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The Ecology of the Bird Cherry-Oat Aphid,
Rhopalosiphum padi (L.) (Hemiptera: Aphididae) in
the Low Rainfall Wheat Belt of South Australia.

By

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TO ELIZABETH ANNE CARTER

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SUMMARY

The lack of adequate summer rainfall in South Australia prevents cereals from being grown during summer and restricts non-cereal grasses to irrigated areas. These included perennial grass pastures and forage crops. *Rhopalosiphum maidis* (Fitch) was found to infest forage crops, but it rarely infested wheat and was not studied. The only other species found was *R. padi* (L.) which occurred in perennial grass pastures. The PAV and RPV types of barley yellow dwarf virus (BYDV) also occurred in these pastures.

In order for *R. padi* to infest wheat, aphids surviving over summer need to produce alate progeny which then migrate. Large numbers of alates were produced in April/May. The numbers produced depended on the numbers of aphids surviving summer. The number surviving was inversely related to the number and frequency of days $\geq 36^{\circ}\text{C}$. Alate production was due to decreasing photoperiod, temperature and crowding. Between 2 and 82% of alates transmitted BYDV and therefore, had the potential to cause significant infections. There were no further flights from pastures.

Alates migrating from pastures infested wheat crops sown between late April and early May, but in South Australia most crops, due to the timing of autumn rainfall, are not sown until late May and so emerge after the flights.

Therefore, most alates land on non-cereal hosts such as annual volunteer grasses. Surveys of wheat crops and annual volunteer grasses in June and July indicated *R. padi* had dispersed across the state.

Alate production in these grasses began in July. Alate production continued through to October. Production was largely due to increasing day length, declining host quality and crowding. Alates infested surrounding wheat crops while many were still tillering and were considered to be the main source of infestation of most crops sown. However, less than 1% transmitted virus indicating they were unlikely to cause significant infections.

In wheat crops, proportions of tillers infested ranged from 0.42 to 0.65. Despite the high proportions of infestation, the proportion of infection was low.

BYDV is unlikely to be a serious risk to wheat farmers unless rains fall earlier in autumn than normal, resulting in more crops emerging during the autumn flights of viruliferous alates.

Declaration

The work presented in this thesis is my own work unless otherwise acknowledged, and has not previously been published or submitted for the award of any degree or diploma. This thesis may be made available for loan or photocopying provided that an acknowledgment is made in the instance of any reference to this work.

Paul J. De Barro

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INTRODUCTION

South Australia has a hot dry climate. Therefore, the phenology of cereal aphids and the epidemiology of barley yellow dwarf virus (BYDV) which they transmit are greatly affected by the influence which climate has on their hosts. As a consequence, whether BYDV is a significant threat to wheat crops in South Australia is largely determined by how well aphid phenology, virus epidemiology and wheat agronomy interlink.

South Australia is the driest state in Australia and much of the state's cropping area (≈ 1.5 million ha) receives between 250 and 500 mm of annual rainfall. This area is known as the low rainfall wheat belt. The remaining cropping area ($\approx 20\,000$ ha) receives greater than 500 mm of annual rainfall, but is considered insignificant in terms of total state production and will be ignored in this study.

The low rainfall wheat belt has mild wet winters with a monthly mean temperature of 11.0 to 11.8°C and hot dry summers with a mean monthly maximum temperature of 37.3 to 38.7°C . The average monthly rainfall of 26 mm is far exceeded by a monthly average evaporation of 216 mm (WARI Biennial Report 1986-1987).

In South Australia the timing of sowing of winter cereals

is firmly linked to rainfall. In a typical year the season "breaks" with "opening rains" in March/April (autumn), and wheat crops are sown in late May or early June. However, in most years some parts of the wheat belt receive sufficient rain to allow crops to be sown in late April or early May. These crops are known as early sown crops. In addition, some areas do not receive rains until mid to late June resulting in sowing being delayed until mid June or early July. These crops are known as late sown crops. The "opening rains" also allow annual volunteer grass species to germinate. These species are widespread, occurring along roadside verges, and in annual pastures and on waste ground.

The lack of adequate summer rainfall in South Australia results in little cereal cropping over summer and it also prevents the survival of most grasses which are not irrigated. Therefore, aphids and viruses can not survive in successive cereal crops, as few are sown during summer and so are forced to over-summer in alternative habitats which I will call refuge areas. These refuge areas are irrigated and composed of non-cereal grasses.

For cereal aphids to infest wheat crops, aphids surviving in refuge areas over summer need to produce progeny which develop wings and then migrate to these crops. Plumb et al. (1986) proposed that the severity of outbreaks in countries with harsh summers reflects how well aphids and BYDV survive in their refuge areas.

RESEARCH PLAN

This study is an attempt to determine whether BYDV is a serious threat to wheat crops in the low rainfall regions of South Australia. It involves the phenology and ecology of cereal aphids which vector BYDV. A parallel study by Dr Monique Henry was undertaken concurrently to examine the epidemiology of BYDV (see chapter 15).

There are 2 possible hypotheses which may be used to explain the annual infestation of wheat crops by cereal aphids. The first is that refuge areas are locally available and in autumn and winter produce sufficient numbers of alates which then fly off to infest and infect wheat crops. The alternative is that local refuges are minor and most aphids infesting wheat come from elsewhere, eg. the south-eastern corner of Australia where the climate is wetter and cooler over summer.

This study examines only the first of these hypotheses.

Because the hot dry summers over much of South Australia restrict grasses to irrigated habitats, both cereal aphids and virus are likely to be restricted to these habitats during summer if they are to survive. Therefore, the first part of this study will be to determine where the refuge

areas for cereal aphids are in South Australia and which species are present.

For cereal aphids in these refuge areas to infest wheat crops, they will need to produce alate progeny which then migrate from the refuge areas into newly sown crops. To answer this, populations within refuge areas will be monitored to determine when aphids migrate. The timing of this migration will further allow speculation as to where these alates mostly migrate. As part of this study, factors which may influence, the numbers of alates produced and the timing of the flights will also be examined as they may indicate the level of threat posed by these migrations.

The distance these aphids migrate, and the timing of their arrival in crops will also be studied to further determine the likely threat of BYDV to wheat crops in low rainfall South Australia. Finally, the colonisation and subsequent development of populations in wheat crops will be studied as a means of assessing the potential for damage.

This thesis is largely presented as a series of manuscripts and therefore involves some repetition.

CHAPTER 1

Cereal aphids in Australia

The distribution and biology of cereal aphids in Australia

Several species of Aphididae and Pemphigidae have been recorded feeding on either roots, leaves, stems or the inflorescences of cereals (Blackman & Eastop, 1985). Records of aphids attacking cereals extend back to the 18th century, but it was not until the early 1950's and the discovery that cereal aphids vectored BYDV that these insects were considered important (Oswald & Houston, 1951, 1953; Vickerman & Wratten, 1979). Since that time the study of cereal aphids increased in Europe, the USA and to a lesser extent South America, New Zealand and Australia. A further escalation of research followed widespread outbreaks of *Sitobion avenae* (Fabricius) (grain aphid) in Europe in 1968 (Bruehl, 1961; Vickerman & Wratten, 1979; Dixon, 1987). Potts and Vickerman (1974) speculated that these outbreaks were due to changes in cropping practices. The resultant increase in pest status has resulted in a substantial increase in the level of research into the ecology and biology of cereal aphids (Dixon, 1987). This work has resulted in the publication of several review

articles (Dean, 1974a; Vickerman & Wratten, 1979; Carter et al., 1980; Dixon, 1987; Irwin & Thresh, 1990) and bibliographies (Foster et al., 1985; Araya et al., 1986, 1987). In Australia however, very little has been published on cereal aphids.

Blackman and Eastop (1985) have described 17 Aphididae and 15 Pemphigidae as being regularly associated with wheat. Of the Aphididae; *Rhopalosiphum padi* (L.) (bird cherry-oat aphid), *R. maidis* (Fitch) (corn leaf aphid), *R. insertum* (Walker) (apple grass aphid), *R. rufiabdominalis* (Sasaki) (rice root aphid), *S. miscanthi* (Takahashi), *Metopolophium dirhodum* (Walker) and *Hysteroneura setariae* (Thomas) (rusty plum aphid) have been recorded in Australia (Eastop, 1966; Carver, 1984; Ridland & Carver, 1987; Hales et al., 1990). A further species, *S. nr fragariae* also occurs and was originally described as *S. fragariae* (Walker), but it appears to be morphologically distinct from this species and the new name has been proposed to avoid confusion (Guy et al. 1986; Hales et al., 1990). In Australia, all have been recorded on wheat with the exception of *H. setariae*. The potentially damaging species *S. avenae*, *Schizaphis graminum* (Rondani) (greenbug), *Sipha flava* (Forbes) (yellow sugarcane aphid) and *Diuraphis noxia* (Mordvilko) (Russian wheat aphid) have yet to be introduced to Australia.

R. padi is the most frequently recorded species in Victoria and Tasmania (Smith & Plumb, 1981; Guy et al.

1987). In South Australia *R. padi* was first recorded in cereals in 1961. It is considered the most important vector of BYDV in most parts of Australia.

M. dirhodum is a recent introduction to Australia being first discovered in 1984 on wheat in New South Wales, Tasmania and Victoria and later in 1987 in South Australia; but it has yet to reach Western Australia (Carver, 1984; Waterhouse & Helms, 1985; ECIMS, Ridland, 1988). It is presumed to have been introduced from New Zealand where it was first recorded in 1981 (Sunde, 1984). In New Zealand and Tasmania it has supplanted *R. padi* as being the most important aphid pest of cereals (Stufkens & Farrell, 1984, 1985, 1986; Johnstone et al., 1990). *M. dirhodum* appears to be a minor species in Victoria (P. Ridland, pers. comm.), but its abundance and importance elsewhere in Australia is unknown.

R. maidis was first recorded in cereals in South Australia in 1954 and was most often associated with barley (ECIMS). In southern Australia, *R. maidis* is common on maize and barley following warm months, but is rarely found in winter and early spring (Johnstone et al., 1990). In Queensland, it is frequently a pest of maize, sorghum and to a lesser extent sugar cane, where it transmits sugarcane mosaic virus (Broadley & Rogers, 1978; P. Allsopp, pers. comm.).

S. miscanthi was first recorded in Australia in 1953 and

in South Australia in 1966. It is believed that the periodic outbreaks of this species in Australia are due to mass migrations into southern Australia from New Zealand (Close & Tomlinson, 1975).

R. insertum has been recorded from South Australia, but its hosts and abundance are unknown (Ridland, 1988). *S. nr fragariae* was first recorded in Tasmania (Guy et al., 1986) and it appears to have displaced *S. miscanthi* in southern Australia. Its abundance in South Australia is unknown.

All species, with the exception of *H. setariae* are known vectors of BYDV and will act as vectors in Australia (Butler et al., 1960; Bruehl, 1961; Blackman & Eastop, 1985; Waterhouse & Helms, 1985; Guy et al., 1986; Ridland, 1988; Ridland et al., 1988).

While *M. dirhodum*, *R. maidis*, *R. padi*, *S. nr fragariae* and *S. miscanthi* have been recorded on wheat in South Australia, their over-summering refuge areas are unknown.

Of the species which are known to occur in South Australia, *R. maidis*, *S. miscanthi* and *R. padi* have been found elsewhere in Australia to have clones which possess differing numbers of chromosomes (Brown & Blackman, 1988; Hales et al., 1990; D. Hales, pers. comm.). The influence of the differing karyotypes on the biological performance of the respective clones is unknown, although there is some

evidence to suggest that the various karyotypes of *R. maidis* have differing host preferences (Brown & Blackman, 1988; D. Hales, pers. comm.). It will, therefore, be necessary to determine the karyotypes of the cereal aphids found in South Australia as any differences may have a profound effect on the phenologies of these species.

None of the Pemphigidae known to feed on wheat overseas have been described in association with the crop in Australia. However, 2 species, *Aploneura lentisci* (Passereni) and *Geoica lucifuga* (Zehntner) have recorded on the roots of several species of Gramineae in Australia (Blackman & Eastop, 1985). The ability of either species to transmit BYDV is unknown although Orlob (1966) reported that *G. utricularia* failed to transmit BYDV.

Lifecycle of cereal aphids

Of the main cereal aphids in Australia *R. padi*, *R. rufiabdominalis*, *R. insertum*, *S. nr fragariae* and *M. dirhodum* are believed to be holoarctic in origin and have evolved an adaptive polymorphism by which they survive cold winters when food is scarce and then rapidly utilise food resources in spring and autumn. This polymorphism involves the production of sexually reproducing morphs prior to autumn/winter followed by the production of asexual morphs in spring. Often associated with this polymorphism is the

alternation between primary (autumn/winter) hosts and secondary (spring/summer) hosts. These species are normally referred to as being holocyclic and heteroecious. *R. maidis* and *S. miscanthi* are both more commonly found in warm temperate and tropical climates and are presumed to be completely anholocyclic and monoecious (Blackman & Eastop, 1985).

Generally, holocyclic heteroecious species in Australia have lost the adaptive polymorphism as winters over much of Australia are mild (Maelzer, 1981). Exceptions can be found around Canberra and Tasmania which both have very cold winters. As a result cereal aphids in Australia normally follow a simple asexual lifecycle in which only anholocyclic, monoecious, parthenogenetic, viviparous females are known. The vestiges of the polymorphism are seen in the production of asexual alate and apterous morphs (Maelzer, 1981).

As only the asexual exules occur their hosts will belong almost exclusively to the Gramineae.

Host ranges in Australia

Most species of aphids are extremely polyphagous within the Gramineae (Blackman & Eastop, 1985). In Australia *R. maidis* has been recorded mostly on panicoid grasses such as

Chenchrus, *Digitaria*, *Echinochloa*, *Eleusine*, *Panicum*, *Pennisetum* and *Sorghum*, but has also been noted on festucoid species belonging to *Avena*, *Hordeum* and *Triticum* (Eastop, 1966; Guy et al. 1987).

In contrast, *R. padi* appears to be more frequently recorded on species belonging to festucoid grasses such as *Avena*, *Bromus*, *Dactylis*, *Festuca*, *Hordeum*, *Lolium* and *Triticum* (Eastop, 1966; Guy et al., 1987). The apparent difference in host preference may reflect the different origins of the 2 species. The preference of *R. padi* for festucoid species reflects this species' holarctic origins where these grasses are more common than the panicoid species. In contrast, the preference for panicoid species demonstrated by *R. maidis* reflects its Asiatic origin where these grass species are more common (Johnstone et al., 1990). *R. padi* has also been reported on non-gramineous hosts and is considered a minor pest of potatoes in Queensland (Cantrell et al., 1983).

M. dirhodum occurs mostly on species of festucoid grasses such as *Bromus* and *Dactylis*, which again may reflect its holarctic origins, but has not been noted on *Lolium perenne* (perennial ryegrass) (Johnstone et al., 1990). *S. miscanthi* has been recorded on several species belonging to *Dactylis*, *Hordeum* and *Triticum* while *S. nr fragariae* has been noted on *Avena*, *Ehrharta*, *Hordeum*, *Trisetum* and *Triticum* (Guy et al., 1987). The host ranges with in Australia of the remaining

species are not known.

Host preference

Overseas host preference studies may have little application in Australia due to differences in cultivars, biotypes and environment. However, Leather and Dixon (1981; 1982) found both *R. padi* alate and apterous exules preferred *L. perenne* to wheat, barley and oats.

Studies and host records in Australia indicate differences in host preferences do occur. *R. maidis* is uncommon on wheat, appearing to prefer barley while *R. padi* prefers wheat to barley (Eastop, 1966; ECIMS). Host preference amongst the other cereal aphids in Australia is unknown. Selective preference of aphid species for different wheat cultivars is unknown as is the level of resistance/tolerance in Australian wheat lines to either the aphids or BYDV. A measure of preference by cereal aphids for certain wheat cultivars has been found in France, but the differences in preference were not always stable from year to year and were smaller than differences caused by different sowing dates of the same cultivars (Dedryver & Di Pietro, 1986). However, wild relatives of barley and oats can possess high levels of resistance to *R. padi* (Weibull, 1988).

The mechanism of host plant selection by cereal aphids has

seldom been studied. Dixon (1971) studied host alternation of *R. padi* between oats and the primary host *Prunus padus*, but as this involved the sexual morphs it is doubtful whether this work has much bearing on the selection of one gramineous host over another.

The availability of the preferred hosts of a species may significantly affect its importance as a vector in a particular area, especially when potential hosts are restricted to localised refuges (Johnstone et al., 1990).

Feeding sites

All cereal aphids found in Australia are phloem feeders and feed predominantly on the leaves, stalks or heads of cereals with the exceptions of *R. insertum* and *R. rufiabdominalis* which feed primarily on the roots and stalk bases (Ridland, 1988).

S. miscanthi and *S. nr fragariae* prefer the upper leaves of wheat and later the heads when they emerge. *M. dirhodum* feeds mainly on leaves, beginning their feeding on the lower leaves and then migrating to the upper leaves as the population increases (Lowe, 1961; Dean, 1974a). The upward movement of *M. dirhodum* coincides with host maturation (Vickerman & Wratten, 1979; Dedryver, 1978). *R. padi* feeds mainly on the lower leaves, behind leaf sheathes and at stem

bases (Dean, 1974a), but also occurs on roots, upper leaves and ears, but to a lesser extent (Vickerman & Wratten, 1979; Jones, 1979, Wiktelius, 1987). The choice of feeding site affects the weight and fecundity of *R. padi* as aphids feeding on wheat stems are heavier and more fecund than those feeding on the flag leaf or ear (Leather & Dixon, 1981).

There appears to be little concern in Australia that cereal aphids damage wheat through direct feeding. Instead, all studies have dealt with the ability of the various species to transmit BYDV (Johnstone *et al.*, 1990, Sward, 1990).

CHAPTER 2

Barley yellow dwarf virus in Australia

BYDV and its vectors

BYDV belongs to the luteovirus group which includes several other economically important viruses including beet western yellows (BWYV) and potato leaf roll. It has a single-stranded RNA genome enclosed in a protein coat and is transmitted persistently by aphids (Burnett, 1984). BYDV is one of the most widely distributed and is vectored by 23 different aphid species (Jones & Lazenby, 1988). Both adults and nymphs transmit BYDV equally well (Plumb, 1974). The virus normally multiplies only in the phloem and spreads rapidly throughout the plant. When more than one strain is present xylem tissue may also be infected (Gildow, 1984). BYDV is not seed borne.

There are 5 types of BYDV known as the New York BYDV types. These are widely used to identify isolates found elsewhere. The MAV type is transmitted specifically by *S. avenae*, SGV type by *Sch. graminum*, RPV type by *R. padi* and RMV type by *R. maidis*. Another isolate PAV is non-specifically transmitted by *R. padi*, *M. dirhodum*, *Sch. graminum* and *S. avenae*. The types vary in virulence, MAV is

mild while PAV and RPV are severe. Each type in turn has several variants which differ in virulence, host range, serological behaviour and vector relationships. There is no cross protection between types (Watson & Mulligan, 1960; Rochow, 1970, 1979; Plumb, 1974; Lister et al., 1984; Gildow & Rochow, 1983; Lister & Sward, 1988).

PAV or a mixture of PAV and RPV are the most commonly detected isolate in Victoria, Tasmania and South Australia (Guy et al., 1987; Sward & Lister, 1987; H. Wallwork, pers. comm.). The Australian isolates of RPV, PAV and RMV appear to be related to the New York types (Sward & Lister, 1988).

Aphids can only become infective with BYDV after they have fed on the infected phloem from infected plants (Burnett, 1984). To be transmitted the virus particles must pass into the alimentary canal where they are transported through the gut epithelial cells into the haemocoel. Virus particles circulate in the haemocoel until they are absorbed by the accessory salivary gland. From here they are excreted along with the saliva during feeding (Burnett, 1984).

R. padi is able to transmit virus to healthy plants in 15 minutes (Watson & Mulligan, 1960). The latent period between uptake and transmission can be as short as 4 days, although at this rate transmission levels are only 10 to 20%. An 8 day latent period achieves greater than 90% transmission (Plumb, 1974). The minimum latent period is 48

hours. For successful inoculation to take place, the virus must be inoculated directly into viable phloem cells with little damage occurring (Gildow, 1984). For this reason attempts at artificial inoculation of BYDV have failed. Ultrastructural examinations of aphid tissue and transmission studies have failed to show any viral replication taking place within aphid vectors (Gildow, 1984).

Symptoms associated with BYDV infection

Most grasses can be infected by BYDV, but few display obvious symptoms. Symptoms displayed in wheat depend upon the time of infection, the strain of virus, the numbers of aphids present, cultivar susceptibility to the virus and environmental conditions such as light and temperature. Loss of green colour in the leaves is the most conspicuous symptom (Rochow, 1961).

In South Australia symptoms range from slight mottling to bright yellow chlorosis starting at leaf tips and extending to the base. Streaking occurs along with reddening or purpling of leaves. Growth reduction, stunting, poor root development and partial sterility (deadheads) may result from early infections (Price & Stubbs, 1963; Wallwork, 1986). Late infections may lead to poor grain formation and filling (ibid).

Symptoms in wheat can take between 7 and 21 days to be apparent. Incubation time of the virus is generally shortest in oats, followed by barley and then wheat. Barley usually turns bright yellow while oats turn a pinkish red (Rochow, 1961). Amongst the cereals, oats usually display the clearest symptoms and is often used as an indicator plant for determining levels of infection in aphids and crops. However, as symptoms may be misinterpreted (D'Arcy, 1984) the enzyme-linked immunosorbent assay (ELISA) should be used to confirm the diagnosis.

The effect of BYDV on the host plant

BYDV has several effects on the host plant. These include cytopathological and physiological alteration of cereal grains, phloem necrosis and infection and destruction of the xylem when plants are infected by more than one strain. In infected barley and wheat, photosynthesis and transpiration decrease while respiration increases. An accumulation of soluble carbohydrates and starch also takes place in the leaves while concentrations in the roots decline. This is thought to be due to destruction of the phloem resulting in blockage of the translocation pathway. Increase of nitrogenous compounds in leaves also occurs which is a possible benefit to phloem feeding aphids (Ajayi & Dewar, 1983). The physiological responses of wheat to virus infection are similar to those which occur during normal

leaf senescence (Gildow, 1984).

Mature plants are less affected by BYDV than younger plants. It is possible that higher temperatures normally associated with older plants are less conducive to virus development. Rochow et al. (1965) found 2 to 5 times more virus in oats grown at 15 to 20°C than at 25°C. Smith and Sward (1982) have shown that wheat at the stem elongation stage is easy to infect, but that longer exposure to infected aphids is needed to significantly reduce yields. BYDV replication may therefore be impaired in older plants. Consequently, the timing of infection of wheat crops is likely to significantly influence the likelihood of economic damage.

Host plants of BYDV

The availability of suitable hosts for BYDV, especially over summer may have a major influence on the likelihood of BYDV being a significant problem. Like cereal aphids, BYDV has a very wide host range, which is not surprising as the two are inextricably linked. Bruehl (1961) lists 34 genera and 97 species of the Gramineae as being susceptible to BYDV. Of the 34 genera, 30 occur in South Australia (Jessop & Toelken, 1986) and include *Avena*, *Bromus*, *Festuca*, *Hordeum*, *Lolium*, *Phalaris*, *Poa* and *Triticum* which together constitute the most commonly occurring cultivated and weed

species in South Australia. BYDV has been recorded in some or all of the above genera. In Tasmania (Guy et al., 1986, 1987), Victoria (Sward & Lister, 1987), New South Wales (Waterhouse & Helms, 1985), Queensland (Greber, 1988) and Western Australia (McLean & Khan, 1983; Jones et al., 1990). This suggests that BYDV is widely distributed across Australia and further suggests there are numerous possible hosts for the disease in South Australia.

Nothing is known of the phenology of cereal aphids or virus epidemiology in South Australia. However, as cereals are not widely sown in summer and the host ranges of both aphids and virus are wide, non-cereal grasses are likely to play an important role in maintaining the aphids and virus over summer. This has been found to be so in other countries in which continuous cereal cropping does not occur.

In New Zealand *L. perenne* in pastures is the major source of BYDV infected aphids in autumn while in South Africa *Themada trianda (australis)* is an important source of infected vectors (Smith & Wright, 1964; Durr & Martin, 1978). Levels of infection greater than 50% BYDV have been found in perennial ryegrass pastures that were 6 to 30 years old (Latch, 1977). Younger pastures had lower levels of infection (Guy et al., 1986). Similar grasses have also been shown to be important sources of BYDV in the USA (Fargette et al., 1982), Canada (Paliwal, 1982) and England (Catherall, 1963).

In Victoria, all cereals and most pasture grasses are susceptible to one or more of the virus isolates (Price, 1970), but infection levels vary with grass species, climate and region. The incidence of BYDV epiphytotics was greater in higher rainfall regions where the survival of perennial grasses, which acted as reservoirs for both the aphid and virus, was suspected as playing an important role (Price, 1970; Smith & Plumb, 1981). These epiphytotics were also associated with cool, moist summers which lead to increased survival of both the aphid and its host plant, followed by dry autumns which were believed to promote aphid dispersal.

However, the presence of grass based pastures does not always indicate an important virus reservoir. Henry (1988) showed that pastures in western France were infected mainly with the RPV type of BYDV which was uncommon in infected cereals. In addition, while early infection of autumn crops in Indiana was due mainly to virus in the local grass reservoir, subsequent larger infections in spring and summer came from elsewhere as the virus present was different from the local type (Lister et al., 1984).

Assuming both cereal aphids and virus are restricted to refuge areas over summer, factors which influence the timing and size of flights may be important in assessing the risk posed by BYDV to wheat crops in South Australia. Such knowledge may also provide a guide when aphids move from

their refuge areas into newly sown crops.

This chapter outlines the construction, use and efficiency of the main method of sampling cereal aphids used in this study. This chapter has been published in the *J. Aust. ent. Soc.* (1991), 31, 207-208

CHAPTER 3

A cheap light-weight efficient vacuum sampler

Abstract

The McCulloch Eager Beaver Blower/Vac R is a cheap, light and efficient tool for sampling aphids in roadside grasses and pastures.

Introduction

Holtkamp and Thompson (1985) described the construction of a lightweight petrol driven vacuum sampler for insects which was lighter and cheaper than existing vacuum samplers and pointed out the benefits of such a unit over existing models. Rather than making such a unit, it is now possible to buy and slightly modify a garden appliance which is readily available from hardware suppliers.

Materials and Methods

The unit in question is a McCulloch Eager Beaver Blower/Vac R. The unit is powered by a 21.2 cc, 2-stroke

petrol engine with an all position diaphragms which allows use in any position. The vacuum tube is 114.3 mm in diameter and is 762 mm in length. At full throttle the unit outputs 78 dB and samples $11.3 \text{ m}^3/\text{min}$ and runs for 35 to 40 minutes. It weighs 5.08 kg and costs \$290.

The McCulloch has several advantages over the Holtkamp/Thompson model. It is lighter, cheaper, has 4 times greater suction, has a muzzle cut in such a way that it fits flush with a horizontal surface and is available as a manufactured item. The only modification necessary is the placement of a snug fitting plastic sleeve plus fine voile bag into the muzzle of the sampler. The sleeve is held in place by a spring clip. After sampling, the sleeve is removed and the bag emptied by turning it inside out into a plastic bag.

During 1989 the vacuum sampler was used to sample cereal aphids in perennial grass pastures and roadside grasses in South Australia. Pastures were sampled by vacuuming a 30 x 30 cm plot of pasture for 30 seconds. Twelve samples (25 plots per sample) were taken from each of 3 pastures during the period February to November. The efficiency of recovery on wet and dry pastures was measured 4 times during this period, by first removing all vegetation and soil to a depth of 1 cm from each of either 10 or 12 plots at each site following a vacuum sample. Efficiency was then estimated as the mean proportion of aphids left in the plots after

vacuuming. All samples were examined in the laboratory and the species, number, age and morph of cereal aphids counted. To test the influence of pasture height on the efficiency of recovery, the height of the tallest vegetation was measured in each plot.

Roadside grasses were sampled by vacuuming 5, 50 m x 14 cm transects in a zig zag fashion along a selected area of grasses. Grasses were vacuumed at a slow walking pace of 25 m/min. This method was chosen to overcome variability in the distribution of different grass species along the roadside verge. Samples were taken between July and the end of August. The efficiency of recovery of *R. padi* was measured on wet and dry grasses at 3 times during this period at 1 site. Following sampling, efficiency was measured by taking 5 strips, each of 2 m x 14 cm, of grass and soil to a depth of 1 cm from each of 2 transects. Efficiency for each transect was then estimated as follows

$$\text{efficiency} = \frac{\text{average number of aphids in the 5 strips} \times 25}{\text{total number of aphids in the transect}}$$

All samples were examined in the laboratory and the species, number, age and morph of aphids counted. Grass height was measured randomly at 10 points within each transect. The influence of height of vegetation and aphid numbers on efficiency of recovery were tested using linear regression and Student's t test (Zar 1984).

Results and Discussion

Sampling efficiencies of *R. padi* ranged from 0.77 ± 0.09 to 0.93 ± 0.02 in pastures of 31-278 mm height with mean aphid densities of 1.68 ± 0.3 to 20.64 ± 0.99 aphids per plot and from 0.6 ± 0.03 to 0.77 ± 0.01 in roadside grasses of 113-730 mm with total aphid densities of 222-17672 aphids per transect. Some samples were taken when the vegetation was wet, but wetness did not appear to adversely affect the performance of the sampler. The sampler was just as efficient at high aphid densities as it was at low aphid densities in pastures ($r^2=0.15$, $P>0.05$) and roadside grasses ($r^2=0.53$, $P>0.05$). Efficiency of recovery was not significantly influenced by the height of vegetation in pastures ($r^2=0.088$, $P>0.05$) and roadside grasses ($r^2=0.021$, $P>0.05$), but overall efficiency was lower on the taller roadside grasses than on the shorter pasture grasses indicating plant height reduced recovery ($t=2.452$, $P<0.05$, 12 df).

Muzzle air velocity of at least 26.8 m/sec is a critical factor in achieving high rates of extraction with vacuum samplers (Southwood, 1978). The muzzle velocity of the McCulloch is 62.6 m/sec which exceeds this requirement by a factor of 2.3. By contrast, recovery efficiencies of less than 50% have been reported for *R. padi* using the D-Vac (Hand, 1986), possibly due to most D-Vac samplers achieving

velocities up to 40.3 m/sec, which is only 65% as powerful as the McCulloch. The greater power of the McCulloch would appear therefore to explain the improved efficiency of recovery and indicates that it is a useful tool for sampling fauna which either lives on the lower parts of plants or soil surface. In addition, the powerful suction has an added benefit in that it helps to dry wet samples by extracting free water and expelling it through the blower tube.

The data pertaining to the D-Vac is based on the widely used Model 1A unit, later modifications (Summers *et al.*, 1984) include the smaller diameter high suction hose and lighter-weight engine and collecting canister. While the high suction hose may result in muzzle velocities comparable to the McCulloch direct comparisons are not possible as vacuum strength was measured as a pressure and not as a rate. Despite this the modified unit is still noisier, more expensive (ca. 2x the cost of the McCulloch) and ≈ 3 times as heavy as the McCulloch.

Recently published work by Brown and Blackman (1988), and Hales et al. (1990) indicated that some species of cereal aphids have biotypes with differing numbers of chromosomes. These biotypes cannot be reliably separated morphometrically, but have been shown to have different host relationships. This chapter examines the karyotypes of several species of cereal aphids found in South Australia in order to determine whether any variability occurred. This chapter has been published in *J. Aust. ent. Soc.* (in press).

CHAPTER 4

Karyotypes of cereal aphids in South Australia with special reference to *R. maidis*

Abstract

R. maidis in South Australia was found to have a karyotype of $2n=8$, regardless of host plant. This contrasts with world-wide records (Brown & Blackman, 1988), where other karyotypes ($2n=9, 10$) are common on host plants other than maize and sorghum. *R. maidis* ($2n=9$) has been recorded consistently in eastern Australia on hosts other than maize. Other cereal aphids in South Australia, namely, *R. padi*, *M. dirhodum* and *S. nr fragariae* had karyotypes as previously recorded in the literature.

Introduction

Recent studies have suggested that the aphid karyotype may influence host choice (Brown & Blackman, 1988; Blackman et al., 1990; Hales pers. comm.). Brown and Blackman (1988) recorded the karyotypes of a large number of samples of *R. maidis* and found chromosome numbers of $2n=8, 9, 10, 11$ and a structurally heterozygous 8. There was some association of

chromosome number with host plant; aphids on *Zea mays* (maize) and *Sorghum* spp. usually had $2n=8$, and aphids on barley (*H. vulgare*) in the Northern Hemisphere usually had $2n=10$, whereas aphids with $2n=9$ occurred on various hosts including *Setaria* spp., *B. catharticus* and *E. crus-galli* in the Middle East, U.S.A and New Zealand. The structurally heterozygous $2n=8$ and the $2n=11$ aphids were less common and occurred only on maize or *Sorghum* spp..

In Australia, Hales (pers. comm.) found $2n=8$ in *R. maidis* on maize (3 samples), and $2n=9$ on other hosts (6 samples). In addition, I have collected *R. maidis* ($2n=9$) on *Se. verticillata* in Melbourne (3 sites) and *El. indica* from Queensland (1 site). *R. maidis* ($2n=8$) has been found on maize and *R. maidis* ($2n=9$) on *E. crus-galli* in Tasmania (Brown and Blackman 1988). Aphids with different karyotypes could not be reliably separated morphometrically.

I have re-grouped the data of Brown and Blackman (1988) and added Hale's and my records for eastern Australia. A log-likelihood ratio (G Test) indicated (Table 4.1) the significant association of $2n=8$ with maize and *Sorghum* spp. ($P<0.001$), of $2n=10$ with Northern Hemisphere barley ($P<0.001$) and of $2n=9$ with grass species other than maize and *Sorghum* spp. ($P<0.05$).

As part of a study of cereal aphids in southern Australia, *R. maidis* was frequently observed on barley, *S. vulgare*,

Table 4.1. The numbers of aphids of different karyotypes of *R.maidis* found on different host plants. The hypothesis of equal occurrence of each karyotype was tested for each host plant(s) with a G-test (df=2).

