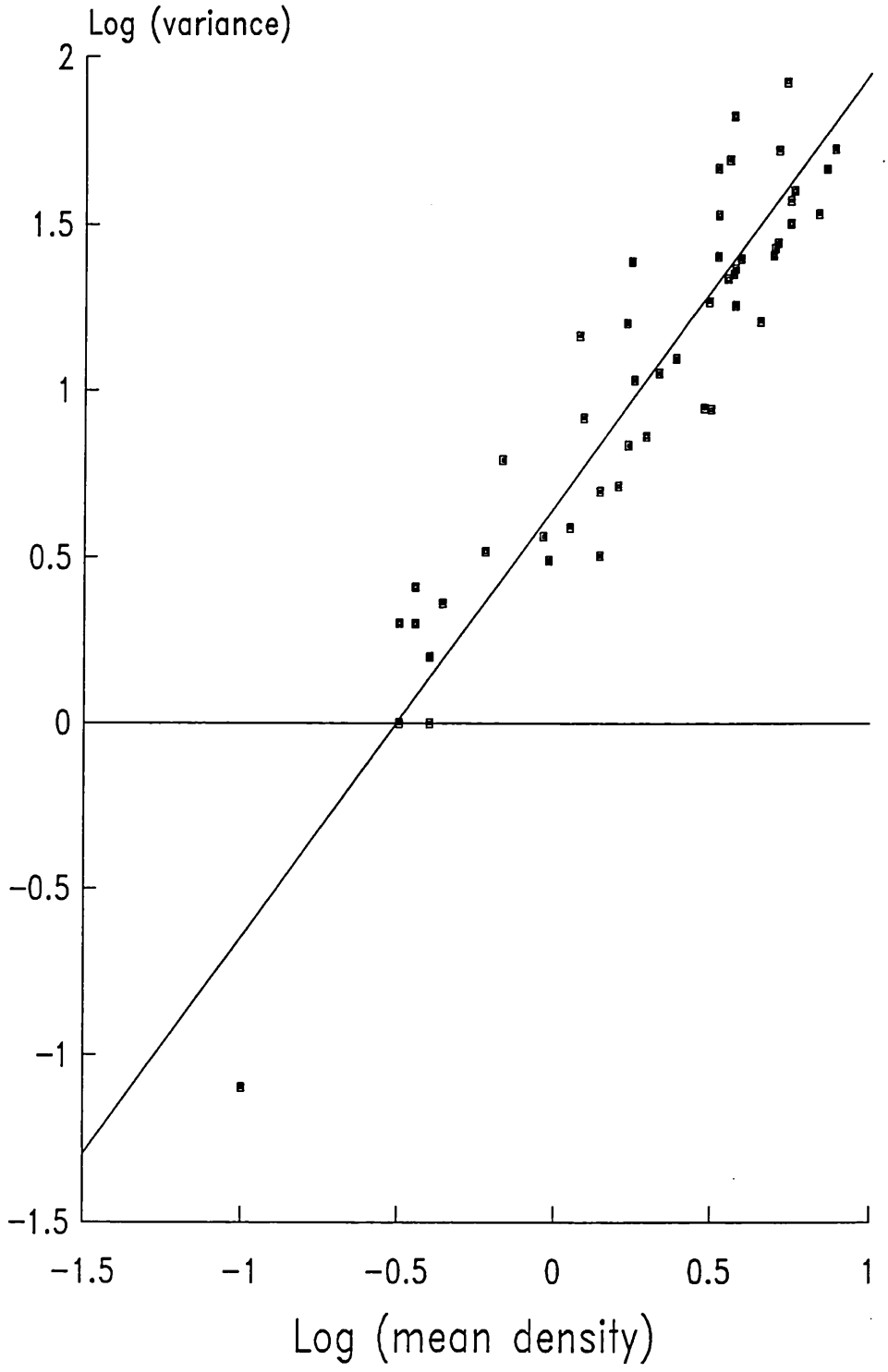


Fig. 2.3 Relationship between log (variance) and log (mean density) of *M. dirhodum* in the field in 1987.

$$\text{Log}(S^2) = \text{Log}(a) + b*\text{Log}(m)$$

where $\text{Log}(a) = 0.6526$; $p < 0.001$

$b = 1.2984$; $p < 0.001$

$r^2 = 0.88$; $p < 0.001$

There was also a significant relationship between the percentage of infested shoots and log transformed aphid density (Fig. 2.4);

$$p = 0.584 + 101.427*\log_{10}(\text{den}); \; r^2 = 0.9353, \; p < 0.001$$

Neither the amount of nitrogen applied nor the application of fungicide resulted in significant effects on aphid densities in samples except on 16 June and 8 July. On 16 June, aphid populations were higher in plots receiving the standard and larger amount of nitrogen than in low nitrogen ones (Fig. 2.5). There were three times more *S. avenae* on plots treated with fungicides compared with those untreated (Table 2.9). The numbers of *M. dirhodum* and the total aphid population were significantly higher on 8 July with increase in the amount of nitrogen applied (Table 2.9). The total aphid population was also significantly affected by the interaction between nitrogen and fungicide (Table 2.10). There were also more *S. avenae* on plots with fungicides than on plots without.

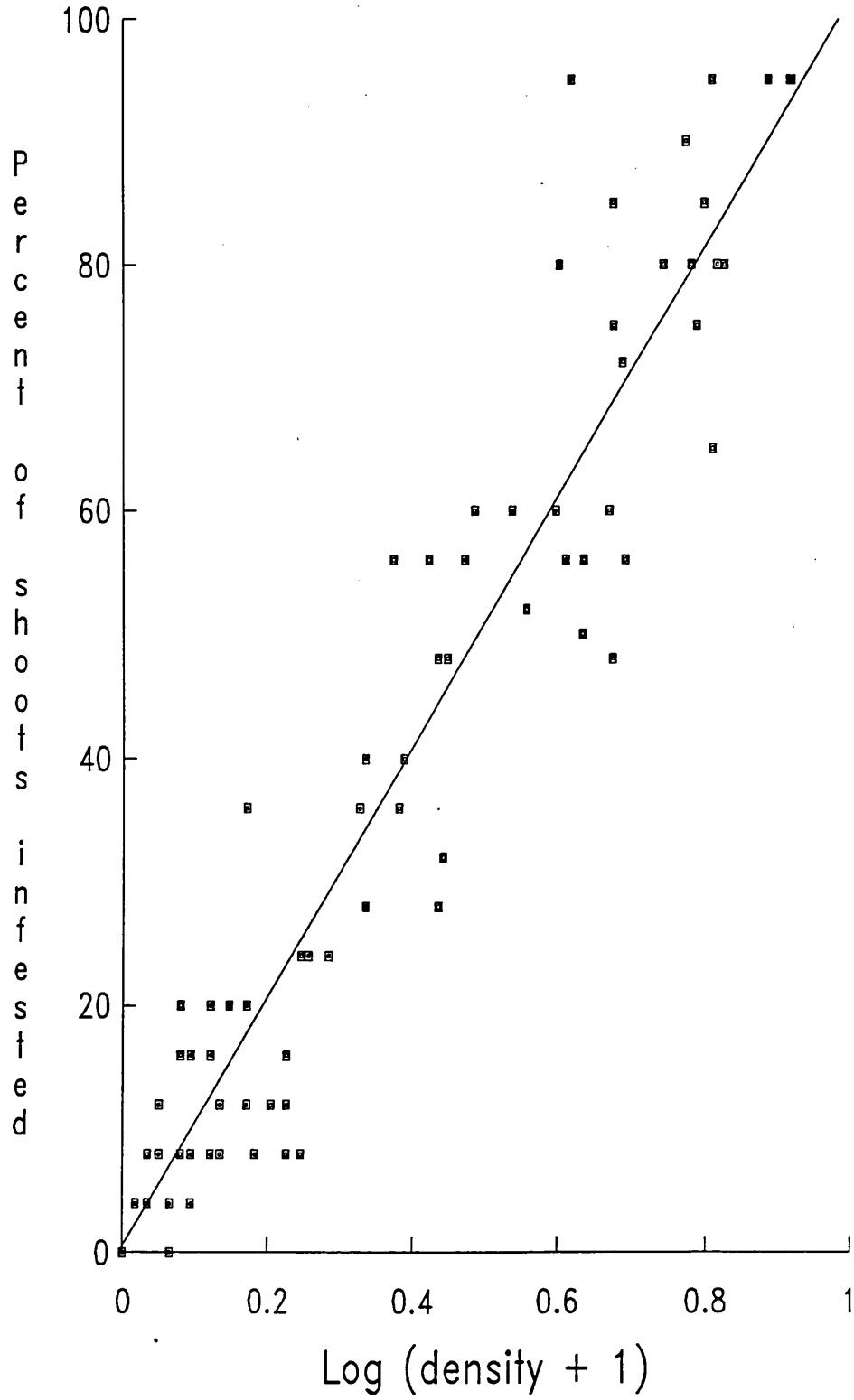


Fig. 2.4 Relationship between percentage of shoots infested by *Metopolophium dirhodum* and its density in 1987.

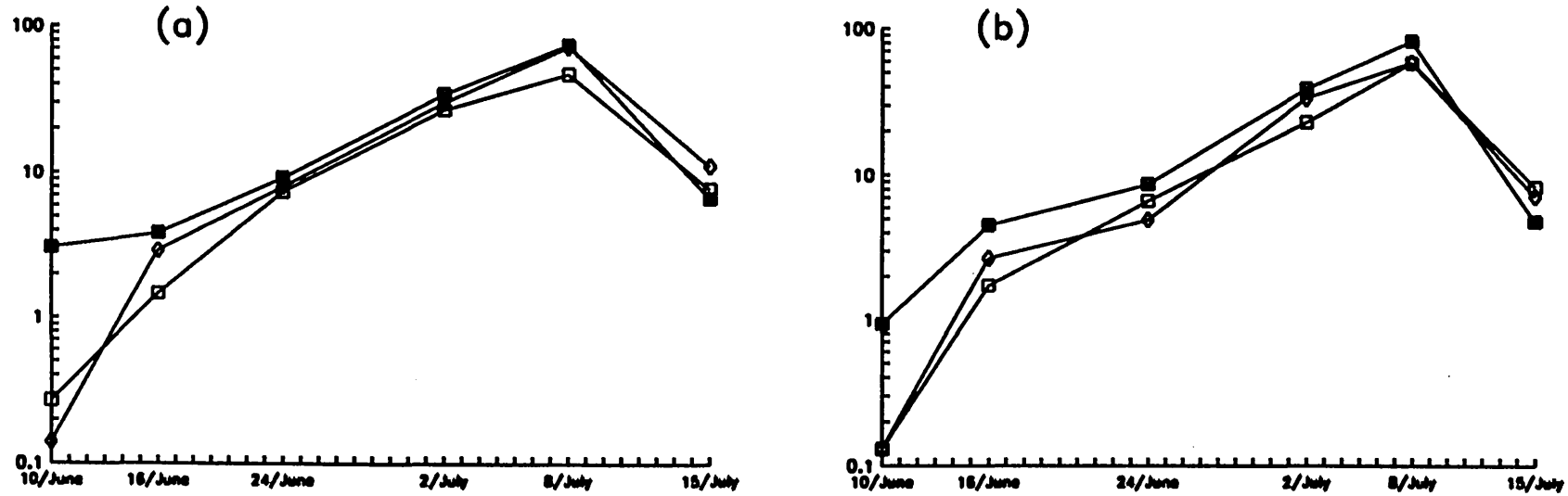


Fig 2.5 Effects of nitrogen and fungicide on aphid population density (N+1/10 shoots) in 1987 ((a) - no fungicide and (b) - fungicide; ⊠ - high nitrogen, □ - standard nitrogen and ◇ - low nitrogen.

Table 2.9 Effects of fungicide and nitrogen on aphid populations on 16 June and 8 July in 1987

		S. avenae on 16 June			*M. dirhodum* on 8 July		
Source of variance	df	ss	ms	v.r.	ss	ms	v.r.
N-rate	2	0.0267	0.0133	0.28	0.1732	0.0866	9.57 **
Fungicide	1	0.3038	0.3038	6.37 *	0.0032	0.0032	0.36
N-rate*fungicide	2	0.2917	0.1438	3.06	0.0009	0.0005	0.05
Residual	10	0.4771	0.0477		0.0905	0.0091	

Table 2.10 Effects of fungicide and nitrogen on total aphid population on 8 July in 1987

Source of variance	df	ss	ms	v.r.
N-rate	2	0.0882	0.0441	16.65 ***
Fungicide	1	0.0002	0.0002	0.08
N-rate*fungicide	2	0.0237	0.0118	4.47 *
Residual	10	0.0265	0.0024	

* ---- $p < 0.05$

** ---- $p < 0.01$

*** ---- $p < 0.001$

2.3.4 Disease assessment

2.3.4.1 *On 1 June*

The area of flag leaf infected with mildew (*Erysiphe graminis*) was not significantly affected by any of the treatments. Mildew infection on the lower leaves was however reduced significantly, from 0.56% to 0.3%, with aphicide treatment, and from 0.56% to 0.29% with fungicide treatment (Table 2.11). The level of mildew infection on the lower leaves increased significantly from 0.15% in the plots with the lowest nitrogen level to 0.93% in the plots with the highest nitrogen level regardless of applications of fungicide.

Septoria spp. infection was not significantly affected by the treatments on the lower leaves although plots treated with aphicide and fungicide were infected 30% less. The incidence of *Septoria* on the lower leaves was 0.6%. Total area infected by all fungal pathogens on flag and other leaves was not significantly affected, although plots treated with aphicide or fungicide were slightly less infected.

2.3.4.2 *On 27 July*

The incidence of mildew on flag leaves was significantly higher in plots with the standard (0.1%) and larger (0.2%) amounts of nitrogen and its interaction with fungicide (Table 2.12). Mildew on the lower leaves was significantly greater in plots with the two higher nitrogen levels ($F_{2,22}=7.02$; $p<0.01$). Again, the highest infection occurred in plots with the highest nitrogen level (0.25%) and plots with the lowest level were free of mildew.

The incidence of *Septoria* on flag leaves was significantly affected by fungicide and aphicide treatments (Table 2.13) but not on other leaves. There were 1.39% and 0.68% of infected area in plots untreated with fungicide and aphicide compared with 0.1% and 0.23% in treated plots respectively ($p < 0.05$, $p < 0.001$ respectively). The incidence of *Septoria* on either the flag or other leaves was not significantly affected by nitrogen levels. The incidence of brown rust (*Puccinia* spp.) was only affected by fungicide treatment on flag leaves ($F_{1,22}=17.73$; $P < 0.001$) where there was 0.12% of infection on flag leaves in plots not receiving fungicide compared with zero in the plots receiving fungicide. The incidence of brown rust was also

affected by aphicide on the lower leaves ($F_{1,22}$=5.28; $p < 0.05$) where infection was 3 times higher on non-aphicide treated plots than on the treated plots, although overall levels were low (0.04% and 0.01% respectively).

The incidence of all diseases on both flag and lower leaves was only affected significantly by the application of fungicide ($F_{1,22}$=26.32; $p < 0.001$ and $F_{1,22}$=6.11; $p < 0.05$ respectively) with more disease in plots not receiving fungicide than in the plots receiving fungicide (Table 2.14). The means of total diseases infected area were 0.74% on flag and 5.1% on the lower leaves.

Table 2.11 Effects of aphicide, fungicide and nitrogen on mildew infection on lower leaves on 1 June in 1987

Source of variance	df	ss	ms	v.r.	
Aphicide(A)	1	0.7049	0.7049	6.04	*
N-rate(N)	2	3.8187	1.9093	16.35	***
Fungicide(F)	1	0.7753	0.7753	6.64	*
A * N	2	0.0790	0.0395	0.34	
A * F	1	0.0818	0.0818	0.70	
N * F	2	0.1304	0.0652	0.56	
A * N * F	2	0.1799	0.0900	0.77	
Residual	22	2.5695	0.1168		

Table 2.12 Effects of aphicide, fungicide and nitrogen on mildew infection on flag leaves on 27 July in 1987

Source of variance	df	ss	ms	v.r.	
Aphicide(A)	1	0.0191	0.0191	0.19	
N-rate(N)	2	3.2688	1.6344	15.99	***
Fungicide(F)	1	0.1891	0.1891	1.85	
A * N	2	0.1286	0.0643	0.63	
A * F	1	0.0000	0.0000	0.00	
N * F	2	0.9461	0.4731	4.63	*
A * N * F	2	0.0380	0.0190	0.19	
Residual	22	2.2486	0.1022		

Table 2.13 Effects of aphicide, fungicide and nitrogen on Septoria on flag leaves on 27 July in 1987

Source of variance	df	ss	ms	v.r.	
Aphicide(A)	1	2.0596	2.0596	4.82	*
N-rate(N)	2	1.9265	0.9633	2.26	
Fungicide(F)	1	12.2854	12.2854	28.78	***
A * N	2	1.0819	0.5409	1.27	
A * F	1	0.0238	0.0238	0.06	
N * F	2	0.3481	0.1740	0.41	
A * N * F	2	1.2162	0.6081	1.42	
Residual	22	9.3923	0.4269		

Table 2.14 The effect of fungicide on all diseases (percentage of leaf area infected) on 27 July in 1987

Fungicide	none	31 + 39 + 59
On flag leaf	1.92%	0.22%
On other leaves	6.67%	3.87%

2.3.5 Natural enemies

The first mummies appeared at the beginning of anthesis but the percentage only increased to 0.4% at the middle milk stage when the aphid population was at the maximum. Its percentage increased to 23.15% at early dough (G. S. 83) when the aphid population declined to 0.8/shoot. Fungal disease increased significantly later in the season (17.42% at the early dough). Coccinellid eggs and larvae, syrphid and lacewing eggs were found during sampling, but numbers were not recorded.

2.4 Results in 1988

2.4.1 Yields

The mean yield was 8.5 t/ha. Aphicide, nitrogen and fungicide showed significant effects on yield ($F_{1,22}=20.59$; $p < 0.001$; $F_{2,22}=9.30$; $p < 0.001$; $F_{1,22}=19.66$; $p < 0.001$ respectively). Yields of plots treated with aphicides were increased by 7.6% (Fig. 2.6a), with fungicide by 7.3% (Fig. 2.6b), and the highest nitrogen level resulted in an increase of 8.74% compared with

the plots receiving the lowest amount of nitrogen. Increases between the low nitrogen and standard levels, and standard and high levels were 5.4% and 3% respectively (Fig. 2.6c).

The average thousand grain weight was 41.3 g. The application of aphicides and fungicides caused 4.5% ($F_{1,22}$=31.55; P < 0.001) and 5.5% ($F_{1,22}$=48.86; p < 0.001) increases of the thousand grain weight respectively but the largest amount of nitrogen caused a slight non-significant decrease (41.7, 41.4 and 40.8g from the lowest to the highest).

The number of grains/m^2 was significantly increased in plots receiving more nitrogen ($F_{2,22}$=26.53; P<0.001). There were 2% more grains in plots receiving the standard amount of nitrogen than that with the lowest nitrogen input and 4.5% more in the plots with the largest amount of nitrogen compared with the standard. Plots treated with aphicide resulted in a 3% increase in number of grains/m^2 ($F_{1,22}$=5.22; P<0.05). The number of grains/ear was not affected significantly by any of the treatments.

2.4.2 Shoot density

The average density of shoots with ears was 433/m^2 from direct counts while the density was 341.3 from the estimate calculated using the first sample. In the direct counts, the densities were the same in plots receiving the standard and high amount of nitrogen (445 shoots/m^2) but significantly lower in the plots receiving the lowest amount of nitrogen (407 shoots/m^2) ($F_{2,16}$=8.1; P<0.001). From the sample estimate, the highest shoot densities occurred in plots treated with fungicide

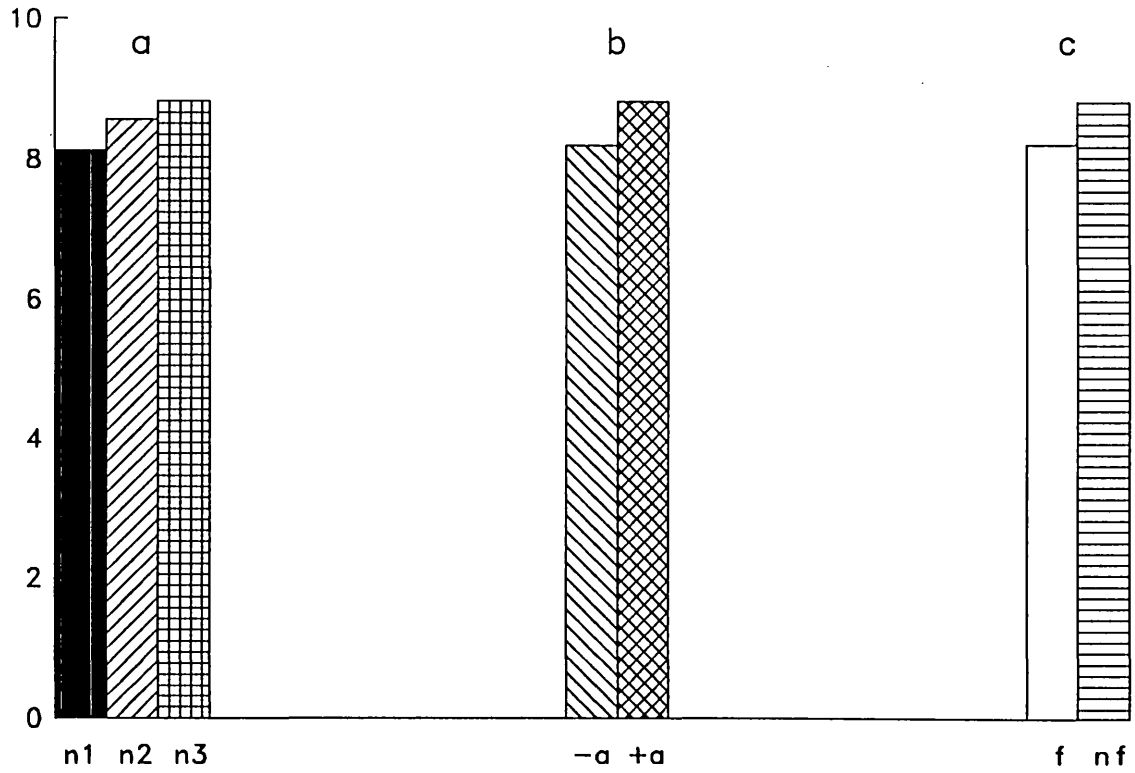


Fig. 2.6 Effects of nitrogen (n1, n2 and n3), aphicide (-a, +a) and fungicide (f, nf) on yields (t/ha) in 1988.

and no aphicide or with aphicide and no fungicide ($F_{1,22}$=5.00; $p < 0.05$) but there were no individual treatment effects.

2.4.3 Plant physiology

Neither total fresh nor dry weights/m^2 in the two samples were significantly affected by any of the treatments (829.6 g and 1326.6 g respectively).

The flag LAI only was increased by applying more nitrogen ($F_{2,22}$=4.94; $P<0.05$) although the other indices also slightly increased with the nitrogen input levels (Table 2.15). The application of fungicides and aphicides also caused increases, but not significantly, in these indices in the first sample (Table 2.15).

Table 2.15. Effects of aphicide, fungicide and nitrogen on LAIs of flag and lower leaves, and stem on 14 June in 1988

	Aphicide		Fungicide		N-rate			Mean
	-	+	-	+	105	140	175	
Flag leaves	1.21	1.32	1.24	1.30	1.14	1.31	1.35	1.27
Other leaves	1.95	2.04	1.95	2.03	1.81	2.02	2.15	1.99
Stem	3.08	3.30	3.20	3.26	3.13	3.20	3.25	3.19
Total	6.24	6.66	6.31	6.59	6.09	6.53	6.74	6.45

Only flag and dead leaf dry weight were significantly affected by nitrogen fertilizer in the first sample (Table 2.16) ($F_{2,22}$=7.72; $p < 0.005$; $F_{2,22}$=4.43; $p < 0.05$ respectively).

Table 2.16 Effects of aphicide, fungicide and nitrogen on dry weights (g)/m^2 of flag, lower and dead leaves, stems and ears on 14 June in 1988.

	Aphicide		Fungicide		N-rates			Mean
	-	+	-	+	105	140	175	
Flag leaves	59.4	61.7	61.7	60.3	55.4	61.6	46.7	60.6
Other leaves	73.1	76.8	73.8	76.1	70.1	75.2	79.5	75.0
Stem	524.9	537.0	529.9	532.1	538.4	542.9	511.6	531.0
Ear	157.9	159.9	158.6	159.2	156.9	159.2	160.7	158.9
Dead	4.04	4.31	4.07	4.28	6.43	4.29	1.80	4.18
Total	819.3	839.7	828.1	832.0	827.2	843.2	800.3	829.7

2.4.4 Aphid populations

Three aphid species were present; *S. avenae*, *M. dirhodum* and *M. festucae*. *S. avenae* was the predominate species during the season. *M. festucae* was abundant early in the season (from 12 May to 25 May), but decreased to zero on 22 July while the percentage of *M. dirhodum* in the total aphid population increased from 22 July (Fig. 2.7).

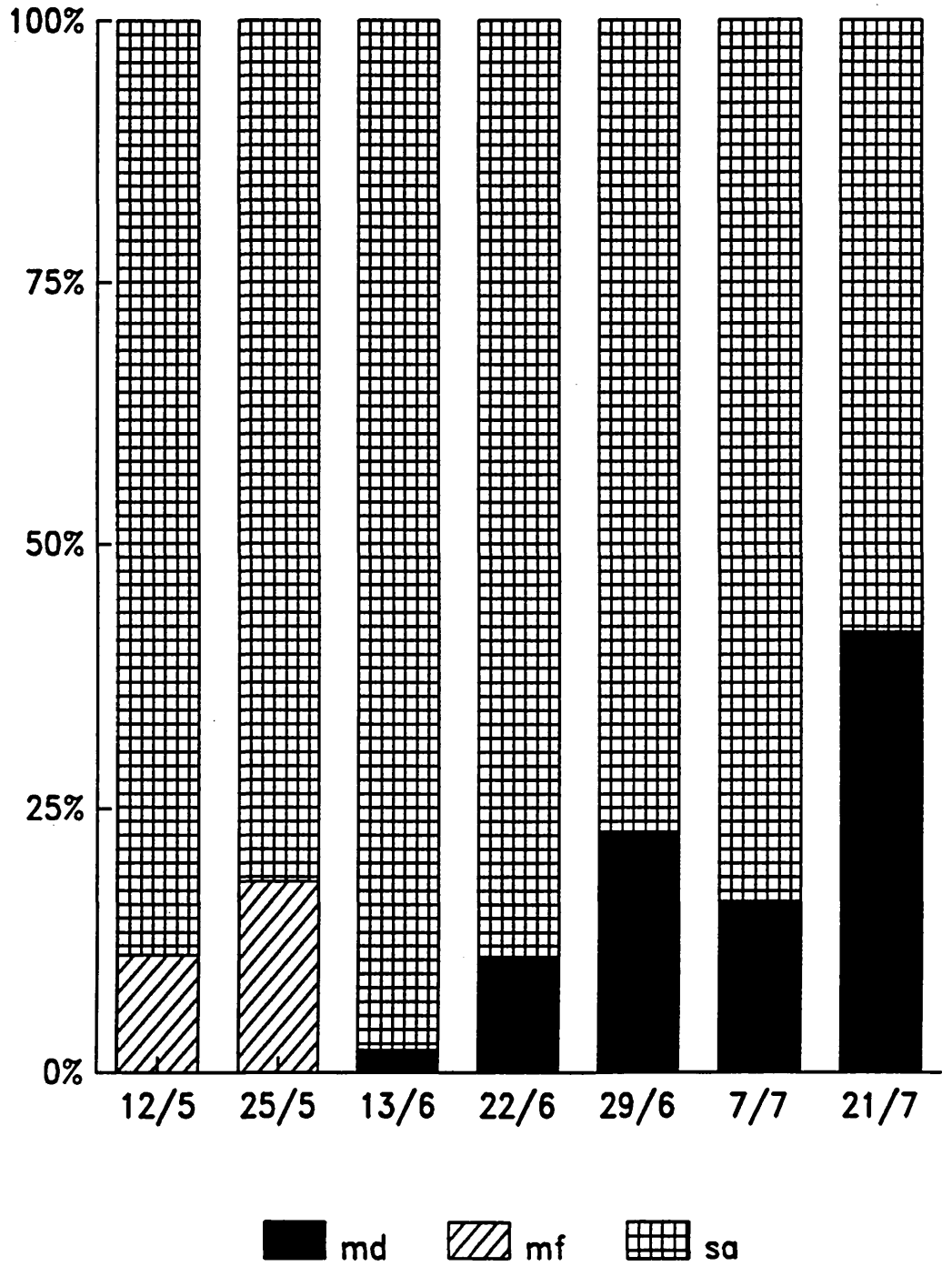


Fig. 2.7 Percentages of each aphid species in 1988 (md - *M. dirhodum;* mf - *M. festucse;* sa - *S. avenae*).

The average peak population occurred on 25th May (1.8 aphids per shoot) although some plots reached particularly high densities of 4.14/shoot on 12 May, 6.74/shoot on 25 May and 5.46/shoot on 3 June. After the population reached the peak, it stayed at a similar level for a long period (48 days) until 7 July, after which it declined slightly (Fig. 2.8). Increases in amount of nitrogen or the application of fungicides did not affect the number of aphids (Fig 2.9 a & b).

The average aphid index was 38 aphid unit days. These indices were not affected by any of the treatments (Fig. 2.10).

2.4.5 Disease assessment

2.4.5.1 *On 14 June*

The incidence of *Septoria* on flag leaves was significantly affected by nitrogen fertilizer ($F_{2,22}=3.79$; $p < 0.05$). Infection occurred only in plots receiving the standard amount of nitrogen (0.23%). Mildew infection on the flag leaves was very low (0.01%) and not affected significantly by any of the treatments. The area infected by *Septoria* on lower leaves was significantly lower as the amounts of nitrogen applied increased ($F_{2,22}=9.37$; $p < 0.01$). Again, the incidence of mildew on the lower leaves was low (0.08%).

2.4.3.2 *On 26 July*

The average yellow area on the flag was 47.78%. The yellow area on flag leaves was significantly lower with application of fungicides ($F_{1,22}=7.14$; $p<0.05$) and with increasing

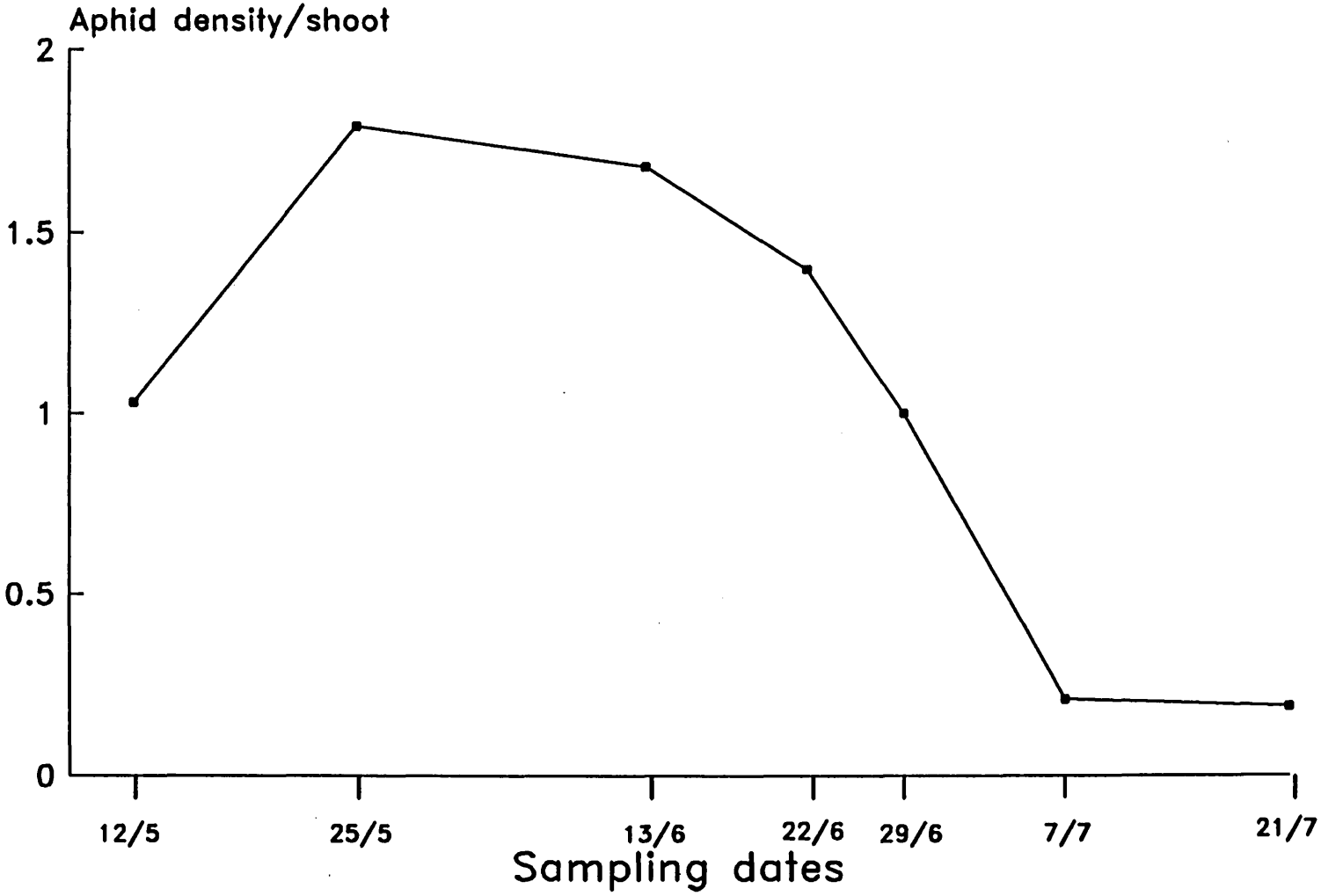


Fig. 2.8 Total aphid density per shoot in 1988

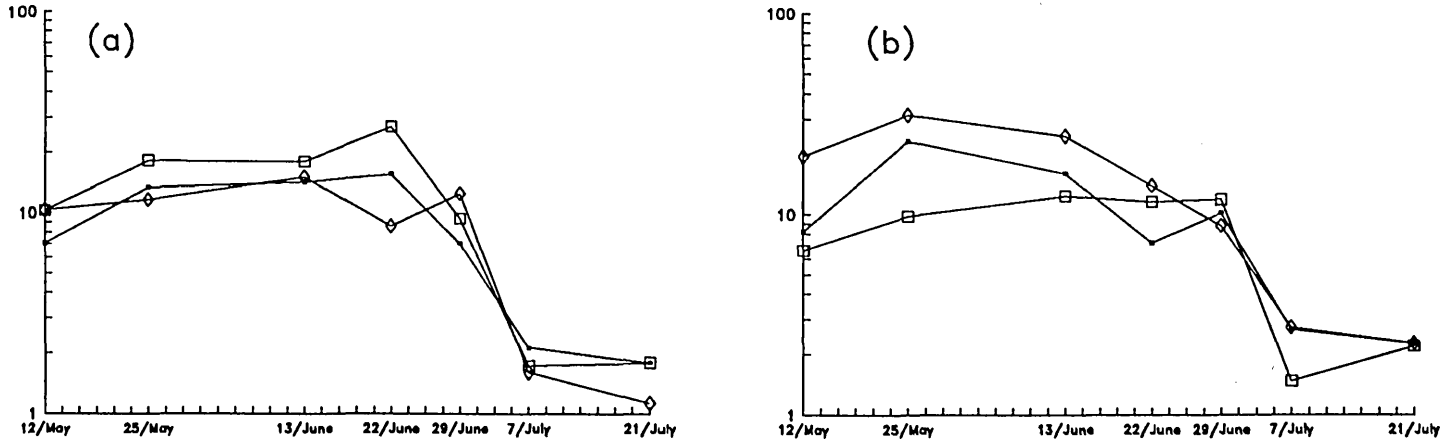


Fig. 2.9 Effects of nitrogen (□- high nitrogen, ◇- standard and ■ - low nitrogen) and fungicide (a - no fungicide and b - fungicide) on total aphid density/10 shoots in 1988.

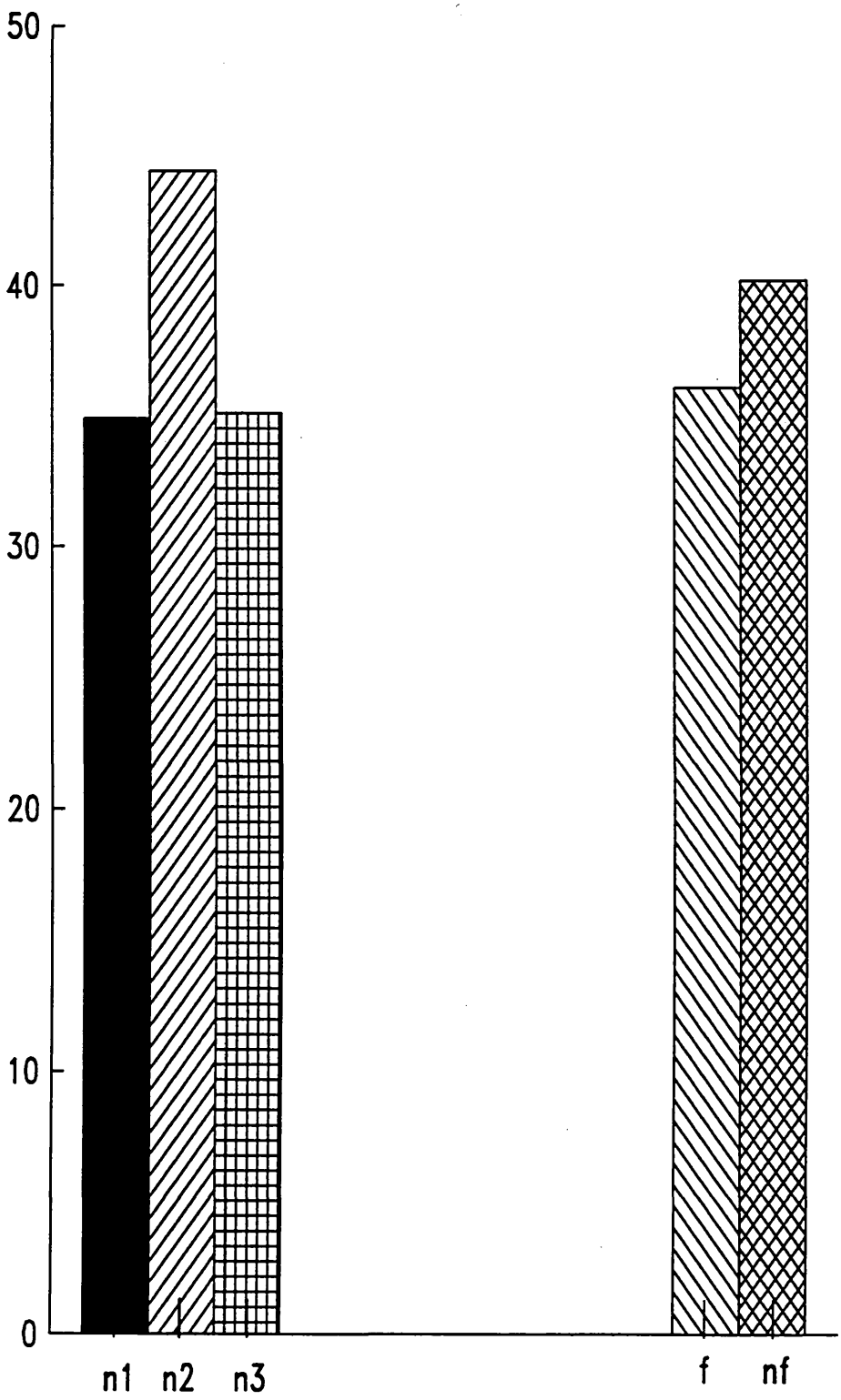


Fig. 2.10 Effects of nitrogen and fungicide on aphid indices in 1988.

amounts of nitrogen ($F_{2,22}$=6.08; p< 0.01). The green flag leaf areas in plots receiving fungicide were 20% higher. The majority of the flag leaves in plots with the low nitrogen level were yellow (65%) while the yellow area decreased from 45.8% to 32.5% in the plots where the nitrogen level was increased from 140kg to 175kg/ha. On the lower leaves, most were yellow (83.3% on average). The total yellow area was 28% greater in plots receiving no fungicide ($F_{1,22}$=10.51; p < 0.01) but was lower in plots receiving the standard and greater amounts of nitrogen fertilizer ($F_{2,22}$=5.48; p < 0.05).

