The epidemiology and forecasting of Barley Yellow Dwarf Virus in autumn-sown cereals

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Thesis submitted to the University of Glasgow for the Degree of Doctor of Philosophy

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December 1991

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ACKNOWLEDGEMENTS

Many thanks are due to Dr G. N. Foster and Dr S. J. Holmes for help and encouragement during both the practical and writing-up stages.

Also of crucial importance were the many farmers who allowed access to their farms for sampling purposes during the three years.

Thanks are also due to many technicians of the Plant and Environmental sciences departments who provided help and assistance:- especially Mrs S. Bone; Mrs S. Gilani; Mrs A. Kelly; and Mr B. Laird for the infectivity indexing work.

Thanks are also due to Mr B. Collison and Mr R. Murray for the Lamb daily weather types and PSC indices respectively. I am also indebted to people too numerous to mention, who collect and identify aphids for the RIS, and who record weather data recorded in the *Monthly Weather Report*.

Finally, I am grateful to the Department of Agriculture for Scotland and the Home Grown Cereals Authority for providing the funds which made this work possible.

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SUMMARY

BYDV is sporadic and potentially damaging to autumn-sown cereals in Britain. Currently, the risk of the disease is assessed during the autumn via Infectivity Indexing (II). However, II has a number of limitations.

Three mild winters in the late 1980s allowed anholocyclic overwintering of aphids in autumn-sown cereals. In the following springs, widespread and sometimes severe BYDV problems were reported from many parts of Britain. This benefited this research, and also highlighted the importance of weather to aphids and BYDV epidemiology.

BYDV occurs as two types: *R. padi*- and *S. avenae*-transmitted BYDV. Monitoring of winter barley revealed that these two types not only differ in their propensity to cause yield loss, but also that they have different pre-conditions. These pre-conditions are weather-related, suggesting that BYDV risk to autumn-sown cereals may be forecast by considering weather patterns in the preceding year. However, the crop sampling also suggests that risk assessments should include aphid monitoring, both in the summer and the autumn: this is necessary if regional differences in BYDV risk are to be identified.

Results of BYDV transmission tests with field-collected aphids were largely consistent with laboratory observations: characteristic vector-specificity and vector-efficiency were encountered, and transcapsidation and

transmission interference appeared to be common. There were significant differences in BYDV transmission, for both *R. padi* and *S. avenae* between host plants, and between years.

Analysis of 12.2 m suction trap catches of cereal aphids drew attention to the sensitivity of aphid populations to weather. Both the temperature of the preceding winter and the current spring affect the size of spring aphid catches. With respect to the size of the autumn migration of *Rhopalosiphum padi*, the temperature of the preceding winter, and the weather of the preceding summer are important, as is the size of the previous autumn's migration.

Sampling of a number of habitats for cereal aphids, identified the importance of cereal fields during the summer, both pre- and post-harvest, to *S. avenae* populations, and ryegrass pasture to *R. padi* populations.

Comparisons of the aphid/BYDV data in winter barley of a region in one season with the comparative data of the following season, suggested local movement of *S. avenae*.

In the three years of study, II failed to assess the BYDV risk to autumn-sown cereals correctly. Apart from mild winters, the failure was due to the importance of aphid morph to *R. padi*-transmitted BYDV. The proportion of the *R. padi* migration which is comprised of exules is crucial to the extent of colonisation of autumn-sown cereals by alatae.

GLOSSARY

ADAS	Agricultural and Development Advisory Service
AFRC	Agriculture and Food Research Council
Alatae	Winged adult aphids
Anholocycly	Type of aphid lifecycle in which reproduction is parthenogenetic throughout the year
Anticyclonic	An area of higher barometric pressure at the surface in which air is sinking at the centre and moving outwards. It is generally associated with dry weather, although anticyclones can be cloudy. In winter, the weather is cold, in summer, it is warm.
Aphidophagous	Aphids comprise whole or part of diet
Apterae	Wingless aphids: adults or nymphs
C	a measure of the difference in frequency of cyclonic and anticyclonic type days over or near to the British Isles. It is positive when cyclonic days predominate.
CET	Central England Temperature. This is the longest temperature series in the world that is constructed from thermometer records: as a monthly series, it extends back to 1659. It is a regional mean, currently calculated with data from the following four sites: Rothamsted, Malvern, Squire's Gate (Blackpool) and Ringway.
Cyclonic	An area of lower barometric pressure at the surface in which air is moving towards the centre and rising. It is generally associated with wet and unsettled weather. In summer, the weather is cool, in the winter usually mild, although it can be cold in the north.
DAFS	Department of Agriculture and Fisheries of Scotland.
DANI	Department of Agriculture of Northern Ireland

Exules	Female aphid form which reproduces parthenogenetically.
Gynoparae	Winged female aphid form which migrates to winter host plant, on which it gives birth to egg-laying females (Oviparae).
Holocycly	Type of aphid lifecycle in which reproduction alternates between parthenogenetic reproduction on secondary host plant(s) in the summer, and sexual reproduction on primary host plant(s) in the winter.
II	Infectivity Indexing. A method of assessing the risk of BYDV to autumn-sown cereals.
Males	Winged form which migrates to winter host plant, on which it mates with the egg-laying females (Oviparae).
Oviparae	The true sexual female. Wingless form which is capable of mating and producing eggs.
P	is a measure of the difference in frequency of days of progressive and blocked synoptic types over the British Isles. It is positive when the bias is towards progressive synoptic types. Progressive types are the westerly weather types identified by Lamb. Blocked synoptic types are the non-westerly Lamb weather types.
Poikilotherm	Cold-blooded animal - body temperature varies with the temperature of the environment although it can be controlled within limits.
RIS	Rothamsted Insect Survey - a network of 12.2 m suction traps which monitor the aerial aphid fauna of Britain.
S	is a measure of the difference in frequency of southerly and of northerly type days over or near the British Isles. It is positive when the bias is southerly.
SAC	Scottish Agriculture College

CHAPTER ONE

Introduction

1.1 **Barley Yellow Dwarf Virus - the problem**

Barley Yellow Dwarf Virus (BYDV) is the most important virus disease affecting cereals in Britain (George, 1982), regularly causing damage to autumn-sown crops in some regions (A'Brook & Dewar, 1980; Hill, 1982). It is one of several damaging plant viruses (luteoviruses) affecting crops in temperate latitudes which are transmitted by aphids (Hemiptera: Aphididae). The manner of transmission is termed persistent (Rochow, 1970), because once an aphid has acquired the virus, it remains capable of transmitting the virus to a number of uninfected plants for several days or more (Rochow, 1963). The ability to transmit BYDV depends to some extent on the time allowed for feeding there being a minimum threshold for a group of aphids to attain maximum probability of transmission: this is termed the latent period (Rochow, 1963). BYDV is not transmitted from parents to their progeny, therefore to be viruliferous, an aphid must acquire the virus from an infected host plant. Nor is BYDV seed-transmitted (Rochow, 1970; Eweida *et al.*, 1988), therefore new plant infections in the field are only achieved by aphid activity.

BYDV is a plant virus that has both effective methods of spreading to new sites and of perennation at current sites of infection (Harrison, 1981), these factors accounting for its ubiquity in Gramineae of temperate regions and for its worldwide distribution. Surveys of ryegrass pastures in Britain by Doodson (1967), Catherall

et al. (1982) and Holmes (1985) have revealed high levels of infection, and abroad, testing for BYDV in wild grasses (e.g. *Lolium perenne*) has also revealed extensive infection (Oswald & Houston, 1953; Guy *et al.*, 1986; Kurppa *et al.*, 1989).

For the spread of BYDV, and for many other plant viruses that have an insect vector, vector activity is more important than vector numbers, as it spreads into cereal crops when climatic conditions favour vector migration (Harrison, 1981). In Britain, few winter cereal crops are unaffected by BYDV when winters are sufficiently mild to allow survival and activity of virginoparae (Oakley, 1989).

In affected fields, BYDV is characterised by the occurrence of patches of stunted plants with leaf discolouration, which is most intense at the distal ends of leaves: reddish-purple in oats (*Avena sativum*), chrome-yellow in barley (*Hordeum vulgare*) and red and yellow in wheat (*Triticum aestivum*) (George, 1982). In common with other luteoviruses, BYDV has a greater yield effect on crop plants the earlier the growth stage at the time of infection, sometimes causing plant death at very early growth stages (Endo & Brown, 1963).

The occurrence of the disease in discrete patches scattered throughout fields is the result of two phases of aphid activity. The first of these is the primary spread, either by alatae immigrating into fields or by apterae

walking (Ferrar, 1968) from grasses or volunteers (either buried by ploughing or present on the surface). If these aphids transmit BYDV to a crop plant, a source of infection is established, each aphid having the potential to transmit BYDV to several plants. The second phase of aphid activity is the secondary spread. This is the development of patches of infected plants from single infected plants. This occurs when an aphid larviposits on an infected plant establishing an apterous aphid population which progressively disperses onto adjacent crop plants infecting them in the process. The size of the infected patch mainly depends on aphid activity which is dependent on temperature and on the time before cold weather halts aphid activity (George, 1982).

Depending on whether alatae or apterae are involved, BYDV has two types of gradient of virus spread (Thresh, 1976). For alatae which are very active, the gradients are shallow, because plants infected by one viruliferous aphid are scattered over a wide area. For apterae, which are relatively sessile, the gradients are steep, because plants infected by one viruliferous aphid are close together (often adjacent).

1.2 **Methods of control of BYDV**

Only virus spread caused by apterae (secondary spread) leads to economic damage in cereals because adjacent plants can compensate for the scattered dead or stunted neighbours

associated with alatae-introduced BYDV. Economic damage to cereals is prevented by controlling the aphid populations (Plumb, 1986). However, the method of aphid population control depends on whether the primary introducers of the virus were alatae or apterae. In the former case, there is a period of approximately one month between the arrival of the alate immigrants and the development of the damaging virus spread by apterae. In the latter case, damaging virus spread can develop sooner for two reasons. Firstly, the number of apterae walking from ploughed-in grass or grass weeds can be large, so that a relatively high proportion of the crop plants become infected during the primary spread causing severe damage (Plumb, 1988). Secondly, apterae are more fecund than alatae (Wratten, 1977) resulting in aphid populations that spread BYDV infections to neighbouring plants to develop more quickly than infections established by alatae.

Control of BYDV introduced by alatae Field-trials have consistently shown that in early-sown cereal crops, an aphicide applied during the last week of October or the first two weeks of November controls virus spread and increases yield in aphid-infested crops (George, 1982; Plumb, 1986; McGrath & Bale, 1990). An insecticide treatment at this time prevents the damaging secondary spread by apterous aphids.

Control of BYDV introduced by apterae Field-trials by ADAS (Carter, 1984) and by the AFRC at Long Ashton (Kendall *et*

al., 1988) have shown that pre-treatment of aphid-infested ploughed-in grass leys or cereal stubbles with aphid-infested grass weeds and/or volunteers (Figure 1.1), whether or not ploughing subsequently occurred with desiccant herbicides reduces BYDV incidence in succeeding winter cereal crops (Kendall *et al.*, 1988).

Not only are late autumn insecticide-applications effective at controlling aphid populations, they are also cheap (Hill, 1988). The low cost of treatment coupled with the serious yield-loss that BYDV may cause in individual crops in certain years has led to the practice of "insurance spraying" (Blake, 1991), particularly in areas where BYDV is a frequent problem. However, research has shown that in most years, only crops drilled prior to the middle of September may benefit from treatment (George, 1982; Plumb, 1986; McGrath & Bale, 1990).

This thesis is not about control of BYDV. This subject has been dealt with elsewhere (Kendall & Smith, 1981a; Kendall *et al.*, 1988; Plumb, 1986; Plumb, 1988; McGrath, 1989; McGrath & Bale, 1990). The epidemiology and forecasting of BYDV are the subjects of this thesis.

1.3 **The Duality of BYDV**

Two types of BYDV are recognised in Britain: *R. padi*-transmitted and *S. avenae*-transmitted BYDV (McGrath & Bale, 1990). This distinction arises, partly because of the relationships between the different strains of BYDV and the

Figure 1.1 A cereal stubble field heavily infested by barley volunteers which were infested by cereal aphids.

different aphid species capable of transmitting them (Rochow, 1969), and partly due to the differing dispersal behaviours of the aphid species.

In Britain, three strains of BYDV occur, their names being acronyms which relate to the aphids which transmit them: RPV transmitted by *Rhopalosiphum padi* (Linnaeus), PAV transmitted by *R. padi* and *Sitobion avenae* (Fabricius) (formerly *Macrosiphum*) and MAV transmitted by *S. avenae* and *Metopolophium dirhodum* (Walker) (Plumb, 1974). Both RPV and PAV are known as "severe" strains, because they induce relatively severe symptoms in cereals compared with the "mild" strain, MAV (Plumb, 1974). However, serologically, PAV and MAV are closely-related whereas RPV is more distinct (Aapola & Rochow, 1971).

Although *S. avenae* transmits PAV under laboratory conditions (Rochow, 1969), in the field, it is mainly associated with mild BYDV symptoms and the MAV strain (Plumb, 1974). However, McGrath (1989) found that, in the Vale of York, *S. avenae* was transmitting both MAV and PAV, but the distinction was nevertheless still valid. This was largely because of the different dispersal behaviours of these two aphid species which determine the extent of crop damage.

Every species has a characteristic spatial disposition of its individuals (Taylor, 1971), which is a product of both the species and the environment. For *R. padi* on cereal

plants, dense aggregations of individuals are characteristic, particularly on the lower leaves, but sometimes covering all the aerial parts of the plant (George, 1982). In contrast, *S. avenae* tends to be found singly on cereal plants except at later growth stages when it forms dense colonies on ripening ears (McGrath & Bale, 1990). This scattered distribution was found to be associated with the greater inclination of *S. avenae* to move from its host plant relative to *R. padi* (McGrath, 1989).

In the context of BYDV spread, the different behaviours mean that apterous *S. avenae* have a shallower gradient of BYDV spread than apterous *R. padi*. This is because their greater activity disperses the virus to a number of plants over a wide area relative to *R. padi*.

It is because of the differing severity of the BYDV strains associated with the two aphid species and the differing dispersal behaviours, that contrasting damage thresholds of BYDV infection have been applied to these two types of BYDV: 5% of tillers infected for *R. padi*-transmitted BYDV (Kendall & Smith, 1981a) and 10% for *S. avenae*-transmitted BYDV (McGrath, 1989). For *S. avenae*, 10% of tillers infected was related to populations of aphids greater than 10% of plants infested (McGrath, 1989). The aggregated distribution of *R. padi* infestations (George, 1982) makes definition of such a relationship for this aphid more difficult.

1.4 The need for forecasting BYDV risk to autumn-sown cereals

BYDV is a sporadic disease only causing damage to autumn-sown crops in certain years and in certain regions of Britain (A' Brook, 1974). Because of the sporadic nature of the disease, and the harmful side-effects of insecticides in cereal ecosystems, prophylactic spraying is not encouraged and a need for the forecasting of autumns in which insecticide applications are required has arisen (Plumb, 1988). Furthermore, because of the distinctions between BYDV introduced by apterae and alatae, and BYDV introduced by *R. padi* and *S. avenae*, farmers need to know the risks from each type, so that they may choose the appropiate control strategy.

Before discussing the current methods of forecasting BYDV risk to autumn-sown cereals in Britain, it is relevant to summarise the history of forecasting the risk of two other aphid-transmitted virus diseases of crops in Britain: those of sugar-beet (*Beta vulgaris*) and potato (*Solanum tuberosum*).

1.5 Forecasting the risk of the virus diseases of sugar beet

There are two important virus diseases of sugar beet. The first, the beet yellows, is comprised of two semi-persistent viruses: Beet Mild Yellowing Virus (BMYV) and Beet Yellows Virus (BYV) (Russell, 1970). The second, Beet Mosaic Virus (BMV), is transmitted in a non-persistent

manner (Russell, 1971).

In common with BYDV, only early infection seriously affects yield by interfering with carbohydrate metabolism (Watson, 1942), and seed transmission does not occur (Watson *et al.*, 1951). An early observation was that the beet yellows can be found in most crops, but that losses due to the disease occurred in only a few fields (Watson, 1942).

Two aphid species were found to be important: *Myzus persicae* (Sulzer) and *Aphis fabae* (Scopoli). As a result of surveys from 1940-48 in which the number of aphids on leaves and the number of yellow patches in crops were recorded, a relationship was eastablished between virus incidence and aphid numbers (Watson *et al.*, 1951).

The next task was to discover the reasons for the higher numbers of aphids in the diseased fields. It was observed that beet yellows (BMYV & BYV) and BMV were more prevalent in areas where sugar beet and mangold seed-crops were grown. Because some of these seed-crops were in their second year of growth, a high proportion of them was both virus infected and aphid-infested. These crops were therefore local sources of viruliferous alatae. BMV being a non-persistent virus, was only found in crops close to seed-crops, because aphids were seldom infective after more than one feed (Watson *et al.*, 1951).

Measures employed to control aphids and viruses in the

seed-crops since 1950 decreased the spread of the viruses, especially of BYV and BMV. However, BMYV increased in importance, because a number of grass weeds present in hedge bottoms and other sites around farms were found to be hosts of the virus (Russell, 1965). Control of such weeds is not a viable option.

Mild winters allow overwintering of aphids on wild grasses and in crops (Turl, 1983). Thus positive relationships were found between virus incidence in sugar beet crops and air temperature in late winter and early spring (Hurst, 1965). In 1959, a spray warning scheme based on aphid surveys in sugar beet crops was implemented in England (Hull, 1968). It was altered in the 1970s to include predictions of virus incidence in late August, based on the knowledge of the relationship between late winter and spring weather and virus incidence in crops later in the season (Watson *et al.*, 1975). Currently, the forecast equations include the level of the previous year's virus incidence in sugar beet crops, the mean temperature in January and February and the predicted timing of the spring migration of *M. persicae* (Harrington *et al.*, 1989). A regional forecast is made in March giving growers up to a month's warning of the need to apply insecticide granules at the time of sowing in years when the risk is predicted to be high.

1.6 **Forecasting the risk of the virus diseases of potatoes**

There are two main virus diseases of potato: a persistent virus, potato leaf roll (PLRV) (Peters, 1970), and a semi-persistent virus, potato virus Y (PVY) (Delgado-Sanchez, 1970).

In common with BYDV, early infection can cause serious yield loss by interfering with carbohydrate metabolism (Cadman & Chambers, 1960). An important distinction between BYDV and the virus diseases of potato is that most ware crops contain a small proportion of infected plants at the beginning of each season whereas winter barley starts the season totally uninfected. This is because seed potatoes are bulked-up vegetatively, and because virus symptoms do not appear in the season of infection. This has led to the practice of "roguing" of plants showing virus symptoms early in the season, to remove these sources of infection (Shaw, 1955).

Three aphid species are commonly found on potato, *M. persicae*, *Macrosiphum euphorbiae* (Thomas) and *Aulocorthum solani* (Kltb.), but only the former species is an important virus vector (Fisken, 1959). A series of experiments in different parts of England and Wales from 1941-47 on the spread of PLRV and PVY showed that PLRV was correlated with the number of alate *M. persicae* caught on sticky traps throughout the potato growing season or with counts of aphids per 100 leaves (Broadbent, 1950a). An observation on the incidence of aphids on potato crops was that they were

more abundant in eastern areas due to the greater frequency of days meteorologically favourable for aphid flight (Davies, 1939) and this explained the historical practice of growing seed potatoes in the cooler parts of the north and west. Another observation was that aphid populations on potato crops developed sooner and reached greater numbers near to urban areas because of the abundance of suitable aphid overwintering sites in such areas in the form of wild and cultivated Cruciferae (Shaw, 1955).

Scotland is an important seed potato growing area, because PLRV and PVY spread slowly (Woodford *et al.*, 1977). However, serious PLRV outbreaks followed a series of mild winters in the early 1970s, when aphids migrated in May colonising the potatoes at an early growth stage and before roguing of infected plants could be carried out (Turl, 1980).

Two warning schemes have been employed in Scotland to minimise virus incidence in seed potato crops. The first scheme involved the prediction of the timing of the spring migration of *M. persicae* using mathematical models based on winter temperature data (Turl, 1980), and the size of the same migration based on measures of the overwintering success of the weed-hosts of *M. persicae* (Turl, 1983). This strategy enabled growers to apply insecticide granules at planting time when early migrations of *M. persicae* were forecast. The second scheme monitored the arrival and

development of aphids on potato crops that had not received insecticide granule treatment, and advised the seed potato growers on whether or not spraying was necessary later in the season (Woodford *et al.*, 1977).

1.7 **Current methods of forecasting BYDV risk to autumn-sown cereals in Britain**

BYDV forecasting schemes are operated in Britain by government agencies to provide farmers in their locality with relevant BYDV forecasts and risk assessments for autumn-sown cereals. The main scheme operated by the AFRC and ADAS at a number of sites in England, by SAC at Auchincruive, Ayr, in Scotland and by DANI at Newforge Lane, Belfast, in Northern Ireland, is the Infectivity Index (II) (Plumb, 1986). This method relies on alate aphid catch data obtained from one of a network of 12.2 m suction traps (Macaulay *et al.*, 1988) covering Britain and western Europe (Tatchell & Woiwod, 1990).

To understand II, it is necessary to understand the reasons for, the use and limitations of, the suction traps. The network of suction traps was established by the Rothamsted Insect Survey (RIS) in the 1960s to monitor the flying stages of insect pests which could then be related to pest populations on crops (Taylor, 1973). The justification for aerial sampling in preference to crop sampling was two-fold. Firstly, many crop pests are migrants which redistribute their populations over large geographical areas necessitating that pest control be

organized on a scale greater than individual farms. Secondly, crop sampling is not feasible in all crops, and even within one crop, several samples per field are required to obtain an estimate of the variation within the crop because insects on crops are highly aggregated (Taylor, 1973).

Two important advantages of sampling aerial populations of insects instead of crop infestations are: firstly, their distribution in the air is random, thus one sample gives both the mean and the variance of the population, and secondly, many different crop pests are sampled simultaneously at little extra cost (Taylor, 1973).

The height of 12.2 m was chosen after inspection of vertical profiles of insect density, because it was high enough to exclude most local flying insects (particularly Nematocera) and low enough to sample from the densest layer of migrating, randomly dispersed, aerial population of insects, especially aphids (Taylor & Palmer, 1972).

The hypothesis that the size of aphid populations on crops could be determined by the size of the suction trap catch of alatae of the same species was unproven at the time. However, the first obstacle was to determine the size of the agricultural land area around the trap which the suction trap catch was relevant to. This was achieved by firstly comparing trap catches (over periods varying from one day to several months) from a pair of traps 1.43 km

apart and subsequently from transects of a number of traps covering hundreds of kilometres. It was established that there were strong between-trap correlations of daily catches over distances up to hundreds of kilometres for whole insect Orders such as Thysanoptera, for whole families such as Aphididae, and for single, small species such as the frit fly *Oscinella frit*, (L.), thus suggesting that large areas could be adequately sampled with a small number of suction traps (Taylor, 1973).

Having satisfied the condition that the 12.2 m suction trap sampled on a scale that was useful for regional pest forecasting purposes, attention focused on the potential of the trap for forecasting particular pests. From 1969 to 1972, entomologists collaborated with RIS by providing crop counts of seven species of cereal aphids on 24-44 spring-sown cereal fields throughout Scotland, England and Wales. The immigration of these pests into cereal crops was investigated by comparing the dates a species was first recorded in crop samples with dates the same species was recorded in the nearest suction trap. There were three important results. Firstly, in 89% of the 732 field/trap comparisons, a species was recorded first by the suction traps indicating the greater sensitivity of the traps compared with crop sampling. Secondly, the first catches by suction traps were spread over a shorter number of days than the first catches by crop samples, again indicating the greater sensitivity of the suction traps. Thirdly, the

relationship depended to a large extent on the aphid species involved. For *R. padi*, which is not a pest of spring-sown cereals in Britain, the relationship was good with no cases of the species being detected in crops before being detected in the suction trap catches. However, for *M. dirhodum*, an important pest of spring-sown cereals, on 25% of occasions, the species was detected in crop samples before being detected by the nearest suction trap. One explanation for this difference was that some of the *M. dirhodum* crop infestations were derived from low-level, short distance movements concentrating insects into the crop from local overwintering sources (Taylor, 1973).

RIS has now been collecting data for more than 20 years, and relationships between suction trap catches and crop infestations have been established for some pest species. For example, suction trap catches of the spring migration of *S. avenae* in England have been compared with the populations that develop on cereals later in the season. When less than 10 alatae were found in suction trap samples before the end of anthesis (GS 69), the peak populations developing in the field never reached outbreak level (defined as > 5 aphids per tiller). Thus, it is possible to forecast when an outbreak will not occur. However, when more than fifty were caught in the suction traps, outbreaks did not necessarily occur, because the suction trap catch needs to be interpreted in light of other factors such as the time of year, crop growth-stage,

sowing date and occurrence of natural enemies (Dewar, 1982).

The autumn migration of *Rhopalosiphum insertum* (Walker) to its woody winter host, apples (*Malus* spp.) is an example in which the size of the suction trap catch relates more directly to the aphid population on the host plant. Large numbers of the autumn migrant morphs (gynoparae and males) are produced in the autumn and caught by the suction traps. On reaching a host plant, gynoparae produce apterous oviparae which mate with males after they arrive later in the autumn. The number of oviparae and subsequently eggs, on *Malus* spp. during the autumn, is proportional to the size of autumn suction trap catches of gynoparae. The size of the fundatrix generation which causes the damage in the spring is proportional to the number of eggs laid. Thus, the size of the suction trap catches of gynoparae during the autumn are used to identify springs when inspections of apple trusses should be especially rigorous (Light, 1980).

Two aphid species are regarded as important vectors of BYDV during the autumn in eastern England: *R. padi* and *S. avenae* (Plumb, 1986). Data from the suction traps revealed the very large autumn migrations of *R. padi*, which overwinters both holocyclically on its woody primary host, *Prunus padus*, which is uncommon in eastern England, and anholocyclically on Gramineae (Taylor, 1982). The aphid

morphs which seek *P. padus* (gynoparae & males) fly at a higher height than the exules seeking graminaceous host plants, and are therefore caught more efficiently by suction traps. In contrast, *S. avenae*, which is considered to mainly overwinter anholocyclically on Gramineae (Hand, 1989), although it may show a considerable degree of holocycly in the north (Newton & Dixon, 1988), is seldom common in suction trap catches during the autumn (Plumb, 1986). Nevertheless, it was hypothesised that the size of the suction trap catches of these two BYDV vectors might be related to aphid infestations in nearby autumn-sown cereals. Given knowledge of the relationship between sowing date and BYDV incidence, and the effectiveness of insecticides applied during late October/early November at controlling virus spread introduced by alatae, it seemed that it should be possible to assess the risk of BYDV during the migration of aphids in September and early October, and use this assessment as the basis of a decision to apply an appropiate pesticide (Plumb, 1986).

The use of suction trap data to predict the need for an application of a pesticide to control BYDV spread was only valid if it could be assumed that virus transmission was directly correlated with aphid numbers (Plumb, 1986). During the summer and autumn of 1969-73 (Plumb, 1976), and during all autumns since then (Plumb, 1986), live aphids have been caught in a low level trap at Rothamsted, and tested for their ability to transmit BYDV to indicator

plants, to establish whether this assumption was correct. The conclusion was that the assumption was false and that the proportion of alate aphids that transmitted BYDV to indicator plants fluctuated from week to week and between seasons in different years, but that no more than 11.5% of the annual catch of any species transmitted BYDV (Plumb, 1986).

The relationship between numbers of alate aphids trapped and the number able to transmit BYDV was also investigated in west Wales from 1970-79 where BYDV is a problem in autumn-sown cereals (A'Brook & Dewar, 1980). They concluded that both the numbers and percentage infective of BYDV vectors in west Wales differ from those described by Plumb (1976) for eastern England. More infective vectors were caught during the autumn in west Wales in contrast to eastern England where most were caught in the summer, and more of them were comprised of *Rhopalosiphum* spp. (both *padi* and *insertum* were important vectors). Also, the proportion of trapped aphids that transmitted BYDV was greater in west Wales although there were also large between year differences. A'Brook & Dewar (1980) concluded that epiphytotics of BYDV in autumn-sown cereals in west Wales were due to large numbers of infective vectors, particularly *Rhopalosiphum* spp. A' Brook (1981) later developed mathematical models based on weather data that could forecast the numbers of *Rhopalosiphum* spp. caught by suction traps during the autumn, by 1 September,

thereby obtaining an estimate of the numbers of infective vectors.

Thus, it was established that the proportion of alatae flying in the autumn that were able to transmit BYDV to indicator plants differed both between years and regions. Experiments were conducted at Rothamsted and Woburn to test whether a forecasting scheme that considered both the number of migrating aphids as measured by the suction traps, and the proportion which were able to transmit BYDV as measured by trapping with a low level trap, gave a better estimate of subsequent crop infection than numbers of migrating aphids alone. The Infectivity Index was devised to integrate these two factors:

Infectivity Index =	No of aphids caught by suction trap	x	proportion that transmit BYDV at 1 m

An index was calculated separately for *R. padi* and *S. avenae*, for each week of the autumn migration starting the week containing 1 September. This method enabled the risks to crops of different sowing dates to be assessed, because each crop accumulated all the weekly Infectivity Indexes from its emergence date (often estimated from its sowing date) until the end of the autumn (Plumb, 1986).

"The results of the regression of yield response to an autumn pesticide on the Infectivity Index of each crop gave a significant correlation for all sowing dates, r = 0.51 (P

< 0.01) but the correlation was better when only September sown crops were considered r = 0.68 (P < 0.01)" (Plumb, 1986).

As a result of these experiments, an accumulated Infectivity Index value of 50 was identified as a threshold level on which to base a decision to spray. Thus, the concept of the Infectivity Index was introduced in 1980. The scheme has since been implemented at other sites throughout Britain, some of which concurrently run field-trials comprised of sequentially drilled plots, to provide validation for the Infectivity Index. At some of these other sites, it has become clear that different thresholds are required and/or modifications made, to the calculation of the Infectivity Index, so as to exclude the holocyclic component of the *R. padi* catch whose contribution to BYDV spread is uncertain (McGrath and Bale, 1989; Gillet *et al.*, 1990; Kendall & Chinn, 1990).

At Long Ashton, a different approach described as a "crop vector index" is used to measure the amount of BYDV spread. It is able to utilise data from irregular or infrequent aphid samples in crops, and therefore uses both numbers of alatae, and the proportion infective, and the numbers of apterae to determine the accumulated infectious aphid-days a crop has been exposed to (Kendall & Chinn, 1990).

1.8 **Aphid lifecycles**

There are two main types of aphid lifecycle: holocyclic and anholocyclic. *R. padi* exhibits both types.

Holocyclic *R. padi* overwinters as an egg on *Prunus padus*, its primary host plant. Two apterous generations feed on *P. padus* in the spring, which are followed by a winged generation, the emigrant. The host plant preference of emigrants changes after the final moult, such that adult emigrants prefer graminaceous host plants which are termed the secondaries. Several parthenogenetic generations are passed on Gramineae before shortening daylength and lower temperatures induce the production of gynoparae and males. Gynoparae migrate to *P. padus* first where they give birth to the wingless oviparae. The males arrive later, and mate with the oviparae which subsequently lay the overwintering eggs (Dixon & Glen, 1971; Leather, 1988).

Anholocyclic Some aphid species breed parthenogenetically throughout the year on their secondary host plants, e.g. *S. avenae* in southern Britain on Gramineae (Hand, 1989). *R. padi* too may occur as anholocyclic clones on Gramineae throughout the year. Anholocycly is considered to be derived from holocycly when the primary host plant is dropped by an aphid species (Kennedy & Stroyan, 1959).

1.9 **Biology, meteorology and education**

It is common knowledge that biology and meteorology are closely-related: the association between the major climate and vegetation belts being a global example. The

activity of all poikilotherms is dependent on temperature, and the relationships between dates of first suction trap catch of cereal aphids and weather data in Britain illustrate this statement (Turl, 1980; Walters & Dewar, 1986; Harrington *et al.*, 1990).

Biology has long been a part of Britain's education curriculum, whereas meteorology has only recently become a part of the science curriculum in England & Wales, and the environment curriculum in Scotland (Duncan, C., 1991). These must be studied by all pupils, and this must bode well for biology.

1.10 **Meteorology and aphids**

Weather was found to be a factor in the epidemiology of the aphid-transmitted virus diseases of sugar beet (section 1.5) and potato (section 1.6). Weather data has been a factor in the forecast equations which are used to assess the risk from the virus diseases of these two crops, to identify whether or not insecticide treatments are required (Woodford *et al.*, 1977; Harrington *et al.*, 1989).

A major objective of this thesis was to examine the extent to which BYDV incidence in autumn-sown cereals can be explained, and perhaps, forecast on weather data alone. Weather may affect both aphid numbers and aphid activity (Taylor, 1963). Given the association of BYDV with mild winters (Oakley, 1989), this was partly achieved by relating incidence and extent of BYDV infection in winter

barley crops in the three years of the study, to preceding winter weather data. Another approach was to analyse suction trap catches of alate cereal aphids using weather data up to one year previous. In these analyses, the dependency of aphid flight on current weather conditions was recognized (see section 2.4 and Chapter 3).

1.11 **General aims of the BYDV project**

1) To evaluate the use of II as a method of forecasting BYDV risk to autumn-sown cereals in south-west and central Scotland by monitoring a number of winter barley crops in different regions over three seasons.

2) To develop new methods of forecasting BYDV risk to autumn-sown cereals.

3) To identify the factors that determine the incidence of *R. padi*-transmitted BYDV.

4) To identify the factors that determine the incidence of *S. avenae*-transmitted BYDV.

5) To identify the factors that determine the regional differences in the incidence of BYDV in south-west and central Scotland.

6) To identify the factors that determine the incidence of BYDV which is primarily introduced locally by apterae.

Attempts were made to ascertain the whereabouts of cereal aphids on farms throughout the year, and to

determine the extent of BYDV infection in Gramineae other than cereal crops. Such knowledge may be necessary to a complete understanding of BYDV epidemiology.

CHAPTER TWO

General Materials and Methods

2.1 **The aphids**

Six species of cereal aphid were encountered during sampling from June 1988 to May 1991. Vagrant aphids were occasionally sampled but, in this thesis, the word aphids refers to one or more of the following species: *Metopolophium dirhodum* (Walker), *M. festucae sensu stricto* (Stroyan), *Rhopalosipum insertum* (W.), *R. padi* (Linnaeus), *Sitobion avenae* (Fabricius) and *S. fragariae* (W.). Nomenclature follows that of Hille Ris Lambers (1966).

2.1.1 **Aphid identification**

Aphids from ryegrass pasture in 1988 were removed to the laboratory prior to identification. Experience gained during this season enabled most subsequent identification to be done in the field with a hand lens. When identification was uncertain using a hand lens, or when aphids were too numerous to count and identify in the field, identification was done in the laboratory. Alatae of uncertain identity and many alate *Rhopalosiphum* spp. were identified by preparing a slide for microscope study by transmitted light. Most apterae were identified in the field but any of uncertain identity were usually identified with the aid of a binocular microscope or rarely by preparing as a slide.

Difficulties were encountered in identifying apterous *Sitobion* to species. In one habitat, "wild grasses in hedge bottoms", *fragariae* was certainly present (Chapter 6),

otherwise, it was generally assumed that the species involved on winter barley, grass weeds in cereals and ryegrass pastures was *avenae*.

2.1.2 **Aphid collection**

Aphids were collected from fields throughout aphid sampling work for two purposes; identification and testing for the ability to transmit BYDV to indicator plants.

For transport to the laboratory, a fine paint brush was used to transfer aphids from their host plants to glass tubes (7.1 cm long and 1.8 cm in diameter). No substrate was provided except for 1st and 2nd instar nymphs which were transferred on the leaf on which they were found. From April to September 1988-90 (when insolation was strong), on leaving the field, the aphids were transferred from glass tubes to Petri-dishes containing damp filter paper, and placed in a chilled Dewar flask before transport to the laboratory.

2.1.3 **Aphid sampling methodology**

Aphids from a range of different habitats were sampled; ryegrass pastures, cereal fields both pre- and post-harvest and grasses in hedge bottoms. The methodology used in the first season for ryegrass pastures and winter barley crops was improved in subsequent seasons. Table 2.1 summarises the sampling procedure, frequency and duration of sampling for each habitat.

Table 2.1 Details of the aphid sampling work carried out during the three year BYDV project.

Habitat and season	No of regions	Sampling duration	Sampling frequency	Number of fields sampled	Number of sampling areas	Definition of a sampling area
Ryegrass pasture						
1988	4	Jun-Aug	monthly	17	6	1 - 1.5 m^2
1988	4	Sep	various	17	5 *or 10*	1 - 1.5 m^2
1990	5	Apr-Oct	various	22	5 *or 10*	1 - 1.5 m^2
Winter barley						
1988/89	3	Oct-Nov	weekly	5	5	tray of oat seedlings
1988/89	3	Oct-Nov	weekly	5	25	1 m^2
1988/89	6	Apr-Jun	monthly	45	10	single barley plant
1989/90	5	Sep-Nov	bi-monthly	26	10 *or 20*	1 m of drill
1989/90	5	Apr-Jun	monthly	26	10	1 m of drill
1989/90	4	Sep	various	16	10	various [a]
1990/91	3	Oct-Nov	weekly	20	10	1 m of drill
1990/91	3	Dec	monthly	20	10	1 m of drill
1990/91	3	May	monthly	20	10	1 m of drill
Hedge bottoms						
1990	5	May-Sep	monthly	-	-	single plant

numbers in *italics* denote occasional replication.