Host	Karyotype*			n	Probability, df=2
	8	9	10		
Maize/ <i>Sorghum</i> spp.	57	3	1	61	P<0.001
Northern Hemisphere barley**	4	1	15	20	P<0.001
Other grasses***	7	17	7	31	P<0.05

* Less common karyotypes 2n=11 and 2n=8 (heterozygous) have been omitted

** Includes "ex culture" records, clones may have originated on other field hosts

*** Includes Southern Hemisphere barley and all host plants not otherwise listed, but excludes samples where the host was unidentified

Japanese pearl millet (*E. utilis*) and volunteer panicoid grasses during summer. In winter it occurred on barley and oats (*Avena sativa*), and on volunteer festucoid grasses such as *Bromus* spp. (brome grasses), *Hordeum* spp. (barley grasses) and *Avena* spp. (wild oats). Other species of cereal aphids, especially *R. padi* (L.), were also found in diverse habitats and on numerous host species.

In order to interpret the apparent local migration of *R. maidis*, it was necessary to determine whether karyotypically different forms were associated with particular graminaceous host plants and/or habitats in South Australia.

Materials and Methods

Aphids were collected from a range of host plants at numerous sites across the County Light, Adelaide Plains, Lower and Upper Murray Valley and Southeast regions of South Australia (Table 4.2). The four species of aphids were collected when they were most abundant. *R. padi*, *M. dirhodum* and *S. nr fragariae* were collected during winter and *R. maidis* mainly during summer. Karyotypes were determined by the method described by Hales and Lardner (1988).

Results

The karyotypes for *R. padi* ($2n=8$, 71 aphids from 25 sites), *M. dirhodum* ($2n=18$, 14 aphids from 7 sites) and *S. nr fragariae* ($2n=18$, 11 aphids from 7 sites) agree with those previously published (Blackman & Eastop 1985; Hales et al. 1990). In contrast, all samples of *R. maidis* (Table 4.2) examined had only one chromosome number: $2n=8$. This contrasts with the situation in eastern Australia.

Discussion

These results simplify the interpretation of South Australian population data as a single population with $2n=8$ is present and may colonise the various host plants sequentially. However, further data are required to define the geographic and environmental limits of the $2n=9$ karyotype found in eastern Australia, and until they are available one should assume that both $2n=8$ and $2n=9$ karyotypes could be present in a given area, and could have distinctive host plant preferences.

Hales et al. (1990) suggested that in parthenogenetic aphids, chromosomal rearrangements permitted new environmental relationships (e.g. insecticide resistance, temperature tolerance, host plant relationships). The absence of the $2n=9$ form from South Australia is difficult

Table 4.2. Karyotypes (2n) of *R. maidis* on different hosts across South Australia.

Species	Number of sites	Locality	Number of aphids	2n
<i>R. maidis</i>				
<i>A. fatua</i> (w)	1	MP	6	8
<i>B. catharticus</i> (s)	2	WA,L	7	8
<i>B. diandrus</i> (w)	2	P,S	5	8
<i>Cenchrus longispinus</i> (s)	1	WA	4	8
<i>Digitaria ciliaris</i> (s)	3	K,B,L	4	8
<i>Echinochloa crus-galli</i> (s)	3	WA,L,RE	15	8
<i>E. utilis</i> (s)	1	MB	2	8
<i>Eleusine indica</i> (s)	2	WA,B	2	8
<i>Eragrostis cilianensis</i> (s)	2	B,L	2	8
<i>H. vulgare</i> (w)	3	A,P,M	20	8
<i>H. vulgare</i> (s)	6	MG (2 crops)	5	8
<i>Setaria pumila</i> (s)	3	WA,K,L	15	8
<i>S. verticillata</i> (s)	3	WA,B,L	12	8
<i>S. viridis</i> (s)	3	K,RE,L	10	8
<i>Sorghum vulgare</i> (s)	6	L,MG (5 crops)	16	8
Total	37		125	

(w)=winter, (s)=summer, A=Avon, B=Berri, K=Kingston, L=Loxton, M=Mallala, MB=Mount Barker, MG=Murray Bridge, MP=MtPleasant, P=Palmer, RE=Renmark, S=Sedan, WA=Waikerie

to explain. One possibility is that the chromosomal rearrangements may bring with it disadvantages that become important in the high summer temperatures of South Australia (although $2n=9$ has been recorded from the Middle East and Queensland), or perhaps it is a recent introduction to the east coast of Australia and has not yet spread to South Australia.

This chapter describes the determination of the low temperature threshold and thermal constant for *R. padi*. This information is used later to assess the theoretically possible numbers of generations completed between early sown and normal sown crops.

CHAPTER 5

Studies on the biology of apterous *R. padi*

Abstract

The low temperature threshold and thermal constant for *R. padi* were estimated as 4.16°C and 105.49 day-degrees, respectively. The low temperature threshold is well below the mean minimum temperature experienced in winter in low rainfall South Australia indicating that *R. padi* can develop throughout the year.

Introduction

The bird cherry-oat aphid, *R. padi*, is the principal vector of the PAV and RPV types of barley yellow dwarf virus (BYDV) in Australia. Despite the interest this disease has attracted in Australia in recent years, little is known of the biology of *R. padi* in Australia.

Numerous studies on the biology of *R. padi* have been carried out in the Northern Hemisphere (Markkula & Myllymaki, 1963; Villanueva & Strong, 1964; Dean, 1974b; Leather & Dixon, 1981; Kuroli, 1984; Araya & Foster, 1987;

Williams, 1987). In contrast, only one study, on the development of *R. padi*, has been reported from Australia (Zaidi, 1981). This study was carried out at 10, 15, 18, 23, 25 and 28°C using barley leaf disks. The straight line regression of these data indicated rate of development per day (RD) and temperature (T) could be related by the following equation; $RD = 1.06T - 6.19$. Using this equation the low temperature threshold was estimated as being 5.84°C, and the thermal constant as 94.15 day-degrees.

This study aims to follow the development of apterous *R. padi* from birth to the beginning of reproduction. These data will be used to estimate the low temperature threshold and thermal constant for *R. padi* so that estimates can be made of the numbers of generations the aphid goes through in the field.

Materials and Methods

Only the biology of apterous *R. padi* was studied as apterous individuals have both a shorter development time and a higher rate of reproduction than alates. Apterous individuals therefore, contribute more to the increase in numbers than alates (Markkula & Myllymaki, 1963; Wratten, 1977; Dixon & Howard, 1986).

The development from birth to the beginning of

reproduction was conducted in constant temperature rooms set at 11, 15 and 20°C (all $\pm 0.1^\circ\text{C}$) (L:D 11:13). The temperatures chosen reflected the mean temperatures in Adelaide during autumn-spring. Two pre-germinated wheat seeds (cv. Halberd) were sown in a 15 cm pot with University of California soil, thinning to 1 plant after emergence. Plants were kept in a screen house and were transferred to constant temperature rooms 5 days before experimentation, to equilibrate. A total of 40 pots were used at each temperature. Plants were used for experimentation when they reach Zadoks growth stage 24/25 (Tottman & Broad, 1987).

Adult *R. padi* were collected from wheat plants growing in the field at the Waite Institute and placed onto moist filter paper to reproduce, thereby ensuring offspring were virus free. This was necessary as aphids developing on virus infected plants have a different biology to those developing on virus-free plants (Gildow, 1980; Araya & Foster, 1987). A newly deposited nymph was then transferred using a camel hair brush to the base of the main tiller, where it was caged. The cages used were the same as those described in chapter 7. Nymphs were allowed to develop until they had reached the fourth instar. At this stage nymphs were identified as being either alatoid or apterous.

At each temperature 21 apterous nymphs were allowed to develop into reproducing adults. The mean length of time taken for nymphs to complete their development at each

temperature was determined. The inverse of each mean, multiplied by 100, was plotted against temperature and a simple regression was then used to fit a line through the points.

To test the hypothesis that the equations of the lines of best fit from Zaidi (1981) and this study were not significantly different, the slopes and intercepts of the 2 lines of best fit were compared using the methods outlined in Zar (1984).

Results and Discussion

The rate of development (RD) of *R. padi* increased with temperature (T) ($P < 0.001$, $r^2 = 0.95$) (Fig. 5.1). From the equation of the straight line; $RD = -3.951 + 0.948T$ the low temperature threshold was estimated to be 4.16°C with a thermal constant of 105.49 day-degrees. The mean minimum temperature in low rainfall South Australia is $\approx 8^{\circ}\text{C}$ indicating that *R. padi* is able to continue to develop throughout the year.

The comparison of the line of best fit from this study with that from Zaidi (1981) showed that the lines were not significantly different ($P > 0.05$).

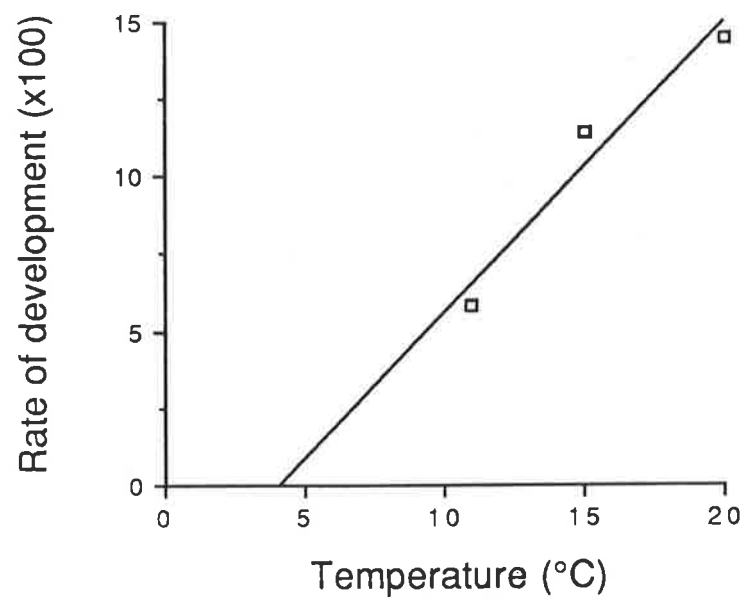


Fig. 5.1. The rate of development (RD) of *R. padi* at 3 temperatures (T); 11, 15 and 20°C and the straight line regression of the data ($RD = 0.95T - 3.95$).

As there is no significant difference between the 2 Australian studies, the equation of the regression line fitted to the data from this study will be used to estimate the numbers of generations possible over a given length of time. These estimates will be made by calculating day-degrees using a modification of Allen's (1976) modified sine wave program. This program was provided by Dr R. Laughlin and requires daily maximum and minimum temperatures, and the equation of the line of best fit. The daily maximum and minimum temperatures were taken from recordings made at the Waite Agricultural Research Institute. The program computes the daily and cumulative heating day-degrees. Heating day-degrees are those units above the low temperature threshold. To determine the number of generations over a given period of time, the cumulative number of heating day-degrees was divided by the thermal constant. This program was used to calculate an estimate of the difference in the number of generations completed in early and normal sown crops (see Chapter 11).

The following chapter discusses the search for cereal aphid refuge areas and the subsequent study of the phenology of *R. padi* in refuge areas. This chapter has been published in *Ann. appl. Biol.*

CHAPTER 6

The role of refuge areas in the phenology of *Rhopalosiphum padi* in low rainfall cropping areas of South Australia

Abstract

Extensive surveys of possible aphid habitats in South Australia indicated that irrigated perennial grass pastures in the Mt Lofty Ranges and Lower Murray Valley were summer refuges for *R. padi*. Large numbers of aphids build up in these pastures each year during autumn (April and May) with numbers peaking in May. The size of the May peak was related to the number of aphids surviving the summer. The proportions of alates were highest in May and August/September. Both peaks coincided with a photoperiod of between 11.2 and 11.6 hrs, and multiple regression suggested that aphid density, photoperiod and temperature were all significant determinants of alate production.

Introduction

The low rainfall wheat belt of South Australia covers the cropping area (≈ 1.5 million hectares) which receives between 250 and 500 mm of annual rainfall (Fig. 6.1) (Aust. Bureau

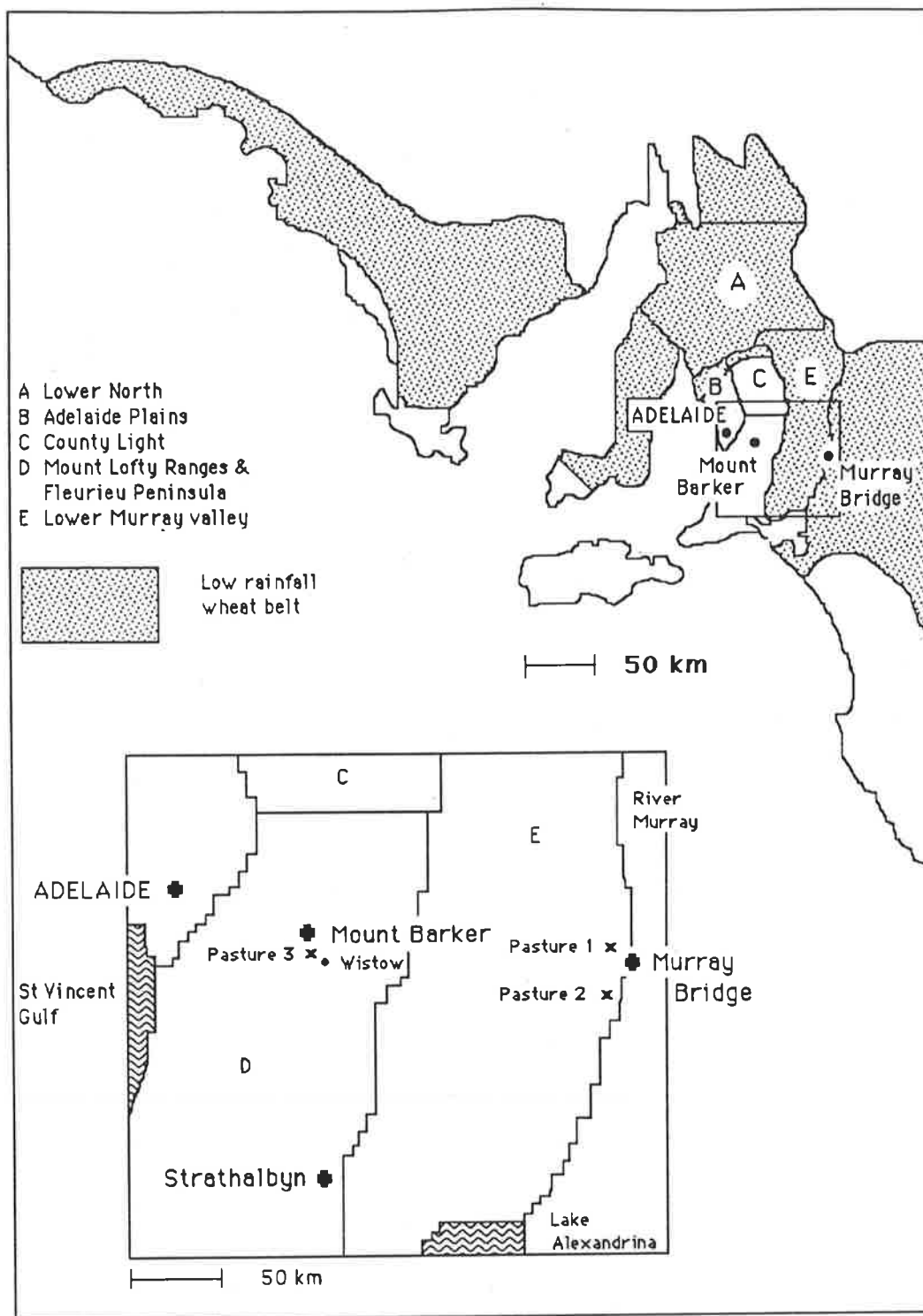


Fig. 6.1. Map of the southern portion of South Australia indicating the low rainfall wheat belt (shaded) together with the areas surveyed for possible cereal aphid summer refuges. The inset illustrates the locations of the 3 pastures used in the study.

Stat. 1988/89). It has mild wet winters with a daily mean temperature of 11.0 to 11.8°C and hot dry summers with a monthly mean maximum temperature of 37.3 to 38.7°C. The average monthly rainfall of 26 mm is far exceeded by a monthly average evaporation of 216 mm (WARI Biennial Report 1986-1987). In a typical year the season "breaks" with "opening rains" in April, and the winter-growing wheat crops are sown in late May or early June.

In South Australia, wheat is host to several species of cereal aphids. The most abundant species are *R. padi*, *M. dirhodum* newly recorded in South Australia in 1987 and *S. nr fragariae* occur less frequently (Economic Insects Database (ECIMS), South Australian Department of Agriculture). In Australia, *S. nr fragariae* was originally described as *S. fragariae*, but it appears to be morphometrically distinct from this species and the temporary name has been proposed to avoid confusion (Hales et al., 1990). *R. maidis* is another commonly occurring species, but it appears to prefer barley and is rarely recorded on wheat (ECIMS, 1988). *R. rufiabdominalis*, *R. insertum* and *S. miscanthi* are uncommon. All species of cereal aphids in South Australia are anholocyclic and hence all alates produced will seek grass hosts.

While cereal aphids cause some damage through feeding (Rautapaa, 1976), their ability to act as vectors for barley yellow dwarf virus (BYDV) is of greater concern. Of the 5

distinct New York types or isolates of BYDV (Rochow, 1979), PAV is the most frequently encountered and RPV is less common in South Australia (Henry et al., in press). *R. padi*, *M. dirhodum* and *S. nr fragariae* are all able to transmit PAV although *S. nr fragariae* is considered an inefficient vector (Hales et al., 1990).

BYDV is recognised as a significant disease of cereals throughout Australia, causing losses estimated at 2% or US \$40 M per annum (Johnstone et al., 1990; Sward, 1990). However, the estimates of BYDV severity were obtained in areas where summers are milder than those in South Australia and so may not be applicable here. The disease is more widespread and damaging in high rainfall (>500 mm) areas, and it tends to be only a sporadic, often local problem in low rainfall areas (Sward, 1990). The apparent increased incidence and severity of BYDV in high rainfall areas is thought to be due to the local presence there of over-summering perennial grasses which act as reservoirs for both the aphids and viruses (Price, 1970; Vickerman & Wratten, 1979; Smith & Plumb, 1981).

The lack of adequate summer rainfall for annual plant growth in South Australia results in there being very little cereal cropping over summer and it also prevents the survival of most grasses which are not irrigated. Consequently, in summer, grasses are restricted to habitats such as irrigated perennial grass pastures, irrigated forage

crops such as sorghum (*S. vulgare*) and millet (*E. utilis*), and irrigated recreational areas such as ovals and lawns. Grasses in these habitats include species of *Lolium*, *Bromus*, *Dactylis*, *Paspalum*, *Hordeum*, *Festuca*, *Phalaris*, *Avena*, *Sorghum* and *Echinochloa*, and all are potential hosts for both the different species of cereal aphids and the different types of BYDV (Doncaster, 1957; Eastop, 1966; Blackman & Eastop, 1985; Carver, 1984; Guy, Johnstone & Morris, 1987; ECIMS, 1988). These habitats may therefore act as refuge areas for aphids and may directly influence which species are present and how many survive to multiply during autumn and give rise to progeny which fly off to infest newly emerged wheat crops. The numbers of cereal aphids which survive in these refuges may therefore influence the extent to which BYDV affects yields.

Two possible hypotheses may explain the annual infestation of wheat crops by cereal aphids. The first suggests that refuge areas are available within the low rainfall areas and in autumn and winter produce sufficient numbers of alates which then fly off to infest and infect wheat crops. An alternative hypothesis is that local refuges are minor and most aphids infesting wheat come from the south-eastern corner of Australia where the climate is wetter and cooler over summer. This chapter examines the first hypothesis.

Materials and Methods

Survey of possible refuge areas

A survey of possible refuge areas was carried out from mid-November to mid-January 1989 to find cereal aphids. Possible refuges surveyed were irrigated perennial grass pastures, summer forage crops and "recreational areas". The areas included in the survey are shown in Fig. 6.1 and comprised: the Adelaide Plains (4 "recreational areas"), County Light (3 "recreational area", 3 forage crops), Lower North (4 "recreational areas", 4 forage crops), the Lower Murray Valley south of Swan Reach (2 "recreational areas", 2 forage crops, 5 pastures), the Mount Lofty Ranges from Mount Barker to Meadows (3 "recreational areas", 2 forage crops, 3 pastures) and the southern Fleurieu Peninsula (2 "recreational areas", 2 forage crops, 4 pastures).

Pastures and "recreational areas" were sampled with a suction device called the McCulloch Eager Beaver Gas Blower/Vac R (Chapter 3). Two 100m diagonal transects from each pasture, lawn or oval surveyed were sampled with the device whilst walking at 25 m/min. Summer forage crops were surveyed by removing the terminal leaf roll from 25 plants selected at random from within the crop. Aphids in each sample were identified and counted in the laboratory.

Aphids in irrigated perennial grass pastures

Three pastures were chosen from those originally surveyed. Pasture 1 was a mix of perennial ryegrass (*L. perenne*), cocksfoot (*D. glomerata*) and clover (*Trifolium* spp.) and was irrigated by overhead sprinkler. Pasture 2 was a mix of perennial ryegrass, paspalum (*P. dilatatum*) and clover and was irrigated by flooding to the depth of 2 to 3 cm. Both pastures were near Murray Bridge in the Lower Murray Valley (Fig. 6.1). Pasture 3 was a mix of fescue (*F. arundinacea*), perennial ryegrass and clover, and was irrigated by overhead sprinkler; it was situated near Mount Barker in the Mount Lofty Ranges (Fig. 6.1).

Pasture composition

Pasture composition was determined in each of the 3 pastures on 4 occasions in 1989 and twice in 1990 using the Levy point quadrat method (Crocker & Tiver, 1948). Twelve quadrats were measured in February and April, 1989, and 10 in May and June, 1989 and February and June, 1990. The main grass species were identified and recorded separately while occasional grasses and all broadleaved species were pooled into separate groups.

Numbers of aphids

From each pasture a 200 x 50 m portion was selected and divided into 25 sub-areas. A single 30 x 30 cm (900cm²) plot was then selected at random from each sub-area and vacuumed for aphids for 30 seconds. The aphids in each of the resultant 25 sample units were counted separately and later pooled for the sample.

Pastures were sampled in 1989 and 1990. A sample from each pasture was first taken in February and then monthly except in May and June when 2 samples, 2 weeks apart, were taken. Sampling ceased in November of each year.

Each sample was examined in the laboratory, the aphid species identified (Eastop, 1966 and Blackman & Eastop, 1985 were used to confirm identifications) and counts made of the numbers of alate adults, alatoid third and fourth instars, apterous adults and apterous third and fourth instars. Alatoid and apterous nymphs were identified using the presence of wing buds, and both were separated from the first and second instars on the basis of size. Third and fourth instars were pooled, and first and second instars were not included in the counts. The proportion of alatoid nymphs was determined by dividing the number of alatoid nymphs by the total number of nymphs counted.

To check whether the number of alates in the sampled

pastures in April and May were typical for all pastures, 25 sample units from each of a further 10 pastures were taken in mid-May of each year.

The changing number of alates produced across the pasture refuges was estimated as the pooled mean per hectare for the three pastures at each sample date. The mean was then multiplied by 10,000 - the approximate area of irrigated perennial grass pastures in the Lower Murray Valley, Mount Lofty Ranges and Fleurieu Peninsula.

The proportion of alatoid nymphs

Since the number of alates produced in autumn may determine the severity of BYDV outbreaks, we attempted to develop one or more predictors of alate production. We did this by regressing the change in the proportion of alates between one sample date (n) and the next ($n+1$), on the variables which were most likely to be important determinants of alate development, namely photoperiod, temperature and aphid density .

Photoperiod was defined as the number of hours of light between sunrise and sunset at the time of sampling and photoperiod values were taken from the sunrise/sunset data in the South Australian Government Gazette, Proof of Sunrise and Sunset Act. Temperature was taken as the mean daily

maximum temperature between one sample date (n) and the next sample date (n+1), and was obtained from the Bureau of Meteorology, Murray Bridge and Mount Barker stations. Aphid density was obtained from the aphid samples.

Statistical analysis

When more than two samples were to be compared, data were tested for homogeneity and normality using the Fmax test and Shapiro-Wilks test, respectively. Where $F > F_{max}$ or $P < 0.05$, data were transformed to $\sqrt{(x+0.1)}$. Data were then analysed using analysis of variance (ANOVA); when $P < 0.05$, means were compared using the Tukey test of multiple comparisons ($\alpha = 0.05$). When only two samples were compared, a t-test was used. Sampling efficiency was measured 4 times during the year (Chapter 3).

Results

Survey of possible refuge areas

No cereal aphids were found in any of the recreational areas sampled. Aphids were present in all forage crops and perennial pastures sampled, but only *R. maidis* was found on the forage crops while *R. padi* was the only species present

in the pastures.

Summer forage crops were considered unlikely to play a major role in the phenology of cereal aphids on wheat as only *R. maidis* was ever found. In addition, the area usually sown is <1000 ha and as most crops are ploughed in by the end of March, well before the earliest sowings of wheat, forage crops are unlikely to be important in the epidemiology of BYDV. By contrast, perennial grass pastures are widespread throughout the irrigated areas of the Lower Murray Valley, the Mount Lofty Ranges and the Fleurieu Peninsula (see Fig. 6.1) and together cover $\approx 10,000$ ha. The presence within these pastures of *R. padi* together with both the PAV and RPV types of BYDV (M. Henry, pers. comm.) suggest that they have the greatest potential to act as refuge areas.

Pasture composition

The composition of each of the 3 selected perennial grass pastures did not change during the year (1989: ANOVA, $P > 0.05$, 3,40 df; 1990: t-test, $P > 0.05$, 18 df). Pasture 1 was composed mostly of *L. perenne* (0.48-0.51, 1989; 0.52, 1990) and *D. glomerata* (0.13-0.18, 1989; 0.14-0.19, 1990). Pasture 2 was mostly *L. perenne* (0.52-0.56, 1989; 0.43-0.47, 1990) and *P. dilatatum* (0.10-0.12, 1989; 0.21-0.23, 1990). Pasture 3 was a mix of 3 grass species, *F. arundinacea*

(0.30-0.41, 1989; 0.42-0.45, 1990). *L. perenne* (0.22-0.24, 1989; 0.21-0.26, 1990) and *D. glomerata* (0.21-0.27, 1989; 0.06-0.08, 1990). Other species of grasses comprised less than 6% of the total plants present.

Aphids in irrigated perennial grass pastures

The survey of 10 irrigated pastures in mid-May 1989-90 gave numbers of alate nymphs ranging from 6.10 to 44.30 per sample in 1989 and from 10.20 to 52.20 in 1990. The three pastures sampled throughout gave numbers in the middle of these ranges and so provided a reliable estimate of numbers across the refuge areas.

The mean numbers of all aphid stages and in each pasture for 1989 and 1990 are given in Fig. 6.2; and in Fig. 6.3 are given the mean numbers and the numbers of alatoid nymphs and alate adults for August-November, 1989. The numbers were obviously smaller during February to May, 1989 than in the same months in 1990, and in each year the numbers were highest in May (Fig. 6.2).

The lower numbers observed during February and March 1989 compared with numbers for the same period in 1990 may have been caused by cooler weather in 1990 than in the same period in 1989. Temperatures $\geq 36^{\circ}\text{C}$ have been shown to cause

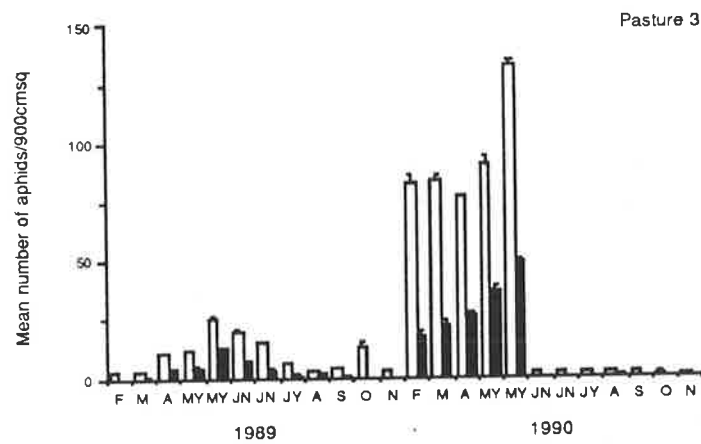
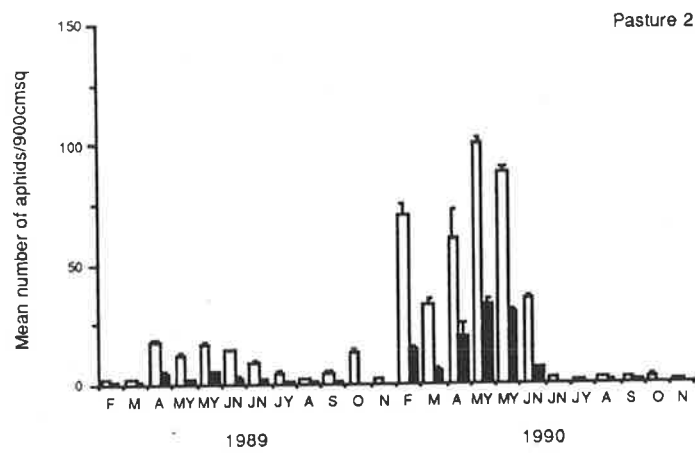
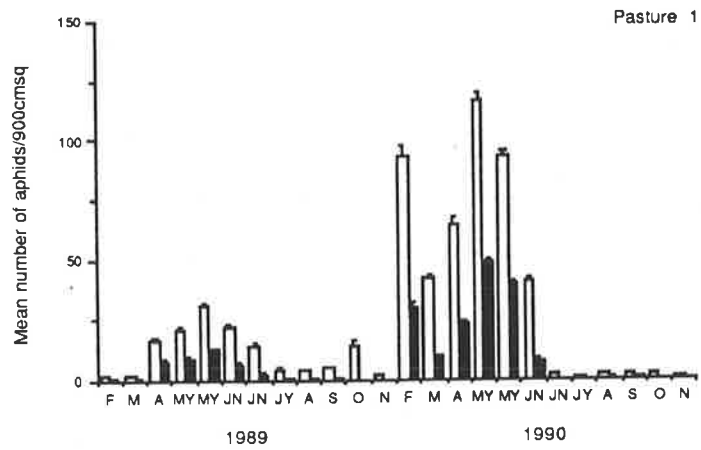


Fig. 6.2. Mean numbers of all stages of *R. padi* $\pm$ S.E. ($\square$) and of *R. padi* alate nymphs $\pm$ S.E. ($\blacksquare$) in perennial grass pastures in pastures 1, 2 and 3 during 1989 and 1990.

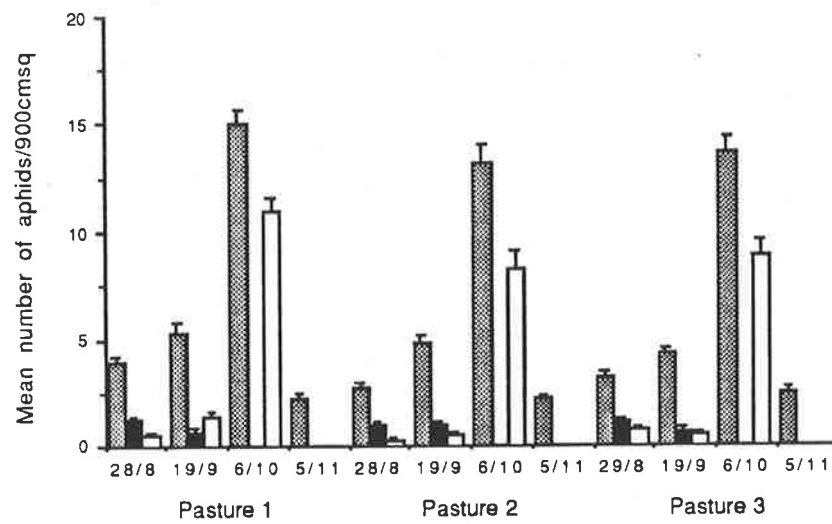


Fig. 6.3. Mean numbers of all stages of *R. padi* $\pm$ S.E. (■), the mean number of alate nymphs $\pm$ S.E. (■) and alate adults $\pm$ S.E. (□) during the period October to November 1989 for each of the three pastures sampled.

considerable aphid mortality (De Barro & Maelzer, unpublished). In 1989 there were 12 and 20 days on which the maximum daily temperature was $\geq 36^{\circ}\text{C}$ in the Mount Lofty Ranges and Lower Murray Valley respectively, while only 4 and 8 days were $\geq 36^{\circ}\text{C}$ in 1990 (Bureau of Meteorology, Kent Town, S.A.).

After the May peak in each year, the numbers declined and remained low for much of the remainder of the sampling period with the exception of October 1989, when a small increase in numbers occurred (Fig. 6.2). This was probably due to alate adults migrating to the pastures from other areas because no alatoid nymphs were present in the pastures at that time (Fig. 6.3). A similar increase was not observed in 1990 although again alate adults were recovered from these pastures in the absence of alatoid nymphs.

A significant decline ($P < 0.01$, 2,72 df) was observed in the mean number of aphids in pasture 2 in the first May sample of 1989 (Fig. 6.2). It was possibly due to flooding caused by local rains. Another significant decline ($P < 0.01$, 2,72 df) in the number of aphids (transformed) in pastures 1 and 2 was observed in March 1990 and was possibly associated with hot weather 9 days earlier. No such decline was observed in pasture 3, possibly because of lower temperatures in the Mount Lofty Ranges.

The proportion of alatoid nymphs

The proportions of nymphs which were alatoids at each sampling time in each pasture are given in Fig. 6.4 for 1989-90. No alates were produced in October or November of either year (Fig. 6.4). Proportions peaked in May in all pastures in both years and corresponded with the peak in mean numbers. The proportions in April-May each year were similar (Fig. 6.4). However, the mean numbers of alatoid nymphs were much greater in 1990 than in 1989 in all pastures (Fig. 6.2), indicating that flights from pastures in 1990 were potentially much larger than those in 1989.

A second smaller peak was observed in August 1989, and August/September 1990 (Fig. 6.4). The August 1989 peak was significantly higher than the number in the adjacent samples in pastures 2 ($P < 0.05$, 2,72 df) and 3 ($P < 0.01$, 2,72 df), but not in pasture 1. In August 1990 the proportion of alatoids at pasture 3 was much greater than that in the July or September samples and did not require analysis (Fig. 6.4). The proportions of alates produced in July, August and September, 1990 for pastures 1 and 2 were not significantly different.

The changes in the proportion of alatoids [$t(n) - t(n+1)$] in each pasture as well as the photoperiod at $t(n+1)$ are plotted in Fig. 6.5 against sample date (t) for each year.