Three diseases were found: *Septoria*, brown rust and mildew. The incidence of mildew was the lowest (0.16%) and not affected by any of the treatments. *Septoria* infection was 4.6% on the flag leaves and 9% on the lower leaves on average. It was significantly higher on the flag leaves (8.7%) ($F_{1,22}$=7.07; p<-0.05), and on the lower leaves (10.1%) ($F_{1,22}$=9.29; p<0.01) in plots not receiving fungicides. On the lower leaves, there was 4 times more *Septoria* (17.5%) in plots receiving the highest amount of nitrogen than in plots receiving the two lower levels (4.5% at both levels).

The incidence of brown rust on average was 6.8% on the flag leaves which was higher than on the lower leaves (1.3%). It was significantly lower on the flag leaves ($F_{1,22}$=26.99; p<0.001) and on the lower leaves ($F_{1,22}$=12.77; p < 0.01) in plots receiving fungicides. The flag leaves in plots receiving fungicides had much less infection of brown rust (2.0%) than those not receiving them (11.6%).

2.4.6 Natural enemies

A total of thirty one coccinellid eggs, 21 syrphid eggs, three lacewing eggs and one staphylinid was recorded on 900 shoots in the plots not receiving aphicide at the middle booting (G.S. 45). These numbers slightly increased at the middle anthesis (G.S.65). Then they remained at a similar level in the next three samples to early milky stage (G.S. 73). Two coccinellids were recorded in the samples when the aphid population decreased to 0.22/shoot at the end of milk stage (G.S. 79). The number of mummies recorded accounted for 10.8% of the total aphid population and remained at that level until the milk stage (G.S. 71). A few mummies were found after the milk stage when the aphid population started decreasing. The level of fungal disease was low during the sampling period (less than 3%).

2.5 Results in 1989

The mean yield was 8.5t/ha. Aphicide, nitrogen and fungicide did not have significant effects on yield.

Three aphid species were present; *R. padi*, *S. avenae* and *M. dirhodum*. *S. avenae* and *M. dirhodum* were abundant during the season but the latter was predominate with a maximum density on 8 June (Fig. 2.11). *R. padi* was abundant for a short period in the summer (from 24 May to 22 June) (Fig. 2.11).

Significantly less *S. avenae* was presented in plots receiving fungicides only on 16 June ($F_{1,11} = 7.00$; $p < 0.05$). Nitrogen and fungicide did not affect the aphid densities of *M. dirhodum*

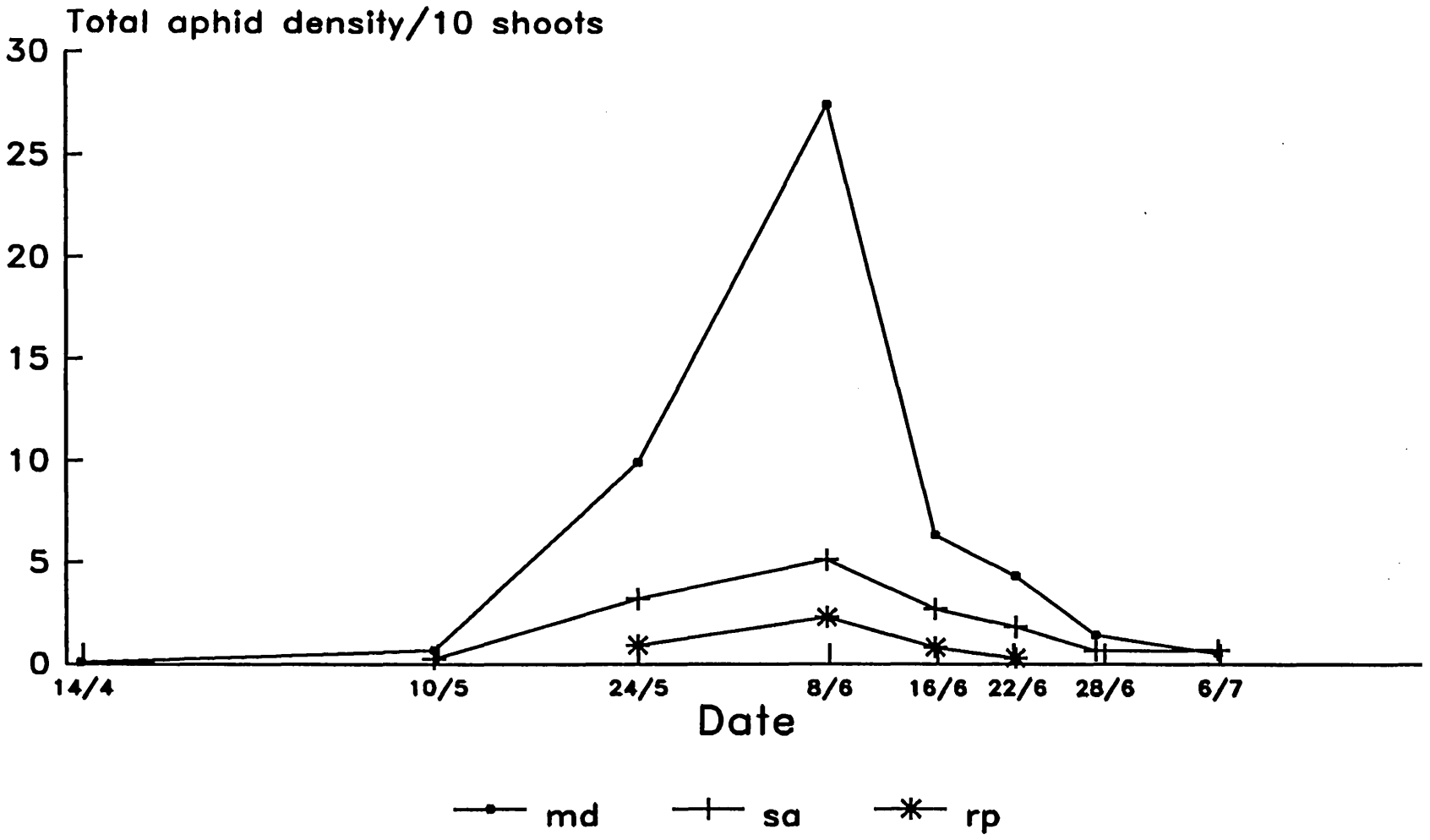


Fig. 2.11 Aphid densities per 10 shoots in 1989 (md - *Metopolophium dirhodum*; sa - *Sitobion avenae*; rp - *Rhopalosiphum padi*).

and *R. padi* in each sample date, and the densities of *S. avenae* in the other samples except on 16 June.

The average total LAI was 6.5. The LAIs of flag, other leaves and stems were not significantly affected by any of the treatments (Table 2.17).

Table 2.17 Effects of aphicide, fungicide and nitrogen on LAIs of flag and lower leaves, and stem in 1989.

	Aphicide		Fungicide		N-rate			Mean
	-	+	-	+	80	120	160	
Flag leaves	1.37	1.32	1.30	1.40	1.29	1.41	1.34	1.35
Other leaves	1.79	1.79	1.68	1.90	1.78	1.82	1.76	1.79
Stem	3.38	3.34	3.27	3.45	3.34	3.42	3.42	3.36
Total	6.54	6.45	6.26	6.74	6.31	6.66	6.53	6.5

The mean mildew and brown rust infection on all leaves was small (0.02% and 0.04% respectively) although *Septoria* infection was higher (1.56%)

Aphicide, fungicide and nitrogen did not have significant effects on mildew and *Septoria* infection. Significantly more brown rust on all leaves was presented in plots not receiving fungicides (0.08%) compared with zero in the plots receiving fungicides ($F_{1,21} = 28.5$, $p < 0.001$).

2.6 Discussion

Non-protein amino acids affect aphid colonisation in crops (Jordens-Rottger 1979). In addition, Kowalski and Visser (1980) found that changes in amino acids levels did not correlate with aphid population development, and stated that the response of aphids to the proportion of non-protein to protein amino acids in leaves was a behavioral one at the time of settling in the crop. Dewar (1980) observed differences in populations but not rate of the population growth on plots with different levels of applied nitrogen. In this study, no significant differences were found in aphid populations or on population development among plots receiving different amounts of nitrogen, except the peak density of *M. dirhodum* (and hence total population) in 1987. Aphid populations in plots may need to be higher to show any significant effects of nitrogen, although the accumulated aphid indices were significantly higher in plots receiving higher amounts of nitrogen.

Colonization of the cereal aphids was late in 1987 (Fig. 2.5) and were dominated by *M. dirhodum*. The high percentage of parasitism and fungal pathogens late in the season may have prevented the aphid population increase. Parasitoids and predators were abundant early in the season in 1988. This may have prevented initial build-up of the aphid population and kept the aphid population at a consistent low level during the favourable crop growth stage. Winder (1990) found that aphid densities were lower in unbarriered plots compared with those in barriered ones where colonizations by ground predators had been prevented.

Incidence of plant diseases were low in the three years. Although effects of nitrogen and fungicide were significant on the diseases and also consequently on yield. The diseases were not common to interact with aphid population development. Furthermore, densities of *M. dirhodum*, which is a leaf-feeder and most likely to interact with the leaf diseases, were low in the three years.

The effect of nitrogen was significant on the accumulated aphid index in 1987, but application of aphicide did not significantly increase yield. This may indicate the economic threshold of *M. dirhodum* is high (George, 1974). Controlling aphids in 1988 resulted in an increase of the thousand grain weight (Wratten, 1975; Wratten *et al.*, 1979) and significant yield increase. This indicates that infestations of *S. avenae* can result in significant yield losses at densities below the economic threshold of five/ear (George, 1974) when the aphids are present for a long period.

Higher nitrogen results in more dry matter, larger leaf area, more grains/m^2 and higher yield. However, the yield increase did not always respond linearly to the increase of nitrogen input (Walker & Ludecke, 1982). The application of fungicides increased the thousand grain weight in both years and the grains/m^2 in 1987.

CHAPTER THREE: BIOLOGICAL STUDIES OF THE APHID

3.1 Introduction

Development rate, reproductive rate and survival rate are important in determining the rate of aphid population increase (Carter *et al.*, 1982). They are affected by several factors including host plant and temperature. These effects have been studied in the laboratory (Dean, 1974; Wratten, 1977) and in the field (Dean, 1973; Dixon, 1977; Cannon, 1984, 1985). However, the results from these studies are inconsistent. For example, the development time of *M. dirhodum* was 30% higher in the field (Cannon, 1984) compared with that in the laboratory at 15° (Dean, 1974). It is important to obtain parameters of population growth in the field in order to understand cereal aphid outbreaks (Cannon, 1984). However, it is not possible to obtain information on individual aphid development and reproduction in the field without the limitation of cages. The influence of crop development and feeding position on population parameters of the rose grain aphid was investigated in the laboratory and further studied, using clip cages, in the field.

3.2 Effects of temperature on development, reproduction and mortality rates

3.2.1 Methods

The experiment, which started in March 1987, was done in a growth cabinet (1m x 1m x 1m) at a series of constant temperat-

ures: 10, 15, 20, 25 and 30°C and a fluctuating temperature: 22-12°C; light:dark 16:8h.

A number of pots (diameter, 7cm) were sown with winter wheat, cv. Avalon, with three seeds per pot in a glasshouse. The number of pots sown varied at each constant temperature from 17 to 31. The mean temperature in the glasshouse was 20°C. After germination one seedling was kept in each pot. When these seedlings had two leaves fully expanded (G.S. 12) they were moved into the growth cabinet and the pots labelled. One apterous adult from a culture kept at 20°C (light:dark 15:9) was confined on the first fully expanded leaf of each seedling, with a clip-cage (diameter:height, 2.5:4cm). The cage and aphid were moved to the next leaf if the caged leaf turned yellow.

Observations were made at 08.00, 13.00, 18.00 and 23.00. As soon as an adult in a cage had produced its first nymphs, the adult was removed and one nymph was kept and the time was recorded. Moult times were recorded when exuviae were found in cages. Once the adults produced their first nymphs, one observation per day (per two days at 20°C) was carried out (at 18.00) and the times of the start of reproduction were recorded. The nymphs produced were removed and the numbers recorded. Individual observations were stopped when an adult had not reproduced for two days or died. Dead or missing aphids during the experiment were also recorded.

3.2.2 Results

3.2.2.1 *Development time*

Development times were similar between different aphid instars at 10°C (Table 3.1). At higher temperature differences in development time between instars were significant (Table 3.1 and Table 3.3). Total development time was shortest at 25°C (Table 3.1). Development time increased at 30°C (Table 3.1). The duration of the 4th instar was the longest at all temperatures except 10°C. The development times of instar I to III were generally very similar. This duration in the pre-reproductive delay at 10°C was about 9 to 10 times higher than that at other temperatures. The average of the fluctuating temperature was 18.67°C. The fluctuation of temperature did not affect the aphid development time (Table 3.1).

Relationships between development rates (y) (the reciprocal of the development times) and temperatures (t) were linear for each instar and the whole generation (birth to start of reproduction) below 30°C (Table 3.2, Fig. 3.1). The development thresholds for each instar were calculated from these equations (Table 3.1). The threshold for the whole generation was -0.26°C. Physiological time, in hourdegrees (H°) was calculated based on -0.26°C (Table 3.3).

Mean apterous adult longevity was longest under the fluctuating temperature regime and was similar to that at 10°C. The shortest reproductive life was recorded at 20°C. Adult

Table 3.1 Development times (hours) of the rose grain aphid, *M. dirhodum* (±Se) at different temperatures on wheat seedlings (G.S.12-30).

Temperature	I	II	III	IV	Pre-reproductive delay	Total+
10°C	118.8 ± 1.1	113.8 ± 9.3	110.5 ± 9.3	111 ± 9.4	98.8 ± 11.4	454.1
15°C	63.7 ± 1.5	69.4 ± 1.8	62.1 ± 2.1	87 ± 1.6	-	273.1
20°C	48.9 ± 0.5	46.3 ± 1.0	49.8 ± 1.0	61.2 ± 1.8	11.1 ± 1.2	206.2
25°C	43.2 ± 1.2	37.6 ± 0.9	40.4 ± 1.3	56.3 ± 0.9	10.4 ± 0.7	177.5
30°C	40.3 ± 1.1	48.3 ± 0.7	50.1 ± 1.5	67.7 ± 2.7	-	206.5
12-22°C	58.8 ± 0.8	45.0 ± 1.5	49.8 ± 1.0	69.6 ± 2.7	13.7 ± 0.6	223.2
Threshold	0.26°C	2.32°C	0.0°C	-6°C		
M*	63	63.1	62.6	74.9		263.5

* average of 10, 15, 20, 25 and 30°C

\- not recorded

\+ totals not including the pre-reproductive delay

Table 3.2 Relationship between development rate (y(i)) (h^{-1}) and temperature (t) for different instars of the rose grain aphid

Instar I, $y(1) = (-2.55 + 9.77t) \times 10^{-4}$ $r = 0.98^{**}$

Instar II, $y(2) = (-3.83 + 1.22t) \times 10^{-3}$ $r = 0.97^{*}$

Instar III, $y(3) = (-8.54 + 103t) \times 10^{-5}$ $r = 0.98^{**}$

Instar IV, $y(4) = (35.8 + 5.96t) \times 10^{-4}$ $r = 0.98^{**}$

A generation, $y = (5.93 + 23.1t) \times 10^{-4}$ $r = 0.98^{***}$

where * $P < 0.01$, ** $P < 0.005$, *** $p < 0.001$

Table 3.3 Development longevities (H°) of the rose grain aphid based on a threshold temperature, -0.26°C

Temperature	I	II	III	IV	Predelay	adult
10°C	1218.9	1167.6	1133.7	1138.8	1013.7	5663.0
15°C	972.1	1059.0	947.6	1327.6	-	5237.0
20°C	990.7	938.0	1008.9	1240.0	224.9	5008.0
25°C	1091.2	947.3	1020.5	1422.1	262.7	7517.0
M	1068.2	1028.0	1027.7	1282.1	500.4	5856.0
Accumulated	1068.2	2096.2	3123.9	4406.0	4906.4	10763.0

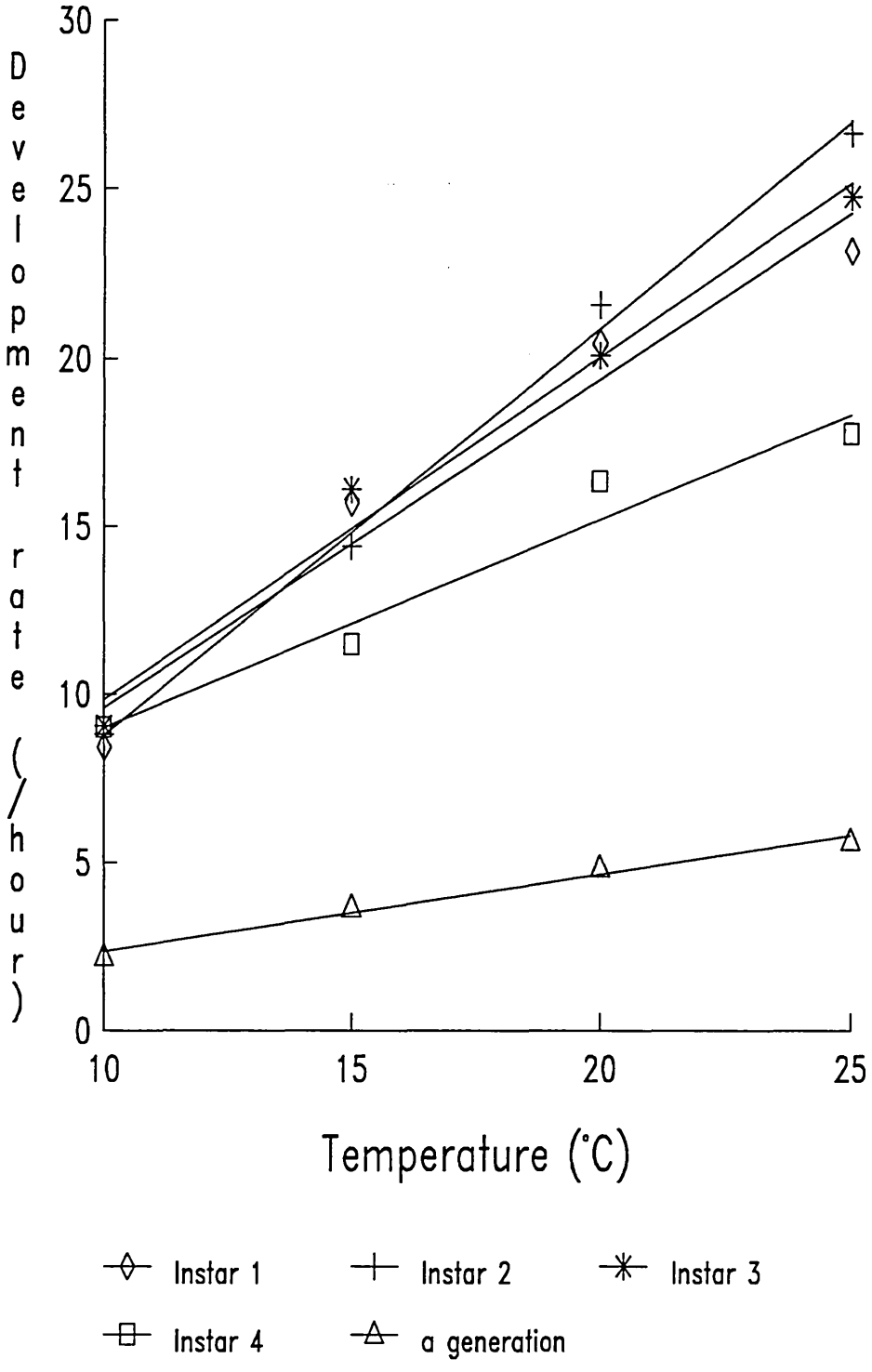


Fig. 3.1 Relationships of development rate (hour^{-1} x 10^{-3}) and temperature for different instars of the rose grain aphid

longevities at 10°C and under the fluctuating temperature were significantly longer than these at 15, 20 and 25°C (Table 3.4).

3.2.2.2 *Reproduction rate*

The largest number of nymphs were produced under the fluctuating temperature regime and the smallest at 20°C although there were no significant difference in fecundity at any temperature (Table 3.4).

Table 3.4 Effects of temperature on adult lifespan and total nymphs produced on wheat seedlings for the rose grain aphid (the same letters in brackets are not significantly different at $p < 0.05$)

Temperature	No. of adults	Mean lifespan(days)	Mean nymphs
10°C	22	23.0(b)	37.5(a)
15°C	22	14.3(a)	36.6(a)
20°C	18	10.3(a)	32.0(a)
25°C	16	12.4(a)	33.6(a)
12-22°C	18	23.8(b)	41.0(a)

The daily reproductive rate was highest at 20 and 25°C (3 nymphs per day) twice that at either 10°C or the fluctuating

temperature regime. Reproductive rates were significantly lower at 10°C and the fluctuating temperature regime compared with those at 15, 20 and 25°C ($p < 0.001$). The numbers of nymphs produced per two days were more evenly distributed over longer periods at 10°C and the fluctuating temperature regime compared with those at 15, 20 and 25°C (Fig. 3.2). Peaks in the reproductive rates occurred later, and were smaller, at lower temperatures (Fig. 3.2). Most nymphs (81% and 73%) were produced in the first eight days of reproduction at 20 and 25°C respectively, while over the same period 55%, 35% and 35% were produced at 15, 10 and 12-22°C respectively.

The intrinsic rate of increase was lowest at 10°C and increased to a maximum at 25°C (Table 3.5). Mean longevities of the aphids decreased as the temperature increased. The net reproductive rate varied at different temperatures with the highest under the fluctuating temperature regime and lowest at 25°C (Table 3.5).

3.2.2.3 *Mortality rate*

Nymphal mortalities were lowest at 20°C (5%), highest at 25°C (20%) and 11 ± 1% at the other temperatures. The percentages of adults surviving decreased more rapidly at higher temperatures except at 20°C (Fig. 3.3). All adults died after 36 days under the fluctuating temperature regime (the longest time) and 16 days at 20°C (the shortest time) (Fig. 3.3).

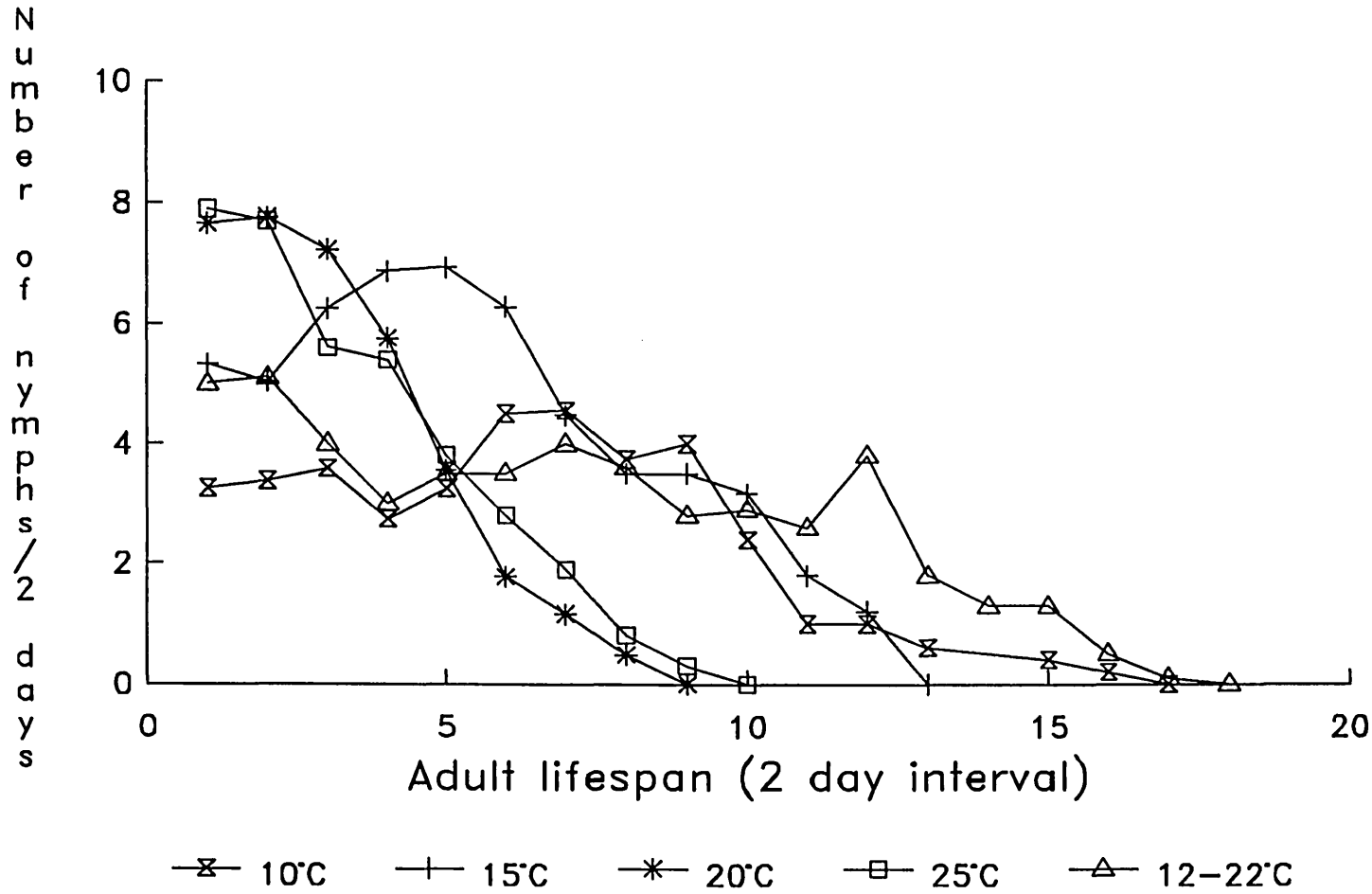


Fig. 3.2 Effects of temperature on reproduction and adult lifespan of the rose grain aphid

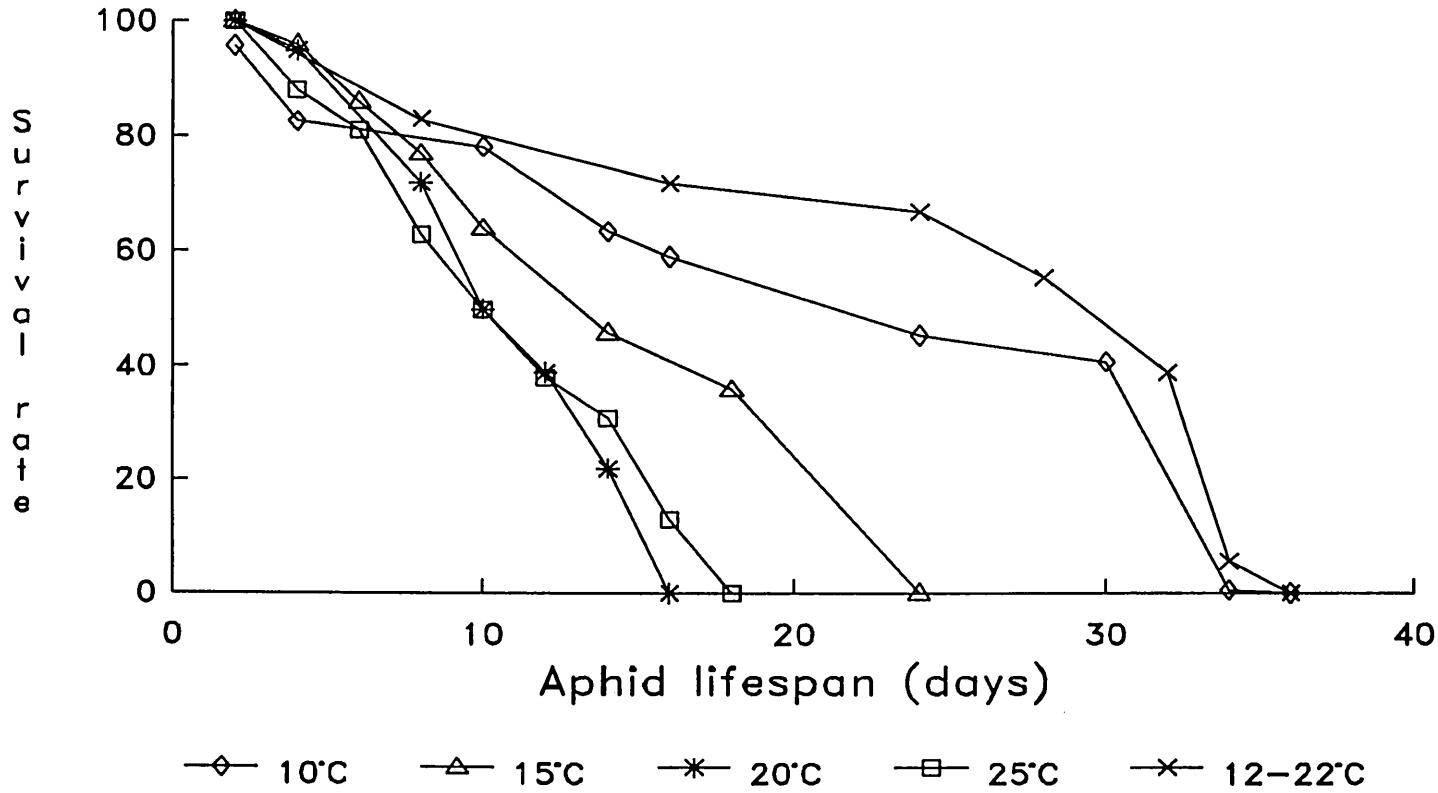


Fig. 3.3 Survival rate (%) of apterous adults of the rose grain aphid at different temperatures

Table 3.5 Life table parameters of the rose grain aphid at different temperatures

Temperature	R_o	T_c	r_m	λ
10°C	25.56	30.88	0.105	1.111
15°C	32.01	19.84	0.175	1.191
20°C	27.42	14.41	0.230	1.258
25°C	21.06	12.31	0.248	1.281
12-22°C	36.73	21.2	0.170	1.185

where R_o is the net reproductive rate (the number of times by which the population multiplies per generation); T_c is the cohort generation time ; r_m is intrinsic rate ($r_m = \ln R_o/T_c$) and λ is the finite rate for increase ($\lambda = e^{rm}$).

3.3 Effects of nitrogen on development, reproductive and mortality rates in the field

3.3.1 Methods

A field study was carried out on the effects of nitrogen on the aphid population development of *M. dirhodum* in conjunction with the crop loss experiment (for details of the experiment, see Chapter 2). Three plots without fungicide and aphicide in each of the three blocks were selected. At middle anthesis (G.S.

65), on 27 June, 45 flag leaves were caged (2.5 x 4cm), 5 in each plot. The chosen leaves were two rows in from plot edges to avoid an edge effect. One adult was put into each cage, and examined once a day. After the start of reproduction one nymph was kept in each cage. The generation length, numbers of nymphs produced per adult in 8 days and of dead aphids were recorded. The experiment was stopped when the flag leaves senesced.

3.3.2 Results

Mean generation length (from birth to the start of reproduction) and fecundity in 8 days were slightly higher at the standard nitrogen level (Table 3.6). However. there was no significant effect of nitrogen on development and fecundity of *M. dirhodum*. Mean generation length was 10.9 days and mean number of nymphs produced in 8 days was 22.6. Mortality was over 30% at the three nitrogen levels (Table 3.6).

Table 3.6 The effect of nitrogen on development, reproduction and mortality rates of *M. dirhodum*

Nitrogen levels (kg/ha)	Average generation length	Average number of nymphs in 8 days	Mortality (%)
80	10.4 ± 1.60	22.6 ± 3.63	38
120	11.7 ± 1.32	24.3 ± 3.70	32
160	10.7 ± 1.77	21.0 ± 3.63	33

3.4 Effects of crop growth stages on development, reproduction and mortality rates

3.4.1 Methods

Winter wheat cv. Avalon was sown in 30 pots (diameter: 10cm) in a greenhouse on 1 Jan. 1988. One plant was kept in each pot and transferred to a bigger pot (diameter: 14cm) at the beginning of tillering (G.S. 20). Fungicide was sprayed four times to ensure that mildew (*E. graminis*) developing on the plants was controlled. As each plant developed many tillers, four of the best grown shoots, including the main stem, were kept and the rest were removed in each pot at the beginning of stem elongation (G.S. 30). Nicotine was applied to remove unwanted aphids four days before the introduction of aphids.

Plants were moved to a constant environment room at 19 ± 1°C and day:night length, 16hrs:8hrs two days before the aphids were introduced.

The aphids were introduced at two crop stages; start of booting (G.S. 40) and flowering (G.S. 60). Five apterous adult aphids were introduced onto each plant, using clip cages, at the start of booting. Three of these aphids were individually confined on the flag, second and third leaves on the main shoot, and the other two aphids were caged on the flag leaves of two earliest tillers in each pot. There were eight replicates. At the start of flowering, three apterous adults were caged on each flag leaf of three shoots (including the main shoot) in each

pot, replicated ten times.

The positions of aphids feeding on the main flag, tiller flag, second and third leaves were recorded. Three observations were made during nymphal development stages at 08:00, 14:00 and 20:00. Moulting, death or missing aphids were recorded. After the aphids had started to reproduce, observations were made once a day. The numbers of nymphs produced per day were recorded, along with the death and loss of any adults.

3.4.2 Results

3.4.2.1 *Effects of feeding position*

Feeding position did not affect total development time or that for each instar separately (Table 3.7 and Table 3.8).

Feeding position did not significantly affect either the reproductive lifespan or the total nymphs produced although nymphs fed on the flag leaves had longer lifespans and produced more nymphs, than the nymphs which had fed on the second leaves. These in turn had longer lifespans and produced more nymphs than those on the third leaves (Table 3.8). Mean daily reproductive rates were similar for aphids feeding on either the flag or second leaves (3.2 nymphs/day) and the rate was smaller when aphids had fed on the third leaves (2.6) although they were not significantly different. No significant effects of the aphids feeding on main shoots and the other shoots were found.

3.4.2.2 *Effects of crop growth stage*

Development time, length of reproductive period and fecundity were significantly affected by crop growth stage (Table 3.9). Aphids which had fed from booting (G.S. 40) to middle inflorescence (G.S. 55) had shorter development times (197 hrs) than those on later stages (start of anthesis G.S. 60 to middle milk G.S. 75) (221 hrs). Mean lifespan of the adults from middle inflorescence to middle milk (G.S.55-75) was 2.3 times longer than that during middle milk to early ripe (G.S.75-83) and fecundity was 14 nymphs higher than that during the later stage, which was 32 nymphs/adult.

Daily reproduction was always higher and adult lifespan longer when the adults had fed on winter wheat from middle inflorescence to early milk stage than from middle milk to early ripe stage (Fig. 3.4b). Moreover, more than 90% of the adults survived and produced nymphs over a period of 11 days before numbers gradually decreased at the low crop growth stages while fewer survived in the later treatment (Fig. 3.4a).

The cohort generation time(T_c) feeding during the two crop growth ranges were similar to that on seedlings at the same constant temperature (20°C) (Table 3.5). However, the net reproductive (R_o) and, therefore, the intrinsic rates (r_m) were higher during the mid-inflorescence to mid-milk stage (38.91 and 0.2573 respectively), and lower during the middle milk to early doughy ripe stage (23.1 and 0.2165 respectively) than that on the seedlings (Table 3.5).

Table 3.7 Effects on nymphal development of the rose grain aphid feeding on flag leaves of the main shoot and tillers, second and third leaves

Source of variance	d.f.	ms	F	signf. level
Instar I	3/29	26.96	0.65	NS
Instar II	3/29	22.45	0.49	NS
Instar III	3/29	47.21	0.75	NS
Instar IV	3/28	18.03	0.11	NS
Repr. delay	3/28	52.75	1.45	NS
Total	3/28	42.4	0.33	NS

3.5 Effects of crop growth stage and crowding on alate production

3.5.1 Method

Winter wheat seedlings, c.v. Avalon, were taken from the field in mid-February and replanted in 60 pots (14cm in diameter) in a greenhouse (20°C). The plants were moved to a constant environment cabinet (1x1m), light:dark 16:8 at a constant temperature of 20°C.