[a] various forms of stubble sampling.

Aerial aphid populations were sampled at 12.2 and 1.2 m height by Rothamsted suction traps (Macaulay *et al.*, 1988) and "commode" traps (see Chapter 11) respectively.

A total of six regions in south-west and central Scotland were visited for sampling during the course of the project. Figure 2.1 shows these regions.

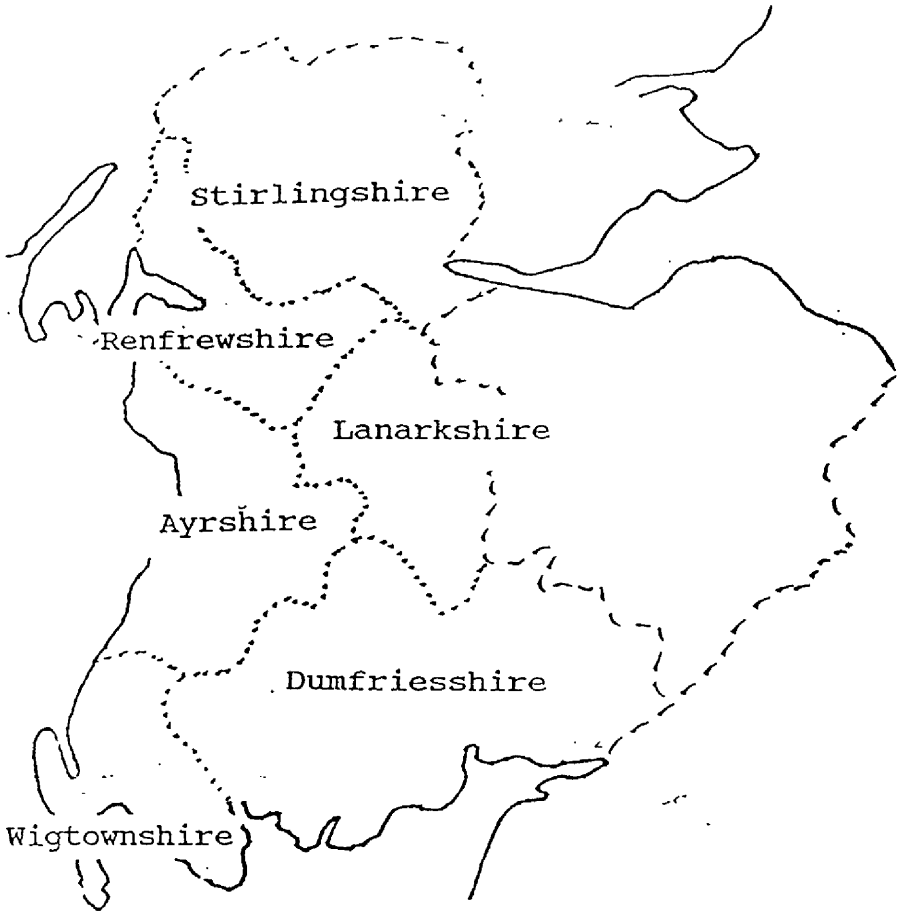


Figure 2.1 Regions of south-west and central Scotland in which aphid sampling was undertaken in the three years of study.

2.2 **The Virus**

Antisera used to detect BYDV segregated isolates into the three strains: RPV, PAV and MAV. Monoclonal antibodies to these three strains were used, therefore one isolate could react with only one of the antisera (Pead & Torrance, 1988; Torrance *et al.*, 1986).

2.2.1 **Enzyme-Linked Immunosorbent Assay (ELISA)**

2.2.1.1 **Objectives of the use of ELISA**

The technique was used to identify BYDV and the specific strain (RPV, PAV or MAV) in field collected plant material, in plant material artificially inoculated in the laboratory and in plant material to which aphids transmitted BYDV during the course of aphid transmission tests.

2.2.1.2 **Preparation of buffers**

Phosphate buffer saline with Tween (PBS-TWEEN) prepared as follows:-

80 g NaCl *
2 g KH_2PO_4 *
29 g Na_2HPO_4 *
2 g KCL *
5 ml Tween 20
2 g NaN_3
10 l distilled water

The chemicals marked with an asterisk were initially dissolved in 1 l of distilled water. Five millilitres of Tween 20 and 2 g NaN_3 were added before making up to 10 l with distilled water.

Coating buffer:- 1.59 g Na_2CO_3
2.93 g $NaHCO_3$
0.2 g NaN_3
1 l distilled water

Coating buffer was stored at 5°C.

Substrate buffer:- 2 g NaN_3 *
97 ml diethanolamine *
800 ml distilled water
4-6 ml 0.3 M HCL

After adding the chemicals marked with an asterisk to the distilled water, the pH was adjusted to 9.8 with 2 ml aliquots of 0.3 M HCL. This was made up to 1 l of buffer with more distilled water. Thus prepared, the buffer was stored at 5°C in a brown glass bottle.

Extraction buffer:- 5 g polyvinylpyrrolidone (PVP)
0.5 g albumin
250 ml PBS

A paste was made before making up to full quantity with PBS. Fresh extraction buffer was made for each day's use and not stored.

2.2.1.3 **Healthy plant samples**

For healthy oat samples, four cultivars were used: Coast Black, Maris Tabard, Dula and Pennal. The seed of the two former cultivars became unobtainable, therefore Dula (recommended by IACR Rothamsted) was used until comparisons with other oat varieties identified Pennal as a good indicator plant. For healthy barley samples, three cultivars were used according to the availability of seed:

Igri, Vixen and Magie. For all grass samples collected from winter barley fields and hedge bottoms, perennial ryegrass was used as the healthy control.

2.2.1.4 **Arrangement of samples on immunological plates**

Three Nunc II immunological plates (Gibco Ltd) were used in each test, one for each BYDV strain: RPV, PAV and MAV. Each sample was placed in duplicate wells in each immunological plate, one above the other within one column. The first column (outer wells) was always the "blank". Initially, other outer wells of each immunological plate were not used for test samples, thus 26 samples were tested in each plate. In later tests, all immunological plate wells were used, enabling 40 samples to be tested. In every test, there were three healthy samples and one known to be infected for each strain. In 1988, the known infected cereal leaf material for each strain was tested in separate duplicate pairs of wells, later they were combined in one known infected sample. The healthy and the known infected samples occupied the same position on the immunological plates in each test.

2.2.1.5 **Washing of immunological plates**

PBS-TWEEN was used at all stages. During 1988, an automatic plate washer (Dynatech; Figure 2.2) was used, the soaking time between washes being set at 90 seconds. In all subsequent tests, immunological plates were washed using a

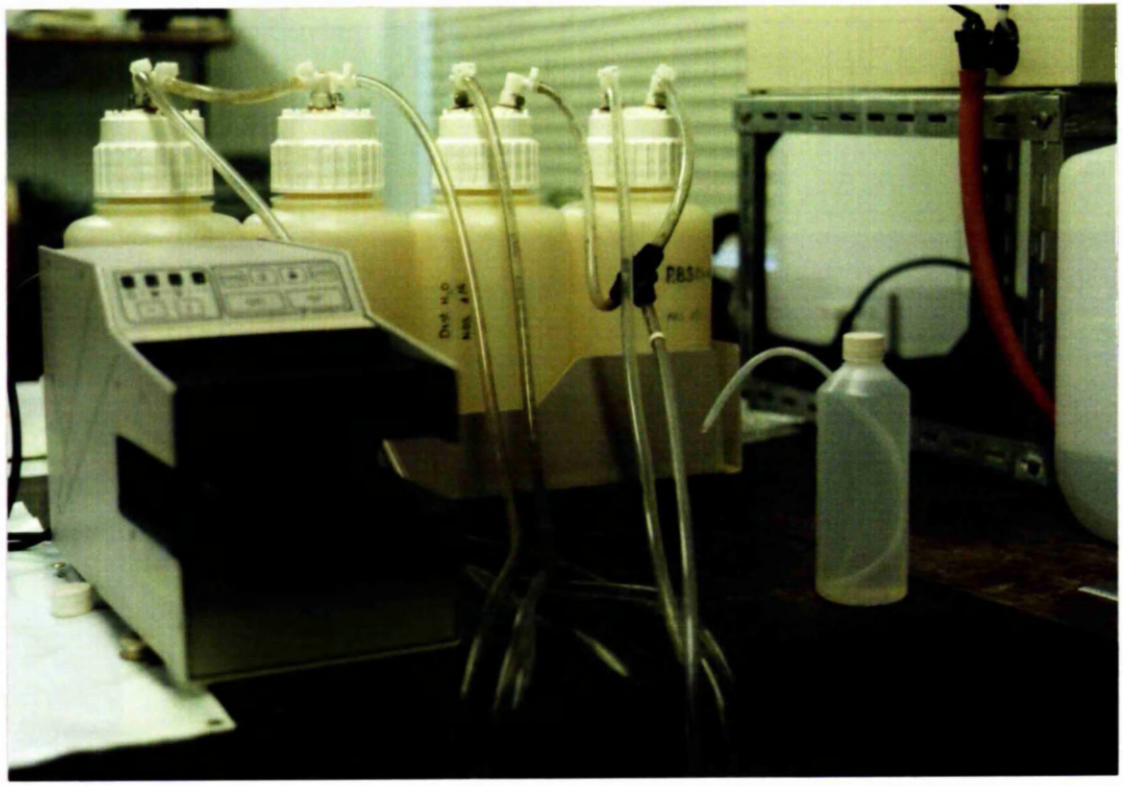


Figure 2.2 Contrasting plate washing technologies: a Dynatech automatic plate washer; and a Griffin & George 500 ml polythene squeeze washbottle.

500 ml polythene squeeze washbottle (Griffin and George Ltd.; Figure 2.2), because the automatic plate washer sometimes failed to wash all immunological plate wells properly. The washbottle produced a powerful jet of PBS-TWEEN which was directed into each immunological plate well. The immunological plate was held at an angle, the top of the plate lowest, and the top row was washed first, so that the bottle's jet entered empty plate wells. The wells were filled with PBS-TWEEN and a soaking time of 90 seconds was allowed between washes. After washing, the immunological plates were firmly tapped well-side down onto a paper towel to remove excess liquid and allowed to dry for 2 - 5 minutes.

2.2.1.6 **Methods of sap extraction**

Two methods of plant sap extraction were used in the course of the project. Initially, all samples were prepared using the "Mortar and Pestle" method of sap extraction. From April 1990 onwards after validation of the technique, the "Seam-roller" method of sap extraction was used for cereal leaf samples. The "Mortar and Pestle" method was used for all grass samples.

Mortar and Pestle method One gram of leaf tissue was cut into small pieces (< 1 cm^2) and placed in a mortar. Liquid nitrogen (enough to half-fill the mortar) was added and the leaf material ground to a fine powder. Extraction buffer (5 ml) was added and the sample ground for a further 45

seconds. The macerated sample was filtered through a square of cheesecloth (10 x 10 cm) and the solid residue discarded. The filtrate was shaken prior to being pipetted into the immunological plates.

Seam-roller method One complete leaf (or part leaf in the case of large leaves) was placed in a clean plastic bag (12 x 6 cm), and approximately 1.7 ml of extraction buffer added. Plant sap was extracted by compressing the leaf with a seam-roller, until the leaf appeared semi-transparent. The solution was then transferred to a centrifuge tube and shaken, before being pipetted into the immunological plates.

Validation of seam-roller method of sap extraction The method was recommended by Dr I. Barker (Central Scientific Laboratory, MAFF, Harpenden), who uses it routinely to test for BYDV in cereal leaves. Therefore, a thorough experimental assessment of the technique was not considered necessary. Initially, longitudinal strips of the same leaves were tested using the two methods. Comparative results were obtained. The performance of the "Seam-roller" method was further examined by using it to detect BYDV in field-collected yellow barley leaves which were suspected of being BYDV-infected. The intended sample was one yellow leaf from five yellow plants in each of the 26 fields surveyed for BYDV in mid-April 1990. Yellow plants were not observed in four fields, and in two others (R4 & R5), the yellowing was considered due to a cause other than

BYDV. The results of this exercise are shown in Table 2.2 In six fields, BYDV was detected in all the yellow leaves collected, in a further seven fields, it was detected in all but one sample. Absorbance values of samples giving positive ELISA tests using this technique were mainly in the range, 0.200 to 0.400. On the basis of these results, which compare quite favourably with infection levels in yellow leaf samples collected in 1989 when the "Mortar and Pestle" method of sap extraction was used, the validity of the "Seam-roller" method of sap extraction was confirmed.

Table 2.2 Validation of the "Seam-roller" method of sap extraction: testing for BYDV in five single leaves collected from each of 22 winter barley fields during mid-April 1990.

	No of samples		No of positive tests for BYDV strain		
Field	tested	infected	RPV	PAV	MAV
Dumfriesshire					
D1	5	3	-	1	2
D2	5	4	-	1	4
D3	5	5	-	-	5
D4	2	1	-	1	-
D5	5	3	2	-	2
D6	5	3	-	1	3
D7	5	1	-	-	1
Totals	32	20	2	4	17
Wigtownshire					
W1	5	3	-	-	3
W2	4	4	-	1	3
W3	5	4	4	3	-
W4	5	5	-	-	5
Totals	19	16	4	4	11

Table 2.2 continued.

Field	No of samples tested	infected	No of positive tests for BYDV strain RPV	PAV	MAV
Ayrshire					
A1	5	2	-	-	2
A2	5	4	-	1	3
A3	5	3	-	2	1
A4	5	4	-	4	1
A5	4	4	1	2	1
Totals	24	17	1	9	8
Renfrewshire					
R1	5	5	-	-	5
R3	5	5	-	-	5
R4	5	-	-	-	-
R5	5	-	-	-	-
Totals	20	10	-	-	10
Stirlingshire					
S2	3	2	-	1	1
S3	5	3	-	2	3
S3	5	4	-	4	-
Totals	8	5	-	3	4
Grand Totals	108	72	7	24	50
	%	67	7	22	46

2.2.1.7 **Stages of the ELISA technique**

The method used was based on the technique described by Clark & Adams (1977). Table 2.3 lists the stages in order of sequence and gives details of the dilution, buffers, incubation and washes for each stage. Each plate received a different treatment at the polyclonal and monoclonal stages when specific antibodies were used. At all other stages, all three plates received identical

Table 2.3 Stages of the ELISA method: the sequence of plate treatments giving the materials, buffers, concentrations, incubation times and the number of washes for each stage.

Stage	Concentration	Buffer	Incubation		No of washes after stage
			Duration	Temp °C	
Polyclonal antibodies[a]	1/1000	coating	3 hrs	37	3
Ground sample	-	extraction	16 "	5	3
Monoclonal antibodies[b]	1/750	PBS-TWEEN	2 "	20	2
Anti-rat phosphatase[c]	1/1000	PBS-TWEEN	2 "	20	2
Substrate[d]	-	substrate	50 mins	20	-

a Polyclonal antibodies:- RPV, PAV, MAV (supplied by Professor Rochow, Cornell University).

b Monoclonal antibodies:- MAC 92, MAC 91, MAFF 2 (supplied by MAFF Central Scientific Laboratory, Harpenden).

c Anti-rat alkaline phosphatase (Sigma no A9529).

d Phosphatase substrate tablets (Sigma no 104-105).

treatments.

The materials listed under "Stage", were added to the specified buffer at the specified concentration. The "blank" column received only buffer at all stages except the substrate. All immunological plate wells received the substrate solution. During incubation, immunological plates were sealed in cling-film, except for substrate incubation.

Preparation of substrate solution and determination of absorbance values Nine phosphatase substrate tablets (Sigma no 104-105) were crushed and dissolved in 66 ml of substrate buffer. This solution was added to each immunological plate well and a time interval of 5 minutes was allowed between immunological plates. After 50 minutes at room temperature, the absorbance value (405 nm) of each well was determined using a Titertek Multiscan plate reader (Flow Laboratories; Figure 2.3).

Volumes The volume of reagent added to each well differed between sap extraction methods. When samples were prepared using the "Mortar and Pestle" method, 200 microlitres of reagent were added to every well at every stage, necessitating the preparation of 18 ml volumes of reagents for each plate. When the "Seam-roller" method of sap extraction was used, 150 microlitres of reagent were added to every well, necessitating the preparation of 14 ml volumes of reagents for each plate.

Figure 2.3 The Titertek Multiscan plate-reader linked to a computer, enabling a more user-friendly output of data to be printed, using the ELISADATA program (The Scottish Office Agriculture & Food Department, Scientific Services, East Craigs, Edinburgh).

2.2.1.8 **Determination of a positive result**

Experiments were not replicated, but the two replicates per sample enabled the recognized variability of ELISA (Sutula *et al.*, 1986) to be considered in the determination of a positive-negative threshold.

Absorbance values were stored on a computer file, in the following format:-

Absorbance values

Sample type	Sample	RPV 1	RPV 2	PAV 1	PAV 2	MAV 1	MAV 2
1	1	.000	.000	.015	.045	.567	.599
3	2	.465	.389	.987	.876	.456	.567

Sample type is either 1 sample being tested
2 healthy sample
3 known infected

A threshold for each BYDV strain was determined by a MINITAB program which calculates the mean of the six healthy readings, and the "**mean** standard deviation" (sd of the two readings per sample) of all the samples tested, i.e. type 1 samples. The threshold is the mean of the six healthy absorbance values plus 3.09 x the "**mean** standard deviation" of type 1 samples. The 3.09 corresponds to a probability of 0.002 for one tail of a Gaussian distribution. If BOTH readings of a sample for a BYDV strain exceeded this threshold, then a positive result for that BYDV strain was accepted.

Several methods of determining a positive and negative threshold are currently in use by BYDV workers: twice the

mean of the healthy controls (McGrath & Bale, 1990) and the mean of the healthy controls plus thrice their standard deviation (Hill & Torrance, 1986) are two examples. These methods are unsatisfactory, mainly because the threshold is determined solely on the basis of the healthy sample absorbance readings. Hill & Torrance (1986) using the second threshold example above, observed that glasshouse grown healthy material gives lower thresholds than uninfected plant material collected from the field, thereby creating a low threshold which uninfected plant material from the field can exceed. Ideally, plant material used for the production of the threshold should be not only of the same host species, but also, of the same age, and grown under similar conditions as samples submitted for ELISA tests (Hill & Torrance, 1986; Sutula *et al.*, 1986).

The threshold used in this project avoids the practical difficulties of growing healthy material in the field and overcomes the shortcomings of the glasshouse healthy material by utilising the greater variability of the field-collected material in the calculation of the threshold. A higher threshold than a threshold determined solely on the basis of healthy plant material (Table 2.4) is obtained which uninfected plant material from the field is unlikely to exceed. However, it has the disadvantage of being influenced by the number of positive samples in the test, because the variation between readings of the same sample is greater the higher the absorbance readings.

Table 2.4 Comparison of threshold values (to determine a positive ELISA result) calculated using variability of field-collected leaf material with those based on variability of healthy material alone; data from two tests of plant material collected during BYDV project.

Sample type	mean of healthies (x)	sd of healthies (sd)	sd of type 1[a] samples (sdw)	x + (3 x sd)	x + (3.09 x sdw)
Barley leaves					
RPV	0.0295	0.0042	0.0262	0.042	0.110
PAV	0.0000	-	0.0292	0.000	0.090
MAV	0.0312	0.0346	0.0438	0.134	0.167
P. annua					
RPV	0.0142	0.0099	0.0492	0.044	0.166
PAV	0.0117	0.0152	0.0384	0.057	0.131
MAV	0.0997	0.0142	0.0353	0.142	0.209

[a] Type 1 samples are samples to be tested. The standard deviation of the two readings per sample is calculated for each sample and the mean value for a type 1 sample determined.

2.2.1.9 **Plant sampling methodology**

Winter barley, grass weeds in winter barley fields, grasses in hedge bottoms and around farm buildings were collected to determine whether or not they were infected with BYDV. The months, frequency and other details of the sampling methodology are shown in Table 2.5 along with the total number of samples tested and the method of sap extraction used.

All plant or leaf samples were placed in polythene bags (12 x 6 cm), sealed with cellotape and stored at -15 ^{o}C until required for testing.

2.3 **Methods of Analysis**

2.3.1 **Statistics**

MINITAB (Version 6.2) was used to perform the following statistical tests:-

Chi-squared	Mann-Whitney
t-tests	Kruskal-Wallis
ANOVA	Regression

2.3.2 **Multivariate analysis**

Data may consist of a large number of variables measured at a number of different sites. Multivariate analysis was developed to help understand and interpret such databases, mainly by reducing the dimensionality. This is possible, either because there are correlations between

Table 2.5 Details of the plant sampling methodology and the plant material collected from farms for BYDV testing by ELISA during the course of the project.

Habitat and season	No of regions	Sampling duration	Sampling frequency	Number of fields sampled	Number of sampling areas	Definition of a sampling area	No of samples	Method of sap extraction
winter barley								
1988/89	6	Apr-May	monthly	44	2 x 5	various[a]	377	M & P
1988/89	5	July	monthly	14	50	green leaf[b]	55	M & P
1989/90	5	Apr-May	monthly	26	5	yellow leaf	216	Seam
1989/90	5	June	monthly	8	5	yellow plant	40	Seam
1989/90	3	July	monthly	9	10	green leaf	107	Seam
1990/91	3	May	monthly	20	5	yellow leaf	100	Seam
P. annua								
1989	5	July	monthly	14	10	one plant	132	M & P
1990	5	May-Jun	monthly	9	10	one plant	176	M & P
1990	3	July	monthly	9	10	one plant	146	M & P
other grasses								
1990 hedge bottoms[c]	-	Apr-Jun	monthly	-	-	one plant	32	M & P
1990	5	May-June	various	-	50	one plant	178	M & P

[a] 1 g leaf samples taken from five patches of yellow and five patches of green plants.

[b] fifty leaves per field tested in five batches of ten.

[c] five weed grass spp. from hedge bottoms on farms.

- not valid M & P Mortar & Pestle Seam Seam-roller

variables measured at each site, or because there are correlations between the data of different sites (Jolliffe, 1990).

A number of different methods of achieving this reduction in dimensionality have been devised. Often, all that is wanted is for the data to be simplified by grouping data from sites with similar levels of variables. This is done by identifying trends in the levels of the variables and ordinating the sites in the order the trend dictates, thus sites with similar levels of variables are grouped together. Once one trend is identified, further trends can be sought by specifying that further trends must be unrelated to the trend(s) already identified. Usually, only the first two or three trends are of interest, because most variation in data is accounted for by a few explanatory variables (Jolliffe, 1990).

To understand the data, the trend must be matched to an environmental variable. There are two classes of multivariate analysis that can be used for this: indirect and direct gradient analysis.

2.3.2.1 **Indirect gradient analysis**

These techniques identify any trends in the data, which may or may not represent an environmental variable. A widely used technique of indirect gradient analysis is principal components analysis (PCA), which assumes that there are linear relationships between variables and the

environment. Principal components are therefore linear functions of the original data which represent trends in the data. The intention is to account for a high proportion of the variation of the variables at the different sites with 2 to 4 PCs (Jolliffe, 1990).

In community ecology, multivariate analysis packages that assume species have unimodal response curves (as opposed to linear) to the environment have been developed. In this thesis, two such packages have been used: TWINSPAN (Hill, 1979a) and DECORANA (Hill, 1979b). These are both based on a technique called, reciprocal averaging (Hill, 1973), which was developed for phyto-sociological studies where the data are samples of the abundance of many species (each with differing environmental requirements). A cross-calibration procedure results in a one-dimensional ordination of both species and samples. Similar samples (on the basis of the calculated sample and species scores) are therefore grouped together and separated from dissimilar samples.

TWINSPAN (Two-Way INdicator SPecies ANalysis; TWINL87)

This is a method of classification for data matrices which express attributes of individuals. It differs from many multivariate analysis packages in two important respects: firstly, only one trend is produced, and secondly, it divides the samples and species into groups on the basis of similarity. Phyto-sociological matrices can be

very large and may contain large numbers of zero values: TWINSPAN does not require the zero values in the original matrix and it does not store a secondary matrix of sample similarities. These advantages enable large data matrices to be analysed using a microcomputer version of the program (Hill, 1979a).

Users of TWINSPAN are required to enter cut-off levels, so that the data can be assigned to categories of abundance (termed "pseudo-species"). For example, if three "pseudo-species" levels are entered, 0, 1 and 5, samples with no species A are assigned "pseudo-species A" 0, others with an abundance 1 to 4 are assigned "pseudo-species A" 1, others with an abundance greater than 4 "pseudo-species A" 2. Thus, categories of abundance of species become a type of species themselves ("pseudo-species") which are necessarily related to lower abundance levels of the same species.

The major output of TWINSPAN is a two-way species-by-sample table (the refined-ordination table - it represents a trend) which identifies the number of groups, sample members of each group and the relationships between groups. In addition, the species are classified into groups on the basis of their relationships with the sample classification.

DECORANA (DEtrended CORrespondence ANAlysis; DECL87)

This analysis is an elaboration of the technique, reciprocal averaging. It overcomes a disadvantage of reciprocal averaging which is that the second and subsequent sample ordinations tend to be strongly related to the first. DECORANA avoids this by insisting not only that there shall be no correlation between sample ordinations, but also that there shall be no systematic relationship of any kind. In other words, DECORANA ignores any trends in the samples that have any similarities with trends detected earlier in the analysis (Hill, 1979b).

The program detects the four most important trends and the first three are normally studied to see whether or not they represent any known environmental variable. This is done by plotting ordination diagrams using sample scores from two of the the three trends identified by DECORANA. Ideally, groupings identified by TWINSPAN are reproduced by one of the three ordination diagrams plotted using trends 1, 2 or 3. Separation of TWINSPAN end-groups can then be explained on the basis of an environmental variable.

2.3.2.2 **Direct gradient analysis**

These techniques are obliged to match one or a combination of environmental variables which have been measured for each site, to the trends they detect in the data.

CANOCO (CANOnical Community Ordination; CANOCO 2.1)

This is an extension of DECORANA, and it seeks to relate the composition of species comminities to their environment. The trends it detects are linear combinations of environmental variables. The relative importance of different environmental variables in determining the species communities can be explored by removing the effects of environmental variables that are known to be important (usually by previous use of CANOCO), thereby separating out the residual variation for further analysis. The particular environmental requirements of a species can be identified using this facility (Ter Braak, 1986; Ter Braak, 1987).

The conventional presentation of CANOCO outputs for community ecology data is a biplot (first and second most significant trends) showing the relationships between species assemblages and environmental variables. This method is successful when the assemblages have largely different environmental requirements, but is not helpful when the environmental requirements are more similar. The latter situation applies to the aphid and BYDV data collected from winter barley crops in this thesis. The chosen method of presentation is explained in Chapter 4.

2.4 The Lamb daily weather types and PSC indices

Biologists sometimes study animals or plants in a specific locality. In these circumstances, the most relevant weather data are measured by climatological

stations in that locality. For the biologist whose field of study is more regional (e.g. west of Scotland, the UK), climatological station data are too parochial, being influenced by local topography, and their relevance diminishes with increasing distance from the station. This problem can be overcome by calculating means from a number of climatological stations scattered around the field of study, e.g. the central England temperature (Manley, 1974). This approach, although cumbersome, can provide meaningful data, but the weather at a site not contributing data to the mean could be quite unrelated. An alternative approach is to avoid site-specific climate data altogether, and work with synoptic weather patterns (i.e. the distribution of atmospheric (barometric) pressure at sea-level).

The weather over the British Isles and surrounding regions can be classified on a daily basis using the Lamb catalogue of daily weather types (Murray & Lewis, 1966). This catalogue is a slightly modified version of the original classification put forward by Lamb (1950): the latter consists of eight directional types each subdivided into three categories (e.g. westerly is subdivided into cyclonic (low pressure) westerly, straight westerly and anticyclonic (high pressure) westerly), and two nondirectional types (cyclonic and anticyclonic). In addition, there are some days on which the weather is unclassifiable under any of these types. The number of days in each month or season with each of the 27 Lamb daily

weather types can therefore be calculated.

A shortfall of the Lamb classification is that it is subjective to some extent. Data for the period 1976-89 were obtained from the Meteorological Office at Bracknell (more recent data unobtainable from this source; currently available from: The climatic research unit, the University of East Anglia).

Murray & Lewis (1966) devised the PSC indices to measure in a succinct and meaningful way the main characteristics of the synoptic situation around Britain over long periods, using the daily weather types over the British Isles identified by Lamb (1950). For a precise description of the synoptic situation around the British Isles, better techniques are available (e.g. summarising pressure data with eigenvectors; Murray, 1991). However, for the biologist who wants synoptic information of a season over a large area such as Scotland, a simple and concise summary of the synoptic situation may be all that is required. Furthermore, details such as temperature and rainfall must be easily derived from the summary, but because of the large field of study, the accuracy of the information for specific sites is not paramount. PSC indices are ideal for this purpose.

The indices are briefly described below:

P is a measure of the difference in frequency of days of progressive and blocked synoptic types over the British

Isles. It is positive when there is a bias towards progressive types. Progressive synoptic types are the westerly weather types identified by Lamb. Blocked synoptic types are the non-westerly Lamb weather types.

S is a measure of the difference in frequency of southerly and of northerly type days over or near the British Isles. It is positive when the bias is southerly.

C is a measure of the difference in frequency of cyclonic and anticyclonic type days over or near to the British Isles. It is positive when cyclonic days predominate.

The indices by themselves do not have any significance unless they can be compared with some standard. Indices for the 100 year period 1869-1968, were used to produce quintile boundaries for each index in each month and for each meteorological season (Murray & Benwell, 1970). A month's classification can therefore be summarised as $P_xS_xC_x$ where x is a quint (an integer from 1 to 5, a convention used with PSC indices, R. Murray, personal communication). Months with an index of quint 3 are therefore average, and months with indices of quints 1 or 2, or 4 or 5, below and above average respectively. Experience has shown that the PSC indices are very useful as parameters for specifying large-scale anomalous circulations which cause long periods of unseasonable weather in the British Isles (Murray & Benwell, 1970).

Monthly PSC indices and quints were obtained from R. Murray for the period 1976-90. Seasonal indices were calculated by adding monthly indices together. Seasonal quints were obtained by allocating each seasonal index to the appropiate quint using the relevant quintile boundaries presented in Murray & Benwell (1970).

A month or season can therefore be summarised using either the Lamb catalogue of daily weather types or the PSC indices. The relationships between PSC indices, rainfall sunshine and temperature have been examined at a number of sites over Britain (Perry, 1968; Perry, 1969; Murray & Benwell, 1970; Murray, 1972), and with regional means (Central England Temperature (CET) and England & Wales Rainfall (EWR), Murray & Lewis, 1966). However, it is important to be aware that the correlations for any parameter vary between sites. For example, the P index is more related to rainfall in Scotland than in England, whereas C is significantly correlated with rainfall in each month in both countries (Murray & Benwell, 1970).

The PSC indices relate to the synoptic situation over the whole British Isles, therefore inferences made about weather in a wide field of study such as western Scotland may be more sound than those made from site-specific meteorological data. To make these inferences, an appreciation of the effects of a particular synoptic type on different regions of Britain is required by users of PSC indices and the Lamb daily weather types. It can be argued

that users of conventional weather data should also have an appreciation of synoptic weather types if inter-regional comparisons in the same time period are intended. For example, it is wrong to assume that the north always has lower temperatures than the south: this depends on the synoptic type.

Use of the Lamb daily weather types and PSC indices in aphidology These two techniques may be of use whenever information on weather of a region is required rather than on weather at a specific site. Also, the Lamb daily weather types enable spells of weather to be studied (e.g. the number of days without appreciable rain or the number of days with a certain wind direction) and for singularities of weather type at specific dates of the year to be identified (Lamb, 1950). PSC indices condense the daily information into a mean synoptic type for a period such as a month or season. This enables, for example the wettest regions to be easily identified.

Aphid flight Wind speed and temperature data are often available from climatological stations close to suction traps. However, different aphid species have different temperature take-off thresholds (Taylor, 1963) and varying methodology produces different values (Walters & Dixon, 1984). Also, it is difficult to quantify the inhibitory effect of wind speed on aphid flight and both wind speed

and temperature can vary over small distances, being greatly influenced by topography.

In contrast, the Lamb daily weather types and the PSC indices provide a neat summary of the synoptic patterns around the British Isles in a period, from which the approximate relative number of days favourable for insect flight in different parts of Britain, and the general favourability for insect flight, can be inferred. This is because parameters such as wind speed and temperature are correlated with the Lamb daily weather types. Although a precise number of days favourable for flight cannot be obtained, the favourability of different springs or summers for aphid flight are easily compared, and the most favoured regions pinpointed.

Aphid overwintering Virginoparae are less cold-hardy than eggs (Bale, 1989). In Britain, anholocyclic overwintering of aphids in cereals only occurs during mild winters (Oakley, 1989). Winters with intense freezing spells in the north, but not in the south, and *vice versa* are easily identified using PSC indices, without resorting to daily or monthly weather values at a number of sites in Britain.

CHAPTER THREE

The effects of winter and spring weather on spring aphid numbers

3.1 Introduction

A number of suction traps in England and Scotland have been in operation for at least 15 years, a few of them for more than 20 years. Their data provide a continuous record which can be analysed to determine the effects of weather on the numbers of alatae of an aphid species, which should be related to the number of aphids of that species on its host plants (Tatchell & Woiwod, 1990).

It is necessary to understand the factors affecting spring suction trap catches if they are to be related to the numbers of aphids on host plants. In the context of BYDV, it is desirable to know the numbers of cereal aphids overwintering anholocyclically on autumn-sown cereals.

The sporadic incidence of BYDV in Britain is in part due to variations in the severity of winter weather (Oakley, 1989) which affects the extent of anholocyclic overwintering by aphids in cereals. Aphids overwintering in the viviparous state (anholocycly) are much less cold-hardy than eggs (holocycly (Bale, 1989)), and in countries such as Sweden where winters are very cold, anholocyclic overwintering of aphids in cereal crops is rare (Kurppa *et al.*, 1989). By studying the numbers of alatae of anholocyclic cereal aphid species caught by suction traps in the spring, the regional distribution and extent of overwintering of aphids in cereals can be crudely assessed.

The number of aphids in suction trap samples is

influenced by four main factors: seasonality; the effect of weather on aphid flight; the effect of wind speed on trapping efficiency; and the reservoir of alatae available (Taylor, 1962; Dewar, 1982; Tatchell, 1982). The two meteorological variables that are most critical to aphid flight are temperature and windspeed (Dewar, 1982). There is a species-specific temperature threshold below which insects are unable to take-off (Taylor, 1963), and a lower one below which they are unable to fly (Cockbain, 1961). Walters & Dixon (1984) determined median take-off thresholds for *S. avenae*: using daily suction trap data and air temperature recorded in a Stevenson screen, it was determined to be 16^{o}C, whereas in the laboratory, it was 19^{o}C. When temperature was not limiting, high winds were found to delay but not to inhibit take-off both in the field and in the laboratory. All aphids eventually flew, even from favourable hosts. When conditions for flight are favourable, trap catches must be limited by the number of aphids flying in the vicinity of the trap.

Aphid problems in British crops during the spring often follow early crop colonisation associated with mild winters (Harrington *et al.*, 1990). Several workers have attempted to predict the date of the first aphid catch at specific suction traps to estimate the time of crop colonisation in specific localities. Winter weather data recorded at a site close to the relevant suction trap are the model predictors. For many anholocyclic pest aphid

species, good models have been produced and these have been incorporated into forecasting systems (Turl, 1982; Walters & Dewar, 1986; Harrington *et al.*, 1989). For holocyclic species such as *S. fragariae* and partially holocyclic species such as *R. padi*, fewer significant relationships have been found.

Walters & Dewar (1986) found significant relationships for *S. avenae* only in the more southerly traps of Britain, and concluded that it may overwinter holocyclically in the north. However, anholocyclic overwintering in winter barley by *S. avenae* occurred in Scotland in both 1988/89 and 1989/90 (Chapter 4). There are differences in the variability of both weather and aphid catches between the north and south of Britain, which may have influenced the relative number of significant relationships between dates of first aphid catch by suction traps and winter temperature data, obtained using regression.

3.1.1 **Climatic differences between the north and south of Britain**

It is common knowledge that the north is colder than the south of Britain. However, there are important seasonal differences in the magnitude of this temperature gradient. To obtain an accurate comparison of the climates of low ground of north and south Britain representative of the cereal growing areas, two long and synchronous temperature records are required. For this purpose, a comparison of Manley's central England temperature series (CET; Manley,

1974) and Mossman's Edinburgh data (Mossman, 1896) is the only option. The greatest difference in mean temperature is in summer (1.1 ^{o}C) and the least in winter (0.3 ^{o}C) (Table 3.1).

Table 3.1 A comparison of annual and seasonal temperatures (^{o}C) of Edinburgh and central England 1764-1896 (from Duncan, K., 1991).