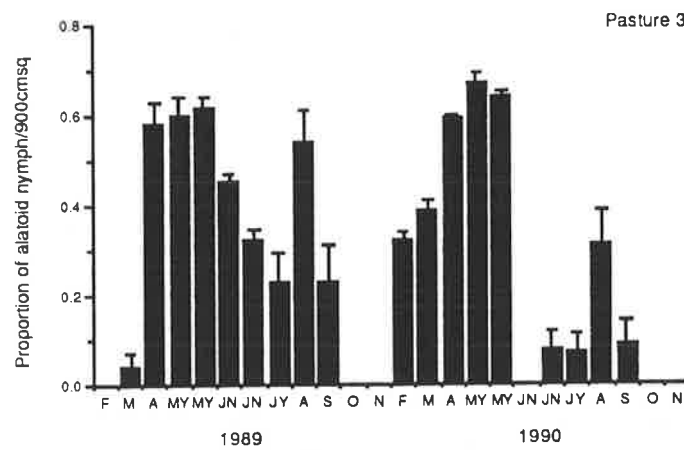
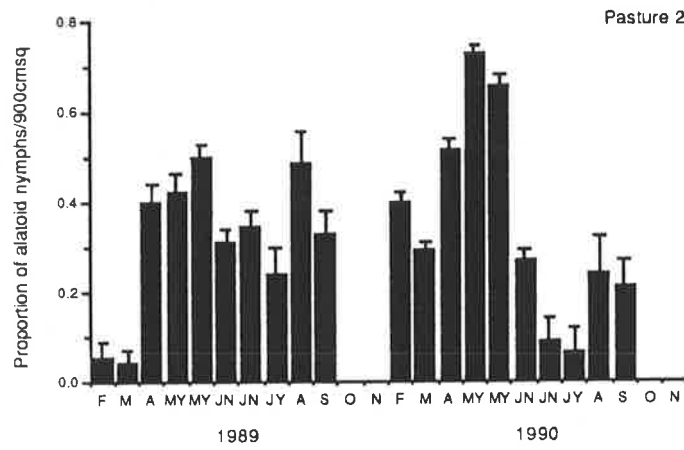
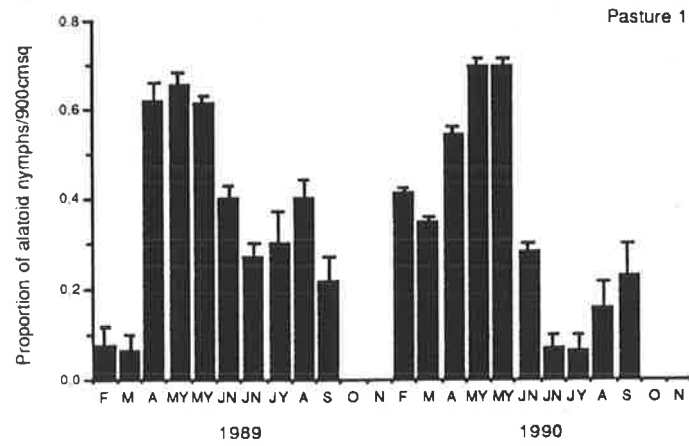


Fig. 6.4. Mean proportion of alatoid nymphs $\pm$ S.E. produced in pastures 1, 2 and 3 during 1989 and 1990.

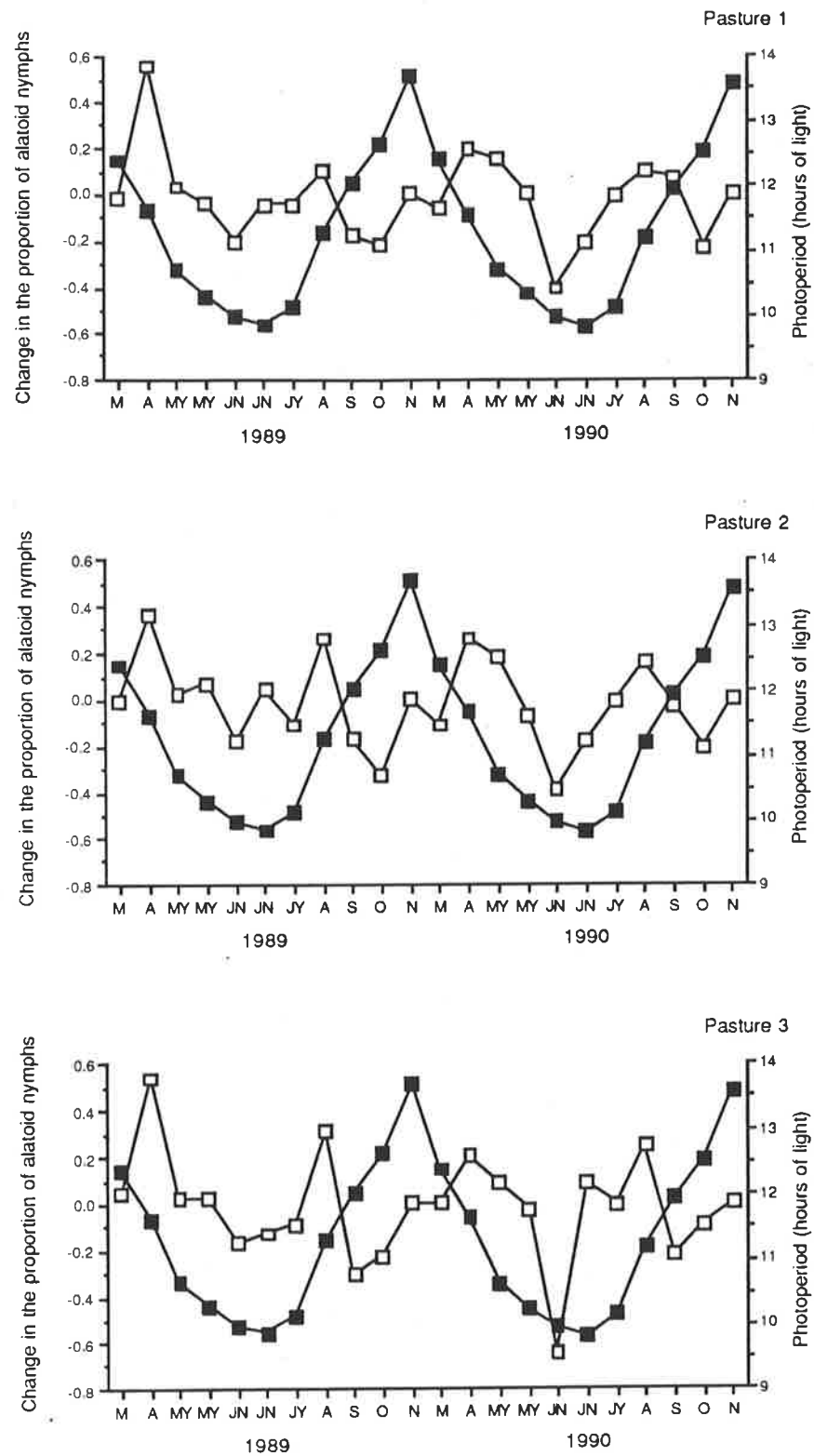


Fig. 6.5. The change in the proportion of alaroid *R. padi* between $t(n)$ and $t(n+1)$ (□) and the photoperiod at $t(n+1)$ (■) for each pasture during 1989 and 1990.

The aphid data show two peaks in each year in each pasture. All the peaks are in April and August each year and each coincides with a photoperiod of 11.2 and 11.6 hours per day suggesting that photoperiod was an important determinant of alate development.

To test whether alate production was correlated with photoperiod and also with aphid density and temperature in the critical period of February-May, the data from all 3 pastures and for both years were pooled and multiple regression was used to test the dependence of the proportion of alatoid nymphs on photoperiod, aphid density and temperature.

The correlation matrix for the selected variables (Table 6.1) show a significant negative correlation between the proportion of alatoid nymphs and temperature and photoperiod ($P < 0.001$) and a positive correlation with aphid density ($P < 0.001$). There is also a correlation between temperature and photoperiod ($P < 0.001$).

Also given in Table 6.1 is the r^2 and its significance for the regression of the proportion of alatoid nymphs on each of the independent variables, separately. As may be expected from the correlation matrix, the regressions on aphid density, photoperiod and temperature were all highly significant ($P < 0.001$).

Table 6.1. The regression of the proportion of alatoid nymphs on: temperature (T), photoperiod (P) and aphid density (D); initially on each one separately, and then on the best combination. df = degrees of freedom; r^2 = proportion of variance explained; P = probability value of r. The correlation matrices are also provided. ** P<0.01, ***P<0.001

Regression Analysis					Correlation Matrix		
Independent Variable	df	r^2	For addition to regression; t to enter	P	Proportion of alatoid nymphs	Temperature	Photoperiod
February to May only in 1989/1990							
Temperature	28	0.601		<0.001	-0.784***		
Photoperiod	28	0.595		<0.001	-0.781***	0.711***	
Aphid Density	28	0.333		<0.001	0.597***	-0.318	-0.263
Combinations of variables							
T + P	27	0.745	3.26	<0.001			
T+P+D	26	0.819	4.38	<0.001			
all months in 1989 + 1990							
Temperature	70	0.000		>0.05	0.033		
Photoperiod	70	0.221		<0.001	-0.428***	0.574***	
Aphid Density	70	0.442		<0.001	0.682***	0.315**	-0.108
Combinations of variables							
D+P	2,69	0.597	4.63	<0.001			

The data (Appendix 1) were then further analysed, with each independent variable being included in the regression equation in order of its correlation with the proportion of alatoid nymphs (alprop). The addition of photoperiod (P) and aphid density (D) to temperature (T) significantly improved the regression ($r^2=0.82$, $P<0.001$, Table 6.1), which was expressed by the following equation:

$$\text{alprop} = 1.900 - 0.023T - 0.085P + 0.002D$$

Because temperature and photoperiod were equally influential, it did not matter which variable was first included in the regression.

To test whether alate production was correlated with aphid density, photoperiod and temperature over the entire sampling period, all the 1989 and 1990 data from all 3 pastures were pooled into a single data set.

In this data set the proportion of alatoid nymphs was highly correlated with aphid density ($P<0.001$) and negatively correlated with photoperiod ($P<0.001$) (Table 6.1). Photoperiod and temperature were again highly correlated ($P<0.001$) while density and temperature were also correlated ($P<0.01$) (Table 6.1). Again, as expected from the correlation values, the separate regressions of the proportion of alatoid nymphs on aphid density and photoperiod were highly significant ($P<0.001$; Table 6.1).

The data were similarly analysed by multiple regression with aphid density being included first. The addition of photoperiod significantly improved the regression ($r^2=0.60$, $P<0.001$, Table 6.1) which was expressed by the following equation:

$$\text{alprop} = 0.928 + 0.005D - 0.065P$$

Discussion

Photoperiod and crowding caused by large numbers of aphids are important determinants of alate development (Johnson, 1965 & 1966; Dixon, 1985). It is interesting to notice that in experiments (Chapter 7), crowding plus a photoperiod of 11 hours at 15°C, induced maximal alate development in *R. padi*. The mean temperatures in April and August, when a photoperiod of 11.2 - 11.6 hours coincided with peak alate production in the field (Fig. 6.5) are 17.2 and 12.0°C, respectively. This suggests that crowding and photoperiod rather than temperature are key determinants of alate development in perennial grass pastures during autumn.

High temperatures are also known to cause increased aphid mortality (Tamaki et al., 1980; Allen, 1984; De Barro & Maelzer, submitted), and in most years, such as 1989, probably keep aphid numbers below the threshold at which

crowding induces alate development. But in cool summers, such as that of 1990, heat induced aphid mortality is reduced and many more alates can be produced at mean daily temperatures of 22°C.

The result of fewer aphids surviving the 1989 summer was a smaller population in the subsequent autumn leading to a smaller production of alates. This reduced production may have resulted in fewer aphids transmitting BYDV and a much reduced risk of the disease causing yield losses.

The critical period for dispersal of *R. padi* from the pasture refuge areas is April-May. The greatest numbers of alates are being produced then and weather is probably most suitable for long range dispersal. Alates produced during June may have less opportunity for long range migration because day length is minimal (≈ 10 hrs) and mean temperatures almost at their lowest ($\approx 11.8^\circ\text{C}$).

The numbers of alates produced during April/June may be a critical factor in the subsequent infection of wheat crops. An estimate was therefore needed of the number of alates being produced in each of the two years to gauge whether the summer pastures could be considered important sources of infestation for wheat crops. It was estimated, using the pooled mean numbers for each sample date from the 3 pastures sampled, that numbers in the 10 000 ha of perennial pastures ranged from 6.06 (60.6 alates/m²) to 11.30 (113.0 alates/m²)

billion alates in 1989 and 0.19 (1.9 alates/m²) to 44.10 (441.0 alates/m²) billion alates in 1990.

These estimated numbers of alates suggest that the perennial grass pastures are indeed, important refuges for *R. padi* and are capable of producing very large numbers of alates during April and May. Furthermore, pastures have also been found to be reservoirs for both PAV and RPV. Between 1.7 and 20.4% of alate nymphs taken from these pastures during April-May transmitted one or other of the types in 1989, between 3.0 and 13.9% in 1990, and between 18.1 and 82.0% in 1991 (De Barro & Henry, unpublished data). Similar findings have been made in Tasmania (Guy et al., 1987; Sward & Lister, 1988).

In South Australia, most crops are not sown until late May or early June and therefore, only early sown crops, i.e. crops sown in late April or early May, are at risk from infestation by the large numbers of alates leaving the summer refuges at that time. Most alates which succeed in finding hosts once they leave pastures may do so by landing on volunteer grasses. These grasses generally emerge soon after the opening autumn rains and occur in a range of habitats including roadside verges, waste land and annual pastures. It is proposed that the perennial grass pastures directly supply the migrant aphids which infest early sown crops, but aphids infesting later sown crops are more likely to originate from other sources such as volunteer grasses

which are colonized earlier. The role of annual volunteer grasses in the infestation and infection of wheat crops in low rainfall South Australia is discussed in Chapter 10.

The study of the pasture refuge areas indicated that:

- (a) alates were produced in large numbers in April and May.
- (b) photoperiod and aphid density may be important determinants of alate development.
- (c) high temperatures may be involved in reducing aphid numbers in February and March.

The 2 following chapters describe experiments designed to determine; whether photoperiod, aphid density and temperature were significant determinants of alate production and what effect high temperatures had on aphid numbers. These chapters have been submitted to *Entomol. exp. appl.* and *Ecol. Ent.*

CHAPTER 7

The role of temperature, photoperiod, crowding and plant quality on the production of the alate viviparous females of the bird cherry-oat aphid, *R. padi*

Abstract

Experiments indicated that for offspring of apterous *R. padi*, photoperiod and crowding were the most important determinants of wing development whereas crowding and plant quality were more significant for the next generation. Plant quality became increasingly important as temperature increased while crowding became less so. More alates developed on plants previously infested with aphids, indicating that aphid feeding reduced plant quality. High temperature suppressed alatoid production, but could be overcome by crowding. Temperature appeared to influence wing development indirectly rather than directly by acting on the aphid through the plant. Adult weight and potential fecundity were also reduced for aphids which fed on previously infested plants.

Introduction

R. padi is the principal species of cereal aphid infesting wheat in the sub-500 mm rainfall areas of South Australia (Chapter 6). In Australia, it is anholocyclic, viviparous (Ridland, 1988) and a vector of the PAV and RPV types of barley yellow dwarf virus (BYDV) (Johnstone *et al.*, 1990).

R. padi has a wide host range, covering most of the commonly occurring Gramineae in South Australia (Eastop, 1966; Guy *et al.*, 1987). However, the low rainfall during summer in South Australia restricts grass growth and development to areas where irrigation occurs. These habitats include perennial grass pastures which provide the most important summer refuges for both *R. padi* and BYDV (Chapter 6; Henry *et al.* in press). With the onset of autumn aphids multiply in numbers, and some of their progeny then develop wings and fly off to infest newly sown wheat crops (Chapter 6).

Wing development in aphids is usually governed by 4 interacting factors: crowding, photoperiod, plant quality and temperature (Johnson, 1965, 1966a, 1966b; Lees, 1966; Maelzer, 1981; Kawada, 1987). These factors have been investigated for *R. padi* in several studies e.g., crowding and plant quality for *R. padi* feeding on the primary host *Prunus padi* L. and grasses (Dixon, 1971), and photoperiod

and temperature for the production of gynopare and males (Dixon & Glen, 1971; Dixon & Dewar, 1974); but no studies have compared all 4 factors in the same experiment.

Crowding, photoperiod and temperature were all proposed as being involved in the development of alate *R. padi* in irrigated perennial grass pastures in South Australia (Chapter 6). It was further proposed that crowding and photoperiod acted directly whereas temperature acted indirectly by maintaining numbers below the threshold at which crowding induced alate development occurred.

The aims of this study were to determine experimentally which of the 4 interacting factors were principally involved in the development of alate *R. padi* viviparous females and to then compare these with those suggested to be involved in perennial grass pastures.

Materials and Methods

Aphids

For each experiment, apterous adult *R. padi* were collected from small colonies (<30 aphids) on tillering wheat plants growing in pots in a glasshouse. An individual adult was placed on a young (Zadoks growth stage 10, Tottman & Broad, 1987) wheat seedling (cv. Halberd) growing in a 35 ml

polystyrene cup on 1.4% agar. The cup was then sealed with a semi-transparent plastic lid. Three hundred cups were set up in this way and stored at 20°C (L:D 12:12). Newly deposited young, <2 hrs old were then removed and placed onto fresh seedlings as before. A total of 600 cups were set up in this manner. The nymphs were then allowed to develop into adults. Offspring were removed and discarded until most adults had commenced reproduction. At this stage nymphs were removed for experimentation within 2 hrs of being deposited.

Plants

For all plants used in the experiments, 2 pregerminated wheat seeds (cv. Halberd) were sown in 15 cm pots with University of California soil mix, watered regularly and fertilised with the slow release fertiliser "Osmocote". Seedlings were thinned to 1 plant after emergence.

For each temperature 180 pots were sown. Plants were grown in a glasshouse under natural light and were used for experimentation when between 4 and 7 tillers had developed (Zadoks growth stages 24-27). Five days prior to the first experiment the 20 most dissimilar plants were discarded and the remainder were divided into 2 equal groups and transferred into walk-in constant temperature rooms set at either 11 or 14 hrs light to equilibrate.

Under each photoperiod in the first experiment, 20 plants were caged, but no aphids were added to these cages. A further 20 plants were left uncaged. These plants were not used until the second experiment. The remaining 40 plants were caged with aphids for use in the first experiment.

Cages

Cages were made from transparent plastic hinged boxes (30x30x30 mm, model 12R, Grant Austin Box Manufacturers) and were a modified version of the cage described by Singh and Painter (1964). A 20 mm diameter hole was cut in the top and bottom of each box and covered with fine gauze. A 5 mm hole was melted into the middle of the rim of one half of the box so as to form a semi-circular groove into which a wheat stem fitted. The rims of both halves of the cage were lined with "Blutac" to form a seal.

First Generation

The temperatures and photoperiods chosen reflected the ranges found in South Australia. The average daily mean temperature found during winter, autumn/spring and summer and the average photoperiod which occurs during autumn/spring and summer were chosen. It was hoped that by

using these conditions, comparisons between the experiments and events in perennial grass pastures could be drawn.

Combinations of treatments were carried out at 3 constant temperatures: 11, 15 and 20°C (all $\pm 0.1^\circ\text{C}$). At each temperature there were 2 photoperiods: 11 and 14 hrs light, and 2 levels of aphid crowding: crowded and uncrowded. There were 20 replicates of each treatment, and in each replicate 16 newly born nymphs were confined in a cage to a separate plant.

For each crowded treatment, the 16 first instars were enclosed in an 8ml glass vial for 4 hrs at 20°C before being placed into a cage this was to ensure that each aphid was in contact with other aphids for much of the time. Preliminary trials showed that the 16 nymphs when placed into the cage and then attached to the stem, rapidly moved onto the plant and commenced feeding with little or no prolonged contact. For the alternative uncrowded treatment, each nymph was kept in a separate vial for 4 hrs before 16 were chosen and placed into a cage. Each cage was then clipped onto the lower stem of the main tiller of a plant at the auricle of the first leaf, the region of the wheat plant where *R. padi* is most commonly observed in South Australia.

Nymphs were allowed to develop until the 4th instar at which time they were examined for the presence of wing buds. Any alatoid nymphs present were discarded as these are less

likely to produce offspring of the same form (Noda, 1959).

Second Generation

Treatments comprised 3 constant temperatures x 2 photoperiods x 2 levels of crowding x 3 levels of plant quality. The temperatures: 11, 15 and 20°C, and photoperiods: 11 and 14 hrs were the same as those used in the previous experiment. The 2 levels of crowding were; aphids crowded and aphids which were not crowded as first instars in the first experiment. The 3 levels of plant quality comprised: plants infested in the first generation, denoted as pi, plants caged without aphids in the first generation, denoted as npic, and plants uncaged without aphids in the first generation, denoted as npiu. Treatments were replicated 10 times. In each treatment, 10 apterous nymphs from the first generation were caged onto the base of the main tiller (1 plant/pot).

All nymphs were allowed to complete their development and then reproduce for 2 days at 20°C, 3 days at 15°C and 4 days at 11°C. The different numbers of days of reproduction were to ensure that a similar number of progeny were deposited in each treatment, thereby maintaining the same degree of crowding across treatments.

To further determine the influence of plant quality on R.

padi, the 10 adults from each replicate were removed after the required period of reproduction and weighed as a group. After weighing, aphids from each treatment were pooled and 20 were then selected at random, dissected and the number of embryos counted using the method described in Adams & van Emden (1972). Nymphs produced in the second generation were allowed to develop to the 4th instars, at which stage the numbers of nymphs with and without wing buds were counted.

Statistical analyses

Data was analysed for each of the 3 temperatures separately as interactions may be different at different temperatures and could be lost if data were pooled. All data were found to be homogeneously distributed between treatments after analysis using the Fmax test. Data in each generation were analysed using ANOVA (model 1). (SAS Release 5.18, SAS Institute Inc., USA, procedure GLM). Where $P < 0.05$ means were compared using the Tukey test of multiple comparisons ($\alpha = 0.05$).

Results

First generation

The mean proportion of alates developed in each treatment is given in Table 7.1. At 15°C there was a significant difference between the treatments in the proportion of alates that developed ($df=3,76$, $P<0.05$). More alates developed at 11 hrs photoperiod than at 14 hrs ($df=1,76$, $P<0.001$) while crowded treatments yielded more alates than the uncrowded ($df=1,76$, $P<0.001$). Photoperiod and crowding interacted strongly ($df=1,76$, $P<0.001$) with the greatest proportion of alates developing in the 11 hrs photoperiod, crowded treatment.

At both 11 and 20°C there were initially no significant differences between treatments in the proportions of alates developing ($df=3,76$, $P>0.05$) (Table 7.1). However, when the data for photoperiod were pooled in a further one-way ANOVA, crowding was significant ($df=1,78$; 11°C, $P<0.05$; 20°C, $P<0.01$), with more alates developing in crowded treatments than in uncrowded treatments (Table 7.1).

Second generation

For each temperature, the mean number of nymphs produced

Table 7.1. Mean proportion of alate *R. padi* developing on wheat (cv. Halberd) in the first generation from crowded and uncrowded nymphs at 11, 15 and 20°C under 11 and 14 hrs photoperiod

			mean proportion of alates							
			11°C			15°C		20°C		
	n		11 hrs	14 hrs	Means for photo*	11 hrs	14 hrs	11 hrs	14 hrs	Means for photo*
crowded	20	mean	0.05	0.04	0.05	0.34	0.04	0.04	0.02	0.03
		S.E.	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.01
uncrowded	20	mean	0.02	0.02	0.02	0.10	0.01	0.01	0.01	0.01
		S.E.	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.00

*photo = pooled photoperiod

in each treatment are presented in Table 7.2. There was no significant difference between the total number of nymphs in each treatment at each temperature ($df=11,108$, $P>0.05$). There were also no significant interactions between photoperiod, plant quality and crowding ($P>0.05$) nor was there any significant difference in numbers for photoperiod ($df=1,108$, $P>0.05$), plant quality ($df=2,108$, $P>0.05$) or crowding ($df=1,108$, $P>0.05$) (see means in Table 7.2). When the data were pooled within each temperature, a one-way ANOVA further suggested no significant differences between temperatures (Table 7.2, $df=2,357$, $P>0.05$). The level of crowding in each treatment was therefore considered to be the same.

The mean proportions of alates which developed at 11°C and 15°C are presented in Table 7.3. At each temperature there was a significant difference between treatments in the proportions of alates which developed ($df=11,108$, $P<0.001$) (Table 7.3). But there were no significant differences between any of the interactions ($P>0.05$) nor was there a significant difference between photoperiods ($df=1,108$, $P>0.05$). So the photoperiod data were pooled (see Table 7.3 for pooled means) and the ANOVA recalculated.

The subsequent ANOVA for each temperature was also significant ($df=5,114$, $P<0.001$), but the interaction between plant quality and crowding was not significant ($df=2,114$,

Table 7.2. Mean number of *R. padi* nymphs produced on wheat (cv. Halberd) at 11, 15 and 20°C under 11 and 14 hrs photoperiod on plants with and without a previous aphid infestation, pi=previous aphid infestation, np=no previous aphid infestation, the “c” and “u” denote caged and uncaged treatments respectively. (*photo = photoperiod)

mean number of nymphs											

Table 7.3. Mean proportion of alate *R. padi* developing on wheat (cv. Halberd) in the second generation from apterous adults of the first generation at 11, 15 and 20°C under 11 and 14 hrs photoperiod on plants with and without a previous aphid infestation. pi=previous aphid infestation, npic=no previous aphid infestation, the “c” and “u” denote caged and uncaged treatments respectively.

			mean proportion of alates								
			11°C			15°C			20°C		
Treatment	n		11 hrs	14 hrs	Means for photo*	11 hrs	14 hrs	Means for photo*	11 hrs	14 hrs	Means for photo*
pi crowded	10	mean ±S.E.	0.38 ±0.06	0.34 ±0.06	0.36 ±0.01	0.78 ±0.02	0.77 ±0.01	0.77 ±0.01	0.83 ±0.03	0.85 ±0.02	0.84 ±0.01
pi uncrowded	10	mean ±S.E.	0.10 ±0.03	0.10 ±0.03	0.10 ±0.01	0.31 ±0.02	0.32 ±0.02	0.31 ±0.01	0.81 ±0.02	0.85 ±0.01	0.83 ±0.01
npic crowded	10	mean ±S.E.	0.19 ±0.05	0.22 ±0.02	0.20 ±0.01	0.61 ±0.01	0.63 ±0.03	0.63 ±0.01	0.71 ±0.03	0.69 ±0.02	0.69 ±0.02
npic uncrowded	10	mean ±S.E.	0.06 ±0.02	0.06 ±0.02	0.06 ±0.00	0.18 ±0.01	0.19 ±0.01	0.18 ±0.01	0.68 ±0.01	0.69 ±0.02	0.66 ±0.02
npiu crowded	10	mean ±S.E.	0.23 ±0.05	0.18 ±0.01	0.21 ±0.01	0.63 ±0.02	0.62 ±0.02	0.62 ±0.02	0.69 ±0.02	0.70 ±0.03	0.70 ±0.02
npiu uncrowded	10	mean ±S.E.	0.06 ±0.02	0.07 ±0.02	0.05 ±0.01	0.18 ±0.02	0.18 ±0.02	0.18 ±0.01	0.69 ±0.02	0.64 ±0.03	0.68 ±0.01
Pooled means for plant quality											
pi	40	mean ±S.E.	0.23 ±0.02			0.54 ±0.04			0.83 ±0.01		
npic	40	mean ±S.E.	0.13 ±0.01			0.40 ±0.04			0.68 ±0.01		
npiu	40	mean ±S.E.	0.13 0.01			0.40 ±0.04			0.69 ±0.01		
Pooled means for crowded and uncrowded											
crowded	60	mean ±S.E.	0.26 ±0.01			0.67 ±0.01			0.74 ±0.01		
uncrowded	60	mean ±S.E.	0.07 ±0.01			0.23 ±0.01			0.73 ±0.01		

*photo = photoperiod

$P > 0.05$). So each variable was then analysed separately using a one-way ANOVA.

At both 11°C and 15°C , there was a significant difference between the pooled means for (Table 7.3) plant quality ($\text{df}=2,117$, $P < 0.001$) and multiple comparison analysis showed a greater proportion of alates developed on the pi plants (Table 7.3) than on npic or npiu plants. In addition, significantly more alates developed from progeny whose parents were crowded in the first generation ($\text{df}=1,118$, $P > 0.001$) than from uncrowded parents (see pooled means for crowded and uncrowded in Table 7.3).

The mean proportions of alates which developed at 20°C are also presented in Table 7.3. At 20°C there was again a significant difference in the proportion of alates developing ($\text{df}=11,108$, $P < 0.001$) (Table 7.3). But, again, none of the interactions showed a significant difference ($P > 0.05$) and of the main effects, only plant quality gave a significant difference between treatments ($P < 0.001$, $\text{df}=2,108$). The data for photoperiod and crowding were therefore pooled (see pooled means in Table 7.3), and the subsequent ANOVA for plant quality showed that a greater proportion of alates developed on pi plants than on either the npic or npiu plants ($P < 0.001$, $\text{df}=2,108$) (Table 7.3).

As the photoperiod data were not significantly different for any of the temperatures tested they were then pooled.

The data for npic and npiu were also pooled as again there was no significant difference between them. The data for all temperatures were then combined to test, using ANOVA, the influence of plant quality, crowding and temperature on alate development.

The means for the combined data for each of the 3 temperatures are listed, according to treatment, in Table 7.4. The ANOVA showed that the means were significantly different ($df=11,348$, $P>0.001$). There was no significant interaction between crowding and plant quality ($df=2,348$, $P>0.05$); however, the interactions between temperature and crowding ($P<0.001$, $df=2,348$), temperature and plant quality ($P<0.001$, $df=2,348$) and temperature, plant quality and crowding ($P<0.001$, $df=1,348$) were all significant.

As before, plant quality showed a significant difference ($df=1,348$, $P<0.001$), with a greater proportion of alates developing on pi plants. Crowding ($P<0.001$, $df=1,348$) was also significant with more alates developing from parents which were crowded as nymphs. Significant differences also occurred between temperatures ($P<0.001$, $df=2,348$) as the proportion of alates which developed, increased with increase in temperature.

Crowding had greater effect at the lower temperatures (11 and 15°C) with a greater proportion of alates developing in the crowded treatments than in the corresponding uncrowded

Table 7.4. The influence of plant quality, crowding and temperature on alate development in second generation *R. padi*, pi=previous aphid infestation, npi=no previous aphid infestation. Treatment means with different letters are significantly different ($P<0.05$).

Treatment	Temperature (°C)	Number of replicates	Mean proportion ($\pm$ S.E.) of alates
pi crowded	20	20	0.838 $\pm$ 0.008 ^a
npi crowded	20	40	0.697 $\pm$ 0.008 ^c
pi uncrowded	20	20	0.830 $\pm$ 0.007 ^a
npi uncrowded	20	40	0.675 $\pm$ 0.008 ^c
pi crowded	15	20	0.773 $\pm$ 0.007 ^b
npi crowded	15	40	0.624 $\pm$ 0.006 ^d
pi uncrowded	15	20	0.313 $\pm$ 0.005 ^e
npi uncrowded	15	40	0.184 $\pm$ 0.008 ^f
pi crowded	11	20	0.360 $\pm$ 0.009 ^e
npi crowded	11	40	0.205 $\pm$ 0.006 ^f
pi uncrowded	11	20	0.102 $\pm$ 0.007 ^g
npi uncrowded	11	40	0.059 $\pm$ 0.008 ^g

treatments (Table 7.4). Plant quality was more important at 20°C as more alates developed on pi plants than on np1 plants regardless of crowding.

The mean grouped adult weight in each treatment for each temperature is given in Table 7.5. At each temperature there was a significant difference in mean weights between treatments ($df=11, 1.001$). None of the interactions were significant ($P>0.05$). In addition, there was no significant difference between photoperiods ($df=1, 108, P>0.05$), or between crowded and uncrowded treatments ($P>0.05, df=1, 108$). Only plant quality was significant ($df=2, 108, P<0.001$). The data for photoperiod and crowding were pooled and the subsequent 1-way ANOVA for plant quality showed that adults which fed on pi plants were significantly lighter ($df=2, 108, P<0.001$) than those which fed on either np1c or np1u plants.