Table 3.8 Effect of feeding position on development (hours) and fecundity of the rose grain aphid

Feeding position	No.	Development I	II	III	IV	pre-pro-ductive delay	Total	Fecundity Adult lifespan	Nymphs produced per adult
Main flag leaves	6	51.3±3.3	43.3±1.9	44.8±1.5	59.0±5.7	11.3±3.1	198.5±6.3	15.4±1.6	51.8±8.4
Tiller flag leaves	13	47.0±1.7	41.3±1.5	50.5±2.4	56.4±3.2	5.6±1.4	196.5±2.7	14.8±1.0	49.6±3.9
Second leaves	8	48.6±1.4	44.6±3.5	47.6±3.9	56.4±4.9	9.9±1.5	197.2±4.5	13.8±1.9	46.4±8.9
Third leaves	6	50.7±3.3	43.9±2.5	48.2±0.2	59.2±5.4	8.3±3.2	201.9±3.3	11.7±1.3	31.7±5.7

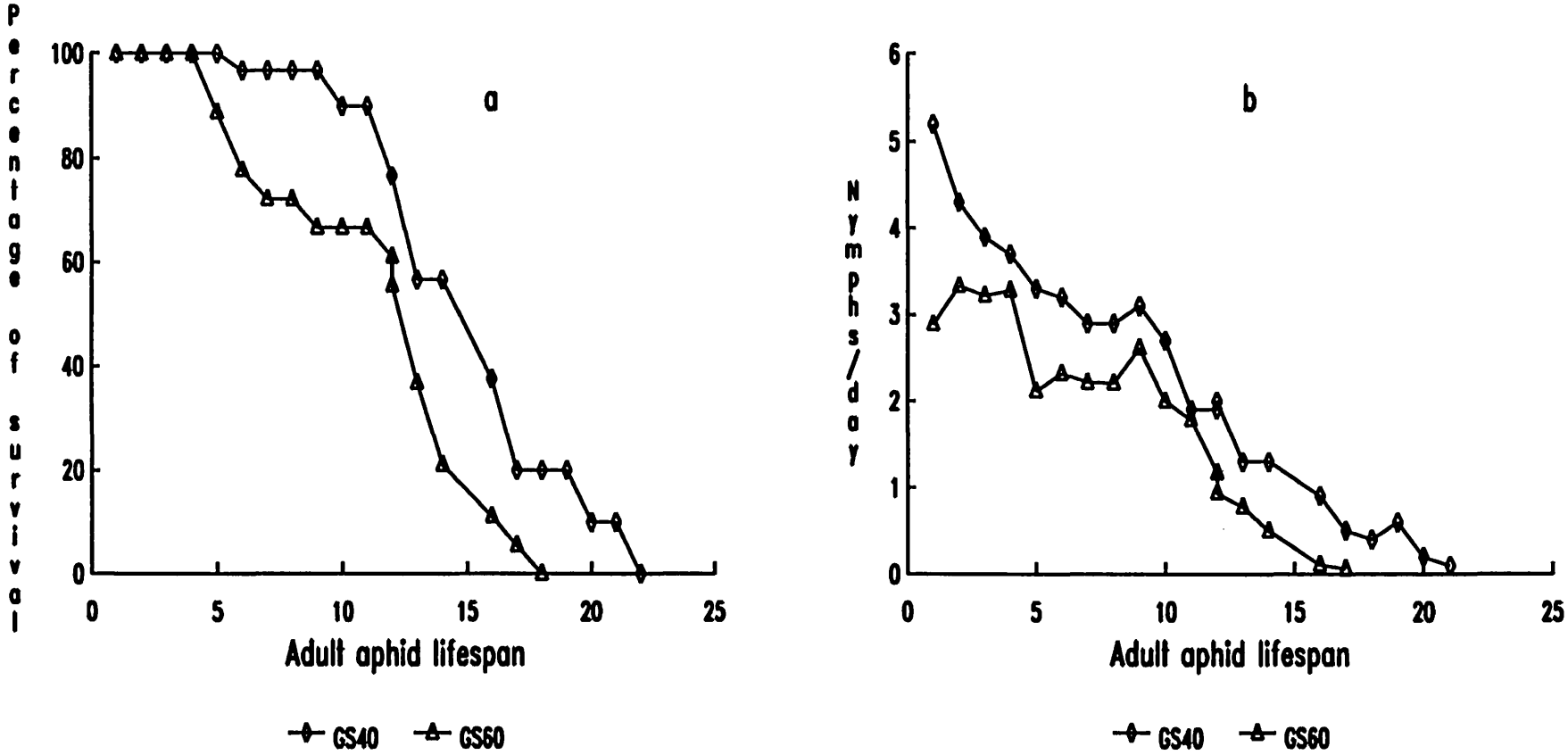


Fig. 3.4 Effects of crop growth stage (GS40 and GS60 are initial rearing stages) on (a) aphid survival, and (b) reproduction, of the rose grain aphid

Table 3.9 Effects on the rose grain aphid feeding on winter wheat from booting to middle inflorescence compared with that from anthesis to middle milk

Source of variance	d.f.	ms	F	signif. level
Development time	1/34	5210.4	6.58	< 0.05
Length of reproductive period	1/33	1322	8.17	< 0.01
Total nymphs	1/33	2978.5	10.81	< 0.005

Newly born nymphs were introduced at the beginning of booting (G.S. 40), mid-inflorescence (G.S. 55), mid-milky (G.S. 75) and beginning of dough (G.S. 80). Three levels of aphid density (1, 5 and 10) were caged (2.5 x 4cm) at each crop stage. Treatments were replicated ten times. Observation were made once a day (18:00). The numbers of fourth instar alatiform aphids were recorded. The same number of nymphs from the second generation were maintained for another generation and the numbers of the fourth instar alatiform nymphs they produced were also recorded.

3.5.2 Results

There was no difference in alate production between the first and second generation, and no alates were produced before

the beginning of anthesis regardless of aphid densities, except 4% of nymphs were alatiform at mid-booting with 10 aphids per cage. Forty to 66% of nymphs were alatiform at mid-milk and beginning of dough with 10 aphids per cage, and about 10% with only one aphid per cage. The relationship between alate production (p_{al}, %) and aphid density (d) and crop growth stage (gs) was estimated from the data after the start of anthesis (G.S. 60) because percentage of alatiform nymphs produced was low before the start of anthesis:

$$p_{al} = -572.94 + 4.6931d + 14.5784gs - 0.092728gs^2$$

$$F_{3/9} = 6.77,\ p < 0.05$$

3.6 Effects of insecticide on aphid survival

3.6.1 Methods

Winter wheat, c.v. Avalon, was grown in a greenhouse (20 ±1°C), one plant per pot (14cm in diameter). Twelve pots of plants at the start of anthesis (G.S. 60) and twelve at the start of tillering (G.S. 20) were sprayed evenly from above with pirimicarb using a hand sprayer to give a rate equivalent to 280g of 50% pirimicarb in 200 l ha^{-1}. Twelve pots of tillering plants were sprayed with water as the control.

Two hours after spraying when the chemical had dried, seventeen to twenty five aphids were confined using a clip cage on each plant. The aphids were examined 24 hours after the introduction and the numbers alive and dead in each cage were

recorded. The live aphids were then removed. The trial was repeated every two days for 14 days.

3.6.2 Results

Aphid mortalities due to pirimicarb were calculated by subtracting a natural mortality obtained from the control (10.2%) from the mortalities when the pirimicarb was applied. Mortalities of the treated aphids on seedlings and flowering plants were similar (Fig. 3.5). The mortality remained at about 90% for 4 days and then quickly decreased linearly (Fig. 3.5). A quadratic equation was calculated between the time (x_d) after spray and the percentage of aphids killed (y_m), combining the mortality data from the two crop growth stages:

$$y_m = 90.3078 + 0.2602x_d - 0.4575x_d^2$$

$$r = -0.978,\ p < 0.001$$

3.7 Discussion

Dean (1974) investigated the effects of temperature on the biology of cereal aphids (*S. avenae, M. dirhodum* and *R. padi*) on barley leaf discs at 2.5°C intervals over a range of 10°C to 30°C. Development rate of *M. dirhodum* increased to a maximum at 20°C and then declined with increase in temperature. The development rate was assumed to be zero at 30°C when all aphids died. However, the assumption may be unrealistic, especially under field conditions, as temperatures fluctuate and rarely reach 30°C for long periods in Britain. In this study, the aphids

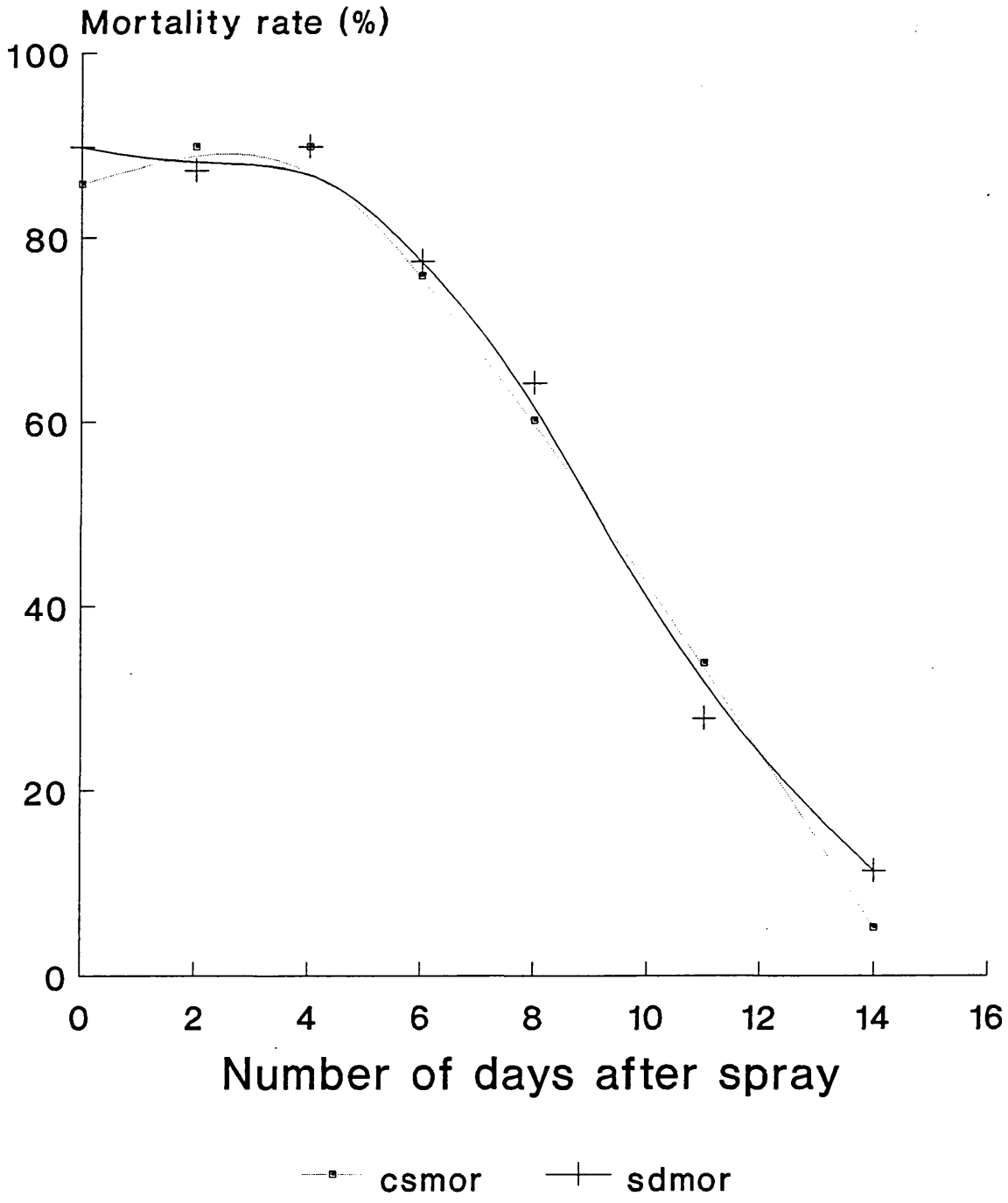


Fig. 3.5 Effects of pirimicarb on mortality of the rose grain aphid (sdmor is at G.S.20, csmor is at G.S.60)

successfully developed to the adult stage at 30°C although they failed to reproduce. This suggests that the upper threshold for reproduction is lower than that for development.

Dean (1974) used quadratic and inverse quadratic equations to relate development time and rate to temperature respectively. However, the optimum temperature for development from the two equations was different (20.3°C from the quadratic equation and 22.2°C from the inverse quadratic one). Two simple linear regressions provide a good fit to these data (Cannon, 1981) (Fig. 4.6). In the present study, linear regression models described the relationship between development rate and temperature at different aphid growth stage as Cannon (1984) had done from field studies.

The first three instars, measured in an intensive winter wheat field trial (Cannon, 1984), had a similar development time as in this study. But, the development time of the fourth instar was much longer than that in this study. The total development time was longer than that in this study and that from Dean (1974) which was the shortest. The difference possibly reflect the conditions under which the experiments were undertaken as *M. dirhodum* prefers barley to wheat (see Chapter 2) and field conditions may also be more adverse to aphid growth. Aphid growth was not affected by fluctuating temperatures compared with constant temperatures (Cannon, 1984), which was also found in this study (Table 3.1).

The optimum temperatures for development and reproduction

cannot be obtained from the field studies (Cannon, 1984). In this study, the shortest development time was at 25°C, five degrees higher than that from the study of Dean (1974). Pre-reproductive periods were longer, especially at low temperatures than those recorded by Dean (1974).

Hu and Gui (1985) obtained development thresholds for individual instars of *M. dirhodum* and the full generation from a life table study which ranged from 1 to 2°C. But, in the present study, the fourth instar had a threshold of -6°C while thresholds of the other instars were approximately 0°C.

Cereal aphids are more fecund on older wheat plants (Leather & Dixon, 1981; Watt, 1979), but more fecund on young plants when feeding on barley (Leather & Dixon, 1981; Thornback, 1983). *M. dirhodum* also favours barley to wheat (Dean, 1973; Thornback, 1983). In laboratory studies using discs made from young barley leaves, the mean fecundity increased from 44 to 61 with increase in temperature from 10°C to 20°C, but with a decrease in the reproductive lifespan from 18 to 13 days respectively. In the present study, fecundity was much less than that on barley leaf discs (Dean, 1974), but the adult aphids produced more nymphs with longer reproductive periods at low temperatures. Furthermore, aphids were more fecund when they fed during the flowering period than when the cereals had ripened as they are less suitable for the aphid growth.

In a laboratory experiment using barley seedlings at 20°C, Wratten (1977) obtained an average daily reproductive rate of

apterae of 3.4 (day 1 to 5), 2.7 (day 5 to 10) and 2.0 (day 10 to 20). The peak rate (4.9) occurred 2 and 3 days after reproduction started before decreasing gradually. In contrast, the reproductive rate of *S. avenae* is more consistent over the first fifteen days with a similar pattern on oat ears and leaves in a laboratory trial (Watt, 1979). This study shows that the peak number and the time of the peak were affected by temperature. As temperature increased, the peak moved towards the beginning of reproduction and the peak numbers increased (Fig. 3.2). The rates became more consistent when the aphids were reared at low temperatures. In a field study, Cannon (1984) observed the average reproductive rate on winter wheat as 4.2 nymphs per day, however the number was obtained without knowledge of adult ages and cannot be taken as the daily reproductive rate of individuals.

The majority of *M. dirhodum* are initially found on lower leaves and then move up to the flags as the lower leaves become senescent (Wratten, 1975; Cannon 1981; Dean, 1973). Watt (1979) in a field trial and Thornback (1983) in the laboratory found no evidence of the effect of feeding position on reproductive rate of *M. dirhodum*, which is in agreement with the results from this study except the aphids which had fed on flag leaves were slightly more fecund than these on the second or third leaves.

Hu & Gui (1985) found that intrinsic rate of increase of *M. dirhodum* was affected by temperature. The rates are similar to those in this study at the respective temperatures although the net reproductive rate (R_o) and mean age of the aphids (T_c) were different in these studies. Middle inflorescence to middle

flowering were the most favourable stages for aphid reproduction with the highest intrinsic rate of increase which the middle milk to dough stages were less favourable than seedlings.

The high adult mortality recorded at 20°C in this study may have been due to a late infestation of mildew (*E. graminis*) on the seedlings, which may also have affected the reproductive rate at this temperature.

Nitrogen has a significant effect on development and reproductive rates of *M. dirhodum* under controlled conditions using an artificial diet (Thornback, 1983; Veijken, 1979) but no significant effect was found in the field trial (Table 3.5). The aphids were confined to green flag leaves which probably supplied sufficient nitrogen for their development. Alternatively, the effects of nitrogen are likely to be different for artificial diet, compared with wheat at a later growth stage with different nitrogen levels. Part of the explanation of the high mortality in the field (Table 3.6) was that the young nymphs and alates became stuck to the clip cage walls.

The introduced nymphs in the first generation were from a crowded culture and a proportion of these aphids could already be alate in the alate production study. However, no alates developed in the cage with one nymph in the first generation. Therefore, data from both generations were combined for the analysis.

Effectiveness of pirimicarb on the rose grain aphid was

similar for young seedlings and mature wheat plants. Mortality was above 50% for eight days. Its effectiveness could be reduced due to bad weather conditions.

CHAPTER FOUR: THE MODEL

4.1 The cereal aphid system

A systems analysis approach was used to study the interactions between weather, crop and aphids.

The cereal aphid system can be described in terms of three types of variable and their interactions (Fig. 4.1): i) State variables are quantities which can be measured at any instant, for example, aphid population size; ii) Rate variables determine the relative speed at which the state variables change and are affected by the current state and driving variables, for example, development rate; iii) Driving variables are those that influence the state of the system, but are not affected by the system, for example, temperature. The relationships between variables are expressed as two types of flow: material flow (for example, individual aphids between state variables) and information flow (Fig. 4.1).

Components in each subsystem may interact with each other, and also with ones in other subsystems. To identify such relationships an interaction matrix was constructed (Fig. 4.2) (Holt *et al.*, 1987).

4.2 Development of the Model

The model simulates population development of *M. dirhodum*, its damage potential and strategies to control it on winter

Fig. 4.1 Relational diagram of population growth and development of *Metopolophium dirhodum* (where rectangles represent state variables; valves rate variables; parentheses driving variables; solid arrows material flow and dotted arrows information flow).

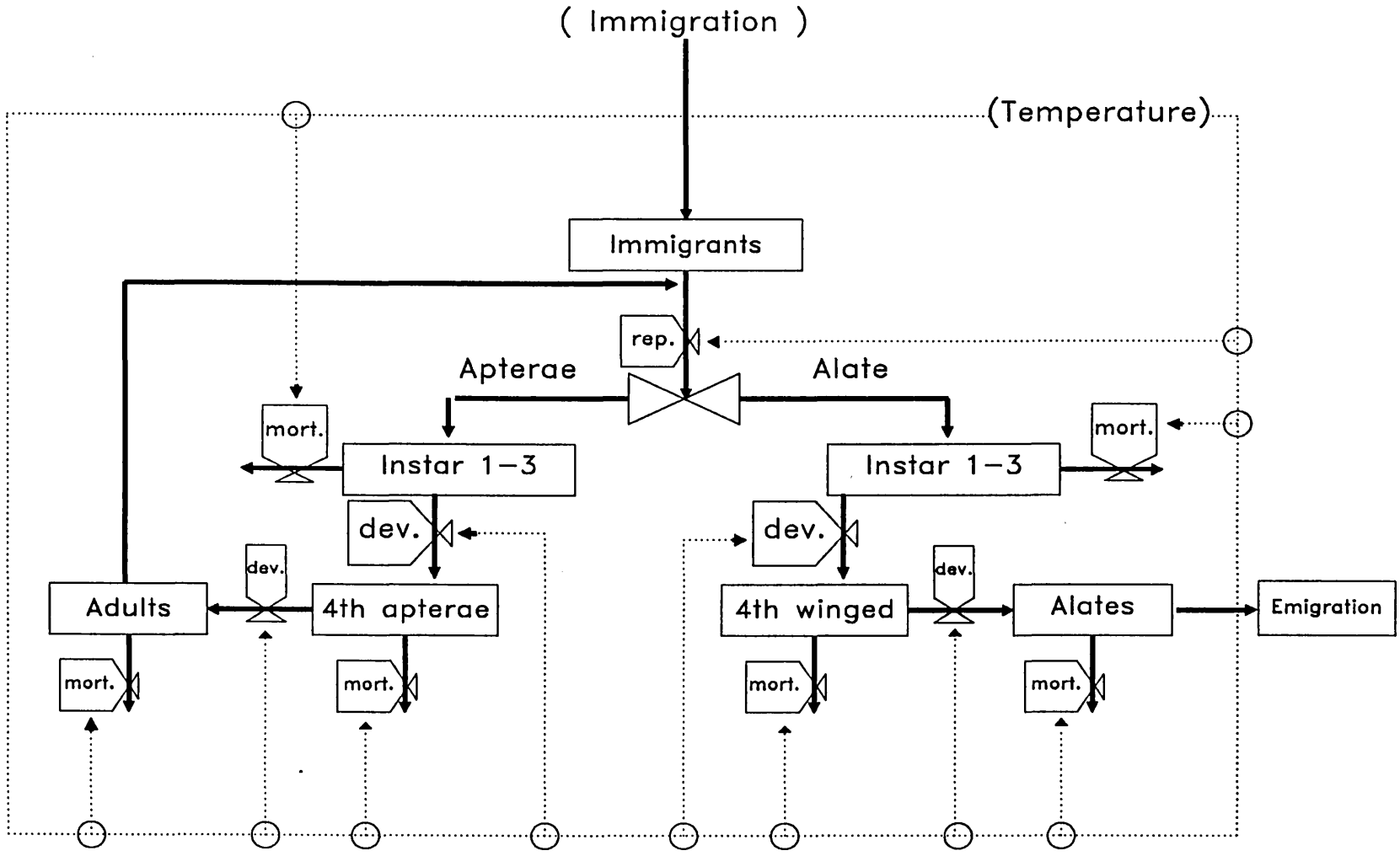
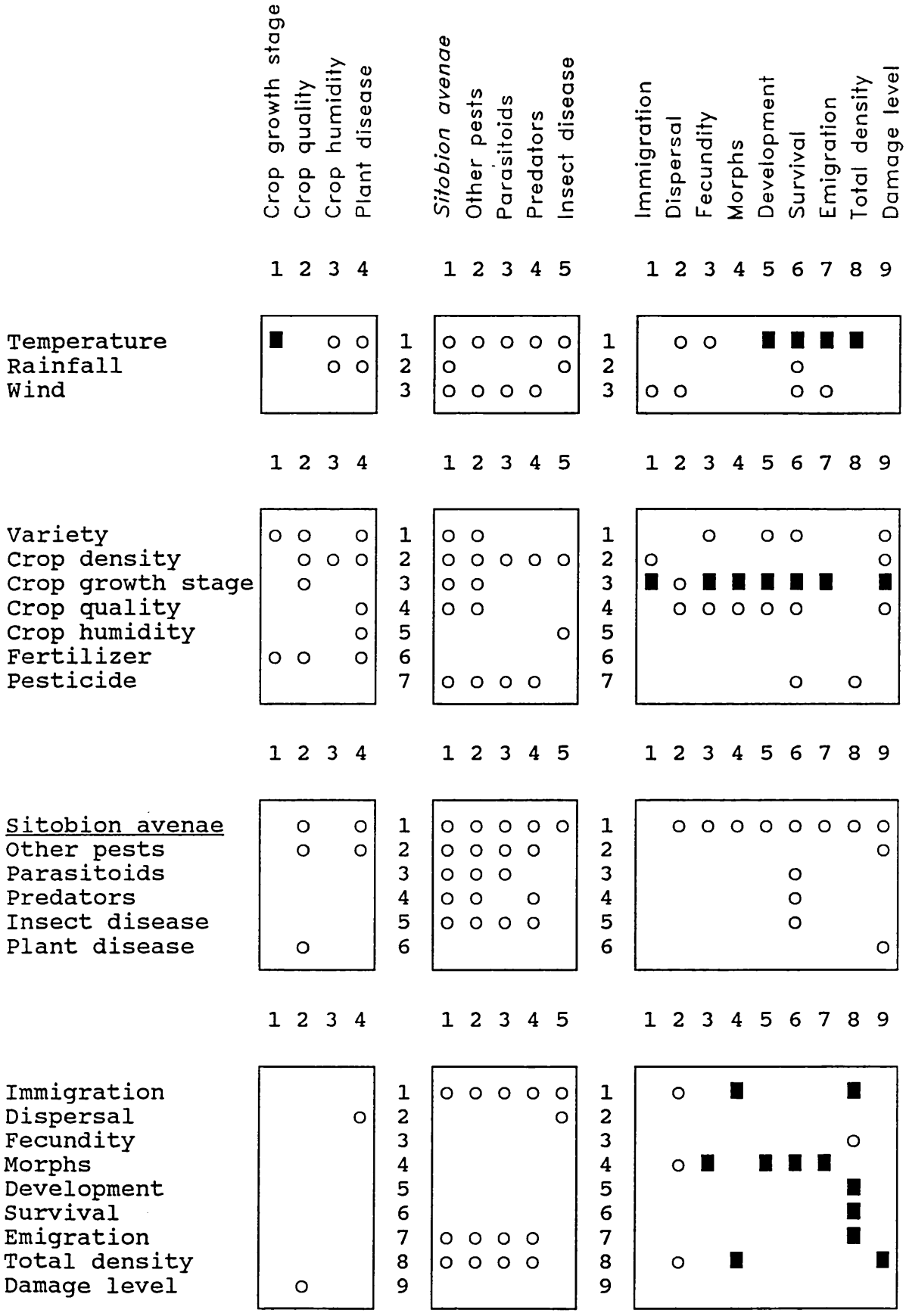

(Immigration)
(Temperature)
Immigrants
rep.
Apterae
Alate
mort.
Instar 1–3
mort.
Instar 1–3
dev.
dev.
dev.
dev.
Adults
4th apterae
4th winged
Alates
Emigration
mort.
mort.
mort.
mort.

Fig. 4.2 Relationships between components in the *Metopolophium dirhodum* system (symbols in cells indicate direct effects of row components on corresponding column components; ■ represents relations between elements incorporated in the model; O indicates that relationships or interactions may exist but are not included in the model; blank cells indicate that no relationships are thought to exist between respective elements)


Crop growth stage
Crop quality
Crop humidity
Plant disease
Sitobion avenae
Other pests
Parasitoids
Predators
Insect disease
Immigration
Dispersal
Fecundity
Morphs
Development
Survival
Emigration
Total density
Damage level
1 2 3 4
1 2 3 4 5
1 2 3 4 5 6 7 8 9
Temperature
Rainfall
Wind
Variety
Crop density
Crop growth stage
Crop quality
Crop humidity
Fertilizer
Pesticide
Sitobion avenae
Other pests
Parasitoids
Predators
Insect disease
Plant disease
Immigration
Dispersal
Fecundity
Morphs
Development
Survival
Emigration
Total density
Damage level

wheat in summer in England. The model, which is deterministic, was written in Fortran 77 and run on a Vax/vms system. The model is listed in Appendix I together with a description of the variables used in the model. The model consists of the following sections (Fig. 4.3).

4.2.1 Initialization and Data Input

Array dimensions (size and number of elements) of variables and types of variables (real or integer) are declared where necessary. Values of variables and parameters are input as follows:

i) Variables with a single value: number of sensitivity analyses; indices of changed values for parameters in the sensitivity analyses; dates on which the model starts and ends; latitude of the site (51 at Rothamsted); the highest and lowest mortalities caused by insecticides; number of shoots per square metre; initial crop stage; grain price, £/t; wheeling loss due to the insecticide application (%) and its application costs, and threshold temperature for aphid development.

ii) Variables in arrays: daily maximum and minimum temperatures; suction trap samples.

iii) Logic variables: LEAP, leap year (yes) or not; CTOUT, controlling output data; skip variables, skipping certain procedures or using alternative data in the model.

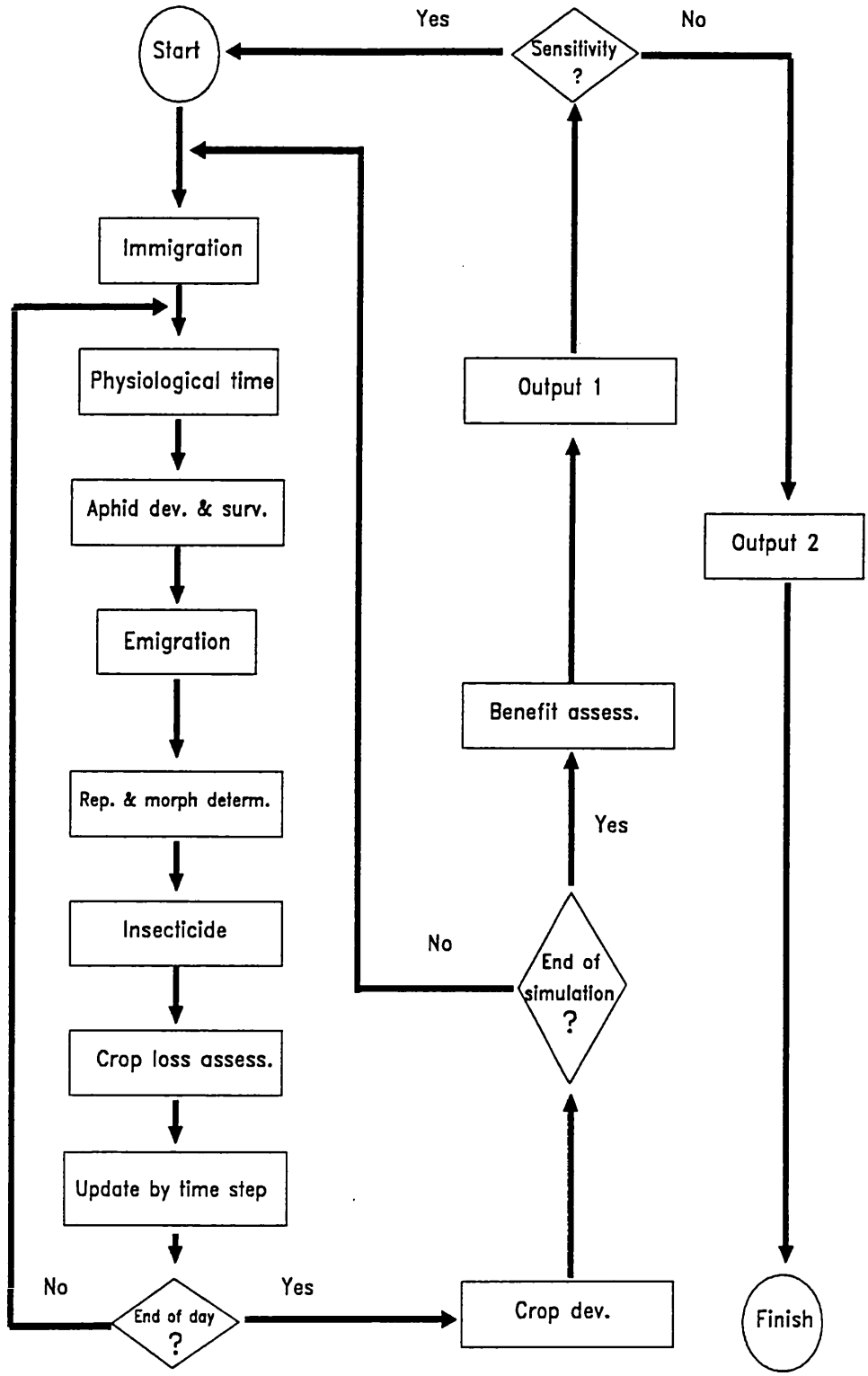


Fig. 4.3 Flow diagram of the model

4.2.2 Migration

M. dirhodum overwinters primarily holocyclically in east England, and colonies in the cereal crops originate from immigrants (Dean, 1973; Carter *et al.*, 1982). The model is therefore initialized by migration as the only aphid input source.

A network of suction traps has been operated since 1968 (Taylor, 1977). Its data have been used in the advisory service to forecast aphid populations (Bartlet *et al.*, 1990). The number of immigrant *R. padi* and the maximum density in spring cereal fields are positively correlated, so that suction trap catches can be used to forecast aphid population trends with a population growth model (Wiktelius, 1982). Carter *et al.* (1980) obtained a significant correlation between the number of *S. avenae* caught in the suction trap (12.2m) at Brooms Barn and the number in yellow water traps placed in cereal fields near Norwich. This suggests that the number of immigrants can be estimated from suction trap samples. Suction traps have been used to estimate the immigrants landing on cereals in several simulation models (Carter, 1979; Winder, 1990).

The suction trap was designed and standardized for insect survey sampling (Taylor & Palmer, 1979). The suction trap includes two density profiles: vertical and horizontal. In the vertical profile, the mean density of flying aphids diminishes with height according to the expression (Johnson, 1957):

$$f(Z) = C(Z + Z_e)^{\lambda} \qquad (4.1)$$

where $f(Z)$ is the density at height Z, C is a constant or scale factor related to population size, λ is a regression coefficient or gradient of density and Z_e is a measure of the departure from linearity on logarithmic co-ordinate.

Therefore the total number of insects in a given volume of air in space (Tim) can be integrated between two heights, z_1 and z_2, giving the horizontal profile.

$$Tim = \int_0^s \int_{z_1}^{z_2} C(z + z_e)^{\lambda} dz ds \qquad (4.2)$$

where s is the area of the horizontal profile.

The mean daily density gradient λ, ranges from -0.5 to -1.5 for aphids. Alternatively, the total number flying at a certain height in the air could be estimated from a simple regression equation using the mean density gradient of -1.0 as the regression coefficient (b) if the density profile is not measured (Johnson, 1957).

$$Log\ D = a + bLog(Z) \qquad (4.3)$$

where D is aphid density and Z is height.

The rate at which these aphids are deposited on the ground depends on the duration of flight (Taylor & Palmer, 1972). The deposition rates with mean flight times and density gradients

from 0 to -2 are presented in Table 4.1 (Taylor & Palmer, 1972). For aphids, an average flight time is 2 hours (Johnson, 1957; Taylor, 1958) with a density-height gradient of -1.0 (Johnson, 1957, Calnaido *et al.*, 1965). Therefore, a deposition rate of 237 aphids ha^{-1} is obtained for each aphid caught in a trap. However, this rate underestimates the number of alate *S. avenae* landing on cereals by a factor of 40 (Carter *et al.*, 1982).

Table 4.1 Estimated landing rates per aphid in suction trap samples (After Taylor & Palmer, 1972)

Density gradient	Mean flight time (hours)						
b	0.5	1	2	4	8	12	24
	Landing rate/ha/day						
0	10319	5159	2580	1290	645	430	215
-0.5	1660	830	415	207	104	69	34
-1.0	949	474	237	118	59	39	20
-1.5	2016	1008	504	252	126	84	42
-2.0	10319	5159	2580	1290	645	430	215

Aphids caught in a suction trap represent the aerial population from and/or to cereal fields. In May and June, most of the alates are emigrants from the primary host or grasses. As cereal crops ripen and the aphid population increases, an increasing proportion of the aphids develops into alates and starts to emigrate. These emigrants from cereals predominate in the trap

samples later in the season. Therefore, a simple algorithm (Equation 4.4) was used to estimate the number of immigrants from the total number in the trap (Fig. 4.4), where the proportion of immigrants (I) in suction trap samples (I_c) is dependent on the current crop growth stage (S_c), the crop stage when emigrants first appear (P_1) and the crop growth stage when all alates are emigrants (P_2).

$$I = I_c \left(1 - \frac{S_c - P_1}{P_2 - P_1}\right) \qquad (P_2 \geq S_c \geq P_1 \;\&\; P_1 \neq P_2) \qquad (4.4)$$

The number of these alates caught in suction trap is transformed to immigrants landing per shoot and multiplied by 40 (Equation 4.5).

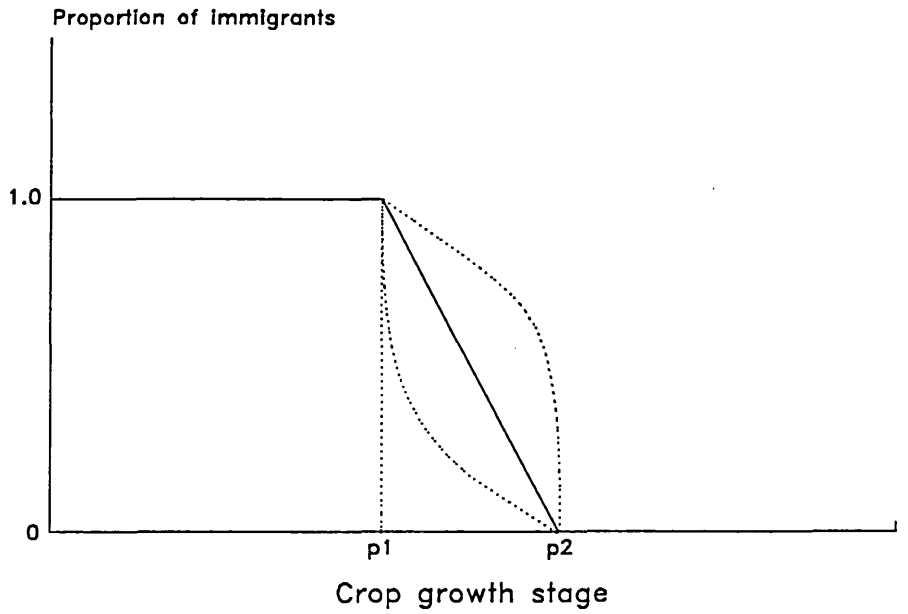


Fig. 4.4 Proportion of alates in suction trap samples estimated as immigrants (dotted lines indicate possible alternative transformations).

$$D_{imm} = I*237*40/sh \qquad (4.5)$$

where sh is 5000000, the number of shoots/ha.

These immigrants are assumed to reproduce immediately after settling on cereals and remain until they die. Alates which develop in the field are assumed to emigrate after moulting to the adult stage.

4.2.3 Physiological time calculation

The rate of development of insects is primarily determined by temperature. Insects have to receive certain amounts of accumulated temperatures (above a temperature threshold below which they stop developing) to develop from one stage to the next. These accumulated temperatures are called 'physiological time' and are expressed in day or hour degrees. Hughes (1962) introduced a method to update insect development on a physiological time scale instead of calender time. This method has been widely used in many simulation studies. In the current model, the aphid population is updated on a physiological time scale, but the output is presented in real time. This allows direct comparison with field data.