	Annual	Winter	Spring	Summer	Autumn
Central England	9.1	3.6	8.1	15.2	9.4
Edinburgh	8.3	3.3	7.2	14.1	8.6
Mean difference	0.8	0.3	0.9	1.1	0.8
Difference between annual & seasonal mean difference		-0.5	+0.1	+0.3	0.0

Winter weather To anholocyclic aphids, the difference of 0.3^{o}C in mean winter temperature between central England and eastern Scotland, may be of less importance than the incidence of spells of weather when the temperature is below 0^{o}C. These spells of weather may be divided into three groups:- anticyclonic conditions with clear skies and light winds when air frosts occur nightly, but during the day, air temperatures usually climb a few degrees above freezing; northerly airstreams giving freezing temperatures day and night, especially in the north; easterly airstreams giving freezing temperatures day and night, especially in the south. The latter type of freezing weather can give conditions of freezing temperature on low ground over wide areas for long periods (Eden, 1991). The cold is most

intense on low ground in the south of Britain (Murray & Benwell, 1970), because of the short sea crossing at the southern end of the North Sea, whilst in northern Britain, cold airstreams from either the north or the east must cross long sea stretches at temperatures several degrees above $0^{o}C$.

Winter temperature data for the period 1976-90 (obtained from the Monthly Weather Report) from three sites representative of the major cereal growing area of Scotland and three sites representative of the major cereal growing area of England, were analysed to compare the relative incidence of spells of freezing weather. These six sites (Table 3.2) were also close to a Rothamsted suction trap.

The mean winter temperature at these six sites varies from 3.4 ^{o}C at Lossiemouth and East Craigs to 4.0 ^{o}C at Writtle (Table 3.3; Appendix 1). However, in the months of January and February, the coefficients of variation (sd/mean) of mean temperature of the three English sites were greater than those of the Scottish sites (except Januaries at East Craigs). This greater variability at the English sites was further investigated by compiling rankings of the ten winter months with the lowest mean temperature at any of the six sites (Table 3.4), the greatest number of air frosts at any of the six sites (Table 3.5), and the greatest number of days with snow lying at 0900 GMT at any of the six sites (Table 3.6).

Table 3.2 Details of the six climatological stations which relate to six 12.2 m Rothamsted suction traps.

Climatological station	Altitude	Latitude	Longitude	National grid reference	Suction trap site
Lossiemouth	6	57 43N	03 20W	NJ 213699	Elgin
Dundee	45	56 28N	02 56W	NO 422313	Dundee
East Craigs	61	55 57N	03 19W	NT 183735	East Craigs
Brooms Barn	75	52 16N	00 34E	TL 753657	Brooms Barn
Rothamsted	128	51 48N	00 21W	TL 132134	Rothamsted
Writtle	32	51 44N	00 26E	TL 677069	Writtle

Table 3.3 Winter temperatures at the six suction trap sites in Britain 1976-90.

	Mean temperature °C / coefficient of variation											
Month	Lossiemouth		Dundee		East Craigs		Brooms Barn		Rothamsted		Writtle	
Dec	3.9	0.48	4.2	0.39	4.1	0.49	4.6	0.39	4.5	0.40	4.9	0.37
Jan[a]	3.0	0.53	3.1	0.58	2.9	0.72	3.3	0.67	2.9	0.76	3.5	0.63
Feb[b]	3.3	0.46	3.5	0.47	3.2	0.59	3.4	0.68	3.2	0.69	3.6	0.61
Winter[c]	3.4	0.33	3.6	0.33	3.4	0.41	3.8	0.37	3.5	0.40	4.0	0.33

t-test between the English and Scottish sites:

coefficients of variation:

[a] t = -1.12, df 4, N.S. [b] t = -3.14, df 4, P = 0.035

mean winter temperature:

[c] t = 1.8, df 4, N.S.

coefficient of variation (sd/mean)

Table 3.4 Ranking of the ten coldest months at the six climatological stations.

Site	Month	Mean monthly temperature °C
Rothamsted	February 1986	-2.2
Brooms Barn	February 1986	-1.6
Writtle	February 1986	-1.3
Rothamsted	January 1979	-1.3
East Craigs	December 1981	-0.8
Brooms Barn	January 1979	-0.6
Writtle	January 1979	-0.3
Rothamsted	December 1981	-0.3
Brooms Barn	December 1981	-0.3

Table 3.5 Ranking of the ten frostiest months at the six climatological stations.

Site	Month	No of days with air frost
East Craigs	January 1979	27
Rothamsted	January 1979	27
Lossiemouth	December 1981	26
Brooms Barn	February 1986	25
Rothamsted	February 1986	25
Brooms Barn	January 1979	24
Writtle	January 1979	24
Rothamsted	January 1985	24
Brooms Barn	January 1985	24
Writtle	February 1986	24

Table 3.6 Ranking of the ten months with the greatest number of days with snow lying at 0900 GMT at the six climatological stations.

Site	Month	No of days with snow lying
Rothamsted	February 1986	22
Brooms Barn	December 1981	22
East Craigs	February 1986	21
Rothamsted	January 1979	21
Dundee	February 1986	20
Dundee	January 1984	19
Dundee	January 1979	18
Writtle	January 1985	18
Writtle	February 1986	18
Dundee	January 1982	17

One, two and five Scottish entries feature in the rankings of mean temperature, frost days and snow lying days respectively. The relatively high altitude of Rothamsted (128 m), the low altitude of Lossiemouth (6 m), and the relative proximity of the North Sea to the Scottish sites will have affected these rankings to some extent. However, the main factor that probably accounts for these rankings is the incidence of freezing spells of the easterly type, which result in very low temperatures in southern Britain. Evidently, the mean winter temperature difference of 0.3 ^{o}C between the north and south of Britain glosses over within site variation in the winter weather of Britain which should have important implications for anholocyclic overwintering of cereal aphids.

Spring weather The difference of 0.9°C in the mean spring temperature of north and south Britain (Table 3.1) could have implications for both aphid population growth in cereals and aphid flight, the latter because each species has a minimum temperature threshold below which they are unable to take-off (Taylor, 1963).

The mean daily maxima at the six sites for the months April to June are shown in Table 3.7 (Appendix 2). In all three spring months, the three English sites had greater mean daily maxima than the Scottish sites, indicating that the difference between mean daily maxima between the north and south of Britain is greater than the difference between sites of either region. Mean spring daily maxima generally decreased with increasing latitude, the value of Writtle being 3°C above that of Elgin. The coefficients of variation varied only a little between sites, and the values were the same at all six sites in the spring as a whole.

3.1.2 **Differences in the spring suction trap catches of England & Scotland**

More cereal aphids in spring are caught by the English suction traps relative to those of Scotland (Table 3.8; Appendix 3). In both May and June, and in both countries, *R. padi* and *S. avenae* were generally more numerous than *M. dirhodum* and *S. fragariae*.

Table 3.7 Spring temperatures at the six suction trap sites in Britain 1976-90.

Maximum temperature / coefficient of variation

Month	Lossiemouth		Dundee		East Craigs		Brooms Barn		Rothamsted		Writtle	
Apr	10.2	0.13	10.8	0.13	10.7	0.13	11.8	0.12	11.7	0.12	12.4	0.12
May	13.6	0.10	14.0	0.08	14.1	0.09	15.8	0.10	15.7	0.10	16.5	0.10
Jun	15.8	0.08	17.1	0.07	16.9	0.07	18.7	0.10	18.6	0.10	19.5	0.09
Spring[a]	13.2	0.06	14.0	0.06	13.9	0.06	15.4	0.06	15.3	0.06	16.2	0.06

t-tests between the mean daily maxima of the English and Scottish sites:

[a] t = 5.1, df 4, P = 0.007

Table 3.8 Mean numbers of cereal aphids caught by the English and Scottish suction traps in May and June 1976-90.

	Numbers of aphids							
	May				June			
Site	Md	Rp	Sa	Sf	Md	Rp	Sa	Sf
Elgin								
Mean	3.6	3.3	2.5	0	4.3	44	61	3.1
cv	3.6	3.3	3.5	-	2.8	3.3	3.7	2.5
Dundee								
Mean	1.2	5.2	7.1	0.1	17	67	198	2.9
cv	3.0	2.5	3.5	3.0	1.5	2.1	3.7	1.4
East Craigs								
Mean	5.5	29	5.9	0.5	24	176	124	6.4
cv	2.4	1.7	3.2	1.4	22	2.6	3.5	1.3
Brooms Barn								
Mean	10	47	30	3.3	155	214	387	15
cv	2.2	2.0	1.9	1.9	1.8	1.8	1.9	1.4
Rothamsted Tower								
Mean	11	54	31	2.9	126	145	291	16
cv	2.4	2.3	1.8	1.4	2.0	2.4	1.7	0.8
Writtle								
Mean	24	105	53	11	449	240	609	26
cv	2.2	2.6	1.5	1.5	2.8	1.9	2.2	0.7

Md *Metopolophium dirhodum* Rp *Rhopalosiphum padi*

Sa *Sitobion avenae* Sf *Sitobion fragariae*

cv coefficient of variation (sd/mean)

Table 3.9 Differences between the spring aphid totals of England & Scotland 1976-90 (England totals minus Scotland totals).

	Numbers of aphids							
	May				June			
Spring	Md	Rp	Sa	Sf	Md	Rp	Sa	Sf
1976	17	143	108	11	6363	2427	9924	36
1977	2	10	14	1	20	28	118	16
1978	2	-5	-1	0	21	32	16	26
1979	3	6	0	0	6	13	0	27
1980	-2	-70	82	12	0	-54	1415	43
1981	-1	48	122	29	-2	187	142	51
1982	14	10	52	6	284	-23	297	28
1983	5	9	40	0	138	254	1029	70
1984	0	-4	4	1	282	6	1909	45
1985	2	17	7	1	50	-15	83	41
1986	-1	0	0	0	26	-28	2	12
1987	8	-28	25	3	118	-124	274	17
1988	21	158	496	74	67	941	1898	144
1989	189	1561	377	81	1559	1085	-3841	98
1990	276	658	149	27	1332	-65	298	17
Mean	36	168	98	16	684	311	904	45
cv	2.5	1.5	1.6	2.3	2.2	3.1	0.8	2.4

Md *Metopolophium dirhodum* Rp *Rhopalosiphum padi*

Sa *Sitobion avenae* Sf *Sitobion fragariae*

cv coefficient of variation

Occasionally, the Scottish suction trap catches are greater than those of England (negative values in Table 3.9) although 12 of the 15 negative values were between -1 and -30. More individuals of *S. fragariae* were always caught by the English suction traps relative to those of

Scotland. The few occasions when the Scottish suction traps caught more *M. dirhodum* than the suction traps of England involved no more than two individuals. Greater differences in the size of the English and Scottish suction trap catches occurred in the month of June (Table 3.9) when the mean numbers of aphids caught are greater (Table 3.8).

3.1.3 **The aims of the analyses**

Given that both winter and spring weather may influence spring suction trap catches, the spring catches of cereal aphids at the six sites (Table 3.8) were analysed to ascertain the relative importance of winter and spring weather, and whether or not their importance depends on the suction trap site (i.e. the north or south of Britain). Conventional weather data from specific sites (Table 3.2) and PSC indices (relating to the whole British Isles; section 2.4) were used in the analyses.

3.2 **Methodology**

Aphid data The six suction trap sites (Table 3.2) were chosen because they had been in operation since the mid-1970s, and because they were representative of the major cereal growing areas of England & Scotland. The data for the period 1976-90 were obtained from the *Aphid Bulletin* produced by RIS. These data are not always complete or verified. However, the purpose of the analysis was to compare the magnitude of the cereal aphid catches in the

spring months (the aphid spring was the months: April to June) at the six sites using multivariate analysis. For this purpose, the data presented in the *Aphid Bulletin* were adequate.

Monthly totals (April to June) were calculated for *M. dirhodum*, *R. padi*, *S. avenae* and *S. fragariae* for each year from 1976-90 for the six suction traps.

Weather data Monthly values of mean daily temperature (December to February), number of days with air frost (December to April), number of days with snow lying at 0900 GMT (December to March) and maximum daily temperature (April to June) were obtained from the *Monthly Weather Reports* for the period December 1975 to June 1990 for the six climatological stations (Table 3.2).

PSC indices were calculated (section 2.4) for each meteorological winter (December to February) and for each meteorological spring (March to May) in the years 1976-90.

The remaining methodology of these analyses is described within the Results (section 3.3), because of their *a posteriori* nature.

3.3 **Results**

3.3.1 **The distribution of cereal aphid suction trap catches during the spring using CANOCO**

The 12 aphid totals (4 aphid species x 3 months) at each site in each year were the samples (a total of 90).

CANOCO was used to ordinate the sites, so that sites with relatively large aphid catches in April and May were at one end, and sites with no aphids early in the spring and many aphids in June, were at the other end. Because weather variables in the same month are often correlated, separate analyses were carried out on the monthly values of mean daily temperature, number of days with air frost, number of days with snow lying at 0900 GMT and maximum daily temperature.

Of the 90 samples, only 33 were deemed *active* (i.e. they qualified to be included in the ordination) by CANOCO, because of the absence of aphids in April and May in most years at some sites, and the absence of aphids at all sites in all three months in a few years (e.g. 1979). Fewer Scottish samples (6) were deemed *active* than English samples, because of the lower trap catches of Scotland (Table 3.8).

The eigenvalue of the first trend identified by CANOCO in each of the separate analyses (Table 3.10) indicates the relative importance of the four types of weather parameter to the spring aphid catches at the six sites. Within an analysis, the weather variable most related to environmental axis 1 (i.e. the one with the highest correlation coefficient in the Correlation Matrix of the CANOCO output) is most related to the first trend. As expected, low values of the two temperature parameters and

high values of the frost and snow parameters were associated with few aphids in April and May, and many aphids in June. Clearly, the number of March days with snow lying is the most important parameter.

Table 3.10 Eigenvalue of the first trend in each CANOCO analysis of the spring aphid totals (33 samples) at the English and Scottish sites.

Parameter with highest correlation coefficient	Month	Eigenvalue
Mean daily temperature	February	0.261
No of air frosts	December	0.201
No of days with snow lying at 0900 GMT	March	0.631
Daily maximum temperature	May	0.237

The importance of these four parameters was investigated further by examining their values in the years (1977, 1978, 1979 & 1986) when few aphids were caught in suction traps at any of the six sites during the spring (which were therefore deemed *not active* by CANOCO [Table 3.11]).

All four years had at least one cold winter month with frequent frost, and three also had cold springs. These findings suggest that the importance of these four weather parameters (Table 3.10) applies to the 90 samples and not just to the 33 deemed *active* by CANOCO.

Table 3.11 Features of the winter and spring of four years in which few cereal aphids were caught (samples deemed *not active* by CANOCO) by the English and Scottish suction traps during the period April to June.

Year	Features
1977	Cold, frosty and snowy December & January. Cold spring.
1978	Cold and frosty January & February. Cold spring.
1979	Cold, frosty and snowy January & February. Snowy March. Cold spring.
1986	Cold, frosty and snowy February.

The spring parameter, mean daily maximum temperature in May, is different from the winter weather parameters. In theory, if samples from sites with mean daily May maxima below the 1976-90 average (at that site) are excluded, the relative importance of the winter weather parameters should be clearer. This is because cool Mays are likely to have a greater number of days when the temperature is below the minimum temperature threshold for take-off (Taylor, 1963). This theory was tested by three further CANOCO runs (again, a separate analysis for each weather parameter - the number of active samples was reduced to 21 by the exclusion of these samples). The eigenvalues of the first trend of each of these three analyses (Table 3.12) were lower and more similar to each other than those obtained when samples with cold Mays were included.

Table 3.12 Eigenvalue of the first trend in each CANOCO analysis of the spring aphid totals at the English and Scottish sites after samples with cold Mays were excluded (21 samples).

Parameter with highest correlation coefficient	Month	Eigenvalue
Mean daily temperature	December	0.158
No of air frosts	March	0.211
No of days with snow lying at 0900 GMT	January	0.120

The greater similarity of eigenvalues in Table 3.12 might indicate that cold weather in any winter month (December to March) is critical, in contrast to the previous analyses which identified cold late-winter months as being most important (the number of March snow days and mean temperature in February). However, a March parameter, the number of days with air frost, again had the highest eigenvalue.

In view of the greater eigenvalues in the analyses in which samples with cold Mays were included (Table 3.10), a further CANOCO run (33 samples) was made with the following three weather parameters which were associated with the greatest eigenvalues: number of days with snow lying in March, February mean temperature and the mean daily maximum temperature in May. The latter two weather parameters accounted for 80% of the variation of the first trend (eigenvalue 0.243) in the spring aphid data (number of days with snow lying in March was omitted by CANOCO

because it had negligible variance).

Summary of section 3.3.1 Both cold winter weather (low temperature, frost and snow) and low temperatures in May accounted for the small spring suction trap catches of cereal aphids. There was a tendency for late winter weather variables to account for more variation in the aphid data than early winter variables.

3.3.2 **The classification of spring cereal aphid totals by TWINSPAN**

In this analysis, data of four cereal aphid species were pooled in the same TWINSPAN "sample" (i.e. a spring), because the purpose was to examine whether or not climatic differences between the north and south of Britain affected spring suction trap catches. Data of single cereal aphid species might be affected by regional differences other than climate. For example, spring catches of *R. padi* might be affected by the differing distribution of *P. padus* between the north and south of Britain.

The four aphid species totals in each of May and June (the April data were excluded because in most years, no aphids were caught) at the three English suction trap sites were added together to create monthly England totals for each cereal aphid species for May and June of each year 1976-90. Comparative Scotland totals were created from data of the three Scottish suction trap sites. The 15 samples grouped by TWINSPAN were the England & Scotland aphid

totals in both May and June of 1976-90 (16 TWINSPAN "species" - 4 aphid species totals in both May and June for each country). The "pseudo-species" setting of TWINSPAN was set to create 6 categories (Table 3.13).

The PSC indices of the preceding winter, the current spring and the current May (CANOCO identified mean daily maxima in May as being most critical to the spring aphid catches - section 3.3.1) of each of the springs 1976-90 are shown in Table 3.14.

The four TWINSPAN end-groups were pooled to form two new groups: group A representing years in which there were many cereal aphids caught by the suction trap catches of both countries in spring, and group B representing years in which there were fewer cereal aphids caught by the suction trap catches of both countries in spring. Using contingency tables which showed the distribution of PSC quints in the preceding winters and current springs of the years in each group (A & B), similarities in preceding winter and current spring weather were sought for years with high or low cereal aphid catches (Tables 3.13 & 3.15).

Springs in which there were many cereal aphids caught in both England & Scotland (group A - Table 3.15) tended to be preceded by winters with a high P quint (i.e. very progressive synoptic types - westerly winds more frequent than normal) and a high S quint (i.e. southerly winds much more frequent than normal).

Table 3.13 TWINSPAN refined-ordination table after 3 divisions; spring aphid totals of England & Scotland, 1976-90.

"Pseudo-species" levels

Spring

			Year	1 1 9 8 0 1	1 1 9 9 7 2	1 1 9 8 7 7	1 1 9 8 8 2	1 1 9 8 7 3	1 1 9 9 8 4	1 1 9 7 8 8	1 1 9 9 7 9	1 1 9 7 8 5	1 1 9 9 8 6	1 1 9 9 6 6	1 1 9 9 8 8	1 1 9 9 7 9	1 1 9 9 8 0	
ENG	MAY	Sf		2	2	1	1	1	-	1	-	-	1	-	2	2	2	2	00
SCO	MAY	Rp		2	2	1	2	2	1	1	1	-	-	-	2	1	3	3	00
SCO	MAY	Sa		1	2	-	-	-	-	1	1	-	-	-	1	1	3	1	00
ENG	JUNE	Sf		2	2	2	2	2	2	2	2	2	2	2	2	3	3	2	0100
ENG	MAY	Sa		2	3	2	2	2	2	1	-	-	1	-	3	3	3	3	010100
SCO	MAY	Sf		1	-	-	-	-	-	-	-	-	-	-	1	1	1	1	010100
SCO	MAY	Md		1	2	-	1	1	-	-	1	-	-	1	1	1	3	1	010100
ENG	JUNE	Rp		2	3	2	2	2	3	3	2	2	2	2	4	4	4	3	010101
ENG	JUNE	Sa		4	3	3	3	3	4	4	2	-	2	2	5	4	4	3	010101
ENG	JUNE	Md		2	2	2	3	3	3	3	2	1	2	2	4	3	4	4	01011
SCO	JUNE	Rp		2	2	1	2	3	2	3	2	2	2	2	2	3	4	3	01011
SCO	JUNE	Sa		2	2	1	1	1	1	2	1	-	1	2	2	3	4	2	011
SCO	JUNE	Sf		2	2	-	1	1	1	1	1	1	1	1	2	2	2	2	011
SCO	JUNE	Md		2	2	-	2	1	-	-	1	1	1	1	2	2	3	3	011
ENG	MAY	Rp		1	2	2	2	2	2	1	1	1	2	-	3	3	4	3	1
ENG	MAY	Md		1	2	1	2	1	1	-	1	1	1	-	2	2	3	3	1
				0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	
				0	0	1	1	1	1	1	1	1	1	1					
						0	0	0	0	0	1	1	1	1					
						1		2			3				4				

ENG English total SCO Scottish total

Md *Metopolophium dirhodum* Rp *Rhopalosiphum padi*

Sa *Sitobion avenae* Sf *Sitobion fragariae*

"Pseudo-species" levels (numbers of aphids)

- = 0 1 = 1 to 9 2 = 10 to 99

3 = 100 to 999 4 = 1000 to 9999 5 = > 9999

Table 3.14 PSC quints of the preceding winter, the current spring and the current May of the spring cereal aphid catches 1976-90.

Quints

	Preceding winter			Current spring			Current May		
Year	P	S	C	P	S	C	P	S	C
1976	4	2	1	3	5	2	5	5	4
1977	1	3	5	3	3	4	1	2	3
1978	2	4	4	1	4	3	1	2	1
1979	1	4	4	5	1	5	5	4	5
1980	1	3	5	1	1	3	1	2	3
1981	4	1	1	1	5	5	1	5	5
1982	1	5	3	4	3	1	5	5	3
1983	4	2	2	2	3	5	1	4	5
1984	2	5	4	1	1	1	1	1	2
1985	1	3	2	1	2	5	1	2	4
1986	1	3	5	5	5	5	5	5	5
1987	1	3	2	5	5	3	3	5	3
1988	2	5	3	5	4	3	1	5	4
1989	5	5	2	4	4	4	3	3	1
1990	3	5	4	5	4	1	1	2	2

Springs in which there were fewer cereal aphids in both England & Scotland (group B - Table 3.15) tended to be preceded by winters with a low P quint (i.e. blocked synoptic types - westerly winds less frequent than normal) and a high S quint. The C quint of the preceding winter appears to be less important. Given that both the P and S indices are positively correlated with mean temperature in the winter months (Murray & Benwell, 1970), these results are consistent with the winter weather parameters found to be important by CANOCO (section 3.3.1) in respect of P, but the high S indices of preceding winters of both groups (Table 3.15) illustrates the desirability of using

Table 3.15 Contingency tables examining the distribution of PSC quints in each group (derived from TWINSPAN end-groups, Table 3.13); spring aphid totals of England & Scotland.

P quint in winter

Gp	1	2	3	4	5
A	1	1	1	2	1
B	6	2	-	1	-

P quint in spring

Gp	1	2	3	4	5
A	2	-	1	1	2
B	3	1	1	1	3

P quint in May

Gp	1	2	3	4	5
A	4	-	1	-	1
B	5	-	1	-	3

S quint in winter

Gp	1	2	3	4	5
A	1	1	1	-	3
B	-	1	4	2	2

S quint in spring

Gp	1	2	3	4	5
A	1	-	-	3	2
B	2	1	3	1	2

S quint in May

Gp	1	2	3	4	5
A	-	2	1	-	3
B	1	3	-	2	3

C quint in winter

Gp	1	2	3	4	5
A	2	1	1	1	1
B	-	3	1	3	2

C quint in spring

Gp	1	2	3	4	5
A	1	1	2	1	1
B	2	-	2	1	4

C quint in May

Gp	1	2	3	4	5
A	1	1	1	2	1
B	1	1	3	1	3

Gp Groups A is groups 1 and 4 in Table 3.13 - many aphids in spring
B is groups 2 and 3 in Table 3.13 - fewer aphids in spring

\- denotes zero

combinations of PSC indices (Murray, 1972). The Central England Temperature (CET) tends to be warmer than average when the combination of a high P and a high S quint (progressive southerly) occurs in a winter month whereas winter months in which the combination of a low P and a high S occurs are colder than average (Murray, 1972).

In the spring, high P and S quints were also found to be associated with large spring catches of cereal aphids (group A - Table 3.15), again indicating the importance of milder than average weather (Murray, 1972). Springs with fewer cereal aphids (group B) tended to have a high C quint (i.e. cooler and wetter than normal [Murray & Benwell, 1970; Murray, 1972) which is consistent with knowledge about aphid flight (section 3.1). When the weather in the month of May alone is considered, a low P quint and a high S quint are associated with large numbers of aphids in the spring (group A - Table 3.15). This combination of quints in May is associated with above average temperatures (Murray, 1972). This association is corroborated by a high proportion of Mays having a high C quint in springs with fewer cereal aphids (group B - Table 3.15). The C quint in May is positively correlated with rainfall in both England & Scotland (Murray & Benwell, 1970).

The relationships between the PSC quints and temperature (Murray & Lewis, 1966; Murray & Benwell, 1970; Murray, 1972) are supported by the mean temperature of the winters in England (mean of mean winter temperature at the

Table 3.16 Comparison of mean winter temperature and mean daily maxima in spring of the three English sites with the three Scottish sites 1976-90.

	Mean temperature °C of preceding winter		Mean daily maxima °C of current spring	
Spring	Scotland	England	Scotland	England
1976	4.9	4.4	14.8	18.1
1977	2.2	3.2	13.0	14.2
1978	2.6	3.6	13.3	14.8
1979	1.6	1.5	13.0	15.3
1980	3.5	4.4	14.6	15.9
1981	4.0	3.9	13.9	14.8
1982	2.2	2.2	14.3	16.6
1983	3.4	4.1	12.0	15.0
1984	3.6	4.0	14.1	15.2
1985	3.2	2.3	13.1	15.0
1986	2.5	2.7	13.2	15.2
1987	3.1	3.0	13.2	15.5
1988	4.4	5.0	14.2	15.7
1989	6.3	5.9	14.3	16.6
1990	4.4	6.3	14.3	16.7
Mean	3.5	3.8	13.7	15.6
cv	0.35	0.35	0.06	0.06

Regression between spring & winter temperature:

Scotland r = 0.546, df 13, P = 0.04

England r = 0.418, df 13, N.S.

Regressions between winter PS indices and winter temperature (df 13):

	Scotland:		England:	
P values	r = 0.822,	P < 0.001	r = 0.763,	P = 0.001
S values	r = 0.032,	N.S.	r = 0.253,	N.S.

Regressions between spring C indices and maximum daily temperature (df 13):

Scotland: r = 0.733, P = 0.002 England: r = 0.518, P = 0.05

3 English sites) and Scotland (mean of mean winter temperature at the 3 Scottish sites), and the mean daily maxima of the springs in England & Scotland (using the comparative figures, Table 3.16).

This is best demonstrated by the relationships (Table 3.16) between the P indices and mean temperature of the winters (1976-90) in both Scotland and England, and the C indices and mean daily maximum temperature of the springs (1976-90) in both Scotland and England.

Summary of section 3.3.2 Large spring suction trap catches of cereal aphids were associated with preceding winters and current springs with high P and S quints. Small spring suction trap catches of cereal aphids were associated with preceding winters with low P and high S quints, and current springs with high C quints. Comparisons with conventional weather data generally confirmed the established relationships (Murray & Lewis, 1966; Murray & Benwell, 1970; Murray, 1972) between PSC indices and conventional meteorological data. Therefore, in other words, mild springs which are preceded by mild winters have large suction trap catches of cereal aphids and *vice versa*. Both winter and spring weather are important to spring suction trap catches of cereal aphids.

3.3.3 The classification of differences in spring cereal aphid totals between Scotland and England by TWINSPAN

TWINSPAN was also used to group springs with similar differences in cereal aphid numbers between England &

Scotland (8 TWINSPAN "species": 4 aphid species differences in each of May and June; negative values were considered as zero - Table 3.9). The end-groups (Table 3.17) were very similar to those obtained when the spring aphid totals of England & Scotland were classified (Table 3.13) indicating that springs in which there were large differences between the aphid totals of England & Scotland were the same as those in which there were large numbers of aphids in both countries (and *vice versa*). Springs in which there were large differences in aphid numbers between England & Scotland in May were separated by TWINSPAN, from those in which there were large differences in June. The former group of years was the same as those in which there were large aphid numbers during the spring.

However, there were three years which markedly changed positions between the two TWINSPAN ordinations (Tables 3.13 & 3.17): 1983, 1984 and 1985. This indicates that in these years, the difference between the aphid numbers caught in the English and Scottish suction traps was less related to the size of the total aphid catches, relative to other years. The first two of these had springs in which low aphid numbers were caught by the Scottish suction traps, whereas in England, moderate numbers were caught. In 1985, relatively few cereal aphids were caught in either England or Scotland.

Table 3.17 TWINSPAN refined-ordination table after 3 divisions; differences in spring aphid totals between England & Scotland 1976-90.

"Pseudo-species" levels

Spring

Year	1 1	1 1 1 1	1 1 1 1 1	1 1 1 1	
	9 9	9 9 9 9	9 9 9 9 9	9 9 9 9	
	8 8	7 8 8 8	7 7 8 8 8	7 8 8 9	
	0 1	7 2 5 7	8 9 6 3 4	6 8 9 0	
MAY Md	1 1	1 2 1 1	1 1 1 1 1	2 2 3 3	000
JUNE Rp	1 3	2 1 1 1	2 2 1 3 1	4 3 4 1	001
JUNE Sa	4 3	3 3 2 3	2 1 1 4 4	4 4 1 3	001
JUNE Sf	2 2	2 2 2 2	2 2 2 2 2	2 3 2 2	001
JUNE Md	1 1	2 3 2 3	2 1 2 3 3	4 2 4 4	001
MAY Sa	2 3	2 2 1 2	1 1 1 2 1	3 3 3 3	01
MAY Sf	2 2	1 1 1 1	1 1 1 1 1	2 2 2 2	01
MAY Rp	1 2	2 2 2 1	1 1 1 1 1	3 3 4 3	1
	0 0	0 0 0 0	0 0 0 0 0	1 1 1 1	
	0 0	1 1 1 1	1 1 1 1 1		
		0 0 0 0	1 1 1 1 1		

Md *Metopolophium dirhodum* Rp *Rhopalosiphum padi*

Sa *Sitobion avenae* Sf *Sitobion fragariae*

"Pseudo-species" levels (numbers of aphids)

1 = 0 to 10 2 = 11 to 99

3 = 100 to 999 4 = > 999

The weather of the preceding winter and the current spring of each of these three years was examined using PSC quints and conventional weather data, so that meteorological reasons for these three years being different might be found.

These three years did not have similar PSC quints in the preceding winters (Table 3.14). The winter of 1983 was $P_4S_2C_2$ which normally suggests that the winter was milder than average (Murray, 1972). A high P quint alone in winter is positively correlated with mean temperature in both the north and south of Britain whilst a low S quint suggests that the north would have the coldest weather (Murray & Benwell, 1970). The winter of 1984 was $P_2S_5C_4$ which is normally associated with colder than average temperatures (Murray, 1972) and a high C quint indicates that the north would be colder than the south (Murray & Benwell, 1970). The winter of 1985 was $P_1S_3C_2$ which is normally associated with lower than average temperatures (Murray, 1972), and the low P and low C quint implies that the south would be colder because of the occurrence of easterly airstreams (section 3.1).

These inferences can be judged by examining the mean temperature data of these three winters at the six climatological stations (Tables 3.18 to 3.20).

Table 3.18 Mean temperature of the winter months 1982/83.

	Mean temperature ^{o}C					
Month	L	D	EC	BB	R	W
December[a]	2.7	3.3	3.3	4.1	3.9	4.3
January	5.0	5.3	5.3	6.3	5.9	6.7
February	2.0	1.9	1.5	1.4	2.2	1.8
Winter[b]	3.2	3.5	3.4	3.9	4.0	4.3

t-tests between the English and Scottish sites:

a t = 4.3, df 4, P = 0.012

b t = 4.7, df 4 P = 0.009

Table 3.19 Mean temperature of the winter months 1983/84.

	Mean temperature ^{o}C					
Month	L	D	EC	BB	R	W
December	5.7	5.5	5.6	5.3	4.8	5.4
January[a]	0.7	1.7	1.9	3.3	3.3	4.0
February	4.3	3.7	3.7	3.1	2.9	3.4
Winter[b]	3.6	3.6	3.7	3.9	3.7	4.3

t-tests between the English and Scottish sites:

a t = 4.8, df 4, P = 0.009

b t = 1.9, df 4, N.S.

Table 3.20 Mean temperature of the winter months 1984/85.

	Mean temperature ^{o}C					
Month	L	D	EC	BB	R	W
December	5.0	5.3	5.1	5.4	4.7	5.1
January[a]	2.2	1.5	0.9	0.1	0.0	0.4
February[b]	3.1	3.3	2.7	1.4	1.7	1.9
Winter[c]	3.4	3.4	2.9	2.3	2.1	2.5

t-tests between the English and Scottish sites:

a $t = -3.5$, df 4, $P = 0.026$

b $t = -6.0$, df 4, $P = 0.0039$

c $t = -4.6$, df 4, $P = 0.01$

Key for Tables 3.18 to 3.20

L Lossiemouth D Dundee EC East Craigs

BB Brooms Barn R Rothamsted W Writtle

Winter temperature averages in Table 3.7

Contrary to inferences drawn from the PSC quints, the winter of 1984 was warmer than average in both countries, although it was $0.4^{o}C$ colder in Scotland. Otherwise, the conventional weather data from the six sites confirm the inferences associated with the PSC quints. In the winters of 1983 and 1984, one month was markedly colder in Scotland

relative to England whereas in 1985, two months were markedly colder in England.

The spring of 1983 was $P_2S_3C_5$ (May being $P_1S_4C_5$), the high C quint indicating rainfall greater than average (Murray & Benwell, 1970), and therefore suggesting that it was a cool and unsettled spring. The spring of 1984 was $P_1S_1C_1$ (May being $P_1S_1C_2$) indicating that the spring had more northerly winds than average and was anticyclonic. This implies that it was a warmer and drier spring than average (Murray, 1972). The spring of 1985 was $P_1S_2C_5$ (May being $P_1S_2C_4$), similar to the spring of 1983. Springs with a low P quint and a high C quint (blocked and cyclonic) such as 1983 and 1985, tend to be associated with lower than average CET (Murray, 1972). The combination of a low S quint and a high C quint in spring (frequent northerly winds and cyclonic) as in 1985 normally gives lower than average temperatures compared to a high S and high C as in 1983 (Murray, 1972). Thus, in 1985, the spring was probably the least favourable for aphid flight (section 3.1) as indicated by PSC quints.

These inferences can be judged by examining the mean daily maxima temperature data of these three springs at the six climatological stations (Tables 3.21 to 3.23).

Table 3.21 Mean daily maximum temperature of the spring months 1983.

	Mean maximum temperature ^{o}C					
Month	L	D	EC	BB	R	W
April	8.3	9.2	9.1	11.1	10.8	11.8
May	11.2	10.9	11.3	14.0	14.0	14.9
June	15.6	16.4	16.3	18.9	18.9	20.2
Spring[a]	11.7	12.2	12.2	14.7	14.6	15.6

t-test between the English and Scottish sites:

[a] t = 8.2, df 4, P = 0.0012

Table 3.22 Mean daily maximum temperature of the spring months 1984.

	Mean maximum temperature ^{o}C					
Month	L	D	EC	BB	R	W
April	11.4	10.8	11.5	12.8	12.8	13.3
May	12.5	14.1	14.3	13.0	13.3	13.9
June	15.9	18.5	17.3	18.7	19.3	19.8
Spring[a]	13.3	14.5	14.4	14.8	15.1	15.7

t-test between the English and Scottish sites:

[a] t = 2.4, df 4, N.S.

Table 3.23 Mean daily maximum temperature of the spring months 1985.

	Mean maximum temperature ^{o}C					
Month	L	D	EC	BB	R	W
April	10.6	10.9	11.1	12.6	12.3	13.5
May	12.6	13.6	13.5	14.6	14.5	15.7
June	14.9	15.6	15.4	16.8	17.0	17.8
Spring[a]	12.7	13.4	13.3	14.7	14.6	15.7

t-test between the English and Scottish sites:

[a] t = 4.5, df 4, P = 0.011

Key for Tables 3.21 to 3.23

L	Lossiemouth	D	Dundee	EC	East Craigs
BB	Brooms Barn	R	Rothamsted	W	Writtle

Spring temperature averages in Table 3.7

In the springs as a whole, England had similar and below average mean temperature in the three years, whereas in Scotland, there were greater differences between years. In 1984, the spring was warmer than average in Scotland, but colder than average in England. However, two of the springs (1983 & 1985) were significantly colder in Scotland than in England. In the Junes of both 1983 and 1984, England had warmer than average daily maximum temperatures (see Table 3.7 for 1976-90 averages) whereas in 1985, mean

daily maxima were below average in both May and June in both England & Scotland. This suggests that 1985, as indicated by PSC quints, was the poorest of the three springs for aphid flight, although in May, it had the higher temperatures than in either 1983 or 1984.