The mean potential fecundity in each treatment for each temperature is presented in Table 7.6. Potential fecundity was significantly different within each temperature ($P<0.001, df=11, 228$). The interactions were again not significant ($P>0.05$). Furthermore, neither photoperiod ($df=1, 228, P>0.05$) nor crowding ($df=1, 228, P>0.05$) were significant whereas plant quality was significant ($df=2, 228, P<0.001$). Consequently, the data for photoperiod and plant quality were pooled and a 1-way ANOVA for plant quality calculated. The mean potential fecundities of aphids which

Table 7.5. Mean grouped adult weights (n=10) of *R. padi* developing on wheat (cv. Halberd) at 11, 15 and 20°C under 11 and 14 hrs photoperiod on plants with and without a previous aphid infestation, pi=previous aphid infestation, npi=no previous aphid infestation, the "c" and "u" denote caged and uncaged treatments respectively.

weights of <i>R. padi</i> (10 ⁻¹ g)											
			11°C			15°C			20°C		
Treatment	n		11 hrs	14 hrs	Means for photo*	11 hrs	14 hrs	Means for photo*	11 hrs	14 hrs	Means for photo*
pi crowded	10	mean	0.145	0.145	0.145	0.138	0.138	0.138	0.139	0.141	0.140
		±S.E.	±0.002	±0.003	±0.002	±0.002	±0.002	±0.001	±0.002	±0.002	±0.001
pi uncrowded	10	mean	0.143	0.141	0.142	0.141	0.137	0.139	0.136	0.138	0.137
		±S.E.	±0.001	±0.002	±0.001	±0.003	±0.001	±0.001	±0.002	±0.002	±0.001
npic crowded	10	mean	0.158	0.157	0.158	0.160	0.162	0.160	0.153	0.151	0.153
		±S.E.	±0.002	±0.002	±0.002	±0.002	±0.002	±0.001	±0.002	±0.002	±0.001
npic uncrowded	10	mean	0.161	0.157	0.157	0.160	0.162	0.160	0.152	0.154	0.152
		±S.E.	±0.002	±0.001	±0.001	±0.001	±0.001	±0.001	±0.002	±0.002	±0.002
npiu crowded	10	mean	0.158	0.159	0.157	0.159	0.161	0.161	0.151	0.154	0.152
		±S.E.	±0.006	±0.003	±0.001	±0.002	±0.002	±0.001	±0.002	±0.002	±0.001
npiu uncrowded	10	mean	0.156	0.157	0.159	0.161	0.160	0.161	0.154	0.150	0.153
		±S.E.	±0.001	±0.002	±0.001	±0.001	±0.002	±0.001	±0.002	±0.002	±0.001
Pooled means for plant quality											
pi	40	mean	0.144			0.139			0.138		
		±S.E.	±0.001			±0.0012			±0.001		
npic	40	mean	0.158			0.160			0.152		
		±S.E.	±0.001			±0.001			±0.001		
npiu	40	mean	0.158			0.161			0.153		
		±S.E.	0.001			±0.001			±0.001		
Pooled means for crowded and uncrowded											
crowded	60	mean	0.154			0.153			0.148		
		±S.E.	±0.001			±0.002			±0.001		
uncrowded	60	mean	0.153			0.153			0.147		
		±S.E.	±0.001			±0.001			±0.001		

* photo = photoperiod

Table 7.6. Mean potential fecundity of *R. padi* developing on wheat (cv. Halberd) at 11, 15 and 20°C under 11 and 14 hrs photoperiod on plants with and without a previous aphid infestation, pi=previous aphid infestation, np=no previous aphid infestation, the "c" and "u" denote caged and uncaged treatments respectively.

		mean potential fecundity (embryos)									
		11°C			15°C			20°C			
Treatment	n		11 hrs	14 hrs	Means for photo*	11 hrs	14 hrs	Means for photo*	11 hrs	14 hrs	Means for photo
pi crowded	20	mean ±S.E.	23.05 ±0.37	22.70 ±0.39	22.88 ±0.27	20.95 ±0.30	21.00 ±0.31	20.98 ±0.21	22.00 ±0.49	21.90 ±0.42	21.95 ±0.42
pi uncrowded	20	mean ±S.E.	21.00 ±0.50	22.35 ±0.41	21.68 ±0.34	20.40 ±0.37	21.00 ±0.38	25.38 ±0.29	21.45 ±0.43	21.45 ±0.33	25.18 ±0.30
npic crowded	20	mean ±S.E.	25.70 ±0.67	24.95 ±0.59	25.48 ±0.37	25.00 ±0.48	25.05 ±0.39	25.03 ±0.31	25.25 ±0.55	24.90 ±0.54	25.08 ±0.38
npic uncrowded	20	mean ±S.E.	25.00 ±0.54	25.45 ±0.68	25.55 ±0.40	24.70 ±0.51	24.75 ±0.38	20.70 ±0.27	24.55 ±0.49	24.25 ±0.42	21.45 ±0.27
npiu crowded	20	mean ±S.E.	25.80 ±0.51	24.35 ±0.51	25.33 ±0.44	25.46 ±0.40	25.28 ±0.43	24.33 ±0.34	25.30 ±0.44	25.25 ±0.55	25.08 ±0.31
npiu uncrowded	20	mean ±S.E.	25.40 ±0.59	25.70 ±0.55	25.23 ±0.43	24.35 ±0.50	24.30 ±0.48	24.73 ±0.31	25.15 ±0.42	25.00 ±0.47	24.40 ±0.32
Pooled means for plant quality											
pi	80	mean ±S.E.	22.28 ±0.22			20.84 ±0.17			21.70 ±0.21		
npic	80	mean ±S.E.	25.31 ±0.27			24.85 ±0.23			25.13 ±0.21		
npiu	80	mean ±S.E.	25.28 ±0.31			24.88 0.22			24.74 ±0.25		
Pooled means for crowded and uncrowded											
crowded	120	mean ±S.E.	24.43 ±0.23			23.79 ±0.24			24.07 ±0.24		
uncrowded	120	mean ±S.E.	24.15 ±0.28			23.25 ±0.24			23.64 ±0.22		

*photo = photoperiod

fed on pi plants were significantly ($df=2,237$, $P<0.001$) lower than those which fed on npic and npiu plants.

Discussion

Crowding strongly influenced alate development in both generations. These results agree with previous observations made with *R. padi* as well as with other aphid species (Noda, 1958; Johnson, 1965; Lees, 1966; Dixon & Glen, 1971; Watt & Dixon, 1981).

Photoperiod also significantly influenced wing development, but only at 15°C in the first generation when more alates developed under short days. Short days in combination with crowding induced the development of more alate *Aphis craccivora* Koch exules than at long days when alate development appeared to be suppressed (Johnson, 1966b). However, this study showed, in the first generation at 15°C, a greater proportion of alates developed under short days with uncrowded aphids than at other temperatures indicating photoperiod was able to influence wing development in the absence of crowding. The failure of photoperiod to influence wing development at the other temperatures indicated that photoperiod, while not necessarily interacting with crowding to induce alate development, did appear to act with temperature.

Not all nymphs exposed to alate inducing cues in the first generation developed wings, indicating all aphids were not equally influenced. This may be explain in terms of the species'. If all offspring from individuals exposed to alate inducing cues developed wings, a chance exists that none will find a new host at that time. By having some progeny which either cannot develop wings or require a greater stimulus than others to do so, the risk of extinction of the local population is reduced by "spreading the risk", as proposed by den Boer (1968).

In the second generation, photoperiod failed to significantly influence alate development. This is possibly because the effects of photoperiod were masked by more influential determinants. Alternatively, as Lees (1966) suggested, the progeny of apterous adults on which photoperiod has already acted were no longer influenced and so by producing mostly apterous progeny, were better able to compete with others of the same species for the available food source. The latter again makes sense from the point of view of "spreading of risk" and the reduced chance of extinction of a local population.

The influence of temperature on wing development appeared to act both directly and indirectly on *R. padi*. In the first generation fewer alates developed at 11 and 20°C than at 15°C under the same photoperiods. High temperatures have also been reported to suppress alate development (Johnson,

1965, 1966b) possibly by increasing the activity of the corpora allata which controls aphid metamorphosis (Hales, 1976). The lack of alate development at 20°C and short days supports this mechanism.

The lack of alate development at 11°C plus short days was unexpected. Since alate development appears to be suppressed by high temperatures, and as short days appear to promote wing development, it was expected that more alates would have developed at 11°C short day than actually occurred. A possible explanation is that in South Australia a mean temperature of 11°C to 11.8°C (Waite Biennial Report, 1985/86) occurs during winter when conditions may be less conducive to dispersal. Consequently, *R. padi* may have adapted to produce alates during spring and autumn when the chance of dispersing to new hosts is greatest.

Temperature may also indirectly influence alate development, by affecting the speed at which hosts become unsuitable (Maelzer, 1981). Data from the second generation experiment supports this mechanism as pi plants supported a greater proportion of alates at 20°C regardless of crowding than occurred at the lower temperatures. It was also noted that the quantity of honey dew produced increased with temperature indicating aphid feeding activity also increased with temperature. Therefore, under the artificial conditions and apparent increased feeding by aphids, plants may have become less suitable sooner at 20°C, resulting in

the increased alate development. The production of alates at 20°C also suggests that reductions in plant quality may be able to overcome any suppression of alate development by high temperatures.

The weights of apterous adults on plants not previously infested were similar to those found on Halberd in the field and indicates the quality of plants used in the experiment were comparable to those in crops. The declines in adult weight and fecundity and the increased production of alates when forced to feed on plants previously infested with aphids suggests plant quality was strongly influenced by aphid feeding and reduced plant suitability for later generations.

The results support the roles of crowding, photoperiod and temperature in alate production in perennial grass pastures. In addition plant quality is also an important determinant, but is less likely to be important in autumn as temperatures are low, and head production, which is known to induce alate production (Kieckhefer, 1975), is not occurring. The action of photoperiod and crowding, independent of plant quality is supported by the results from the first experiment, but the nature of the influence of temperature is still unclear as the results support both direct and indirect - through the plant influences.

CHAPTER 8

Influence of high temperatures on the survival of the bird cherry-oat aphid, *Rhopalosiphum padi* in irrigated perennial grass pastures in South Australia

Abstract

A field experiment in perennial grass pastures showed that the survival of *R. padi* was reduced when aphids were exposed to air temperatures $\geq 36^{\circ}\text{C}$ (32°C at the base of the sward). The longevity, rate of reproduction and fecundity of individuals also declined as temperature increased. Aphids were also affected by the duration of exposure. The results of the field experiment were later corroborated by sampling an aphid population on critical days over summer and regressing aphid numbers on daily maximum temperature and duration of exposure to temperature. A model is proposed to estimate the numbers of aphids which survive in refuge areas over summer in relation to temperature-induced mortality.

Introduction

In summer and early autumn, *R. padi* is the most abundant of the species of wheat infesting cereal aphids found in the

sub-500mm rainfall areas of South Australia. During this period *R. padi* is restricted mainly to irrigated perennial grass pastures in the Lower Murray Valley and Mount Lofty Ranges (Chapter 6). As well as providing a refuge for *R. padi*, perennial grass pastures also harbour the PAV and RPV types of the barley yellow dwarf viruses (BYDV) transmitted by this species (Henry et al., in press).

In autumn, large numbers of alates migrate from these pastures to infest recently emerged annual grasses, including newly sown wheat crops. The number of migrants is dependent on the numbers of aphids surviving the summer. In February/March 1989, mean aphid numbers per 900 cm² of pasture ranged from 1.80 to 2.56 whereas, in 1990, they ranged from 33.16 to 92.28. The subsequent mean numbers of alatoid nymphs produced in mid-May 1989 ranged from 5.36 to 12.52 in contrast to 29.96 to 49.04 in 1990 (Chapter 6).

The smaller numbers of aphids in 1989 may have been due to the hotter summer. As early as 1919, declines in aphid numbers in the field have been attributed to high temperatures (Chaine, 1919). Recently, Tamaki et al. (1980) found temperatures between 31.6 and 42.3°C decelerated population growth for *Myzus persicae* (Sulzer); and in South Australia, 2 consecutive days with daily maximum temperatures $\geq 38^{\circ}\text{C}$ caused a high mortality of *Therioaphis trifolii* (Monell) forma *maculata* (Allen, 1984).

If *R. padi* is similarly adversely affected by high temperatures in summer, we may be able to predict the size of the surviving aphid population at the end of summer. This study aimed to elucidate, by manipulating temperatures in the field, the effect that high temperatures may have on the survival-rate, adult longevity, rate of reproduction and fecundity of *R. padi*.

Materials and Methods

Field experiment

The experiment was carried out in an irrigated pasture at Victor Harbour, 70 km south of Adelaide. The portion of the pasture chosen for the experiment was an almost pure stand of perennial ryegrass (*L. perenne*) with an average height of 11 cm.

The experiment was carried out in mid-January on a cloudless day with the shade temperature ranging from 22 to 27°C during the course of the experiment and a south easterly breeze of <1 knot.

Temperature was manipulated within plots of pasture to give treatments of either 32 or 35°C for 1, 2 or 3 hrs, or 38 or 40°C for 1, 2 or 2.75 hrs. There were 6 replicated

plots of the 32 and 35°C treatments and 4 of the 38 and 40°C treatments. A further 16 plots were included as the control; 8 of these were sampled at the beginning (Before control) and 8 at the end (After control) of the experiment. The total of 76 plots were randomised within one block with 1 m spacings between plots.

Each plot was 30 cm x 30 cm and temperature within it was raised by covering the pasture with a 30x30x0.5 cm sheet of transparent glass. Previous experiments had determined how to supplement the glass sheet with other materials to obtain different temperatures at the base of the ryegrass where *R. padi* was commonly found.

To obtain 32 and 35°C, the glass was supported on a wire frame which was either 14 cm or 6 cm high respectively, and the sides of the frame were enclosed in Xiro plastic (transparent plastic sheeting containing numerous holes). The top of the frame was lined with strips of sponge rubber to provide a uniform seal between the frame and the glass plate. To obtain 38°C the glass was simply placed onto the surface of the pasture; and to obtain 40°C the plot was covered with a 30x30x2.5 cm wooden frame with the glass resting on its top.

Preliminary trials with the different enclosures showed a temperature gradient of <1°C between the top and the base of the pasture. So temperatures were recorded only at the base

of the pasture in 2 randomly selected plots from each treatment. Measurements were made at 15 min intervals using a Fluke 52 K/J thermometer. Temperatures for the 32, 35 and 40°C treatments were maintained at the desired level by sliding the glass plate across the frame to allow hot air to escape more rapidly. For the 38°C treatments, the glass plate was slightly raised on the leeward side with a small stone. Each required temperature was achieved within 30 to 45 minutes of the plot being enclosed.

Each plot was sampled with a vacuum sampler (Chapter 3) at the completion of its exposure. Samples were stored at 15°C for 24 hrs to allow any unconscious aphids to revive. Aphids were first divided into dead and alive individuals, and then separated into the 5 morph groupings of; apterous adults, alate adults, apterous nymphs, alatoid nymphs and first-second instars.

Pasture height

Pasture height also influences temperature at the base of a sward because taller swards are cooler than shorter ones. Pasture height was measured at 30 points within each of 21 pastures across the Lower Murray Valley and Mt Lofty Ranges in February - March to obtain an average summer pasture height which could be used to predict the effect of temperature.

Adult longevity, rate of reproduction and fecundity

Longevity, rate of reproduction and fecundity were measured by taking surviving apterous third instars from each of the treatments and caging them individually onto wheat seedlings (1 aphid/seedling, cv. Halberd). Apterous individuals were selected because they were the dominant morph and probably contributed more to population increase than alates. After the final (4th) moult, the number of days survived and the number of progeny produced on each day was noted for each aphid. Eight aphids from each of the 32 and 35°C treatments and 8 from the 38°C for 1 and 2 hrs duration treatments were used, but only 4 nymphs from the 38°C for 2.75 hrs survived to be used, and none survived at 40°C.

Statistical analysis

Data were first tested for homogeneity of variance using the Fmax test. Means were compared using either ANOVA and Student's t-test. LSD ($\alpha=0.05$) was used to separate means when more than 2 were being compared and $P<0.05$.

Population numbers in relation to temperature

A perennial ryegrass, fescue (*F. arundinacea*), cocksfoot (*D. glomerata*) and clover (*Trifolium* spp.) pasture was sampled at Mt Barker during January/March 1991. Sampling commenced in mid-January and continued with samples being taken every 4 to 6 days until mid-March. Each sample comprised between 30 and 60 sample units.

For comparison, 4 samples (25 sample units/sample) were also taken from a perennial ryegrass, paspalum (*P. dilatatum*) and clover pasture at Murray Bridge. Two were collected in February, 1 in March and 1 in early April.

Samples were collected and processed as described in Chapter 3, but here first and second instars were included in the counts as a pooled group.

Results

Field experiment

The estimated mean number (per plot) of live plus dead aphids of each of the 5 morph groupings were very similar in all 14 treatments, and an ANOVA applied to the numbers of each morph grouping, in turn, indicated no significant

differences between treatments ($df=13,62$, $P>0.05$).

Another ANOVA applied to the overall total of all morph groupings also indicated no significant differences between treatments. The aphids were therefore distributed uniformly across all treatments; and their mean numbers are given in Table 8.1.

The mean numbers of live aphids in the before and after control plots (Table 8.1) were also not significantly different ($df=14$, $P>0.05$) for both the individual morph grouping and the overall totals (Table 8.1). Therefore, any mortality significantly greater than that occurring in the controls could be attributed to heat stress.

The mean proportion of mortality for each morph grouping, and the mean proportion of mortality over all morphs, are given for each treatment and each control in Table 8.2. Separate ANOVAs applied to the proportions of mortality for each morph grouping and to the proportions of mortality over all morphs, indicated significant differences between treatments and controls ($df=13,62$, $P<0.001$). Analysis using the LSD was then used to separate the means of all treatments.

First and second instars were the most susceptible to heat stress with mortality significantly greater than the controls starting at 32°C for 3 hrs duration (Table 8.2).

Table 8.1. The mean numbers, over all 14 temperature treatments, of alive + dead *R. padi* in a perennial ryegrass pasture at Victor Harbour during summer 1991. Also given are the mean numbers in the before control and after control plots. The standard errors are given in brackets.

Treatment	Alate adults	Alatoid nymphs	Apterous adults	Apterous nymphs	First-second nymphs	Total
Before Control	2.6 (0.37)	4.0 (0.4)	6.9 (0.3)	10.6 (0.5)	25.8 (0.6)	48.8 (0.7)
After Control	2.3 (0.4)	4.0 (0.3)	7.3 (0.3)	10.0 (0.7)	26.0 (0.7)	49.3 (1.1)
Overall treatment mean	2.6 (0.5)	3.0 (0.4)	7.1 (0.5)	10.2 (0.8)	24.3 (0.9)	47.3 (1.4)

Table 8.2. The effect of high temperatures on *R. padi* in a perennial grass pasture at Victor Harbour during summer 1991. The mean proportion of mortality of the different morph groupings and the mean proportion for all aphids totalled are given along with the standard errors in brackets.

Mean proportion of mortality							n
Treatment	Alate adults	Alatoid nymphs	Apterous adults	Apterous nymphs	First-second nymphs	Total	
Before Control	0.10 (0.07)	0.05 (0.05)	0.02 (0.02)	0.02 (0.02)	0.01 (0.01)	0.02 (0.01)	8
After Control	0.06 (0.06)	0 (0.00)	0.04 (0.02)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	8
40°C 1 hr	0.75 (0.14)	0.85 (0.09)	0.96 (0.04)	1.00 (0.00)	1.00 (0.00)	0.97 (0.01)	4
40°C 2 hrs	0.94 (0.06)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.01)	4
40°C 2.75 hrs	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	4
38°C 1 hr	0.94 (0.06)	0.44 (0.09)	0.52 (0.12)	0.25 (0.04)	0.96 (0.02)	0.70 (0.01)	4
38°C 2 hrs	0.92 (0.08)	0.56 (0.09)	0.83 (0.04)	0.61 (0.07)	1.00 (0.00)	0.86 (0.01)	4
38°C 2.75 hrs	0.85 (0.09)	0.71 (0.17)	0.76 (0.06)	0.91 (0.04)	1.00 (0.00)	0.92 (0.03)	4
35°C 1 hr	0 (0.00)	0 (0.00)	0 (0.00)	0.05 (0.05)	0.50 (0.04)	0.29 (0.03)	6
35°C 2 hrs	0.06 (0.06)	0.06 (0.06)	0 (0.00)	0.23 (0.05)	0.64 (0.03)	0.37 (0.02)	6
35°C 3 hrs	0.54 (0.07)	0.69 (0.10)	0.47 (0.08)	0.53 (0.06)	0.87 (0.03)	0.70 (0.03)	6
32°C 1 hr	0 (0.00)	0 (0.00)	0.02 (0.02)	0.02 (0.02)	0.06 (0.01)	0.04 (0.01)	6
32°C 2 hrs	0 (0.00)	0 (0.00)	0.04 (0.03)	0.03 (0.02)	0.17 (0.03)	0.10 (0.02)	6
32°C 3 hrs	0.06 (0.06)	0 (0.00)	0.08 (0.05)	0.03 (0.02)	0.43 (0.04)	0.25 (0.02)	6
l.s.d. (0.05, 62 df)							
n1,n2							
8, 8	0.14	0.14	0.09	0.08	0.05	0.04	
6, 6	0.17	0.16	0.11	0.09	0.06	0.05	
4, 4	0.20	0.19	0.13	0.11	0.08	0.06	
8, 6	0.16	0.15	0.19	0.08	0.06	0.05	
8, 4	0.18	0.17	0.12	0.10	0.07	0.06	
6, 4	0.19	0.18	0.12	0.10	0.07	0.06	

For the remaining morph groupings, no significant mortality occurred at 32°C. Apterous nymphs were less susceptible than first and second instars to heat stress as significant mortality started at 35°C for 2 hrs duration (Table 8.2). Alate and apterous adults and alatoid nymphs were the most tolerant, but all suffered significant mortality at temperature/duration combinations >35°C for 2 hrs duration (Table 8.2).

The high temperature threshold

To further quantify the influence of the treatments on the mortality of aphids, the mean proportion of mortality over all morphs (M) was regressed, by multiple regression, on log temperature (logT) and duration (D) of exposure by the equation:

$$M = -9.191\log T + 0.118D - 13.950 \quad (r^2=0.970, \text{ df } 9, P<0.001)$$

The threshold for mortality at 32°C was determined by substitution into the equation to be 1 hr. This threshold is based on temperatures at the base of the sward.

To use this threshold information to predict mortality, we needed to establish the relation between the temperature at the base of the sward, sward height and the daily maximum temperature in a standard climatological (Stephenson)

screen.

So, temperatures at the bases of 5, 10 and 15 cm swards (St) and air temperatures within a Stephenson screen (Ss) were determined for 3 hot days in Jan-Feb. The relationships are illustrated in Fig. 8.1 and were fitted by the following equations (Fig. 8.1):

$$5 \text{ cm; } Ss = 136.49 - 13.326St + 0.049407St^2 - 0.0055417St^3$$

$$(r^2 = 0.993) \quad (2.1)$$

$$10 \text{ cm; } Ss = -21.94 + 1.5294St + 0.0492505St^2 - 0.0010585St^3$$

$$(r^2 = 0.994) \quad (2.2)$$

$$15 \text{ cm; } Ss = 13.332 - 1.2003St + 0.11575St^2 - 0.0017267St^3$$

$$(r^2 = 0.997) \quad (2.3)$$

The average pasture height during February and March across 21 pastures was determined in both months as 9.7 cm. So equation 2.2 was used to convert the threshold temperature of 32°C at the base of a 10 cm high pasture to a threshold of 36°C in a Stephenson screen.

Influence of high temperatures on adult biology

The mean longevity of adults, their mean fecundity and their mean rate of fecundity, generally declined with increases in temperature and duration of exposure (Table 8.3). However, the properties of aphids exposed to 32°C for

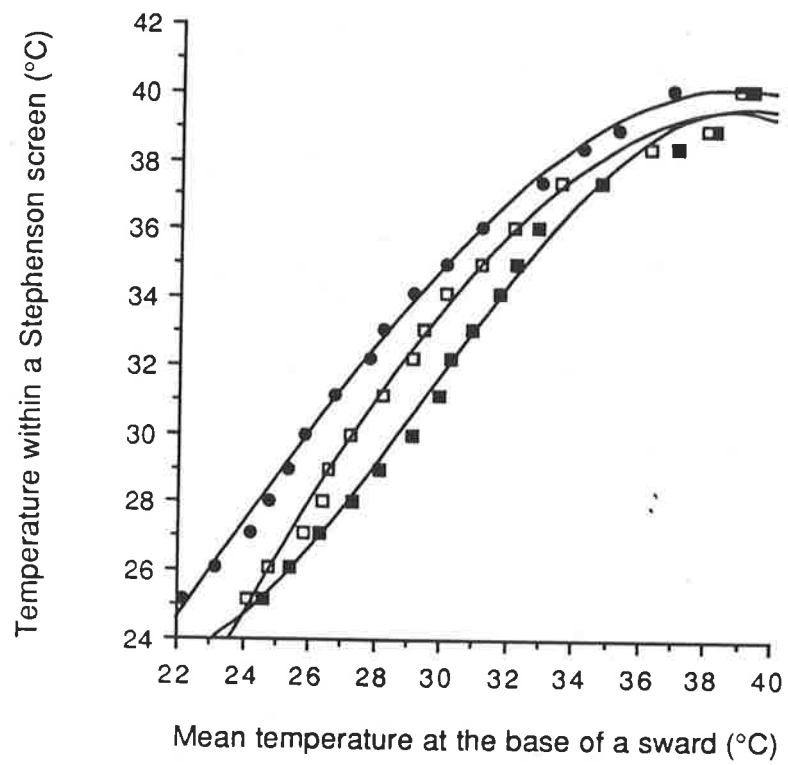


Fig. 8.1 . Mean temperatures at the base of 5 (■), 10 (□) and 15 (●) cm pasture swards compared with temperatures within a Stephenson screen.

Table 8.3. The effect of high temperatures on the mean longevity, mean fecundity and rate of fecundity per adult per day of *R. padi*. Standard errors are given brackets.

Treatment	n	Mean adult longevity	Mean number of progeny	Mean number of Ny/adult/day
Control	8	8.9 (0.4)	15.9 (0.6)	1.8 (0.1)
38°C 1 hr	8	5.6 (0.2)	6.3 (0.3)	1.1 (0.1)
38°C 2 hrs	8	5.3 (0.2)	5.9 (0.4)	1.1 (0.1)
38°C 2.75 hrs	4	5.3 (0.2)	5.8 (0.3)	1.1 (0.1)
35°C 1 hr	8	7.0 (0.3)	9.1 (0.5)	1.3 (0.1)
35°C 2 hrs	8	6.0 (0.3)	9.0 (0.4)	1.5 (0.1)
35°C 3 hrs	8	6.1 (0.3)	8.4 (0.5)	1.4 (0.1)
32°C 1 hr	8	8.6 (0.4)	15.4 (0.9)	1.8 (0.1)
32°C 2 hrs	8	8.6 (0.4)	16.4 (0.6)	1.9 (0.1)
32°C 3 hrs	8	8.3 (0.4)	12.6 (0.5)	1.5 (0.1)
l.s.d. (0.05, 66 df)				
n1,n2				
8, 8		0.9	1.5	0.2
4, 8		1.1	1.8	0.3

1 or 2 hours were not different to those of the controls.

Temperatures and population numbers in 1991

The mean total number of aphids and of individual morphs at Mt Barker peaked on 3 occasions during January/March, 1991 (Fig. 8.2). Each of the first 2 peaks was followed by a sharp decline in numbers, with all morphs being affected (Fig. 8.2). Both periods of decline were associated with a daily maximum temperature above the postulated 36°C threshold (Fig. 8.2). No other decline in numbers was observed during the sampling period. In particular, there was no decline in numbers after 26 February despite the maximum temperature reaching 35°C on 2 days; and aphid numbers increased steadily to a higher peak on 3 April when sampling ceased.

For comparison, the numbers of aphids on 6 sample dates in a pasture at Murray Bridge are given in Fig. 8.3 with their respective maximum daily temperatures. The numbers were much lower than those at Mt Barker until mid-March and seem to be associated with hotter and more frequent "hot" days. They only started to increase after mid-March when maximum temperatures were lower than the suggested threshold of 36°C (Fig. 8.3).

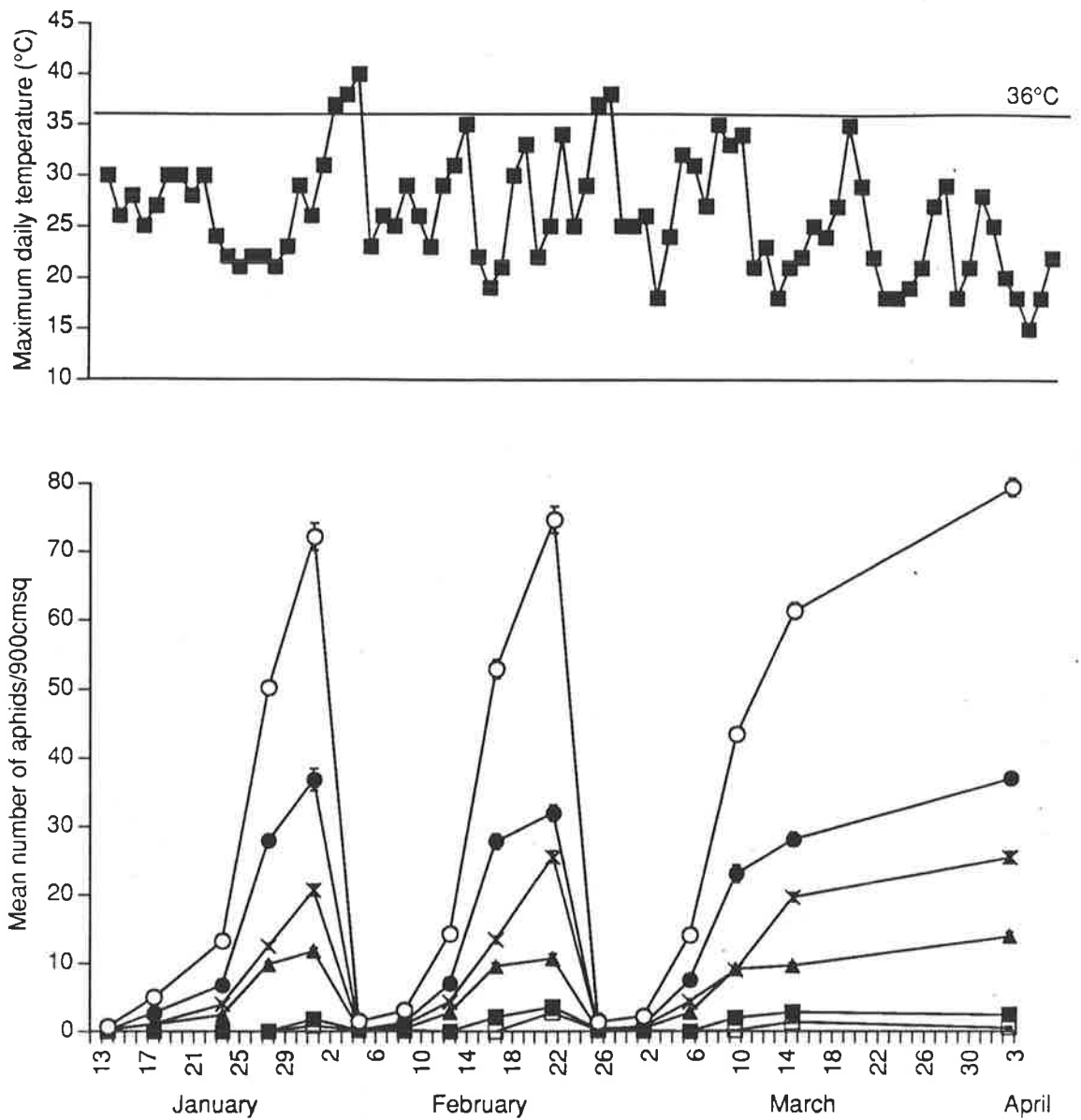


Fig. 8.2. The maximum daily temperatures and the mean numbers of alate adults (□), alatoid nymphs (■), apterous adults (▲), apterous nymphs (X), first/second instars (●) and total numbers of *R. padi* (○) present in an irrigated perennial grass pasture at Mount Barker, South Australia during January - April 1991.

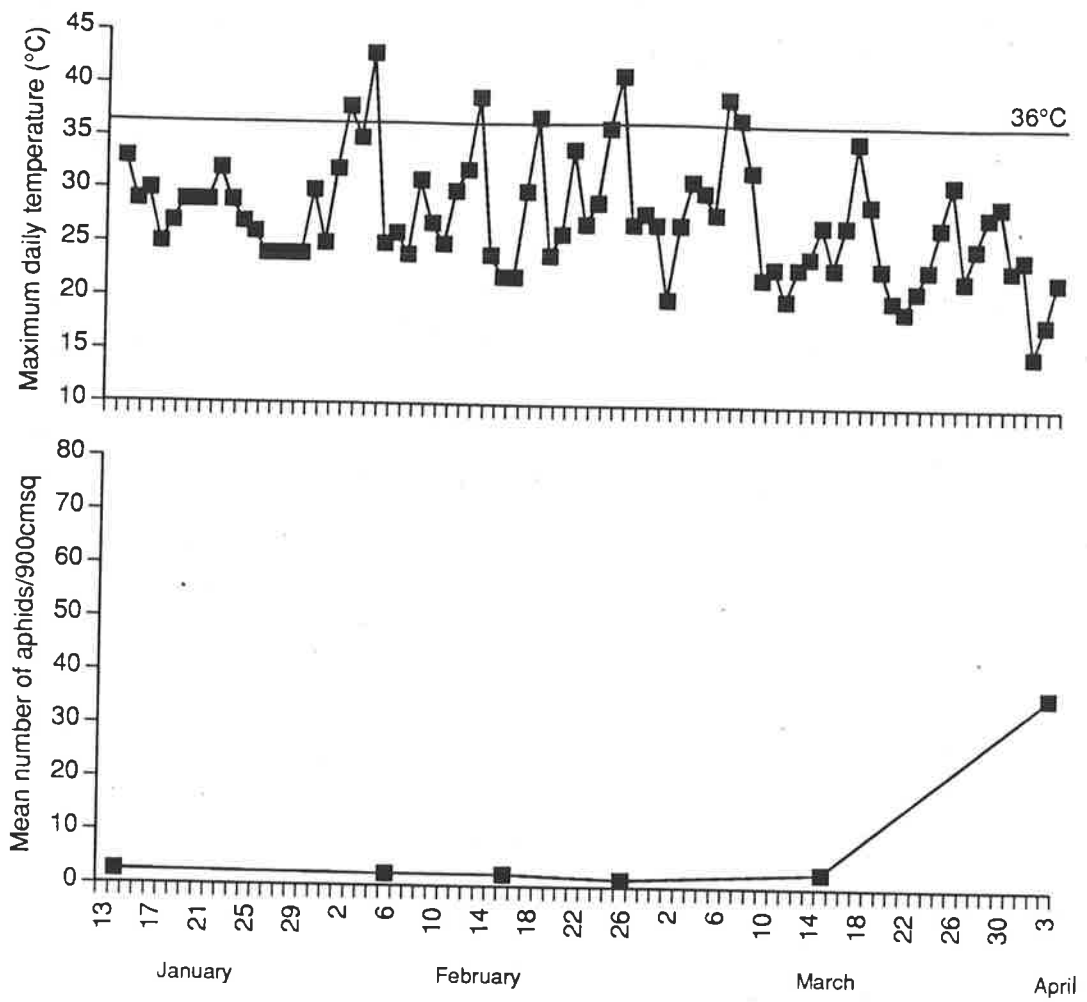


Fig. 8.3. The maximum daily temperatures and the mean total number of *R. padi* present in an irrigated perennial grass pasture at Murray Bridge, South Australia during January - April 1991.

The likelihood of occurrence of days $\geq 36^{\circ}\text{C}$

Data for Mt Barker (Fig. 8.2) clearly show that *R. padi* numbers were able to recover rapidly in March-April despite massive mortality occurring at the end of February. However, data for Murray Bridge (Fig. 8.3) indicate that recovery was slower when numbers were still low in mid-March. This slowing in the rate of population increase at Murray Bridge is almost certainly due to the decline in temperatures during autumn (mid-March onwards) (Fig. 8.3). Consequently, mortality caused by heat stress in January and February is likely to have a lesser impact on the number of alates produced in April and May if no further days $\geq 36^{\circ}\text{C}$ are experienced in March. Therefore, the critical period for assessing the likely impact of high temperatures on aphid numbers is the first 14 days of March.