Temperature data are usually recorded as maximum and minimum temperatures each day. Hourly temperatures are estimated from these temperatures. Daily maximum and minimum temperatures are assumed to occur at 14:00 and sunrise respectively. The actual time of sunrise is dependent on latitude and the time of the year. Hourly temperature are assumed to change according to a sine curve (Fig. 4.5) which is represented by three equations:

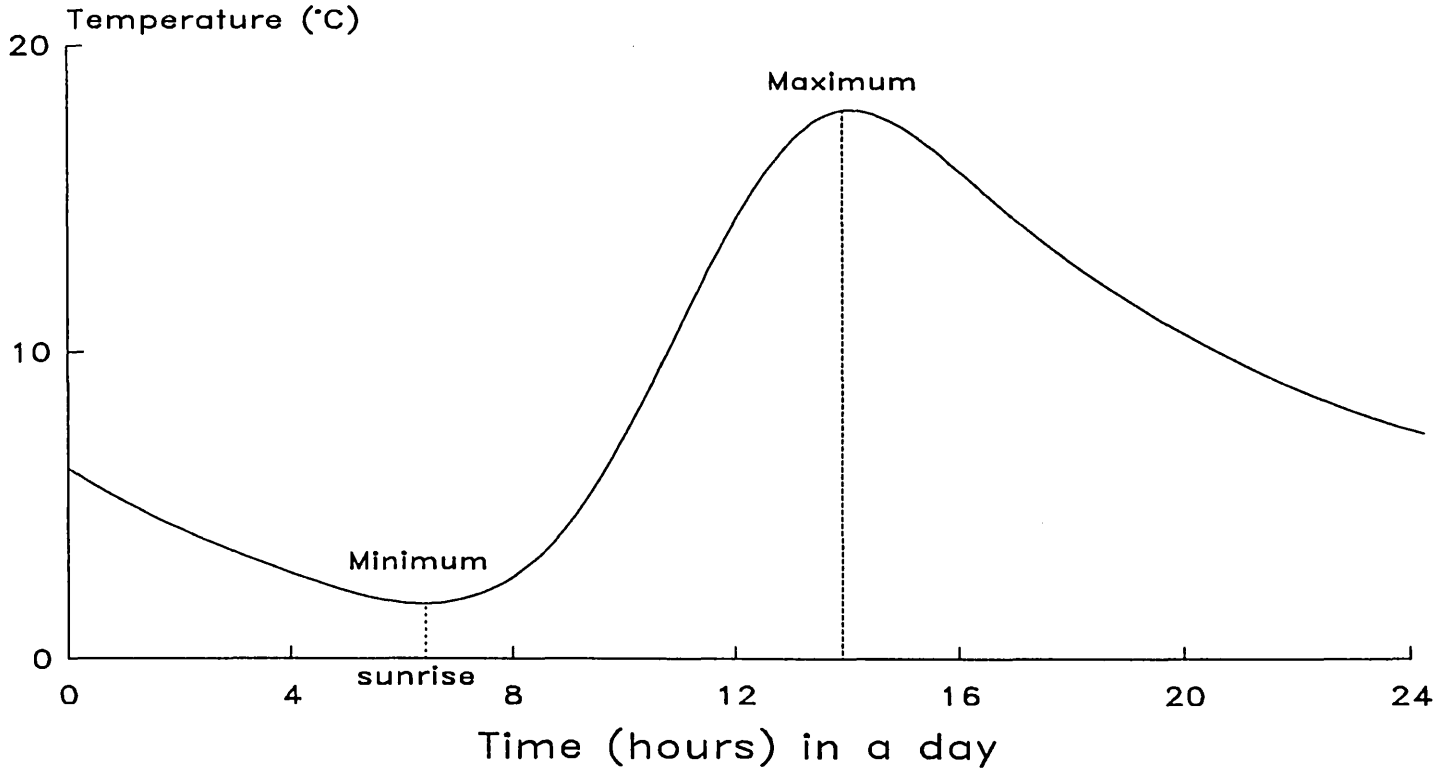


Fig. 4.5 The curve used to calculate hourly temperatures of each day.

When $i \leq Tr$

$$t(i) = (y_{max}(d-1) - y_{min}(d)) * (\cos[(i - 2Tr - 10)\pi / (10 - Tr)/2 + (y_{max}(d-1) + y_{min}(d))/2 \quad (4.6)$$

When $Tr < i < 14$

$$t(i) = (y_{max}(d) - y_{min}(d)) * \{-\cos[(i - Tr)\pi/(14 - Tr)]\}/2 + (y_{max}(d) + y_{min}(d))/2 \quad (4.7)$$

When $i \geq 14$

$$t(i) = (y_{max}(d) - y_{min}(d+1)) * \cos[(i - 14)\pi/(10 - Tr)]/2 + (y_{max}(d) + y_{min}(d+1))/2 \quad (4.8)$$

Where y_{max} --- the maximum temperature the day before

y_{min} --- the minimum temperature the day after

i --- time (1 to 24 hour)

t --- hourly temperature

Tr --- time of sunrise

d --- The day concerned

π --- 3.1416

A development threshold was calculated from Dean's (1974) study of cereal aphids on barley leaf discs in the laboratory (Table 4.2). Two significant lines describe the data (Fig. 4.6):

$$d_{v1}(t) = (0.522 + 0.24\ t) * 10^{-3}$$

$$r = 0.98, \quad p = 0.01 \quad (t \leq 20°C) \quad (4.9)$$

$$d_{v2}(t) = (8.917 - 0.198\ t) * 10^{-3}$$

$$r = 0.99, \quad p = 0.05 \quad (t > 20°C) \quad (4.10)$$

Assuming the relationship of d_{v1} is true below 10°C, the development threshold is -2.2°C. To calculate physiological time (hour-degrees, H°), the hourly temperatures are converted to H° by adding 2.2 when these temperatures are between -2.2°C and 20.0°C (Equation 4.11). When the temperatures are between 20.0°C and 27.5°C, the development rates are calculated by Equation 4.10 and then the physiological time is calculated from Equation 4.12:

$$H° = t(i) + 2.2 \qquad (-2.2°C \leq t(i) \leq 20°C) \quad (4.11)$$

$$H° = d_{v1}^{-1}\{d_{v2}[t(i)]\} + 2.2 \qquad (20°C \leq t(i) \leq 27.5°C) \quad (4.12)$$

The physiological time is zero if $t(i) < -2.2°C$ or $t(i) > 27.5°C$

Data from experiments in this study (see Chapter 3) are also incorporated. The physiological time is calculated above a development threshold, -0.26°.

Reproductive rates, number of nymphs per hour-degree per day, are calculated assuming a reproductive threshold of 5°C. Hour-degrees are assumed to be half when the temperature was between 5 and 10, and 20 and 25°C, and one eighth when the temperature is over 25°C as the reproductive rate was significantly reduced at these temperature regimes (Dean 1974a; Hu & Gui 1985).

4.2.4 Development and survival

Development times are from excised barley discs Dean (1974). The longevities measured in hours are multiplied by the temperature above the development threshold of -2.2°C (Fig. 4.6) to convert to an hour degree scale (Table 4.2). The length of the alatiform fourth instar is assumed to be 1.5 times that of apterae based on studies of *Brevicoryne brassicae* (Hughes, 1963). The length of the life span of apterous adults is dependent on crop growth stage. It is the length obtained from Dean (1974b) before the end of inflorescence (G.S. 59) and doubled between the end of inflorescence and early milk (G.S. 73) and is halved at later growth stages (Watt, 1979). The alate adult life span is assumed to be half of the apterous adult life span before the end of inflorescence (Wratten, 1977).

The development data in this study (Table 3.3) are also incorporated into the model.

Watt (1979) observed that survival (SUR) was dependent on crop growth stages. Apterous alate adult survival rate is 0.89 before early milk (G.S. 73) and 0.54 after this growth stage (Watt, 1979). Nymphal survival rate is 0.87 before early milk (G.S. 73) and 0.23 afterwards. Then, these survival rates are transformed to rates per hourdegree over a time scale.

$$SURi = Sur^{**[(\Sigma h°i)/Li]} \qquad (5.13)$$

Table 4.2 Development lengths (H°) of *M. dirhodum* above -2.2 (after Dean, 1974b) (The mean values exclude that at 27.5°C).

Temp.(°C)	1st instar	2nd instar	3rd instar	4th instar	rep-delay	total
10	1029.68	916.22	935.74	1212.68	280.6	4309.04
12.5	940.8	924.64	1026.06	1273.02	238.14	4140.99
5	899.56	823.88	963.2	1049.2	247.68	3928.48
17.5	902.26	957.24	1095.23	1203.67	131.99	4343.85
20	961.26	883.56	916.86	1165.5	202.02	4158.06
22.5	1029.99	1000.35	1190.54	1536.34	358.15	5011.63
25	1047.2	1093.44	1234.88	1689.12	1123.36	6106.4
27.5	1375.11	1541.43	2168.1	-	-	-
m	972.96	942.79	1051.8	1304.22	368.85	4571.21

The nymphs and adults at any given state are represented by an array A_N $(A_{1,\ 2,\ 3,\ \cdots,\ k;\ k+1,\ \cdots,\ l;\ l+1,\ \cdots,\ m;\ m+1,\ \cdots,\ o;\ o+1,\ \cdots,\ N})$ where $A_{1,\ldots,\ k}$ is designated to the first instar, $A_{k+1,\ \ldots,\ l}$ second instar and so on. Another vector, associated with this population vector A_N, is X_N, which has the same length as A_N and in which each element represents the age of these aphids in the corresponding element in the A_N array (Fig. 4.7).

Updating of individuals from one element to the next, i.e. from A_r to A_{r+1} occurs on a real time scale. The age of these individuals is also updated from X_r to X_{r+1} by adding the number

of hourdegrees over the time step. For computing convenience, updating starts with the oldest age class:

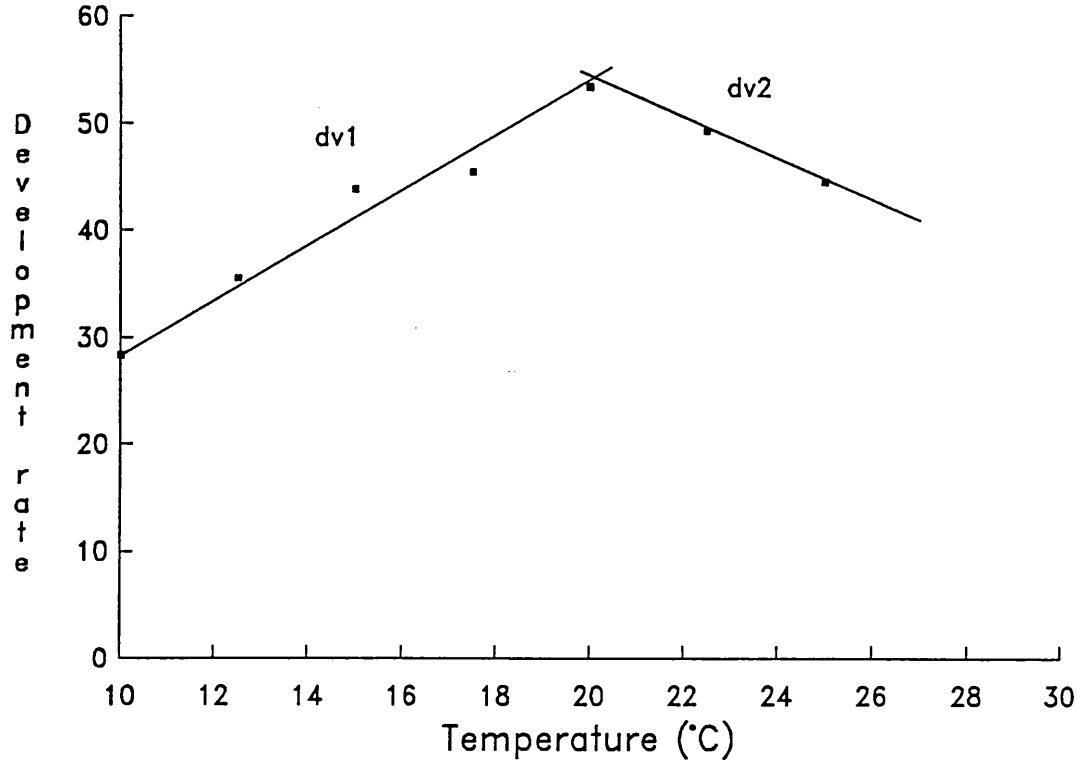


Fig. 4.6 The relationship between development rate (dv, hour^{-1} x 10^{-4}) and temperature (t).

$$A_r = A_{r-1} \tag{4.14}$$

$$X_r = X_{r-1} + H^\circ \tag{4.15}$$

then the updated individuals stored in A_{r-1} and X_{r-1} are deleted so that individuals in younger age classes can be updated.

$$A_{r-1} = 0.0$$

$$X_{r-1} = 0.0$$

Updating from one instar to an older one and from the fourth instar to the adult stage depends on the physiological time in the age vector X_N (Fig. 4.7). For instance, if X_m is greater than or equal to the development length of the first instar, the individuals in the A_m cell are moved to the next elements in both vectors (A_{m+1}, X_{m+1}) and become the second instar. The numbers of individuals are modified by a survival factor (SUR(i) in each updating as they are moved to the next element in the A_N:

$$A_r = A_{r-1} * SUR(i) \qquad (4.16)$$

where SUR(i) is the survival rate of each development stage over a physiological time scale which is the length of each updating; i is 1, 2, 3, 4, 5 for the first, second, third, fourth and adult respectively and the survival rate of four nymphal stages is the same.

Numbers of individuals in each aphid growth stage (i) are summarised:

The first instar; $$T(1) = \sum_{i=1}^{k} A(i) \qquad (4.17)$$

The second instar; $$T_g(2) = \sum_{i=k+1}^{l} A(i) \qquad (4.18)$$

The third instar; $$T_g(3) = \sum_{i=l+1}^{m} A(i) \qquad (4.19)$$

The fourth instar; $$T_g(4) = \sum_{i=m+1}^{o} A(i) \qquad (4.20)$$

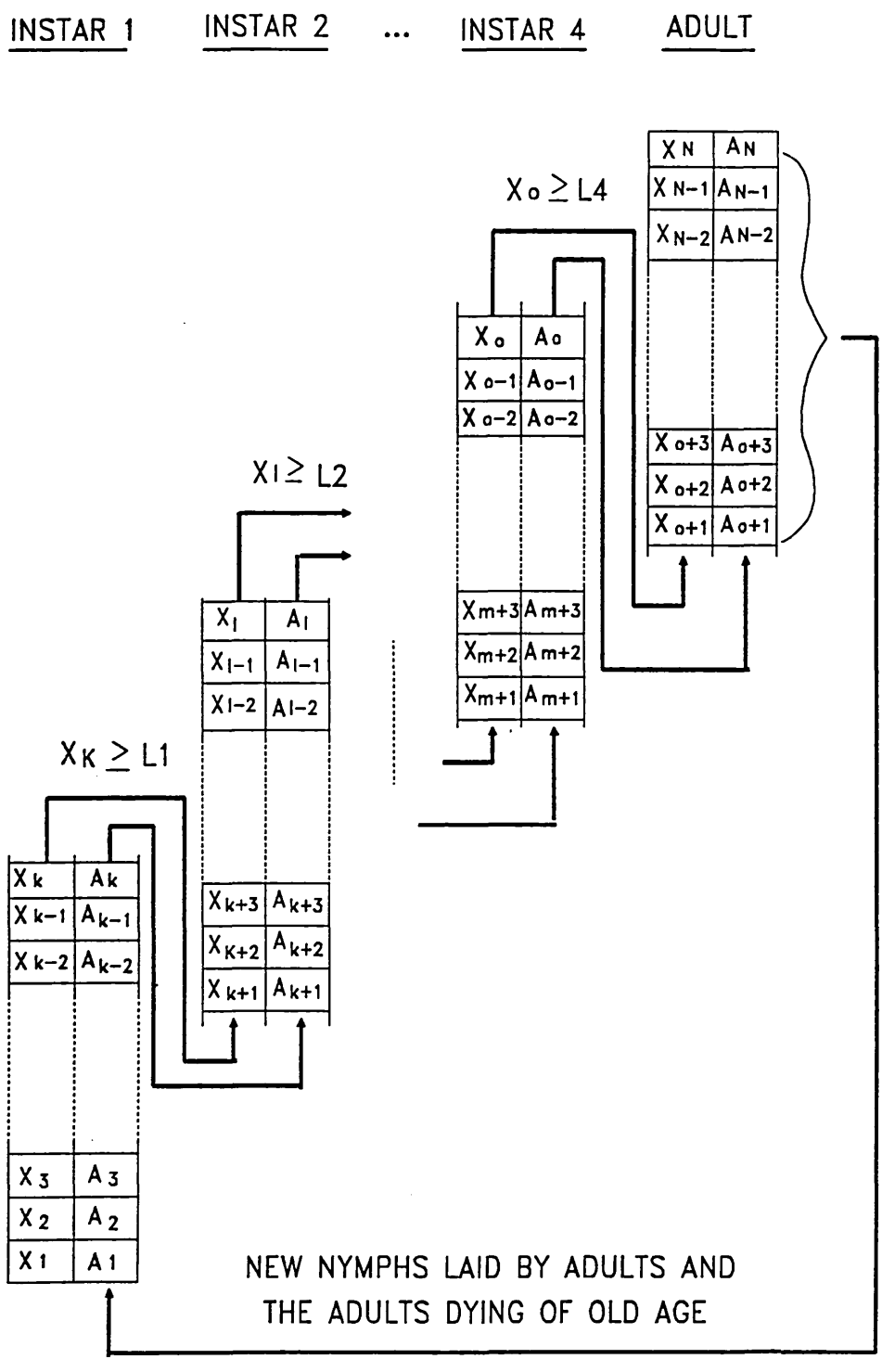


Fig. 4.7 Diagram for updating the aphid population development

The adult; $$T_g(5) = \sum_{i=o+1}^{N} A(i) \qquad (4.21)$$

Total population; $$T_g = \sum_{i=1}^{5} T(i) \qquad (4.22)$$

where g is for apterae or alatae.

4.2.5 Reproduction and morph determination

Immigrants landing on cereals are assumed to mature and produce nymphs as soon as they settle on cereals, while apterous adults, which develop in the field, have to pass through a pre-reproductive delay (see Chapter 3). Alatae and apterae have a marked difference in reproductive rate (Wratten, 1977). Reproduction also depends on temperature and crop growth stage (Dean, 1974b; Wratten, 1978; Watt, 1979 & see Chapter 3). The reproductive rate of apterae is calculated as an average of those at 10, 15, 20 and 25°C (Dean, 1974b) and is 0.00839 nymphs/hourdegree/apterous adult. The rate is assumed as the rate on winter wheat but is modified by 2/3 for the period before the start of anthesis (G.S. 60) (see Chapter six), and between early milk (G.S. 73) and early ripe (G.S.83), and modified by 4/5 for the period between the start of anthesis and early milk stage (Thornback, 1983). Apterae are more fecund than alatae, producing 27.42% more nymphs (after Wratten, 1977). Alate reproduction rates, therefore, are calculated from the apterous rates multiplied by 0.7848.

The reproductive rate obtained on winter wheat seedlings in this study is 0.00614 nymphs/hour-degree/adult. This rate is

used as an alternative to the above from the literature in the model. Modifications of this rate on crop growth stage and morphs are done as above.

Nymphs born on cereals are either apteriform or alatiform. The morph of an aphid is determined at birth in many aphid species (Dewar, 1977) which is also used in the model. The percentage of alatiform nymphs (P_n) born from the aphid population on cereals is dependent on aphid density (AP_{dn}) and crop growth stage (crstage) on *S. avenae* (Carter *et al.*, 1982);

$$P_n = -27.189 + 0.026AP_{dn} + 0.847\text{crstage} \qquad (4.23)$$

This relationship is also used in this model and is reasonable for *M. dirhodum* from the simulation study (See Chapter 5).

4.2.6 Crop development model

Crop growth stage affects the population growth of *M. dirhodum* (see Chapters 1 and 3). Therefore a crop growth stage submodel was included in the aphid model. The decimal code of crop growth stage (Zadoks *et al.*, 1974) was used in the model. Carter (1985) developed a polynomial equation (4.24) to describe the relationship between crop growth stage and the accumulated physiological time above a crop development threshold (6°C):

$$\text{crstage} = 26.336 + 0.173\text{tot} - 0.000125\ (\text{tot})^2 \qquad (4.24)$$

4.2.7 Insecticide

Insecticide treatments are incorporated to study effects on

aphid population development. The insecticide can be applied up to three times in the model. There is little information on insecticide persistence in the field (Rmr_{Tap}, mortality rate). Therefore, an exponential decay (Fig. 4.8) is used with maximum and minimum mortality rates (R_{pp} and R_{bb} respectively) set arbitrarily at 90% and 25% respectively. If the mortality rate falls below 25%, the rate is set to zero.

$$Rmr_{Tap} = R_{pp}e^{**((\log(Rbb)/Lgt)*Tap)} \qquad (4.25)$$

where Lgt is the period of the insecticide persistence; Tap is the time after spray.

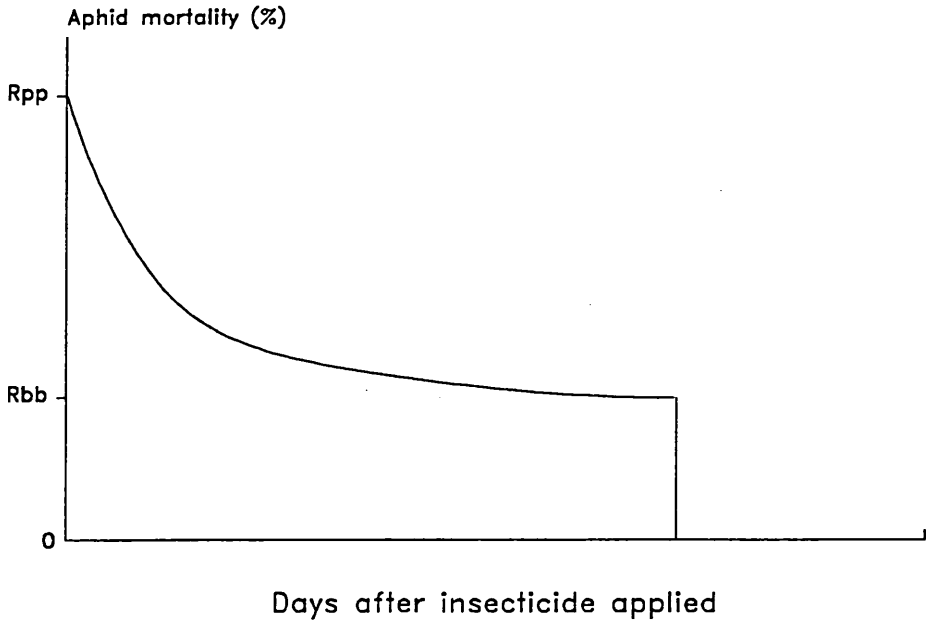


Fig. 4.8 Relationship between insecticide persistence and period after it is applied (R_{bb} is the lowest and R_{pp} the highest mortality).

A relationship derived from this experimental study is incorporated in the model as the alternative (see Chapter 3)

4.2.8 Crop yield loss

The rate of aphid damage is measured as a proportion of the potential yield per aphid unit per day (see Equation 4.28) and depends on crop growth stage (Table 4.3) (Wratten *et al.*, 1979; Lee et *al.*, 1981 and Holt *et al.*, 1984). When the crop development is before the start of stem elongation (G.S. 41), it is assumed that the rose grain aphid does not cause yield reduction or the damage is compensated for by the crop (Wratten *et al.*, 1979). The data from Holt *et al.* (1984) is used for the period between the start of stem elongation (G.S. 41) and the middle of inflorescence (G.S. 55), because the damage might occur in the late infestation due to the long infestation periods in these experiments. The values for other periods were obtained by calculating the mean from various data sets.

Yield loss in proportion to the potential yield was calculated daily (Equation 4.26) and depended on the damage rate (Rl_i) and aphid units (Ap_i) on the day.

$$L_i = Ap_i Rl_i \qquad (4.26)$$

These daily values are accumulated to give the total yield loss (Tl_i) up to that day (Equation 4.27). The aphid units in a day were calculated as in equation 4.28 (see Chapter 1).

$$Tl_i = \Sigma L_i \qquad (4.27)$$

$$Ap_i = (\Sigma Nu13_i)/3 + \Sigma(Nuap4_i + Nuap_i + Nual4_i + Nual_i) \quad (4.28)$$

where $Nu13_i$, $Nuap4_i$, $Nuap_i$, $Nual4_i$ and $Nual_i$ are numbers of individuals in the first to third instar, the fourth apterous instar and apterous adult, and the fourth alatiform instar and alate adult respectively.

Table 4.3 Yield loss as a proportion of the potential yield per aphid unit day

Crop stage	Proportional yield loss	Reference or assumption
<G.S. 40	0.0	assumption
G.S.≥40 - <55	1.556×10^{-4}	Holt *et al.* (1984)
G.S.≥55 - <60	3.765×10^{-4}	Wratten *et al.* (1979)
G.S.≥60 - <70	4.87×10^{-4}	Lee *et al.* (1981)
G.S.≥70 - <77	3.83×10^{-4}	Holt *et al.* (1984)
G.S.≥77 - <83	1.92×10^{-4}	Holt *et al.* (1984)
≥G.S. 83	0.0	assumption

4.2.9 Control strategies

Three control strategies against *M. dirhodum* are considered: non-control, prophylactic control and control based on a forecast. The economics of these strategies depend on the aphid population levels on crops, cost of control (George & Gair, 1979), the expected yield, the probability of an outbreak (P_{ot}) and the accuracy of any available forecast (P_{fr}) (Watt, 1983). Profitability of these strategies is compared at particular

times when control decisions have to be made. The prophylactic control, here, was defined as crop growth stage treatment.

The economics of the non-control and prophylactic control strategies (B, £/ha) are presented as functions of aphid damage (L_{ap}), expected yield (y_e), the cost of control (C_{ctl}), wheeling loss (w_{ls}) and grain price (y_{pr}) if the probabilities of an outbreak or non-outbreak are 100% (Table 4.4).

Table 4.4 A payoff matrix of non-control and prophylactic control strategies under non-outbreak and outbreak situations

	Non-control	Prophylactic
Non-outbreak	$B_{nn} = y_e * y_{pr}$	$B_{ny} = y_e * y_{pr} * (1 - w_{ls}) - C_{ctl}$
Outbreak	$B_{yn} = y_e * y_{pr} * (1 - L_{ap})$	$B_{yy} = y_e * y_{pr} * (1 - w_{ls}) * (1 - Ls_{ctl}) - C_{ctl}$

Where Ls_{ctl} is the damage caused by the aphid population after an insecticide application.

Aphid outbreaks only occur occasionally and forecasting systems are unlikely to be perfect in their accuracy (Watt, 1981). Therefore, the comparison of these strategies should take these elements into account. The economics of these strategies in financial values can be written:

Non-control: $$C_{bn} = B_{yn}P_{ot} + B_{nn}(1 - P_{ot}) \quad (4.29)$$

Prophylactic control: $$C_{pc} = B_{ny}(1 - P_{ot}) + B_{yy}P_{ot} \quad (4.30)$$

Control based on forecast: $C_{fc} = B_{nn}(1 - P_{ot})P_{fr} + B_{yy}P_{ot}P_{fr} + B_{ny}(1 - P_{ot})(1 - P_{fr}) + B_{yn}P_{ot}(1 - P_{fr})$ (4.31)

The three strategies are compared by subtracting from each other when a decision is needed to decide at a particular crop growth stage:

$C_{pc} - C_{bc}$; $C_{fc} - C_{pc}$ and $C_{fc} - C_{bn}$

4.2.10 Output

All outputs are formatted and headings are added except where data are used for graphs. Total aphid density, numbers of 1st to 3rd instar nymphs, 4th instars and adult apterae and alatae, crop growth stage, daily and accumulated yield loss and profitability of insecticide treatment and comparison of the three control strategies are output at noon, each day (Output 1, Fig. 4.3). At the end of the simulation, all input data are printed to ensure that the model has read the data correctly (Output 2, Fig. 4.3).

CHAPTER FIVE: SIMULATION RESULTS

5.1 Introduction

Four contrasting years were used to validate the model: 1979, 1985, 1986 and 1987 at Rothamsted, Harpenden, England (latitude, 51). Large numbers of migrants of *M. dirodum* were caught in suction traps and high densities of the aphid were recorded on crops in Britain in 1979 (Taylor *et al.*, 1980). The aphid density in 1985 was also high but lower than that in 1979. Numbers of the aphid were below damaging levels in the other two years.

Verification of the model was done. Variables in the model were checked to ensure that they worked in the expected manner.

The model was run with time steps ranging from one hour to 12 hours. The predictions of the aphid population in 1979 from these simulations were similar (Fig. 5.1). But the time of executing the model was eight times faster at 12 hours (9.82 seconds) than at one hour (1.4 minutes). Therefore all further simulation studies were done using the 12 hour time step.

5.2 Source of aphid field data at Rothamsted

1979

Field data were from a multidisciplinary wheat experiment (Rothamsted Report, 1980) and an integrated aphid control study

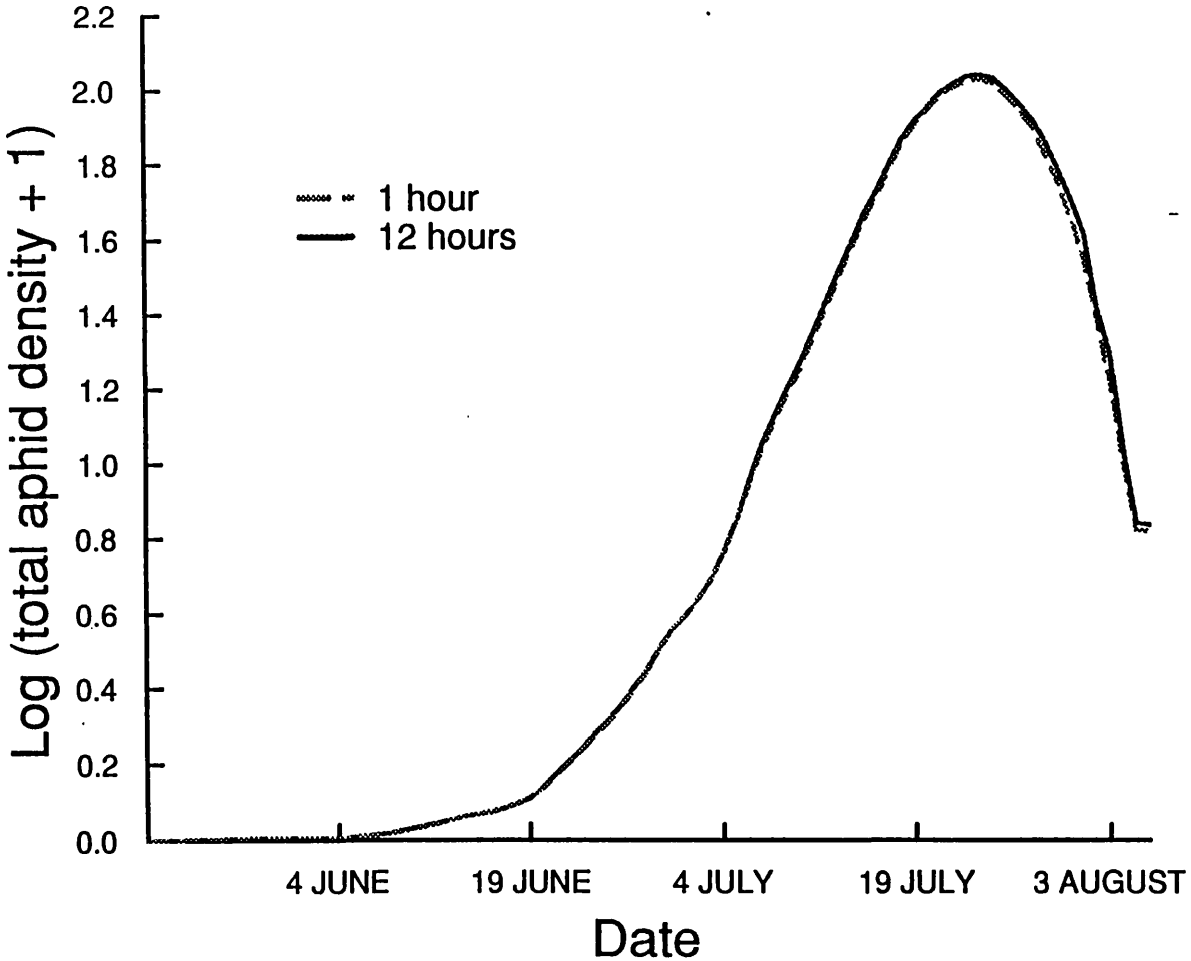


Fig. 5.1 Simulated aphid populations from the model in 1979 at time steps of one and 12 h.

(Dean *et al.*, 1980). The multidisciplinary experiment had eight treatments (make of drill, irrigation, sowing dates, different levels of nitrogen, timing of nitrogen inputs, autumn pesticide, summer pesticide and fungicide) (total 134 plots). Aphid densities were sampled in plots without summer pesticide treatment on 25 June, 10, 16 and 24 July on 25 shoots per plot. These aphid densities were then calculated according to early or late sown plots, and the densities for each instar and adult alates and apterae were also calculated from the samples. Finally, the aphid densities in plots sprayed with summer pesticides were also sampled. The integrated aphid control study had four treatments (control, aphicide, biological control and multichemical control) replicated three times (12 plots). The aphid densities were from samples on 10 shoots per plot in the control treatment. The cultivar in both studies was Hustler.

1985

Aphid densities were from an aphicide persistence study (Carter *et al.*, 1989). Treatments were single applications of various aphicides on two occasions. The total aphid densities were obtained from eight plots receiving no aphicides.

1986

Total aphid densities were estimated from 12 plots receiving no aphicide in an aphicide persistence study (Carter *et al.*, 1989).

1987

The aphid data were extracted from the field experiment described in Section 2.2 (Table 2.8).

5.3 Validation of the model for four years

5.3.1 1979

The model slightly underestimated the field populations early in the season but predicted the observed data well later in the season in both the early and late sown crops (Fig. 5.2 A and B). The predictions were slightly better in the latter. The model also predicted the date on which the maximum density was observed in both early and late sown cereals (Table 5.1). After the peak density, the predicted population declined rapidly as the crop became unfavourable to aphid growth. However, there were no further aphid counts after the maximum number was observed in the field.

The model overestimated the field aphid population in the integrated aphid control study. However, the dates on which the maximum number was predicted and observed in the field were similar (Fig. 5.3).

The model predicted the resurgence after the first aphicide was applied but the peak density of the resurgence was lower than the maximum number observed in the field (Fig. 5.4). The observed field population remained high while the population from the model decreased to a much lower level after the second aphicide application.

The model, when it used data on development, reproduction and alate production from this study, predicted the aphid

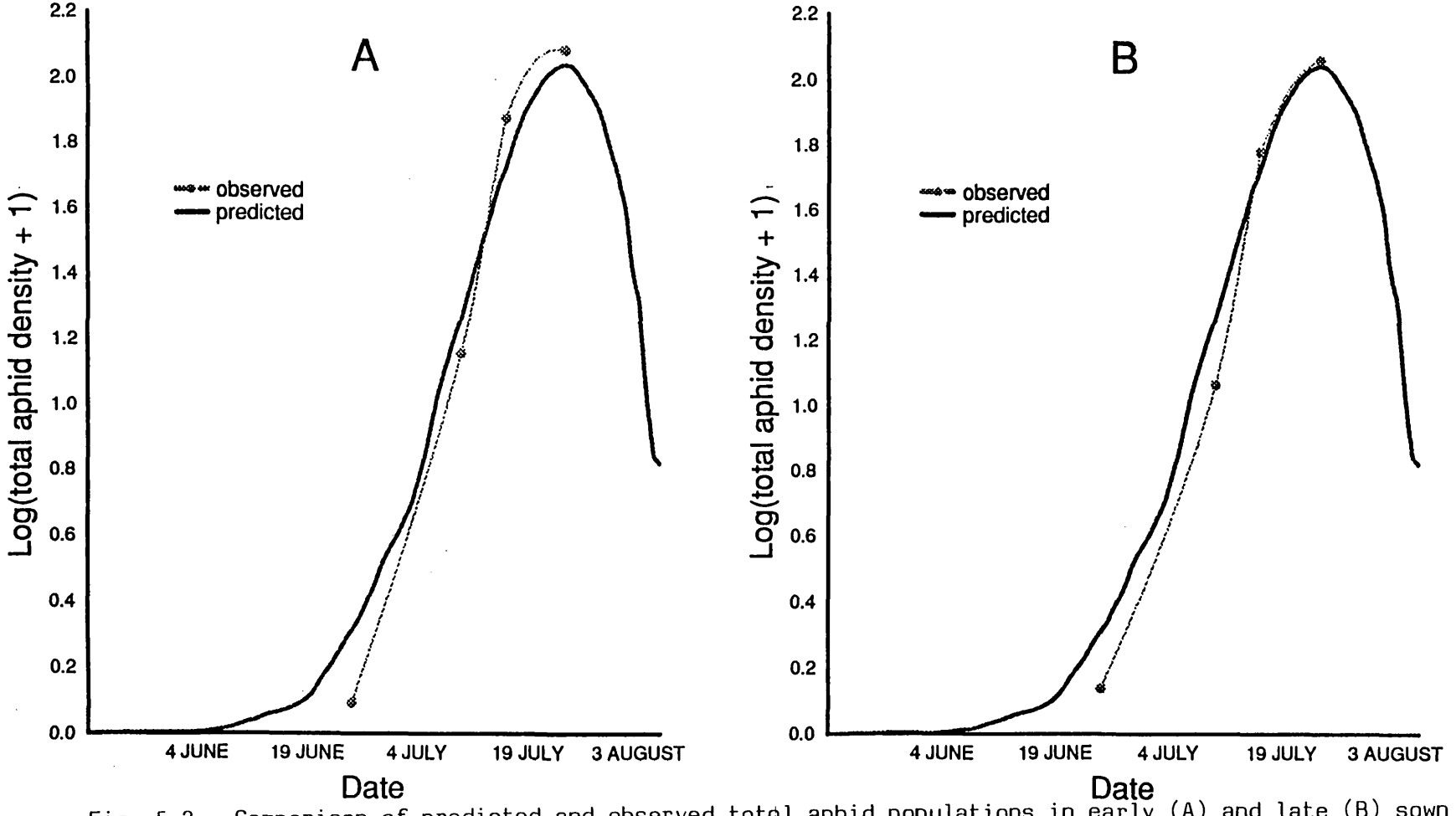


Fig. 5.2 Comparison of predicted and observed total aphid populations in early (A) and late (B) sown plots in 1979.