A relevant weather parameter when comparing suction trap catches of England & Scotland is the temperature gradient between the two countries. This is because aphids have a temperature threshold below which they are unable to take-off (Taylor, 1963). In the spring as a whole, central England is on average 0.9^{o}C warmer than Edinburgh (Table 3.1). The mean daily maxima temperature data of the three English sites were pooled to obtain England temperature means and the Scottish data were pooled to obtain comparative temperature means for Scotland. The difference in the mean daily maxima between England & Scotland in May and June of the springs 1983-85, is compared with the mean difference in May and June 1976-90 in Table 3.24.

In 1983, the north-south temperature gradient was unusually intense in both May and June. In 1984, May was slightly cooler in England than in Scotland whereas in June, the temperature difference was close to average. 1985 was about average in this respect in both months.

Table 3.24 The difference in mean daily maximum temperature between England & Scotland during May and June 1983-85.

	Temperature difference °C	
Year	May	June
1983	3.2	3.2
1984	-0.2	2.1
1985	1.7	1.9
Mean difference 1976-90	2.1	2.3

The summary (Table 3.25) of the weather of the preceding winters and springs of 1983-85 indicates possible reasons for the differences between the cereal aphid numbers caught in the English and Scottish suction traps being less related to the size of the total aphid catches in these three years, relative to other springs.

Summary of section 3.3.3 The largest differences between the cereal aphid catches of the Scottish and English suction traps were found in springs when the size of catches was large, and *vice versa*. In three springs (1983, 1984 & 1985), the difference in catch sizes between Scotland and England was less related to the sizes of suction trap catches in both countries. Unusual winter and spring weather (Table 3.25) was identified as the possible explanation.

Table 3.25 Summary of the weather of the preceding winters and springs of 1983-85.

Year	Comments
1983	Significantly (P = 0.012) colder December (1982) in Scotland.
	Very cold spring in Scotland.
	Intense temperature gradient between Scotland & England in spring.
1984	Significantly (P = 0.009) colder January in Scotland.
	Above average spring temperatures in Scotland but below average in England. May in England was slightly cooler than in Scotland.
1985	Significantly (P = 0.01) colder winter in England.
	Colder than average spring, particularly in Scotland, both May and June being below average at all 6 sites.

3.4 **Discussion**

3.4.1 **Anholocycly and holocycly**

Theoretically, the numbers of anholocyclic aphid species caught by suction traps in spring may vary more between years than the numbers of holocyclic species. This is because mild winters favour anholocycly, whereas cold winters have the opposite effect. In contrast, holocyclic species are more independent of the severity of winter weather (Bale, 1989).

Although anholocyclic overwintering of *M. dirhodum* (Turl, 1980) and *S. fragariae* (Hand, 1989) has been

observed, these two species are considered to be largely holocyclic in Britain (George, 1982). In comparison, both *R. padi* and *S. avenae* overwinter anholocyclically (Dean, 1974a; George, 1974; Dewar & Carter, 1984; Hand, 1989), although *R. padi* regularly overwinters holocyclically on *P. padus* too in northern Britain (Taylor, 1982).

These statements on the manner of overwintering by cereal aphid species are supported by the mean numbers caught in both May and June by the three suction traps in both England & Scotland (Table 3.8) and by the difference in numbers between the suction trap catches of England & Scotland (Table 3.9). The mean numbers of the species that can overwinter anholocyclically in large numbers (i.e. *R. padi* & *S. avenae*) were generally greater than the mean numbers of the more holocyclic species (*M. dirhodum* & *S. fragariae*) (Table 3.8). The numbers of the two anholocyclic species which are more sensitive to winter weather differed most between England & Scotland, sometimes being more numerous in Scotland than in England (Table 3.9). In the period 1976-90, six winters have been colder in England relative to Scotland (Table 3.16 - mean of 3 sites in each of England & Scotland).

3.4.2 **Winter and spring weather**

The study of winter weather (section 3.1) has shown that either the north or the south of Britain can be colder in winter. In the spring, there is a greater difference in

temperature between the north and south than in winter (Table 3.7). In the period 1976-90, the mean daily maximum of the meteorological spring has never been warmer in Scotland than in England although the odd spring month has been warmest in Scotland (Table 3.24).

Hurst (1969) compared the average values of accumulated temperature above threshold values during the spring and summer for different areas of Britain 1931-60. In the spring, the values for eastern Scotland (at sea level) above threshold values of 5.5^{o}C and 10^{o}C are 70 and 43% respectively of the values of central England (at sea level). The comparative figures for the summer are 80 and 65% and the figure for a threshold of 15.5^{o}C is only 30% of the value of central England.

Therefore, the spring weather is more likely to be the major factor accounting for the greater numbers of cereal aphids being caught by the English suction traps than those of Scotland (Table 3.9), than winter weather.

This theory can be tested by examining aphid and temperature data from springs preceded by the mildest winters (1976, 1988, 1989 & 1990) when spring numbers were least limited by the incidence of freezing weather in either England or Scotland (Table 3.26).

Clearly, the greatest difference in suction trap catches between England & Scotland occurred in June 1976 when there was the largest difference in mean daily maxima

(5°C) between these two countries. The negative values (i.e. aphid catches were greater in Scotland) occurred when the differences in temperature were relatively small. However, no significant relationships were found when the differences for each species ($\log_{10}$ (n + 1) transformation - negative values transformed to zero) were regressed on the temperature differences.

Table 3.26 Comparison of the monthly difference in aphid numbers between England & Scotland in Mays and Junes following the mildest four winters, and the difference in monthly mean daily maximum temperature between England & Scotland in the same months (calculated from data from same sites used to calculate aphid number differences).

	Differences in aphid numbers				
Year	Rp	Sa	Sf	Md	Temperature difference °C
May					
1976	143	108	11	17	3.6
1988	158	496	74	21	2.4
1989	1561	377	81	189	3.6
1990	658	149	27	276	3.6
June					
1976	2427	9924	36	6363	5.0
1988	941	1898	144	67	0.3
1989	1085	-3841	98	1559	2.7
1990	-65	298	17	1332	1.8

Md *Metopolophium dirhodum* Rp *Rhopalosiphum padi*

Sa *Sitobion avenae* Sf *Sitobion fragariae*

Of course, the reservoir of alate aphids which might be caught by suction traps would not have been the same size after these four mild winters and they would probably

not have been of equal size in the north and south of Britain. These factors might account for the non-significant relationships between temperature and aphid number differences between the north and south of Britain.

3.4.3 **PSC indices and conventional weather data**

The comparison of PSC quints with conventional weather data in the meteorological winter and spring seasons identified the merits and pitfalls of PSC indices.

The merits are that combinations of indices neatly summarise the synoptic character (the distribution of atmospheric pressure at sea level) of a season around the British Isles, from which regional characteristics, and most importantly, regional differences, can be extrapolated by users with an appreciation of synoptic weather patterns. Furthermore, the use of the quintile boundaries provide an easy method of comparing the weather of a month or season with the long-term average synoptic situation for that month or season.

A pitfall of PSC indices is that the relationships between indices and weather parameters such as temperature and rainfall, differ between months and between regions in the same month. Many of these relationships are known and are published (Murray & Lewis, 1966; Murray & Benwell, 1970; Murray, 1972), but the knowledge is incomplete. If the PSC indices are used to estimate weather variables at a site where these relationships have not been studied,

errors might arise.

An advantage of conventional weather data is that precise measurements of a weather parameter are obtained at each site, whereas PSC indices enable only estimates to be made for a weather variable.

In this Chapter, assemblages of aphid species were analysed which ruled out the use of regression on conventional weather data as an analytical tool. Using TWINSPAN and contingency tables, the importance of the P index in winter and the C index in spring was identified. This was confirmed by comparisons with conventional weather data in the winter and spring seasons. This demonstrates that PSC indices can be used in *Aphidology* (see section 2.4 for further uses).

3.4.4 **Forecasting spring aphid migrations using winter weather data**

Turl (1980) examined the effects of winter and spring temperature on the date of first catch of nine species of cereal and potato aphid in three Scottish suction traps. Significant correlations between winter and spring (November to April) temperatures and first catches of aphids were found for all species except *R. padi*. Most correlations were negative indicating that the colder the temperatures, the later aphids were caught in suction traps. The periods showing significance varied from species to species and from trap to trap. The periods of highest

significance lay in the January to April period, with February being the most important single month (Turl, 1980).

These results suggested that the date of first aphid catch at specific suction traps could be predicted in advance, on the basis of temperature in the preceding winter, thereby providing an indication of the time of spring colonisation of crops (Turl, 1980).

Other analyses similar to those of Turl (1980) have been applied to suction trap catches in both the south and north of Britain (Walters & Dewar, 1986; Harrington *et al.*, 1990). Again, winter temperature, particularly in January and February, was found to be more important than early spring temperature. For largely anholocyclic species, good relationships were found with winter temperature, as might be expected. For some holocyclic species (*Acyrthosiphon pisum* (Harris) and *M. dirhodum*), numbers caught tended to be positively related to spring temperature (Harrington *et al.*, 1990).

Walters & Dewar (1986) examined the relationship between temperature (November to April) and first suction trap record for *S. avenae* (a largely anholocyclic species) and *S. fragariae* (a largely holocyclic species) over a range of latitudes in Britain and other parts of western Europe. For *S. fragariae*, no relationships were found at any latitude. For *S. avenae*, relationships were found only

in the south, with temperature in January and February being most important. Because there appears to be an association between lifecycle strategy (anholocycly or holocycly) and the effects of winter temperature on date of first suction trap catch, it was hypothesised that *S. avenae* is mainly holocyclic in the north, as suggested by Turl (1980). Collection of *S. avenae* clones has shown that over 90% in Scotland are holocyclic whereas in southern England, most were anholocyclic (Newton & Dixon, 1988).

It is now known that *S. avenae* is at least partially anholocyclic in Scotland (Chapter 4). The failure to obtain significant relationships in the north for *S. avenae* (Walters & Dewar, 1986) may not have been because this species mainly overwinters holocyclically in this part of Britain as suggested, but may have been due to the smaller variation in temperature during January and February in the north relative to southern England (Table 3.3). Also of relevance is the lower mean numbers of *S. avenae* caught by the suction traps of Scotland relative to those of England (Tables 3.8 & 3.9). In Scotland in May and June, fewer than ten *S. avenae* were caught by the three Scottish traps combined in 13 and 7 of the 15 years respectively. These relatively low numbers in Scotland are associated with the later dates of first aphid catch in higher latitudes (Walters & Dewar, 1986).

The greater variability of temperature in late winter

(Table 3.3) may explain why temperature in February has most often been related to dates of first aphid catch (Turl, 1980; Harrington *et. al.*, 1990). This greater variability is associated with the recognised singularity of anticyclonic long spells of weather in February, such that record frosts occur in cold winters (Lamb, 1950). Recently, February 1986 was an extreme example (Tables 3.4 to 3.6).

In the CANOCO analysis (section 3.1.3) which is also sensitive to the relative variability of the explanatory variables, February and March parameters were found to be most important, although any cold winter month apparently had adverse effects on anholocyclic overwintering by cereal aphids. Perhaps, freezing spells in late winter may have a greater impact on spring aphid numbers than early winter freezing spells, because the size of the overwintering population is likely to be relatively small at this time of year. On the other hand, a very cold December would have a very negative effect on the numbers of aphids overwintering anholocyclically no matter how mild the temperature in January and February. Also, the fact that a late winter month is closer in time to the spring would increase the likelihood of finding a relationship between date of first aphid catch in the spring and winter temperature.

The lack of significant relationships when dates of first catches of holocyclic aphid species were regressed on

winter temperature data (Walters & Dewar, 1986; Harrington *et al.*, 1990), is supported by the lower mean numbers of holocyclic species being caught by the six suction traps during the spring relative to anholocyclic species (Table 3.8).

An aphid species is more likely to be caught by a suction trap when it is more abundant in the vicinity of the trap. Early in the spring, the small size of aphid populations must limit the size of suction trap catches and affect their sensitivity (Taylor, 1963), thereby influencing the dates of the first aphid catches, which is the theory behind these regressions. The greater incidence of spring months with zero catches (Table 3.13) for holocyclic species (25) relative to anholocyclic species (16) may contribute to the lack of relationships found for holocyclic species.

The importance of current weather to the size of suction trap catches has been observed by several workers (A'Brook, 1981; Dewar, 1982; Walters & Dixon, 1984). During May and June at Rothamsted from 1965-79, high wind speeds and low temperatures on 48% of days were unsuitable for cereal aphid flight (Walters & Dixon, 1984).

The significantly lower spring temperatures encountered in the north of Britain (Table 3.7) must surely result in fewer days being above the minimum temperature threshold for take-off. The time spent at temperatures above the

threshold has more effect than mean temperature on the size of daily trap catches (Taylor, 1963). Also, at higher temperatures, a greater proportion of aphids able to fly, will do so (Walters & Dixon, 1984), and they will be more active (Taylor, 1963). These statements are supported by the spring suction trap data which show fewer aphids being caught by the suction traps of Scotland than those of England (Tables 3.8, 3.9 & 3.26). Again, this would reduce the likelihood of obtaining significant relationships between winter temperature and date of first aphid catch in the north.

Regressions where temperature in winter and spring months were pooled showed that high temperatures during the winter and the spring usually correspond with large numbers of aphids caught up to 1 July (Harrington *et al.*, 1990). In the period 1976-90, the four mildest winters (1976, 1988, 1989 & 1990) were all followed by mild springs, and three of the four coldest winters (1977, 1979, & 1986) were followed by cold springs (Table 3.16). In Scotland, there is a positive relationship between mean winter temperature and spring daily maximum temperature from 1976-90 (Table 3.16), whereas in England, there is not. However, the fact that the mildest and coldest winters in the period 1976-90 tended to be followed by springs with a similar character creates the likelihood of finding spring temperature to be less important using regression for two reasons. Firstly, spring temperature is less

variable than winter temperature (Tables 3.3 & 3.7), and secondly, it is related to winter temperature to some extent.

In meteorology, it is known that mild winters (especially if they are dry too) are often followed by warm summers (Ratcliffe, 1991a). Such relationships form the basis of seasonal forecasting, because there is a belief that seasonal weather types such as hot, dry summers tend to have pre-conditions which are different to those of cool, wet summers (Ratcliffe, 1991b). However, the relationship is not absolute, and sometimes, the less likely event of a cool, wet summer following the pre-conditions of a hot, dry summer occurs.

From 1976-90, there has been a relationship between winter and spring temperature, particularly in the north of Britain. However, in years when a cold spring follows a mild winter, aphid forecasts made using regressions of winter temperature will be inaccurate. There is a need to consider the effects of spring weather on aphid numbers in crops and on aphid flight when forecasts are made. The RIS data should be analysed, and aphid forecasts made, using methods which discriminate between winter and spring weather, such as the combination of TWINSPAN and PSC indices.

Summary Analysis of the spring suction trap catches of cereal aphids suggest that they can be greatly influenced

by the incidence of freezing weather in the region of the trap during the preceding winter; the temperature of the spring; and the presence of an aphid species in the area prior to the winter.

There is a linear relationship between the timing of the spring migration of cereal aphids and latitude, such that dates of first aphid catches are later at higher latitudes (Walters & Dewar, 1986). Lower winter temperatures at higher latitudes have been offered as an explanation for this (Walters & Dewar, 1986). In some winters (Tables 3.4, 3.5, 3.6 & 3.16), temperatures are lower in England than in Scotland, suggesting that some other factor is critical to the timing of the spring migration of cereal aphids. Spring temperature (Tables 3.7 & 3.16) is likely to be this factor.

Higher temperatures result in greater numbers of aphids on their host plants, and therefore more alatae. Higher temperatures also result in more days exceeding the minimum threshold for take-off and therefore more alatae are caught by suction traps (Taylor, 1963).

The higher spring temperatures in England enable virginoparae that have overwintered to reproduce more quickly on their host plants producing alatae earlier in the spring. Therefore, in England, alatae colonise crops earlier in greater numbers, and reproduce more quickly. In Scotland, the lower spring temperatures mean slower reproduction and fewer days when aphid flight is possible.

CHAPTER FOUR

Identification of the factors affecting the incidence and the regional distribution of BYDV during three winter barley seasons: 1988/89, 1989/90, 1990/91

4.1 Introduction

The rise in the importance of BYDV Since BYDV was discovered in Britain in 1954 (Watson & Mulligan, 1957), large changes in the methods of cereal production have occurred. A major change has been the switch from spring to autumn drilling for a large proportion of the cereal acreage, because of the larger yields of the winter varieties (Plumb, 1988). For example, in the five years to 1984, the areas of winter barley and winter wheat both doubled to 0.9 and 1.8 M ha respectively (Barnes, 1984). With this change, the incidence of BYDV in cereals has increased (Hill, 1988). Again for reasons of higher yield, there has been a pressure to drill winter cereal crops in September, this also contributing to the rise in the importance of the disease (Plumb, 1988), because of the relationship between crop drilling date and BYDV incidence (George, 1982; Plumb, 1986; McGrath & Bale, 1990).

Another big change has been the increase in the use of agrochemicals in cereal production. The UK cereal acreage treated by insecticides, molluscicides and herbicides almost doubled between 1977 and 1982, whereas that treated by fungicides increased by a factor of five (Carter, 1984).

It has not been possible to identify the effects of these agrochemicals on cereal ecosystems, because the fauna prior to their use was unknown (Vickerman, 1977). The use of herbicides to control weeds in cereal fields may have caused the measured decrease in insect abundance of recent

years (Southwood & Cross, 1969). The increased problem of aphids in agriculture may be associated with the increased use of agrochemicals (Baranyovits, 1973).

Both generalist predators and aphid-specific invertebrate natural enemies are known to consume aphids in cereal crops (Vickerman & Sunderland, 1975). Comparisons between the autumn aphid counts and incidence of BYDV in winter barley plots drilled after conventional ploughing and plots direct drilled suggest that natural enemy predation may be adversely affected by conventional ploughing, leading to greater aphid numbers and BYDV incidence (Kendall *et al.*, 1988).

Therefore, both agrochemicals used to control other pests and diseases, and agronomy methods, may have contributed to the rise in the importance of BYDV in Britain in recent years.

The geographical distribution of BYDV in Britain BYDV isolates transmitted by *R. padi* tend to be more common in the south and west of Britain whereas isolates transmitted by *S. avenae* tend to predominate in the north and east (Plumb, 1974). South and west Wales (A'Brook & Dewar, 1980) and south-west England (Kendall & Chinn, 1990) are areas where problems of *R. padi*-transmitted BYDV are most common, whereas in the Vale of York, *S. avenae* is considered to be the main vector (McGrath & Bale, 1989). At Rothamsted, both

aphid species are important vectors (Plumb, 1986). In Scotland, most BYDV problems have been associated with *R. padi* (Holmes, 1985), although data for Scotland presented in this Chapter show that the importance of the different types of BYDV can differ between years in the same region, and between different regions in the same year.

These regional differences in the importance of *R. padi*- and *S. avenae*-transmitted BYDV suggest that climate may be a factor in determining which vector is most important in a region, and weather may be a factor in the severity of BYDV problems in autumn-sown cereals.

Direct transfer and the "green bridge" The severe damage to autumn-sown cereals from *R. padi*-transmitted BYDV which is associated with the ploughing-in of grass leys not killed off with desiccants (Carter, 1984; Plumb, 1988) is the result of apterous aphids walking directly from one crop onto next season's crop, via the "green bridge". However, the "green bridge" is not necessarily a previous crop in the form of a grass ley, but may be grass weeds and/or volunteers in the stubble of a previous cereal crop (Plumb, 1988).

Destruction of weed and/or grass reservoirs of virus diseases which can be transmitted to agricultural crops by insects is an important disease control measure (van Emden, 1965). To prevent the direct transfer of apterous aphids, the use of desiccants to treat grass leys and stubbles

with grass weeds and/or volunteers is recommended ten to 14 days prior to ploughing when the succeeding crop is a winter cereal.

Aims of analyses The aphid and BYDV data collected over three seasons are initially analysed to test for regional differences in aphid and BYDV incidence. Further analyses attempt to explain the results of the first analyses at a more biological level.

4.2 General Methodology in winter barley

4.2.1 Field naming

In each winter barley season, differing numbers of regions and differing numbers of fields were sampled. Within each season, the fields were labelled with the first letter of their region name, and a number which relates to the alphabetical order of the farms visited in that region.

4.2.2 Aphid sampling

In each of the three winter barley seasons, sampling began at the one-leaf stage (GS 11, Tottman & Makepeace, 1979). The term, autumn sampling refers to all sampling between crop emergence and 31 December. Winter sampling refers to all sampling between 1 January and 31 March. Spring sampling refers to all sampling between 1 April and 31 June.

4.2.3 **Plant sampling**

The extent of BYDV infection in winter barley crops was assessed in April and/or May in each of the three seasons. It was assessed visually (as a percentage of the total crop), and by collecting leaf samples which were subsequently tested for BYDV by ELISA. Plants with yellow leaf discolouration were identified as being "probably BYDV-infected". The type of yellow leaf discolouration looked for in barley plants was chrome yellow discolouration at the distal ends of leaves (George, 1982), sometimes accompanied by dark brown blotches. However, certain types of plant with yellow leaf discolouration were rejected as being "probably BYDV-infected": damaged leaves showing yellow leaf discolouration; plants with pale yellow leaf discolouration characteristic of nitrogen deficiency; and feeble yellow plants characteristic of waterlogged soil.

On occasions, ten well-established *Poa annua* (L.) plants were collected from tramlines in winter barley fields and tested for BYDV by ELISA (Mortar & Pestle). Plants expressing symptoms of BYDV were not looked for, because BYDV is symptomless in most grasses (Oswald & Houston, 1953; Kurppa *et al.*, 1989).

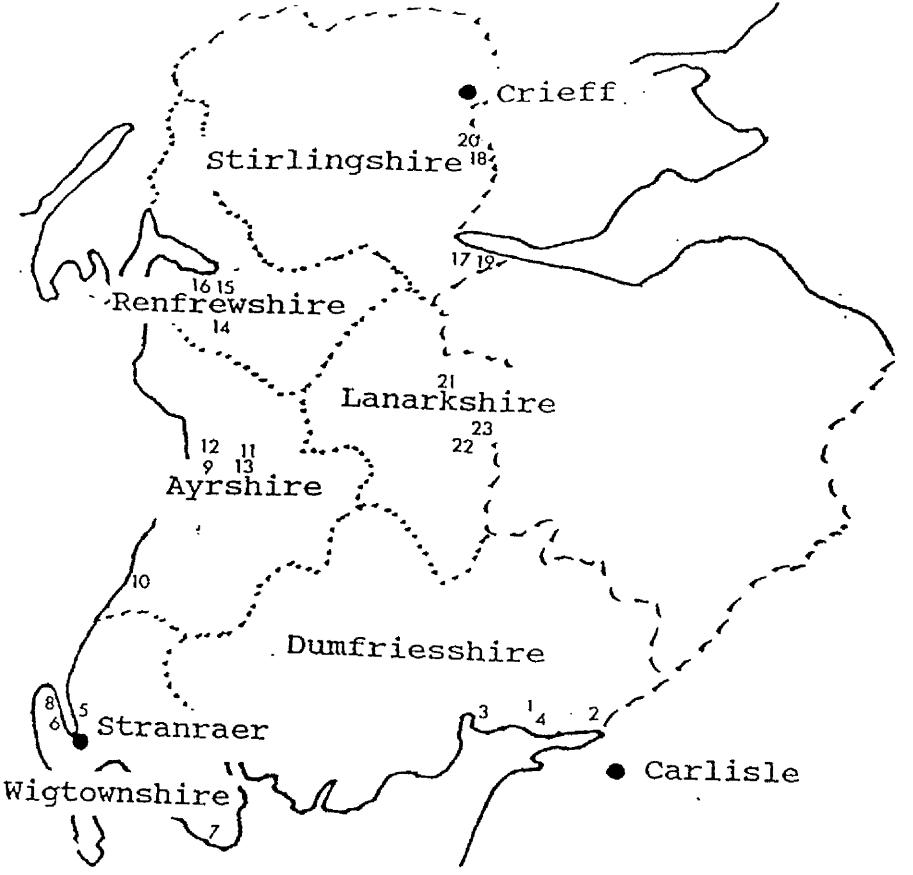
4.3 BYDV epidemiology in winter barley, 1988/89

4.3.1 Methodology for aphid sampling in winter barley, autumn 1988, winter and spring 1989

Winter barley fields in three regions were sampled during the autumn and winter: Wigtownshire, Ayrshire and Stirlingshire. In the spring 1989, winter barley fields in Dumfriesshire, Renfrewshire and Lanarkshire were also sampled (Figure 4.1).

Autumn sampling Five fields were sampled weekly for aphids, using two methods, from crop emergence to mid-November. Two fields were visited in Ayrshire and Wigtownshire and one in Stirlingshire. All fields except the Stirlingshire field were sampled once more in late November using method 2, making a total of eight visits.

Method 1:- trays (40 x 29 x 9.5 cm [cat-litter, Midland Oak]), which were painted "Sulphur" yellow to attract aphids constituted the sampling areas. Each contained 15 oat seedlings (cv. Maris Tabard) at the two leaf stage (GS 12). Five were placed in a north-south line 50 metres apart in each field, the first tray being placed 50 metres from a field boundary. At the end of each week, aphids present on the oat seedlings were counted and identified, and the plants were removed to the glasshouse, sprayed with Pirimor (ICI, 50% w/w pirimicarb as a water dispersible granule - dilution rate 0.5 g/l) and grown on for four weeks. Plants showing yellow leaf discolouration were tested for BYDV by ELISA.



Dumfriesshire			
1. Charlesfield (Hoddom & Kinmount estate)	D1	D2	
2. Gretna House	D3	D4	
3. Kelton	D5	D6	D7
4. Spittalriddinghill	D8	D9	D10
Wigtownshire			
5. Beoch	W1		
6. Kirranrae	W2		
7. Physgill	W3	W4	
8. Portencalzie	W5		
Ayrshire			
9. Auchincruive estate	A1		
10. Girvan Mains	A2		
11. Muir	A3	A4	
12. Newlands	A5		
13. Barskimming estate	A6	A7	
Renfrewshire			
14. Arkleston	R1	R2	R3
15. Barrangary	R4	to	R8
16. Erskine Home	R9	R10	R11
Stirlingshire			
17. Bonnyhill	S1	S2	
18. East Third	S3		
19. Myrehead	S4	S5	
20. Shearerston (Colquazie estates)	S6	S7	
Lanarkshire			
21. Auchnotroch	L1		
22. Chesterhall	L2	L3	
23. Coulterhaugh	L4	L5	

Figure 4.1 Locations of crops sampled in winter barley season 1988/89.

Method 2:- each week, plants in approximate 1 m^2 areas were examined at 10 metre intervals along the north-south line the trays were aligned. Any aphids on plants were counted and identified.

Winter sampling W2, W5 and A3 were sampled in January using method 2 described above. A1, a field on the Auchincruive estate was sampled twice in early February. On both occasions, three 50 x 1 m strips of crop were selected, and five 1 m^2 areas at 10 m intervals along this strip were examined for aphids. Aphids were counted and identified.

Spring sampling In the spring of 1989, 45 winter barley fields were visited once in late April or early May. These fields were selected, either because they had been sampled during the previous autumn, or because farmers had observed patches of yellow plants in them. A second visit was made to 16 of these fields in May. On both visits, during a circuit of each field using tramlines, ten randomly selected plants within a metre swath either side of the tramlines were examined for aphid species incidence. When more than one species was present, the more numerous species was noted as the predominant species.

4.3.2 Results for aphid sampling in winter barley, autumn 1988, winter and spring 1989

Autumn sampling, 1988 Tables 4.1 and 4.2 show the results for the aphid sampling using yellow trays. Fifteen of the 2520 oat seedlings placed in fields within the yellow trays

during the seven week period were infested by aphids at the time of examination. Twelve *Rhopalosiphum* spp. and nine *S. avenae* were counted on these 15 oat seedlings. Eighteen of these aphids were recorded in the two Wigtownshire fields.

Table 4.1 Cumulative total numbers of yellow trays placed weekly in each field with at least one aphid-infested oat seedling (out of a total of 35 trays in each field); winter barley, autumn 1988.

	Total number of trays	
Field	*Rhopalosiphum* spp.	*S. avenae*
W2	2	1
W5	2	5
A3[a]	0	0
A5	0	0
S7	1	1
Totals	5	7

[a] 28 trays only.

Two of the 2520 plants grown on in the glasshouse developed leaf yellow discolouration, and ELISA tests (Mortar and Pestle method) showed that both these plants, each from a different Wigtownshire field, were infected with the RPV strain.

Table 4.2 Total numbers of aphids on oat seedlings within the 35 yellow trays placed in each field, and the number of oat seedlings out of a total of 525 placed in each field which were infested by at least one aphid; winter barley, autumn 1988.

	No of aphids (No of oat seedlings infested)	
Field	*Rhopalosiphum* spp.	*S. avenae*
W2	3 (1)	2 (2)
W5	7 (6)	6 (3)
A3[a]	0 (0)	0 (0)
A5	1 (1)	0 (0)
S7	1 (1)	1 (1)
Totals	12 (9)	9 (6)

[a] 28 trays only.

The numbers of *R. padi* and *S. avenae* in 25 m^2 of crop in each field on each of the eight visits are shown in Table 4.3, whereas Table 4.4 and Figure 4.2 show the cumulative total numbers of *Rhopalosiphum* spp. (alate *insertum* included) and *S. avenae* in each field during the eight visits after a total of 200 m^2 of crop had been examined. A much greater proportion of the *Rhopalosiphum* population was alate compared with *S. avenae*.

Table 4.3 Weekly numbers of aphids in 25 m^2 of each crop; winter barley, autumn 1988.

Numbers of *Rhopalosiphum padi*

	Week beginning								
	October					November			
Field	4	11	18	25	31	7	14	28	T[a]
W2	6	1	1	0	1	3	0	2	14
W5	3	0	4	8	4	16	0	2	37
A3	3	2	0	0	0	0	0	0	5
A5	1	0	0	0	0	1	0	1	3
S7	0	1	3	0	0	0	0	-	4
Totals	13	4	8	8	5	20	0	5	63

Numbers of *Sitobion avenae*

	Week beginning								
	October					November			
Field	4	11	18	25	31	7	14	28	T[a]
W2	10	2	4	10	10	15	19	10	80
W5	0	0	1	10	4	1	10	6	32
A3	4	4	0	4	5	5	1	1	24
A5	4	1	0	0	7	6	4	1	23
S7	7	6	2	1	5	2	1	-	24
Totals	25	13	7	25	31	29	35	18	183

[a] field totals for the whole autumn - no sampling

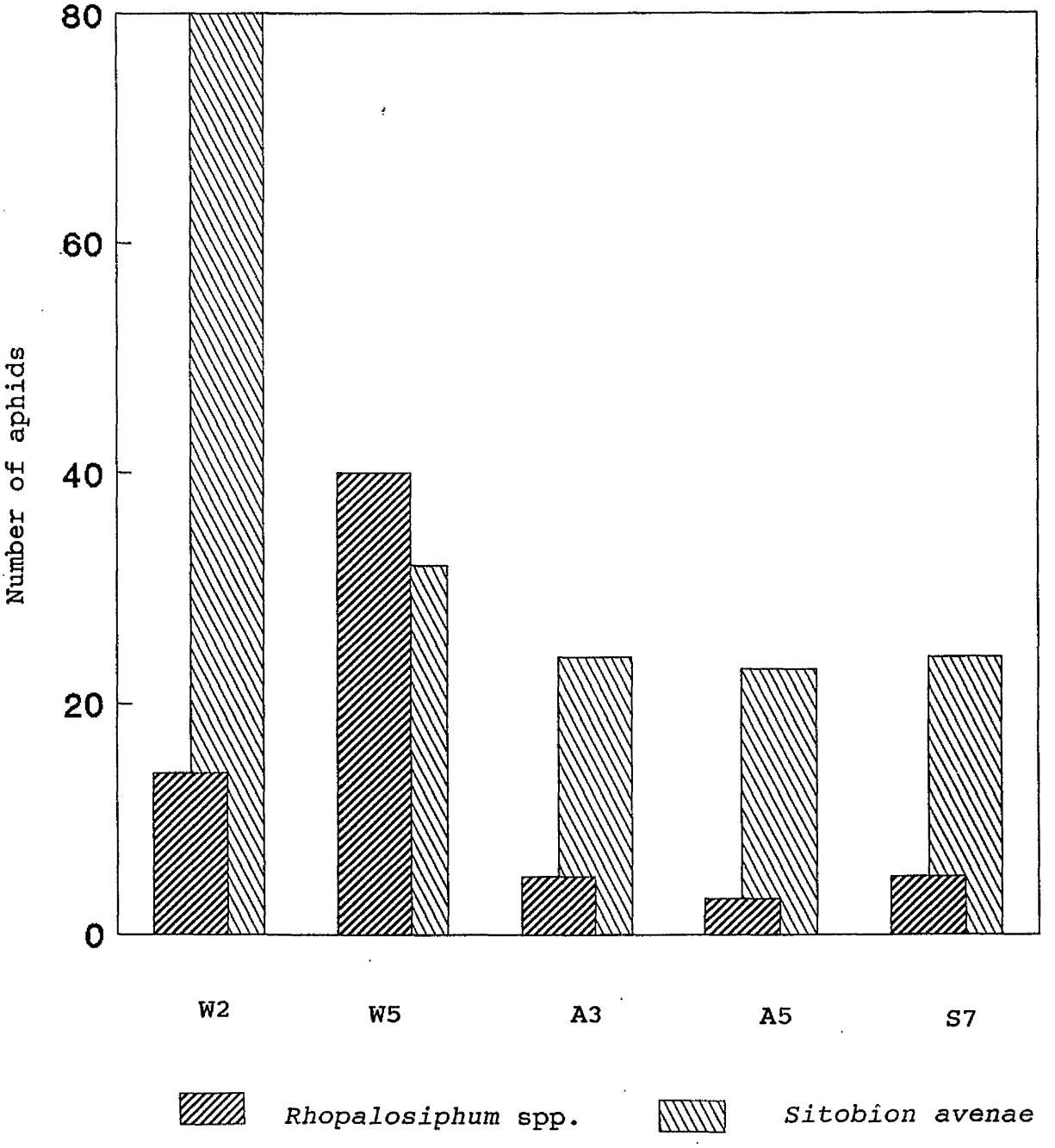


Figure 4.2 The cumulative total numbers of *Rhopalosiphum* spp. and *Sitobion avenae* in five winter barley crops sampled weekly between early October and mid-November 1988 and once in late November 1988.

Table 4.4 The cumulative total number of aphids in 200 m^2 of each winter barley crop after eight visits to each field during the autumn 1988. Data are same as shown in Table 4.3 except *Rhopalosiphum insertum* is included.

	Rhopalosiphum spp.			*Sitobion avenae*		
Field	alatae	apterae	both	alatae	apterae	both
W2	8	6	14	4	76	80
W5	17	23	40	2	30	32
A3	4	1	5	1	23	24
A5	1	2	3	2	21	23
S7[a]	5	0	5	5	19	24
Totals	35	32	67	14	169	183

[a] seven visits only.

A Chi-squared test between the two aphid totals (Table 4.4) of each field gave a significant result ($x^2_{(4)} = 42.9$, $P < 0.001$) indicating that there were differences in the ratios of the numbers of *Rhopalosiphum* spp. to the numbers of *S. avenae* in each field. In W5, 72 aphids were sampled, 56% were *Rhopalosiphum* spp., of which 93% were *padi*. In W2, 94 aphids were sampled, 85% of these being *S. avenae*. In A3, A5 and S7, fewer aphids were sampled and apterous *S. avenae* predominated. Overall, 73% of the aphids counted in winter barley crops in the autumn of 1988 were *S. avenae*.

The two Wigtownshire fields in which greater numbers of aphids were present in the crop, also had a greater number of trays containing infested oat seedlings, a

greater number of aphids on the oat seedlings, and more oat seedlings infested, at the time of examination (Tables 4.1 & 4.2). Relationships between the aphid totals obtained using the two methods of sampling were tested by linear regression. Using a $\log_{10}(n + 1)$ transformation, a significant positive relationship between the two measurements in each field was obtained for *Rhopalosiphum* spp. ($r = 0.886$, df 3, $P < 0.05$; Figure 4.3). The comparative test for *S. avenae* gave a non-significant result ($r = 0.460$, df 3, N.S.).

The agronomic details of each field (Table 4.5) show that all five winter barley crops were sown between the 16 and 22 September 1988 and followed a previous cereal crop. Four of the fields had been two years in cereals. W5, the field with most *R. padi*, differed in having a non-cereal crop (oilseed rape) in 1986/87.

Table 4.5 Agronomic details of winter barley fields in which aphids were sampled; autumn 1988.

Field	Sowing date	Cultivar	Crop grown in season 1986/87	1987/88
W2	16/9/88	Magie	WB	WB
W5	21/9/88	Plaisant	OSR	WB
A3	16/9/88	Igri	WB	WB
A5	22/9/88	Magie	SB	SB
S7	20/9/88	Magie	WW	SB

OSR oilseed rape
WB winter barley
SB spring barley
WW winter wheat

$y = 1.05x + 0.55$

Test of $\beta = 0$ $t = 3.31$, df 3, $P < 0.05$

Test of $\beta = 1$ $t = 0.16$, df 3, N.S.