The probability of high aphid mortality in each of the weeks in February-March was estimated from temperature records (1925-1991) for the Waite Institute in Adelaide which is 30 km from Mt Barker and has similar temperatures. Table 8.4 shows the proportion of years with at least 1 day $\geq 36^{\circ}\text{C}$ in each week. The data show a marked decline in proportion after the first 2 weeks in March. If the data for those first 2 weeks are pooled, the proportion increases to 0.38, indicating that lethal high temperatures occur in those 2 weeks in about 4 years out of 10.

Table 8.4. The proportion of years with at least 1 day $\geq 36^{\circ}\text{C}$ in each of the weeks of February and March. Probabilities were calculated using the daily maximum temperature records for the Waite Institute (1925-1991).

February				March			
1 - 7	8 - 14	15 - 21	22 - 28	1 - 7	8 - 14	15 - 21	22 - 28
0.38	0.41	0.30	0.30	0.26	0.15	0.02	0.03

Discussion

The estimates of mortality were based on the numbers of aphids which died either during the experiment or in the subsequent 24 hours. These may be underestimates, especially at the lower temperatures because of the "delayed-action" effect of high temperatures which may result in mortality at some later critical stage (Andrewartha & Birch, 1954). The surviving third instars successfully completed their development, indicating this is unlikely for third instars; but further studies should be made of the longer term effects of heat stress on younger instars.

An upper temperature threshold for development is often a mortality threshold because development does not usually stop until the aphid dies. Upper temperature thresholds have been found to be between 34 and 40°C for several species of aphids (Chaine, 1919; Broadbent & Hollings, 1951; Harrison & Barlow, 1973; Allen, 1984). The estimated threshold is dependent on the rate of acclimatization, with higher mortality following rapid rather than gradual temperature increases (Chaine, 1919; Andrewartha & Birch, 1954). In South Australia, "heat waves" are usually preceded by several days on which temperatures are 5 to 10°C cooler. Consequently, *R. padi* is often faced with rapid increases in temperature and the mortalities in the field are likely to well reflect those recorded in the experiment.

Acclimatization is an important factor which needs to be born in mind when attempting to determine high temperature thresholds. Short exposures to high sub-lethal temperatures either on the same day or the day preceding exposure to possibly lethal high temperatures improves insects' chance of survival (Bursell, 1970). In contrast, exposures to constant high temperatures do not give insects the chance to acclimatize, and so thresholds from such experiments underestimate insects' tolerance to high temperatures (Bursell, 1970). As a consequence, Villanueva & Strong (1964) and Zaidi (1981), using constant temperatures, estimated thresholds 5 and 2°C lower, respectively, than the 32°C (at the base of the sward) proposed here.

Another possible cause of differences in estimated high temperature thresholds is that light intensities used in laboratory experiments are often equivalent only to those which occur in winter and so fall well short of the intensities needed to simulate summer. Such low light intensities could result in different plant physiologies which affect aphid biology.

High temperatures and population dynamics

Apart from the high mortality of aphids at temperatures $\geq 36^{\circ}\text{C}$ (32°C at the base of the sward), the data of Fig. 8.3

also suggest that aphid population growth up to each peak was being suppressed by one or more processes as numbers increased. There is no evidence that sub-lethal temperatures, which reduce fecundity, longevity and the rate of development of other aphid species, have any direct influence on *R. padi* (Broadbent & Hollings, 1951; Villanueva & Strong, 1954; Tamaki et al., 1980).

Sub-lethal temperatures may also reduce plant quality, for some aphid species, by increasing the speed at which the plant matures (Maelzer, 1981) or by increasing the numbers of aphids feeding on it (Tamaki et al., 1980). However, plant quality is likely to be reduced for *R. padi* only when head development begins (Forbes, 1962; Kieckhefer, 1975), which does not occur in pastures until spring. A density-related process is also unlikely to be involved in population growth because even at the highest numbers of aphids per sample, the mean density of aphids per tiller was less than 1 (De Barro unpublished data).

It was tentatively concluded, therefore, that predation was the most likely process which was suppressing aphid population growth up to each peak in numbers depicted in Fig. 8.2. An experimental test of this hypothesis is reported in a Chapter 9.

Predicting the survival of R. padi in pastures over summer

The suggested threshold of 36°C can be used to assess the probability of survival of aphids in the summer refuge areas. Chapter 6 and Henry (unpublished data, Chapter 15) have shown that these pastures are an important source of viruliferous aphids which infest wheat crops in autumn. In addition, Chapter 14 has shown there is no evidence to support the occurrence of large migrations into South Australia from elsewhere during autumn. Therefore, by assessing the probability of aphids survival in pastures over summer, and coupling this with other variables such as the production of alates in the refuge areas, timing of the opening rains and sowing date, it may be possible to predict the likelihood of outbreaks of BYDV in wheat crops in the low rainfall wheat belt of South Australia.

Temperatures $\geq 36^{\circ}\text{C}$ reduced aphid numbers. However, another factor or factors appeared to be acting to reduce the rate of increase. The following chapter describes an experiment aimed at determining whether natural enemies were having a significant effect on aphid numbers in pastures and if so, which species were considered to be the more important. This chapter has been published in *Ann. app. Biol.*

CHAPTER 9

The impact of spiders and high temperatures on cereal aphid *R. padi* numbers in an irrigated perennial grass pasture in South Australia.

Abstract

Spiders were the most important group of aphid natural enemies in an irrigated perennial grass pasture. The Lycosidae and Linyphiidae were the only families encountered. An exclusion experiment found predation by spiders to be an important factor in controlling aphid numbers. Together with high temperatures, they maintained aphid numbers at a lower than expected level.

Introduction

Irrigated perennial grass pastures are an important summer refuge area for *R. padi* and the PAV and RPV types of barley yellow dwarf viruses (BYDV) which it transmits (Chapter 6, 1991a; Henry et al., in press). The numbers of aphids surviving in pastures over summer influence alate numbers produced in autumn (Chapter 6). Survival through the summer was shown experimentally to depend on the frequency of

lethal high temperatures (Chapters 8). However, the experiments also indicated other variables were depressing the aphids' rate of increase, and predation was proposed as the most likely one.

Numerous studies have suggested that generalist predators, such as the Carabidae, Staphylinidae and the Araneida are important in controlling aphid numbers, especially in the colonisation phase when densities are low (Vickerman & Wratten, 1979; Chiverton, 1987). Similar studies have not been done with cereal aphids in Australia, but in dryland lucerne pastures, native predators and introduced parasites were important in maintaining low populations of spotted alfalfa aphids (*T. trifolii* forma *maculata*) during spring (Allen, 1984).

Predators could similarly help to maintain lower numbers of *R. padi* in summer refuge areas. An experiment was therefore conducted to test whether aphid numbers in refuge areas could be influenced by manipulating both temperature and predators.

Materials and Methods

The experiment was carried out in early autumn in an irrigated pasture comprising fescue (*F. arundinacea*), perennial ryegrass (*L. perenne*), cocksfoot (*D. glomerata*)

and clover (*Trifolium* spp.). The pasture (4 ha) was at Mount Barker in the Mount Lofty Ranges, South Australia and was used for grazing dairy cattle (50 cattle/ha/day). It was bordered by further pastures and irrigated using sprinklers with timing and frequency of irrigation dependant on temperature. No agrochemicals were applied.

Plots of pasture were caged to either exclude or contain natural enemies. Table 9.1 describes the experimental design. A total of 120 plots, each 195 cm², were laid out in a 12x10 completely randomized design. There were 90 treatment and 30 control plots. The later were used to account for any cage effect. All treatment plots were caged at time zero (T0) (6/3/91) whereas the control plots were left uncaged. Each cage was a cylindrical piece of PVC piping (200 mm x 157 mm (length x I.D.), Hardie Iplex TM, WPSO 160) with 25 mm embedded into the soil. The open end was covered with a fine voilé and held in place with a rubber band. The cage surface area was 195 cm².

At T0 the treatment plots were prepared. The 30 plots designated as "enemies removed" were vacuum sampled for 15 sec. using a McCulloch Eager Beaver Blower/Vac R (Chapter 3). Any predators, parasitoids (adults and mummies) and diseased aphids present were discarded. All remaining material was returned to the plots from which they came. Each of the 30 plots designated "enemies returned" was vacuum sampled, the material removed and then returned

Table 9.1. The number of plots of each treatment sampled on the 3 sample dates.

Treatment	T0 (6/3/91)	T1 (15/3/91)	T2 (3/4/91)	
enemies removed		10	10	
enemies removed + heat at T2			10	
enemies returned		10	10	
enemies returned + heat at T2			10	
enemies undisturbed		10	10	
enemies undisturbed + heat at T2			10	
control	10	10	10	
totals	10	40	70	120

without further disturbance. The remaining 30 caged plots were left untouched and labelled "enemies undisturbed".

After preparing the treatment plots, 10 control plots were vacuum sampled (Table 9.1). The material collected from each was sorted and aphids identified, separated into alate and apterous adults, alatoid and apterous third/fourth instars, and first/second instars, and counted. Alatoid and apterous nymphs were identified using the presence of wing buds, and both were separated from the first/second instars on the basis of size. No aphid parasitoids, aphid-specific predators, or any diseased aphids were found in any of the samples. Generalist predators were the only natural enemies found and these were removed for identification.

The remaining 110 plots were left until numbers in the surrounding pasture had increased to between 13 and 14 aphids/195 cm² (T1, 15/3/91). This was roughly equivalent to the pre-peak numbers observed in this pasture in a study of high temperatures and their influence on aphid mortality (Chapter 6). Ten plots of each of the treatments plus control were then vacuum sampled (Table 9.1). Aphids and natural enemies were treated as before.

The remaining 70 plots were left until T2 (3/4/91) so that aphid numbers had the opportunity to increase past the peak numbers observed in the earlier study (Chapter 6). On this day, the cage of each plot designated as "enemies present +

heat", "enemies removed + heat" and "enemies undisturbed + heat" was covered with a glass plate. The remaining caged plots were left untouched.

Temperatures were noted at the base of the pasture every 15 minutes within 2 glass covered cages and 2 voilé covered cages using a Fluke 52 K/J thermometer TM. Temperatures increased from 17°C to 22°C in the voilé covered cages (these were 1-2°C above ambient) and from 18°C to 34°C in the glass covered cages. Temperatures in the glass covered cages remained above 32°C (the high temperature mortality threshold at the base of a pasture sward (Chapter 8)) for 2 hrs. The total duration of heating was 2.75 hrs. The control plots were left untouched. All plots were sampled after the heat treatment had been completed. Samples were stored at 5°C for 6 hrs before counting to allow unconscious aphids to revive. All live aphids and live plus dead spiders were counted. Spiders were identified by Dr M. Harvey, Western Australian Museum.

Results

Of the Insecta, only a single specimen of *Platycoelus* sp. (Carabidae) was found. The remaining predators were spiders, of which Lycosidae (1 species, undetermined) and Linyphiidae (6 species: *Erigone* sp.; *Eperigone fradeorum* (Berland); 4 species undetermined) were the only families

represented. *Erigone* sp. and the unidentified lycosid species were the most numerous.

No alate adults or alatoid instars were present in the control plots at T0. The mean numbers of apterous adults, apterous and first/second instars over all 10 plots were respectively: 0.8 ± 0.3 , 1.3 ± 0.3 and 1.7 ± 0.3 . The mean total was 3.8 ± 0.5 .

At T1, data (Table 9.2) were transformed using $\sqrt{(x+0.1)}$ to ensure homogeneity and then analysed using one-way ANOVA. The numbers of alate and apterous adults, and alatoid instars were highest in the "enemies removed" plots. However, there were no differences between numbers in the control, "enemies returned" and "enemies undisturbed" plots. The total number of aphids as well as the numbers of apterous and first/second instars were also greatest in the "enemies removed" plots. However, in each case, there were more aphids in the control plots than in the "enemies returned" and "enemies undisturbed" plots (Table 9.2).

The data (Table 9.3) for the numbers of aphids at T2 were also transformed ($\sqrt{(x+0.1)}$). The control was omitted from the initial analyses as only differences between treatments were being tested. The numbers of aphids differed among treatments ($df=5,54$, $P<0.001$), but there was no significant interaction between predation and high temperature exposure for either individual morphs or total numbers.

Table 9.2. Mean number and $\sqrt{(x+0.1)}$ mean $\pm$ S.E. of *R. padi* at T1 (15/3/91) for the 10 plots in each treatment.

Treatment	Alate adult		Alatoid third/fourth instar		Apterous adult		Apterous third/fourth instar		First/Second instar		Total number of <i>R. padi</i>	
	Mean	$\sqrt{(x+0.1)}$ (S.E.)	Mean	$\sqrt{(x+0.1)}$ (S.E.)	Mean	$\sqrt{(x+0.1)}$ (S.E.)	Mean	$\sqrt{(x+0.1)}$ (S.E.)	Mean	$\sqrt{(x+0.1)}$ (S.E.)	Mean	$\sqrt{(x+0.1)}$ (S.E.)
enemies removed	2.9	1.7 (0.1)	1.6	1.3 (0.1)	4.3	2.1 (0.1)	10.6	3.3 (0.1)	12.3	3.5 (0.1)	31.7	5.6 (0.1)
enemies returned	0.1	0.4 (0.1)	1.0	1.0 (0.1)	2.0	1.4 (0.1)	1.9	1.4 (0.1)	1.8	1.3 (0.1)	6.8	2.6 (0.1)
enemies undisturbed	0.3	0.5 (0.1)	0.9	0.9 (0.1)	1.8	1.3 (0.1)	2.0	1.4 (0.1)	1.8	1.3 (0.1)	6.8	2.6 (0.1)
control	0.2	0.5 (0.1)	0.8	0.9 (0.1)	2.1	1.5 (0.1)	4.8	2.2 (0.1)	6.8	2.6 (0.1)	14.7	3.8 (0.1)
s.e.d. (36 df)		0.2		0.1		0.1		0.1		0.1		0.1

Table 9.3. Mean number and $\sqrt{(x+0.1)}$ mean $\pm$ S.E. of *R. padi* at T2 (3/4/91) for the 10 plots in each treatment.

Treatment	Alate adult		Alatoid third/fourth instars		Apterous adult		Apterous third/fourth instars		First/Second instars		Total number of <i>R. padi</i>	
	Mean	$\sqrt{(x+0.1)}$ (S.E.)	Mean	$\sqrt{(x+0.1)}$ (S.E.)	Mean	$\sqrt{(x+0.1)}$ (S.E.)	Mean	$\sqrt{(x+0.1)}$ (S.E.)	Mean	$\sqrt{(x+0.1)}$ (S.E.)	Mean	$\sqrt{(x+0.1)}$ (S.E.)
enemies removed*	24.9	5.0 (0.2)	31.7	5.6 (0.2)	19.4	4.4 (0.2)	29.9	5.5 (0.2)	58.6	7.6 (0.3)	164.5	12.8 (0.3)
enemies removed + heat	25.0	5.0 (0.1)	28.6	5.3 (0.2)	13.7	3.7 (0.1)	10.1	3.1 (0.2)	0.8	0.8 (0.2)	78.2	8.8 (0.1)
enemies returned*	-	-	-	-	2.1	1.4 (0.2)	2.7	1.6 (0.1)	5.8	2.4 (0.2)	19.0	3.1 (0.2)
enemies returned + heat	-	-	-	-	1.7	1.3 (0.1)	1.2	1.1 (0.1)	0.3	0.5 (0.1)	3.2	1.8 (0.1)
enemies undisturbed*	-	-	-	-	2.1	1.4 (0.1)	2.6	1.6 (0.1)	5.3	2.3 (0.2)	10.0	3.2 (0.2)
enemies undisturbed + heat	-	-	-	-	2.0	1.4 (0.1)	1.5	1.2 (0.1)	0.6	0.7 (0.1)	4.1	2.0 (0.1)
control	-	-	-	-	3.2	1.8 (0.1)	5.9	2.4 (0.1)	8.6	2.9 (0.1)	18.5	4.3 (0.1)
*s.e.d. (27 df) for treatments						0.2		0.2		0.3		0.3
Pooled means for heat												
heated					7.9	2.4 (0.3)	11.7	2.9 (0.4)	23.2	4.1 (0.5)	61.7	6.4 (0.9)
unheated					5.8	2.1 (0.2)	4.3	1.8 (0.2)	0.6	0.7 (0.1)	28.5	4.2 (0.6)

To test the influence of predation on aphid numbers, the 3 heat treatments were omitted (Table 9.3). Only alate adults and alatoid instars occurred in the "enemies removed" plots. For the remaining morphs as well as the overall total, more aphids were present in the "enemies removed" plots than in the remaining treatments ($df=2,27$, $P<0.001$). However, there was no difference between the numbers of aphids in the "enemies returned" and the "enemies undisturbed" plots.

The influence of high temperatures on aphid numbers was tested by pooling the data for the 3 heat treatments and comparing these with the pooled data for the 3 unheated treatments (Table 9.3). Exposure to high temperatures in the caged plots had no effect on alate and apterous adults (18 df, $P>0.05$), and alatoid instars (58 df, $P>0.05$). However, declines in the numbers of both apterous and first/second instars as well as an overall decline in the total numbers of aphids (58 df, $P<0.001$ for each morph grouping) were observed.

To determine whether predation or high temperature led to a greater decline in the numbers of each morph grouping, each of the heated treatments was compared with its unheated counterpart. There were no significant differences between the numbers of alate and apterous adults, and alatoid instars in each of the 3 treatment pairs. However, there were always significantly fewer apterous and first/second

instars in the heated treatment than in the corresponding unheated treatment. The total number of aphids was also significantly lower in each of the heated treatments.

A significant cage effect was determined after comparing the control data (Table 9.3) with the 3 treatments. As expected, there was a significant difference ($df=3,36$, $P<0.001$) between treatments and control for each morph grouping as well as the total. More aphids were present in the "enemies removed" plots than in the control plots. In contrast, there were fewer aphids in the "enemies returned" and "enemies undisturbed" plots than in the control.

The mean total number of spiders at T0 was 3.1 ± 0.5 (Table 9.4). No spiders were present in the "enemies removed" plots at T1 (Table 9.4). Comparisons among the remaining treatments and control showed fewer spiders present in the control.

At T2 there was an overall significant difference in spider numbers ($5,54$ df , $P<0.001$, Table 9.4) among treatments. The interaction between spider numbers and exposure to high temperatures was not significant. No spider mortality was noted. Also, no difference was found between spider numbers in each heated treatment and its unheated counterpart so the data for each pair of treatments were pooled and compared with the control.

Table 9.4. Mean numbers $\pm$ S.E. of juvenile spiders and the mean total number $\pm$ S.E. of spiders at T0, T1 and T2 for the 10 plots in each treatment.

Treatment	Time of sampling	Mean number of juvenile spiders	Mean total number of spiders	
control	T0	1.2 $\pm$ 0.5	3.1 $\pm$ 0.5	
enemies removed	T1	0	0	
enemies returned	T1	1.3 $\pm$ 0.4	2.9 $\pm$ 0.5	
enemies undisturbed	T1	0.9 $\pm$ 0.2	2.3 $\pm$ 0.3	
control	T1	0.5 $\pm$ 0.2	1.7 $\pm$ 0.2	
s.e.d. (27 df)			0.2	
				Pooled means
enemies removed	T2	0	0.2 $\pm$ 0.1	
enemies removed+ heat	T2	0	0.1 $\pm$ 0.1	0.2 $\pm$ 0.1
enemies returned	T2	3.8 $\pm$ 0.8	4.6 $\pm$ 0.9	
enemies returned + heat	T2	3.8 $\pm$ 0.7	4.4 $\pm$ 0.8	4.5 $\pm$ 0.6
enemies undisturbed	T2	2.7 $\pm$ 0.3	3.6 $\pm$ 0.4	
enemies undisturbed + heat	T2	3.1 $\pm$ 0.6	4.5 $\pm$ 0.7	4.1 $\pm$ 0.4
control	T2	0.8 $\pm$ 0.2	2.3 $\pm$ 0.3	
s.e.d. (66 df)				0.8
<u>Pooled means for heat</u>				
heated	T2		3.0 $\pm$ 1.2	
unheated	T2		2.8 $\pm$ 1.5	

There was a significant difference (3,66 df, $P < 0.001$) among the treatments and control. More spiders were present in the "enemies returned" and "enemies undisturbed" plots than in the "enemies removed" plots (Table 9.4). Also, there were approximately 50% fewer spiders in the control than in the "enemies returned" and "enemies undisturbed" plots.

The greater numbers of spiders in the caged plots was due to the increased numbers of juveniles (Table 9.4). This may explain the preferential decline at T1 in the numbers of apterous and first/second instars between caged and uncaged plots with predators (Table 9.2) as the juveniles were more likely to have preyed on the smaller instars. Disturbance had no negative effect on the numbers of spiders.

Discussion

Generalist predators had a major impact on aphid numbers as their removal led to a 15 to 16 fold increase in aphid numbers. In conjunction with lethal high temperature exposure, they caused even greater declines in numbers than did heat stress alone.

The presence of spiders significantly reduced the numbers of each of the different aphid morphs. In the case of alate adults and alatoid instars, spiders may have reduced numbers

either through selective predation or by reducing numbers to below the level at which crowding induces alate development. This phenomena has recently been proposed (Wellings, 1991) and suggests natural enemies may be useful in disrupting aphid migration. Furthermore, younger instars also appeared more vulnerable to predation, but further study is needed on this.

The control suggests that both aphid mortality and spider numbers were greater in the caged plots from which natural enemies were not removed. Consequently, for the real influence of spiders on aphid numbers to be assessed, further experiments using uncaged pasture would be needed.

In Australia, most studies of pasture aphids' natural enemies have been associated with species infesting *Medicago* spp.. Only one study has dealt with cereal aphids (Ridland, 1988). In that study, the hemerobiid lacewing, *Micromus tasmaniae* (Walker) and the syrphid *Melangyna viridiceps* (Macquart) were the most commonly observed Sternorrhyncha-preferred predators while Carabidae and Staphylinidae, along with Lycosidae and Linyphiidae were the most numerous generalist predators.

In New South Wales, lycosids and linyphiids were also commonly found in lucerne crops (Bishop & Holtkamp, 1982). They are also recorded as important aphid predators in European studies of aphids in cereal crops (Nyffeler & Benz,

1979; Sunderland et al., 1986). This study did not attempt to define specific relationships between the different predator species and *R. padi*. Further studies involving antibodies against aphids (Chiverton, 1987) would be useful in determining which species and what proportions thereof fed on *R. padi*.

The lack of Sternorrhyncha-preferred natural enemies is not surprising given the large fluctuations in aphid numbers caused by lethal high temperatures in summer and early autumn (Chapter 8). Fluctuations would result in a discontinuous food source, thereby preventing numbers of these natural enemies from building up. In contrast, generalists are able to persist during periods of low aphid density by feeding on other prey (Vickerman & Wratten, 1979) and consequently, the occurrence of aphids in pastures over summer is analogous to the colonisation phase in cereal crops. The lack of generalist predatory insects was surprising as they are common later in the year (unpublished data), indicating they may be unable to survive heat stress.

Heating had no effect on the numbers of adults and alate instars, while numbers of apterous and first/second instars were significantly reduced. First/second instars were the most affected by heating. These results confirm those from a previous experiment (Chapter 8) and adds further support to the hypothesis that lethal high temperatures play a dominant role in determining aphid numbers over summer.

This study did not, expose aphids to the extreme temperatures ($\geq 39^{\circ}\text{C}$) which cause aphid mortality to exceed 90% (Chapter 8). In such circumstances the impact of predation may be inconsequential. Therefore, natural enemies are likely to be more important in years when summer temperatures are not extreme.

The importance of BYDV in low rainfall South Australia is unknown. However, if BYDV causes economic reductions in yield, it may be possible to reduce its impact by augmenting natural enemy numbers in the pasture refuge areas, thereby reducing the numbers of aphids at the start of autumn. Alate production in pastures occurs mainly in late April/May (Chapter 8). Therefore, a decline in aphid numbers in early autumn may result in them being below the critical threshold at which density-dependent production of alates occurs. This would lead to a reduction in alate numbers produced in late April/May. Reduction in alate numbers may in turn significantly reduce the spread of BYDV to cereal crops and consequently, the risk of infection.

The results from the study of refuge areas indicated that large numbers of alates were being produced in perennial grass pastures during April and May. While some of these aphids may settle in the same or neighbouring pastures many will leave the pastures altogether. Some of these aphids will fail to locate a host and perish, but others will locate a host successfully.

I have considered there to be 2 groups of hosts available to alates leaving pastures in April and May. The first are wheat crops which are sown in late April or early May and emerge during the period of peak flights. There are however, in a normal year, very few of these crops available as most crops are not sown until after mid-May and consequently do not emerge until after the autumn flights.

The second are the annual volunteer grasses. These grasses are usually widespread across the state during the period of peak flights from pastures. It is thought that the majority of alates which successfully locate a non-pasture host do so by landing on these annual volunteer grasses.

The following 2 chapters detail the study of annual volunteer grasses along roadside verges and cereal crops.

The chapter on annual volunteer grasses along roadside verges details the proposed pattern of dispersal of aphids

from the pasture refuge areas. The phenology of *R. padi* in these roadside grasses is also described with the aim of determining when alates are produced.

The chapter dealing with cereal crops describes the surveys of early, normal and late sown crops across the low rainfall wheat belt. It examines the hypothesis that early sown crops have more aphids than later sown crops.

CHAPTER 10

The role of volunteer grasses in the phenology of *R. padi* in the low rainfall belt of South Australia

Abstract

R. padi was the first species of cereal aphids to colonise annual grasses across the state each year. Numbers were higher in the Lower Murray Valley than in the Mount Lofty Ranges or Adelaide Plains. At all locations, numbers generally increased until grasses reached the boot stage after which they declined. Alate production commenced in late July in response to crowding, but thereafter plant age and photoperiod were more important determinants. *M. dirhodum* and *S. nr fragariae* first appeared in annual grasses in late July.

Introduction

Irrigated perennial grass pastures in the Lower Murray Valley and Mount Lofty Ranges of South Australia are summer refuges for both *R. padi* and the PAV and RPV types of barley yellow dwarf virus (BYDV) which it transmits (Chapter 6; Henry et al., in press). Grasses occurring in other

habitats at this time are not suitable for *R. padi* (Chapter 6). During autumn, large numbers of alate *R. padi* develop in these pastures. Alate production peaks in the second half of May with numbers declining to very low levels in June (Chapter 6). Up to 80% of alatoid nymphs collected from these pastures between 1989 and 1991 were able to transmit the PAV or RPV types of BYDV (De Barro & Henry, unpublished data).

Much of the South Australian wheat belt receives less than 500 mm of annual rainfall and because of the dry summer the timing of the autumn rainfall indicates when sowing is able to commence. Regions which receive soaking rains in March or early April (early rains) may have wheat sown in late April or early May. As a consequence, plant emergence coincides with the autumn flights of *R. padi* from perennial pastures, exposing these crops to the risk of infestation and subsequent infection with BYDV. Regions which receive rains in late April/May usually have wheat sown in late May/June. These crops, emerge after the peak autumn aphid flights and have a much reduced risk of infestation from aphids migrating from perennial grass pastures. These crops make up the majority of those sown each year. Therefore, most aphids migrating from pastures in autumn and successfully locating a suitable host in April or May must land on non-cereal hosts. The most widely available non-cereal hosts in autumn are the annual grasses. These grasses begin to emerge soon after the first rains in March

(these rains while usually not sufficient to allow sowing, do allow the germination of annual grasses species) and occur over much of the state's agricultural area in a wide range of habitats including roadside verges, annual pastures and waste ground.

Annual grasses are considered important as they have the potential to link aphids in the perennial grass pastures with wheat crops by providing numerous sites in which both aphid populations and virus can develop. These aphid populations may then produce alates which infest and infect surrounding wheat crops.

This paper examines the role which annual grasses play in the phenology of *R. padi* by studying the colonisation and subsequent population development in roadside grasses at several locations in South Australia.

Material and Methods

Aphid surveys

Roadside grasses were vacuum sampled using the method described in Chapter 3. The method involved vacuuming 5, 50m x 14 cm transects in a zig zag fashion along a selected area of grass. Grasses were vacuumed at a slow walking pace of

25m/min. An initial survey was carried out on the 20 June in each of the years, 1989, 1990 and 1991. Each of the surveys involved sampling 18 locations along a north-west/south-east transect between Mallala and Mannum, and 22 locations along the Lower Murray Valley between Murray Bridge and Sedan (Fig. 10.1). Two sample units were collected at each location.

The sample units were examined in the laboratory and the aphid species identified (Eastop, 1966; Blackman & Eastop, 1985 and Hales et al., 1990 were used to confirm identifications). Few, if any of the nymphs collected were alatoid, so only the total number of aphids in each sample unit were recorded.

The grasses at all locations in 1989 and 1991 were mostly at growth stage (GS) 21 whereas in 1990 grasses were at GS 9/11 (Zadoks growth stages; Tottman & Broad, 1987). Grasses were older in 1989 and 1991 because rain fell over much of South Australia in early autumn. This led to the widespread emergence of annual grasses during late March/early April. However, in 1990, opening rains did not fall until late June, delaying widespread grass emergence until early July.

Later, different surveys were conducted to determine whether aphids were able to reach the northern edges of the wheat belt. In these extended surveys, grasses were

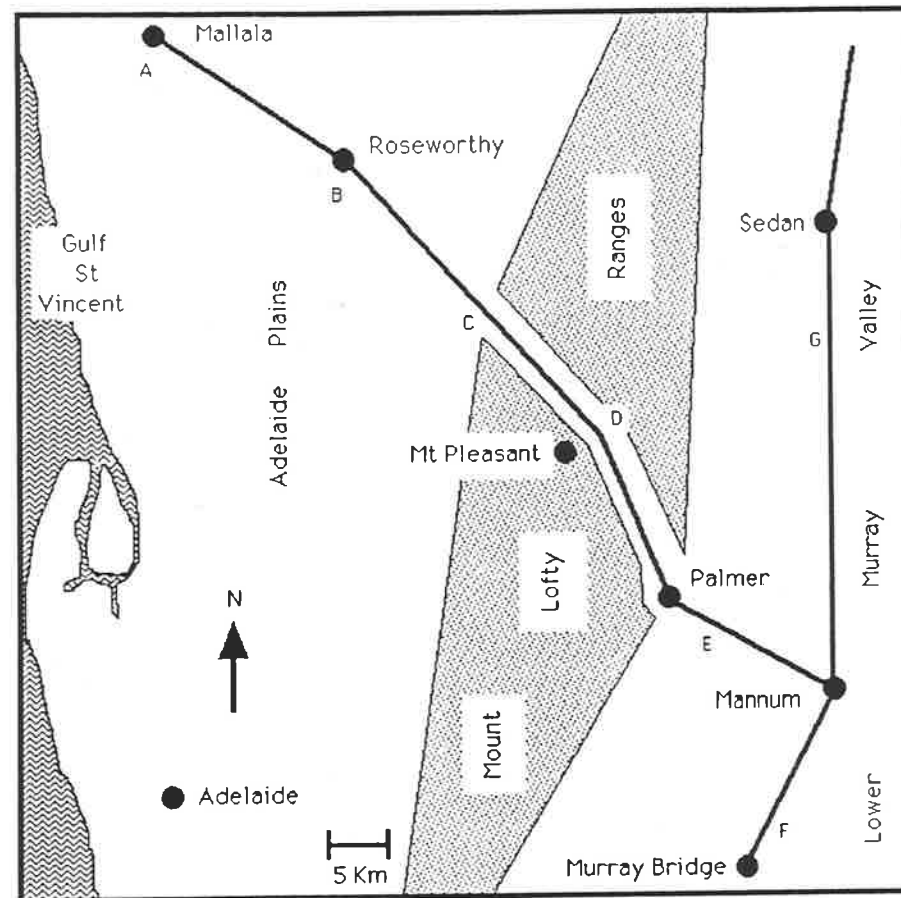
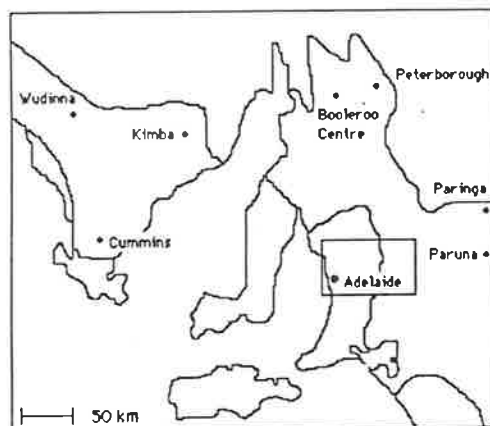


Fig.10.1. Map of the low rainfall wheat belt of South Australia showing the locations of grasses sampled in the extended surveys. The enlarged area indicated by the inset shows the routes of the June surveys. The sites indicated by A-G show the locations at which the population studies were carried out.

searched for aphids. Aphids were noted as being either present or absent at each of 2 locations in the Upper North (Booleroo Centre & Peterborough), 3 in the Eyre Peninsula (Wudinna, Cummins & Kimba) and 2 in the Murray Mallee (Paringa & Paruna) in July 1989 and 1991, and July/August 1990 (Fig. 10.1).

Population study

Population studies of wheat-infesting cereal aphids were carried out at each of 3 locations between Murray Bridge and Sedan and 4 locations between Roseworthy and Mannum in each of the years, 1989, 1990 and 1991 (Fig. 10.1). In both 1989 and 1991, 4 samples, each composed of 5 sample units, were collected between July and August while in 1990 sampling was carried out between July and September. Each of the 4 samples was taken at a different stage of grass growth namely, tillering (GS 23/25), stem elongation (GS 31), boot (GS 45/47) and anthesis (GS 65). Growth stages at the time of sampling were uniform across the different sites.

For these samples, counts for *R. padi* were made of alate and apterous adults, alatoid and apterous third and fourth instars. Alatoid and apterous nymphs were identified using the presence of wing buds, and both were separated from the first and second instars on the basis of size. Third and fourth instars were pooled, and first and second instars

were not included in the counts. The proportion of alatoid nymphs was determined by dividing the number of alatoid nymphs by the total number of third and fourth instars.

Grass composition

Grass species composition was measured each year at each location, once in July and once in August. At each location, 2 sample units of 50 grasses were collected at random. Grasses were identified to genus only, using a key (Pearce unpublished) and were confirmed by Dr J. Gardiner (Taxonomic Botanist, Waite Institute). It was not possible to separate, to species level, immature plants of several of the commonly occurring annual grasses.

The production of alatoid nymphs

Since the production of alates in winter/spring may determine how well aphids move from annual grasses into cereal crops and hence influence the severity of BYDV outbreaks, we attempted to develop one or more predictors of alate production. We did this by regressing the proportion of alates produced on the variables which were most likely to be important determinants of alate development, namely photoperiod, temperature, aphid density and plant quality as indicated by the plant age.