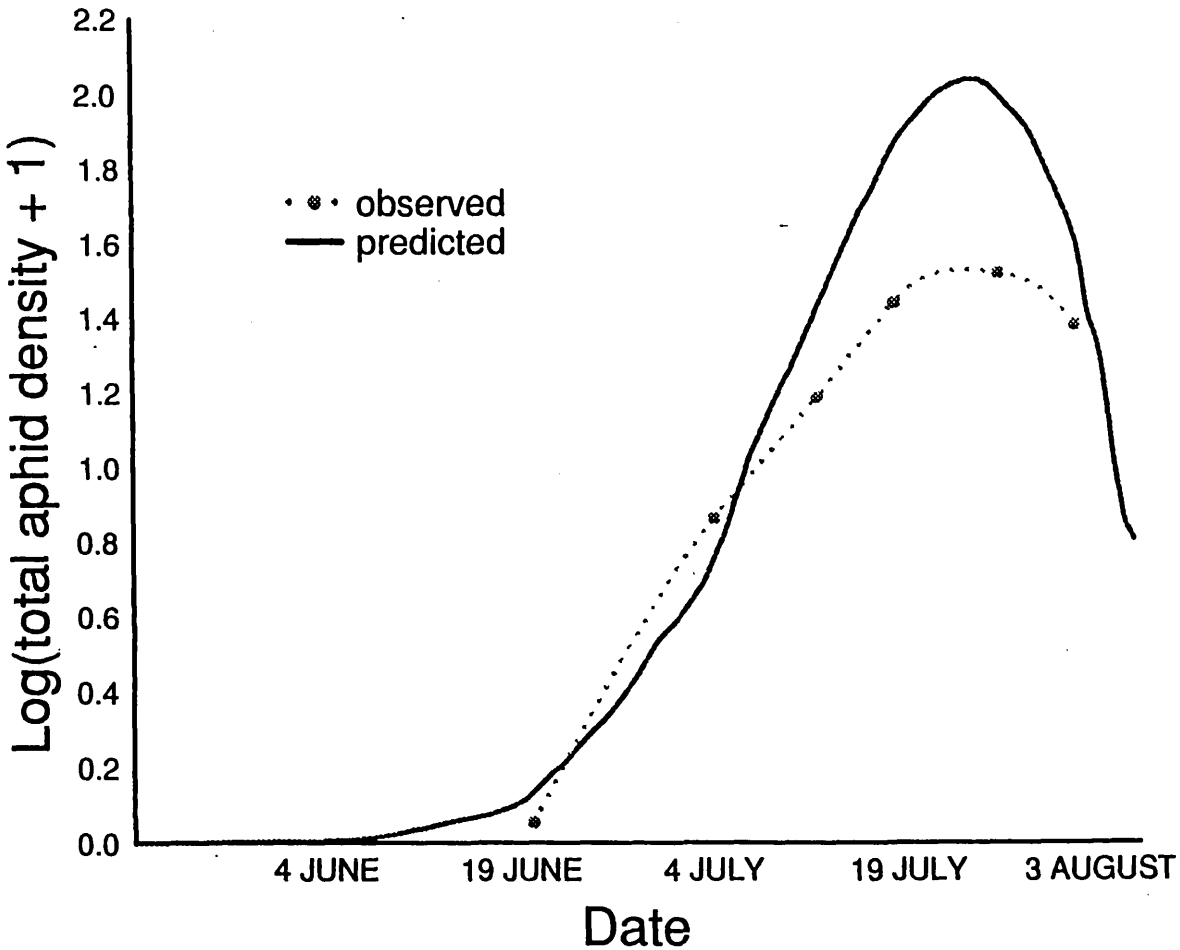


Fig. 5.3 Comparison of predicted and observed total aphid populations from the integrated control study in 1979

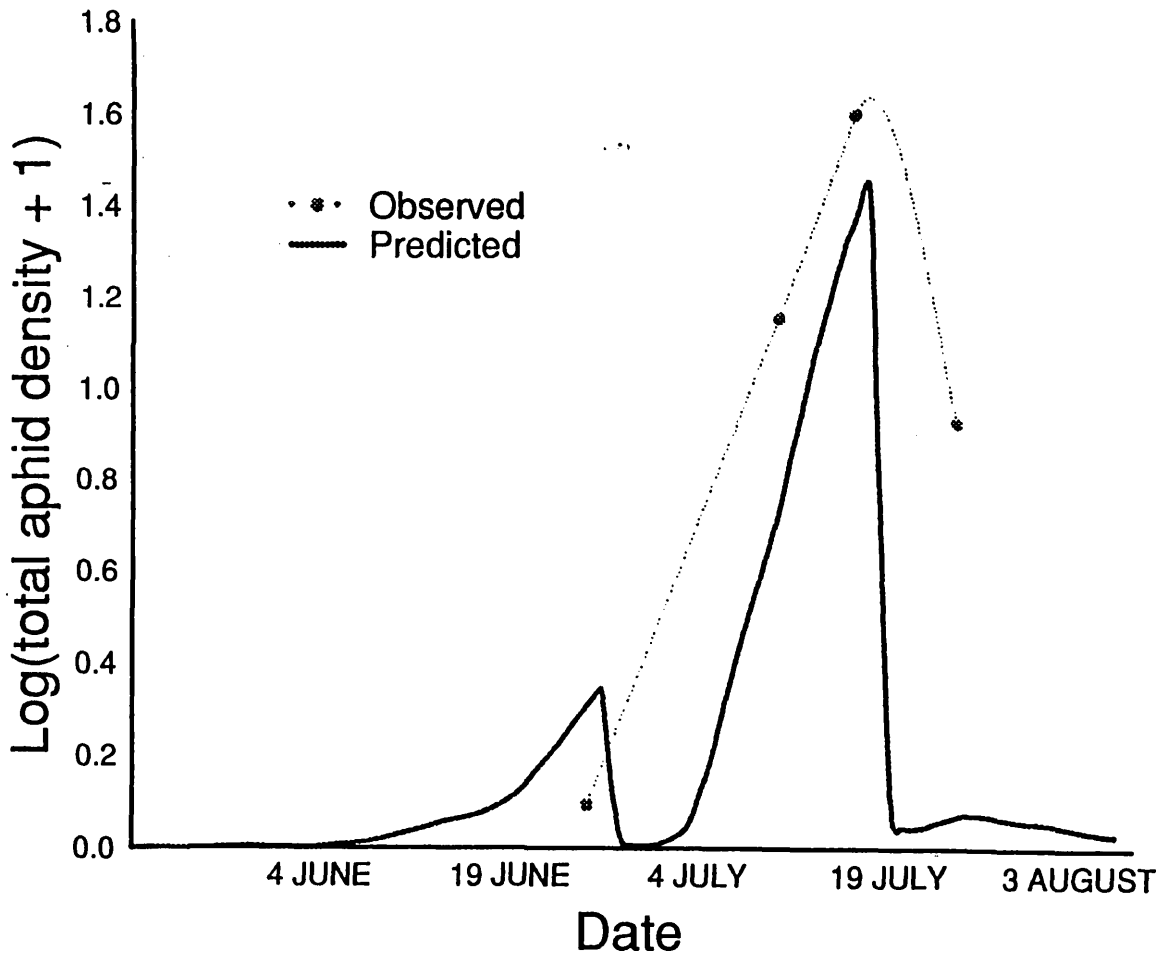


Fig. 5.4 Comparison of predicted and observed total aphid populations after aphicides were applied in the multidisciplinary experiment in 1979.

population better early in the season than that using these data from literature. The maximum density was slightly less than that using the data from literature and also slightly underestimated the observed maximum density (Fig. 5.5).

The model predicted the total nymphal density well in the early sown cereals because most of the aphid population in the field and in the model consisted of nymphs (Fig. 5.6 A). The model also accurately predicted the apterous adult density, especially early in the season (Fig. 5.6 B). The prediction of the alate adult density was higher than that observed until the predicted maximum density when the predicted population declined early (Fig. 5.6 C). However, the total alate density was low (Table 5.1).

5.3.2 1985

The model predicted the increase of the total aphid population in the field early in the season (Fig. 5.7 A). But it overestimated the observed density later in the season by 45 aphids/shoot at the peak density (Fig. 5.7 A). The date of the maximum density from the model was seven days later than that on which the maximum density was observed in the field (Table 5.1).

6.3.3 1986

The model did not predict the initial field population (which started 18 days later than the model) and overestimated the maximum density in the field (Fig. 5.7 B). However, these densities from the model and the field were low (the maximum was 8/shoot in the model and 2/shoot in the field).

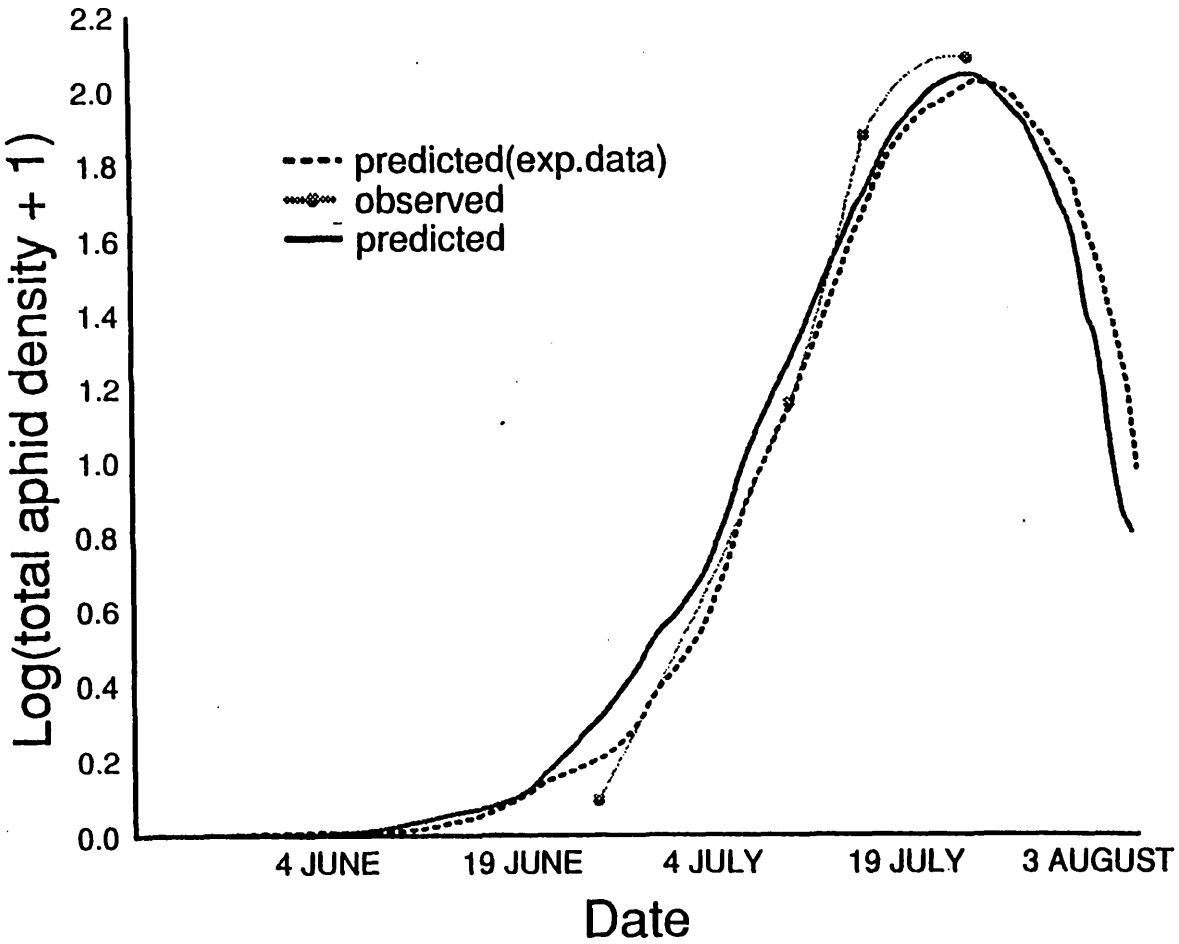


Fig. 5.5 Comparison of predicted and observed total aphid populations using development, reproductive rate and alate production rate data from this study in the model in 1979.

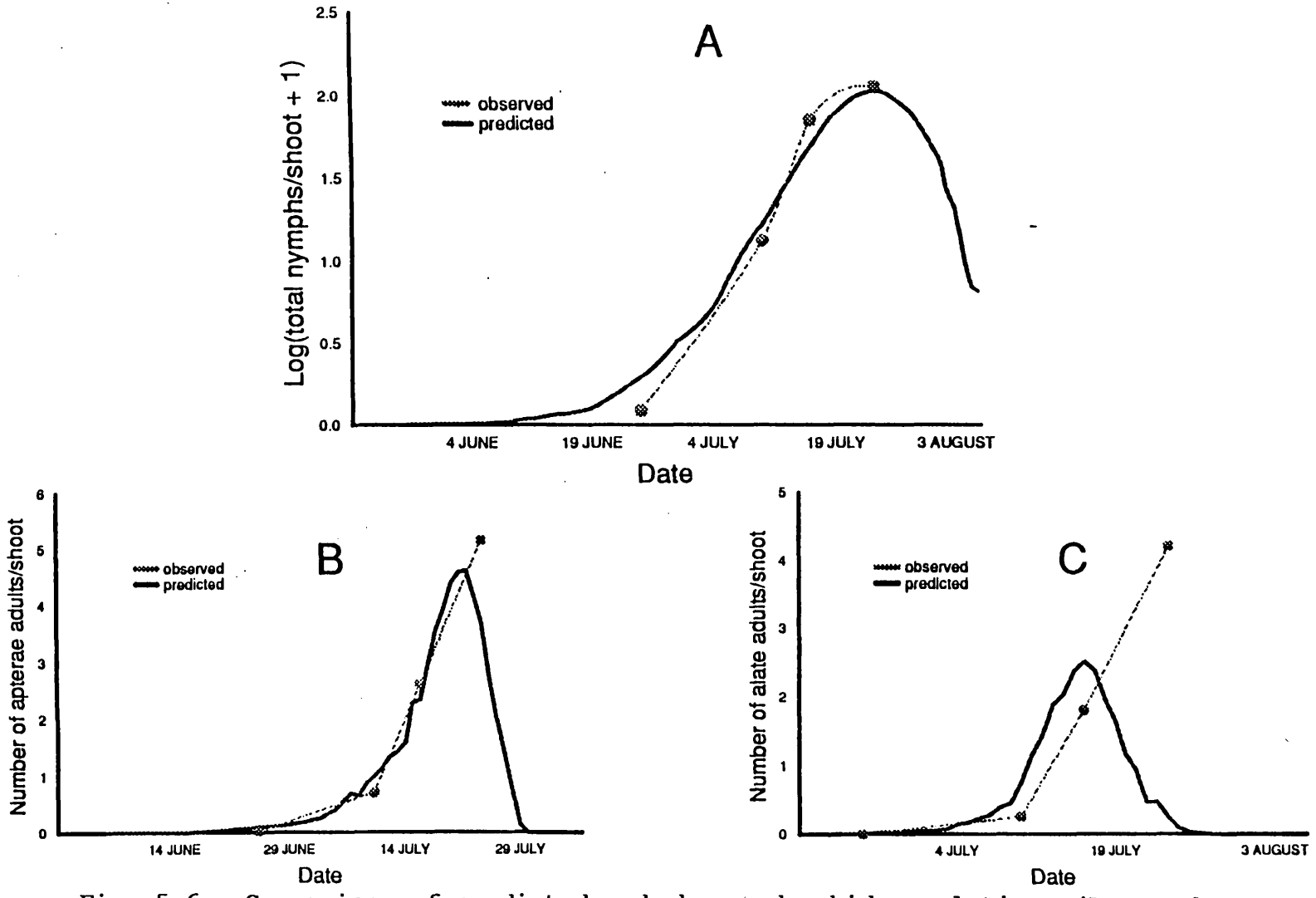


Fig. 5.6 Comparison of predicted and observed aphid populations (A, nymphs; B, apterous adults and C, alate adults) in early sown plots in 1979.

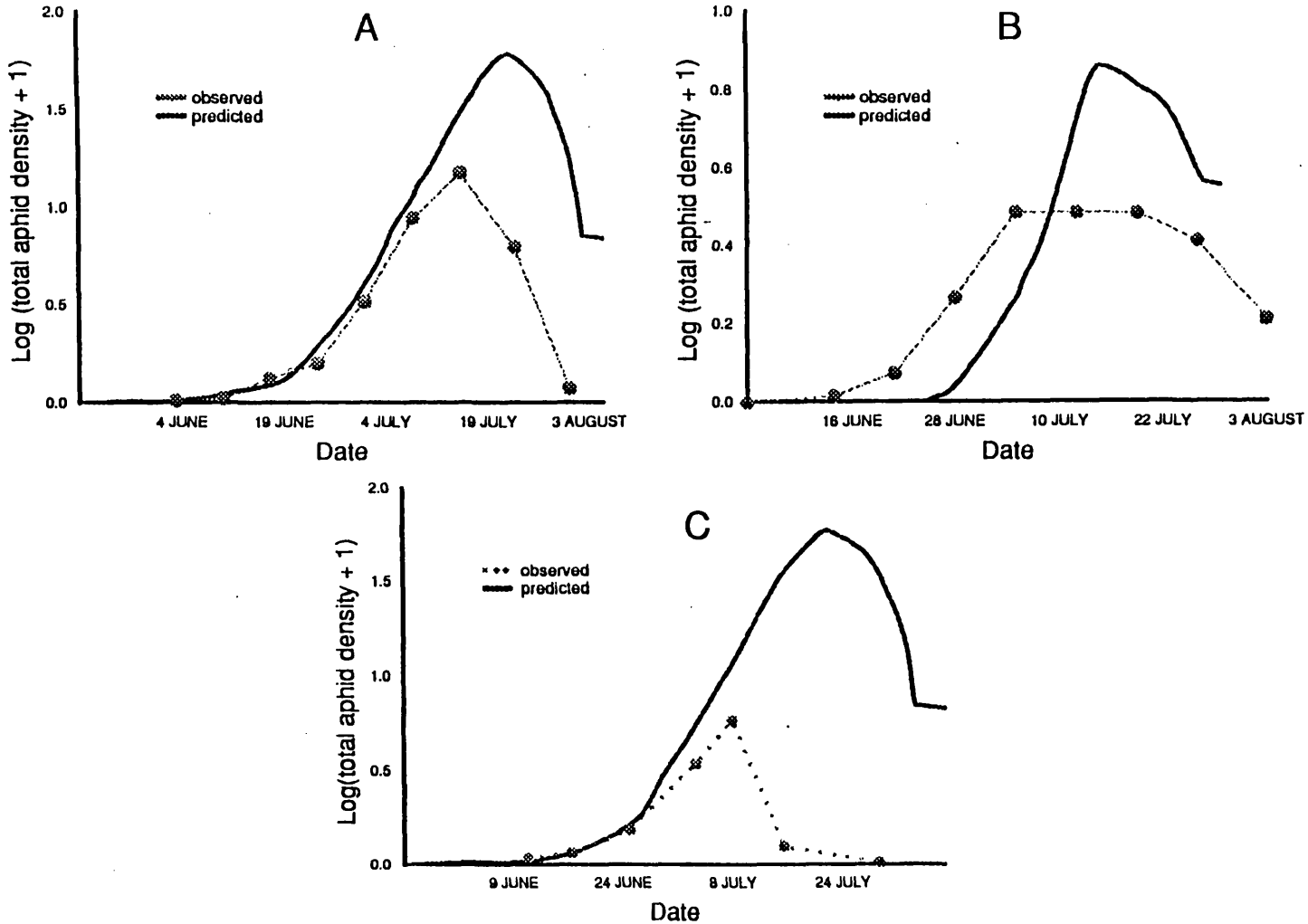


Fig. 5.7 Comparison of predicted and observed total aphid populations (A), in 1985; (B), in 1986 and (C), in 1987.

6.3.4 1987

The densities predicted by the model were similar to those observed in the field early in the season. Then the density was predicted to increase more rapidly to a maximum of 51.3/shoot while the population observed in the field increased slowly to a maximum of only 4.85/shoot before decreasing 14 days earlier than predicted by the model (Fig. 5.7 C).

Table 5.1 A summary of model validation results for 1979, 1985, 1986 and 1987

		Model prediction		Field observation	
Year	Items	Peak date	Peak no.	Peak date	Peak no.
1979	Total	24 July	109.1	24 July	113.4
	Nymph	24 July	105.2	24 July	111.7
	Apterae	22 July	4.6	24 July	6.2
	Alate	16 July	2.5	24 July	4.2
Experimental data		25 July	104.8	24 July	113.4
1985	Total	22 July	59.0	15 July	14.2
1986	Total	17 July	8.0	7-21 July	2.1
1987	Total	22 July	51.3	8 July	4.9

5.4 Sensitivity analysis

Sensitivity analysis was done to gain an understanding of the aphid population dynamics in the aphid/plant system, and to evaluate the importance of the parameters in the model, which

have important effects on the aphid population. Ten parameters were analyzed: temperature, development length, initial crop stage, reproduction, survival, alate production, immigration, initial crop growth stage of the migration transformation (IMST), migration transformation period (IMPR) and insecticide persistence. The range of changes was set at a constant 20% more or less of the standard inputs of these parameters except some parameters where specified in particular sections. Two years, one outbreak year (1979) and one year when the observed field population was low (1987), were chosen for the sensitivity study and the results from these simulations were compared for each parameter.

5.4.1 Temperature

Temperature had an important effect on aphid population development (Fig. 5.8). A reduction of 20% in the daily maximum and minimum temperatures resulted in an increase of the aphid peak density of 210% in 1979 and 68% in 1987, and led to a delay in the peak density of ten days in 1979 and 13 days in 1987 (Table 5.2). In contrast, an increase of 20% in these temperatures led to a reduction in the peak density of 74.3% in 1979 and 70% in 1987, and resulted in earlier dates of the peak density (13 days 1979 and 12 days in 1987) (Table 5.2). In both years, the populations, when temperature had been increased or decreased, were maintained for less time after the peak density than that of the standard input (Fig. 5.8). A 20% reduction in temperature dramatically increased the yield loss, especially in 1979, while an increase of the same amount resulted in much less yield loss in both 1979 and 1987 (Table 5.2).

5.4.2 Development time

A 20% increase or decrease of the development time slightly decreased the peak aphid density in 1979 (Fig. 5.9 and

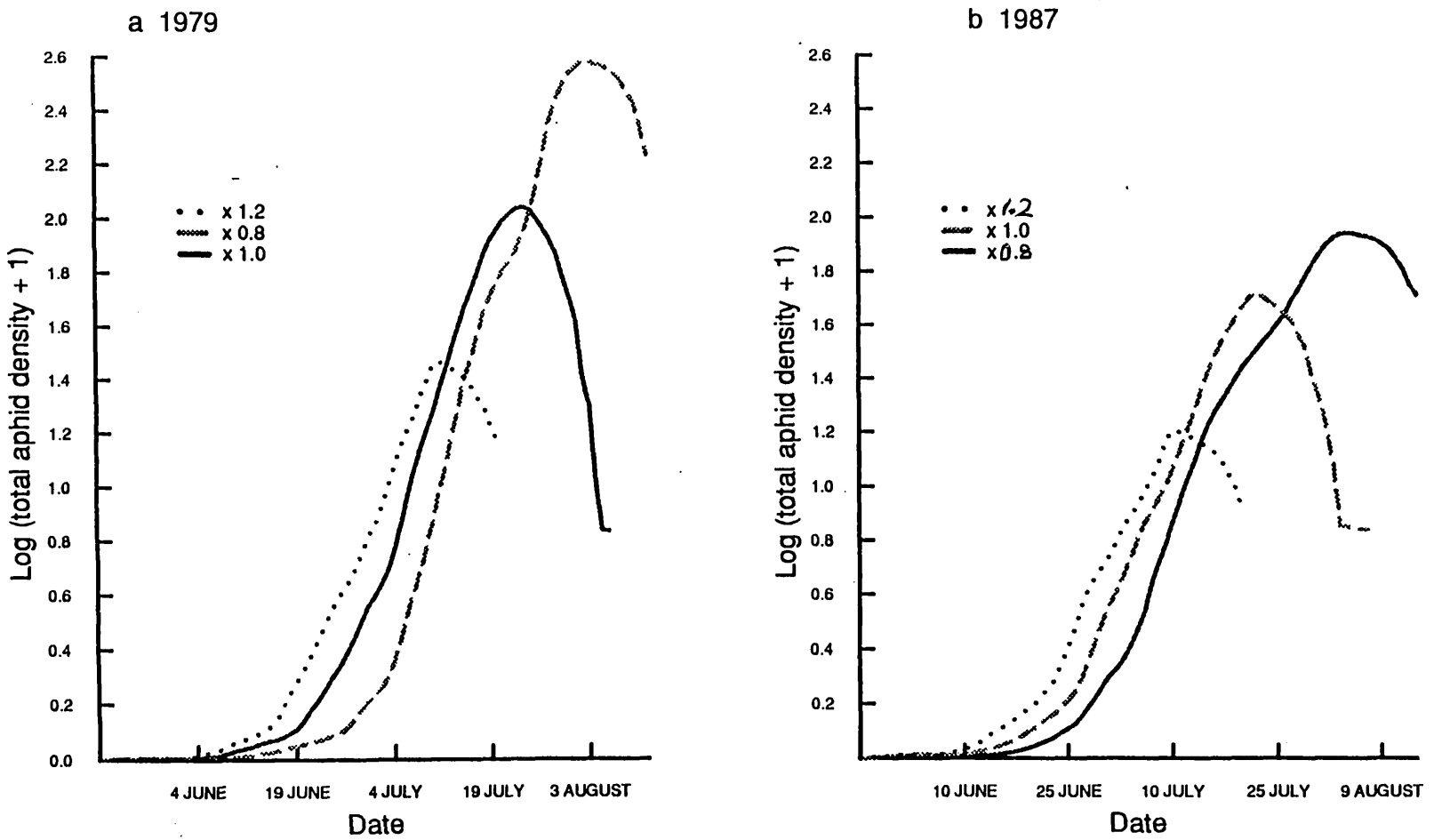


Fig. 5.8 Effects of changes in daily maximum and minimum temperature on predicted aphid population development.

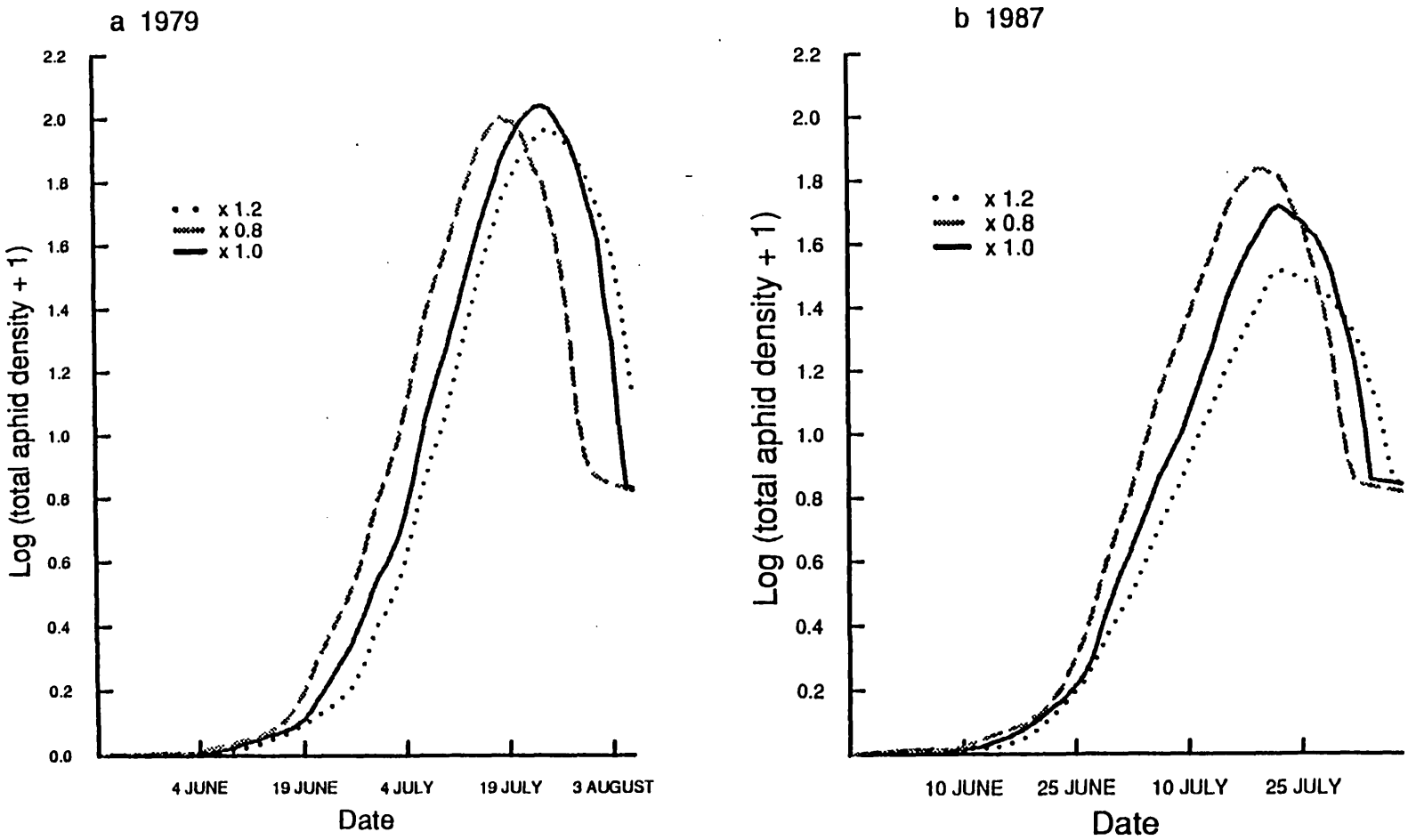


Fig. 5.9 Effects of changes in development time on predicted aphid population development.

Table 5.2). In contrast, an increase of 20% in the length caused a reduction of the maximum population density of 38.2% while a reduction of 20% led to an increase of 31.2% in the peak density in 1987. The change in the development time affected the dates of maximum densities in both years (Table 5.2). The 20% decrease led to earlier dates; 7 days in 1979 and 2 days in 1987. The 20% increase resulted in only a slightly later date of the peak density in 1979 (one day) but there was no effect in 1987 (Table 5.2). A 20% reduction in the development time resulted in 5.7% and 4% more yield loss while the 20% increase caused 3.7% and 1.7% less yield loss than that from the standard simulation in 1979 and 1987 respectively.

5.4.3 Initial crop growth stage

Changes to the initial crop growth stage did not affect the early increase phase of populations in either year (Fig. 5.10). However, a reduction of 20% in the crop growth stage increased the maximum density by 20% in 1979 and 70% in 1987. A 20% increase decreased the maximum density by 44.5% in 1979 and 64.3% in 1987. The earlier initial crop growth stage caused a slightly delayed peak density, one day in 1979 but five days in 1987. The later initial crop growth stage led to a slightly earlier peak density in 1979 (two days) and much earlier in 1987 (eight days). The 20% decrease in the initial crop stage led to 7.7% and 7.1% more yield loss while an increase of the same amount caused 7.1% and 3.2% less yield loss than that from the standard simulation in 1979 and 1987 respectively.

5.4.4 Reproduction

Changes in the reproductive rate affected slightly initial population development in both years (Fig. 5.11). An increase of 20% in the rate increased the peak density by 34.8% in 1979 and 67% in 1987 while a decrease of 20% in the rate resulted in a reduction of the peak density by 34.9% in 1979 and 49.3% in 1987 (Table 5.2). The increase or decrease in the reproductive rate

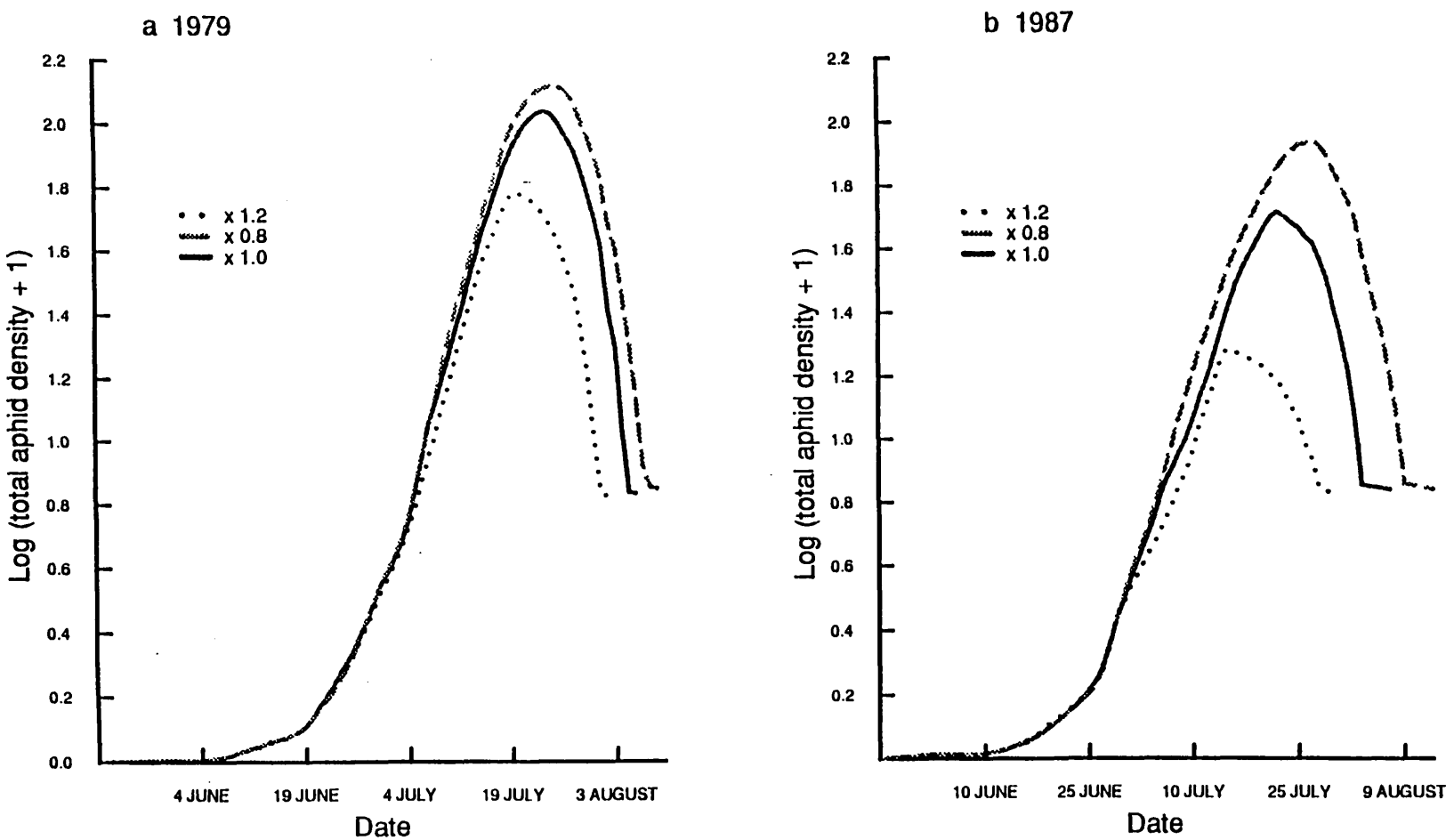


Fig. 5.10 Effects of changes in the initial crop growth stage on predicted aphid population development.

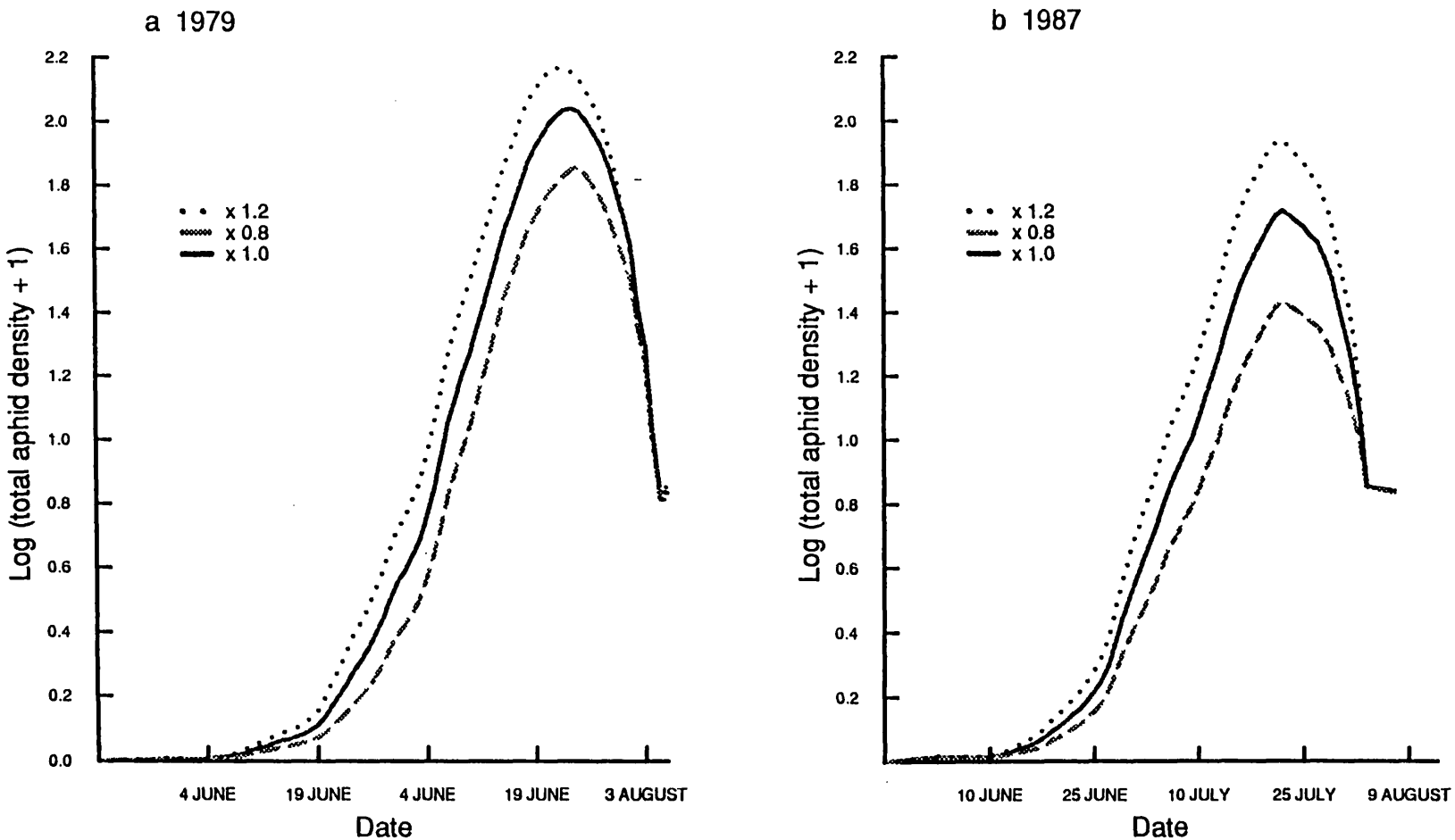


Fig. 5.11 Effects of changes in reproductive rate on predicted aphid population development.

by the same amount only slightly affected the date of the peak density in 1979 and had no effect in 1987 (Table 5.2). A 20% reduction in reproductive rate led to 4.5% and 2% less yield loss while an increase of the same amount resulted in 5.9% and 2.9% more yield loss than that from the standard simulation in 1979 and 1987 respectively.

5.4.5 Survival

Changes in survival rate affected the aphid population development at the start of the simulation (Fig. 5.12). An 10% increase of the survival rate on its standard value, 0.89, which was near the maximum survival rate (1.00) led to an increase of the peak density by 23.8% in 1979 and 41.7% in 1987. A 20% decrease of the standard rate decreased the peak density by 41.3% in 1979 and 51.1% in 1987. These changes slightly affected the date of the peak density in 1979 only (Table 5.2). A 20 % reduction in survival rate resulted in 5% and 2.3% less yield loss while a 10% increase caused 3.5% and 1.6% more yield loss than that from the standard simulation in 1979 and 1987 respectively (Table 5.2).