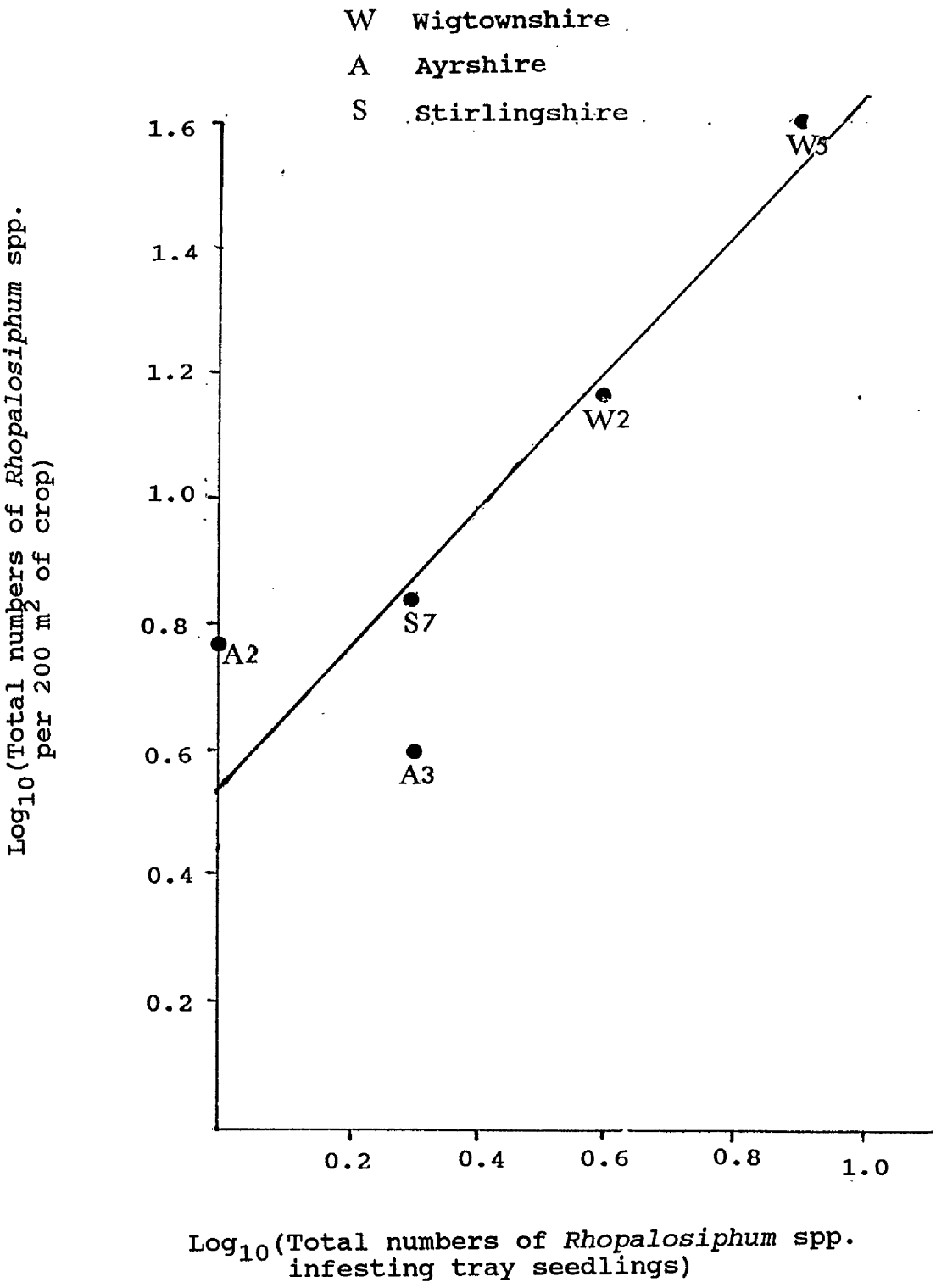


Figure 4.3 Relationship between the numbers of *Rhopalosiphum* spp. in the crop, and the numbers infesting the yellow trays containing oat seedlings; winter barley autumn 1988.

Winter sampling, 1989 The total numbers of apterous *R. padi* and *S. avenae* found on 25 January 1989 in three of the winter barley fields sampled during the autumn 1988 are shown in Table 4.6. Aphids were found in all three fields.

Table 4.6 Total numbers of *Rhopalosiphum padi* and *Sitobion avenae* in 25 m^2 of crop in three fields on 25 January 1989.

	Numbers of aphids	
Field	*R. padi*	*S. avenae*
W2	0	10
W5	10	0
A3	5	5
Totals	15	15

A1, a winter barley crop on the Auchincruive estate, was sampled twice in late winter 1989. Table 4.7 shows the number of apterous *R. padi* and *S. avenae* found in this field on each date.

Table 4.7 Total numbers of *Rhopalosiphum padi* and *Sitobion avenae* in 15 m^2 of crop on each of two visits to A1.

	Numbers of aphids	
Date	*R. padi*	*S. avenae*
6/2/89	6	2
8/2/89	11	9
Totals	17	11

Spring sampling, 1989 The regional incidence of the three cereal aphid species in winter barley crops in the spring of 1989 is shown in Table 4.8 and Figure 4.4. The number of plants out of the ten that were examined that were aphid infested and the incidence of each cereal aphid species are shown in Table 4.9 for each field. At least one of the ten barley plants examined in each field was infested by at least one aphid in 25 of the 45 crops on the first visit to each field. In a further 11 fields, no aphids were found on the ten examined plants but aphids were observed in the crop: these fields are given aphid infestation values of 0.5 in Table 4.9.

Table 4.8 Incidence of cereal aphids in different regions of south-west & central Scotland in the spring 1989; winter barley 1988/89.

Region	No of fields	No of fields with aphid species[a]		
		Rp	Md	Sa
Dumfriesshire	10	1	4	10
Wigtownshire	5	4	2	2
Ayrshire	7	2	0	4
Renfrewshire	11	1	0	10
Stirlingshire	7	0	1	7
Lanarkshire	5	0	0	0
Totals	45	8	7	33

[a] observed on ten examined plants or elsewhere in crop.

Rp *Rhopalosiphum padi* Md *Metopolophium dirhodum*
Sa *Sitobion avenae*

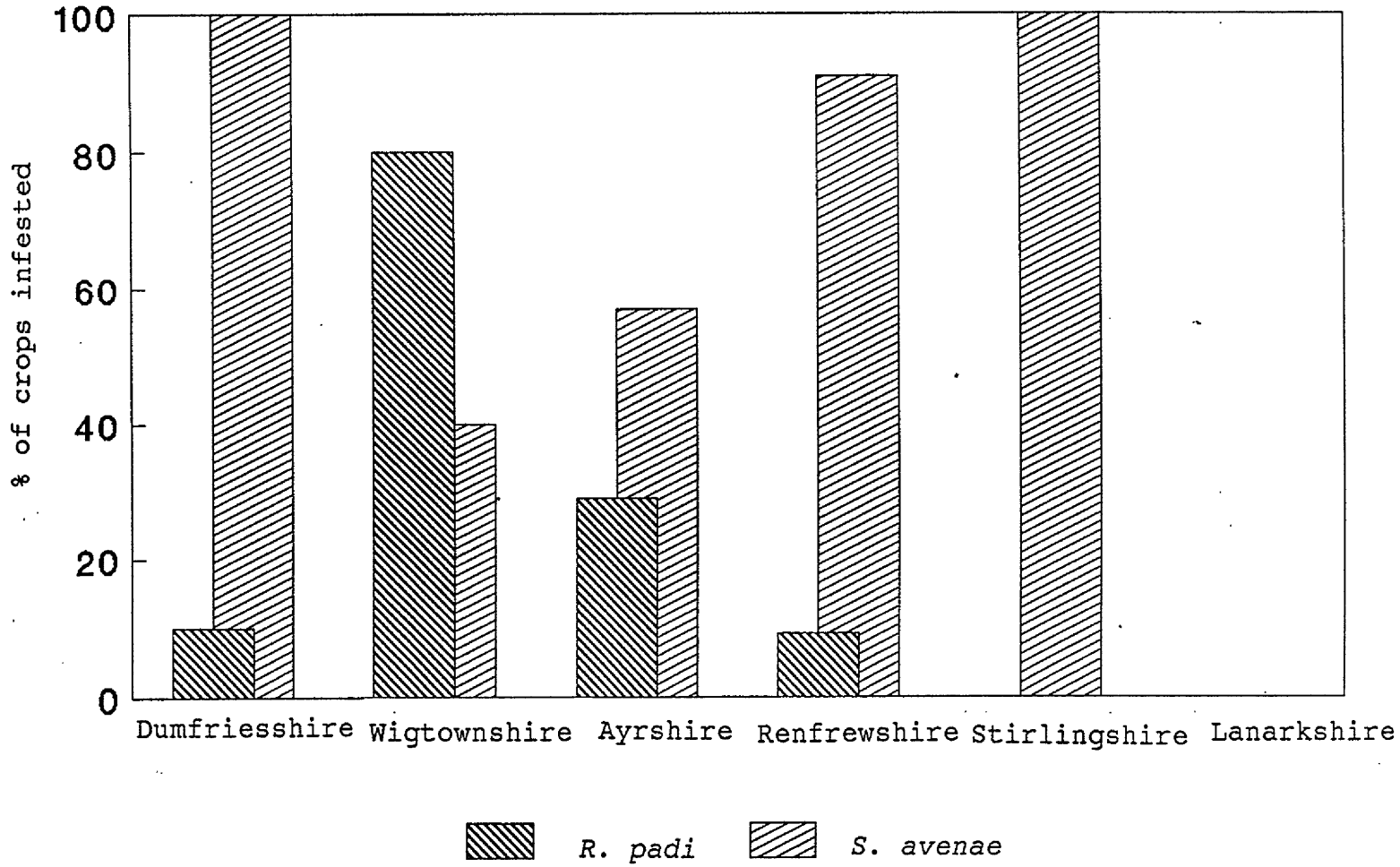


Figure 4.4 The percentage of sampled crops in each region infested by *Rhopalosiphum padi* and *Sitobion avenae* in the spring 1989.

Table 4.9 Incidence of *Metopolophium dirhodum*, *Rhopalosiphum padi* and *Sitobion avenae* in each field in the spring of 1989 and the numbers of plants out of the ten examined which were aphid infested; winter barley 1988/89.

Field	Incidence of aphid species[a]			Number of plants[b] infested
	M. dirhodum	*R. padi*	*S. avenae*	
Dumfriesshire				
D1	-	-	2	0.5
D2	-	-	2	1
D3	1	-	2	5
D4	1	-	2	8
D5	1	-	2	8
D6	1	-	2	9
D7	-	-	2	8
D8	-	1	2	5
D9	-	-	2	4
D10	-	-	2	2
Wigtownshire				
W1	-	2	-	7
W2	1	2	1	5
W3	-	2	-	0.5
W4	-	2	-	0.5
W5	1	2	1	8
Ayrshire				
A1	-	1	2	8
A2	-	-	-	0
A3	-	-	2	0.5
A4	-	-	2	1
A5	-	1	2	6
A6	-	-	-	0
A7	-	-	-	0
Renfrewshire				
R1	-	-	2	0.5
R2	-	-	2	8
R3	-	-	2	7
R4	-	-	2	2
R5	-	-	-	0
R6	-	-	2	2
R7	-	-	2	0.5
R8	-	-	2	0.5
R9	-	-	2	0.5
R10	-	1	2	10
R11	-	-	2	5

Table 4.9 continued.

Field	Incidence of aphid species[a]			Number of plants[b] infested
	M. dirhodum	*R. padi*	*S. avenae*	
Stirlingshire				
S1	-	-	2	1
S2	-	-	2	1
S3	-	-	2	0.5
S4	-	-	2	5
S5	-	-	2	5
S6	1	-	2	0.5
S7	-	-	2	0.5
Lanarkshire				
L1	-	-	-	0
L2	-	-	-	0
L3	-	-	-	0
L4	-	-	-	0
L5	-	-	-	0

a - aphid species not observed.

1 aphid species observed but not predominant.

2 aphid species predominant.

b 0.5 denotes no aphids found on ten examined plants but aphids found elsewhere in crop.

Seventy-three per cent of fields were infested by *S. avenae* compared with 18 and 16% for *R. padi* and *M. dirhodum* respectively. *S. avenae* was found in all regions except Lanarkshire where no aphids were observed, whilst *R. padi* although observed in four regions, was numerous only in Wigtownshire. *M. dirhodum* was present in low numbers in three regions, most of these in the southernmost regions of Dumfriesshire and Wigtownshire.

The aphid infestation data (percentage of the ten examined plants which were aphid infested for each field shown in Table 4.9) were analysed to test whether there were aphid infestation associations with the following four factors: region, previous cropping type, sowing date or predominant aphid species. The five *regional* means of aphid infestation are given in Table 4.10, the five *previous crop type* means in Table 4.11, the three *predominant aphid species* means in Table 4.12 and the four *sowing date category* means in Table 4.13.

Table 4.10 *Regional* means and standard deviations of aphid infestation; winter barley 1988/89.

Region	n	mean	sd
Dumfriesshire	10	50.1	32.1
Wigtownshire[a]	5	40.4	37.6
Ayrshire	7	21.6	33.8
Renfrewshire	11	31.3	37.2
Stirlingshire	7	17.6	22.5
Lanarkshire	5	0.0	-

[a] 4 of the 5 fields received a spring insecticide application prior to the survey.

Variance ratio for ANOVA: 1.72, df 4, 35, N.S. (Lanarkshire excluded).

Table 4.11 *Previous crop type* means and standard deviations of aphid infestation; winter barley 1988/89.

Previous crop	n	mean	sd
Ryegrass pasture	3	56.7	51.3
Oilseed rape	6	43.3	36.1
Spring barley	14	33.7	30.7
Winter barley	15	21.1	31.7
Winter wheat	7	14.7	29.1

Variance ratio for ANOVA: 0.96, df 4, 40, N.S.

Table 4.12 *Sowing date* category means and standard deviations of aphid infestation; winter barley 1988/89.

Sowing date category	n	mean	sd
Early September	9	41.3	35.2
Late September	29	25.1	31.3
Early October	4	35.0	43.6
Late October	3	26.7	46.2

Variance ratio for ANOVA: 2.25, df 2, 42, N.S

Table 4.13 *Aphid type* means and standard deviations of aphid infestation; winter barley 1988/89.

Aphid species	n	mean	sd
R. padi	5	40.4	37.6
S. avenae	31	36.1	33.6
No aphids	9	-	-

t = 0.45, df 34, N.S.

The eighteen group means (of the four factors) of aphid infestation are ranked in Figure 4.5. Important characteristics of these data were that all the standard deviations were high and the distributions were skewed towards zero. Two aphid infestation means were above 50%, the *previous crop type*, "ryegrass" and the *region*, "Dumfriesshire" compared with 13 aphid infestation means in the range 14 to 44%.

For *previous crop type*, the aphid infestation means varied from 56.7% for "ryegrass" to 14.7% for "winter wheat". *Region* showed the widest distribution. "Dumfriesshire" had a mean of 50.1% compared with "Ayrshire" and "Stirlingshire" with approximately 20% each and "Lanarkshire" with 0%. "Wigtownshire" had a mean of 40.4% which was the same as the mean of *predominant aphid species*, "*R. padi*", this association being an important feature of these and the crop yellowing data. *Sowing date categories* were aggregated in the range 25 to 41%, and were

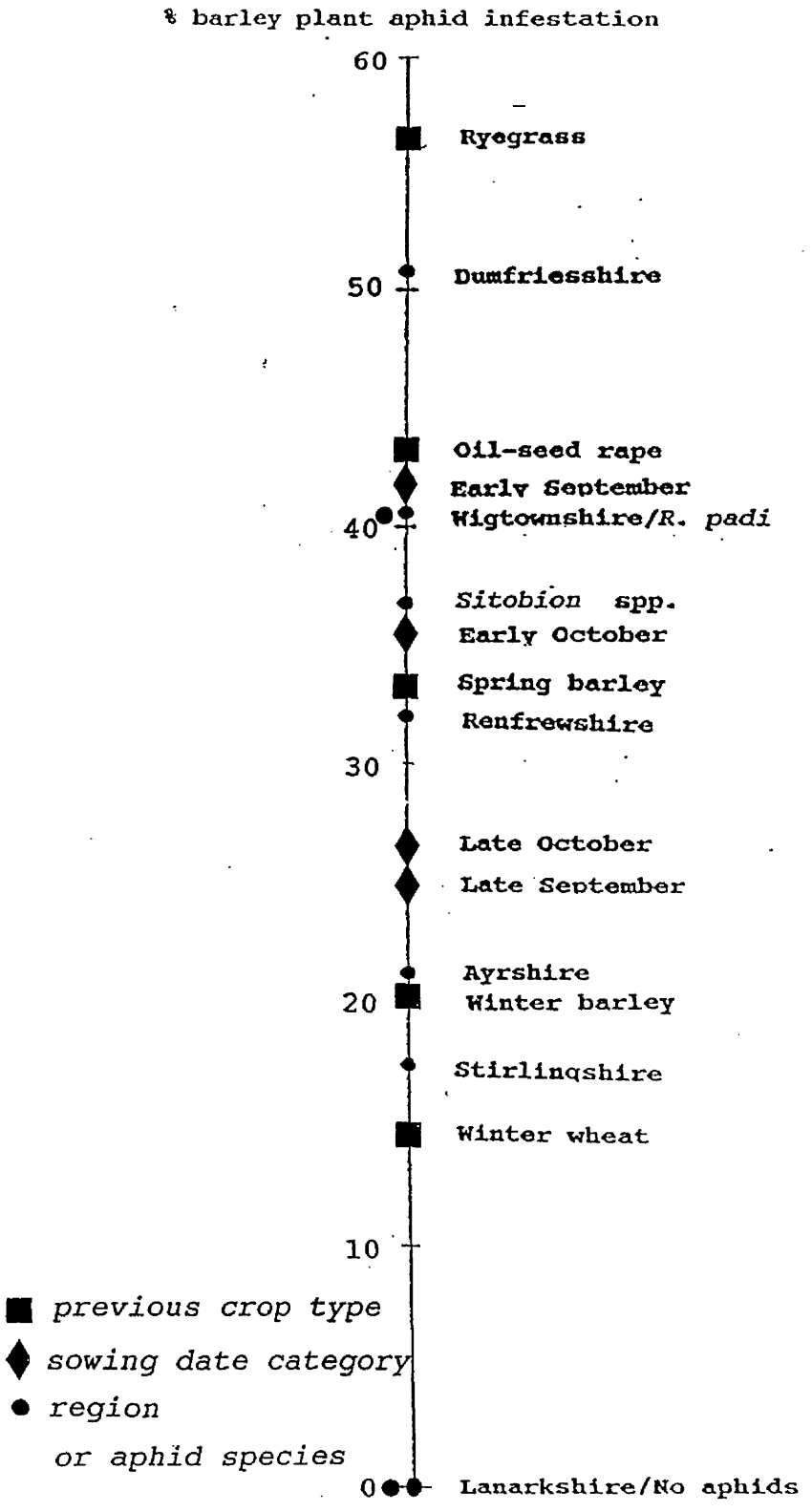


Figure 4.5 The distribution of the 18 means of barley plant aphid infestation; spring 1989.

not ranked with the earliest sowing date having the greatest level of aphid infestation. The distribution of *predominant aphid species* showed that "*R. padi*" and "*S. avenae*" had similar means. Two aphid infestation means were zero; the *region*, "Lanarkshire" and the *predominant aphid species*, "no aphids".

Variation of the aphid infestation data within three of the four factors was analysed using single factor analysis of variance (ANOVA). "Lanarkshire" data were excluded in the test for region, because none of the 50 plants examined in "Lanarkshire" was aphid infested. All three ANOVA variance ratios were non-significant owing to the amount of variation between fields within factors. The factor, *predominant aphid species*, was not tested, using analysis of variance, because of the group "no aphids". Using a t-test, the difference between the "*R. padi*" and "*S. avenae*" aphid infestation data was found to be non-significant ($t = 0.45$, df 34).

4.3.3 **Methodology for BYDV survey, spring 1989**

The 45 winter barley crops sampled for aphids in the spring 1989 were also surveyed for BYDV.

To assess which BYDV strains were present, several leaves from one yellow plant (to obtain a 1 g leaf sample) in five randomly selected yellow patches were collected during a circuit of each field using the tramlines. Symptomless infection was assessed by collecting several

leaves from one green plant (to obtain a 1 g leaf sample) in five randomly selected green areas of the crop. Samples were tested for BYDV by ELISA (Mortar and Pestle method).

In each field, three BYDV symptom categories were assessed; (a) incidence of patches in which plant death had occurred (attributable to BYDV infection).

(b) incidence of patches of stunted yellow plants (chrome-yellow discolouration at the ends of leaves) appearing as yellow saucer-shaped depressions in the crop.

(c) incidence of patches of plants which had a spikey appearance and had leaves which were twisted and showed signs of "turning yellow".

4.3.4 **Results of BYDV survey, spring 1989**

Yellow plants (Figure 4.6) were found in all 45 winter barley crops in the six regions during late April/early May. Thirty-eight fields contained patches of yellow plants (Figure 4.7) on the first visit.

The percentage of yellow and green leaf samples that gave a positive ELISA test for each BYDV strain in each region is given in Table 4.14 (for samples collected on the first visit). Overall, for yellow leaf samples, 63, 12 and 11% of leaves tested were infected with the MAV, PAV and RPV strains respectively. The comparative figures for green leaf samples were 8, 9 and 4%.

Figure 4.6 Barley plants showing characteristic symptoms of BYDV: a generally spikey appearance with chrome-yellow discolouration at distal ends of leaves.

Figure 4.7 A winter barley crop with extensive areas comprised of patches of yellow plants characteristic of BYDV. This crop was the worst case of *S. avenae*-transmitted BYDV in the spring of 1989.

Table 4.14 Incidence of BYDV strains in yellow and green leaf samples collected from winter barley crops in the spring 1989.

Region	Yellow leaves: Number of fields sampled	Yellow leaves: Number of leaves tested	Yellow leaves: Percentage of positive tests for BYDV strain RPV	Yellow leaves: Percentage of positive tests for BYDV strain PAV	Yellow leaves: Percentage of positive tests for BYDV strain MAV	Green leaves: No of leaves tested	Green leaves: Percentage of positive tests for BYDV strain RPV	Green leaves: Percentage of positive tests for BYDV strain PAV	Green leaves: Percentage of positive tests for BYDV strain MAV
Dumfriesshire	10	52	4	6	52	38	3	-	5
Wigtownshire	5	26	73	58	77	24	25	42	21
Ayrshire	7	25	-	4	48	18	-	6	6
Renfrewshire	11	50	-	6	70	53	-	6	6
Stirlingshire	7	33	-	-	88	32	-	3	9
Lanarkshire	5	10	-	10	10	21	-	5	-
Totals	45	196				186			
		%	11	12	63		4	9	8

- no samples gave positive ELISA test for strain

Leaf samples collected from 16 fields on a second occasion during the spring were not tested because the data were not required. Table 4.15 shows the estimated percentage area of each crop comprised of patches of yellow plants on the first visit and the number of positive BYDV tests for the yellow and green leaf samples (regional totals also provided).

Table 4.15 The incidence of each BYDV strain in the yellow and green leaf samples and the percentage area of each winter barley crop comprised of yellow plants; BYDV survey, spring 1989.

	No of positive tests for BYDV strain							
	Yellow leaves				Green leaves			
Field	n	RPV	PAV	MAV	n	RPV	PAV	MAV	% of crop yellow
Dumfriesshire									
D1	10	2	2	2	0	-	-	-	1
D2	4	-	1	-	0	-	-	-	0.5
D3	4	-	-	2	3	-	-	-	0.5
D4	5	-	-	2	5	1	-	-	0.5
D5	5	-	-	4	5	-	-	2	10
D6	5	-	-	5	5	-	-	-	15
D7	5	-	-	4	5	-	-	-	15
D8	4	-	-	2	5	-	-	1	50
D9	5	-	-	4	5	-	-	-	10
D10	5	-	-	2	5	-	-	-	1
Totals	52	2	3	27	38	1	-	2	
Wigtownshire									
W1	5	5	3	5	5	-	2	2	75
W2	5	-	1	5	5	1	2	2	50
W3	6	5	6	4	5	2	3	-	50
W4	5	4	4	1	5	-	1	1	4
W5	5	5	1	5	4	3	2	-	75
Totals	26	19	15	20	24	6	10	5	

- no appreciable yellowing in crop or no positive ELISA test for BYDV strain in the leaf samples.

Table 4.15 continued.

	No of positive tests for BYDV strain							
	Yellow leaves				Green leaves			
Field	n	RPV	PAV	MAV	n	RPV	PAV	MAV	% of crop yellow
Ayrshire									
A1	5	-	-	2	5	-	-	1	1
A2	5	-	1	5	0	-	-	-	50
A3	5	-	-	-	0	-	-	-	0.5
A4	5	-	-	-	0	-	-	-	0.5
A5	5	-	-	5	5	-	1	-	0.5
A6	0	-	-	-	3	-	-	-	-
A7	0	-	-	-	5	-	-	-	-
Totals	25	-	1	12	18	-	1	1	
Renfrewshire									
R1	5	-	-	2	5	-	-	1	-
R2	4	-	1	4	4	-	-	-	10
R3	5	-	-	-	5	-	1	-	-
R4	4	-	1	4	5	-	-	-	4
R5	4	-	-	1	5	-	-	-	3
R6	5	-	-	5	5	-	-	-	5
R7	5	-	-	3	5	-	-	-	0.5
R8	5	-	-	4	5	-	1	1	5
R9	4	-	-	3	5	-	-	-	0.5
R10	5	-	-	5	5	-	1	1	50
R11	4	-	1	4	4	-	-	-	1
Totals	50	-	3	35	53	-	3	3	
Stirlingshire									
S1	4	-	-	4	5	-	-	1	1
S2	4	-	-	4	5	-	-	-	5
S3	5	-	-	5	5	-	-	1	0.5
S4	5	-	-	5	5	-	-	-	0.5
S5	5	-	-	4	2	-	-	1	5
S6	5	-	-	2	5	-	1	-	0.5
S7	5	-	-	5	5	-	-	-	0.5
Totals	33	-	-	29	32	-	1	3	
Lanarkshire									
L1	3	-	-	1	3	-	-	-	
L2	3	-	1	-	3	-	1	-	1
L3	4	-	-	-	5	-	-	-	0.5
L4	0	-	-	-	5	-	-	-	-
L5	0	-	-	-	5	-	-	-	-
Totals	10	-	1	1	21	-	1	-	

On the second visit to 16 of the 45 fields, the estimated percentage area of each crop comprised of patches of yellow plants had not noticeably changed. Dumfriesshire, Wigtownshire, Ayrshire and Renfrewshire all had at least one field in which 50% of the crop was comprised of patches of yellow plants. Fields without patches of yellow plants were distributed as follows: two in both of Ayrshire and Renfrewshire and three in Lanarkshire. Plant death occurred in all five Wigtownshire fields (Figure 4.8), but was not observed in fields of any other region. A general "spikey and crisp" appearance of crops was observed in all regions.

There was a significant difference in the ratios of BYDV strains between the yellow leaf samples of Wigtownshire and all other regions (pooled to avoid low expectations, $[x^2_{(2)} = 58.9, P < 0.001]$), because RPV and PAV were only common in the Wigtownshire yellow leaf samples. In the green leaf samples, there was a significant difference in the ratios of the RPV + PAV strains to the MAV strain between Wigtownshire and all other regions (pooled to avoid low expectation $x^2_{(1)} = 4.1, P < 0.05$), because the incidence of the RPV + PAV strains was much greater than the incidence of MAV in Wigtownshire. In Wigtownshire, all three strains were present in at least 50% of yellow leaf samples and in more than 20% of green leaf samples. In all other regions except Lanarkshire, only MAV was present in more than 48% of yellow leaf samples and no strain was present in more than 10% of green leaf samples.

(b)

Figure 4.8 Plant symptoms associated with *R. padi*-transmitted BYDV in Wigtownshire in the spring of 1989: (a) a patch with severely-stunted plants including areas where plant death has occurred, (b) the field view.

In Lanarkshire, yellow leaf samples were difficult to obtain, thus twice as many green samples were collected as yellow ones. Two yellow and one green Lanarkshire leaf samples gave a postive result, two for the PAV and one for the MAV strain.

Similarity of BYDV strain incidence in the yellow and the green leaf samples was tested for by a Chi-squared test between the "all regions" BYDV strain ratios of yellow and green leaf samples ($x^2_{(2)} = 20.7$, $P < 0.001$). The significant result indicates that the BYDV strain incidences were dissimilar due to the scarcity of MAV in the green leaf samples relative to its abundance in the yellow leaf samples.

The estimates of the percentage area of each crop comprised of patches of yellow plants were analysed to test whether there were associations between the extent of BYDV infection and the following four factors: region, previous cropping type, sowing date and predominant aphid species. The five *regional* means of crop yellowing are given in Table 4.16 and Figure 4.9, the five *previous crop type* means in Table 4.17, the three *predominant aphid species* means in Table 4.18 and the four *sowing date category* means in Table 4.19.

Table 4.16 *Regional* means and standard deviations of percentage areas of each crop comprised of patches of yellow plants; winter barley 1988/89.

Region	n	mean	sd
Dumfriesshire	10	10.4	15.2
Wigtownshire	5	50.8	29.0
Ayrshire	7	7.5	18.7
Renfrewshire	11	7.2	14.5
Stirlingshire	7	1.9	2.2
Lanarkshire	5	0.3	0.5

Variance ratio for ANOVA: 7.23, df 5, 39, $P < 0.001$

Table 4.17 *Previous cropping* means and standard deviations of percentage areas of each crop comprised of patches of yellow plants; winter barley 1988/89.

Previous crop	n	mean	sd
Ryegrass pasture	3	41.7	38.2
Winter barley	15	13.6	24.1
Winter wheat	7	8.2	18.5
Oilseed rape	6	6.3	5.2
Spring barley	14	5.6	13.2

Variance ratio for ANOVA: 1.69, df 4, 40, N.S.

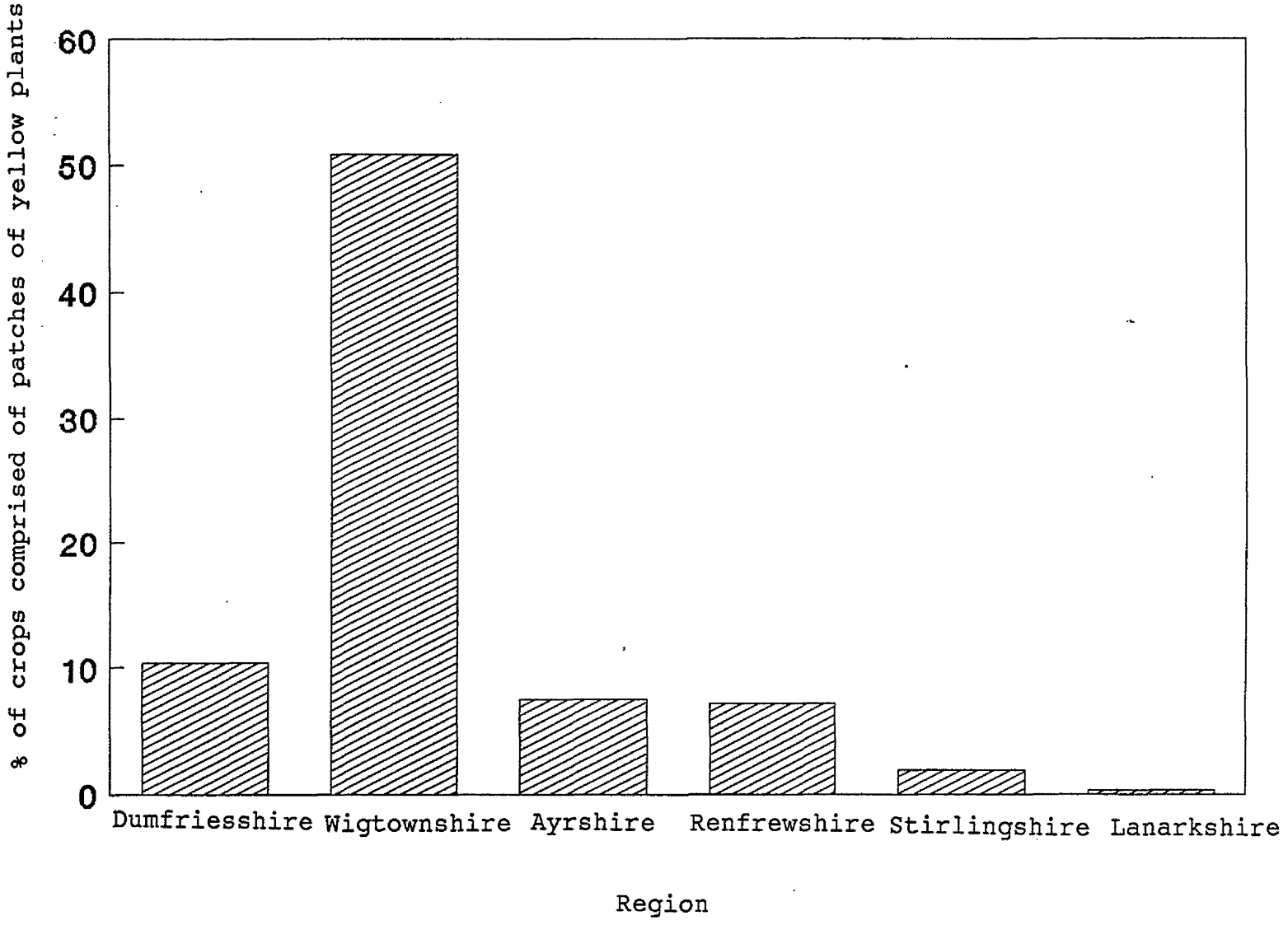


Figure 4.9 The mean percentage area of winter barley crops comprised of patches of yellow plants in each region; spring 1989.

4.18 *Sowing date category* means and standard deviations of percentage areas of each crop comprised of patches of yellow plants; winter barley 1988/89.

Sowing date category	n	mean	sd
Early September	9	31.4	35.2
Late September	29	10.6	19.5
Early October	4	14.3	23.9
Late October	3	0.3	0.6

Variance ratio for ANOVA: 0.13, df 2, 42, N.S.

Table 4.19 *Predominant aphid species* means and standard of percentage areas of each crop comprised of patches of yellow plants; winter barley 1988/89.

Aphid species	n	mean	sd
R. padi	5	50.8	29.0
S. avenae	31	6.3	12.5
No aphids	9	6.1	16.5

Variance ratio for ANOVA: 16.03, df 2, 42, $P < 0.001$

These 18 group means (of the four factors) of percentages of the crops comprised of patches of yellow plants are ranked in Figure 4.10. Important characteristics of these data were that all the standard deviations were high and the distributions were skewed towards zero. The

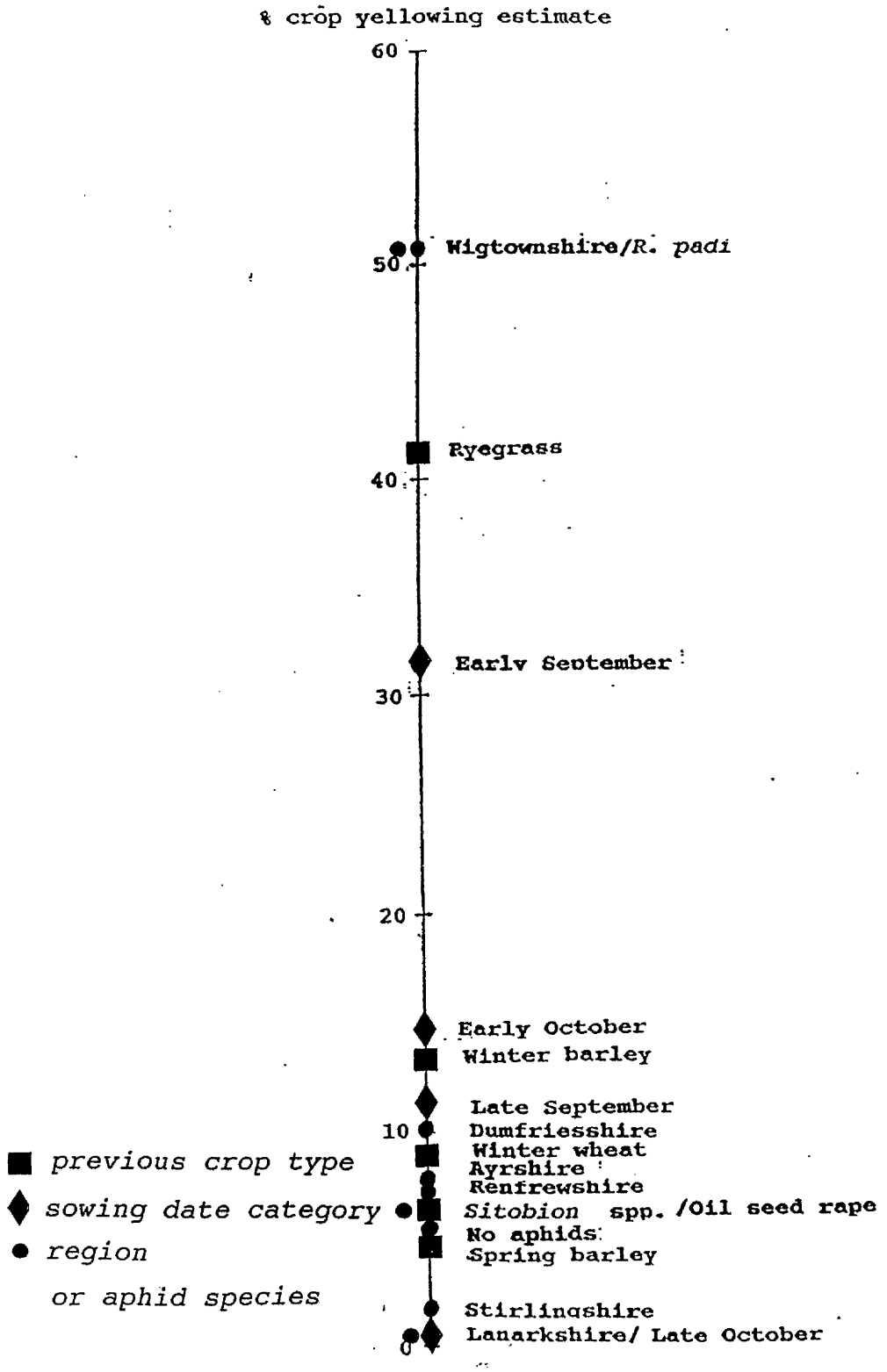


Figure 4.10 The distribution of the 18 means of percentage of winter barley crops comprised of patches of yellow plants; spring 1989.

latter characteristic is due to the fact that 58% of fields had crop yellowing estimates of 1% or less, thus the distribution of the 18 means in Figure 4.10 is also skewed towards zero. This is in contrast to the barley plant aphid infestation means in Figure 4.4 which are normally distributed. Two crop yellowing means were above 50%, the *region*, "Wigtownshire" and the *predominant aphid species*, "*R. padi*", whilst another four were in the range 13 to 42%. Nine crop yellowing means were grouped closely together between 5 and 11% whilst another three were below 2%. The three lowest means belonged to two *regions*, "Stirlingshire" and "Lanarkshire", and the *sowing date category*, "late October".