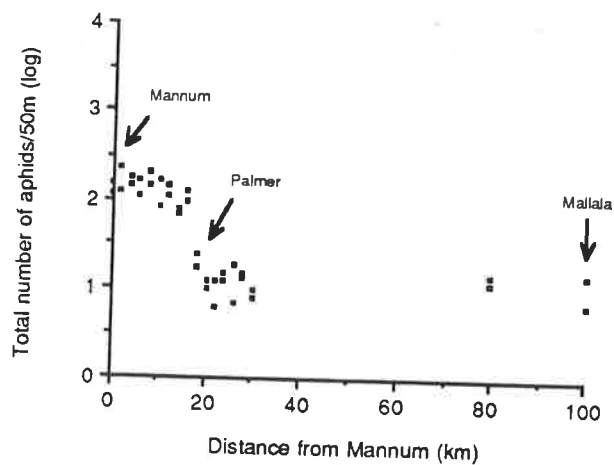
Photoperiod values were taken from the sunrise/sunset data in the S.A. Govt Gazette, Proof of Sunrise and Sunset Act, and photoperiod was defined as the number of hours of light between sunrise and sunset at the time of sampling. Temperature was the mean maximum temperature between sample date (n) and sample date (n+1), and was provided by the Bureau of Meteorology, Murray Bridge and Mount Barker stations. Aphid density was determined using the aphid samples from the population study while plant age, namely tillering, stem elongation, boot and anthesis, were those found at the time of sampling in the population study.

Results

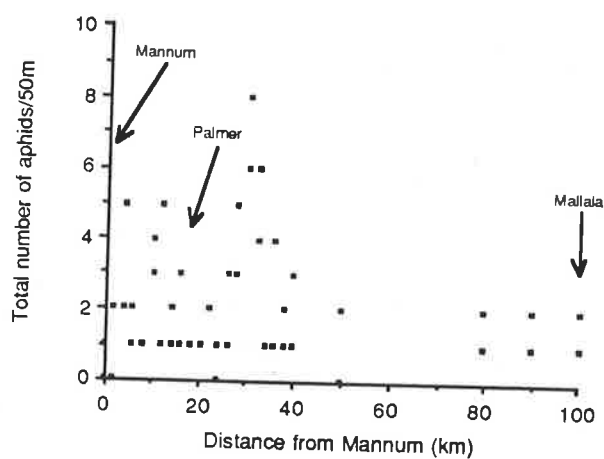
Aphid surveys

R. padi was the only wheat infesting species of aphid found in annual grasses in each of the 3 initial surveys in June. The Mallala-Mannum transect (Fig. 10.1) showed that numbers in 1989 and 1991 (Fig. 10.2) were highest in the Lower Murray Valley, east of Palmer. In addition, the transect along the Lower Murray Valley (Fig. 10.1) showed that numbers in 1989 and 1991 (Fig. 10.3) were generally scattered evenly along the valley. The exception was an area 4 to 6 km north and south of Punthari where many more

1989



1990



1991

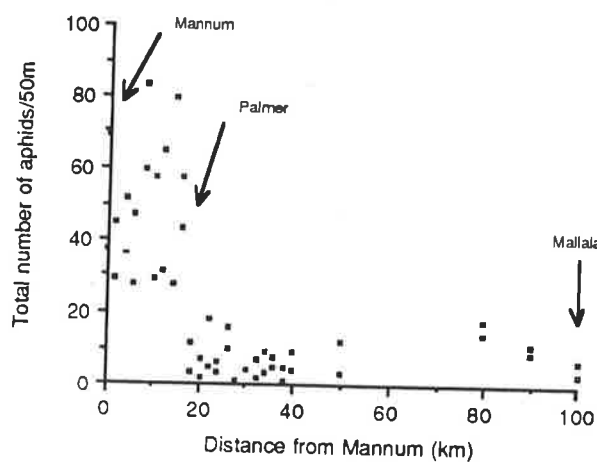
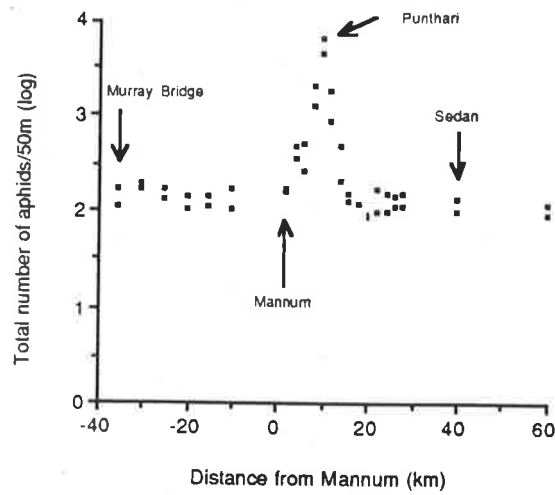
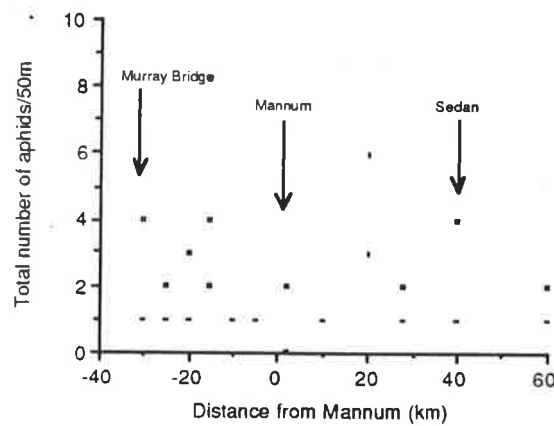


Fig.10.2. The total number of *R. padi* in annual volunteer grasses sampled along roadside verges between Mallala and Mannum in June, 1989, 1990 and 1991. Notice that because of the much larger numbers in 1989, the numbers are expressed as a log scale.

1989



1990



1991

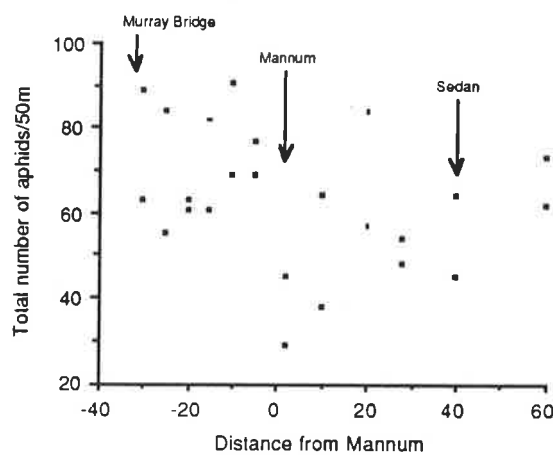


Fig.10.3. The total number of *R. padi* in annual volunteer grasses sampled along roadside verges between Murray Bridge and Sedan in June 1989, 1990 and 1991. Notice that because of the much larger numbers in 1989, the numbers are expressed as a log scale.

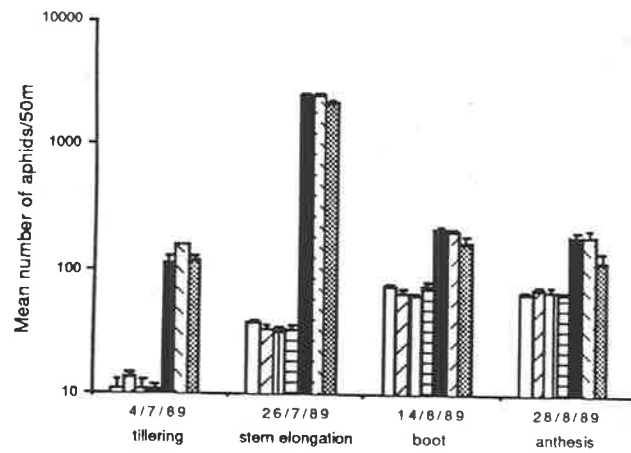
aphids were obviously present (Fig. 10.3). No other "hot spots" occurred in the 2 remaining years. No clear pattern of aggregation was evident in 1990 (Fig. 10.2, 10.3) as very few aphids were found. The numbers of aphids infesting grasses in 1989 were greater than the numbers present in 1991 (Fig. 10.2, 10.3).

The extended surveys of annual grasses in July each year showed *R. padi* was present at the northern extents of the Eyre Peninsula, Upper North and Murray Mallee in 1989 and 1991 whereas no aphids were found in 1990. These data indicate that in a "normal" year, *R. padi* is able to disperse from the irrigated perennial grass pastures in the south to the northern edges of the wheat belt. No other species of wheat infesting aphid were ever found in these surveys.

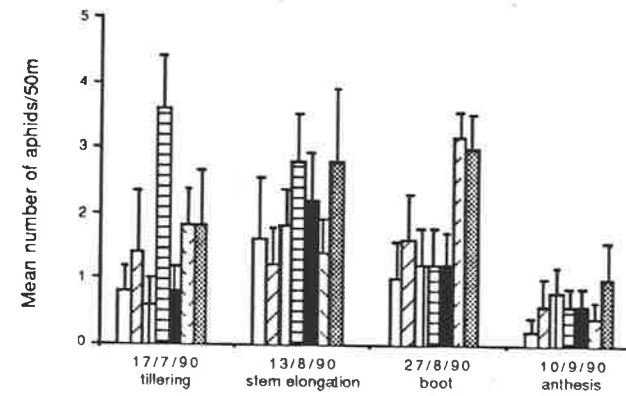
Population study

The mean numbers of *R. padi* at each of the 7 locations of population study are given in Fig. 10.4. The Lower Murray Valley followed the trend indicated by the June surveys in the sense that they were almost always greater than those found in the Mount Lofty Ranges and Adelaide Plains (Fig. 10.4) on the same sample date. In 1989 and 1991 the mean numbers of *R. padi* in the Lower Murray Valley peaked in late July (Fig. 10.4) followed by a sharp decline as grasses

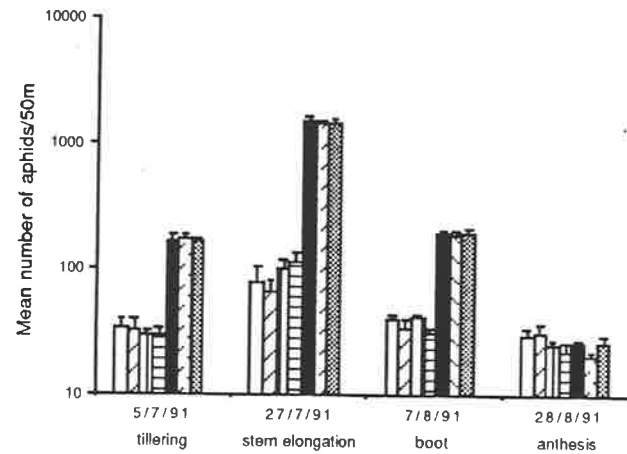
1989



1990



1991



145

Fig. 10.4. The mean number of *R. padi* in annual volunteer grasses at 4 locations; A (□), B (▨), C (▤) and D (▥) in the Adelaide Plains and Mount Lofty Ranges, and 3 locations E (■), F (▣) and G (▧) in the Lower Murray Valley. Grasses were sampled at 4 different growth stages; tillering, stem elongation, boot and anthesis.

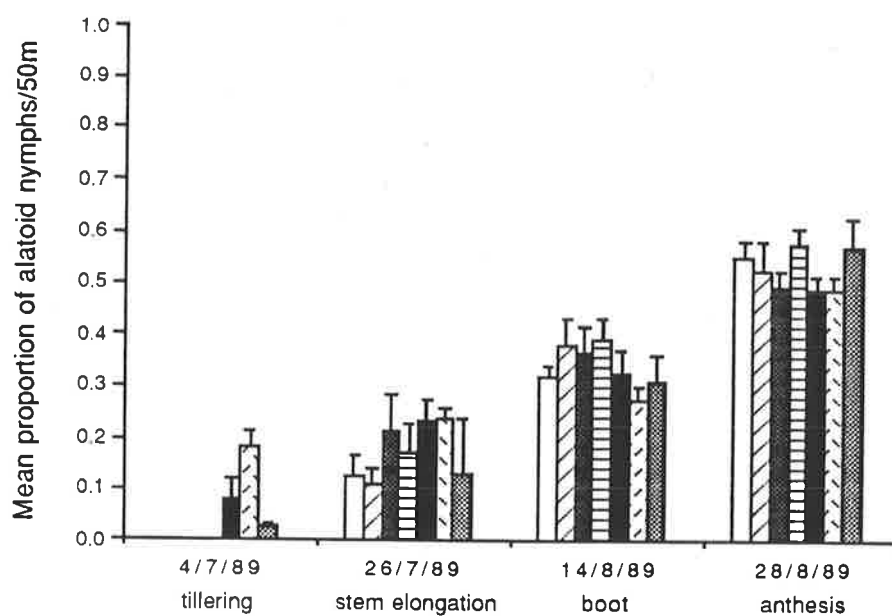
commenced head development (boot stage) in August.

No clear trend in population increase occurred in the Adelaide Plains or Mount Lofty Ranges (Fig. 10.4). In 1989, numbers increased slowly during July before reaching a plateau in late August whereas, in 1991 numbers followed a similar trend to that experienced in the Lower Murray Valley. No trends could be established for the data from 1990 as numbers at all locations were too low, and further analysis is restricted to the data for 1989 and 1991.

While the population studies did not include June, the surveys showed alatoid nymphs were found only at the "hot spot" at Punthari in 1989 when unusually large numbers of aphids occurred (Fig. 10.2). Alate production in annual grasses during June therefore appears to be an uncommon occurrence which is associated with an unusually high density of aphids.

After June, in each year, the proportion of alatoid nymphs increased at all locations (Fig. 10.5). No alates were produced in either years during early July in the Adelaide Plains or Mount Lofty Ranges (Fig. 10.5) whereas, alates were produced in the Lower Murray Valley. This difference is again associated with higher densities of aphids in the Lower Murray Valley than in the other locations (Fig. 10.4) and supports the role of aphid density in promoting the early production of alates. Alate production occurred at

1989



1991

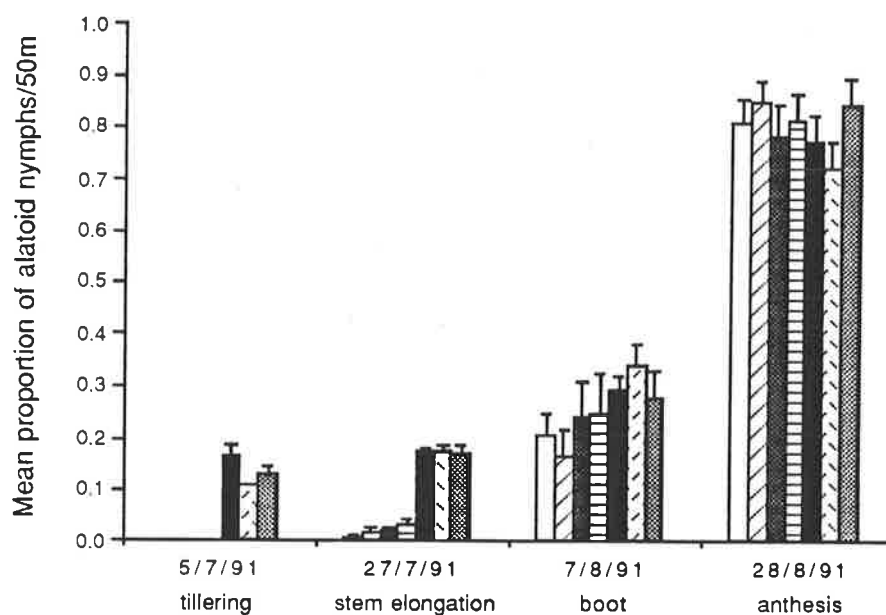


Fig. 10.5. The mean proportion of alataid *R. padi* nymphs in annual volunteer grasses at 4 locations; A (□), B (▤), C (■) and D (▥) in the Adelaide Plains and Mount Lofty Ranges, and 3 locations E (■), F (▤) and G (■) in the Lower Murray Valley. Grasses were sampled at 4 different growth stages; tillering, stem elongation, boot and anthesis.

all locations (Fig. 10.5) in late July and increased markedly in August, especially in 1991.

Both *M. dirhodum* and *S. nr fragariae* first appeared in annual grasses in late July 1989 and 1991, and in early August 1990. Local refuges for either species are not known.

Grass composition

At each of the 7 locations of population study, grass composition remained constant ($P > 0.05$, 2 df). Three genera of annual grasses, *Bromus* (brome grass), *Hordeum* (barley grass) and *Avena* (wild oats) were commonly found at each of the 7 locations. Other genera occasionally collected included *Lolium*, *Phalaris*, *Cynodon*, *Poa*, *Lophochloa*, and *Ehrharta*. *Bromus* made up between 20 and 58% of grasses while *Hordeum* and *Avena* ranged from 12 to 36%, and 0 to 32% respectively. Other species of grasses comprised between 0 and 36% of the total grasses present.

The production of alatoid nymphs

Photoperiod, temperature, plant age and aphid density were considered to be important determinants of alate development. An understanding of which factors could be used as predictors of alate production was considered

important, as the number of alates produced may determine the timing of the spread of aphids from annual grasses into the surrounding wheat crops, and in turn influence the severity of BYDV outbreaks.

To test whether alate production was correlated with any environmental factor, the 1989 and 1991 data for the 3 Lower Murray Valley locations were pooled into a single data set, and the 1989 and 1991 data for the 4 Adelaide Plains/Mount Lofty Ranges locations were pooled into another data set.

Each data set was then analysed using multiple regression to test the dependence of the proportion of alatoid nymphs as a function of photoperiod, aphid density, plant age and temperature (Appendix 2, Table 2.1; Table 2.2).

The correlation matrix for the selected variables for the Lower Murray Valley (Table 10.1) shows a highly significant correlation between the proportion of alatoid nymphs and both photoperiod and plant age. There is also a very high correlation between photoperiod and plant age ($P < 0.001$), which is not surprising, and between aphid density and temperature (negative correlation, $P < 0.01$).

Also given in Table 10.1 is the r^2 value, and its significance for the regression of the proportion of alatoid nymphs on each of the independent variables, separately. As may be expected from the correlation matrix, the regressions

Table 10.1. The proportion of the variance (r^2) explained when fitted individually by each of the independent variables; aphid density, photoperiod, plant age and temperature, and the combination of independent variables which best fitted the data. The correlation matrices are also provided. * $P < 0.01$, ** $P < 0.001$

Correlation Matrix								
Independent Variable	df	r^2	For addition to regression; t to enter	P	Proportion of alate nymphs	Aphid Density	Photoperiod	Plant Age
Lower Murray Valley								
Aphid Density	22	0.060		>0.05	-0.345			
Photoperiod	22	0.858		<0.001	0.891**	-0.294		
Plant Age	22	0.872		<0.001	0.875**	-0.263	0.991**	
Temperature	22	0.045		>0.05	0.068	-0.561*	-0.108	-0.090
Adelaide Plains & Mount Lofty Ranges								
Aphid Density	30	0.033		>0.05	0.022			
Photoperiod	30	0.872		<0.001	0.936**	0.282		
Plant Age	30	0.813		<0.001	0.905**	0.286	0.991**	
Temperature	30	0.008		>0.05	-0.200	-0.226	-0.292	-0.289
Combinations of variables								
P+pA*	29	0.900	3.03	<0.001				
P+pA+D*	28	0.962	6.96	<0.001				

* Photoperiod (P), Plant Age (pA), Aphid Density (D)

on photoperiod and plant age were highly significant ($P < 0.001$).

The data were then further analysed by multiple regression, with each independent variable being added to the regression equation in order of its correlation value with the proportion of alatoid nymphs. Addition of further independent variables to either photoperiod or plant age had no significant influence on the regression, indicating that either variable could be used as a predictor of alate production (Table 10.1). This suggests that aphid density, while associated with the early production of alates, is unimportant in the overall production of alates between early July and late August.

In the data set for the Adelaide Plains and Mount Lofty Ranges, the proportion of alatoid nymphs was again highly correlated with photoperiod ($P < 0.001$) and plant age ($P < 0.001$) (Table 10.1); and photoperiod and plant age were also, again, highly correlated ($P < 0.001$; Table 10.1). Again, as expected from the correlation values, the separate regressions of the proportion of alatoid nymphs on photoperiod and plant age were highly significant ($P < 0.001$; Table 10.1).

However, for this data set, the addition of aphid density and plant age significantly improved the regression ($r^2 = 0.97$, $p < 0.001$, Table 10.1). The relationship between

the proportion of alatoid nymphs (alprop), photoperiod (P), plant age (pA) and aphid density (D) can be expressed by the following equation:

$$\text{alprop} = - 11.668 + 1.2179P - 0.29598pA - 0.0027198D$$

Discussion

One possible cause for the difference between numbers of aphids infesting grasses in 1989 and 1991 was the greater occurrence of heavy showers of rain in 1991. Heavy showers of rain have been previously noted as a mortality factor of cereal aphids (Dean & Wilding, 1971). They were considered to have been a likely mortality factor in 1991 as the grass canopy in mid-June was open, allowing rain drops to strike the base of the plants where the aphids were feeding.

In Chapter 6 it was estimated that at least 4 times as many alates were produced in pastures during autumn in 1990 than in 1989, yet numbers in roadside grasses reflected a completely opposite trend. The likely explanation is based on the close relationship between the emergence of the annual grasses and rainfall. The delay in rainfall until late June in 1990 led to a delay in the emergence of grasses until after the autumn flights from pastures. As a consequence, most alates migrating from pastures in April/May 1990 were likely to have failed to land on annual

grasses.

The surveys showed that numbers of *R. padi* were higher in the Lower Murray Valley than elsewhere. This suggests that the majority of alates leaving the perennial grass pastures in the Lower Murray Valley fail to fly over the Mount Lofty Ranges which rise $\approx 500\text{m}$ above the level of the pastures. Aphids are weak fliers and rely on wind to disperse widely (Dixon, 1985). Therefore, the apparent failure to fly over the Mount Lofty Ranges may be due to a lack of convective air currents over the Lower Murray Valley during autumn (R. Farrow, pers. comm.). This suggests that the ranges provide an effective barrier to westerly migration, forcing aphids to first move northwards before the ranges become low enough to allow westward migration and so shortening the potential distance travelled west of the refuge areas. The role of the Mount Lofty Ranges as a barrier to westward migration could also be enhanced by westerly air streams being forced to rise up over the ranges, becoming compressed and thereby increasing the height of the barrier (H. Dingle, pers. comm.).

The arrival of *M. dirhodum* and *S. nr fragariae* was associated in each year with the movement across the country by a high pressure system (Australian Bureau of Meteorology). These systems produce warm northerly winds ideal for aphid flight. It is therefore possible that these species migrated into South Australia from source areas

located in northern New South Wales. *R. padi* may also migrate into South Australia at the same time, but whether this occurs is at present unknown.

The comparative lack of aphids in roadside grasses in the Mount Lofty Ranges was unexpected considering the large numbers of alates produced in the perennial pastures in this area (Chapter 6). This suggests that alates leaving pastures in the Mount Lofty Ranges failed to disperse widely. The apparent failure to disperse widely may be due to the presence of large numbers of trees. Tall objects such as trees can disrupt aphid dispersal by increasing turbulence (Dean & Luuring, 1970). In contrast, the Lower Murray Valley is virtually treeless leaving very little to obstruct aphid dispersal. Consequently, I suggest that alates produced in the Mount Lofty Ranges contribute less to the numbers reaching wheat crops, than alates leaving pastures in the Lower Murray Valley.

R. padi prefers grasses which have yet to reach the boot stage (Wiktelius et al., 1990). Once grasses have reached boot, *R. padi* becomes restless and begins to produce alatoid offspring. Such alate production is thought to reflect a decline in plant quality. The commencement of head development (boot stage) is largely driven by increasing day length, so it is not surprising that the correlation matrices showed very high correlations between photoperiod and plant quality (Table 10.1).

The results clearly indicate that either photoperiod or plant age is a useful predictor of alate production and that aphid density was less important and temperature had no significant influence at all. Photoperiod was also considered an important determinant of alate production in irrigated perennial grass pastures (Chapter 6). However, while aphid density and temperature were considered very influential in pastures, their roles in promoting alate development in annual volunteer grasses seems much reduced. Aphid density appeared to have an influence early on which is then overshadowed by photoperiod and plant age. Whether plant age was involved in alate production in pastures is not known, but is considered unlikely as the peak period of alate production in pastures occurs in autumn when days are short and pasture grasses are tillering.

Smith and Sward (1982) suggested that wheat crops inoculated with BYDV infective *R. padi* at the first node stage of stem elongation, suffered little or no significant reductions in yield, whereas crops infected before tillering suffered significant yield reductions. Similar reductions have been noted elsewhere (Bremmer, 1965; Doodson & Saunders, 1970a & b). In a normal rainfall year, by the time alates are dispersing from annual grasses, only early sown wheat crops will have reached the first node stage of stem elongation, with the majority either yet to reach the tillering stage or at some stage within the tillering

phase. Consequently, many of the normal and late sown crops are still vulnerable to infection and subsequent reductions in yield.

The extended survey of annual grasses carried out in July showed that *R. padi* had spread to the northern ends of the wheat belt indicating widespread dispersal. In addition, the sampling of roadside grasses in July and August showed alate production in annual grasses commenced in July. Therefore, annual grasses do provide numerous sites scattered throughout the wheat belt in which aphid populations can develop. Furthermore, these aphid populations produce alates when wheat crops are still vulnerable to infection and losses in yield.

Annual grasses therefore provide a link between the pasture refuge areas and wheat crops, and provided BYDV is present in the annual grasses, and alates dispersing from these grasses are viruliferous, they have the potential to allow major disease outbreaks to occur. In addition, in years when late rains delay the emergence of annual grasses until June, the link between pastures and crops may be broken as few alates from pastures infest the grasses. This leads to a much lower production of alates later in the year. In such years the risk of BYDV would be considered remote.

CHAPTER 11

Surveys of wheat crops in low rainfall South Australia between 1989 and 1991

Abstract

The proportions of infestation and the total numbers of aphids in crops from the Eyre Peninsula, Lower and Upper North and the Murray Mallee were positively correlated with crop age. No aphids were ever found colonising late sown crops indicating these crops were much less at risk from BYDV than earlier sown crops. Early sown crops were considered to be at the most risk of damage as these crops had the greatest proportions of infestation at an early age.

Introduction

Barley yellow dwarf virus (BYDV) is recognised as a significant disease of cereals throughout Australia causing losses estimated at 2% or US \$40 M per annum (Johnstone et al., 1990; Sward, 1990). However, the disease is more widespread and damaging in high rainfall (>500 mm) areas, and it tends to be only a sporadic, often local problem in low rainfall areas (Sward, 1990). The apparent increased

incidence and severity of BYDV in high rainfall areas is thought to be due to the local presence there of over-summering perennial grasses which act as reservoirs for both the aphids and viruses (Price, 1970; Smith & Plumb, 1981). However, the above estimates of BYDV severity were obtained in areas where summers are milder than those in South Australia and so may not be applicable here.

In South Australia, irrigated perennial grass pastures in the Lower Murray Valley and Mount Lofty Ranges are summer refuges for both *R. padi* and the PAV and RPV types of BYDV which it transmits. During autumn large numbers of alate *R. padi* develop in these pastures. Alate production peaks in the second half of May with numbers declining to very low levels in June (see Chapter 6).

Because of the low rainfall conditions under which much of the state's wheat is grown, the sowing date is closely linked to when the first autumn rains occur. These rains usually begin in the latter half of March, with sizeable falls of 25 to 50mm occurring in late April or early May. In such years farmers tend to begin sowing in mid to late May. These crops are considered to be "normal" sown crops whereas those not sown until mid June to early July are considered late sown. Both the normal and "late" sown crops emerge after the peak autumn flights of aphids from pastures have passed, and are considered to have a lesser chance of infestation and subsequent infection with BYDV.

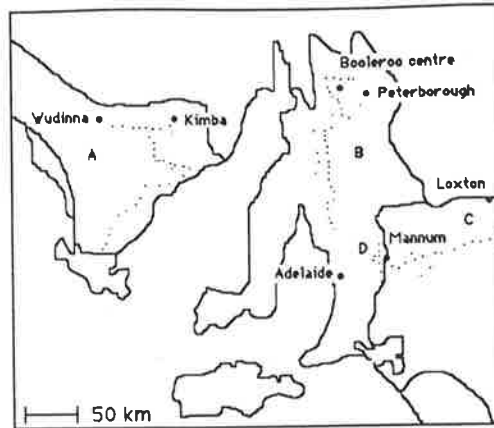
However, in each year some areas receive sufficiently heavy rains in early to mid-April to allow farmers to commence sowing in late April or early May. These "early" sown crops usually make up only a small proportion of the overall total area sown, but because they emerge during the peak autumn flights, they are considered to have a greater risk of infestation and subsequent infection with BYDV.

This study aims to test the hypothesis that early sown crops have more aphids than later sown crops and are therefore at greater risk from infestation with *R. padi*.

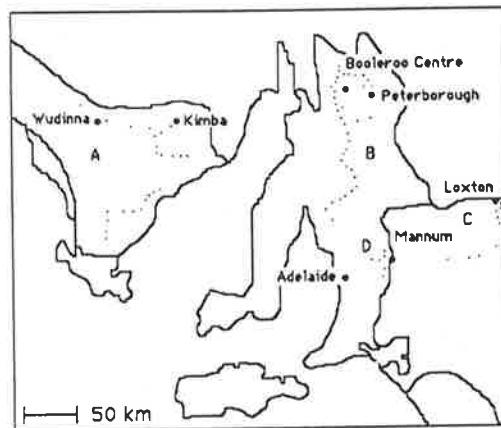
Materials and Methods

Wheat crops from across the low rainfall wheat belt were surveyed in July, 1989 and 1991, and July/August 1990. To determine which particular crops were to be chosen in the survey in any year, the low rainfall wheat belt was divided into 4 regions; the Eyre Peninsula, the Upper and Lower North, the Murray Mallee and the Lower Murray Valley (Fig. 11.1). Within each region, rainfall data obtained from the Australian Bureau of Meteorology were used to locate areas of early, normal and late rains. An area was considered to have received useful rain if at least 25 mm of rain fell over 1 or 2 days.

1989



1990



1991

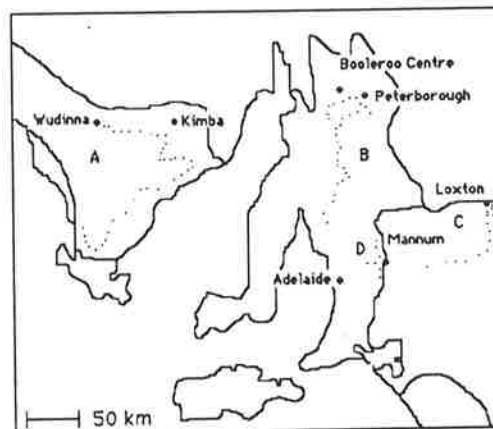


Fig. 11.1. Map of South Australia showing the locations of wheat crops (.) sampled in the (A) Eyre Peninsula, (B) Lower and Upper North, (C) Murray Mallee and (D) Lower Murray Valley in 1989, 1990 and 1991.

Within each of these areas, crops were chosen across the range of growth stages available. Growth stages used to describe crop age were based on Zadoks growth stages (Tottman & Broad, 1987) and were assigned to the predominate growth stage present in each crop. The different aged crops were assumed to reflect the different sowing dates, with the most advanced crops being sown earliest and the least advanced being sown latest. The routes taken for the 3 surveys and the locations of the crops sampled are illustrated in Fig. 11.1.

In 1989, 97 crops were surveyed, 33 in the Eyre Peninsula, 37 in the Lower and Upper North, 19 in the Murray Mallee and 8 in the Lower Murray Valley. In 1990, 80 crops were surveyed, 24 in the Eyre Peninsula, 36 in the Lower and Upper North, 14 in the Murray Mallee and 6 in the Lower Murray Valley; in 1991, 89 crops were surveyed, 36 in the Eyre Peninsula, 30 in the Lower and Upper North, 16 in the Murray Mallee and 7 in the Lower Murray Valley.

From each crop selected, 2 parallel transects of 50 plants each were searched for aphids. Each transect started at the crop edge with plants being sampled at roughly 1 m intervals. Each plant was selected at random and then thoroughly searched for aphids. Only the total number of each species of aphid found on each plant was recorded. The mean proportion of infestation and the mean total number of aphids was estimated for each crop.

Results and Discussion

The data are given, for each year separately in Appendix 3, Tables 1 and 2. The frequency of distribution of each of the variables was highly skewed, so correlations between the variables could not be calculated with the usual parametric correlation. Instead, the mean proportion of infestation and the mean total of aphids for each crop were ranked, and the ranks were related to those of crop growth stage by a Spearman rank correlation test (Zar, 1984).

In 1989 both the proportions of infestation and the total numbers of aphids in crops from the Eyre Peninsula, Lower and Upper North, and the Murray Mallee were positively correlated with crop age (Table 11.1). All crops in the Lower Murray Valley were at the same growth stage so the correlation could not be tested.

No aphids were found in any of the crops surveyed in 1990 despite a range of early to late sown crops being available (Table 11.1). Why this was so is not clear. Unlike 1989 and 1991, 1990 was a drought year in which rains did not fall over much of the state until late June, resulting in crops being sown late. The only exceptions were the northern edges of the wheat belt where April rains led to early sowing. In addition, the previous chapter showed how

Table 11.1. The range of crop age, the range of the total number of *R. padi* and the range of the proportion of infestation in wheat crops in the Eyre Peninsula, Lower and Upper North, Murray Mallee and Lower Murray Valley of South Australia in July, 1989 and 1991, and July/August 1990. Also given is each correlation coefficient and its probability for the correlations with crop age of, (a) total number of aphids, and (b) proportion of tillers infested.

Region	Number of crops sampled	Crop age	Total number of aphids			Proportion of infested tillers		
			Range	Correlation coefficient	P	Range	Correlation coefficient	P
1989								
Eyre Peninsula	33	21-27	0-200	0.283	<0.001	0-0.37	0.402	<0.001
Lower & Upper North	37	21-25	5-112	0.402	<0.001	0.01-0.39	0.694	<0.001
Murray Mallee	19	12-24	1-221	0.570	<0.001	0.02-0.32	0.678	<0.001
Lower Murray Valley	8	22	31-104	0.195	-	0.13-0.28	0.159	-
1990								
Eyre Peninsula	24	11-31	-	-	-	-	-	-
Lower & Upper North	36	11-31	-	-	-	-	-	-
Murray Mallee	14	11-59	-	-	-	-	-	-
Lower Murray Valley	6	9-12	-	-	-	-	-	-
1991								
Eyre Peninsula	36	21-31	0-17	0.566	<0.001	0-0.15	0.569	<0.001
Lower & Upper North	30	11-26	0-9	0.694	<0.001	0-0.08	0.694	<0.001
Murray Mallee	16	10-25	0-20	0.829	<0.001	0-0.15	0.832	<0.001
Lower Murray Valley	7	11-13	-	-	-	-	-	-

the lack of early and normal rains led to a delay in the emergence of annual volunteer grasses until well after the autumn aphid flights from perennial grass pastures. In such years crops, which are not infested by alates migrating from pastures, are unlikely to be infested by large numbers of alates dispersing from annual volunteer grasses, as poor initial colonisation leads to the production of only small numbers of alatoid nymphs later in the year.