5.4.6 Alate production

Population densities were similar early in the season before the peak density was reached in both years (Fig. 5.13). However, an increase of 20% in the rate of alate production reduced the peak density by 19.4% in 1979 and 20.6% in 1987 while a reduction of 20% in the rate increased the peak density by 28% in 1979 and 23.5% in 1987. The effects of these changes on the date of peak density were slight in 1979 with no effect in 1987 (Table 5.2). An increase or decrease in alate production rate by 20% slightly decreased or increased yield losses (by 1%) in both years (Table 5.2)

5.4.7 Immigration

Changes in the immigration rate affected aphid population development from the start of the simulation in both years (Fig. 5.14). However, the increase or decrease of 20% only slightly increased or decreased the maximum aphid density by 11.1% or by

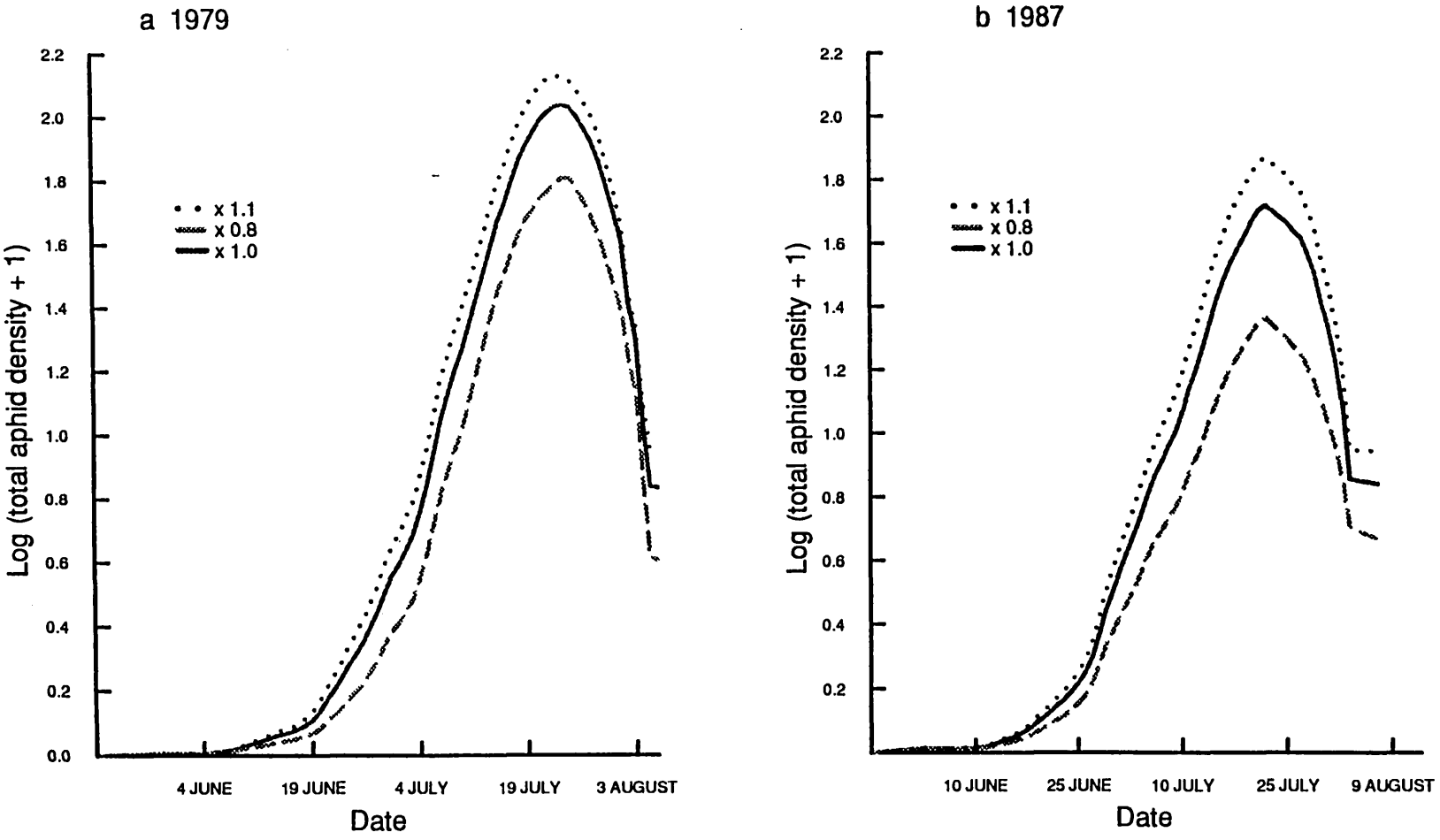


Fig. 5.12 Effects of changes in survival rate on predicted aphid population development.

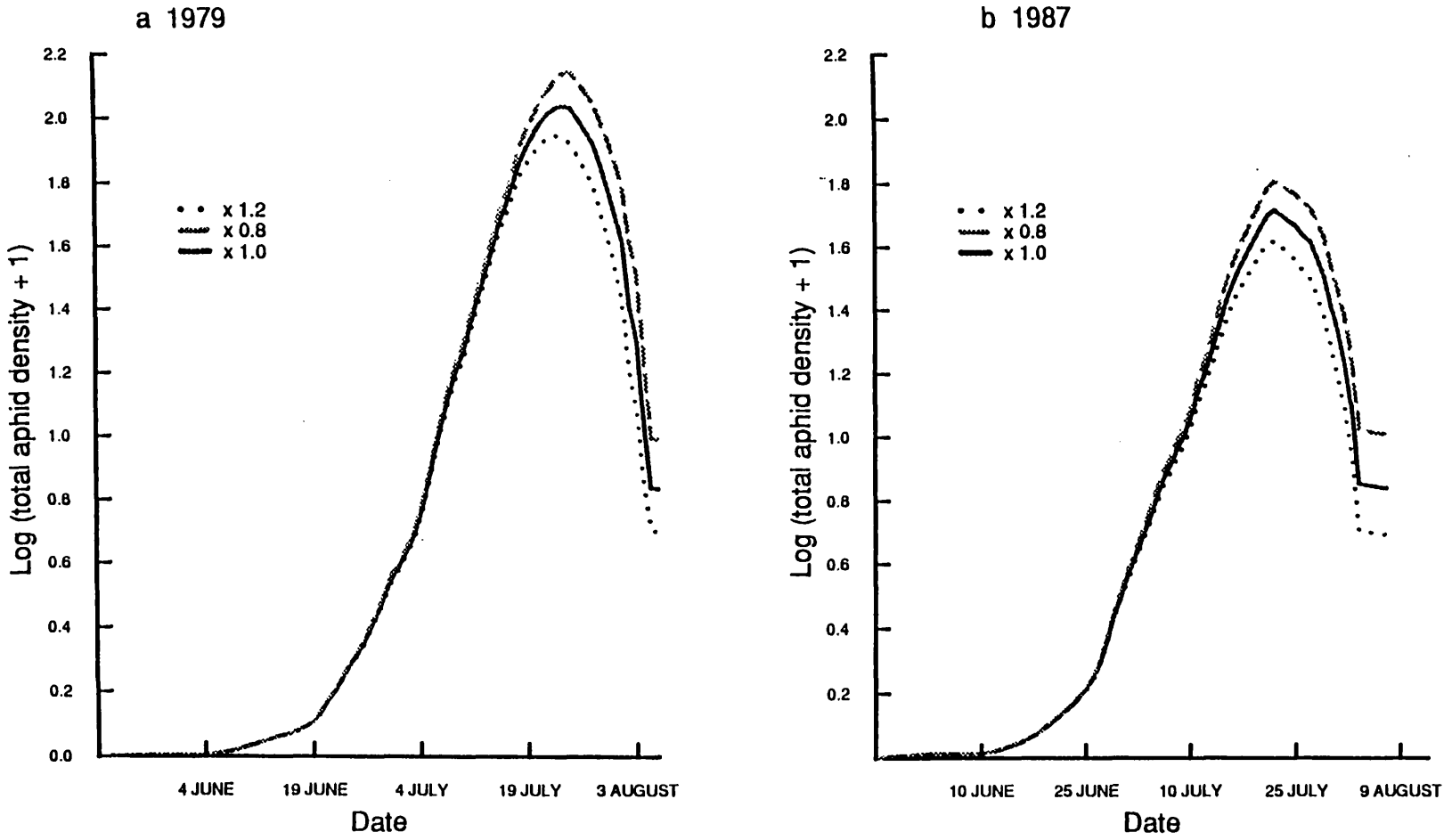


Fig. 5.13 Effects of changes in alate production rate on predicted aphid population development.

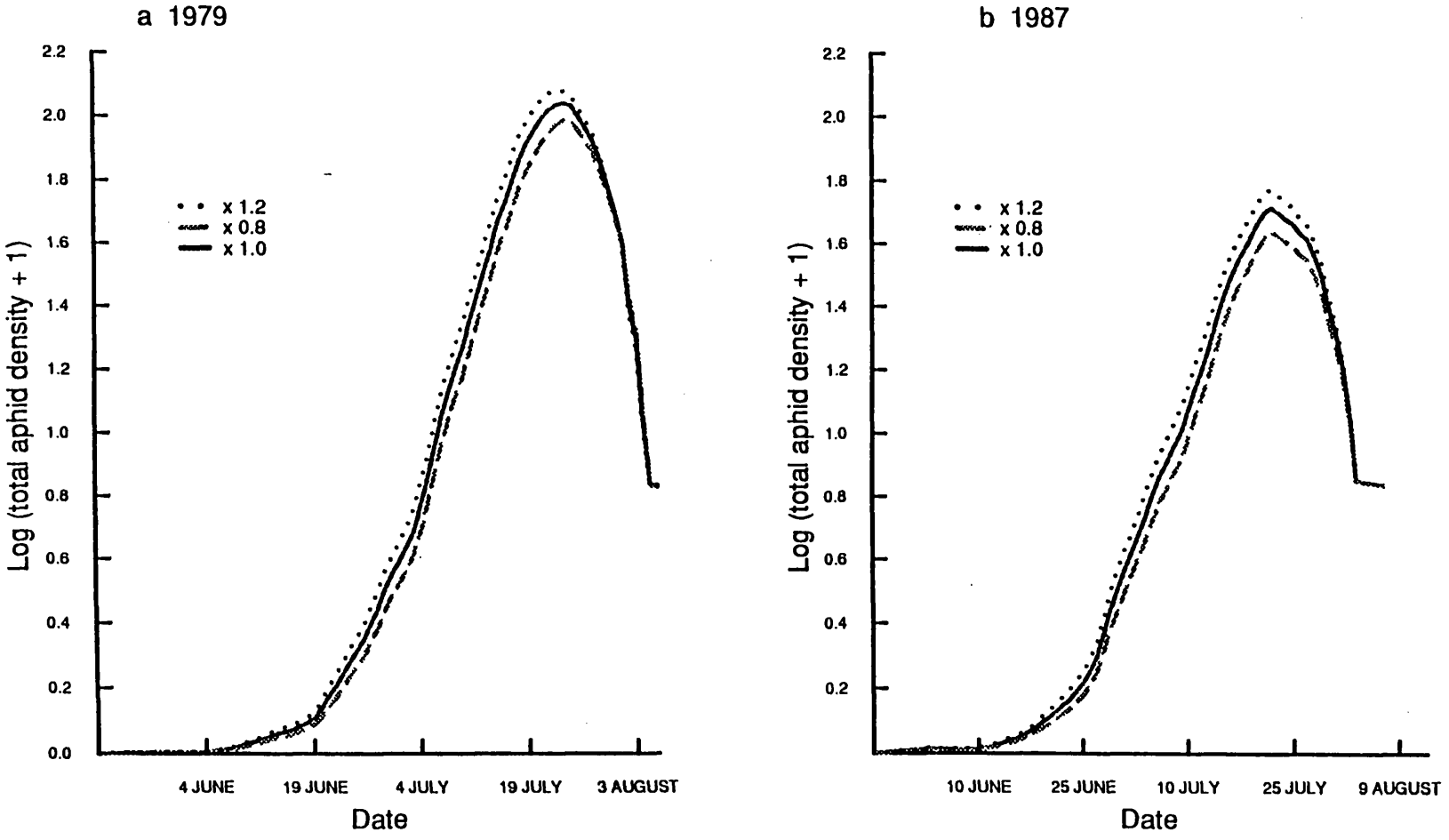


Fig. 5.14 Effects of changes in immigration rate on predicted aphid population development.

11.7% respectively in 1979, and by 14.7% or 16.0% respectively in 1987 (Table 5.2). These changes did not affect the date of the peak density in either year (Table 5.2). These changes only slightly affected the yield loss in both years (Table 5.2).

5.4.8 Initial crop growth stage for immigration transformation

The peak aphid density was increased by 22.4% in 1979 and 15.9% in 1987 and occurred one day later in 1979 when the transformation started 10 units of crop growth stage later (Fig. 5.15 and Table 5.2). When the transformation started 10 units earlier, the peak density was decreased by 29% in 1979 and 12.7% in 1987, and occurred one day later in 1979. The changes in this parameter slightly affected the yield loss in both years althoght a reduction of 10 units in crop growth stage led to much less yield loss in 1979 (Table 5.2).

5.4.9 The period of the immigration transformation

Population development and maximum aphid densities of the prediction for several transformation periods; G.S.0, 5 and 10 were slightly different in 1979 and similar in 1987 (Fig. 5.16 and Table 5.2) to the standard simulation. The dates of these peaks in each years were the same except for the period of 10 G.S. in 1979 (Table 5.2). The yield losses were similar to that in the standard simulation for each year (Table 5.2).

5.4.10 Insecticide persistence

The insecticide was applied once at the beginning of the milky ripe stage (G.S. 70). The maximum kill rate was 90% at the time of application and minimum rate 25% after a persistence period. The persistence was set at three levels; one, three and seven days. The population decreased to nearly zero immediately after the insecticide was applied in both years (Fig. 5.17). The population then recovered rapidly to a maximum which was half of the original population on 25 July when the persistence was one

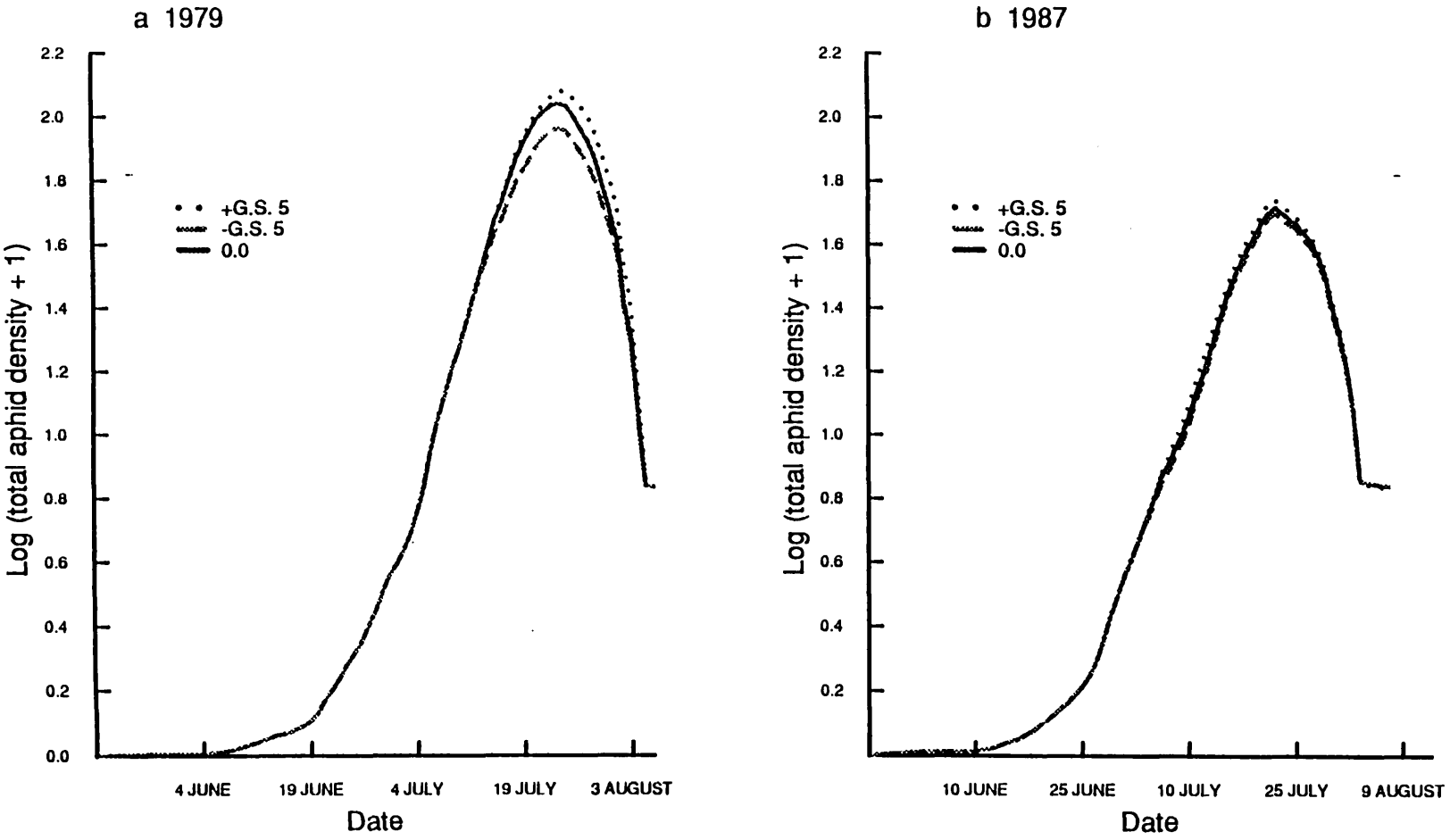


Fig. 5.15 Effects of changes in crop growth stage on predicted aphid population at which the immigration modification started.

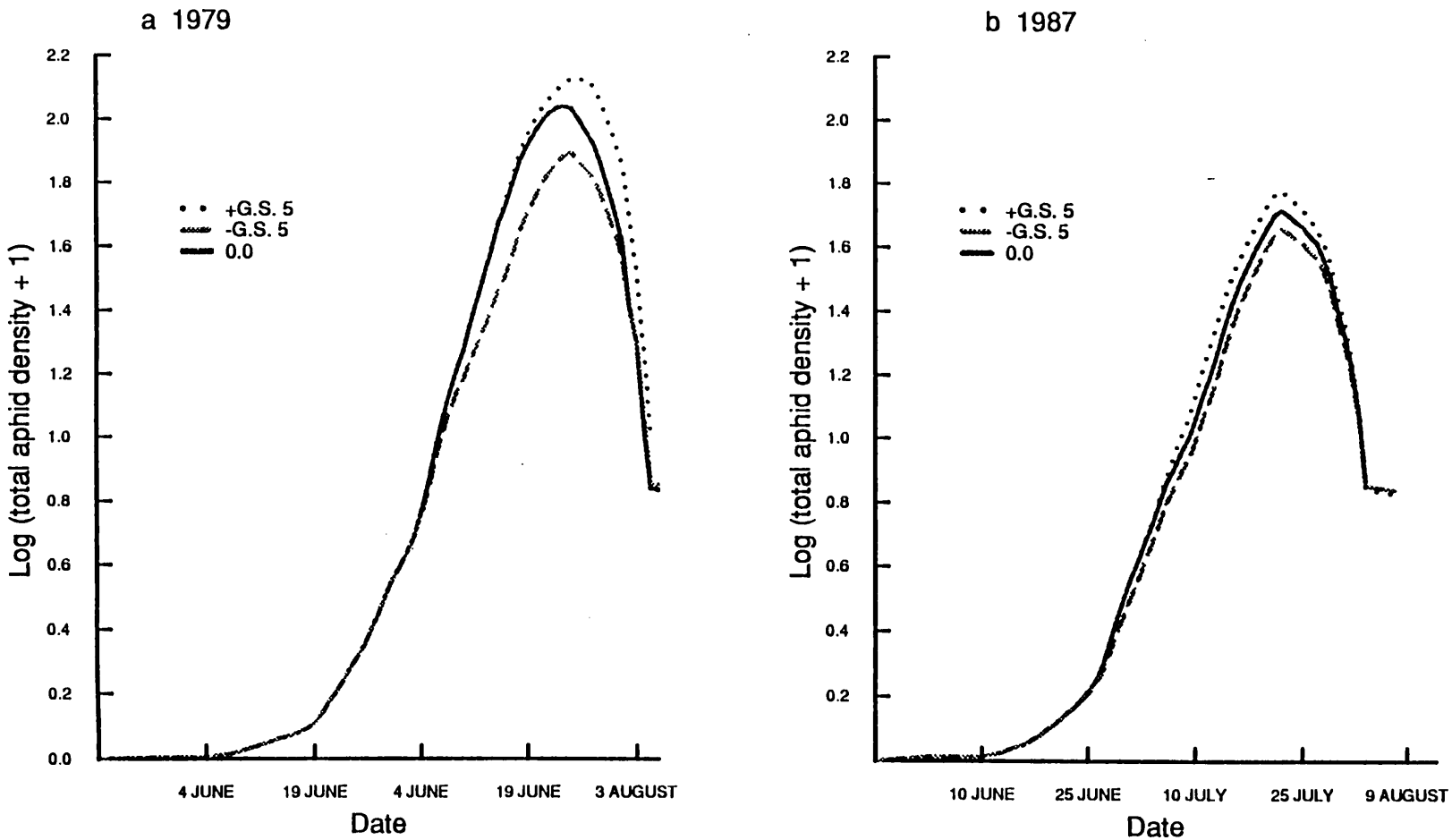


Fig. 5.16 Effects of changes in length of immigrationon predicted aphid population development .

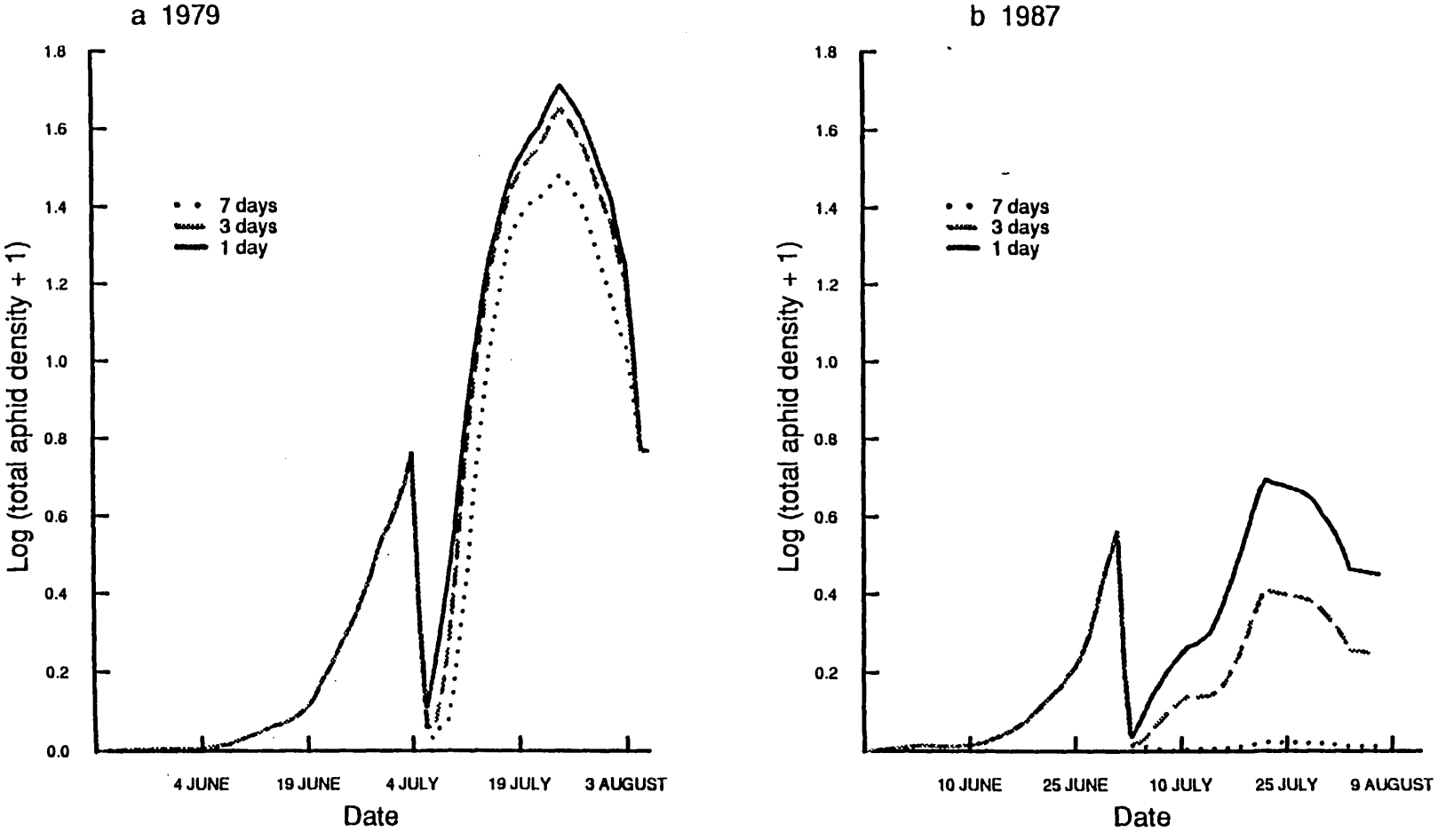


Fig. 5.17 Effects of changes in insecticide persistence on predicted aphid population development.

day, 44/shoot when at three days and 29.5 when it was seven days in 1979. However, in 1987, the population was reduced to a maximum of 3.95/shoot when the persistence was one day, 1.58/shoot when it was three days on 22 July and zero when the persistence was seven days (Fig. 5.17). The yield loss with longer insecticide persistence was only slightly lower than that with persistence of one day in both years (Table 5.2).

5.5 Yield loss and control studies

These studies were done on the aphid population in 1979 because the population was high enough to cause economic yield loss. Grain price was assumed to be £100 /t. Wheelling losses due to application of the insecticide were 3% of the potential yield (Entwistle & Dixon, 1987; Watt, 1983), and the cost of insecticide and labour was £13.5/ha (Anon., 1989). Data for the rest of the parameters in the model remained the same as in the previous simulations.

The final accumulated yield loss was 11.5% in 1979 which was used in the control-benefit analysis study. Most yield loss occurred from the late milk ripe (G.S. 77) to early dough (G.S. 82) when the crop had the highest aphid population density (Fig. 5.18).

Longer persistence of the insecticide increased the net return of control linearly (Fig. 5.19).

Profit was analyzed when the insecticide was applied once at different crop growth stages. Profit started to increase when the spray was applied at the beginning of anthesis (G.S. 60) to a maximum at middle milky ripe stage (G.S. 75) before decreasing

Table 5.2 Summary of sensitivity analyses

Year		1979			1987		
Parameters	criteria	peak date	peak no.	yield loss(%)	peak date	peak no.	yield loss(%)
Standard		24/7	109.1	11.5	22/7	51.3	4.5
Temperature	-20%	3/8	384	90.7	4/8	86.4	24.9
	+20	11/7	28	2.1	10/7	15.1	1.2
Development	-20%	17/7	100.7	17.2	20/7	67.3	8.4
	+20%	25/7	93.4	7.8	22/7	31.7	2.7
Initial crop growth stage	-20%	25-26/7	131	19.2	27/7	87.2	11.6
	+20%	20/7	60.5	4.4	15/7	18.3	1.3
Reproduction rate	-20%	25/7	71.1	7.0	22/7	26.0	2.5
	+20%	23/7	146.9	17.4	22/7	85.6	7.4
Survival rate	-20%	25/7	64.0	6.5	22/7	22.0	2.2
	+10%	23/7	135.0	15.0	22/7	72.6	6.1
Alate production rate	-20%	25/7	139.5	12.8	22/7	63.3	5.0
	+20%	23/7	87.8	10.3	22/7	40.7	3.9
Immigration	-20%	24-25/7	96.3	9.5	22/7	42.8	3.6
	+20%	23/7	120.0	13.4	22/7	58.8	5.3
Start G.S. of immigration transformation	-10	24/7	77.3	7.8	22/7	44.8	3.8
	+10	25/7	133.5	12.2	22/7	59.4	5.2
Period of transformation	-5	24/7	90.9	10.3	22/7	28.3	4.3
	+5	25/7	119.2	11.8	22/7	57.0	4.7
Insecticide persistence	one day	25/7	50.5	3.7	22/7	4.1	0.5
	3 days	25/7	44.1	3.1	22/7	1.6	0.4
	7 days	25/7	29.5	2.2	22/7	0.1	0.3

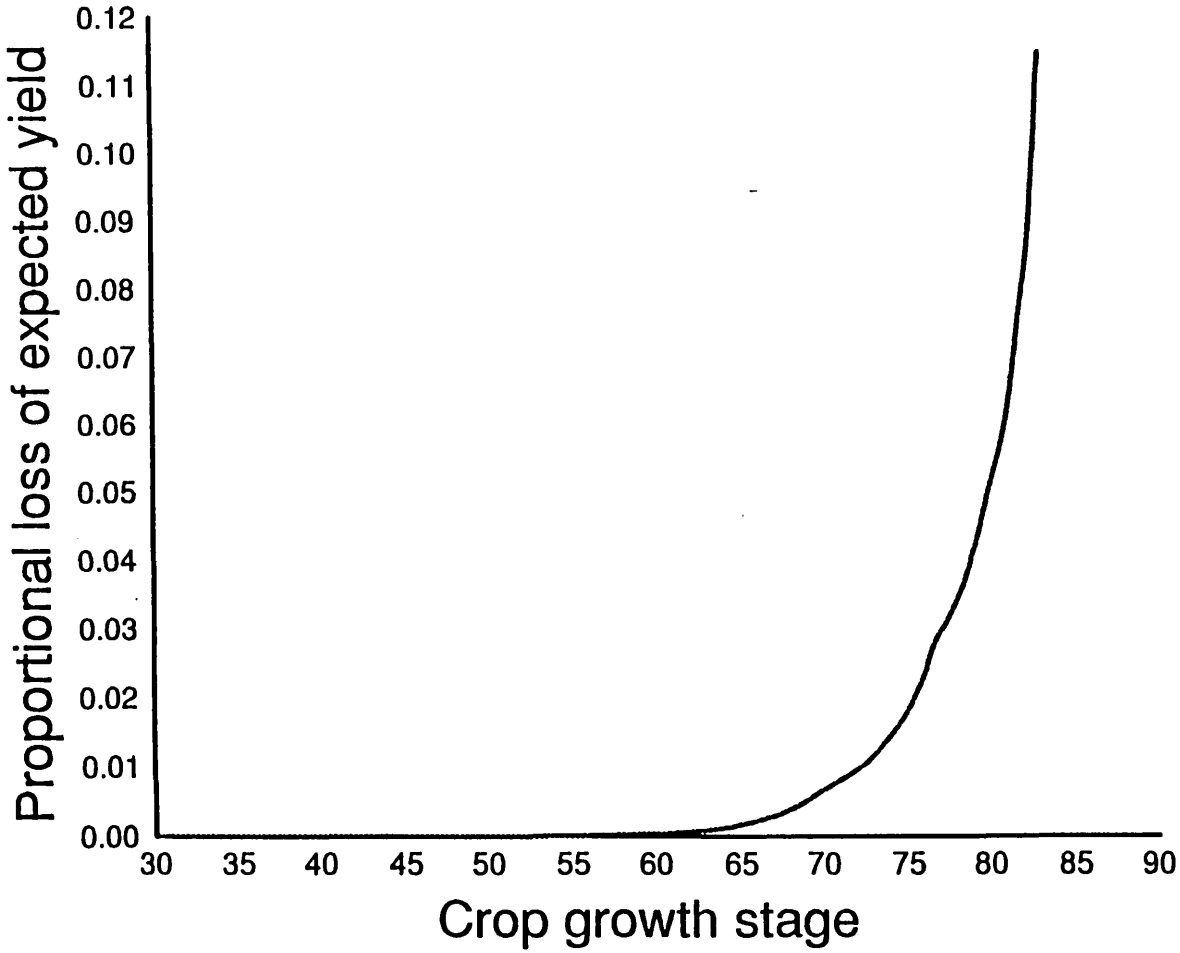


Fig. 5.18 Predicted accumulated yield loss in 1979.

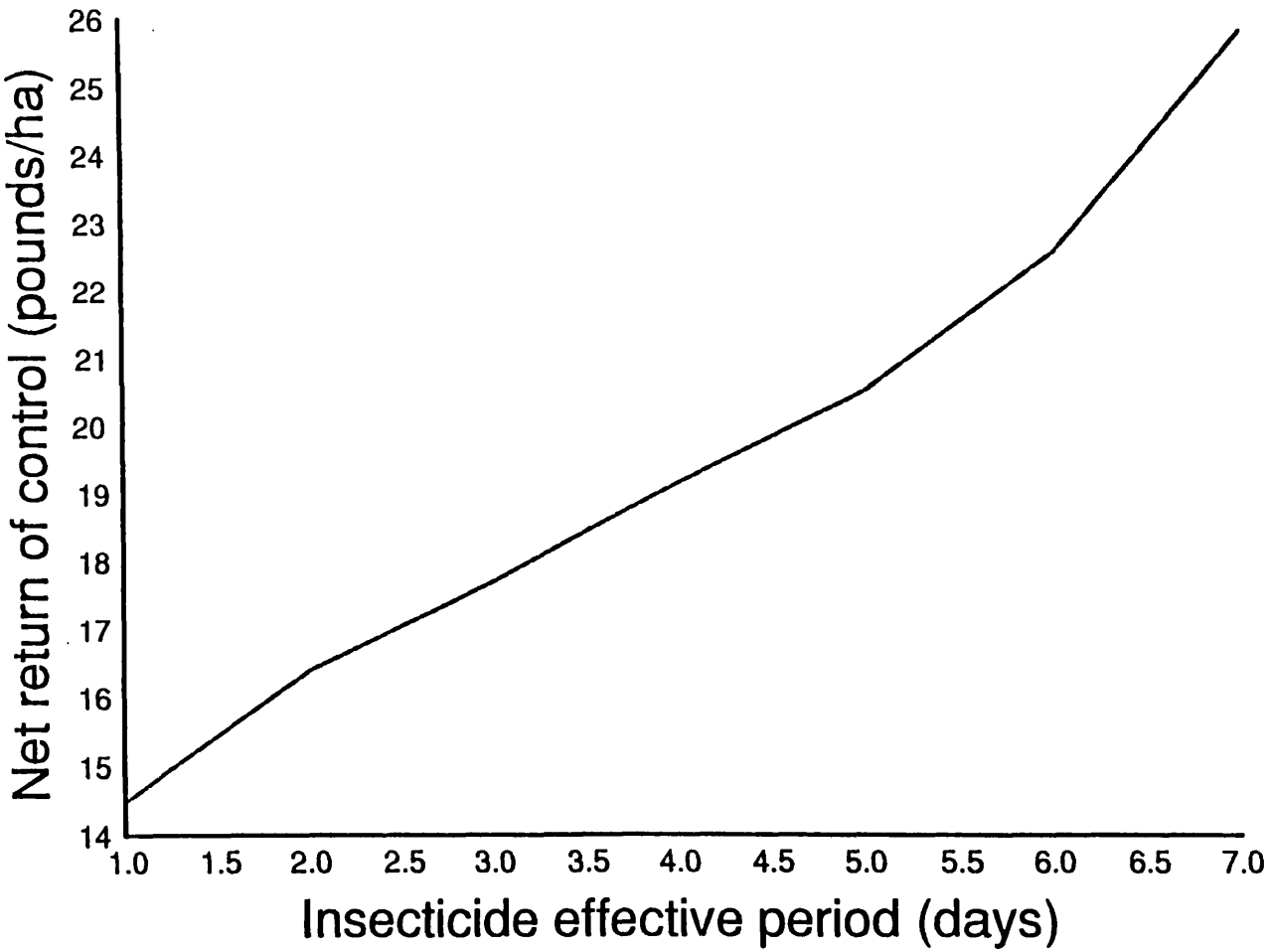


Fig. 5.19 Effects of changes in insecticide persistence on the net return of control.

rapidly (Fig. 5.20). Net return also depended on expected yield; with net return increasing with yield (Fig. 5.20). When two applications were applied with the first application at different crop growth stages and with different intervals between the two applications the highest net return was in the area between the profit line of £21/ha (Fig. 5.21). Combination of the two applications revealed that the highest profit was achieved if the second application was between middle milk stage (G.S. 75) and the beginning of dough (G.S. 82) no matter what crop growth stage the first application was applied. Therefore, one spray was the best strategy if it was applied during mid-milk and the beginning of dough. Secondly, the intensity of the profit lines between £21 to £7/ha on the upper right hand side in Fig. 5.21 mean that the net returns from control are sensitive to the combination of the two applications if two sprays were applied (Fig. 5.21). The net return decreased faster in the upper right hand than the other side in Fig. 5.21.

The net return of different control strategies were compared taking into account the outbreak probability and forecasting accuracy. The aphid population growth simulated in 1979 was used as an outbreak.

The outbreak probability was set at 0.3 during recent years, forecast accuracy for outbreak and no-outbreaks assumed to be 0.8. Spraying according to forecast was a better strategy than prophylactic control but only slightly better against no control. No control was a much better strategy than the prophylactic because the risk of unnecessary aphicide use was high for prophylactic control (70%) (Fig. 5.22 A).