Thus, "region" had the widest range (50.6%) of crop yellowing means: the highest regional mean was "Wigtownshire" with 50.9%, whilst "Lanarkshire" with a mean of 0.3% had the same mean as the *sowing date category*, "late October". The ranges of the other three factors decreased in the following order: *predominant aphid species* (44.7%); *previous crop type* (36.1%); and *sowing date category* (31.1%).

Variation of the percentage crop yellowing data within each of the four factors was analysed using ANOVA. The variation of the percentage areas of crops comprised of patches of yellow plants between *regions* and *predominant aphid species* gave significant results (arcsine

Table 4.20 *Regional* variation in arcsine (% crop yellowing estimates spring 1989); single factor ANOVA.

ANALYSIS OF VARIANCE ON Arcsine % crop yellowing estimate

SOURCE	DF	SS	MS	F	p
Region	5	5941	1188	7.23	0.000
ERROR	39	6407	164		
TOTAL	44	12348			

LEVEL	N	MEAN	STDEV	INDIVIDUAL 95 PCT CI"S FOR MEAN BASED ON POOLED STDEV
Dumfriesshire	10	15.11	13.23	(----*---)
Wigtownshire	5	44.31	19.80	(-----*-----)
Ayrshire	7	8.99	16.03	(---*----)
Renfrewshire	1	11.33	12.59	(---*---)
Stirlingshire	7	6.83	4.21	(---*----)
Lanarkshire	5	1.96	2.75	(-----*-----)

POOLED STDEV = 12.82

0 20 40 60

Table 4.21 *Predominant aphid species* variation in arcsine (% crop yellowing estimates spring 1989); single factor ANOVA.

ANALYSIS OF VARIANCE ON Arcsine % crop yellowing estimate

SOURCE	DF	SS	MS	F	p
Aphid spp.	2	5345	2673	16.03	0.000
ERROR	42	7002	167		
TOTAL	44	12348			

LEVEL	N	MEAN	STDEV	INDIVIDUAL 95 PCT CI"S FOR MEAN BASED ON POOLED STDEV
No aphids	9	7.20	14.61	(----*-----)
S. avenae	31	10.69	11.15	(--*--)
R. padi	5	44.31	19.80	(-------*------)

POOLED STDEV = 12.91

0 16 32 48

transformation of crop yellowing estimates). The analysis of variance tables for these two factors are shown above (Tables 4.20 & 4.21):

P. annua In July 1989, as part of pre-harvest sampling (Chapter 8), ten *P. annua* plants were collected from each of 14 of the 45 winter barley fields from all regions except Lanarkshire (3 fields per region except in Ayrshire). The percentage of the regional totals of *P. annua* collected, which gave positive ELISA tests for each BYDV strain are shown in Table 4.22. Similarity of BYDV infection in yellow cereal leaf samples collected in the spring and in *P. annua* plants collected in July was tested for by a Chi-squared test between the "all regions" BYDV strain ratios in yellow cereal leaf samples and in *P. annua* samples ($x^2_{(2)} = 31.6$, $P < 0.001$). The significant result was due to the much higher frequencies of the RPV and PAV strains in *P. annua* than in yellow cereal leaf samples.

Figure 4.11 shows the scatterplot between the regional percentage BYDV infection of yellow cereal leaf and *P. annua* samples (except Lanarkshire which was not visited for pre-harvest sampling). Although the relationship is not linear (test for linear regression on the arcsine transformed data gave a non-significant result, $r = 0.485$, df 13, N.S.), greater percentages of infection in yellow cereal leaf samples are reflected to some extent, in

greater infection in *P. annua*, particularly for the MAV strain.

Table 4.22 Percentage BYDV infection of *Poa annua* collected in July 1989 for each region.

Region	No of plants tested	Percentage of positive tests for BYDV strain		
		RPV	PAV	MAV
Dumfriesshire	25	48	56	100
Wigtownshire	29	72	83	31
Ayrshire	19	53	58	32
Renfrewshire	29	0	10	76
Stirlingshire	30	3	17	63

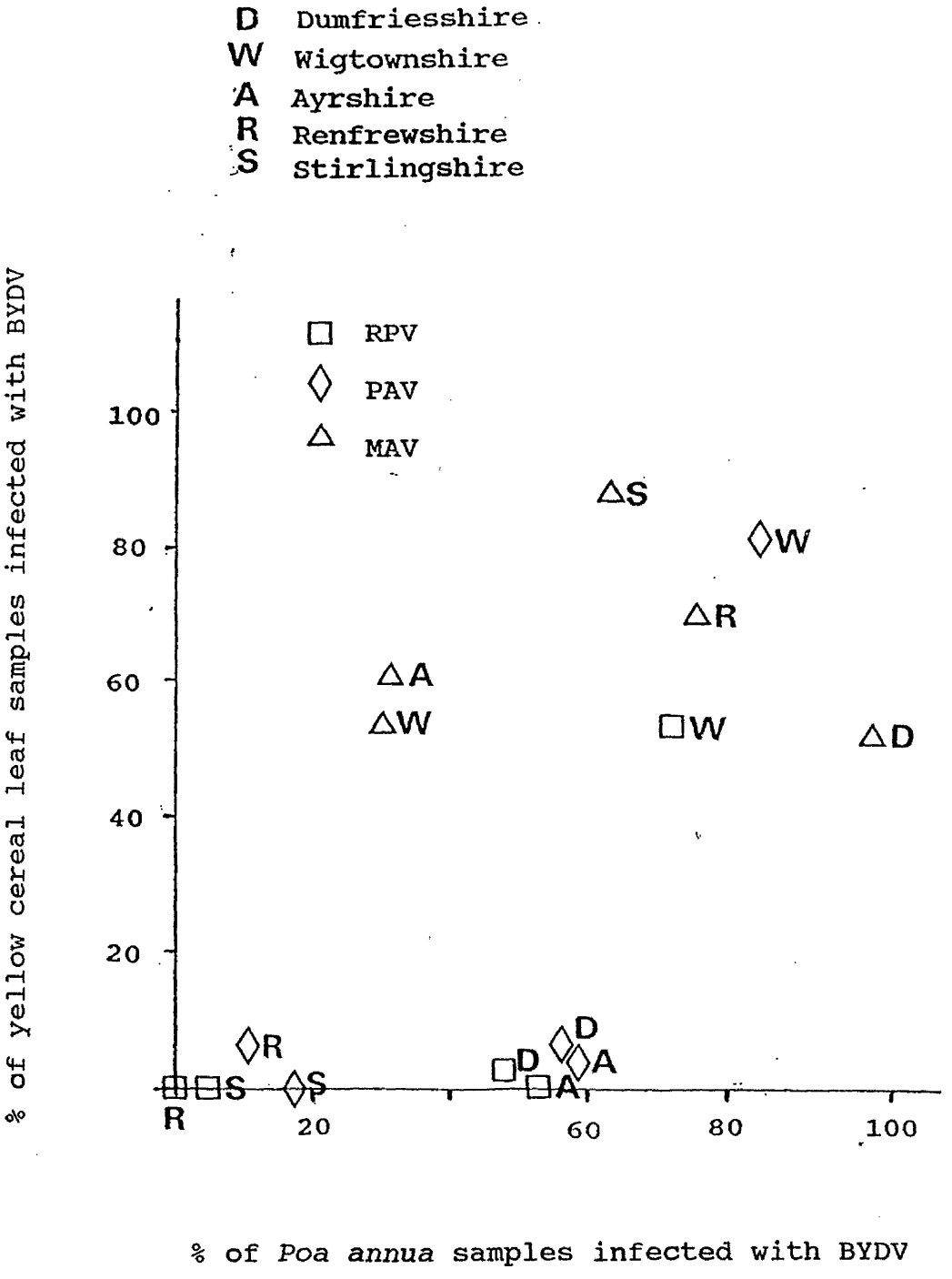


Figure 4.11 Scatterplot between the regional percentage of yellow leaf samples collected in the spring and the regional percentage of *Poa annua* samples collected in July infected with each BYDV strain; BYDV 1988/89.

4.4 BYDV epidemiology in winter barley, 1989/90

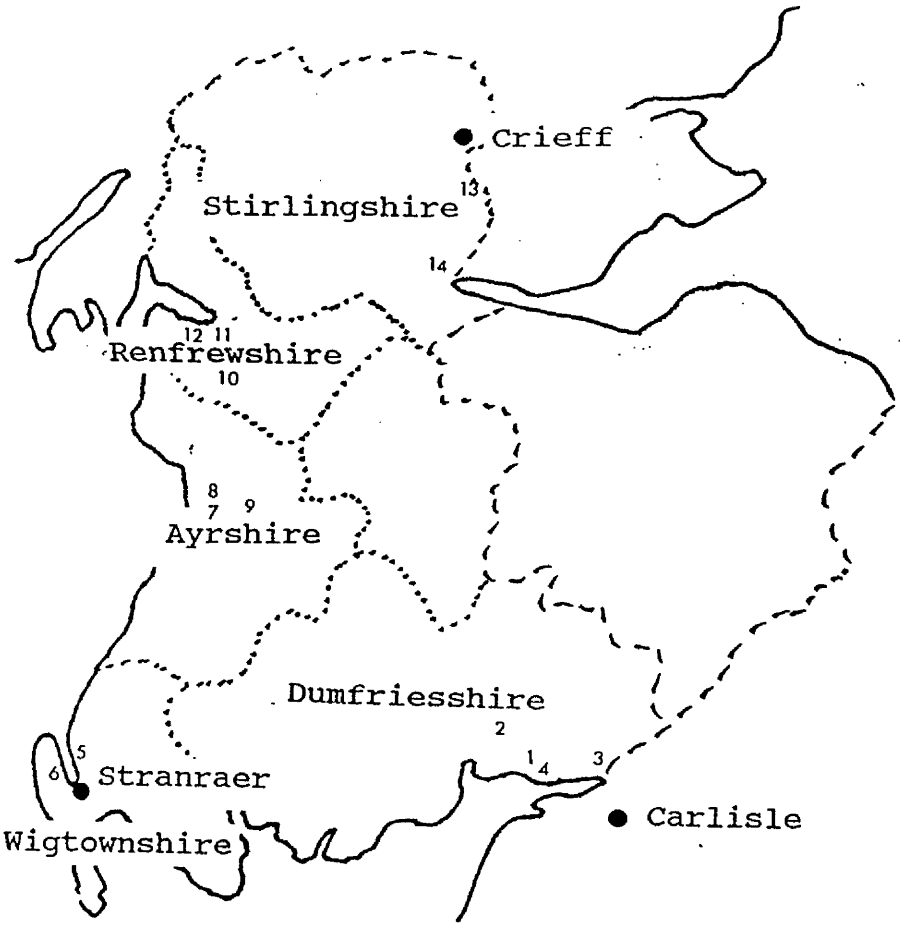
4.4.1 Methodology for aphid sampling in winter barley, autumn 1989, winter and spring 1990

Twenty-six winter barley crops in the following five regions were sampled: Dumfriesshire, Wigtownshire, Ayrshire, Renfrewshire and Stirlingshire (Figure 4.12).

Ten metre lengths of drill were examined during a circuit of each field. Sparse metre lengths of drill (< 50 plants) were not selected. From April, tramlines were used and the metre length samples were selected from a metre wide swath either side of the tramlines. Only one sample was selected from either headland with tramlines at right angles to the interior tramlines. Other samples were selected using tramlines away from headlands.

Aphid colonies instead of aphid individuals were counted in each of these metre lengths. A colony was defined as "a group of aphids numbering one or more". Thus, one adult with eight nymphs is one colony, as is a group of six nymphs without a parent. This method reduces the number of occasions when counting to large numbers is necessary and it gives an epidemiologically meaningful measure of the aphid infestation level, because it records the number of potential sites of patches of infected plants. The numbers of colonies in each metre length for *Rhopalosiphum* spp. and *S. avenae* were noted.

Autumn sampling Bi-monthly sampling commenced during late-September in four Dumfriesshire fields, during October in



Dumfriesshire			
1. Charlesfield (Hoddom & Kinmount estate)	D1		
2. Dryfeholme	D2	D3	
3. Gretna House	D4	D5	
4. Spittalriddinghill	D6	D7	
Wigtownshire			
5. Beoch	W1	W2	W3
6. Kirranrae	W4		
Ayrshire			
7. Auchincruive estate	A1	A2	
8. Newlands	A3		
9. Barskimming estate	A4	A5	
Renfrewshire			
10. Arkleston	R1	R2	R3
11. Barrangary	R4	R5	
12. Erskine Home	R6	R7	
Stirlingshire			
13. Shearerston (Colquazie estates)	S1	S2	
14. Southwood	S3		

Figure 4.12 Locations of crops sampled in winter barley season 1989/90.

21 other fields and during early-November in one Wigtownshire field. In 16 fields, the last autumn visit was in November, making a total of two visits in four fields, three visits in 11 and four visits in one. In the seven Renfrewshire fields and the three Stirlingshire fields, the last autumn visit occurred in mid-December, making a total of three visits in four fields and four visits in six.

Winter sampling Sampling took place in all three winter months. In Ayrshire, three fields were sampled in late January, A1, A2 and A5. In mid-February, three Wigtownshire fields were sampled, W2, W3 and W4. In mid-March, four Ayrshire fields were sampled, A3, A4 and A5 and A2.

Spring sampling All 26 fields were sampled monthly from April to June. Two Ayrshire fields, A4 and A5, were sampled twice in April.

4.4.2 Results of aphid sampling in winter barley, autumn 1989 and winter, spring 1990

Autumn sampling 1989 The total numbers of aphid colonies in each field in each region are shown in Table 4.23. Means of the number of aphid colonies in each field during the whole autumn (in both 1989 & 1990) were not calculated for two reasons. Firstly, there was variability in the number of colonies between sampling dates, which in combination with the differing numbers of visits to each field, would give misleading values. Secondly, fractions of aphid colonies are more difficult to comprehend than whole numbers of aphid colonies.

Table 4.23 Total numbers of *Rhopalosiphum* spp. and *Sitobion avenae* colonies in 26 winter barley fields; autumn 1989.

Field	No of visits	Numbers of aphid colonies	
		Rhopalosiphum spp.	*S. avenae*
Dumfriesshire			
D1	2	1	2
D2	3	4	7
D3	3	3	7
D4	3	0	0
D5	3	1	0
D6	2	0	1
D7	2	0	1
Totals		9	18
Wigtownshire			
W1	3	9	4
W2	3	1	0
W3	2	43	10
W4	3	2	3
Totals		55	17
Ayrshire			
A1	3	5	4
A2	3	4	19
A3	3	0	0
A4	4	47	0
A5	3	83	0
Totals		139	23
Renfrewshire			
R1	4	1	17
R2	4	2	13
R3	4	0	14
R4	3	0	1
R5	3	0	0
R6	3	0	0
R7	3	4	0
Totals		7	45
Stirlingshire			
S1	4	0	0
S2	4	2	1
S3	3	12	0
Totals		14	1

There are two important features of the cumulative total number of colonies in each field during the autumn visits (Table 4.23), and the regional totals (Table 4.23 & Figure 4.13), for *Rhopalosiphum* spp. and *S. avenae*. Firstly, that there was heterogeneity in aphid species incidence within regions, and secondly, that the regional aphid colony totals reflect large aphid colony totals in a minority of fields. For example, in Wigtownshire and Ayrshire, one and two fields respectively, which followed untreated ploughed-in grass leys contributed most of the *Rhopalosiphum* colonies in the form of apterous *padi* (on occasions, > 10 colonies per metre length). These crops were W3, A4 and A5.

There was a significant difference between regions in the ratios of *Rhopalosiphum* colony totals to *S. avenae* colony totals during the autumn 1989 ($x^2_{(4)} = 116.9$, $P < 0.001$, 1 expected count was marginally less than 5). Sixty-two per cent of the total Chi-square value was contributed by the Renfrewshire colony totals, because *S. avenae* was much more numerous than *Rhopalosiphum* spp. in this region, although overall, *Rhopalosiphum* colonies were twice as numerous as *S. avenae* colonies. Also, the Wigtownshire and Ayrshire *Rhopalosiphum* colony totals were large relative to the other regional aphid colony totals.

When the colony totals of W3, A4 and A5 were excluded, a Chi-squared test on the regional ratios of *Rhopalosiphum* colonies to *S. avenae* colonies of Wigtownshire and Ayrshire

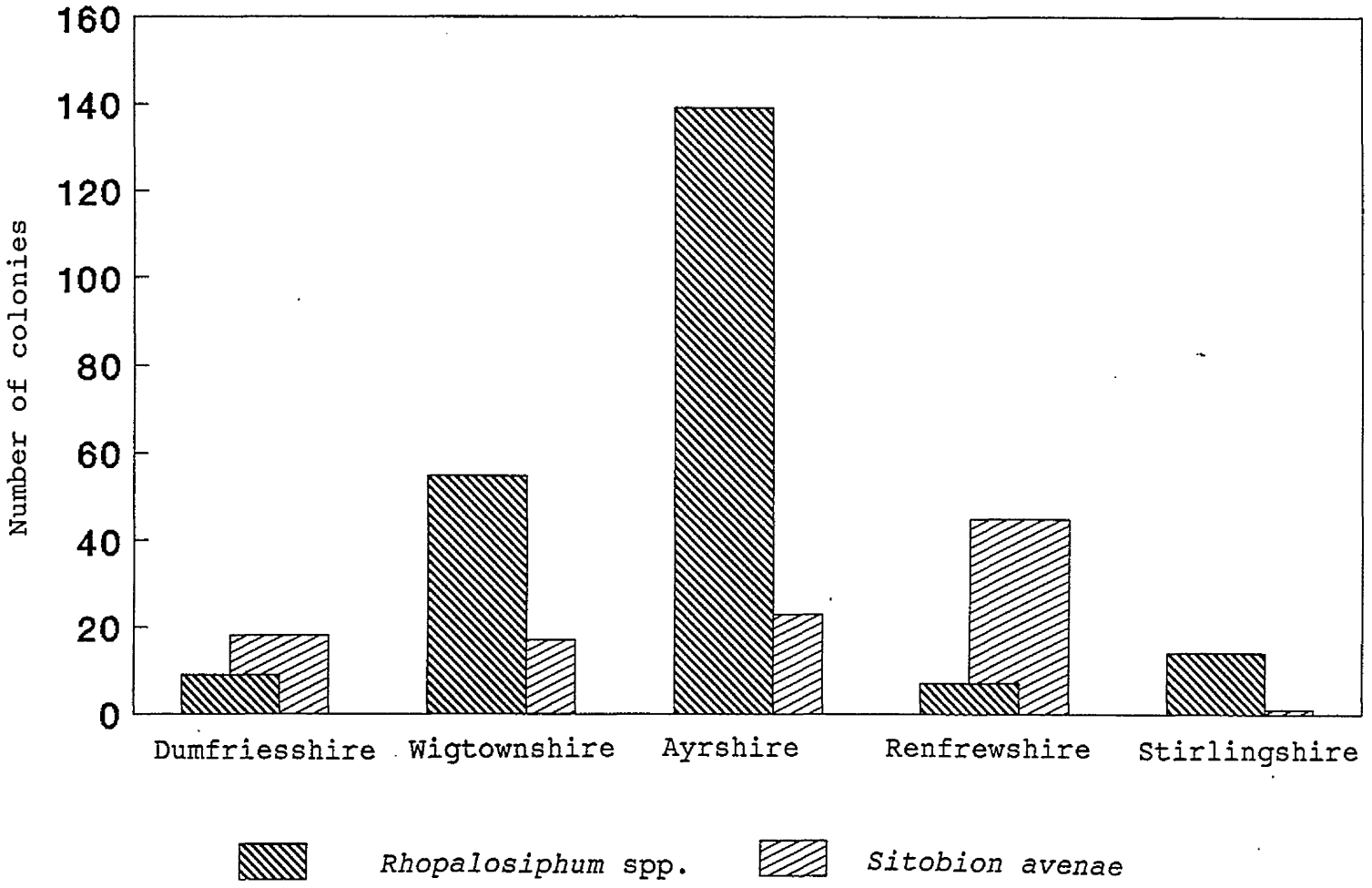


Figure 4.13 The cumulative total numbers of *Rhopalosiphum* spp. and *Sitobion avenae* colonies in winter barley crops of each region during the autumn 1989.

pooled, and the other regions pooled gave a non-significant result ($x^2_{(1)} = 1.24$, N.S.). This indicates that the differences beteween regions in the incidence of aphid species was probably due to the previous cropping type of grass in Wigtownshire and Ayrshire.

Aphids were least common in Dumfriesshire and Stirlingshire during the autumn period 1989, where no more than 12 aphid colonies were recorded in any field.

The large variations in aphid colony numbers between fields during the autumn 1989 were examined in more detail for Ayrshire where three types of aphid infestation were found. The total numbers of aphid colonies (*Rhopalosiphum* spp. plus *S. avenae*) for each metre length on each visit are shown for each Ayrshire field except A3 in Table 4.24. In A3, no aphids were found. A4 and A5 were infested by *R. padi* only, compared with A1 and A2 where aphids of both genera were found. Differences in the number of aphid colonies per metre length, between all five Ayrshire fields, between sampling dates within all Ayrshire fields and between sampling dates within each Ayrshire field were tested using Kruskal-Wallis tests (Table 4.25). There were significant differences between fields, between sampling dates within all Ayrshire fields and between sampling dates in A5 where an insecticide application had reduced the previous high aphid populations to zero.

Table 4.24 Total numbers of aphid colonies (*Rhopalosiphum* spp. and *Sitobion avenae*) for each metre length on each visit to the Ayrshire fields; winter barley, autumn 1989.

	Numbers of aphid colonies per metre length									
Field	1	2	3	4	5	6	7	8	9	10
A1										
18/10	0	0	2	1	0	1	1	0	0	0
3/11	0	0	1	0	0	0	0	1	2	0
21/11	0	0	0	0	0	0	0	0	0	0
A2										
18/10	0	0	0	2	0	0	0	0	0	0
3/11	2	0	0	1	3	1	1	1	0	0
21/11	4	2	1	1	0	0	0	2	0	2
A4										
18/10	0	0	0	2	0	0	8	0	0	0
29/10	2	4	7	1	1	0	5	2	0	0
10/11	0	3	4	1	2	1	0	0	3	1
21/11[a]	0	0	0	0	0	0	0	0	0	0
A5										
18/10	0	0	1	0	0	0	5	0	4	0
29/10	12	25	0	0	0	0	8	20	3	5
10/11[a]	0	0	0	0	0	0	0	0	0	0

[a] received an application of Ambush C prior to visit.

Table 4.25 Kruskal-Wallis tests for differences in the median number of aphid colonies (*Rhopalosiphum* spp. and *Sitobion avenae*) per metre length, between all five Ayrshire fields, between sampling dates within all Ayrshire fields and between sampling dates within each Ayrshire field.

Test	H^b statistic compared with x^2 - distribution
Between fields	H = 23.4, df 4, P < 0.001
Between sampling dates within all Ayrshire fields.	H = 8.2, df 2, P < 0.05
Between sampling dates within A1.	H = 4.6, df 2, N.S.
Between sampling dates within A2.	H = 5.6, df 2, N.S.
Between sampling[a] dates within A4.	H = 4.2, df 2, N.S.
Between sampling dates within A5.	H = 9.3, df 2, P < 0.01

a Data from the 4th visit was not included in Kruskal-Wallis tests to preserve equality of number of visits in each field.

b adjusted for ties.

In south-west and central Scotland as a whole, most alate *Rhopalosiphum* were *insertum* although the majority of *Rhopalosiphum* were apterous *padi* in three fields following untreated ploughed-in grass.

Winter sampling 1990 In A2, two *S. avenae* colonies were

observed in mid-March. No aphids were observed on all other winter visits.

Spring sampling 1990 The cumulative total numbers of aphid colonies in each field during the spring visits are shown in Table 4.26, and the regional colony totals for *Rhopalosiphum* spp. and *S. avenae* in both Table 4.26 and Figure 4.14. There was a significant difference between Wigtownshire, Renfrewshire, and, Dumfriesshire, Ayrshire and Stirlingshire (pooled to avoid low expectation) in the ratios of *Rhopalosiphum* colony totals to *S. avenae* colony totals during the spring 1990 ($x^2_{(2)} = 168.7$, $P < 0.001$). Two regions had higher numbers of aphids: Wigtownshire and Renfrewshire. The two Wigtownshire fields that followed untreated ploughed-in grass leys, W2 and W3, had a resurgence of *R. padi* infestation during the spring, despite each receiving an autumn application of insecticide. In Renfrewshire, three fields on one farm each had *S. avenae* infestations exceeding ten colonies per ten metre lengths in June. No *Rhopalosiphum* and no *S. avenae* colonies were counted during the spring in Dumfriesshire and Stirlingshire respectively.

The relationship between the autumn and spring aphid colony totals differed between regions. In Dumfriesshire, Wigtownshire, Ayrshire and Stirlingshire, the spring regional aphid colony totals were smaller than the autumn totals compared with Renfrewshire where the spring total was larger.

Table 4.26 Total numbers of *Rhopalosiphum* spp. and *Sitobion avenae* colonies in 26 winter barley fields during the spring 1990.

Field	No of visits	Numbers of aphid colonies	
		Rhopalosiphum spp.	*S. avenae*
Dumfriesshire			
D1	3	0	0
D2	3	0	0
D3	3	0	1
D4	3	0	1
D5	3	0	0
D6	3	0	2
D7	3	0	0
Totals		0	4
Wigtownshire			
W1	3	5	1
W2	3	120	0
W3	3	10	2
W4	3	0	8
Totals		135	11
Ayrshire			
A1	3	0	7
A2	3	0	3
A3	3	0	0
A4	4	0	3
A5	3	3	0
Totals		3	13
Renfrewshire			
R1	3	2	33
R2	3	0	14
R3	3	1	19
R4	3	0	1
R5	3	0	0
R6	3	0	1
R7	3	0	1
Totals		3	68

Table 4.26 continued.

Field	No of visits	Numbers of aphid colonies: *Rhopalosiphum* spp.	Numbers of aphid colonies: *S. avenae*
Stirlingshire			
S1	3	2	0
S2	3	0	0
S3	3	0	0
Totals		2	0
Grand Totals		143	96

Relationships between the autumn and spring aphid colony totals (log or $\log_{10}(n + 1)$ transformation) were tested separately for *Rhopalosiphum* and *S. avenae* by linear regression. For *Rhopalosiphum*, the test was non-significant ($r = 0.474$, df 3, N.S.) compared with the test for *S. avenae* which was significant at $P = 0.031$ (Figure 4.15). Fields with large *R. padi* infestations in the autumn 1989 received autumn insecticide applications, thus there was no general relationship between *Rhopalosiphum* colony totals in the autumn and the spring.

The ratios of the "all regions" *Rhopalosiphum* and *S. avenae* colony totals differed between the autumn 1989 and the spring 1990 ($x^2_{(1)} = 4.3$, $P < 0.05$). The scatterplot of the regional autumn and spring aphid colony totals (Figure 4.16) has several important features. Three points were markedly different: the *Rhopalosiphum* totals of Wigtownshire were high in both the autumn and the spring whereas the Ayrshire *Rhopalosiphum* total was high in the

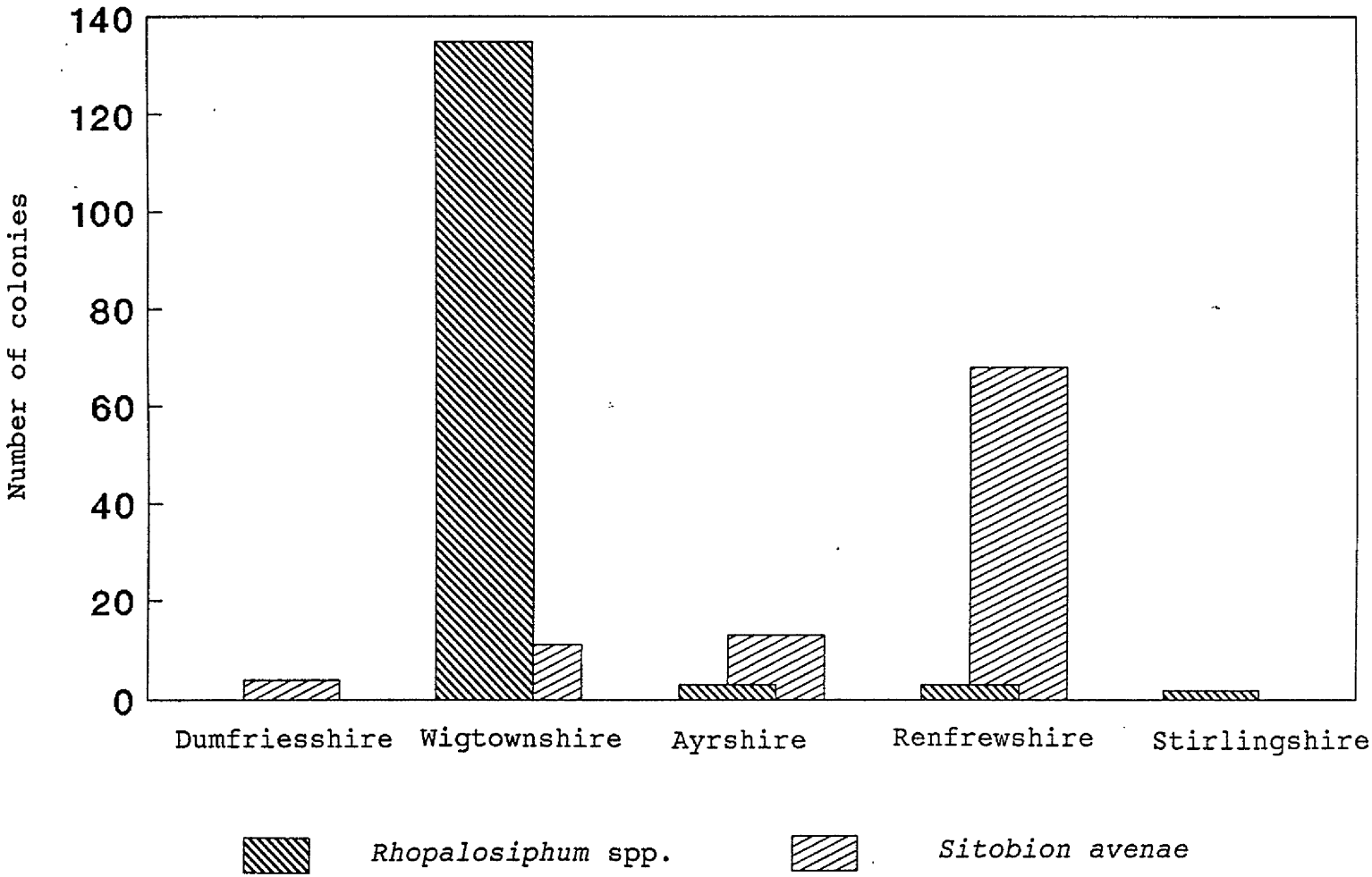


Figure 4.14 The cumulative total numbers of *Rhopalosiphum* spp. and *Sitobion avenae* colonies in winter barley crops of each region during the spring 1990.

Test of $\beta = 0$ $t = 4.35$, df 3, $P < 0.05$

Test of $\beta = 1$ $t = 0.77$, df 3, N.S.

$y = 1.22x - 0.48$

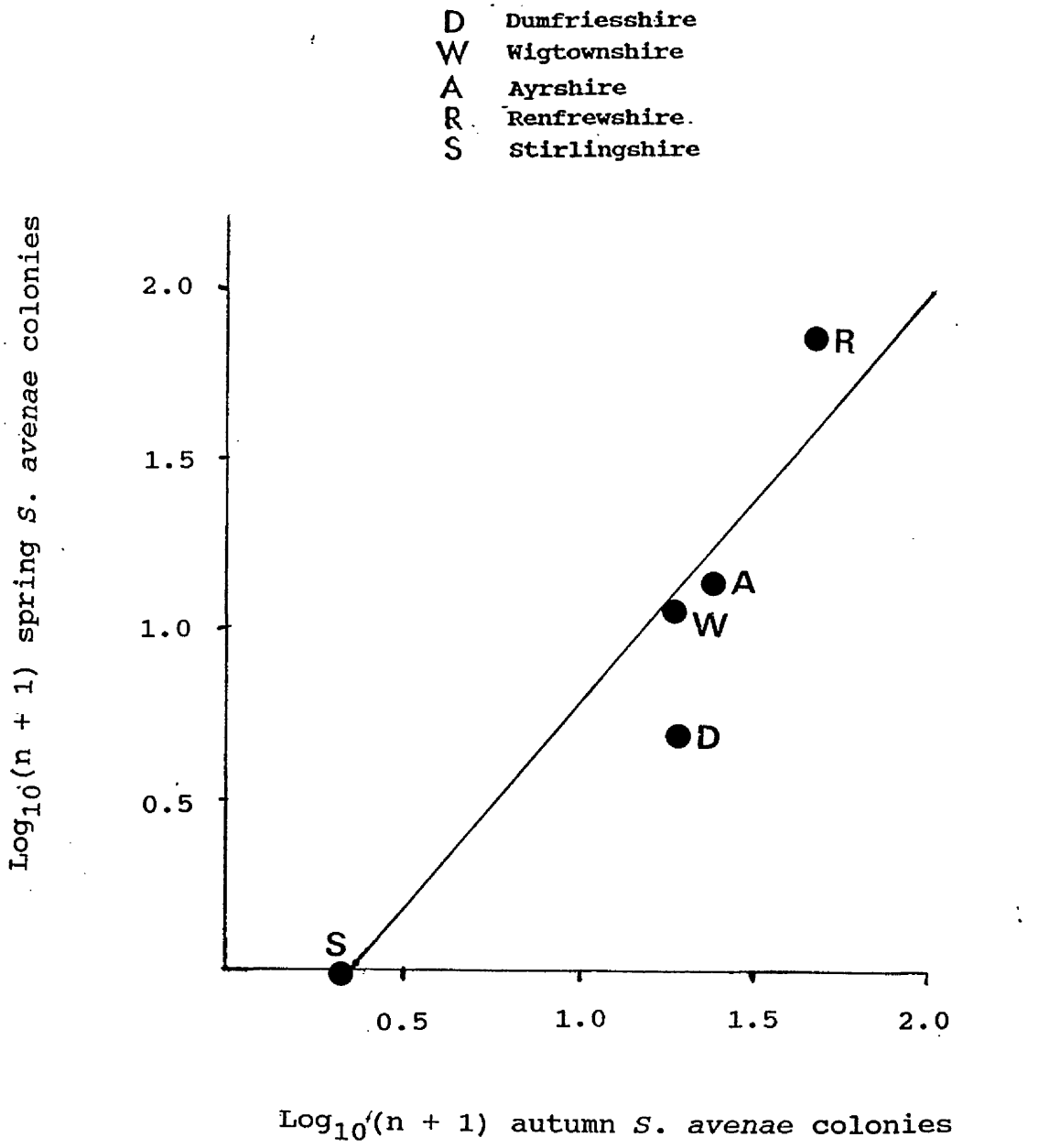


Figure 4.15 Relationship between $\log_{10}(n + 1)$ regional *Sitobion avenae* colony totals counted during the autumn 1989 with those counted in the spring 1990 using the ten one-metre lengths of drill methodology.