The absence of *R. padi* in early sown crops in 1990 was unexpected as these crops emerged during the autumn flights from pastures. A possible explanation may be the lack of hosts between the refuge areas in the south and the early sown crops in the north. It is suggested that aphids may migrate northwards in a series of short flights rather than in one long flight. As a consequence, the lack of suitable hosts along the way may disrupt northward migration by possibly preventing aphids from feeding along the way. This hypothesis goes against the accepted idea of aphid migration in which aphids complete a long flight which may be followed by a series of short hops as the aphid searches for a suitable host (Robert, 1987). However, J. Kennedy (pers. comm.) agrees that my proposed mechanism is quite possible despite there being no published records of it occurring.

An alternative, suggested by R. Farrow (pers. comm.) is that northerly migration is dependent on warm northerly blowing winds, caused by temperature inversions, over the

refuge areas in autumn. A similar situation (Farrow, 1986) found that aphids could migrate longer distances than expected by flying in the warm air of the inversion. Therefore, the failure of aphids to migrate north in 1990 may have been due to the lack of warm northerly direction winds.

The proportions of infestation and the total numbers of aphids in crops surveyed in 1991 were again positively correlated with crop age in the Eyre Peninsula, Lower and Upper North and the Murray Mallee (Table 11.1). No aphids were found in crops from the Lower Murray Valley so the correlations were again not tested.

As aphids were never found in late sown crops it is concluded that more aphids colonized the early and normal sown crops. The same statement can not be applied to the presence of more aphids, and higher proportions of infestation in early sown crops than in normal sown crops. The difference may be caused by more aphids colonizing the early sown crops, but this is not necessarily the case.

Using the modified sine wave program (see Chapter 5) to estimate the number of generations of aphids which could be completed before the crop commences head development, it has been estimated that *R. padi* which colonised early sown crops between April 25 and May 14 may have completed between 1 and 4 generations more than a normal sown crop colonized on May

25. Therefore, it is also possible that the rate of infestation of both crop types was the same, but because aphids had longer to multiply and subsequently spread in early sown crops, the total numbers and proportions of infestation were greater.

In terms of the risk of damage caused by BYDV the end result is the same whether or not the rate of infestation was similar, ie. early sown crops have higher proportions of infestation than normal or late sown crops and consequently have a greater risk of serious damage. Similar conclusions have been made elsewhere; thus Lowe (1961), A'Brook (1974), Jorda et al. (1987) and McGrath and Bales (1990) all found that crops sown so that they emerged during periods of aphid flight suffered greater losses from BYDV than did crops which were sown later.

CHAPTER 12

The phenology of *R. padi* in wheat crops in the low rainfall wheat belt of South Australia

Abstract

R. padi was the first species to infest wheat crops with *M. dirhodum* and *S. nr fragariae* appearing later in the year. The numbers of *R. padi* and the proportion of infested tillers generally peaked in the sample taken before the crop entered the boot stage. Both peaks were followed by a sharp decline in numbers as aphids migrated from the crop. A premature decline in numbers of *R. padi* was noted in 1 crop in 1989; it was associated with a combination of parasitism by *Aphidius similis* Stary & Carver and infection with *Entomophthora* spp.. Numbers of *M. dirhodum* and *S. nr fragariae* and the proportions of infestation were never higher than those of *R. padi*. *R. padi* preferred the lower parts of the plant while the *M. dirhodum* and *S. nr fragariae* occurred on the upper parts. No aphids infested the developing heads.

Introduction

Most of the wheat (≈ 1.5 million hectares) sown each year

in South Australia is grown in the low rainfall wheat belt. Three species of wheat infesting cereal aphids, *R. padi*, *M. dirhodum* and *S. nr fragariae* are commonly found in this region and, of these, *R. padi* is by far the most numerous. Each of the 3 species is able to transmit the PAV type of BYDV, the most common form of the virus in South Australia (M. Henry, pers. comm.).

In Australia, there have been several studies of the epidemiology of BYDV in crops, pastures and volunteer grasses (Mc Lean & Khan, 1983; Mc Lean et al., 1984; Sward & Lister, 1987; Smith & Sward, 1982; Gréber, 1988; Jones et al., 1990; M. Henry, chapter 15). In contrast, there have been no published studies of the phenology or dynamics of cereal aphid populations.

This study examines the phenology of 3 different species of cereal aphids found in commercial crops sampled during 1989-91 and compares the results with those found elsewhere.

Materials and Methods

To determine the phenology of *R. padi* on wheat in South Australia, 2 wheat crops were repeatedly sampled in each of the 3 years of the study. In both 1989 and 1991, 1 crop was sampled at Palmer, 50 km east of Adelaide, and a second crop was sampled at Paskeville, 120 km north-west of Adelaide.

In 1990, a crop near Palmer was again sampled while the second crop was at Mallala, 65 km north of Adelaide. Both 1989 crops (cv. Spear) were sown in the later half of May while the 1990 crops (cv. Spear) were sown in early July. In 1991, the Paskeville (cv. Machete) and Palmer (cv. Spear) crops were sown in late April and early June, respectively.

From each crop, at each sampling data, a 100 x 70 m portion was selected and divided into 28 sub-areas (25 x 10 m). Twenty tillers were then selected at random from each sub-area and searched for aphids. Each tiller was divided into 3 sections; (a) between the crown and the base of the first leaf, (b) stem and leaves above the base of the first leaf and (c) flag leaf and head. The aphids on each portion of each tiller were identified and counted *in situ*. The numbers of each species present were recorded separately for each tiller and the numbers on each portion of the tiller were taken as a measure of the preference of aphids for that part of the tiller.

Sampling commenced when crops were at growth stage 10 or 11. The exception was at Paskeville, 1991 where sampling did not commence until the crop had begun to tiller (GS 21). Sampling continued until September or October when aphids were no longer detectable.

In 1989, the level of aphid mortality caused by entomopathogenic fungi and parasitoids was studied by

collecting 100 third and fourth instar *R. padi* nymphs in late July and again in early August. The nymphs were placed onto tillering wheat plants which were then caged and kept at 20°C (L:D 12:12). The caged plants were inspected daily and any newly deposited nymphs, aphid cadavers or mummies were removed. Cadavers were examined using a compound microscope for fungal fruiting bodies. Each mummy was enclosed in a gelatine capsule and the emerging parasitoid was then sent to Dr M. Carver, CSIRO for identification.

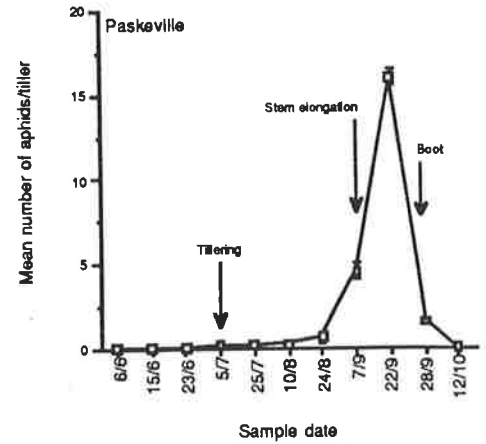
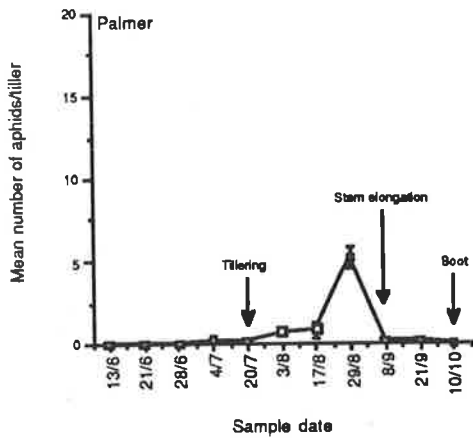
Results

The mean number of aphids per tiller for 1989 and 1991 are presented in Fig. 12.1. There were no aphids in either crop in 1990 and their absence was probably due to a drought which lead to the very late sowing of these crops.

R. padi was the most commonly encountered species, being present in all crops in 1989 and 1991. *M. dirhodum* and *S. nr fragariae* were less common and were only noted in 1991. Neither species developed large populations. All species were evenly scattered over the crop.

R. padi colonised crops at an early age while both *M. dirhodum* and *S. nr fragariae* arrived later in the season (Fig. 12.1). Numbers of *R. padi* usually peaked just before

1989



1991

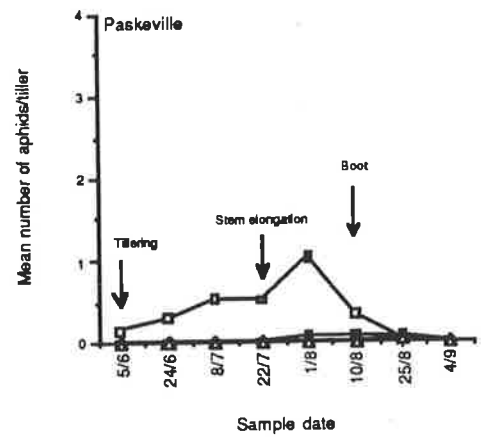
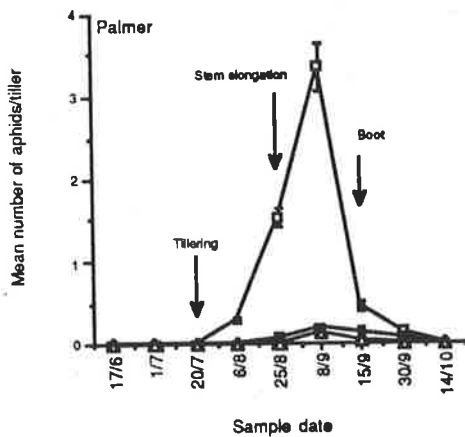


Fig. 12.1. The mean number/tiller of *R. padi* (□), *M. dirhodum* (△) and *S. nr fragariae* (■) at Palmer and Paskeville in 1989 and 1991. The sample dates indicated with an arrow show the growth stage of the crop at that time.

head development (boot) with numbers declining sharply thereafter (Fig. 12.1). The decline in numbers was associated with the production of numerous alatoid nymphs in the earlier samples.

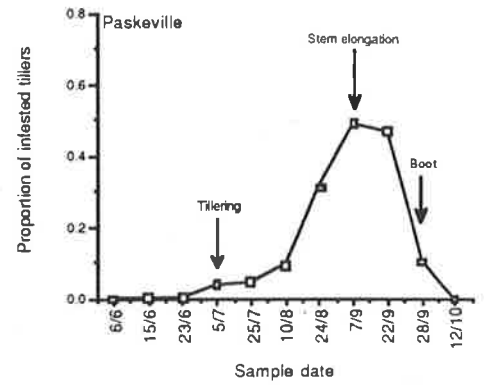
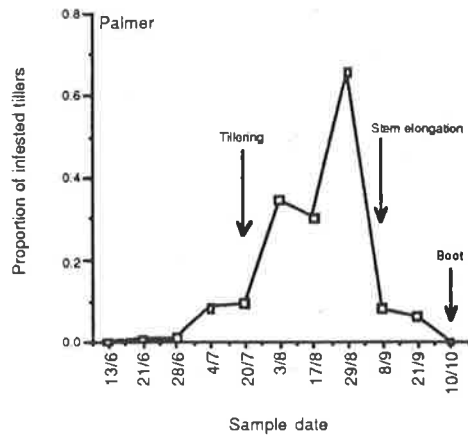
The exception was at Tepko 1989, where numbers declined well before head development. This decline was associated with the presence of numerous aphids mummies belonging *Aphidius similis* Stary & Carver (Hymenoptera: Aphididae) and cadavers containing the entomopathogenic fungus, *Entomophthora* sp..

In both samples 95% of aphids had died within 7 days of collection. *Entomophthora* sp. caused between 8 and 11% of the observed mortality while *A. similis* caused between 68 and 80%.

The proportions of tillers infested by each aphid species are presented in Fig. 12.2. They followed the increase and decline in aphid numbers. There was little association between the mean numbers per tiller and the proportions of tillers infested. In 1989 and 1991, the proportions of tillers infested by *R. padi* ranged from 0.42 to 0.65 during the course of the study whereas, *M. dirhodum* ranged from 0 to 0.06 and *S. nr fragariae* from 0 to 0.05.

The mean numbers of *R. padi* on each of the 3 sections of a wheat tiller are presented in Fig. 12.3. *R. padi* generally

1989



1991

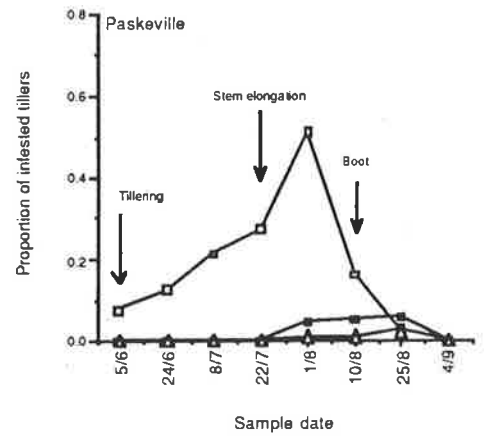
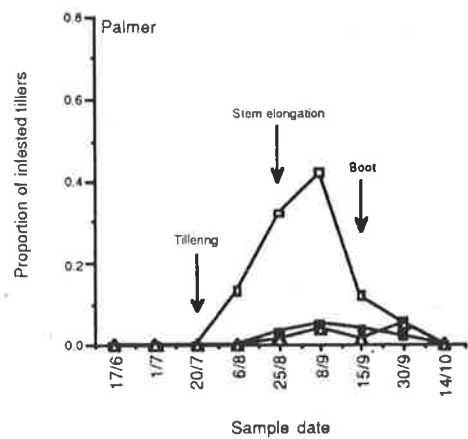
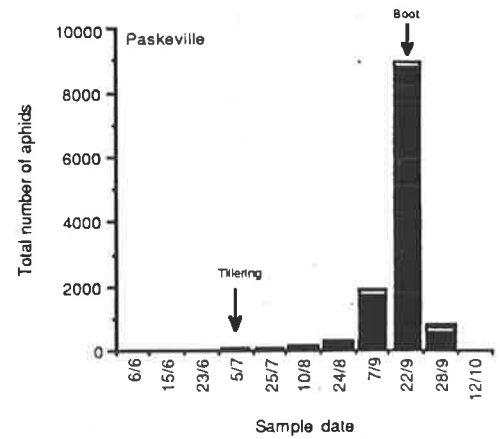
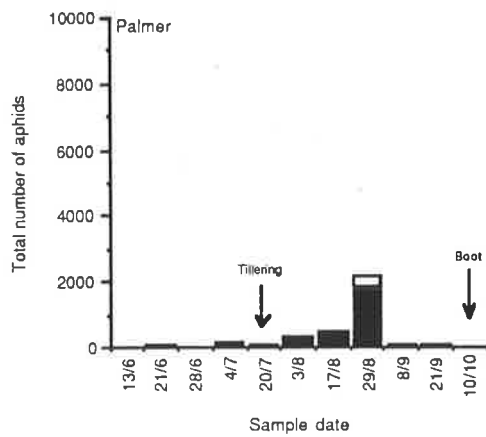


Fig. 12.2. The proportion of tillers infested with *R. padi* (□), *M. dirhodum* (■) and *S. nr fragariae* (Δ) at Palmer and Paskeville in 1989 and 1991. The sample dates indicated by an arrow show the growth stage of the crop at that time.

1989



1991

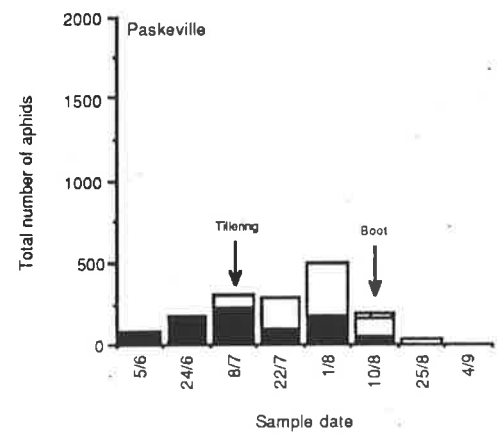
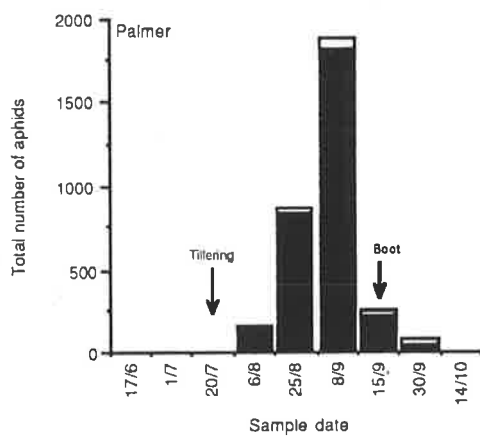


Fig. 12.3. The total number of *R. padi* between the crown and the base of the first leaf (■), on the stem and leaves above the base of the first leaf (□), and on the flag leaf and head (▨) of wheat crops at Palmer and Paskeville in 1989 and 1991.

preferred the lower parts of the tiller and was most commonly observed on the underside of the first leaf. The exception was at Paskeville 1991 where it appeared to prefer the upper leaves. *R. padi* was never found below the soil surface.

M. dirhodum and *S. nr fragariae* were never found on the lower part of the tiller. They initially colonised the upper leaves and could be found evenly distributed between these leaves and the flag leaf when it emerged. Neither species ever colonised the head.

Discussion

R. padi colonised crops well before other species. A similar situation has been noted in New South Wales (W. Milne, pers. comm.).

Both Dean (1973) and Dean & Luuring (1970) noted that *R. padi* tended to first colonise crop margins before moving into the crop. Such a pattern of colonisation does not always occur (Rautapaa, 1976) and may be linked to the presence of hedgerows. Hedgerows are not present in South Australia which may explain the lack of any systematic pattern of colonisation of wheat crops in South Australia.

The preference of *R. padi* for the lower parts of the plant

and *M. dirhodum* for the upper leaves agrees with observations made elsewhere although it was not evident that *M. dirhodum* preferred the flag leaf over other leaves (Dean, 1974a; Wratten, 1975; Leather & Lehti, 1982; Wikteliu, 1987). There are no reports of the feeding site preference of *S. nr fragariae*, but a related species *S. fragariae* also preferred the upper leaves although there was no feeding on the head as observed with the latter species (Dean, 1974).

The association of the decline in *R. padi* numbers with the onset of head development has been reported in studies of the species on oats (Forbes, 1962; Adams & Drew, 1964), barley (Wikteliu & Ekbom, 1985) and wheat (Kieckhefer, 1975; W. Milne, pers. comm.). In addition, the increased production of alatoid nymphs has also been associated with the decline (Adams & Drew, 1964; Carter et al., 1980; Wikteliu et al., 1990).

The failure of both *M. dirhodum* and *S. nr fragariae* to develop large populations suggests environmental conditions in wheat crops in South Australia may be unsuited to each species. Temperature and humidity are suggested as 2 possible limiting factors. These are proposed because *S. nr fragariae* fails to colonise wheat heads in the field yet invariably colonises the heads of the same varieties in glasshouses.

The occurrence of large numbers of parasitized *R. padi* at

Tepko in 1989 was associated with the presence of numerous *R. padi* mummies containing *A. similis* earlier in the year in adjacent annual volunteer grasses growing along the roadside. It is suggested that adult wasps migrated into the adjacent crop in large numbers resulting in the subsequent decline in aphid numbers. This indicates that annual grasses may provide a temporary reservoir in which *Aphidius* spp. may build up and then disperse into surrounding crops. Similar situations have been reported by Stary (1978) and Stary and Lyon (1980) and is the basis pest reduction program operated by The University of Southampton (Wratten, pers. comm.).

Smith and Sward (1982) found the infection of wheat with BYDV at the stem elongation stage resulted in little or no yield reduction whereas crops infected at an earlier growth stage suffered significant reductions. Consequently, infestations by both *M. dirhodum* and *S. nr fragariae* are considered unlikely to cause significant reductions in yield through BYDV transmission as their arrival coincides with the crop entering the stem elongation phase.

Cereal aphids can also cause yield reductions through direct feeding damage. Estimates of a threshold of 20-30 aphids/tiller for *R. padi* and *M. dirhodum* indicate economic losses resulting from direct feeding damage were unlikely to occur (Kolbe, 1973; Wetzell & Freier, 1980). No threshold for *S. nr fragariae* is known, but as numbers were low

economic damage was again considered unlikely.

In general, *R. padi*, *M. dirhodum* and *S. nr fragariae* followed similar phenologies to those described elsewhere (Dixon, 1987). In all cases the proportions of tillers infested by the commencement of stem elongation exceeded 40%, indicating crops were susceptible to significant yield reductions from BYDV provided aphids infesting the crops were viruliferous.

The final 2 chapters dealing with work under taken during the course of this project describes a study involving the use of yellow pan traps as a means of determining when cereal aphids were flying over the state's agricultural areas. The first chapter describes the method of selection of a suitable colour for the pan traps as well as their construction. This chapter has been published in *J. Aust. ent. Soc.* 30, 263-264. The second chapter describes the actual survey which was carried out in 1989 and has been accepted for publication in *J. Aust. ent. Soc.*.

CHAPTER 13

The attractiveness of four colours of traps to cereal aphids in South Australia

Abstract

Pan traps coloured yellow, "bright" green, white and "young wheat" green were tested for their attractiveness to cereal aphids in Adelaide in winter/spring and summer. In winter/spring *R. padi*, *M. dirhodum* and *S. nr fragariae* were attracted most strongly to yellow followed by "bright" green, while *R. maidis* was absent. Only *R. maidis* was trapped in large numbers during summer and again yellow and "bright" green were the most attractive colours.

Introduction

In South Australia wheat crop losses may result from barley yellow dwarf virus (BYDV) transmitted by the cereal aphid *R. padi* (Potter pers. comm.). Other known BYDV vectors frequently encountered are *R. maidis*, *S. nr fragariae* and *M. dirhodum*, although the former is more commonly associated with barley (ECIMS) while the latter 2 species occur in low numbers and are considered

minor vectors (see Chapters 6, 10, 11 & 12).

In the sub-500 mm rainfall areas of South Australia cereal aphids are generally restricted during hot dry summers to irrigated refuge areas. These areas provide a source of aphid infestation and virus infection for wheat crops sown later in the year.

As part of a control strategy it may be possible to detect incoming flights of aphids using coloured water traps. Green (Irwin & Ruesink, 1986) and yellow (Geissler et al., 1987) water traps have been found to be most suitable for attracting cereal aphids, although there is some question as to which colour is the most effective.

The aim of this work was to test the attractiveness of four colours to cereal aphids, so that the most attractive colour could be incorporated in water traps used to monitor aphid flights through a network monitoring system operated by school students across South Australia.

Materials and Methods

The 4 colours compared were yellow, white, "bright" green and "young wheat" green ("yw" green). Yellow, white and "bright" green enamels (Quick Dry Spray Enamels, British Paints Australia) were used because they were claimed by the

manufacturer to be resistant to fading. "Young wheat" green was obtained by initially measuring the reflected spectrum (400 to 700 nm) of sunlight off 20 leaves of young wheat leaves (cv. Warigal, decimal growth stage 23) using a spectroradiometer (Isco spectroradiometer model SR). Dulux Australia Research and Development Laboratories then developed a formula by matching the reflectance spectrum to that of various paint mixes (Fig. 13.1). The reflectance spectra of yellow and "bright" green are also provided (Fig. 13.1); the latter was close to the reflectance spectrum of the "bright" green tile used by Irwin and Ruesink (1986).

Water traps in the form of coloured pan traps were selected for use because they fulfilled the major criteria set out for the aphid monitoring system. These were that the trap be cheaply constructed and easy to use and maintain by the student operators. Each trap was an aluminium foil container (30 x 30 x 3 cm) with a 1 cm diameter gauze covered overflow outlet. It was initially painted with a primer (Quick Dry Spray Enamel, British Paints) to maintain colour and surface integrity and was then painted with one of the four coloured paints. Traps were filled with 1 l of water containing detergent (Palmolive, 1 ml) and formalin (1 ml). All experiments were carried out in 1989 at the Waite Agricultural Research Institute during summer (February) and winter/spring (August/September).

In summer each colour trap was replicated 4 times and

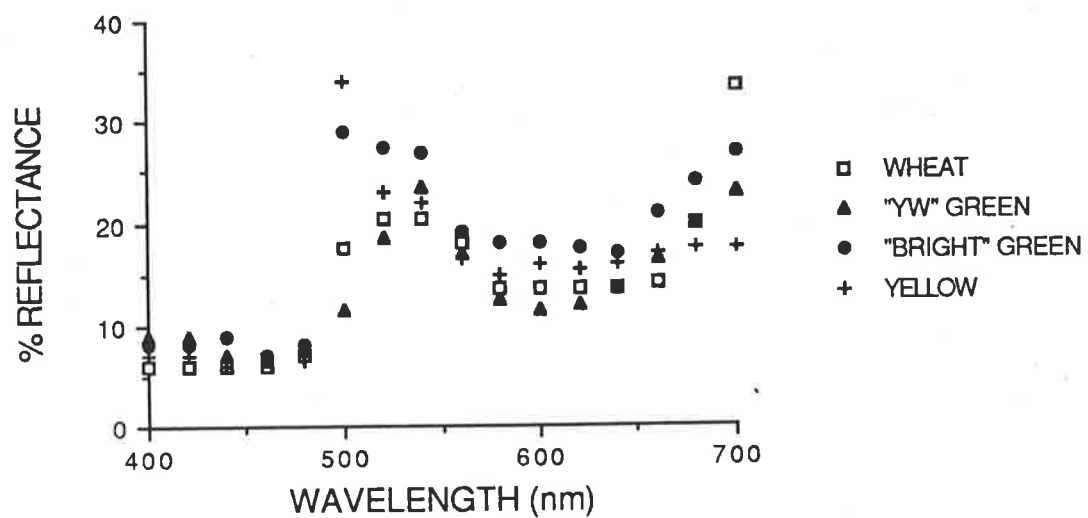


Fig. 13.1. Reflectance spectra of wheat leaves (growth stage 23), "young wheat " green paint made by Dulux Australia for the experiment and "bright" green and yellow paints made by British Paints Australia.

traps were placed on bare soil in 4 square blocks (60 x 60 cm) containing 1 trap of each colour. Each block was 290 cm from its neighbours and trap placement within each block was determined at random. The blocks were in a line running north/south and traps were 4.5 m from the nearest vegetation and 150 m from the nearest object over 1 m high.

The experiment was run for 10 days and commenced in the second week of February. The traps were emptied daily and the aphids removed, sorted into different species and counted or stored in 70% alcohol for later counting.

Most aphids were identified with the EURAPHID key for alate aphids (Taylor & Robert, 1980), supplemented by information in Eastop (1966) and Hales et al. (1990). Data were analysed using the Kruskal-Wallis test together with the nonparametric version of the Tukey test of multiple comparisons.

In winter/spring the experimental design was the same as that used in summer except for the number of blocks which was increased to 12. Trapping commenced in the second week of August and continued for 6 weeks. Two blocks were lost in weeks 5 and 6. Traps were emptied weekly. Data were transformed to $\sqrt{(x+0.1)}$ in order to maintain homogeneity and were analysed using ANOVA followed by the Tukey test of multiple comparisons to separate means.

Results and Discussion

Only *R. maidis*, *R. padi* and *M. dirhodum* were captured during summer, with *R. maidis* predominating. Yellow ($\bar{x}=37.45\pm5.06$) and "bright" green ($\bar{x}=31.05\pm4.36$) were equally attractive to *R. maidis*, whereas white ($\bar{x}=1.50\pm0.25$) and "yw" green ($\bar{x}=1.85\pm0.36$) were poorly attractive ($P<0.01$, 3,156 df). Too few *R. padi* and *M. dirhodum* were caught to allow the testing for colour "preference".

R. padi, *M. dirhodum* and *S. nr fragariae* were the only species caught during winter/spring. Table 13.1 presents the mean number per week (back-transformed) and the range of each species trapped for each colour of trap. The overall 2-way ANOVA indicated that the mean number of aphids trapped per week by colour of trap and week of trapping for *R. padi* ($P<0.01$, 19,212 df), *M. dirhodum* ($P<0.01$, 19,212 df) and *S. nr fragariae* ($P<0.01$, 19,212 df) were significant as were the colour (3 df), week (4 df) and colour x week (12 df) interactions for each species ($P<0.01$). A further 2-way ANOVA, testing the colour interaction and the multiple comparison of means with this ANOVA was used to indicate the "preference" of each species for the different coloured traps. The overall most attractive colour for *R. padi* ($P<0.01$, 3,212 df) and *M. dirhodum* ($P<0.01$, 3,212 df) was yellow followed by "bright" green, while for *S. nr fragariae* ($P<0.01$, 3,212 df) "bright" green was as attractive as

Table 13.1. The mean number (back-transformed) per week of *R. padi*, *M. dirhodum* and *S. nr fragariae* caught in yellow, "bright" green, white and "young wheat" ("yw") green coloured pan traps during August to September, 1989.

Species		Mean number of aphids trapped per week			
		Yellow	"Bright" Green	White	"YW" Green
<i>R. padi</i>	mean	13.81	10.71	0.71	3.62
	range	11.94-15.82	9.08-12.50	0.56-0.88	2.86-4.48
<i>M. dirhodum</i>	mean	3.76	3.10	0.12	0.61
	range	3.03-4.35	2.66-3.59	0.08-0.16	0.46-0.76
<i>S. nr fragariae</i>	mean	4.87	4.08	0.19	0.62
	range	4.31-5.47	3.36-4.65	0.13-0.26	0.49-0.76

yellow. White and "young wheat" green were poorly attractive, although "young wheat" green traps consistently attracted more aphids than white traps.

Yellow was the most suitable colour for attracting all 4 species during summer and winter/spring, although "bright" green was often as effective. This differs from the results of Dean (1973) which showed yellow to be poorly attractive to cereal aphids, but supports other more recent data for *R. padi* (Geissler et al., 1987).

The ability of cereal aphids to survive over summer is important to the epidemiology of BYDV. Plumb et al. (1986) stated that in areas which had harsh summers, the number of aphids surviving to autumn critically influenced the severity of BYDV outbreaks. Yellow pan traps can now be used as a simple method for providing data on flights of cereal aphids in South Australia. This will enable comparisons of aphid phenology with BYDV epidemiology.

CHAPTER 14

A survey of *R. padi* and other wheat infesting cereal aphids flying over South Australia in 1989

Abstract

In 21 trap locations across South Australia *R. padi* was the most commonly trapped species of cereal aphid. *M. dirhodum* and *S. nr fragariae* were rarely trapped at any of the locations other than the Waite Institute. The trap catches of *R. padi* peaked twice. The first, an autumn peak, began in late April and continued through until the end of May, coinciding with the production of alatoid nymphs in perennial grass pastures. The second, winter peak commenced in July and continued through to the end of sampling, coinciding with alatoid nymph production in annual volunteer grasses and wheat crops. *M. dirhodum* and *S. nr fragariae* had only one peak which occurred in winter-spring.

Introduction

There have been two previous studies of aphids flying over parts of Australia. Both studies, O'Loughlin (1963) and Hughes *et al.* (1964; 1965) indicated that pan traps could be

used to measure the seasonal abundance of different species of aphids. O'Loughlin (1963) trapped aphids at 3 locations in Victoria and found trap catches of *R. padi* peaked in autumn and late winter-spring. Hughes et al. (1964) trapped aphids in the Northern Territory (1 location), Queensland (6 locations), New South Wales (4 locations), Victoria (2 locations), Tasmania (2 locations) and South Australia (2 locations). *R. padi* numbers peaked in winter-spring at both the South Australian trap locations.

In Chapter 13 yellow pan traps were also shown to be able to trap the three species of cereal aphids, *R. padi*, *M. dirhodum* and *S. nr fragariae*, commonly found on wheat in the low rainfall wheat belt of South Australia. Hughes et al. (1964) indicated several assumptions involved in the interpretation of pan trap data. Provided these assumptions are accepted, trap data can be used to monitor the seasonal abundance and distribution of aphid species. In this study assumptions (after Hughes et al., 1964) were:

if an aphid species was caught in a trap, that species could be assumed to be present in the area, but the failure to catch a species does not necessarily indicate absence;

if a species was caught consistently at one period of the year, failure to catch it at other times indicates rarity at those times;

if the aphid was trapped consistently over a long period of time, the occurrence of a clearly defined peak extending

over more than one week's catch reflects a true population change;

if an aphid species was trapped consistently at more than one site, failure to trap it at another site was evidence of its rarity at that other site;

absence or rarity at a few or many sites indicates marked localization of the species distribution;

if the spectrum of the commoner species trapped at two sites was similar then the lack of any other species common at one of the sites indicated absence.

Based on these assumptions a pan trapping survey was set up to determine: which species of wheat infesting aphids were present in South Australia; when major flights of each species occurred; whether there was a pattern in the distribution of individual species which might indicate their origin; whether the occurrence of peak aphid flights matched the phenologies of cereal aphids in pastures, in annual volunteer grasses and in wheat crops; and which aphid could be most involved in the spread of barley yellow dwarf virus (BYDV) in South Australia.