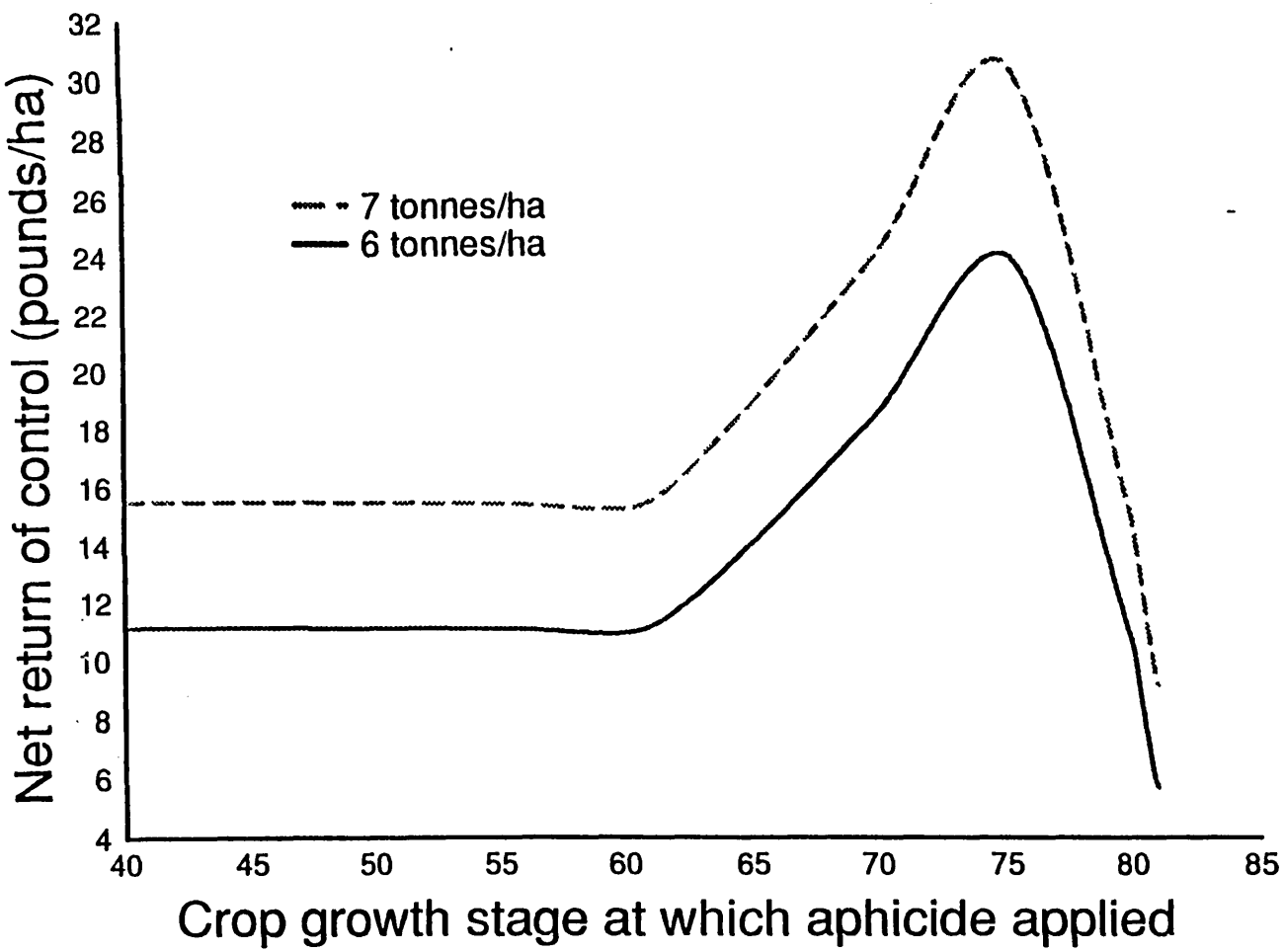


Fig. 5.20 Net return of insecticide control dependent on expected yield at different crop growth stages.

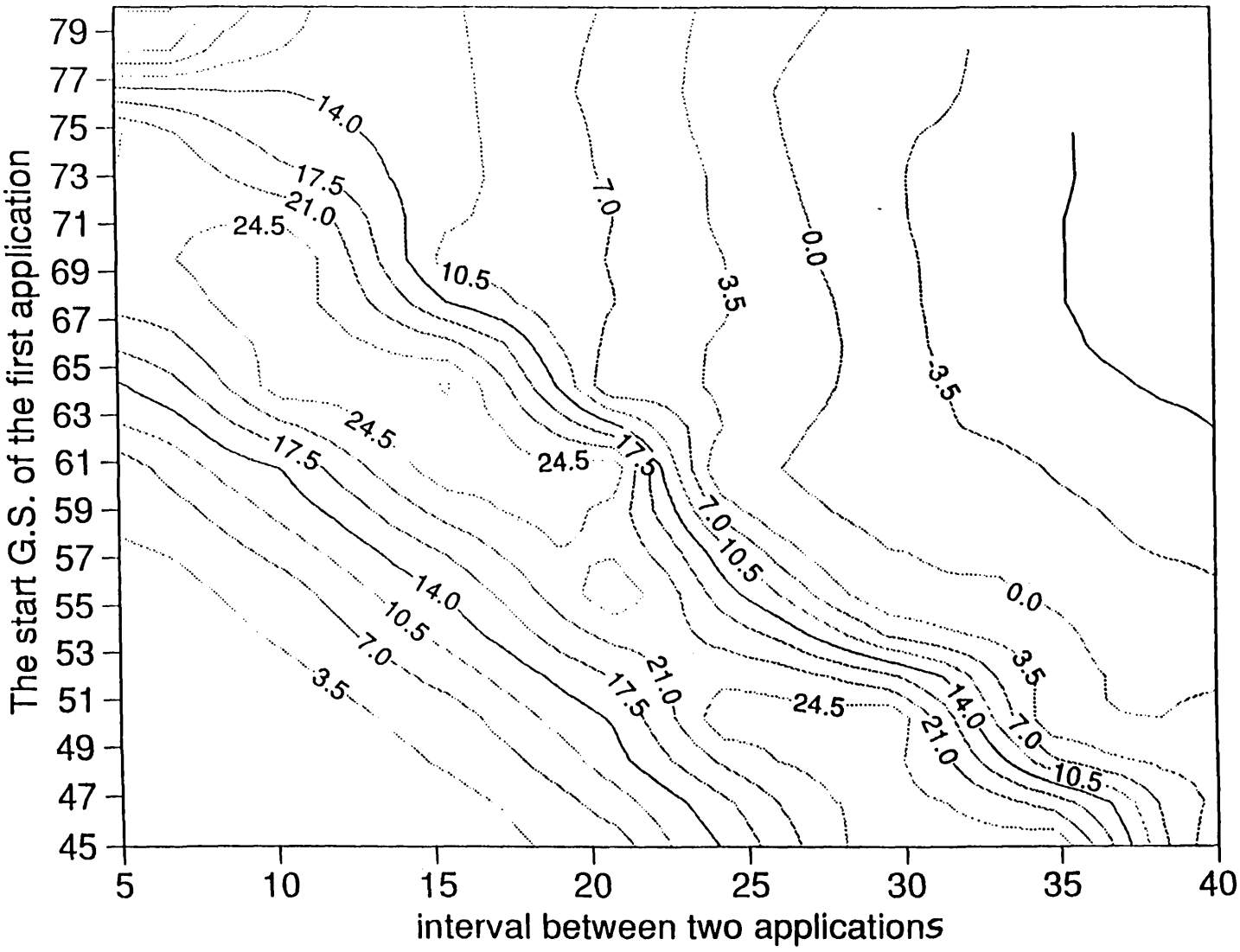


Fig. 5.21 Relationship between net return of control, time of the first spray and interval to the second spray.

If the outbreak probability was 0.8 then spraying according to a forecast was a far better strategy against the no control because the latter resulted in the high risk of severe yield loss especially from mid-flowering (G.S. 65) to late milk stage (G.S. 77). Spraying according to a forecast was similar to prophylactic spraying and was slightly worse than the latter strategy during the milky stage. The prophylactic spraying strategy was more economic than the no control, especially during the milky stage period (Fig. 5.22C).

When the outbreak probability was 0.5, spraying according to a forecast was better than the other two strategies, and no control was a better strategy than the prophylactic spraying before the mid anthesis (G.S. 65) but otherwise after that growth stage (Fig. 5.22B).

In most cases, no control was the best strategy no matter what the outbreak probability and forecasting accuracy were if a control decision had to be made early in the season when aphid population density was low, for instance at mid-booting (G.S. 45) (Fig. 5.23). If the decision was made later in the season, e.g. at the beginning of milky-ripe stage (G.S. 70), spraying according to a forecast was more likely to be a better strategy compared with no-control when the forecasting accuracy and outbreak probability were high (Fig. 5.24). Prophylactic spraying was the worst strategy early in the season, unless forecasting accuracy was very low and the outbreak probability was high (Fig. 5.25) and it only improved slightly, later in the season (G.S. 70) (Fig. 5.26).

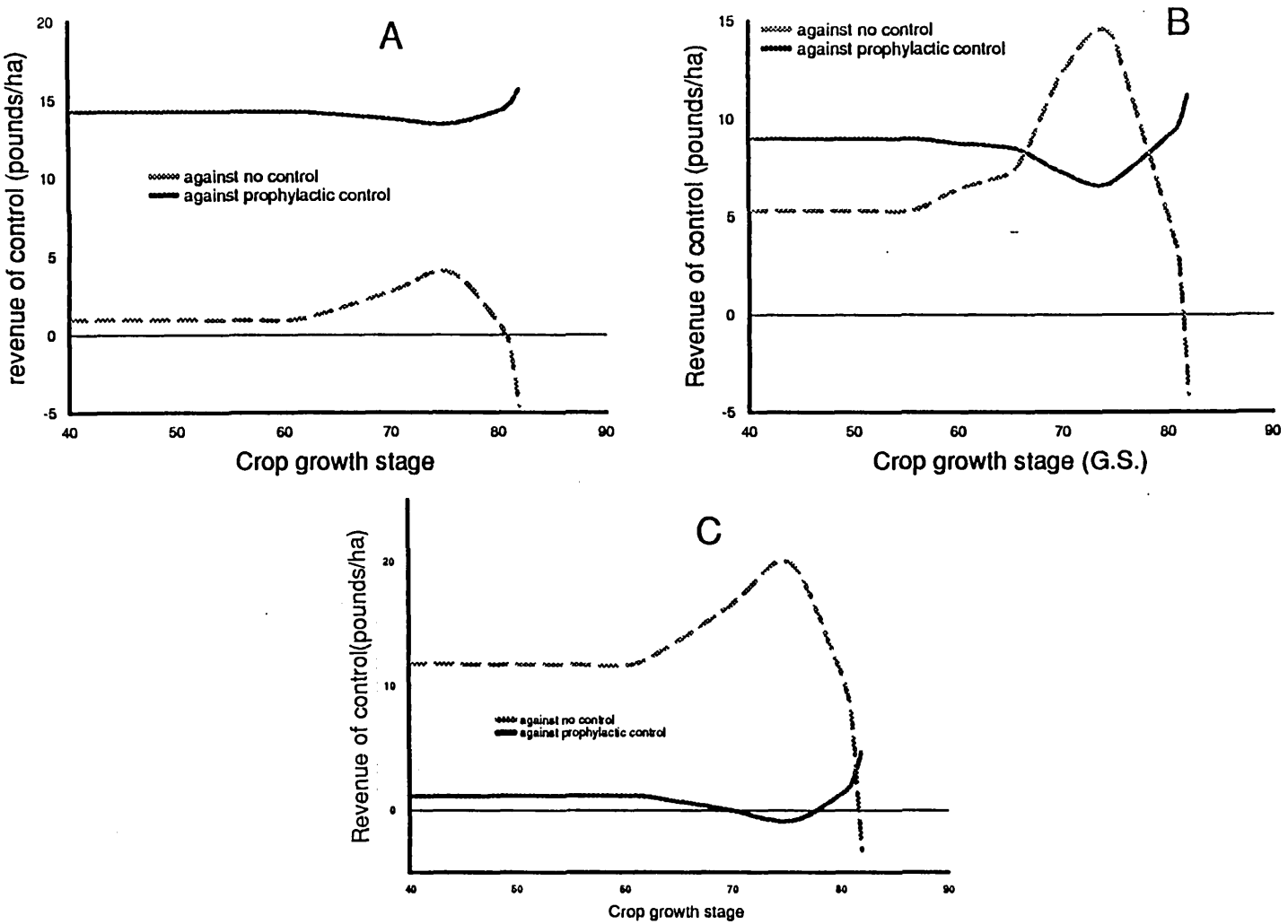


Fig. 5.22 Difference in net return of forecast based control compared with either no control or prophylactic control when the outbreak probability was (A), 0.3; (B), 0.5 and (C), 0.8, and forecast accuracy was 0.8.

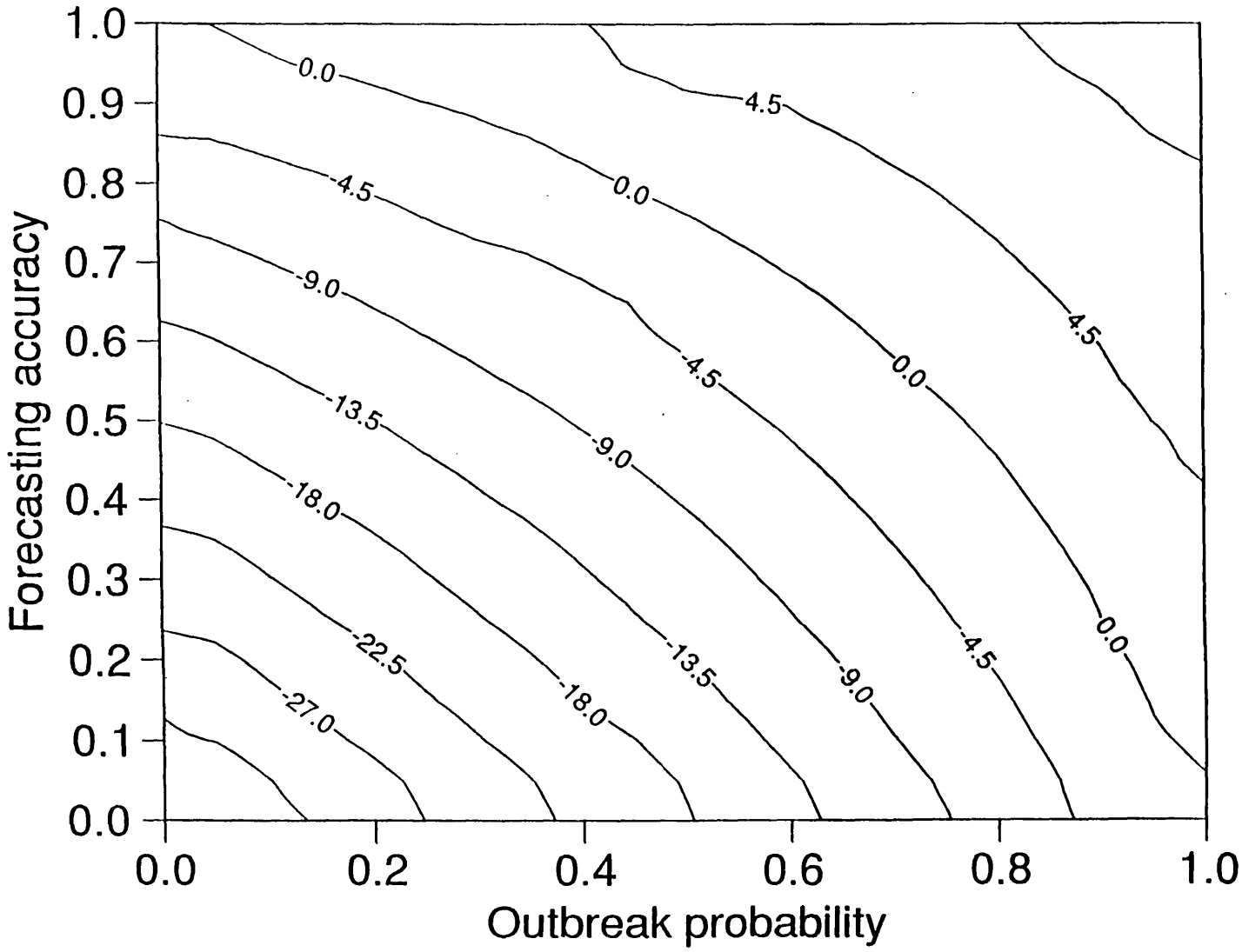


Fig. 5.23 Comparison between forecast based control and no control under different outbreak probabilities and forecast accuracies at mid-booting (G.S. 45), showing net return (£/ha)

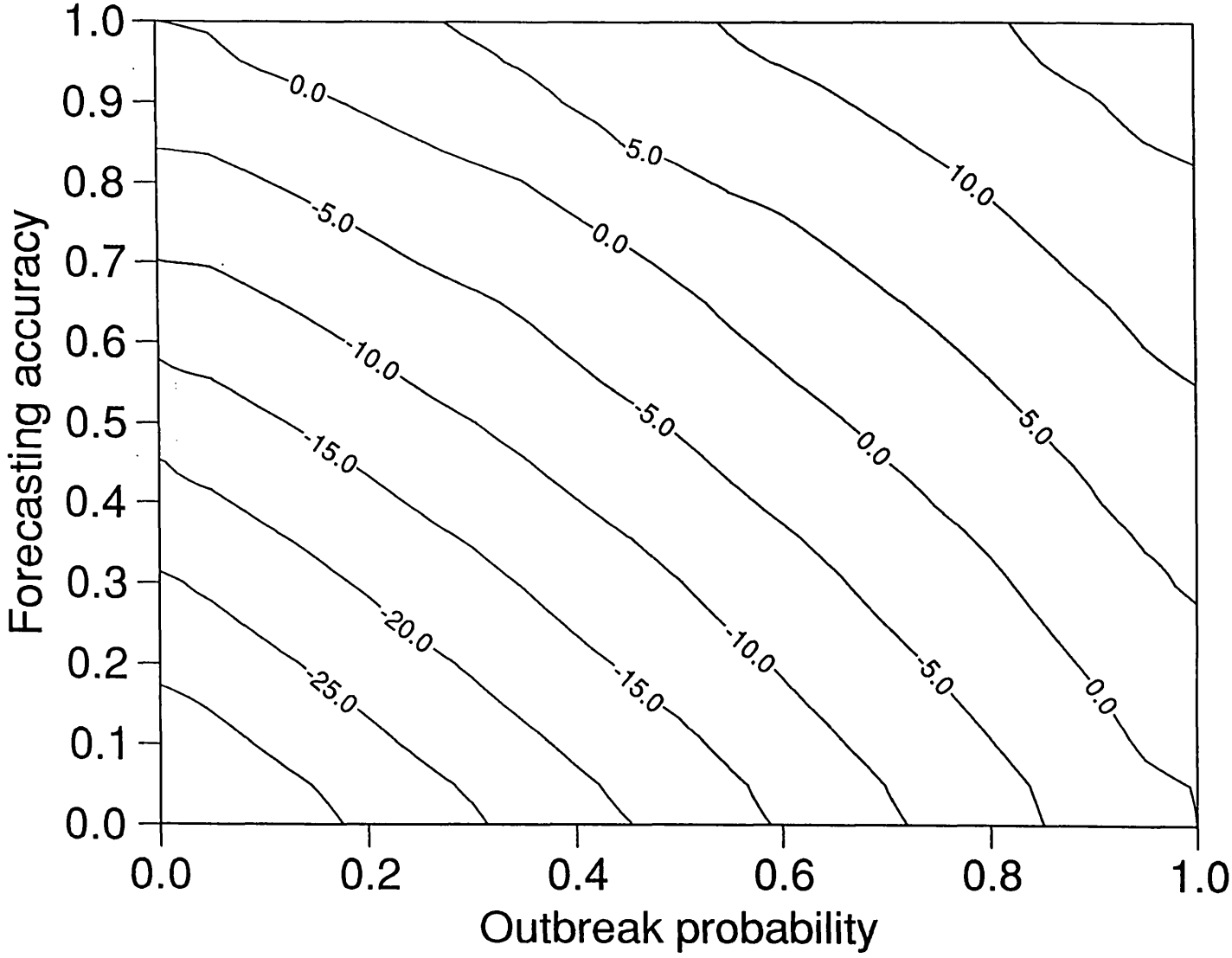


Fig. 5.24 Comparison between forecast based control and no control under different outbreak probabilities and forecast accuracies at milky ripe (G.S. 70), showing net return (£/ha).

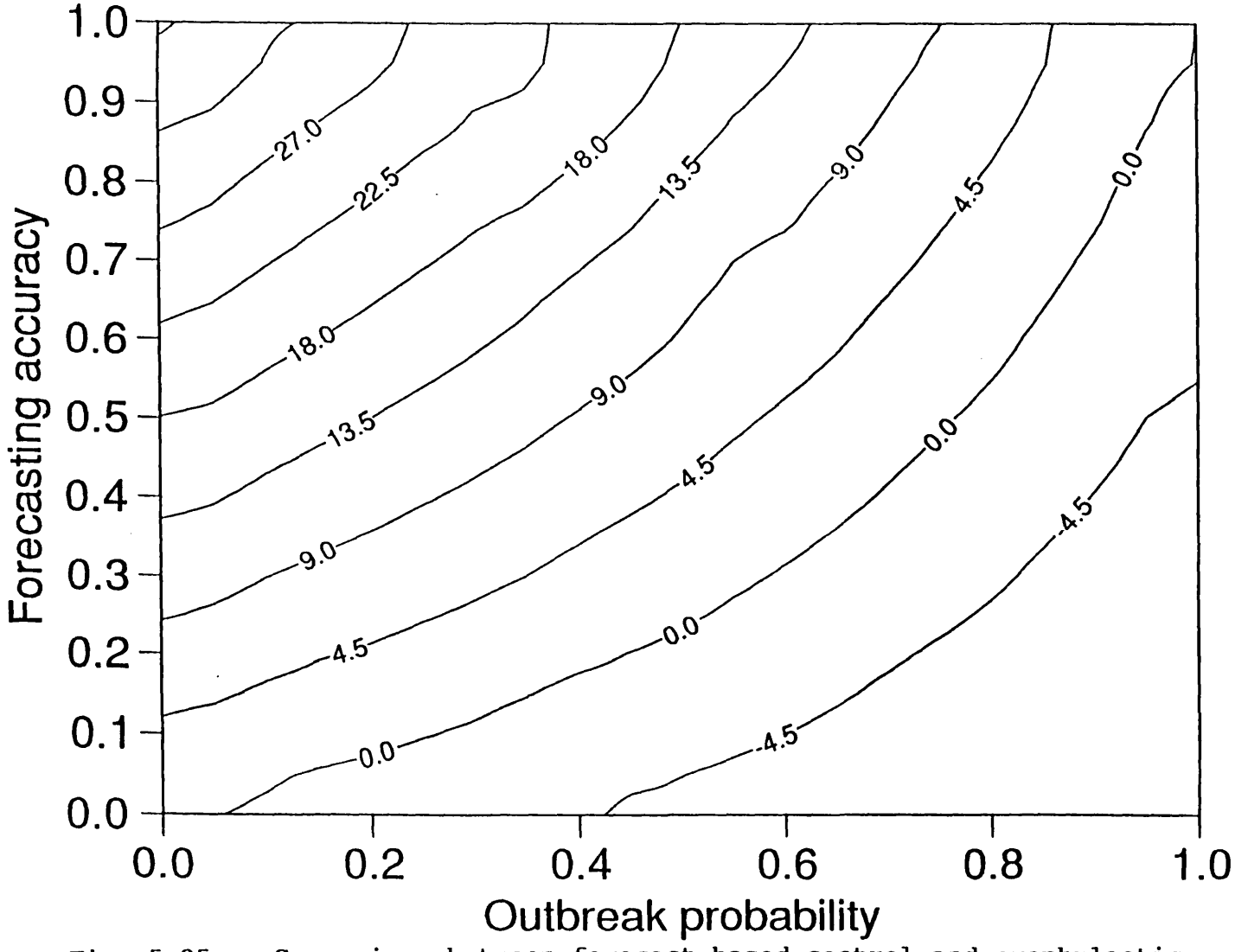


Fig. 5.25 Comparison between forecast based control and prophylactic control under different outbreak probabilities and forecast accuracies at mid-booting (G.S. 45), showing net return (£/ha).

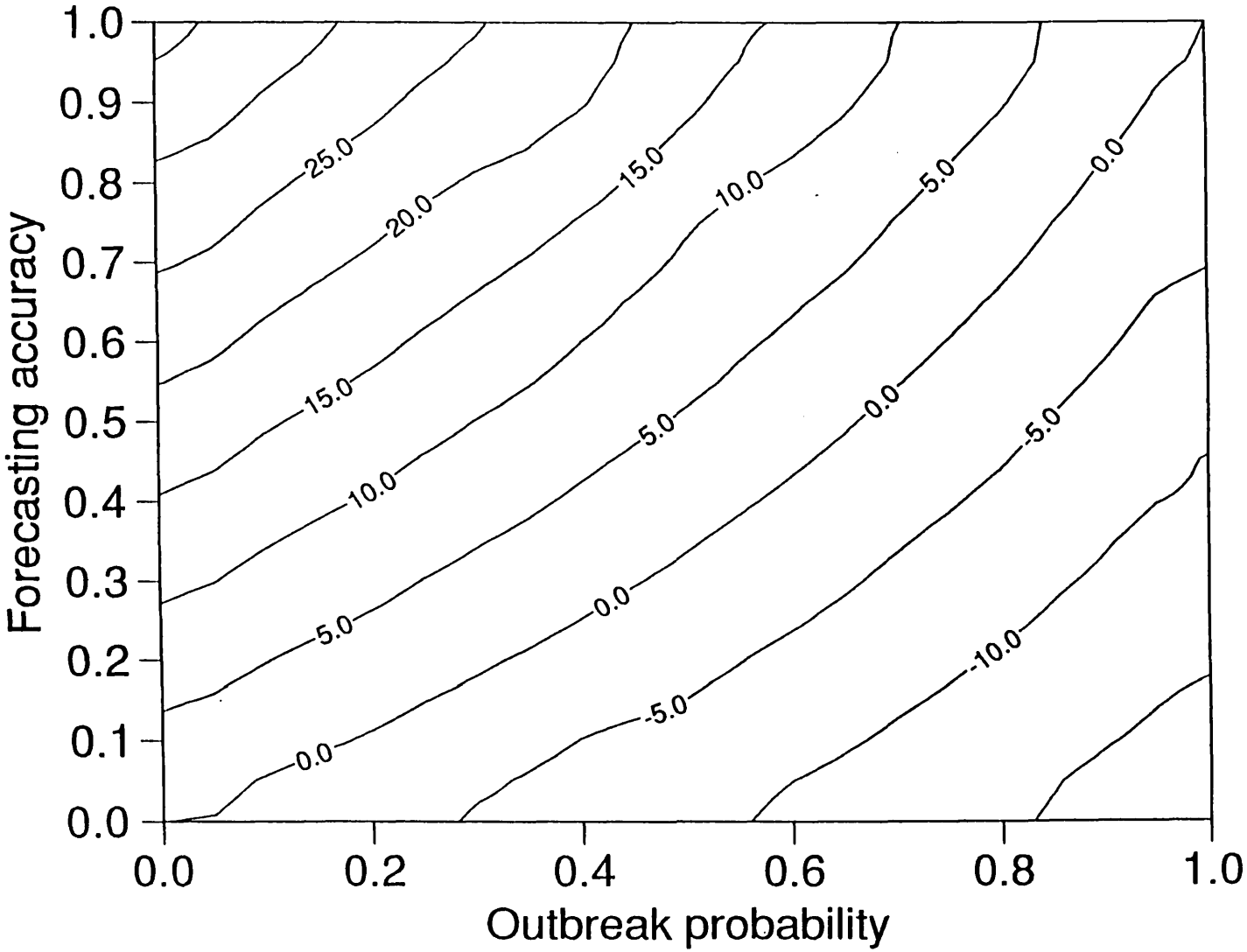


Fig. 5.26 Comparison between forecast based control and prophylactic control under different outbreak probabilities and forecast accuracies at milky ripe (G.S. 70), showing net return (£/ha).

5.6 Discussion

The model predicted the field population well in the multidisciplinary experiment of 1979 when natural enemies had little effect on the increase of the aphid population (Dewar, 1980). The populations in the early sown and late sown plots were similar (Fig. 5.2 A and B). The predictions of alate densities were not good as the predicted numbers declined early (Fig. 5.6 C). This could have been because the alates estimated in the model were all from immigration and the alates which developed in the crop were assumed to emigrate. This may indicate that some of these alates stayed and reproduced on cereals. The predictions of total population densities were also not very good in the biological control trial in 1979. This may have been due to natural enemies such as coccinellids and fungal disease, which arrived late, slowing down the rapid growth of the population (Dean *et al.*, 1980).

The model predictions were not accurate in other years. The model was unable to predict populations in which natural enemies or weather had important effects as it was constructed with only a natural mortality. Natural enemies were abundant and reported to have had significant effects on the field aphid populations in 1985, 1986 (Carter *et al.*, 1989) and they were abundant in 1987 (see see 3.6). Therefore, the predictions of the peak densities from the model were always higher than in the field. Furthermore, the appearance of alates in the suction trap was nearly one month later than they were observed in the field population (Fig. 5.7 A) and consequently the model predicted the

initial field population about 30 days late.

It was difficult to compare the results from the model and in the field in Fig. 5.4 due to too few field counts. However, the model simulated the trend of the resurgence after the first aphicide application. The field population was high after the second aphicide application which may have been because a high level of local immigration from near unsprayed plots with high population densities or the effectiveness of the application on aphid mortality was low.

The model had similar predictions in 1979 when development, reproduction and alate production data from this study and literature were used. However, the model would overestimate the field population if the reproductive rate on barley from the literature was not modified for the rate on wheat in the model (see Chapter 4) (Table 5.2).

The crop growth stage influences the reproduction rate and survival rate (Wratten, 1978; Watt, 1977), which are sensitive factors in aphid population development, as shown by the sensitivity analysis, and it also affects aphid development and alate production (Thornback, 1983; Carter *et al.*, 1982). Therefore it is important in affecting aphid population growth and timing of the maximum population (Fig. 5.10) and hence the final yield loss. Changes in temperature had a large impact on population growth and the final yield loss. It is similar to the finding by Carter (1978) that an increase in temperature resulted in an earlier lower peak aphid density because higher temperature speeded up crop development more than aphid development, so the aphids had less time for development and reproduction (Carter *et al.*, 1982).

Both increase or decrease in the development time slightly reduced the maximum aphid density compared with the standard in 1979, but considerably decreased or increased the maximum density respectively in 1987. The reduction in the development time shortened aphid generation time, which caused the aphid population to increase much faster than the standard early in the season in 1979. The higher density caused the adults to produce alate nymphs which would become emigrants in the field much earlier. Therefore less apterous adults developed and subsequently less nymphs were produced which caused the maximum density to be lower than that in the standard. However, in 1987, the increase of aphid density due to the shorter development time was not high enough to cause a large number of adults to be alate earlier. Changes of alate production also slightly affected the aphid population peak which was because total alate and apterous adult densities in the population were small. Population development was slightly sensitive to immigration and IMPR. Aphid population development was more sensitive to IMST than immigration and IMPR. The yield loss was also sensitive to changes in development time, reproductive rate and survival rate but was less sensitive to changes in alate production rate, immigration, IMST, IMPR or the period of insecticide persistence.

Effects of pesticide persistence on the aphid population varied in the two years. A longer persistence decreased the aphid population to zero in 1987 while the aphid population recovered to a high level shortly after the end of the effective period of the insecticide (Fig. 5.17).

The model from Watt (1983) did not allow the possible resurgence of aphid populations following an insecticide spray.

The aphid population was fixed when it was set in the model. This resulted in the maximum profit occurring when the spray was as early as possible in the season in the control profit analysis. Therefore the model is possible to result in overuse of pesticides. In this study, however, the model allowed the resurgence of the aphid population after a spray. Therefore, the model predicted that the maximum profit occurred when the spray was at early milky stage (G.S. 73). The model also indicated that one spray at the early milky stage was the best control strategy while two sprays were actually applied in the field in 1979 (Prew *et al.*, 1983).

The profit of the three strategies; prophylactic control, no control and control based on a forecast, depended on the outbreak probability and forecasting accuracy (Fig. 5.22). Forecasting was the best strategy when its accuracy was high. Prophylactic control was better compared with no control, especially during middle milky to end of milky stage (G.S.75 to 79) when the outbreak probability was high. However, the outbreak frequency of *M. dirhodum* from recent aphid data is low and in theory the no control will be a better strategy compared to the prophylactic control unless controlling *S. avenae* or disease control with fungicide are considered. Furthermore, the prophylactic control would result in unnecessary environmental pollution.

CHAPTER SIX: GENERAL DISCUSSION

Cereal aphid populations were low in the field in 1987 and 1988. *M. dirhodum* was dominant in 1987 with a maximum of 5/shoot although this was below the economic threshold (30/shoot, George 1975). Consequently, aphicide did not increase yield significantly. *S. avenae* was more common in 1988 and its population was maintained for a long period (30 days) at a approximately 2/shoot which was below the economic threshold (5/ear or 66% infested shoots, Walters, per. comm.). Aphicide did significantly increase yield, which suggests that *S. avenae* causes more damage if its population is maintained for a long period at a lower level than the economic threshold.

Nitrogen significantly increased the accumulated aphid index of *M. dirhodum* in 1987 and yields in both years. The higher aphid index did not reduce the yield. However, effects of neither fungicide on aphid population development nor aphicide on yield loss did not occur, possibly due to the low aphid densities in 1987. Therefore, damage under these yield production levels cannot be compared, as they did not affect aphid infestation levels significantly to affect yields. However, this method of changing levels of inputs to influence production levels is useful in studying economic thresholds of other pests as well as cereal aphids.

The laboratory studies provided useful information on aphid

biology for use in the simulation model. The optimum temperature is 25°C at which the aphid development was shortest and the intrinsic rate was highest while Dean found a slightly lower optimum at 22.5°C. Development time of the aphid on wheat was longer (12%) and fecundity lower (33%) than that on barley discs (Dean, 1974), but the development time and fecundity were similar to Thornback's studies on wheat (1983).

The laboratory experiments confirmed that flowering is the most favourable growth stage for aphid adult survival and fecundity (Watt, 1979). Feeding positions (flag, second and third leaves) on the wheat plant did not affect aphid development and reproduction.

The model accurately predicted rose grain aphid population development in the year when natural enemies did not significantly affect aphid populations i.e in the multidisciplinary experiment, 1979 (Prew *et al.*, 1983). Effects of natural enemies on aphid population development were not included in the model because: i) the main aim of this study was to investigate aphid damage potential and control options; ii) the natural enemy system is very complicated, i.e. many groups of natural enemies; parasitoids, predators and fungal pathogens, and it was not possible at this stage to include them in the model; and iii) quantitative data on natural enemies were not available for the years used to validate the model.

Simulation studies of aphid population dynamics, *Brevicoryne brassicae* (L.) (Hughes & Gilbert, 1968 and Gilbert & Hughes,

1971) and the grain aphid, *S. avenae* (Carter, 1978) concluded that timing of immigration was important in determining the final size of the aphid population later in the season. This was also true in this study. Therefore, sampling on cereals early in spring in the field may be useful when the suction trap is not detecting low aerial aphid population.

In 1979, cold weather in the previous winter delayed crop development (Dewar, 1980). Although there were few immigrants and small field populations in spring, the warm dry weather in July allowed these aphid populations to increase rapidly to very high levels, during a long period of favourable crop growth stages, in the absence of significant effects of natural enemies (Dewar *et al.*, 1980). Sensitivity analysis indicated that slower crop development, by reducing temperature, also increased aphid population sizes. However, the effects of temperature are complex in the model. Lower temperature slowed the rate of the crop development but also reduced the rate of aphid increase. Furthermore, although the low temperature resulted in a higher density this occurred much later than in the standard simulation (Table 5.2). In the field, this may allow natural enemies, which are abundant later in the season, to have a significant effect on population development (Carter, 1978). Therefore, cold weather in the previous winter may be more beneficial for *M. dirhodum* as it delays the crop growth (Dewar *et al*, 1980) and reduces the survival of natural enemies (Majerus & Kearns, 1989), while it does not affect the survival of overwintering eggs of the aphid (Hand & Williams 1980).

The model indicated that the crop growth stage at which

migrants in the suction trap were determined as emigrants was more sensitive compared with the immigration and the length of transformation periods. These parameters and the transformation equation (Eqt 4.4), determined arbitrarily in the model, may not accurately reflect the actual proportions of immigrants and emigrants in the field population. Therefore, more research is needed to establish an accurate relationship between the proportion of immigrants in the suction trap samples, crop growth stage and aphid density in the field.

The model indicated that changes of reproduction and survival were sensitive to aphid population development. This suggests that breeding for resistant wheat varieties to the aphid could be an effective way to reduce aphid infestations (Lowe, 1978; Dixon, 1987).

Carter (1978) indicated that a shorter development time increased the aphid population density a great deal in a simulation study of *S. avenae*. However, in this study, the model indicated that a shorter development time might not be an advantage to the aphid population growth as it caused a high aphid density early in the season which induced a large proportion of emigrants, and therefore reduced the development of the aphid population in the field.

The advantage of this model over another damage model (Watt, Watt et al., 1983, 1984) in the economic analysis of control is that it allowed aphid population resurgence, which might cause further yield loss after the insecticide was applied and took effectiveness of insecticide into account. The model revealed that in

1979 an insecticide treatment during the milky ripe stage was most profitable. But, two insecticide applications in the multidisciplinary experiment in 1979 were done. The first spray during anthesis, applied as a standard treatment, reduced the early population size and the second application during the milk ripe stage controlled the aphid population when the most damage occurred (Prew *et al.*, 1983). The net return of these control was still high (Fig. 5.21) although it was less than that for a single spray due to the additional cost of the extra control.

Control based on a forecasting scheme, even when only 80% accurate, was the best strategy although its value depended on outbreak probability and population densities. Entwistle and Dixon (1987) also found that control decisions based on forecasts from multiple regression analyses were more profitable for *S. avenae*. However, the level of damage used in the profit analysis was relatively high and the *M. dirhodum* population only reached such high level in 1979. Therefore, control on this aphid was unlikely to be profitable with such a low outbreak probability (Fig. 5.23 & 24). However, the grain aphid, *S. avenae* is more damaging than *M. dirhodum* (Rabbinge & Carter 1984) and has had a high outbreak probability in recent years (Watt, 1984). This method can be useful in studying control strategies on other aphids.

More work is needed to improve the model: firstly, effects of natural enemies should be incorporated into the model to improve predictions of aphid populations in non-outbreak years; secondly, field studies are needed to obtain information on insecticide persistence in the field under different weather

conditions; and finally the economic analysis in the model should use an outbreak probability forecasted at the time a control decision is made instead of deriving from the frequency of the outbreaks in recent years. Then the model can be used to make tactical controls in the field.