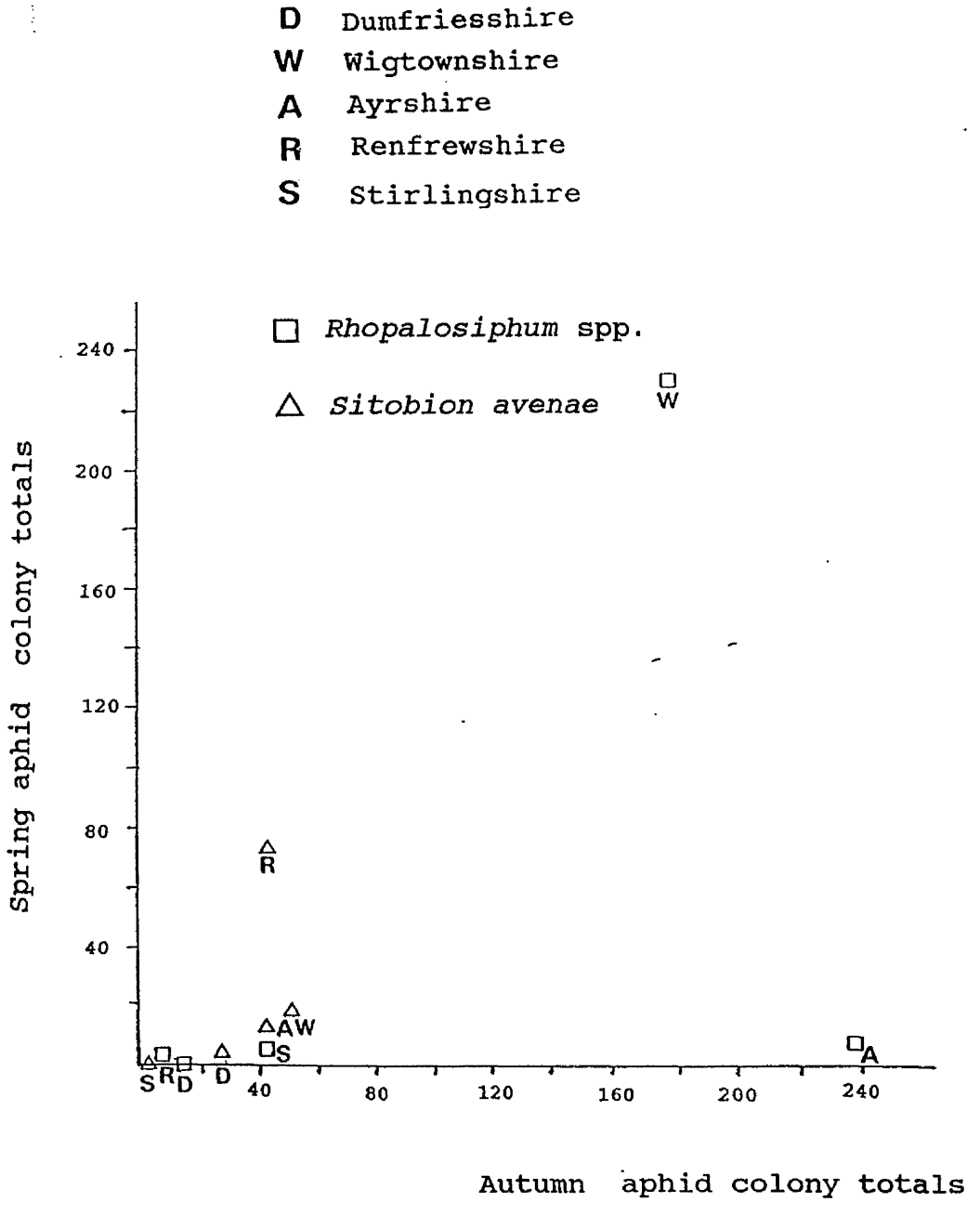


Figure 4.16 Scatterplot between the regional aphid colony totals in the autumn 1989 with regional aphid colony totals in the spring 1990.

autumn and low in the spring. The *S. avenae* total of Renfrewshire was relatively high in both the autumn and the spring. All other points reflected two facts: firstly, autumn totals were larger than spring totals and, secondly, that most regional aphid totals were low in both autumn 1989 and spring 1990.

4.4.3 **Methodology for BYDV survey, spring 1990**

All 26 winter barley crops that were sampled for aphids in the spring of 1990 were also surveyed for BYDV on the same dates. During the April and May visits, single yellow leaves were collected from five randomly selected yellow plants during a circuit of each field using tramlines, and these were tested for BYDV using ELISA (Seam-roller method). In eight fields during early June, several leaves were collected from each of five randomly selected yellow plants to obtain a 1 g leaf sample, during a circuit of each field using tramlines. These were tested for BYDV using the Mortar and Pestle method. In several fields in which patches of yellow plants were present, samples of 10 leaves/patch were taken and tested for BYDV by ELISA (Seam-roller method).

During the May and June visits: the percentage of each crop which was comprised of yellow plants was visually estimated and, if patches were present, their diameter was estimated. The abundance of individual yellow plants was also assessed, either "hard to find" (1 in 100 m^2) or "easy

to find" (1 in 10 m^2).

Ten well-established *P. annua* plants were collected from tramlines in nine fields in May and again in June. Two fields were sampled per region except for Ayrshire where one field was sampled. Other grass species occurred in some winter barley fields, and approximate 1 g leaf samples of a few individuals of these species were also collected on any of the three visits. Samples were tested for BYDV by ELISA (Mortar and Pestle method).

Grass weed infestation, particularly *P. annua*, was assessed on the June visit: either, 1 = scattered plants in tramlines, 2 = appreciable proportion of tramlines carpeted (1 to 5%), or, 3 = extensive weed coverage throughout crop.

4.4.4 **Results of BYDV survey spring 1990**

Individual yellow plants were found in all 26 winter barley crops during late April/early May. In 16 fields, individual yellow plants were relatively "easy to find" but in only three of these crops, the extent of yellowing was considered to exceed 0.1% of the total crop. In 13 of these 16 fields, patches of yellow plants, mostly 0.5 - 1.0 m in diameter were observed, compared with only one field where yellow plants were "hard to find", W1.

The percentage of single yellow barley leaves that gave positive ELISA tests for each BYDV strain in each region (collected on the second visit, because leaf samples

Table 4.27 Percentage of yellow barley leaf samples infected with each BYDV strain collected from winter barley in the spring 1990.

Region	Number of fields sampled	Number of leaves tested		Percentage of positive tests for BYDV strain RPV	PAV	MAV	% of total fields yellow[a] plants	yellow[b] patches
Dumfriesshire	7	34		9	18	26	71	29
Wigtownshire	4	20		20	15	45	75	100
Ayrshire	5	23		22	39	39	80	80
Renfrewshire	7	35		6	14	51	43	29
Stirlingshire	3	13		0	54	31	67	67
Totals	26	125	%	11	24	39	65	54

a % of total fields in which yellow plants were "easy to find"

b % of total fields in which patches of yellow plants were observed.

from first visit were used to validate Seam-roller method of sap extraction - Table 2.2) is given in Table 4.27 along with the percentage of fields with the higher level of abundance of scattered yellow plants (1 per 10 m^2) and the percentage of fields in which patches of yellow plants were observed (Figure 4.17). Overall, 39% of leaves tested were infected with the MAV strain, 24% with PAV and 11% with RPV. For each field, Table 4.28 shows the estimated percentage area of each crop comprised of patches of yellow plants and the number of positive BYDV tests for the yellow leaf samples collected on the second visit. Fields without patches of yellow plants and in which yellow plants were "hard to find", were found in all regions except Wigtownshire. The three fields with the more extensive crop yellowing were A4, A5 & S3.

There was no significant difference between the regional BYDV strain ratios in the barley leaf samples (Dumfriesshire and Wigtownshire pooled compared with Ayrshire, Renfrewshire and Stirlingshire pooled to avoid low expectations, $x^2_{(2)} = 1.65$, N.S.), indicating that BYDV strain incidence was similar in all regions of south-west and central Scotland in the spring 1990. However, the RPV strain was more common in Wigtownshire and Ayrshire, and Stirlingshire differed in having PAV as the predominant strain and RPV absent.

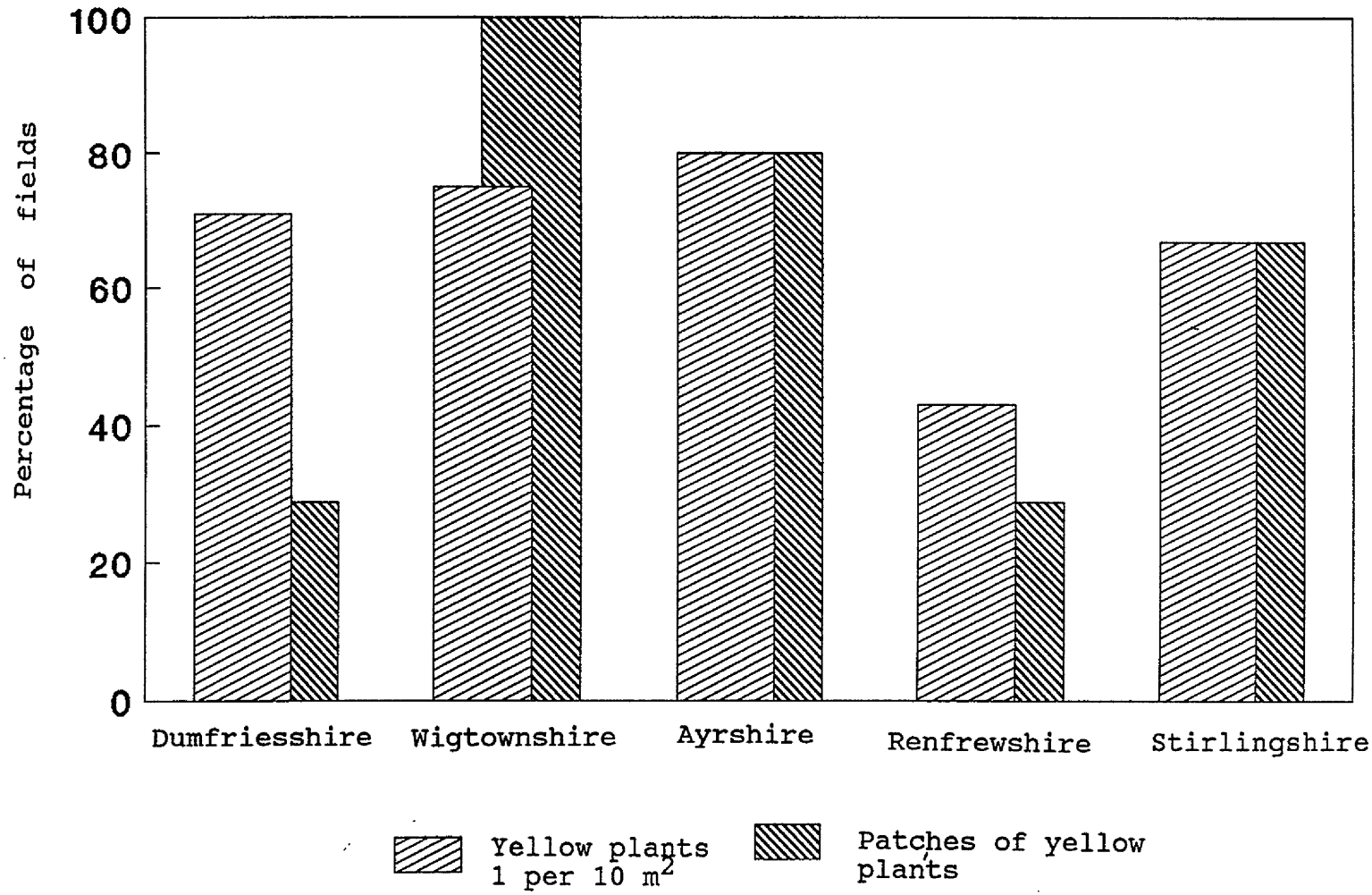


Figure 4.17 The percentages of fields in each region with the higher level of abundance of scattered yellow plants (1 in 10 m^2) and with patches of yellow plants; BYDV in winter barley 1989/90.

Table 4.28 The incidence of BYDV strains in the yellow leaf samples, the abundance of yellow plants, the incidence of patches of yellow plants, and the percentage area of each winter barley crop comprised of patches of yellow plants; BYDV survey, spring 1990.

		No of postive tests for BYDV strain			Incidence of yellow		
Field	n	RPV	PAV	MAV	plants	patches	% of crop yellow
Dumfriesshire							
D1	5	-	-	-	+	+	-
D2	5	-	-	5	+	+	-
D3	5	-	-	2	+	-	-
D4	5	-	-	-	+	-	-
D5	5	-	2	-	+	-	-
D6	4	-	2	2	-	-	-
D7	5	3	2	-	-	-	-
Totals	34	3	6	9	5	2	
Wigtownshire							
W1	5	1	-	3	-	+	-
W2	5	1	3	1	+	+	-
W3	5	2	-	1	+	+	-
W4	5	-	-	4	+	+	-
Totals	20	4	3	9	3	4	
Ayrshire							
A1	5	-	1	5	+	+	-
A2	5	1	1	3	+	+	-
A3	3	-	1	1	-	-	-
A4	5	1	5	-	+	+	1
A5	5	3	1	-	+	+	2
Totals	23	5	9	9	4	4	
Renfrewshire							
R1	5	-	-	5	+	+	-
R2	5	-	-	5	+	-	-
R3	5	-	-	5	+	+	-
R4	5	-	-	-	-	-	-
R5	5	1	-	-	-	-	-
R6	5	1	2	2	-	-	-
R7	5	-	3	1	-	-	-
Totals	35	2	5	18	3	2	

Table 4.28 continued.

Field	n	No of postive tests for BYDV strain RPV	PAV	MAV	Incidence of yellow plants	patches	% of crop yellow
Stirlingshire							
S1	3	-	1	1	-	-	-
S2	5	-	2	3	+	+	-
S3	5	-	4	-	+	+	1
Totals	13	-	7	4	2	2	
Grand Totals	125	14	30	49	17	14	

BYDV strain - strain not detected.

yellow plants + one yellow plant in 10 m^2
- one yellow plant in 100 m^2

yellow patches - absent + present

% crop yellow - denotes < 0.1 %

The two types of plant yellowing percentages were lowest in Renfrewshire and highest in Wigtownshire. In Dumfriesshire, yellow barley plants were "easy to find" in 71% of fields in contrast to the 29% of fields in which patches of yellow barley plants were observed. In all other regions, these two percentages were more similar. A relationship between the percentage of fields in which yellow barley plants were "easy to find" and the number of fields in which patches of yellow barley plants were observed in the same region was tested for by linear regression (arcsine transformation): a non-significant result was obtained ($r = 0.598$, df 3, N.S.).

Ten yellow leaves were collected from patches of yellow plants (sometimes stunted) in nine fields. Most samples were taken from the fields with crop yellowing estimates exceeding 0.1% of the total crop area. Thus, samples were taken from six patches in S3, and samples from two patches in each of A4 and A5. Patches of yellow barley plants were evident in all other fields from which samples were taken. The BYDV strain incidence in the ten leaves of each sampled patch of yellow plants is shown in Table 4.29. A major feature of these data is that PAV was the predominant strain present in these patches of yellow plants, in contrast to the prevalence of the MAV strain in the single yellow leaf samples which were mainly collected from individual yellow plants (Tables 4.27 & 4.28). For each region except Dumfriesshire, differences between the RPV+PAV:MAV strain ratios of the ten yellow leaves per patch and the five single yellow leaves per field data were tested (Table 4.30). Ayrshire was the only region not to give a significant result. There was also a significant difference between the overall BYDV strain ratios of the ten yellow leaves per patch data and the five single yellow leaves per field data ($x^2_{(2)} = 43.2$, $P < 0.001$), confirming that different strains were present in scattered yellow barley plants (mainly MAV) and in patches of yellow barley plants (sometimes stunted [mainly PAV]).

Table 4.29 BYDV strain incidence in ten leaves collected from a patch of yellow plants in nine winter barley fields; BYDV survey, spring 1990.

Field		No infected	No of positive tests for BYDV strain		
			RPV	PAV	MAV
Dumfriesshire					
D1	9/5	-	-	-	-
Wigtownshire					
W2	14/5	6	-	5	1
W2	14/5	4	-	4	-
W3	14/5	9	4	4	2
W4	6/6	4	1	3	-
Totals		23	5	16	3
Ayrshire					
A1	21/5	10	-	-	10
A4	24/4	8	-	8	1
A4	21/5	4	2	2	-
A5	24/4	10	3	10	1
A5	21/5	1	-	1	-
Totals		33	5	21	12
Renfrewshire					
R1	8/5	10	3	7	-
R2	8/5	5	3	2	-
Totals		15	6	9	-
Stirlingshire					
W3	9/5	10	-	10	-
W3	9/5	10	-	9	1
W3	9/5	6	-	6	-
W3	9/5	8	-	8	-
W3	9/5	3	-	3	-
W3	9/5	7	-	7	-
Totals		44	-	43	1

\- no positive test for BYDV strain.

Table 4.30 Results of tests for differences between the regional RPV+PAV:MAV strain ratios of the 10 yellow leaves per patch and the 5 single yellow leaves per field samples.

Region	Test	Significance
Wigtownshire	Exact probability	P = 0.004
Ayrshire	Chi-squared	$x^2_{(1)} = 0.3$, N.S.
Renfrewshire	Chi-squared	$x^2_{(1)} = 19.6$, $P < 0.001$
Stirlingshire	Exact probability	P = 0.0008

Table 4.27 shows that compared with 1989 (Table 4.14), low percentages of the yellow barley leaves were infected with BYDV. Although the Seam-roller method for single leaves was validated using the yellow leaves collected during the first spring visit in 1990, it was considered correct to further investigate this relatively low percentage BYDV infection of yellow leaves. This was achieved by collecting several yellow leaves to obtain a 1 g leaf sample as in 1989, from each of five plants from two fields in each of four regions in early June. These fields were selected to represent the wide range of fields sampled, in terms of the abundance of yellow plants in fields and the number of single yellow leaves that were infected with BYDV. Table 4.31 shows the results of the ELISA tests (Mortar & Pestle method) for the eight fields in which five 1 g leaf samples were collected, and compares these results with those obtained with single yellow

leaves. The results were so similar, that use of a statistical test was not required.

Table 4.31 Comparison of the number of positive ELISA tests obtained by collecting 1 g yellow barley leaf samples with single yellow barley leaf samples; BYDV survey spring 1990.

	Number of positive tests for BYDV strain					
	5 x 1 g leaf samples			5 single leaves		
Field	RPV	PAV	MAV	RPV	PAV	MAV
Dumfriesshire						
D1	0	0	0	0	0	0
D4	0	0	4	0	0	0
Wigtownshire						
W3	1	0	1	2	0	1
W4	0	0	3	0	0	4
Ayrshire						
A1	0	0	4	0	1	5
Renfrewshire						
R1	1	0	5	0	0	5
R4	0	0	0	0	0	0
Stirling						
S2	0	3	0	0	2	3
Totals	2	3	17	2	3	18

P. annua Table 4.32 shows the results of the ELISA tests on *P. annua* collected on two occasions from nine fields during the spring. The percentage of plants infected with each

BYDV strain in each region is shown in Figure 4.18. There were significant regional differences in the BYDV strain ratios of the *P. annua* samples (data from both visits were pooled for each field, and, data from Dumfriesshire, Wigtownshire and Ayrshire were pooled, and, data from Renfrewshire and Stirlingshire were pooled, to avoid low expectations, $x^2_{(2)} = 10.2$, $P < 0.01$) indicating that, as in the yellow barley leaf samples, BYDV strain incidence differed between regions. The differences were due to contrasting levels of abundance of strains rather than presence/absence because all three strains were present in every region except Stirlingshire where RPV was absent. In Wigtownshire and Ayrshire, PAV was most prevalent, in Renfrewshire and Stirlingshire, MAV was most prevalent and in Dumfriesshire, PAV and MAV occurred equally.

In some fields, similar results were obtained for the BYDV infection in *P. annua* samples collected at the two different times. A relationship between the BYDV infection of samples collected in May and the samples collected in June was tested for by linear regression. Data for all three strains were included in the same test, but pairs of data in which one or more zeros occurred were excluded and a $\log_{10}$ transformation made. The non-significant result ($r = 0.126$, df 11, N.S.) indicates that there was no consistent relationship between BYDV infection of *P. annua* collected from the same field on two different occasions.

Table 4.32 Incidence of BYDV strains in *P. annua* collected on two occasions from winter barley fields; BYDV survey, spring 1990.

		Number of positive ELISA tests for BYDV strain					
		RPV		PAV		MAV	
Field	No of[a] samples	May	/June	May	/June	May	/June
Dumfriesshire							
D1	20	0	2	0	5	0	0
D5	19	1	0	1	0	6	0
Wigtownshire							
W3	18	0	0	2	1	0	0
W4	20	1	0	4	0	1	0
Ayrshire							
A2	20	6	3	7	5	6	3
Renfrewshire							
R1	20	2	7	4	3	5	8
R7	20	2	3	6	2	3	9
Stirlingshire							
S2	19	0	0	3	2	3	6
S3	20	0	0	0	2	8	6
Grand Totals		12	15	27	20	32	32

[a] May and June samples pooled.

However, when viewed on wider scale, (Chi-squared test between the "all regions" BYDV strain ratios in *P. annua* on the two occasions, $x^2_{(2)} = 1.3$, N.S.), there was no difference between the infection of the *P. annua* samples collected in May and June.

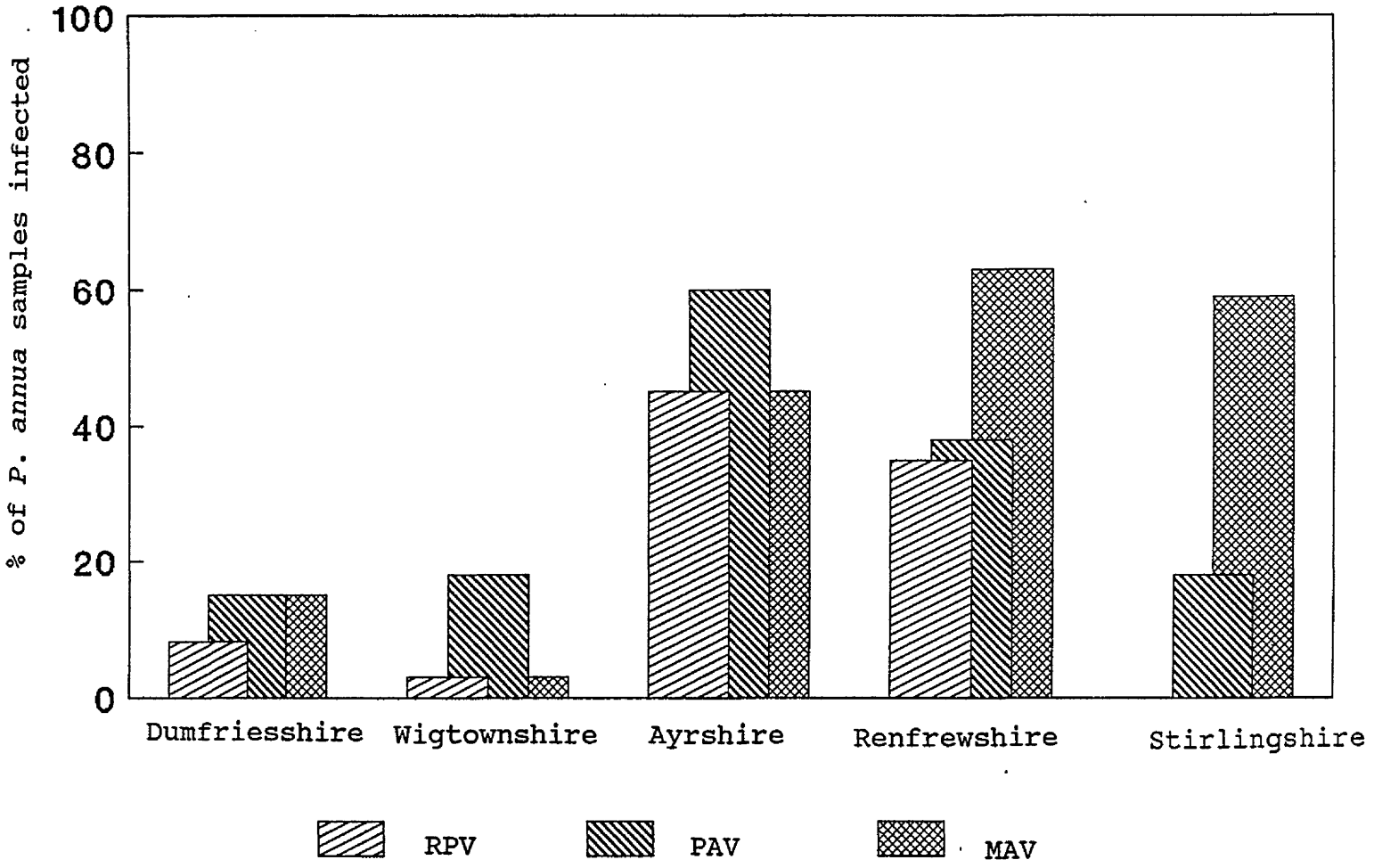


Figure 4.18 The regional percentage of *Poa annua* infected with each BYDV strain; BYDV survey spring 1990.

A relationship between the regional percentage BYDV infection of single yellow barley leaves and *P. annua* samples was tested for by linear regression after arcsine transformations (data for each strain were included in the same test to give 15 pairs of observations). The non-significant result ($r = 0.39$, df 13, N.S.) is reflected by the scatterplot of the regional percentage BYDV infection of the single yellow leaves and the *P. annua* shown in Figure 4.19. Although the relationship is not linear as the test above showed, greater percentages of infection in yellow barley leaf samples are reflected in greater infection in *P. annua*. The highest levels of infection of both barley leaves and *P. annua* were associated with the MAV strain. Mann-Whitney tests on the percentage infection of single yellow barley leaves and *P. annua* pooled for each strain, gave a significant result between the RPV and MAV strains ($W = 72.5$, $P = 0.016$) but the medians of the percentage infections for the RPV and PAV strains ($W = 81$, N.S.), and, the PAV and MAV strains ($W = 90.5$, N.S.) were not different. Another feature of Figure 4.19 is that all Dumfriesshire and Wigtownshire points are grouped on the left of the plot (low BYDV infections in *P. annua*) whereas all Ayrshire and Renfrewshire points are grouped on the right (high BYDV infections in *P. annua*). A Mann-Whitney test on the percentage infections for all three strains in single yellow barley leaves and *P. annua* pooled, for Dumfriesshire and Wigtownshire, compared with the same in Ayrshire and Renfrewshire gave a significant result ($W =$

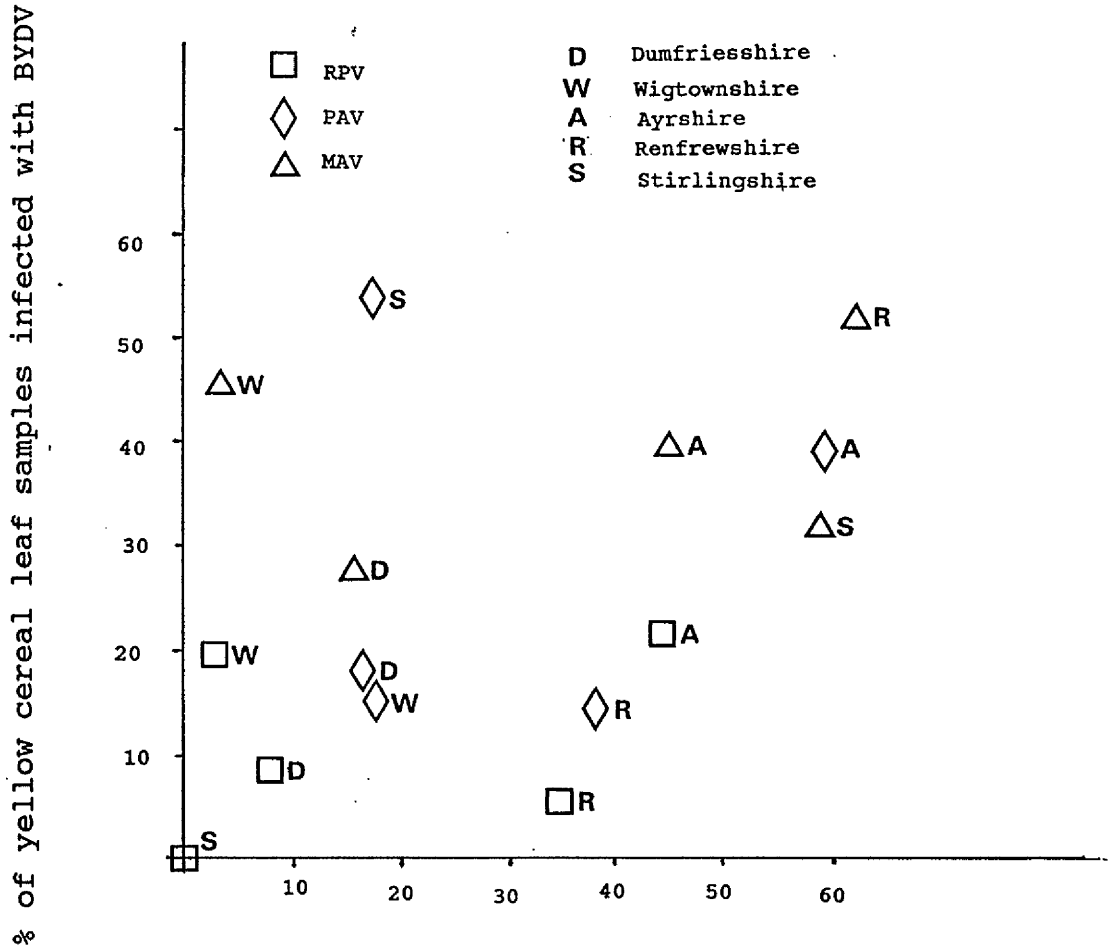


Figure 4.19 Scatterplot between the regional percentage of single yellow cereal leaf samples and the regional percentage of *Poa annua* samples infected with each BYDV strain; BYDV survey spring 1990.

103, P = 0.007) indicating that the medians of the percentage BYDV infections of these two groups differed.

The "all regions" totals of single yellow barley leaf samples infected with the RPV, PAV and MAV strains, were 14, 30 and 49 respectively. The comparative figures for *P. annua* samples were 27, 47 and 64. A Chi-squared test between these two sets of figures gave a non-significant result ($x^2_{(2)}$ = 1.14, N.S.) indicating that in south-west and central Scotland as a whole, BYDV incidence was similar in barley leaves and *P. annua* in the spring of 1990.

Other grass weed species To some extent, the numbers of the six grass weed species collected reflect their relative abundance in winter barley fields (Table 4.33). *L. perenne* was the second most abundant grass weed in winter barley fields after *P. annua*, and all the samples collected were infected with BYDV. All the other species were found only in a small number of fields. The five *H. lanatus* were collected from S3, a field in which cereal leaf samples were predominantly infected by the PAV strain. However, MAV was the strain detected in three of the *H. lanatus*. *Poa trivialis* also showed a high level of BYDV infection, but was present in the headlands of only a few fields.

There was a significant difference between the BYDV strain ratios of *L. perenne* and *P. annua* ($x^2_{(2)}$ = 6.4, P < 0.05, [one expected value marginally less than five]) collected from winter barley fields in the spring 1990. The

PAV strain was relatively rare in *L. perenne*.

Table 4.33 BYDV strain incidence in grass weeds (other than *P. annua*) collected from winter barley fields; BYDV survey, spring 1990.

Grass weed spp.	No of samples	No of positive tests for BYDV strain		
		RPV	PAV	MAV
Holcus lanatus	5	-	-	3
Lolium perenne	12	9	3	10
Phleum pratense	5	1	1	1
Poa trivialis	8	-	5	5

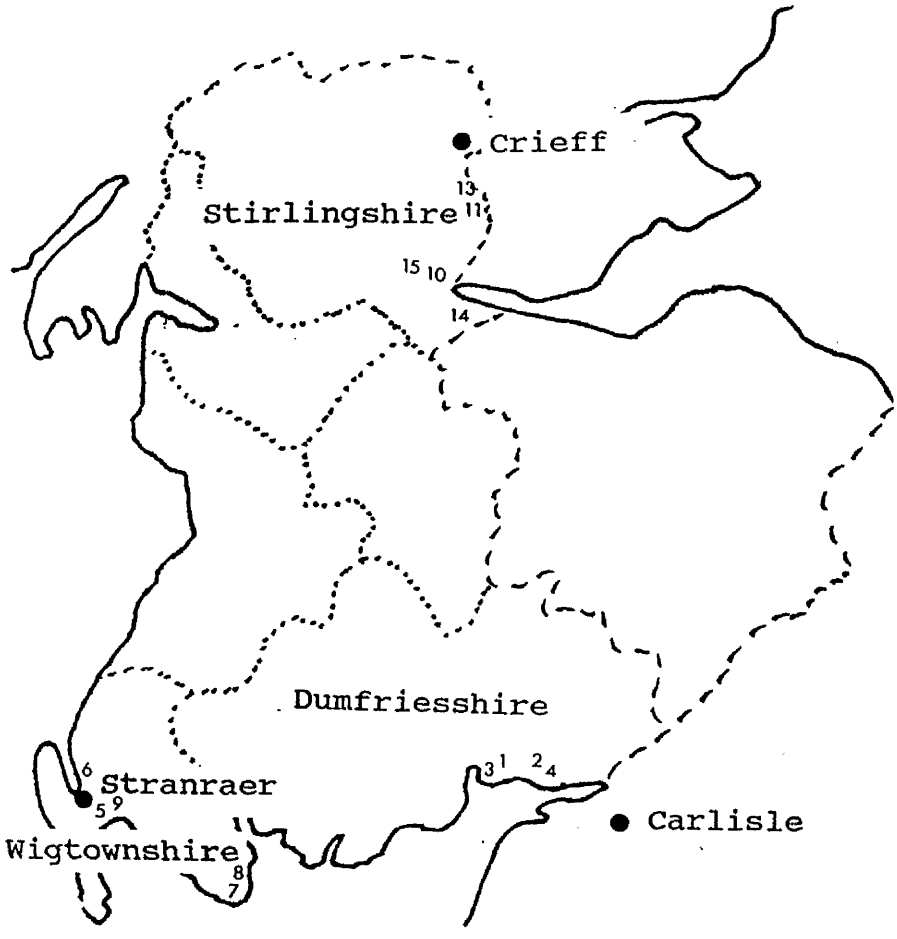
- no positive test for BYDV strain.

4.5 BYDV epidemiology in winter barley, 1990/91

4.5.1 Methodology for aphid sampling in winter barley, autumn 1990, winter and spring 1991

Twenty-five winter barley crops were sampled in the following three regions: Dumfriesshire, Wigtownshire and Stirlingshire (Figure 4.20). The methodology used in 1989/90 was also adopted in 1990/91.

Autumn sampling Weekly sampling commenced in late September 1990 in two Stirlingshire fields and during the first half of October in 18 fields from all three regions. In five fields, sampling commenced in late October. After mid-November, sampling occurred fortnightly until the last



Dumfriesshire			
1. Broadgate	D1		
2. Charlesfield (Hoddom & Kinmount estate)	D2	D3	
3. Kelton	D4	D5	
4. Spittalriddinghill	D6	D7	
Wigtownshire			
5. Barsolus	W1		
6. Beoch	W2	W3	W4
7. Claymoddie	W5	W6	
8. Garlieston Home	W7	W8	
9. Little Genoch	W9		
Stirlingshire			
10. West Cambusdrenny	S1	S2	
11. East Third	S3	S4	
12. Feruyfold	S5		
13. Shearerston (Colquazie estates)	S6	S7	
14. Todhill	S9		

Figure 4.20 Locations of crops sampled in winter barley season 1990/91.

autumn visit in the first half of December.

SAC advisers sampled five of the 25 fields on a weekly or fortnightly basis, commencing from mid to late October. The number of visits to each field varied from two to five.

Eighteen fields were sampled on seven or eight occasions, and another two on nine occasions. Differing crop emergence dates and irregular crop sampling by advisers, and snow lying at two fields of one region in December 1990, all contributed to the variable numbers of visits to the 25 fields.

Winter sampling Three fields were sampled by SAC advisers in early January, two in Wigtownshire and one in Dumfriesshire.

Spring sampling All 25 fields were sampled in May 1991.

4.5.2 Results for aphid sampling in winter barley autumn 1990 and winter and spring 1991

Autumn sampling Table 4.34 shows the cumulative total numbers of aphid colonies in each field during the autumn visits for both *Rhopalosiphum* spp. and *S. avenae*. The regional totals are shown in Table 4.34 & Figure 4.20. Most Stirlingshire fields were sampled on more occasions than Dumfriesshire and Wigtownshire fields because they were drilled earlier. However, the Dumfriesshire aphid colony totals were highest because most Dumfriesshire fields had relatively high aphid colony totals.

There were significant regional differences in the ratios of *Rhopalosiphum* colonies to *S. avenae* colonies ($x^2_{(2)} = 6.7$, $P < 0.05$). The overall totals show that 56% of aphid colonies were *Rhopalosiphum* spp. Stirlingshire was different in that more *S. avenae* were counted in most fields.