Materials and Methods

The 21 trap locations included 20 schools which participated in the state-wide trapping programme (Fig. 14.1). The last location was the Waite Institute. At each

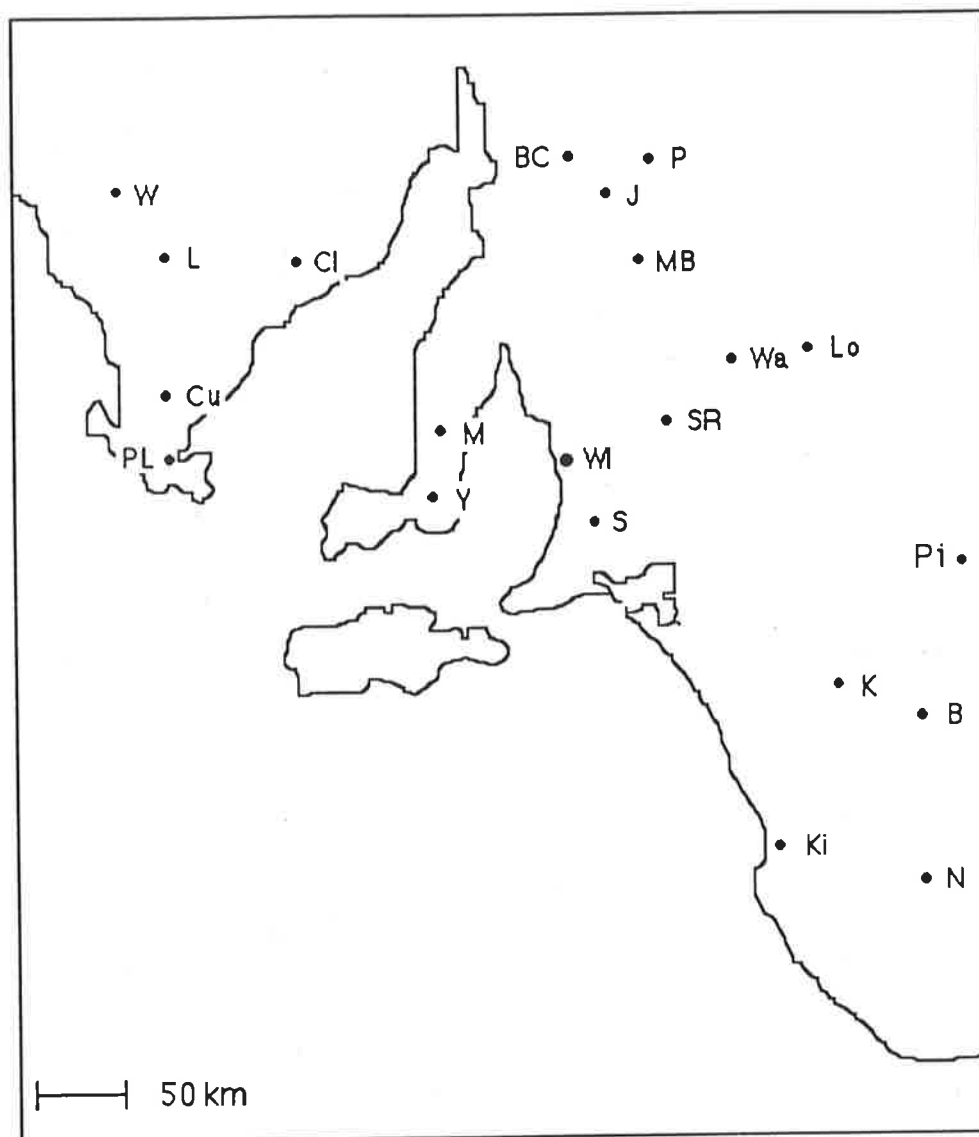


Fig. 14.1. Map of South Australia showing the locations of pan traps. B=Bordertown, BC=Booleroo Centre, Cl=Cleve, Cu=Cummins, J=Jamestown, K=Keith, Ki=Kingston, L=Lock, Lo=Loxton, M=Minlaton, MB=Mount Bryan, N=Naracoorte, P=Peterborough, Pi=Pinnaroo, PL=Port Lincoln, S=Strathalbyne, SR=Swan Reach, W=Wudinna, Wa=Wakerie, Wl=Waite Institute, Y=Yorketown.

location 8 yellow (yellow, Quick Dry Spray Enamel, British Paints) pan traps (Chapter 13) were placed in 2 groups of 4 in a square pattern on bare soil, well away from buildings, trees and other obstructions. Traps were filled with 1L of water containing detergent (Palmolive, 0.001L) and formalin (0.001L). Where possible, traps were positioned near cereal crops, but where none was available, traps were positioned near either a perennial grass pasture or the school oval.

At each location, trapping commenced at the beginning of April and continued through to the end of September. Traps were emptied weekly by pouring the contents through a fine net sieve. All material collected in the net was placed in a vial containing 70% alcohol. Each school was provided with paint and replacement traps to ensure trap quality was maintained during the survey. Aphids were identified using the EURAPHID key to alate aphids (Taylor & Robert 1980) supplemented by information in Eastop (1966) and Hales et al. (1990).

Results

R. padi was the most commonly trapped species at all locations and the numbers caught in each week at each location are listed in Table 14.1. To determine when peaks in the trap catches of *R. padi* occurred, the total numbers of aphids trapped at all locations were pooled for each

Table 14.1. The total number of *R. padi* trapped at 21 locations across South Australia in each week between April and the end of September, 1989. Samples in which no aphids were trapped are left blank. 'M' indicates no sample was collected.

Location of traps	April				May					June				July				August				September			
	1	2	3	4	1	2	3	4	5	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Booleroo Centre	1	3		6	12	1	12	29	35	7	5			8	4	13	23	31		25	23	36	31	24	5
Bordertown	3	1	1		2	1		3	1					M	M	13	23	31		25	23	36	31	24	5
Cleve				5	M	1	14	19	10	5	1	3	M	10	21	43	32	M	M			24	34	27	20
Cummins				1		2	7	4	2	1	2		1	2	9	22	43	3	3	M		29	13	16	2
Jamestown				7	11	5	15	20	15	1		2	1		5	11	29	18		43	12	39	48	11	7
Keith				1	1		6		7		3					9	14	M	M	M		31	25	15	10
Kingston				13	24	18	9	11	1		1	1	2		6	15	21	11	31	19	6	11	21	18	4
Lock	M	M	M	M		1	5	3						38	17	24	21	10	15	7	2	25	19	1	16
Loxton	M			24	23	18	36	48	9	1	3		2		2	11	20	15	9	5	1	3	11	2	6
Minlaton			1		16	2	4	32	8	1		1	1	M	M	M	M	9		M		25	23	11	3
Mt Bryan	M	M	M	M	18		8	14	19	11		2			1	1		1	11	1	23	43	32	3	0
Naracoorte	1	1		27	37	12	15	9	1				M	M	M	M	M	M	M	M		18	11	10	9
Peterborough				14	15		13	29	22	7	1	2			5	9	48	M	M	M		11	22	28	6
Pinnaroo	M			14		15	26	45	11	1			3		5	18	34	22	14	18	11	13	8	M	M
Pt Lincoln	M			9		1	2	6	3			1	1												
Strathalbyn	M			21	13	14	6	1		2		4	8	6	4	22	30	M	M	7	11	11	7	36	10
Swan Reach			1	9	12	11	24	58	17	9	1		3	1	1	12	39	28	31	44	1	2	1	M	M
Waikerie	M	M	1	13	9	27	48	38	12	3		4		M	M	M	M	M	M	M		13	15	10	1
Waite				18	11	33	18	24	16	5	2		1	2	1	13	53	3		15	8	7	21	68	3
Wudinna	M							6	1		1		2					M	16	10	8	2	1		2
Yorketown	M	M	M	M	10	5	6	22	11		1	4		3	22	32	18	M		M	18	10	19	16	4

week. The weekly totals were then divided by the number of locations which collected a sample that week (some schools did not operate the traps in some weeks or the data were missing for other reasons). Thus the mean number of aphids per week per operational location only was calculated, thereby reducing the influence of missing samples.

There were 2 peaks in *R. padi* trap catches (Fig. 14.2). The first, an autumn peak, commenced at the end of April and continued until the end of May. This was followed by a second, winter-spring flight period which began in mid-July and continued until the end of sampling. This pattern occurred at most locations with the exception of the Eyre Peninsula at Wudinna, Lock, Cummins and Pt Lincoln and the Upper Southeast at Keith and Bordertown where there was no first peak.

At all locations other than the Waite Institute, *M. dirhodum* was rarely trapped, with only 1 specimen being found in both the third and fourth weeks of June at Pt Lincoln, and 5 and 11 in the second and third weeks of August respectively, at Swan Reach. *S. nr fragariae* was recorded only at the Waite Institute.

At the Waite Institute, the peak in trap catches for both *M. dirhodum* and *S. nr fragariae* began in the third week of July and continued through to the end of September. Numbers during the peak ranged from 4 to 8 *M. dirhodum* and 1 to 6 *S.*

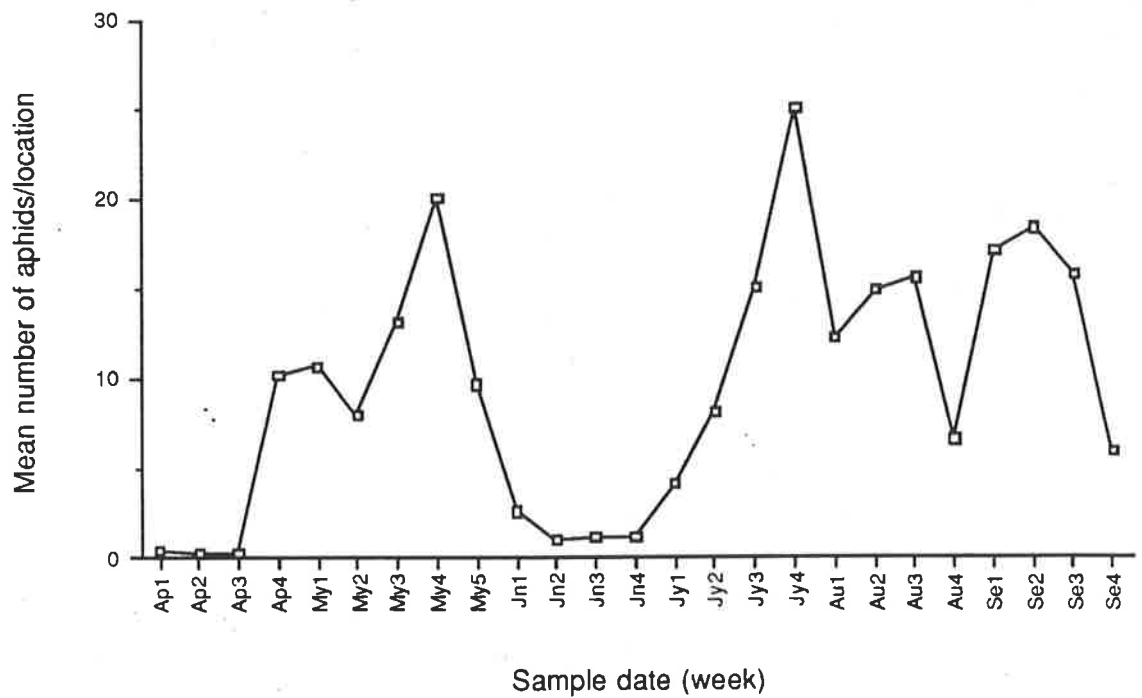


Fig. 14.2. The mean number of aphids trapped across South Australia in each week between April and the end of September, 1989.

nr *fragariae* per week whereas numbers in the remaining weeks were no greater than 2 aphids for both species.

Discussion

The results for *R. padi* from this survey are similar to those reported in the earlier studies of aphids flying over eastern Australia (O'Loughlin 1963; Hughes et al. 1964). No comparisons can be made for *S. nr fragariae* or *M. dirhodum* as neither was recorded in the earlier surveys. *R. padi* was the most common species of wheat infesting cereal aphid trapped. This, together with studies of the epidemiology of BYDV (Henry et al. in press) and ecology of cereal aphids in perennial grass pastures, annual volunteer grasses and wheat crops (De Barro 1991b) suggest that *R. padi* is the principal vector of BYDV in South Australia.

The first peak in trap catches coincides with the production of alate aphids that *R. padi* spreads over much of the state during autumn. Furthermore, the absence of the autumn peak over much of the Eyre Peninsula may be partly due to the Mount Lofty Ranges. These appear to block westward aphid migration and deflect it to the north (Chapter 10).

It was hoped that the survey may have provided some indications as to whether aphids infesting wheat crops in

the low rainfall wheat belt originated either in the Mount Lofty Ranges and Lower Murray Valley or in areas in south eastern Australia, where weather is milder over summer. While there is no clear pattern of spread across the State, the lack of *R. padi* in traps at Keith and Bordertown during autumn, suggests that few aphids were migrating from southeastern Australia into the low rainfall wheat belt.

The second peak coincides with the production of alatoid *R. padi* nymphs in annual volunteer grasses (Chapter 10) and wheat crops (Chapter 12). Also, the trapping of numerous aphids at all locations suggests that dispersal was even more widespread than in autumn. The importance of BYDV in low rainfall South Australia is unknown. However, Smith and Sward (1982) suggested that wheat crops infested with BYDV infective *R. padi* after the first node stage suffered little or no significant reductions in yield. In contrast, crops infected before tillering suffered significant yield reductions. This implies that, provided crops are still young enough when the second flight occurs and alates are viruliferous, there is a potential for widespread infection and subsequent yield loss.

The rarity of *M. dirhodum* and *S. nr fragariae* in most traps compared with their relative abundance at the Waite Institute indicates that the refuges for both species within South Australia are small and of local importance only. Consequently, both species appear to be insignificant in the

epidemiology of BYDV in the low rainfall wheat belt of South Australia. These results agree with observations made in perennial pastures and annual grasses between 1989 and 1991 (Chapters 6 & 10) which suggested that these two species, while occurring regularly each year, were minor vectors compared with *R. padi*.

Yellow pan traps proved to be a useful method of determining which species of wheat infesting aphids were commonly present in South Australia, and when and where major flights of each species occurred. They also showed a good match between trap catches and the phenology of cereal aphids in pastures and annual grasses. However, the trap network did not reveal any clear pattern of spread across the State and consequently there was no indication of the points of origin of any of the species.

CHAPTER 15

The epidemiology of barley yellow dwarf virus in South Australia

As part of the overall attempt to assess the importance of barley yellow dwarf virus in low rainfall South Australia a parallel study of the epidemiology of BYDV was undertaken by Dr Monique Henry. This study was carried out with the cooperation of the author and a brief summary of the results are presented here.

As was the case for *R. padi*, the summer refuges for BYDV were the irrigated perennial grass pastures. Both the PAV and RPV types of BYDV were found in pasture grasses and of these, PAV was the most commonly encountered. Alatoid *R. padi* nymphs collected from these pastures in May and June were found to transmit both types of BYDV. Transmission varied from 2 to 20% ($\bar{x}$ = 8%) in 1989, 3 to 22% ($\bar{x}$ = 9%) in 1990 and 18 to 82% ($\bar{x}$ = 44%) in 1991.

Alatoid nymphs collected from annual volunteer grasses in June, July and August of the 3 years transmitted BYDV at much lower levels (<1%).

Surveys of wheat crops across low rainfall South Australia

found levels of infection in normal and late sown crops to be less than 1%. In contrast, levels of infection in early sown crops ranged from 1 to 10%.

These results indicate:

- (a) that early sown crops in the low rainfall areas have the greatest risk of infection as alates migrating from pastures transmit BYDV at moderate to high levels. However, this risk is not considered sufficiently great to advise farmers to delay sowing as the economic gain from sowing early is thought to be greater than any loss caused by BYDV.
- (b) that normal and late sown crops have a low risk of infection and subsequent yield loss as alates dispersing from annual volunteer grasses transmit BYDV at very low levels.

CHAPTER 16

DISCUSSION

Irrigated perennial grass pastures in South Australia are the major over-summering refuges of the main vector of BYDV to wheat, *R. padi*. In addition, these pastures may be responsible for providing the alates which invade wheat crops in autumn. However, the alternative hypothesis, that local refuges are minor and most aphids infesting wheat come from elsewhere, eg. the south-eastern corner of Australia where the climate is wetter and cooler over summer, has not yet been disproved. Attempts in the past to determine the spatial origins of aphids by trapping airborne alates have provided some indications of origin, but the operation of such networks is expensive and the results, unless supported by detailed meteorological data, are rarely definitive.

Therefore, to adequately test either hypothesis about the origins of *R. padi* which invade wheat crops in South Australia each autumn/winter. It is necessary that individuals occurring in one refuge area be in some way physically distinguishable from those occurring in another. The ability to do so would enable the origin or origins of arrivals in crops to be determined unequivocally.

The need for this type of information can be viewed in the larger context of the migration of pest aphid species in

South Australia. Atmospheric circulation dominates the aerial movement of aphids (Dixon, 1985). However, the detailed meteorological information that would be useful in determining whether air movement over South Australia is conducive to large scale aphid migration from a particular point of origin at a given point in time, is largely unavailable. For example, the influence of the Mount Lofty Ranges on air movement during autumn is understood in broad terms, but how effectively it blocks westward migration of aphids or diverts westerly air streams to the north is poorly understood. Also, how effectively anticyclonic circulation in spring redistributes migrating aphids from western New South Wales into South Australia is also largely unknown as only anecdotal information exists. In terms of those cereal aphids currently occurring in South Australia, there is possibly no great impetus to answer these questions as none appear to be of particular agronomic importance. However, the issue of the origins of aphids in wheat crops in South Australia may become critical if the Russian wheat aphid, *D. noxia*, invades Australia.

In the past decade or so, *D. noxia* has spread from the southern Soviet Union, Iran, Afghanistan and southern Europe into Central Asia, the Middle East, North and South Africa, Mexico, Argentina, Chile, the USA and Canada (Evans et al., 1989; Kieckhefer & Elliott, 1989). In addition, it has reached (most probably on board long-distance aircraft) some of these countries over distances equally as long as those

Australia is from known sources of infestation. Therefore, Australia's isolation, which has protected it in the past, is unlikely to afford it the same protection in the future.

Furthermore, using the CLIMEX computer program Hughes and Maywald (1990) have predicted that some of South Australia's major hard wheat producing regions are at risk from serious infestation and damage when *D. noxia* does invade Australia. However, the same environmental constraints which act on cereal aphids already in South Australia, will almost certainly act upon *D. noxia* in that it will need to migrate to these crops from more favourable over-summering areas. Therefore, definite knowledge of migratory patterns of cereal aphids currently infesting crops in South Australia would be of great benefit in further assessing not only the likely risk of infestation, but also the likely timing of infestations by *D. noxia*.

One technique that has been used successfully to detect the origins of other organisms with an asexual phase in their life cycle involves the detection of enzyme polymorphisms. The nature and frequency of these polymorphisms have been used to distinguish between different populations (Hughes, 1989). However, the generally low level of enzyme polymorphism found in aphids by isozyme electrophoresis (May & Holbrook, 1978; Tomiuk & Wohrmann, 1980; Loxdale & Brookes, 1988) has restricted information on the population structure of many species. As

a consequence, basic information on the number of clones present in a population and the extent of temporal and spatial changes in clonal diversity have been obtained for only a few species (Rhomberg et al., 1985; Loxdale & Brooks, 1988, 1990). The lack of fundamental data on clonal diversity and dynamics in aphids has hindered attempts to examine empirically the spatial origins of many species.

A recent DNA development offers more promise. It is based on the discovery that scattered within the genome of man (Jeffreys et al., 1985a,b) and other vertebrates (Georges et al., 1988) are minisatellite regions comprising short (4-40 base pair) tandem repeat sequences differing in the number of repetitions and giving rise to extensive polymorphism at many loci. Polymorphism is visualized by hybridization of the target DNA to an appropriately labelled probe containing repeats of a common base-pair sequence, so producing individual-specific hybridization patterns or "DNA fingerprints". The increased genotypic discrimination resulting from the exploitation of these so-called hypervariable loci provides a powerful tool for differentiating between closely related individuals and clonal organisms which have hitherto been indistinguishable using other markers.

Recent work (Carvalho et al., 1991) has applied the technique to *Myzus persicae* Sulzer and *S. avenae* and has shown that enough DNA for fingerprinting can be extracted

from a single aphid, that the clones are stable over many generations and that clones within a single aphid species differ. Therefore, should the clonal makeup of populations of *R. padi* elsewhere in Australia differ from those found in the local refuge areas it should now be possible to distinguish between the origins of clones provided sufficient clonal variation between populations exists.

The use of DNA fingerprinting to separate a species into a series of clones has the potential to provide a new dimension to the study of the ecology of asexually reproducing pests. DNA fingerprinting would enable the determination of whether the proportion and frequency of certain clones change over the life of the crop, and whether certain clones have a better "fitness" with respect to colonising a crop than others and are therefore, potentially more damaging than others. In terms of pests which cause little direct damage, but are vectors of disease causing agents, the detection of clones which are better vectors would be equally advantageous. This would enable clones to be ranked in order of their ability to damage crops or transmit disease under a range of environmental conditions. Therefore, depending on the clonal make-up of immigrants, the likelihood of an outbreak may be more accurately assessed.

The application of DNA fingerprinting to certain aphid populations may therefore provide a unique understanding of

the genetics and spatial dynamics of these migratory pests, and lead to considerable improvements in producing and refining pest forecast schemes.

APPENDIX 1

Table 1.1. The proportion of alatoid nymphs and aphid density in 3 pastures between February and November in 1989 and 1990. The photoperiod and temperature on the day of sampling are also provided.

Sample date	Proportion of alatoid nymphs	Photoperiod	Temperature	Aphid Density
February, 89	0.50	13.35	29.50	1.80
March, 89	0.04	12.38	31.69	2.44
April, 89	0.40	11.6	24.57	17.48
May, 89	0.42	10.67	22.46	12.28
May, 89	0.50	10.28	20.00	16.60
June, 89	0.31	9.95	17.94	14.00
June, 89	0.35	9.83	14.77	9.24
July, 89	0.24	10.12	14.81	4.44
August, 89	0.49	11.23	15.12	2.56
September, 89	0.33	12.00	18.00	4.80
October, 89	0.00	12.62	20.53	4.80
November, 89	0.00	13.67	22.20	2.12
February, 89	0.00	13.78	26.14	2.32
March, 89	0.04	12.35	30.03	2.56
April, 89	0.58	11.60	22.52	10.08
May, 89	0.60	10.65	20.38	11.72
May, 89	0.62	10.29	17.14	25.68
June, 89	0.45	9.95	14.50	19.92
June, 89	0.32	9.85	12.27	14.76
July, 89	0.23	10.14	12.25	5.80
August, 89	0.54	11.29	12.61	3.16
September, 89	0.23	12.00	14.88	4.24
October, 89	0.00	12.62	18.06	4.72
November, 89	0.00	13.67	19.63	2.44
February, 89	0.08	13.35	29.50	2.36
March, 89	0.06	12.38	31.39	2.08
April, 89	0.62	11.60	24.57	16.36
May, 89	0.65	10.67	22.46	20.64
May, 89	0.61	10.28	20.00	30.84
June, 89	0.40	9.95	17.94	22.36
June, 89	0.27	9.83	14.77	14.56
July, 89	0.30	10.12	14.81	4.64
August, 89	0.40	11.23	15.12	4.36
September, 89	0.22	12.00	18.00	5.36
October, 89	0.00	12.62	20.53	4.04
November, 89	0.00	13.67	22.20	2.16
February, 90	0.40	13.38	23.93	70.76
March, 90	0.29	12.40	28.12	33.16
April, 90	0.55	11.67	26.40	60.92
May, 90	0.73	10.70	22.83	99.96
May, 90	0.66	10.28	23.20	88.04
June, 90	0.27	9.97	17.00	35.08
June, 90	0.09	9.82	18.38	2.00
July, 90	0.08	10.12	15.54	1.32
August, 90	0.24	11.17	15.95	1.68
September, 90	0.21	11.93	19.54	2.12
October, 90	0.00	12.52	21.67	1.68
November, 90	0.00	13.55	23.40	0.64
February, 90	0.39	13.18	24.15	83.24
March, 90	0.39	12.37	27.95	84.08
April, 90	0.59	11.63	25.40	80.48
May, 90	0.67	10.63	20.80	85.00
May, 90	0.64	10.23	20.07	126.20
June, 90	0.00	9.97	15.00	1.64
June, 90	0.08	9.82	16.07	1.56
July, 90	0.07	10.15	12.58	1.56
August, 90	0.31	11.17	12.68	1.92
September, 90	0.09	11.93	15.34	1.76
October, 90	0.00	12.53	18.00	2.16
November, 90	0.00	13.55	21.20	0.36
February, 90	0.41	13.35	24.80	92.28
March, 90	0.35	12.40	28.12	41.92
April, 90	0.54	11.52	26.88	63.92
May, 90	0.69	10.70	22.44	115.80
May, 90	0.69	10.33	23.62	93.04
June, 90	0.28	9.97	17.39	40.80
June, 90	0.07	9.82	18.38	1.84
July, 90	0.06	10.12	15.54	0.96
August, 90	0.16	11.17	15.95	1.76
September, 90	0.23	11.93	19.54	2.20
October, 90	0.00	12.52	21.67	1.68
November, 90	0.00	13.55	23.40	0.44

APPENDIX 2

Table 2.1. The proportion of alatoid nymphs and aphid density in annual volunteer grasses in the Lower Murray Valley in 1989 and 1991. The photoperiod, temperature and plant age at the time of sampling are also provided.

Proportion of alatoid nymphs	Photoperiod	Temperature	Aphid Density	Plant Age
0.08	9.88	15.0	112.2	1
0.18	9.88	15.0	153.4	1
0.03	9.88	15.0	118.8	1
0.23	10.25	14.2	2513.0	2
0.24	10.25	14.2	2469.0	2
0.13	10.25	14.2	2184.0	2
0.33	10.77	15.4	206.2	3
0.27	10.77	15.4	199.8	3
0.31	10.77	15.4	163.8	3
0.49	11.23	15.5	189.2	4
0.49	11.23	15.5	186.6	4
0.58	11.23	15.5	115.0	4
0.17	9.88	18.9	162.8	1
0.11	9.88	18.9	174.0	1
0.14	9.88	18.9	163.8	1
0.18	10.27	15.1	1547.0	2
0.18	10.27	15.1	1452.0	2
0.17	10.27	15.1	1467.0	2
0.30	10.57	17.3	196.2	3
0.34	10.57	17.3	183.6	3
0.28	10.57	17.3	194.6	3
0.77	11.20	16.5	26.0	4
0.72	11.20	16.5	20.2	4
0.85	11.20	16.5	26.4	4

Table 2.2. The proportion of alate nymphs and aphid density in annual volunteer grasses in the Mount Lofty Ranges and Adelaide Plains in 1989 and 1991. The photoperiod, temperature and plant age at the time of sampling are also provided.

Proportion of alate nymphs	Photoperiod	Temperature	Aphid Density	Plant Age
0.00	9.88	14.7	11.0	1
0.00	9.88	14.7	13.2	1
0.00	9.88	14.7	10.6	1
0.00	9.88	14.7	10.6	1
0.13	10.25	13.4	36.6	2
0.11	10.25	13.4	32.2	2
0.21	10.25	13.4	31.4	2
0.17	10.25	13.4	33.2	2
0.32	10.77	14.6	73.4	3
0.38	10.77	14.6	64.0	3
0.37	10.77	14.6	62.4	3
0.39	10.77	14.6	74.4	3
0.81	11.23	15.3	29.4	4
0.86	11.23	15.3	30.8	4
0.79	11.23	15.3	24.8	4
0.82	11.23	15.3	22.6	4
0.00	9.88	17.6	34.4	1
0.00	9.88	17.6	33.0	1
0.00	9.88	17.6	29.0	1
0.00	9.88	17.6	28.8	1
0.01	10.27	14.8	78.0	2
0.02	10.27	14.8	66.4	2
0.02	10.27	14.8	101.2	2
0.04	10.27	14.8	115.8	2
0.21	10.57	15.9	40.8	3
0.17	10.57	15.9	34.2	3
0.24	10.57	15.9	41.2	3
0.25	10.57	15.9	31.0	3
0.55	11.20	14.2	62.6	4
0.53	11.20	14.2	70.4	4
0.50	11.20	14.2	67.4	4
0.58	11.20	14.2	63.6	4

APPENDIX 3

Table 3.1. Lower Murray Valley, July 1989

Growth stage	Total number of aphids	Proportion of infestation
21	80	0.22
21	88	0.26
22	98	0.18
22	103	0.16
22	57	0.28
22	65	0.24
22	46	0.12
22	31	0.14
22	67	0.22
22	69	0.18
22	101	0.26
22	90	0.22
22	79	0.20
22	65	0.18
22	71	0.16
22	70	0.22

Table 3.2. Murray Mallee, July 1989

Growth stage	Total number of aphids	Proportion of infestation
22	3	0.04
22	2	0.02
12	1	0.02
12	4	0.04
13	13	0.12
13	8	0.08
22	5	0.10
22	5	0.02
22	3	0.04
22	1	0.02
23	42	0.16
23	28	0.18
22	85	0.14
22	79	0.16
24	173	0.20
24	164	0.22
24	160	0.30
24	169	0.32
25	138	0.32
25	174	0.30
21	53	0.16
21	64	0.10
22	49	0.18
22	69	0.14
16	14	0.06
16	9	0.04
16	105	0.08
16	89	0.12
22	78	0.22
22	50	0.26
23	220	0.26
23	194	0.28
13	3	0.04
13	4	0.02
21	5	0.08
21	1	0.04
21	16	0.06
21	12	0.08

Table 3.3. Eyre Peninsula, July 1989.

Growth stage	Total number of aphids	Proportion of infestation
22	2	0.02
22	8	0.10
22	6	0.06
22	8	0.08
24	1	0.02
24	4	0.04
22	4	0.04
22	2	0.04
23	2	0.02
23	1	0.02
22	4	0.04
22	4	0.02
23	4	0.06
23	1	0.02
22	4	0.06
22	2	0.02
24	1	0.06
24	1	0.04
22	9	0.02
22	5	0.02
22	0	0.00
22	0	0.00
22	3	0.10
22	1	0.04
25	42	0.16
25	36	0.18
26	66	0.26
26	74	0.28
23	6	0.06
23	9	0.10
26	62	0.30
26	73	0.28
27	131	0.36
27	128	0.24
26	199	0.34
26	150	0.38
25	98	0.30
25	123	0.34
26	78	0.22
26	113	0.26
25	108	0.24
25	132	0.28
23	102	0.36
23	117	0.24
22	15	0.08
22	11	0.04
22	2	0.02
22	5	0.04
23	4	0.02
23	2	0.02
23	6	0.02
23	4	0.06
23	3	0.02
23	3	0.04
22	2	0.02
22	8	0.04
21	1	0.02
21	3	0.02
32	5	0.04
32	4	0.04
33	4	0.06
33	6	0.04

Table 3.4. Lower and Upper North, July 1989.

Growth stage	Total number of aphids	Proportion of infestation
23	11	0.08
23	17	0.12
23	29	0.12
23	26	0.18
21	6	0.04
21	11	0.06
22	12	0.04
22	19	0.08
22	16	0.16
22	18	0.18
23	9	0.06
23	6	0.06
22	15	0.10
22	5	0.04
23	5	0.02
23	8	0.02
23	7	0.06
23	10	0.04
23	8	0.08
23	6	0.02
24	33	0.18
24	26	0.16
22	32	0.12
22	34	0.22
24	70	0.28
24	88	0.24
24	103	0.34
24	95	0.32
23	90	0.28
23	89	0.22
23	76	0.26
23	100	0.24
23	110	0.36
23	90	0.32
22	56	0.24
22	54	0.22
23	76	0.20
23	85	0.20
23	78	0.26
23	100	0.28
23	42	0.22
23	41	0.20
23	88	0.18
23	97	0.26
23	81	0.22
23	51	0.26
23	81	0.24
23	60	0.28
23	110	0.30
23	80	0.24
23	88	0.22
23	95	0.24
23	111	0.26
23	100	0.28
25	60	0.30
25	46	0.32
25	55	0.26
25	65	0.32
25	68	0.30
25	37	0.22
23	59	0.26
23	94	0.24
24	62	0.22
24	44	0.28
23	99	0.24
23	105	0.26
23	36	0.18
23	26	0.16
22	33	0.20
22	40	0.18
23	38	0.22
23	32	0.22
23	37	0.24
23	41	0.18

Table 3.5. Murray Mallee, July 1991.

Growth stage	Total number of aphids	Proportion of infestation
12	0	0
12	0	0
13	0	0
13	0	0
13	0	0
13	0	0
13	0	0
13	0	0
22	0	0
22	0	0
24	1	0.02
24	3	0.04
13	0	0
13	0	0
21	0	0
21	0	0
26	2	0.04
26	7	0.08
26	1	0.02
26	3	0.04
25	5	0.08
25	2	0.04
24	1	0.02
24	8	0.08
12	0	0
12	0	0
11	0	0
11	0	0
13	0	0
13	0	0
21	0	0
21	0	0

Table 3.6. Eyre Peninsula, July 1991.

Growth stage	Total number of aphids	Proportion of infestation
25	25	0.14
25	9	0.10
21	0	0
21	0	0
24	3	0.04
24	4	0.04
22	0	0
22	0	0
24	3	0.04
24	0	0
26	4	0.04
26	0	0
31	1	0.02
31	0	0
21	0	0
21	0	0
23	0	0
23	0	0
31	0	0
31	0	0
23	0	0
23	0	0
26	2	0.04
26	0	0
27	0	0
27	0	0
26	0	0
26	0	0
24	0	0
24	0	0
23	0	0
23	0	0
21	0	0
21	0	0
21	0	0
21	0	0
31	5	0.06
31	0	0
31	3	0.02
31	10	0.16
25	7	0.10
25	1	0.02
22	0	0
22	0	0
25	4	0.06
25	0	0
22	0	0
22	0	0
31	8	0.10
31	1	0.02
26	5	0.06
26	1	0.02
23	0	0
23	0	0
24	9	0.06
24	0	0
23	0	0
23	0	0
24	18	0.16
24	6	0.08
24	10	0.14
24	16	0.14
23	0	0
23	0	0
24	0	0
24	0	0
22	0	0
22	0	0
31	15	0.14
31	3	0.04
21	0	0
21	0	0

Table 3.7. Lower and Upper North, July, 1991.

Growth stage	Total number of aphids	Proportion of infestation
11	1	0.02
11	0	0
10	0	0
10	0	0
11	0	0
11	0	0
21	0	0
21	0	0
12	0	0
12	0	0
23	0	0
23	0	0
25	15	0.18
25	8	0.12
25	0	0
25	0	0
25	3	0.06
25	16	0.08
25	2	0.10
25	20	0.16
12	0	0
12	0	0
23	2	0.03
23	1	0.02
25	8	0.10
25	8	0.10
11	0	0
11	0	0
11	0	0
11	0	0
11	0	0
11	0	0
10	0	0
10	0	0
12	0	0
12	0	0
10	0	0
10	0	0
11	0	0
11	0	0
10	0	0
10	0	0
10	0	0
10	0	0
12	0	0
12	0	0
13	0	0
13	0	0
11	0	0
11	0	0
10	0	0
10	0	0
11	0	0
11	0	0
10	0	0
10	0	0
10	0	0
10	0	0
10	0	0
11	0	0
11	0	0

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