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Appendix I: The Model

```
************************************************************
*                                                          *
*   A population and control strategy model of Metopolophium *
*                       dirhodum                           *
*                                                          *
*                                                          *
*                       X. Zhou                            *
*                                                          *
*                                                          *
************************************************************
C
C
C  Dimension claim
C
C
C************************************************************
      DIMENSION ALATES(2,1500),AIMM(2,1500),APTERS(2,1500),
     *TMIN(250),TMAX(250),SEN(100,20),SURRA1(5),SURRA2(5),
     *HRDEG(24),HRDREP(24),TMINN(250),TMAXX(250)
C************************************************************
C
C  SEN(I,20) (Sensitivity  analysis) where I respectively:
C  1_Temperature(*),
C  2_Crop growth stage(*),
C  3_Aphid development longevity(*),
C  4_Aphid natural survival rate(*),
C  5_Reproduction rate(*),
C  7_Morph determination(*)
C  6_Immigration(*),
C  8_Immigration transformation starts at crop growth stage P1
C  (P1,P2: the start and finish crop stage of the transformation
C  respectively)
C  9_Transformation period of immigration(+),
C  10_Time step
C  11-Insecticide effective period
C
C  Types of variables are specified
C
      REAL
      LAT,IMM(250),IMMM(250),NEWNY,NWNY,NUMBE1(5),NUMBE2(5),
     *NUMBE(5),LENGT1(5),LENGT2(5)
      INTEGER MM,ND,IG(250)
      CHARACTER*3 LEAP,CTLOUT
C
      COMMON PI,LAT,IDAY
C
C************************************************
C                  1___DATA INPUT                *
C************************************************
C
C  N:      number of sensitivity loops
C  LEAP:   logical variable, leap year(yes) or not(no)
C  CTLOUT: control of output(yes or no)
```

```
C  ISKEXP: use of data from literature(0) or experiments(1 or 2)
C  ISKINT: skip insecticide application(0) or not(1)
C  ISK(x): x=1 to 3, skip each individual applications
C          of insecticides
C  CRSTAG: initial crop growth stage
C  PP1:    start crop growth stage of migration transformation
C  ISG(x): x=1 to 3, crop stages at which insecticides applied
C  ISTART: the day model starts or/and immigration starts
C  IFINIS: the day migration or model stops
C  LAT:    latitude at the  site simulated
C  DRATE:  maximum mortality rate of insecticide
C  BR:     minimum mortality rate of insecticide
C  PRICE:  grain price per tonne
C  CTLOSS: potential yield loss without aphid control
C  WHEEL:  wheeling loss due to control
C  PESCOS: pesticide costs per application
C  TMAXX:  maximum temperature in a day
C  TMINN:  minimum temperature in a day
C  IMMM:   aphid suction trap data
C
      READ(*,*)N,LEAP,CTLOUT
      READ(*,*)((SEN(I,J),J=1,14),I=1,N)
      READ(*,*)ISKEXP,ISKINT,ISK1,ISK2,ISK3
      READ(*,*)CRSTAG,PP1,ISG11,ISG22,ISG33
      READ(*,*)ISTART,IFINIS,LAT,DRATE,BR,TILNO
      READ(*,*)PRICE,CTLOSS,WHEEL,PESCOS,THRE
      READ(*,*)(TMAXX(IDAY),IDAY=ISTART-1,IFINIS)
      READ(*,*)(TMINN(IDAY),IDAY=ISTART,IFINIS+1)
      READ(*,*)(IMMM(IDAY),IDAY=ISTART,IFINIS)
C
C  Array size and some parameters
C
      DATA ISTEP,IMSTEP,PI,TRACON/1500,700,
     *3.145928,40.0/
C
C
C***********************************************
C       2___SENSITIVITY ANALYSIS LOOP START     *
C***********************************************
C
      I=1
      CISTAG=CRSTAG
C
  101 C=CISTAG*(SEN(I,2))
      TOT=(0.1732-SQRT(0.03+(0.0005*(26.3365-C))))/0.00025
C
      DMAX=0.0
C
C  Isen: For time step (integer)
C
      OUPROB=SEN(I,13)
      FRPROB=SEN(I,14)
C
      ISEN=SEN(I,10)
      ISEN2=SEN(I,12)
      P1=PP1+(SEN(I,8))
      P2=P1+(SEN(I,9))
      ISG1=ISG11+ISEN2
      ISG2=ISG22+ISEN2
```

```
      ISG3=ISG33+ISEN2
C
C  Sensitivity analysis for temperature
C
      DO 10 IDAY=ISTART-1,IFINIS+1
        TMAX(IDAY)=TMAXX(IDAY)*(SEN(I,1))
        TMIN(IDAY)=TMINN(IDAY)*(SEN(I,1))
   10  CONTINUE
C
      TAYPAL=0.0237*TRACON/TILNO
C
C  Immigration sensitivity analysis and transformation
C
      DO 20 IDAY=ISTART,IFINIS
        IMM(IDAY)=IMMM(IDAY)*TAYPAL*(SEN(I,6))
   20 CONTINUE
C
C***********************************************
C            3___INSTAR LONGEVITIES             *
C***********************************************
C
C  Development length: (x)L Where x from a to p
C
C   Assumption for adult; If gs>59, apterae length is 1/5 longer
C  if gs>73,then 1/5 shorter; Alate is half of apterae
C  life span all the way
C
C  Alate 4th length: 1.2 times longer than 4th apterae
C
C  Reproduction rate  R(x) Where x is from a to d
C
C   Assumption:  normal reproduction for apterae is 2/3 of
C  results(0.00839)(Dean,1974); then the rates of
C  apterae and alates dependent on crop development
C  stage, the reproduction rates are 1.2 times the
C  normal(Thornback,1983) between G.S. 59 and  G.S. 73;
C  reproduction rates for alate are 0.7848 times
C  that for apterae(Wratten,1977):
C
C using data from literature
C
      IF(ISKEXP.EQ.0)THEN
       DTRESH=THRE
       AL=972.9
       BL=1915.75
       CL=2967.56
       DL=4571.21
       EL=4901.46
       FL=10750.8
       GL=11986.72
       TL=7661.0
       PL=7991.26
       RA=0.00559
       RB=0.00671
       RC=0.004389
       RD=0.005267
C
C  using experimental data
C
```

```
      ELSE
C
        DTRESH=THRE
        AL=1082.75-(63.0*(DTRESH))
        BL=2181.36-(126.1*(DTRESH))
        CL=3307.95-(188.66*(DTRESH))
        DL=5186.7-(303.61*(DTRESH))
        EL=5445.77-(318.56*(DTRESH))
        FL=11628.6-(639.61*(DTRESH))
        GL=12917.3-(706.81*(DTRESH))
        TL=9051.8 -(471.61*(DTRESH))
        PL=9310.8-(486.56*(DTRESH))
        RA=0.006137
        RB=0.007364
        RC=0.004816
        RD=0.005779
      END IF
C
C    LENGT1(x): Where x=1 to 4 for the first to fourth instar
C  development time of aptertae, 5 for the adult
C  LENGT2(x): The longevity of the alate
C
C  LENGT1(4) and LENGT2(4) include reproductive delay
C
      LENGT1(1)=AL*SEN(I,3)
      LENGT1(2)=BL*SEN(I,3)
      LENGT1(3)=CL*SEN(I,3)
      LENGT1(4)=DL*SEN(I,3)
C
      DO 30 LM=1,3
        LENGT2(LM)=LENGT1(LM)
   30 CONTINUE
C
      LENGT2(4)=EL*SEN(I,3)
C
C************************************************
C               4___MODEL STARTS                 *
C************************************************
C
C Outputs are output to specific files
C
      OPEN(8,FILE='TABLE',STATUS='NEW')
      OPEN(9,FILE='PROFIT',STATUS='NEW')
      OPEN(29,FILE='DEGREES',STATUS='NEW')
      OPEN(30,FILE='LOGTOTDEN',STATUS='NEW')
      OPEN(31,FILE='CRSTAGE',STATUS='NEW')
      OPEN(33,FILE='APTERAE',STATUS='NEW')
      OPEN(34,FILE='ALATE',STATUS='NEW')
      OPEN(36,FILE='YLOSS',STATUS='NEW')
      OPEN(37,FILE='INDEX',STATUS='NEW')
      OPEN(32,FILE='LOGNYMPH',STATUS='NEW')
C
C  Control output
C
      IF(CTLOUT.EQ.'YES')THEN
C
C  Print headings of each data set in file 'TABLE'
C
      WRITE(8,1000)
```

```
C
 1000 FORMAT(1H1,'Day',1X,'Date/month',2X,'Nymph1-3',2X,
     * '4th-apte',2X,'4th-alat',2X,'Totalnym',2X,'To-ap-ad',2X,
     * 'To-al-ad',2X,'To-dens*',2x,'Acc-indx',1x,'To-cr-lo',1x,
     * 'crop-stage')
C
      WRITE(8,1001)
 1001  FORMAT(1H ,'---',1x,'----------',2X,'--------',2X,'
     * --------',2X,
     * '--------',2X,'--------',2X,'--------',2X,
     * '--------',2X,'--------',2X,'--------',1X,'--------',
     * 1X,'--------')
      ELSE
       GOTO 98
      ENDIF
   98 CONTINUE
C

      TOLOSS=0.0
      CPINDE=0.0
      DEGREE=0.0
      RDEGRE=0.0
      TDADEG=0.0
C
      DO 102 IDAY=ISTART,IFINIS
C
C   Set longevities,in hour degrees, are input
C  for alate and apterous adults at different crop
C  development stage.
C
      LENGT1(5)=FL*SEN(I,3)
      LENGT2(5)=PL*SEN(I,3)
C
      IF(CRSTAG.GT.59.0)LENGT1(5)=GL*SEN(I,3)
      IF(CRSTAG.GT.73.0)LENGT1(5)=TL*SEN(I,3)
C
C************************************************
C           5__TEMPERATURE PROCESS              *
C************************************************
C
C   As the model is updated on hourly base, temperatures
C  are calculated hourly in a submodel.
C

      CALL DEVTEMP(TMIN(IDAY),TMIN(IDAY+1),
     *TMAX(IDAY-1),TMAX(IDAY),HRDEG,HRDREP,ISEN,
     *ISKEXP,DTRESH)
C
C************************************************
C      6__FROM JULIAN DAY TO DATE, MONTH        *
C************************************************
C
      CALL CALENDER(IDAY,ND,MM,LEAP)
```

```
C
C***********************************************
C                  7___INSECTICIDE                *
C***********************************************
C
C  IDS: The day insecticide is applied
C  C:  Current crop growth stage
C  SURIN(X): x=1 to 3, survival rates correspond to insecticide
C           application
C  TSUR: total  survival  rate after insecticide treatment
C
      IU=SEN(I,11)
      IG(IDAY)=CRSTAG
      IF(ISKINT.EQ.1)THEN
C
C  Application 1
C
       IF(IG(IDAY).EQ.ISG1)IDS1=IDAY
       IF(IG(IDAY).EQ.IG(IDAY-1).AND.IG(IDAY-1).
     * EQ.ISG1)IDS1=IDAY-1
       IF(ISK1.EQ.1.AND.IDAY.GE.IDS1.AND.IDAY.LE.(IDS1+IU))THEN
        CALL INSECTICIDE(IDAY,IDS1,IU,DRATE,SURIN1,BR)
       ELSE
        SURIN1=1.0
       END IF
C
C  Application 2
C
       IF(IG(IDAY).EQ.ISG2)IDS2=IDAY
       IF(IG(IDAY).EQ.IG(IDAY-1).AND.IG(IDAY-1).
     * EQ.ISG2)IDS2=IDAY-1
       IF(ISK2.EQ.1.AND.IDAY.GE.IDS2.AND.IDAY.LE.(IDS2+IU))THEN
        CALL INSECTICIDE(IDAY,IDS2,IU,DRATE,SURIN2,BR)
       ELSE
        SURIN2=1.0
       END IF
C
C  Application 3
C
       IF(IG(IDAY).EQ.ISG3)IDS3=IDAY
       IF(IG(IDAY).EQ.IG(IDAY-1).AND.IG(IDAY-1).
     * EQ.ISG3)IDS3=IDAY-1
       IF(ISK3.EQ.1.AND.IDAY.GE.IDS3.AND.IDAY.LE.(IDS3+IU))THEN
        CALL INSECTICIDE(IDAY,IDS3,IU,DRATE,SURIN3,BR)
       ELSE
        SURIN3=1.0
       END IF
C
       TSUR=SURIN1*SURIN2*SURIN3
C
      ELSE
       TSUR=1.0
      END IF
C
      DO 90 II=1,24/ISEN
       TDADEG=HRDEG(II)
   90 CONTINUE
```

```
C
C************************************************
C           8___LOOP WITHIN A DAY                *
C************************************************
C
      DO 103 IT=1,24/ISEN
        TOTDEN=0.0
C

C   Immigration data transformed to field data and
C  input to the model at noon
C
      IF(IT.EQ.12/ISEN)THEN
       IF(CRSTAG.LT.P1)THEN
         AIMM(1,1)=IMM(IDAY)
       ELSE IF(CRSTAG.GT.P2)THEN
         AIMM(1,1)=0.0
       ELSE
         AIMM(1,1)=ALATC(IMM(IDAY),P1,P2,CRSTAG)
       END IF
      END IF
C
C
C

C************************************************
C                  9___SURVIVAL                  *
C************************************************
C
C   Now the hourdegreely survival rates dependent
C  on growth stage, alates, apterous adults and
C  both nymphs
C
C  For insecticides
C
      SUINS=(TSUR)**(HRDEG(IT)/TDADEG)
C
C  For natural mortality
C
       SURRA1(5)=(0.89*(SEN(I,4)))**(HRDEG(IT)
     *   /(LENGT1(5)-LENGT1(4)))
C
       SURRA2(5)=(0.89*(SEN(I,4)))**(HRDEG(IT)
     *   /(LENGT2(5)-LENGT2(4)))
C
       SURAPN=(0.87*(SEN(I,4)))**(HRDEG(IT)/LENGT1(4))
C
       SURALN=(0.87*(SEN(I,4)))**(HRDEG(IT)/LENGT2(4))
C
       IF(GRSTAG.GT.73.0)THEN
C
         SURRA1(5)=(0.54*(SEN(I,4)))**(HRDEG(IT)
     *     /(LENGT1(5)-LENGT1(4)))
C
         SURRA2(5)=(0.54*(SEN(I,4)))**(HRDEG(IT)
     *     /(LENGT2(5)-LENGT2(4)))
C
         SURAPN=(0.23*(SEN(I,4)))**(HRDEG(IT)/LENGT1(4))
C
```

```
          SURALN=(0.23*(SEN(I,4)))**(HRDEG(IT)/LENGT2(4))
        END IF
C
        DO 40 LS=1,4
          SURRA1(LS)=SURAPN
          SURRA2(LS)=SURALN
   40 CONTINUE
C
C*************************************************
C     10___APHID POPULATION  DEVELOPMENT          *
C*************************************************
C
C  For immigrant adults
C
        ISKIP=1
          CALL DEVSUR(AIMM,IMSTEP,NUMBE,SURRA2
      *   ,LENGT2,HRDEG(IT),SUINS,ISKIP)
C
C  For alates developed in field
C
        ISKI=0
          CALL DEVSUR(ALATES,ISTEP,NUMBE2
      *   ,SURRA2,LENGT2,HRDEG(IT),SUINS,ISKI)
C
C  For apterae developed in field
C
          CALL DEVSUR(APTERS,ISTEP,NUMBE1

      *   ,SURRA1,LENGT1,HRDEG(IT),SUINS,ISKI)
C
C*************************************************
C               11___REPRODUCTION                 *
C*************************************************
C
C  For nymphs laid by the apterae
C
        ARATE=RA
        IF(CRSTAG.GT.59.0.AND.CRSTAG.LE.73.0)ARATE=RB
        IF(CRSTAG.GT.83.0)ARATE=0.0
C

        NEWNY=NUMBE1(5)*HRDREP(IT)*ARATE*SEN(I,5)
C

C  For nymphs laid by alates
C
C  Alates developing in field are assumed to emigrate
C
        ALRATE=RC
        IF(CRSTAG.GT.59.0.AND.CRSTAG.LE.73.0)ALRATE=RD
        IF(CRSTAG.GT.83.0)ALRATE=0.0
C
        NWNY=(NUMBE(5))*HRDREP(IT)*ALRATE*SEN(I,5)
C

C  Aphids are totalled up
C

        DO 50 LT=1,4
```

```
          TOTDEN=TOTDEN+NUMBE1(LT)+NUMBE2(LT)
   50 CONTINUE
C
       TOTDEN=TOTDEN+NUMBE(5)+NUMBE1(5)
C
C*************************************************
C          12___MORPH DETERMINATION                *
C*************************************************
C
C  Decide the proportion of nymphs which will be alatiform
C
C
       IF(ISKEXP.EQ.0)THEN
C
       ALATE=((2.603*TOTDEN+0.847208*CRSTAG-
      *27.18896)/100.0)*SEN(I,7)
C
       ELSE
C
       ALATE=-572.94+4.693*TOTDEN+14.5784*CRSTAG
      *-0.092728*(CRSTAG**2)
       END IF
C
       IF(ALATE.GT.1.0)ALATE=1.0
       ALATES(1,1)=(NWNY+NEWNY)*ALATE
       IF(ALATES(1,1).LT.0.0)ALATES(1,1)=0.0
C
C  Now the number of apterae
C
       APTERS(1,1)=NEWNY+NWNY-ALATES(1,1)
       IF(APTERS(1,1).LT.0.0)APTERS(1,1)=0.0
C

C  Now the totals are calculated.
C

       NUMBE1(1)=NUMBE1(1)+APTERS(1,1)
       NUMBE2(1)=NUMBE2(1)+ALATES(1,1)
       TONY13=NUMBE1(1)+NUMBE1(2)+NUMBE1(3)+NUMBE2(1)+
      *NUMBE2(2)+NUMBE2(3)
       TONYM=TONY13+NUMBE1(4)+NUMBE2(4)
       TOTDEN=TOTDEN+ALATES(1,1)+APTERS(1,1)
C

C  All instars are converted into aphids units.
C

       APHUNI=TONY13/3+NUMBE1(4)+NUMBE2(4)+NUMBE1(5)+
      *NUMBE(5)
C
C  Day and reproductive degrees accumulated
C
       DEGREE=DEGREE+HRDEG(IT)
C
       RDEGRE=RDEGRE+HRDREP(IT)
C

       IF(IT.EQ.12/ISEN)THEN
C
```

```
C************************************************
C                13___CROP LOSS                  *
C************************************************
C
C   The crop loss is calculated by proportion of yield loss
C  over potential yield per aphid unit day.
C
        IF(CRSTAG.LT.41.)CLOSS=0.0
        IF(CRSTAG.GE.41.0.AND.CRSTAG.LT.
     * 55.0)CLOSS=0.0001556
        IF(CRSTAG.GE.55.0.AND.CRSTAG.LT.
     * 60.0)CLOSS=0.0003765
        IF(CRSTAG.GE.60.0.AND.CRSTAG.LT.
     * 70.0)CLOSS=0.000487
        IF(CRSTAG.GE.70.0.AND.CRSTAG.LT.
     * 77.0)CLOSS=0.000383
        IF(CRSTAG.GE.77.0.AND.CRSTAG.LT.
     * 83.0)CLOSS=0.000192
        IF(CRSTAG.GE.83.0)CLOSS=0.0
        DAILOS=APHUNI*CLOSS
        TOLOSS=TOLOSS+DAILOS
        CPINDE=CPINDE+APHUNI
C
        IF(DMAX.LE.TOTDEN)THEN
         DMAX=TOTDEN
         IDYMA=IDAY
        END IF
C
        IF(IDAY.EQ.IDS1)CLOS1=TOLOSS
        IF(IDAY.EQ.IDS2)CLOS2=TOLOSS
C

C************************************************
C                  14___OUTPUT                   *
C************************************************
C
        IF(CTLOUT.EQ.'YES')THEN
          WRITE(8,1002)IDAY,ND,MM,TONY13,NUMBE1(4),NUMBE2(4),
     *    TONYM,NUMBE1(5),NUMBE(5),TOTDEN,CPINDE,TOLOSS,
     *    CRSTAG
 1002     FORMAT(I4,3X,I2,'//',I2,10F10.4)
C
          WRITE(29,1023)IDAY,DEGREE,RDEGRE
          WRITE(30,1021)IDAY,ALOG10(TOTDEN+1)
          WRITE(31,1021)IDAY,CRSTAG
          WRITE(32,1021)IDAY,ALOG10(TONYM+1)
          WRITE(33,1021)IDAY,NUMBE1(5)
          WRITE(34,1021)IDAY,NUMBE(5)
          WRITE(36,1022)CRSTAG,TOLOSS
          WRITE(37,1022)CRSTAG,ALOG10(CPINDE+1)
 1021     FORMAT(2X,I4,F13.5)
 1022     FORMAT(2(3X,F13.4))
 1023     FORMAT(3X,I4,2(4X,F14.4))
          END IF
       ELSE
        GO TO 103
       END IF
  103 CONTINUE
C
```

```
C $$$$$ End of within day loop $$$$$
C
C***********************************************
C              15___CROP DEVELOPMENT             *
C***********************************************
C
      CALL CROPGROWTH(TMAX(IDAY),TMIN(IDAY),TMIN(IDAY+1),
     * TOT,CRSTAG)
C
C***********************************************
C      16___PROFIT ASSESSMENT  OF  CONTROL       *
C***********************************************
C
      IF(CRSTAG.GT.86.3.OR.IDAY.EQ.IFINIS)THEN
C
       IF(ISKINT.EQ.1)THEN
       BRIDGE=ISK1+ISK2+ISK3
       PESCO=PESCOS*BRIDGE
       CALL BENEFIT(PRICE,CTLOSS,TOLOSS,WHEEL,PESCO,
     * OUPROB,FRPROB,CLOS1,CLOS2)
       ELSE
        GO TO 95
       END IF
   95  CONTINUE
C
       WRITE(38,*)IDYMA,DMAX
C
C  Prepare for next sensitivity analysis loop
C
       CRSTAG=CISTAG*(SEN(I+1,2))
       I=I+1
       IF(I.EQ.(N+1))GO TO 901
C
C   Zero all elements in development and survival subprogram
C  in second simulation
C
       DO 60 NI=1,2
       DO 60 NII=1,1500
       APTERS(NI,NII)=0.0
       AIMM(NI,NII)=0.0
       ALATES(NI,NII)=0.0
   60 CONTINUE
C
       ISKIP=1
       CALL DEVSUR(AIMM,IMSTEP,NUMBE,SURRA2
     * ,LENGT2,HRDEG(IT),SUINS,ISKIP)
C
       ISKI=0
       CALL DEVSUR(ALATES,ISTEP,NUMBE2
     * ,SURRA2,LENGT2,HRDEG(IT),SUINS,ISKI)
C
       CALL DEVSUR(APTERS,ISTEP,NUMBE1

     * ,SURRA1,LENGT1,HRDEG(IT),SUINS,ISKI)
C
       TOLOSS=0.0
       IDS1=0
       IDS2=0
       IDS3=0
```

```
C
C
       GO TO 101
C
      END IF
  102 CONTINUE
C
C $$$$$ End of day loop $$$$$
C
  901 CONTINUE
C
C $$$$$ End of sensitivity loop $$$$$
C
C***********************************************
C   17___INPUT DATA ARE FORMATTED AND PRINTED    *
C***********************************************
C
      WRITE(8,1025)
 1025  FORMAT(1H0,2X,'Start',2x,'Finish',2x,'Latitude',
     * 2x,'Leap year',
     * 2x,'Migration tran-start G.S.',2x,'Data
     * (Exp./Literature)',2x,
     * 'Insecticide or not',2x,'Dev. threshold')
C
      WRITE(8,1026)
 1026  FORMAT(3X,'-----',2X,'------',2X,'--------',
     * 2X,'---------',
     * 2X,'-------------------------',2X,'----------
     * -----------',2X,
     * '------------------',2X,'--------------')
C
      WRITE(8,1027)ISTART,IFINIS,LAT,LEAP,P1,ISKEXP,ISKINT,THRE
 1027  FORMAT(3X,I4,4X,I4,5X,F4.1,6X,A4,14X,F4.1,23X,I1,21X,I1
     * ,17X,F5.2)
C
      WRITE(8,1028)
 1028  FORMAT(1H0,2X,'Insecticide',4x,'Application one'
     * ,2x,'Application
     * two',2x,'Application three',2X,'I',2x,'Tiller
     * number',2X,'Kill
     * rate(t)',2x,'Kill rate(b)')
C
      WRITE(8,1029)
 1029  FORMAT(3X,'-----------',4X,'---------------',
     * 2X,'------------
     * ---',2X,'-----------------',2x,'I',2X,'----
     * ---------',2x,'
     * ------------',2x,'------------')
C
      WRITE(8,1030)ISK1,ISK2,ISK3,TILNO,DRATE,BR
 1030  FORMAT(3X,'Skip',18x,I1,16X,I1,17X,I1,10X,'I'
     * ,5X,F6.2,10X,F4.2,10X,F4.2)
C
      WRITE(8,1031)ISG1,ISG2,ISG3
 1031  FORMAT(3X,'Crop stage',11x,I2,15X,I2,16X,I2,10X,'I')
C
      WRITE(8,1032)
 1032 FORMAT(1H0,2X,'Grain price/tonne',3x,'Potential loss',3x,
     * 'Wheel loss',3x,'Spraying cost')
```

```
C
      WRITE(8,1033)
 1033  FORMAT(3X,'-----------------',3X,'--------------',3X,
     * '----------',3X,'-------------')
C
      WRITE(8,1034)PRICE,CTLOSS,WHEEL,PESCOS
 1034  FORMAT(8X,F6.2,13X,F4.2,10X,F6.3,8X,F6.2)
C
      WRITE(8,1006)
 1006  FORMAT(1H0,4X,'Suction trap data output
     * modified by "taypal" relation')
C
      WRITE(8,1007)(IMM(IN),IN=ISTART,IFINIS)
 1007  FORMAT(5F10.3)
C
      WRITE(8,1035)
 1035  FORMAT(1H0,28X,'Sensitivity analysis')
C
      WRITE(8,1036)
 1036  FORMAT(1X,'Temperature',2x,'Crop stage',2x,'
     * Aphid dev. length',2x,
     * 'Survival',2x,'Reproduction',2x,'Immigration')
C
      WRITE(8,1037)((SEN(I,J),J=1,6),I=1,N)
 1037 FORMAT(2x,F5.2,8X,F5.2,11X,F5.2,10X,F5.2,7X,F5.2,8X,F5.2)
C
      WRITE(8,1038)
 1038  FORMAT(2X,'Morph determination',2x,'Imm. tran.
     *G.S.',2x,'Tans.
     *length',2x,'Time step',2x,'Insecticide period')
C
      WRITE(8,1039)((SEN(I,J),J=7,11),I=1,N)
 1039  FORMAT(9X,F5.2,10X,F7.2,9X,F7.2,7X,F7.2,9X,F7.2)
C
      WRITE(8,1011)
 1011  FORMAT(1H0,35X,'Maximum temperature')
C
      WRITE(8,1012)(TMAX(IN),IN=ISTART-1,IFINIS)
 1012  FORMAT(1X,15F7.2)
C
      WRITE(8,1013)
 1013  FORMAT(1H0,35X,'Minimum temperature')
C
      WRITE(8,1014)(TMIN(IN),IN=ISTART,IFINIS+1)
 1014  FORMAT(1X,15F7.2)
C
C
C*****..... THE END.....*****
C
      STOP

      END

C
C************************************************
C                 18___SUBROUTINES                *
C************************************************
C
C  Subroutine 1: Update aphids over their age classes
```

```
C
      SUBROUTINE DEVSUR(APHIDS,ISTEP,TOTAL,SURVIV,
     *ALONG,HRDEG,SUINS,ISKIP)
C
      REAL APHIDS(2,ISTEP),SURVIV(5),ALONG(5),TOTAL(5)
      DO 60 LT=1,5
        TOTAL(LT)=0.0
   60 CONTINUE
C

C  Updating: starting with the old age class
C
      DO 109 I=ISTEP,2,-1
C
C  Age is updated.
C
      APHIDS(2,I)=APHIDS(2,I-1)+HRDEG
      APHIDS(2,I-1)=0.0
      IF(ISKIP.EQ.1)THEN
       IF(APHIDS(2,I).LT
     * .(ALONG(5)-ALONG(4)))J=5
       TOTAL(J)=TOTAL(J)+APHIDS(1,I)
       GO TO 70
      ELSE
       GO TO 80
      END IF
C
   80 CONTINUE
C
C  The IFBLOCK for calculations of
C  different instars and adult stage
C
      IF(APHIDS(2,I).GT.ALONG(4)
     *.AND.APHIDS(2,I).LT.ALONG(5))THEN
C
        J=5
C
      ELSE IF(APHIDS(2,I).GT.ALONG(3)
     *.AND.APHIDS(2,I).LT.ALONG(4))THEN
C
        J=4
C
      ELSE IF(APHIDS(2,I).GT.ALONG(2)
     *.AND.APHIDS(2,I).LT.ALONG(3))THEN
C
        J=3
C
      ELSE IF(APHIDS(2,I).GT.ALONG(1)
     *.AND.APHIDS(2,I).LT.ALONG(2))THEN
C
        J=2
C
      ELSE IF(APHIDS(2,I).LT.ALONG(1))THEN
C
        J=1
C
      END IF
   70 CONTINUE
C
```

```
C    The numbers in the old age class I-1 are moved into I
C   and some die
C
        APHIDS(1,I)=APHIDS(1,I-1)*SURVIV(J)*SUINS
C
C   The element in i-1 is zeroed
C
        APHIDS(1,I-1)=0.0
C
C   Total aphid numbers are summed for each instar
C
        TOTAL(J)=TOTAL(J)+APHIDS(1,I)
C
C   Total up aphids
C
        TOTALS=TOTALS+APHIDS(1,I)
  109 CONTINUE

        RETURN

        END

C
C
C

C   Function 1: Suction trap catches transformed to field data
C
         FUNCTION ALATC(TMM,P1,P2,CRSTAG)
        ALATC=(1-(CRSTAG-P1)/(P2-P1))*TMM
        RETURN
        END
C
C
C
C   Subroutine 2: Hourdegrees for reproduction and development
C
        SUBROUTINE DEVTEMP(MNT1,MNT2,MXT1,MXT2,
       *HRDEG,HRDREP,NN,ISK,DTRES)
C
        DIMENSION TEMP(24),HRDEG(24),HRDREP(24),
       *STHRDG(24),STHDRP(24)
        COMMON PI,LAT,IDAY
        INTEGER NN
        REAL MNT1,MNT2,MXT1,MXT2
        JJ=NN
C

        CALL SUN(RISE)
C
C   Hour temperature during a day

        DO 15 J=1,24
C
C    Hour temperature from last max to next min
C   MXT1- for last day;MNT1- for first day temp.
C
        IF(J.LE.RISE)TEMP(J)=((MXT1
      * -MNT1)*(COS(PI*(J-
```

```
     * 2*RISE-10)/(10+RISE))
     * ))/2.0+(MXT1+MNT1)/2.0
C

      IF(J.GE.14)TEMP(J)=((MXT2
     * -MNT2)*(COS(PI*(J-14)/(10+RISE
     * ))))/2.0+(MXT2+MNT2)/2.0
C

C   Hour temperature from minimum to maximum
C  at the same day
C
      IF(J.GT.RISE.AND.J.LT.14)TEMP(
     * J)=((MXT2-MNT1
     * )*(-COS(PI*(J-RISE)/(14-RISE))))/2.0+(MXT2
     * +MNT1)/2.0
C

C  Physiological time calculation
C
C  development
C
      IF(TEMP(J).LE.(DTRES))STHRDG(J)=0.0
      IF(TEMP(J).GT.(DTRES).AND.TEMP(J).
     * LE.20.0)STHRDG(J)=TEMP(J)-(DTRES)
      IF(TEMP(J).GT.20.0.AND.TEMP(J).
     * LE.27.5)STHRDG(J)=4.167*(8.912-0.178*TEMP(J)
     * )-DTRES
      IF(TEMP(J).GT.27.5)STHRDG(J)=0.0
C
C  ISK: experimental data(1) or literature (0)
C
      IF(ISK.NE.0)THEN
C
       STHRDG(J)=TEMP(J)-DTRES
       IF(STHRDG(J).LT.0.0)STHRDG(J)=0.0
      ELSE
       GO TO 105
      END IF
C
 105  CONTINUE
C
C  Reproduction
C
      IF(TEMP(J).LT.5.0)STHDRP(J)=0.0
       IF(TEMP(J).LT.10.0.AND.TEMP(J).GE.5.
     * )STHDRP(J)=0.5*TEMP(J)
         IF(TEMP(J).LE.25.AND.TEMP(J).GE.10.)
     *    STHDRP(J)=TEMP(J)
          IF(TEMP(J).GT.25.0)STHDRP(J)=0.12*
     *    TEMP(J)
   15  CONTINUE
C
C  Hour degree over time step length
C
      DO 25 IT=1,24/JJ
C
C    Development
C
```

```
      HRDEG(IT)=0.0
C
C     Reproduction
C
      HRDREP(IT)=0.0
   25 CONTINUE
      II=1
      IJ=JJ
      DO 30 IT=1,24/JJ
      DO 35 I=II,IJ
        HRDEG(IT)=HRDEG(IT)+STHRDG(I)
        HRDREP(IT)=HRDREP(IT)+STHDRP(I)
   35 CONTINUE
       II=II+JJ
       IJ=IJ+JJ
   30  CONTINUE
      RETURN
      END
C
C
C
C  Subroutine 3: Crop development
C
      SUBROUTINE CROPGROWTH(TS,X,XS,G,C)
      THRESH=6.0

      DD=0.0

      DO 304 IN=1,2
       Y=TS+X-2.0*THRESH
       IF(X.LT.THRESH)GO TO 301
       B=0.25*Y

       GO TO 303

  301 IF(TS.GT.THRESH)GO TO 302
       B=0.0

       GO TO 303

  302 T=ASIN(Y/(X-TS))
      B=0.125*Y*(1.0-0.63661977*T)+0.079577472*(TS-X)*COS(T)
      IF(B.LT.0.0)B=0.0
  303 CONTINUE

       DD=DD+B

       X=XS
  304 CONTINUE

C
C  Day are summed
c
      G=G+DD

      C=0.173224*G-0.000125*G*G+26.33648
      RETURN
      END
C
```

```
C
C
C  Subroutine 4: Sunrise time is calculated
C
      SUBROUTINE SUN(RISE)
      COMMON PI,LAT,IDAY
      RAD=PI/180.0
      CONV=RAD*LAT
      DEC=-23.4*COS(PI*(IDAY+10.173)/182.621)
      SSIN=SIN(CONV)*SIN(RAD*DEC)
      CCOS=COS(CONV)*COS(RAD*DEC)
      TT=SSIN/CCOS
      AS=ASIN(TT)
      DAYL=12.0*(PI+2.0*AS)/PI
      RISE=12.0-(DAYL/2.0)+0.5
      RETURN
      END
C
C
C  Subroutine 5: Insecticide
C
      SUBROUTINE INSECTICIDE(ID,IDS,IU,DR,S,BR)
       P=ID
       SE=IU
       D=IDS
       S=1-DR*EXP((LOG(BR)/SE)*(P-D))
       IF(S.GT.(1-BR))S=1.0
       IF(S.LT.(1-DR))S=1-DR
       RETURN
       END
C
C
C
C  Subroutine 6: Calculate day and month
C
      SUBROUTINE CALENDER(IDAY,DD,MM,LEAP)
      INTEGER MT(12),MD(12),DD,MM
      DATA (MT(I),I=1,12),(MD(I),I=1,12)/31,59,
     *90,120,151,181,212,243,273,304,334,365,31,28,
     *31,30,31,30,31,31,30,31,30,31/
C
      IF(LEAP.EQ.'YES')THEN
       MD(2)=29
       DO 10 I=2,12
        MT(I)=MT(I)+1
   10  CONTINUE
      END IF
C
      IF(IDAY.LE.MT(1))THEN
       MM=1
       DD=IDAY
      ELSE IF(IDAY.LE.MT(2).AND.IDAY.GT.MT(1))THEN
       MM=2
       DD=IDAY-MT(1)
      ELSE IF(IDAY.LE.MT(3).AND.IDAY.GT.MT(2))THEN
       MM=3
       DD=IDAY-MT(2)
      ELSE IF(IDAY.LE.MT(4).AND.IDAY.GT.MT(3))THEN
       MM=4
```

```
        DD=IDAY-MT(3)
       ELSE IF(IDAY.LE.MT(5).AND.IDAY.GT.MT(4))THEN
        MM=5
        DD=IDAY-MT(4)
       ELSE IF(IDAY.LE.MT(6).AND.IDAY.GT.MT(5))THEN
        MM=6
        DD=IDAY-MT(5)
       ELSE IF(IDAY.LE.MT(7).AND.IDAY.GT.MT(6))THEN
        MM=7
        DD=IDAY-MT(6)
       ELSE IF(IDAY.LE.MT(8).AND.IDAY.GT.MT(7))THEN
        MM=8
        DD=IDAY-MT(7)
       ELSE IF(IDAY.LE.MT(9).AND.IDAY.GT.MT(8))THEN
        MM=9
        DD=IDAY-MT(8)
       ELSE IF(IDAY.LE.MT(10).AND.IDAY.GT.MT(9))THEN
        MM=10
        DD=IDAY-MT(9)
       ELSE IF(IDAY.LE.MT(11).AND.IDAY.GT.MT(10))THEN
        MM=11
        DD=IDAY-MT(10)
       ELSE
        MM=12
        DD=IDAY-MT(11)
       END IF
       RETURN
       END
C
C
C
C  Subroutine 7: Calculate profits of control
C
      SUBROUTINE BENEFIT(PRICE,CTLOSS,CLOSS,WHEEL,PESCOS,
     *OUPROB,FRPROB,CLOS1,CLOS2)
C  Y: expected yield
C  LECO: losses in economic term after insecticide spray
C
      CHARACTER*10 EXPRES(11)
      REAL LECO(11),BENEF(11),Y(11),BNPRP(11),BNFRC(11),
     *BNNCTR(11),BNFRCC(11),BNPRPP(11)
C
      DO 10 I =0,8
       R=I
       Y(I)=6.0+0.5*R
       LECO(I)=CLOSS*Y(I)*PRICE
       SA=1.0-CTLOSS
       SL=(1.0-CLOSS)*(1.0-WHEEL)
C
C Control strategies
C
C  1 no control and no aphid outbreak
C
       PRI1=Y(I)*PRICE
C
C  2 no outbreak and control
C
       PRI2=Y(I)*PRICE*(1.0-WHEEL)-PESCOS
C
```

```
C  3 outbreak and no control
C
       PRI3=Y(I)*PRICE*(1.0-CTLOSS)
C
C  4 outbreak and control
C
       PRI4=Y(I)*PRICE*(1.0-CLOSS)*(1.0-WHEEL)-PESCOS
C
C
C  No control
C
       BNNCTR(I)=PRI1*(1.0-OUPROB)+PRI3*OUPROB
C
C  Prophylactic control
C
       BNPRPP(I)=PRI4*OUPROB+PRI2*(1.0-OUPROB)
C
C
C  Control based on forecasting
C
       BNFRCC(I)=PRI1*(1.0-OUPROB)*FRPROB+PRI4*OUPROB*
     * FRPROB+PRI2*(1.0-OUPROB)*(1.0-FRPROB)+PRI3*
     * OUPROB*(1.0-FRPROB)
C
       BNPRP(I)=BNFRCC(I)-BNPRPP(I)
       BNFRC(I)=BNFRCC(I)-BNNCTR(I)
C
       BENEF(I)=(SL-SA)*Y(I)*PRICE-PESCOS
       IF(BENEF(I).LE.0.0)EXPRES(I)='No benefit'
       IF(BENEF(I).GT.0.0)EXPRES(I)='   Benefit'

   10 CONTINUE
      WRITE(9,1040)(Y(I),I=0,8)
      WRITE(9,1041)(BENEF(I),I=0,8)
      WRITE(21,1043)OUPROB,FRPROB,(BNPRP(I),I=0,2)
      WRITE(22,1043)OUPROB,FRPROB,(BNFRC(I),I=0,2)
      WRITE(9,1042)(EXPRES(I),I=0,8)
 1040 FORMAT(1H0,'Expected yield',9(8x,F4.1))
 1041 FORMAT(1X,'Benefit',7x,9(5x,F7.2))
 1042 FORMAT(15X,9(2X,A10))
 1043 FORMAT(1X,5(2X,F7.2))
      RETURN
      END
```