On certain dates, there were large *S. avenae* colony totals in a few fields. Such dates are shown in Table 4.35 when at least five *S. avenae* colonies were counted in each field. Differences in the distribution of *S. avenae* in the ten one-metre lengths between these five fields were tested for using a Kruskal-Wallis test. The non-significant result (H [adjusted for ties] = 1.64, df 4, N.S.) indicates that the distributions of *S. avenae* colonies in the ten one-metre lengths of each field were not different.

Most *Rhopalosiphum* spp. recorded were alate *R. insertum* which migrated into crops of all three regions and did not reproduce. During November, a greater proportion of the *Rhopalosiphum* colonies were apterous *R. padi*, particularly in Dumfriesshire. Most *S. avenae* colonies were apterous.

Table 4.34 Total numbers of *Rhopalosiphum* spp. and *Sitobion avenae* colonies in 25 winter barley crops; autumn 1990.

Field	No of visits	Total numbers of aphid colonies: *Rhopalosiphum* spp.	*S. avenae*
Dumfriesshire			
[D1 +	4	8	6]
D2	7	14	10
D3	7	15	8
D4	7	6	6
D5	7	15	15
D6	7	13	9
D7	7	8	3
Totals		71	51
Wigtownshire			
[W1 +	5	1	2]
W2	7	5	4
W3	7	3	5
W4	7	8	0
W5	7	5	0
W6	7	5	2
W7	7	4	1
W8	7	6	5
[W9 +	5	4	7]
Totals		36	17
Stirlingshire			
S1	9	4	7
S2	8	1	16
S3	7	6	3
S4	7	1	5
[S5	2	0	2]
S6	8	16	7
S7	8	3	1
[S8	4	5	12]
S9	9	2	1
Totals		33	40
Grand totals		140	108

Totals from bracketed fields were not included in regional totals because sampling frequency by SAC advisers was mostly fortnightly throughout the autumn.

\+ sampled during early January.

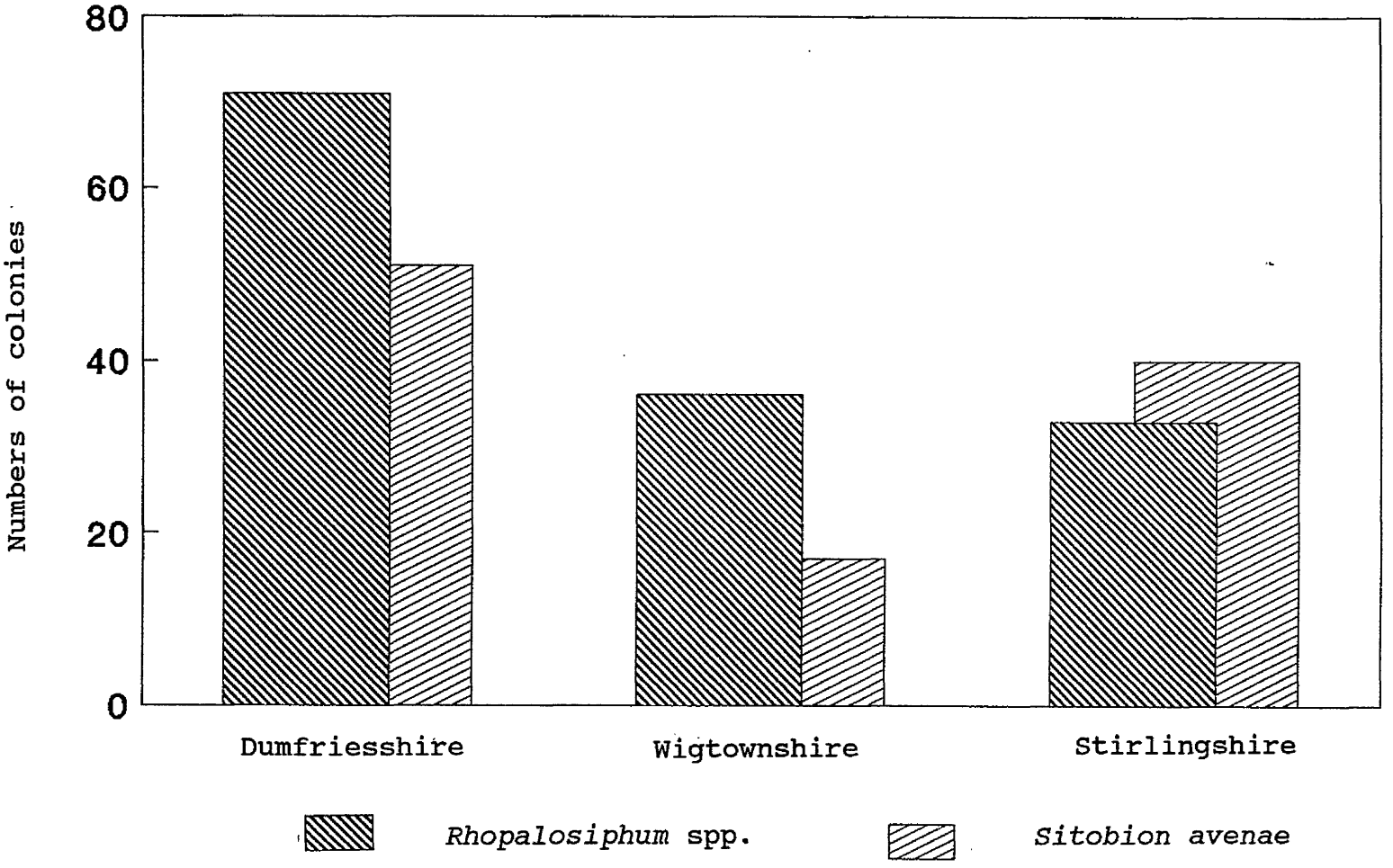


Figure 4.21 The cumulative total numbers of *Rhopalosiphum* spp. and *Sitobion avenae* colonies in winter barley crops of each region during the autumn 1990.

Table 4.35 Numbers of *Sitobion avenae* colonies in each of the 10 one-metre lengths of drill, in field samples in which the cumulative *S. avenae* total was five or more; winter barley, autumn 1990.

	No of *S. avenae* colonies / metre length									
Field	1	2	3	4	5	6	7	8	9	10
D5 25/10	1	0	4	0	0	0	1	0	0	1
D3 25/10	0	1	0	1	0	0	0	0	1	2
S2 4/10	1	0	0	2	2	1	0	1	0	0
12/10	1	0	0	0	3	2	0	1	0	0
S8 15/10	1	0	0	0	1	0	2	0	0	1

Winter sampling No aphids were observed in the three fields sampled in early January 1991 (see Table 4.34).

Spring sampling No aphids were observed in the 25 winter barley crops at the beginning of May 1991.

4.5.3 **Methodology for BYDV survey, spring 1991**

The 25 crops which were sampled for aphids in the spring 1991 were surveyed for BYDV on the same dates. The methodology used in 1990 was also adopted in 1991.

4.5.4 **Results for BYDV survey, spring 1991**

20 fields sampled by the author Yellow plants characteristic of BYDV (section 4.23) were observed in 16 fields, whilst a further two fields contained many plants which were considered yellowed for reasons other than BYDV. Patches (> 0.5 m) of yellow plants were not observed in any field. The percentage of the crop which was comprised of yellow plants was considered to be less than 0.1% in every case.

5 fields sampled by SAC advisers Advisers collected the yellow leaf samples in each field for testing for BYDV. However, owing to the subjective nature of the two measurements of crop yellowing, College advisers were not requested to make these assessments.

The percentage of yellow leaf samples that gave positive ELISA tests for each BYDV strain and the percentage of fields with the higher level of abundance of scattered yellow plants (1 per 10 m^2) are shown in Table 4.36 for each region. There were no significant differences between the regional RPV+PAV:MAV strain ratios ($x^2_{(2)} = 1.7$, N.S.). The highest infection levels occurred in Stirlingshire where 42% of yellow leaves collected were infected with the MAV strain. In Dumfriesshire and Wigtownshire, infection levels for each strain were no more than 30%.

Table 4.36 The percentage of yellow leaf samples infected with each BYDV strain collected from winter barley in the spring 1991.

Region	Number of fields sampled	Number of leaves tested	Percentage of positive tests for BYDV strain RPV	PAV	MAV	% of total fields[a] with yellow plant abundance category 2 1 plant in 10 m^2
Dumfriesshire	6	25	8	24	24	33
Wigtownshire	9	37	3	16	30	14
Stirlingshire	9	45	2	22	42	29

[a] fields sampled by advisers excluded.

The incidence of yellow plants and the results of ELISA tests for BYDV on the five yellow leaves collected from each field are shown in Table 4.37.

Table 4.37 The incidence of BYDV strains in the single yellow barley leaf samples and the abundance of yellow plants in the 20 winter barley fields; BYDV survey spring 1991.

Field	No of samples	No of positive tests for BYDV strain			Incidence[a] of yellow plants
		RPV	PAV	MAV	
Dumfriesshire					
D2	5	1	1	0	2
D3	5	0	0	0	1
D4	5	0	2	4	1
D5	5	1	1	0	2[b]
D6	5	0	2	2	1
D7	0	-	-	-	-[c]
Totals	25	2	6	6	
Wigtownshire					
W1	5	0	0	5	-
W2	5	0	1	1	1
W3	5	0	3	1	1
W4	5	0	0	0	2[b]
W5	1	0	1	0	1
W6	5	1	1	0	1
W7	3	0	0	0	1
W8	3	0	0	0	1
W9	5	0	0	4	-
Totals	37	1	6	11	

Table 4.37 continued.

Field	No of samples	No of positive tests for BYDV strain RPV	PAV	MAV	Incidence[a] of yellow plants
Stirlingshire					
S1	5	0	0	4	1
S2	5	0	1	3	2
S3	5	0	1	3	1
S4	5	0	0	3	1
S5	5	0	4	1	-
S6	5	0	2	1	2
S7	5	0	1	3	1
S8	5	0	0	0	-
S9	5	1	1	1	1
Totals	45	1	10	19	

Key for **Table 4.37**

a
1 one yellow plant in 10 m^2
2 one yellow plant in 100 m^2

b extensive crop yellowing due to a factor other than BYDV

c no yellow plants observed

4.6 Summary of the aphid and BYDV history of the winter barley crops of each region in the three years of the BYDV project

In the preceding sections of this chapter (sections 4.3, 4.4 & 4.5), the aphid and BYDV data of winter barley crops sampled in each season were presented and analysed: essentially to ascertain whether or not aphid and BYDV incidence differed between regions. A brief summary of the aphid and BYDV data of crops in different regions in the three seasons is presented in Table 4.38.

Only in the spring 1989 was BYDV extensive in crops of any region. In that spring, only Lanarkshire crops escaped extensive infection. In the springs of 1990 and 1991, only a few crops had crop yellowing exceeding 1% of the crop although the disease was detectable in nearly all sampled crops.

Winter barley crops in Wigtownshire and Stirlingshire were sampled in the autumn and the spring of all three seasons. In Wigtownshire during the first two autumns, *R. padi* predominated in sampled crops. In the third autumn, relatively few aphids were observed although *Rhopalosiphum* spp. again predominated. In Stirlingshire, only in 1988/89 were aphids numerous.

In Dumfriesshire during the autumn 1989, fewer aphids were sampled than in most other regions whereas in the autumn 1990, more aphids were sampled than in other regions. In the two seasons of sampling in Renfrewshire, *S.*

Table 4.38 Summary of the aphid and BYDV histories of the different regions sampled during the three years of the project.

Region	Autumn 1988	Spring 1989	Autumn 1989	Spring 1990	Autumn 1990	Spring 1991
Dumfriesshire	-	Many *S. avenae*	Few aphids	Few aphids	Many aphids	No aphids
	-	Much MAV	-	Little BYDV	-	Little BYDV
Wigtownshire	Many aphids	Many *R. padi*	Some *R. padi*	Many *R. padi*	Few aphids	No aphids
	-	Much BYDV	-	Little BYDV	-	Little BYDV
Ayrshire	Some *S. avenae*	Many *S. avenae*	Many *R. padi*	Few aphids	-	-
	-	Much MAV	-	Some PAV	-	-
Renfrewshire	-	Many *S. avenae*	Many *S. avenae*	Many *S. avenae*	-	-
	-	Much MAV	-	Little BYDV	-	-
Stirlingshire	Some *S. avenae*	Many *S. avenae*	Few aphids	Few aphids	Some aphids	No aphids
	_	Much MAV	-	Little BYDV	-	Little BYDV
Lanarkshire	-	No aphids	-	-	-	-
	-	Little BYDV	-	-	-	-

N.B. The terms, many, some, few *etc* denote relative numbers within each season. They have no precise definition. See relevant section for further details.

avenae was numerous relative to other regions.

Clearly, regional differences in aphid species and numbers can exist in winter barley crops during the autumn. This may translate into regional differences in BYDV infection in the following spring.

There are two main facets of the regionality encountered in this Chapter. The first is that fields in the same region may have more similar soils, are exposed to similar climates and agriculture, compared with fields of other regions. The second is that differing numbers of fields, and fields with different field/farm variables were sampled in each region. Both these facets of regionality are taken into account in the following analyses which attempt to explain the regional differences at a biological level.

4.7 Classification of winter barley crops and the identification of factors affecting the incidence and the regional distribution of BYDV within each season

4.7.1 Methodology

In this analysis, the aphid and BYDV data already presented for each field are referred to as the "aphid/BYDV variables". In each of the three winter barley seasons, the seasonal incidence of aphid infestations (and in 1988/89, autumn aphid sampling only took place in 5/45 fields) and the extent of BYDV infection differed, resulting in different aphid/BYDV variables being selected in each season. Therefore, TWINSPAN was used to group fields with

similar levels of aphid/BYDV variables within each winter barley season. These groups were named and described on the basis of the aphid/BYDV variables of the field members.

For each field, a number of agronomic and topographic variables were obtained, and for each region, weather data for the months November to March of each season were obtained from the *Monthly Weather Report* by selecting one climatological station to represent all the sampled winter barley crops in a region. These are collectively known as the "field/farm variables". A total of 21 variables were obtained for each field, except in the season 1989/90 when an extra variable, weed abundance was measured. These variables are defined in Table 4.39. For each TWINSPAN end-group, the means of the field/farm variables of each field member were calculated.

DECORANA and CANOCO were used to identify which field/farm variables were important in determining the incidence and the levels of the aphid/BYDV variables within each season.

Sections 4.7.2, 4.7.3 and 4.7.4 present the aphid/BYDV and the field/farm variables for each field, the TWINSPAN end-groups, the TWINSPAN end-group means of the aphid/BYDV and field/farm variables, the DECORANA and CANOCO analyses and the regional weather data for the winter barley seasons 1988/89, 1989/90 and 1990/91 respectively. In each section, the field/farm variables

Table 4.39 List of field/farm variables obtained for each field: definition of each variable and code name used in the analysis.

Variable	Definition	Code name
Altitude	Nearest 10 m (using O.S. 1:50,000)	Alt
Aspect A	Shelter around periphery of field on a scale 0 to 5 (5 very sheltered).	Asp A
Aspect B	Shelter to south and west of field on a scale 0 to 5 (5 very sheltered).	Asp B
Aspect C	Shelter to north and east of field on a scale 0 to 5 (5 very sheltered).	Asp C
Aspect T	Sum of Aspect A, B and C.	Asp T
Cultivar	Most common cultivar was Magie 1 All other cultivars 0	Cul
Desiccant	Desiccant herbicide applied to headlands (h) or entire field (e) prior to ploughing.	Des
Drilling date	Put in category 1, 2 or 3. 0 After 1 October. 1 Between 16 and 30 September. 2 Before 16 September.	Dri
Distance from Carlisle	Nearest km.	Carl
Distance from Crieff	Nearest km.	Crie
Distance from Stranraer	Nearest km.	Stra
Distance from sea	Nearest km from sea or estuary.	Sea
Extent of grass weed infestation in late spring.	Particularly *P. annua* 0 scattered weeds in tramlines. 1 appreciable proportion of tramlines carpeted (1-5%) 2 extensive areas of crop carpeted.	Wee

Table 4.39 continued.

Variable	Definition	Code name
Landuse	Degree of partitioning of farm enterprise between arable and livestock. 0 mostly cereals. 1 major livestock component.	Lan
Previous crop	Order may reflect increasing risk of BYDV 0 spring barley 1 winter wheat 2 winter barley 3 oilseed rape 4 ryegrass ley	Pre
Region	Each county was ascribed a number. 1 Dumfriesshire 2 Wigtownshire 3 Ayrshire 4 Renfrewshire 5 Stirlingshire 6 Lanarkshire	Reg
Soil moisture	Ability of soil to drain quickly. 0 drains very quickly (allows machinery access on day following heavy rain). 1 drains slowly.	Moi
Mean maximum temperature Nov-Mar	Mean of monthly values from climatological station selected to represent the region in which field is situated.	Mx
Mean minimum temperature Nov-Mar	Mean of monthly values from climatological station selected to represent the region in which field is situated.	Mn
Mean lowest minimum temperature Nov-Mar	Mean of monthly values from climatological station selected to represent the region in which field is situated.	Lmn
Total number of frost days Nov-Mar	Total of monthly values from climatological station selected to represent the region in which field is situated.	Fr
Total number of days with snow lying Nov-Mar	Total of monthly values from climatological station selected to represent the region in which field is situated.	Sn

that were important in determining aphid and BYDV incidence in that season were identified.

4.7.2.1 **Season 1988/89**

For each of the 45 fields, the aphid/BYDV variables and field/farm variables (except regional weather variables, regional distances and region number) are shown in Table 4.40. The "pseudo-species" function of TWINSPAN was set to create six categories (Table 4.41). All other settings were the default values. The five groups created by TWINSPAN after three levels of division are shown in the dendrogram (Figure 4.22) and the refined-ordination table (Table 4.41). Characteristic "pseudo-species" and field members of the five TWINSPAN end-groups are shown in Table 4.42. Data from four fields could not be included in the analysis, because all their aphid/BYDV variables were negative. These fields form a sixth group called, "No aphids or BYDV". Another field, L3, had one aphid/BYDV variable with a positive result: Yel 0.5. However, because of the "pseudo-species" settings, it was categorised as a field with all negative aphid/BYDV variables. This field was added to "No aphids or BYDV" which is also included in Table 4.42 and Figure 4.23. The regional weather data are shown in Table 4.43.

Table 4.40 Aphid/BYDV variables and field/farm variables of winter barley crops sampled season 1988/89.

	Aphid/BYDV variables												Field/farm variables										
							Yellow leaves			Green leaves									ASPECT				
Field	Md	Rp	Sa	Ins	Inf	Yel	RPV	PAV	MAV	RPV	PAV	MAV	Dri	Pre	Moi	Alt	Sea	Lan	A	B	C	T	Cul
Dumfriesshire																							
D1	-	-	2	-	1	1	1	1	1	-	-	-	1	2	-	40	3	-	1	2	2	5	1
D2	-	-	2	-	10	0.5	-	1	-	-	-	-	2	1	-	40	3	-	1	2	2	5	1
D3	1	-	2	-	50	0.5	-	-	1	-	-	-	1	-	-	40	2	-	1	2	1	4	-
D4	1	-	2	-	80	0.5	-	-	1	1	-	-	2	-	-	40	2	-	1	3	1	5	1
D5	1	-	2	-	80	10	-	-	1	-	-	1	1	-	1	10	0.5	-	3	3	3	9	-
D6	1	-	2	-	90	15	-	-	1	-	-	-	1	3	1	10	0.5	-	3	2	5	10	-
D7	-	-	2	-	80	15	-	-	1	-	-	-	1	2	1	10	1.0	-	2	2	3	7	1
D8	-	1	2	-	50	50	-	-	1	-	-	1	1	-	1	20	4	-	1	3	2	6	-
D9	-	-	2	-	40	10	-	-	1	-	-	-	1	-	1	20	4	-	1	3	2	6	-
D10	-	-	2	-	20	1	-	-	1	-	-	-	-	2	1	30	4	-	-	2	3	5	-
Wigtownshire																							
W1	-	2	-	1	70	75	1	1	1	-	1	1	2	4	-	30	1	1	1	2	3	6	-
W2	1	2	1	-	50	50	-	1	1	1	1	1	1	2	-	40	1	-	1	3	2	6	1
W3	-	2	-	1	1	50	1	1	1	1	1	-	1	2	-	80	1.5	-	2	4	3	9	-
W4	-	2	-	1	1	4	1	1	1	-	1	1	1	2	-	80	1.5	-	1	1	2	4	-
W5	1	2	1	1	80	75	1	1	1	1	1	-	1	2	1	50	0.5	1	1	3	-	4	-
Ayrshire																							
A1	-	1	2	-	80	1	-	-	1	-	-	1	-	1	1	20	5	1	2	3	2	7	-
A2	-	-	-	1	-	50	-	1	1	-	-	-	1	1	1	10	1	-	2	3	3	8	-
A3	-	-	2	-	1	0.5	-	-	-	-	-	-	1	2	1	100	14	-	2	2	4	8	-
A4	-	-	2	-	10	0.5	-	-	-	-	-	-	1	2	1	100	14	-	3	3	4	10	-
A5	-	1	2	-	60	0.5	-	-	1	-	1	-	1	-	1	30	4	-	1	2	2	5	1
A6	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	70	13	1	3	3	2	8	-
A7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	70	15	1	1	1	3	5	-
Renfrewshire																							
R1	-	-	2	-	1	-	-	-	1	-	-	1	2	1	1	30	10	-	-	5	1	6	-
R2	-	-	2	-	80	10	-	1	1	-	-	-	2	3	1	30	10	-	-	5	1	6	1
R3	-	-	2	-	70	-	-	-	-	-	1	-	2	2	1	30	9	-	2	-	1	3	-
R4	-	-	2	-	20	4	-	1	1	-	-	-	1	3	1	0	6	-	2	2	2	6	1
R5	-	-	-	-	-	3	-	-	1	-	-	-	1	3	1	0	6	-	3	2	2	7	-
R6	-	-	2	-	20	5	-	-	1	-	-	-	1	3	1	10	5.5	-	1	3	-	4	1
R7	-	-	2	-	1	0.5	-	-	1	-	-	-	1	-	1	10	5	-	3	2	3	8	-
R8	-	-	2	-	1	5	-	-	1	-	1	1	1	2	1	10	5	-	3	4	-	7	1
R9	-	-	2	-	1	0.5	-	-	1	-	-	-	1	2	1	30	1	-	3	-	4	7	1
R10	-	1	2	-	100	50	-	-	1	-	1	1	-	4	1	10	0.5	-	4	5	3	12	1
R11	-	-	2	-	50	1	-	1	1	-	-	-	1	3	1	30	0.5	-	2	4	4	10	1

Table 4.40 continued.

	Aphid/BYDV variables												Field/farm variables										
							Yellow leaves			Green leaves									ASPECT				
Field	Md	Rp	Sa	Ins	Inf	Yel	RPV	PAV	MAV	RPV	PAV	MAV	Dri	Pre	Moi	Alt	Sea	Lan	A	B	C	T	Cul
Stirlingshire																							
S1	-	-	2	-	10	1	-	-	1	-	-	1	-	-	1	20	9	-	1	2	3	6	1
S2	-	-	2	-	10	5	-	-	1	-	-	-	-	1	1	20	9	-	3	3	3	9	1
S3	-	-	2	-	1	0.5	-	-	1	-	-	1	1	1	1	60	30	-	3	2	4	9	1
S4	-	-	2	-	50	0.5	-	-	1	-	-	-	1	-	1	40	4	-	1	2	3	6	1
S5	-	-	2	-	50	5	-	-	1	-	-	1	1	-	1	40	3.5	-	2	1	3	6	1
S6	1	-	2	-	1	0.5	-	-	1	-	1	-	1	1	1	50	36	-	3	2	4	9	1
S7	-	-	2	-	1	0.5	-	-	1	-	-	-	1	-	1	50	36	-	1	2	3	6	1
Lanarkshire																							
L1	-	-	-	-	-	-	-	-	1	-	-	-	1	4	1	200	38	-	1	1	1	3	-
L2	-	-	-	-	-	1	-	1	-	-	1	-	1	2	1	230	58	-	1	2	1	4	-
L3	-	-	-	-	-	0.5	-	-	-	-	-	-	1	2	1	230	58	-	1	2	2	5	-
L4	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	210	46	-	3	3	3	9	1
L5	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	210	46	-	3	3	3	9	1

Key for **Table 4.40**

\- denotes zero.

Md Incidence of *M. dirhodum*

Rp Incidence of *R. padi*

Sa Incidence of *S. avenae*

1 present.

2 predominant.

\- absent.

Ins Field received a spring application of insecticide prior tc the survey. This variable was not included in the TWINSPAN analysis, because it was a response to the aphid/BYDV variables in the field, and not a contributory factor as ar autumn application of insecticide would be. None of the 45 fields received an autumn insecticide application in 1988.

Inf Percentage of ten plants infested by at least one aphid. 1% denotes none of the ten examined plants was infested but aphids were seen in the crop.

Yel Percentage of crop comprised of patches of yellow plants.

RPV Incidence of BYDV strain in leaf samples (+/-).

PAV Incidence of BYDV strain in leaf samples (+/-).

MAV Incidence of BYDV strain in leaf samples (+/-).

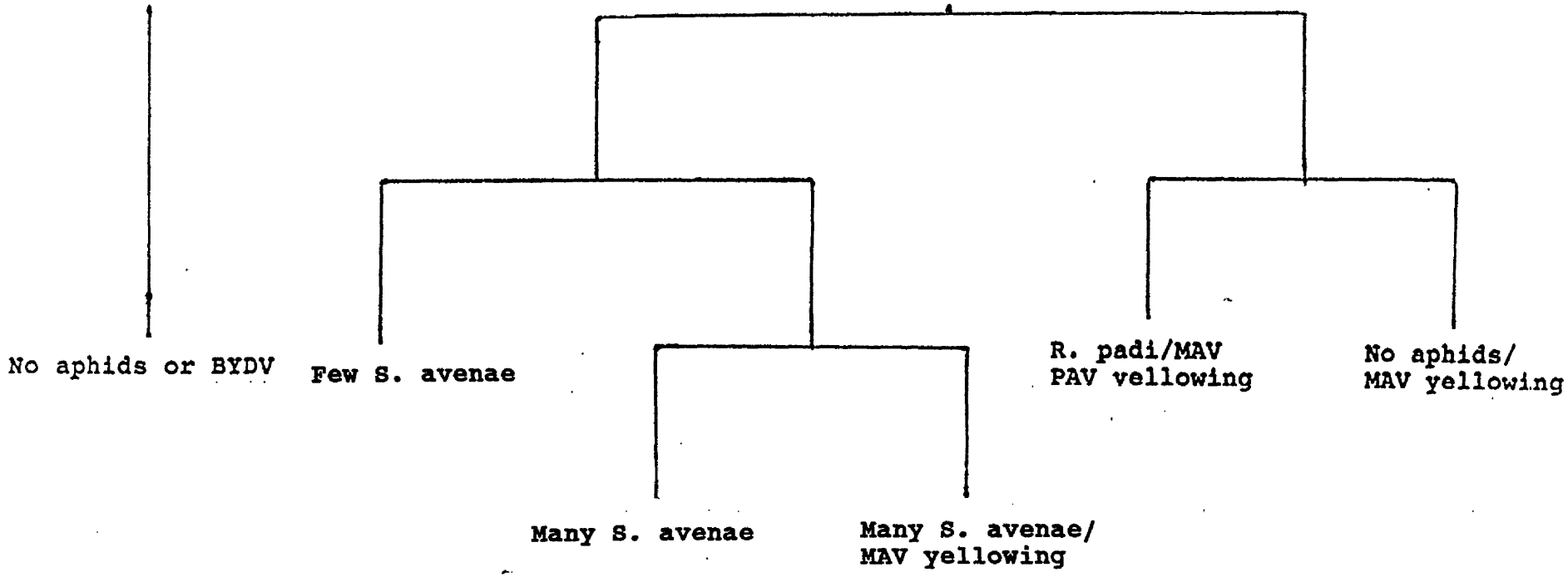


Figure 4.22 Dendrogram showing divisions and end-group names of TWINSPAN classification of BYDV survey 1988/89.

Table 4.41 TWINSPAN refined-ordination table; end-groups of BYDV in winter barley 1988/89.

"Pseudo-species" level

Aphid/BYDV variable	40 fields ordinated to reflect the incidence and levels of abundance of the aphid/BYDV variables	
Inf	1 - 1 1 1 1 1 1 1 1 3 3 3 5 5 5 5 5 5 5 5 5 5 4 3 3 3 3 5 5 5 5 5 5 5 1 1 - - -	00
MAVy	1 1 - 1 1 1 1 1 1 1 - - 1 1 1 1 1 1 - 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 - 1 1	00
Md	- - - - - - - - - 1 - - - - 1 1 - - - - 1 1 - - - - - - - - - - - - 1 1 - - - - -	00
MAVg	1 - - 1 - - - 1 - - - - - 1 - - - - 1 - 1 - - 1 - - - - - - - - 1 1 1 - 1 - 1 - - -	01
Sa	2 - 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 - 1 1 - - - - -	01
PAVg	1 - - - - - - - - 1 - - - - - - - 1 - 1 - - - - - - - - - - - - 1 1 1 1 1 1 1 - -	10
PAVy	- - - - - - - - - - 1 1 - - - - - - - - - - - - - - - - - - - 1 1 1 - - 1 1 1 1 1 1 1 -	10
Yel	3 - - - - - - - - - 1 - - 1 - - - - 1 - 3 3 3 3 3 1 3 3 3 3 1 5 5 5 5 5 5 3 1 5 3	10
Rp	- - - - - - - - - - - - - - - - - - 1 1 - - - - - - - - - - - - 1 1 2 2 2 2 2 - - -	11
RPVg	- - - - - - - - - - - - - - - - 1 - - - - - - - - - - - - - - - - - - - 1 1 1 1 - - -	11
RPVy	- - - - - - - - - - 1 - 1 1 - 1 1 - - -	11
	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1	
	0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 0 0 1 1 1 1 1	
	0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	

Group 2 Group 3 Group 4 Group 5 Group 6

"Pseudo-species" levels

- = 0 1 = 1 2 = 2

3 = 3-24 4 = 25-49 5 = >49

Table 4.42 "Pseudo-species" that characterise TWINSPAN end-groups and the group members; BYDV in winter barley 1988/89.

Characteristic "Pseudo-species"

TWINSPAN end-groups					
1[a]	2	3	4	5	6
Sa 0	Sa 2	Sa 2	Sa 2	Sa 1	Sa 0
Rp 0	Rp 0	Rp 0	Rp 0	Rp 2	Rp 0
Inf 0	Inf 1	Inf 5	Inf 3	Inf 5	Inf 0
MAVy 0	MAVy 1	MAVy 1	MAVy 1	MAVy 1	MAVy 1
Yel 0	Yel 0	Yel 0	Yel 3	MAVg 1	PAVy 1
				PAVy 1	Yel 3
				PAVg 1	
				Yel 5	
A6	R8	D3	D5	D8	W4
A7	L1	D4	D6	R10	L2
L3	A3	S4	D7	W1	A2
L4	R1	A5	S5	W5	R5
L5	R7	A1	D9	W2	
	R9	R3	D10	W3	
	S7		R6		
	S3		S2		
	S6		R4		
	D1		R2		
	D2		R11		
	A4				
	S1				
No aphids or BYDV.	Few *S. avenae*	Many *S. avenae*	Many *S. avenae*/ MAV yellowing.	*R . padi*/ MAV/PAV yellowing.	No aphids/ MAV yellowing.

[a] TWINSPAN could not classify these fields because all of their aphid/BYDV variables were negative.

Table 4.43 Winter weather parameters at the climatological stations selected to be representative of the six regions 1988/89.

	November					December					January					February					March				
	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn
Dumfriesshire	9.1	1.3	-5.0	10	0	10.3	5.1	-1.3	2	0	9.5	4.5	-1.4	3	0	8.7	2.4	-3.0	7	0	9.8	2.1	-2.7	7	0
Wigtownshire	9.4	3.6	-3.5	5	0	9.7	5.9	1.0	0	0	9.2	5.6	0.4	0	0	8.2	3.8	-0.2	1	0	9.1	3.2	-4.0	4	0
Ayrshire	9.5	2.7	-5.6	-	-	9.7	5.9	2.2	0	0	9.5	5.3	1.1	0	0	8.3	3.4	-0.8	1	0	9.1	3.0	-4.0	3	0
Renfrewshire	8.8	2.6	-3.6	7	1	9.7	5.4	1.5	0	0	9.5	4.8	0.2	0	0	8.1	2.3	-2.2	6	3	9.5	2.5	-3.0	3	0
Stirlingshire	9.0	1.2	-5.5	11	0	10.5	4.5	0.3	0	0	9.9	4.7	-1.0	2	0	8.3	2.6	-3.5	5	0	9.7	2.6	-3.0	6	0
Lanarkshire	7.4	-1.1	-11.6	17	5	8.3	2.8	-4.4	7	0	8.0	2.8	-3.6	4	0	6.7	0.4	-10.6	9	6	8.2	0.3	-7.9	13	2

Mx Mean daily maximum temperature °C

Mn Mean daily minimum temperature °C

Lmn Lowest daily minimum temperature °C

Fr Number of days with air frost

Sn Number of days with snow lying 0900 GMT

The TWINSPAN end-group means of the 12 aphid/BYDV variables and the 20 field/farm variables are shown in Tables 4.44 and 4.45 respectively.

Table 4.44 TWINSPAN end-group means of aphid/BYDV variables; BYDV in winter barley 1988/89.

	Mean values of aphid/BYDV variables					
TWINSPAN end-group	Gp 1	Gp 2	Gp 3	Gp 4	Gp 5	Gp 6
Md	0.0	0.1	0.3	0.2	0.3	0.0
Rp	0.0	0.0	0.3	0.0	1.7	0.5
Sa	0.0	1.8	2.0	2.0	1.0	0.0
Ins	0.0	0.0	0.0	0.0	0.5	0.5
Inf	0.0	0.2	6.5	4.9	5.8	0.0
Yel	0.1	0.8	0.5	7.4	58	14
RPVy[a]	0.0	0.1	0.0	0.0	0.5	0.3
PAVy	0.0	0.2	0.0	0.3	0.7	0.8
MAVy	0.0	0.8	0.8	1.0	1.0	0.8
RPVg[b]	0.0	0.0	0.2	0.0	0.5	0.0
PAVg	0.0	0.2	0.3	0.0	0.8	0.5
MAVg	0.0	0.3	0.2	0.2	0.7	0.3

[a] yellow leaf samples

[b] green leaf samples

Table 4.45 TWINSPAN end-group means of field/farm variables; BYDV in winter barley 1988/89.

TWINSPAN end-group	Mean values of field/farm variables					
	Gp 1	Gp 2	Gp 3	Gp 4	Gp 5	Gp 6
Dri	0.6	1.1	1.2	0.9	1.0	1.0
Pre	0.8	1.4	0.5	1.8	2.3	2.0
Moi	1.0	0.8	0.7	1.0	0.5	0.8
Alt	158	57	32	18	38	80
Sea	36	16	4.5	4.0	1.4	17
Lan	0.4	0.0	0.2	0.0	0.3	0.0
Asp A	2.2	1.9	1.3	1.7	1.7	1.8
Asp B	2.4	2.2	2.0	2.7	3.3	2.0
Asp C	2.6	2.7	1.7	2.6	2.2	2.0
Asp T	7.2	6.8	5.0	7.1	7.2	5.8
Reg	4.8	3.8	2.8	2.8	2.2	3.8
Stra	105	130	113	117	50	80
Carl	103	130	96	98	123	121
Crie	100	74	111	106	163	128
Cul	0.4	0.6	0.5	0.6	0.3	0.0
Mx	8.3	9.2	9.3	9.4	9.2	8.8
Mn	2.2	3.2	3.5	3.2	4.0	3.3
Lmn	-5.1	-2.4	-2.0	-2.2	-1.6	-2.9
Fr	32	22	20	24	14	21
Sn	7.8	2.2	0.7	1.5	0.7	4.3

In the DECORANA, all settings used were the default values. Data from the four fields with wholly negative aphid/BYDV variables were excluded from the analysis. The DECORANA sample scores for axes 1 and 3 (the first and third most significant trends) are plotted as an ordination diagram in Figure 4.23. These two axes were chosen because the TWINSPAN end-groups were separated most using them. Axis 1 (eigenvalue 0.791) accounts for 76% of the variance whereas axis 3 (eigenvalue 0.092) accounts for only 9%.

Table 4.46 and 4.47 show the presentation of CANOCO chosen in this thesis. In each Table, the species rankings show the ordination of the aphid/BYDV variables in the first two trends, whereas the biplot rankings show the ordination of the field/farm variables in the first two trends. The weighted correlation values relate to the field/farm variables and indicate the relative importance of the field/farm variables to that trend.

For example, in Table 4.46, the species rankings of trend 1 show that *R. padi*-transmitted BYDV variables have been separated from *S. avenae*-transmitted BYDV variables. The biplot rankings and weighted correlations of trend 1 indicate that distance from Stranraer is the most important field/farm variable, because its weighted correlation value is much greater than the others. Thus, *S. avenae*-transmitted BYDV was associated with increasing distance from Stranraer, and *R. padi*-transmitted BYDV proximity to Stranraer. The species rankings of the second trend

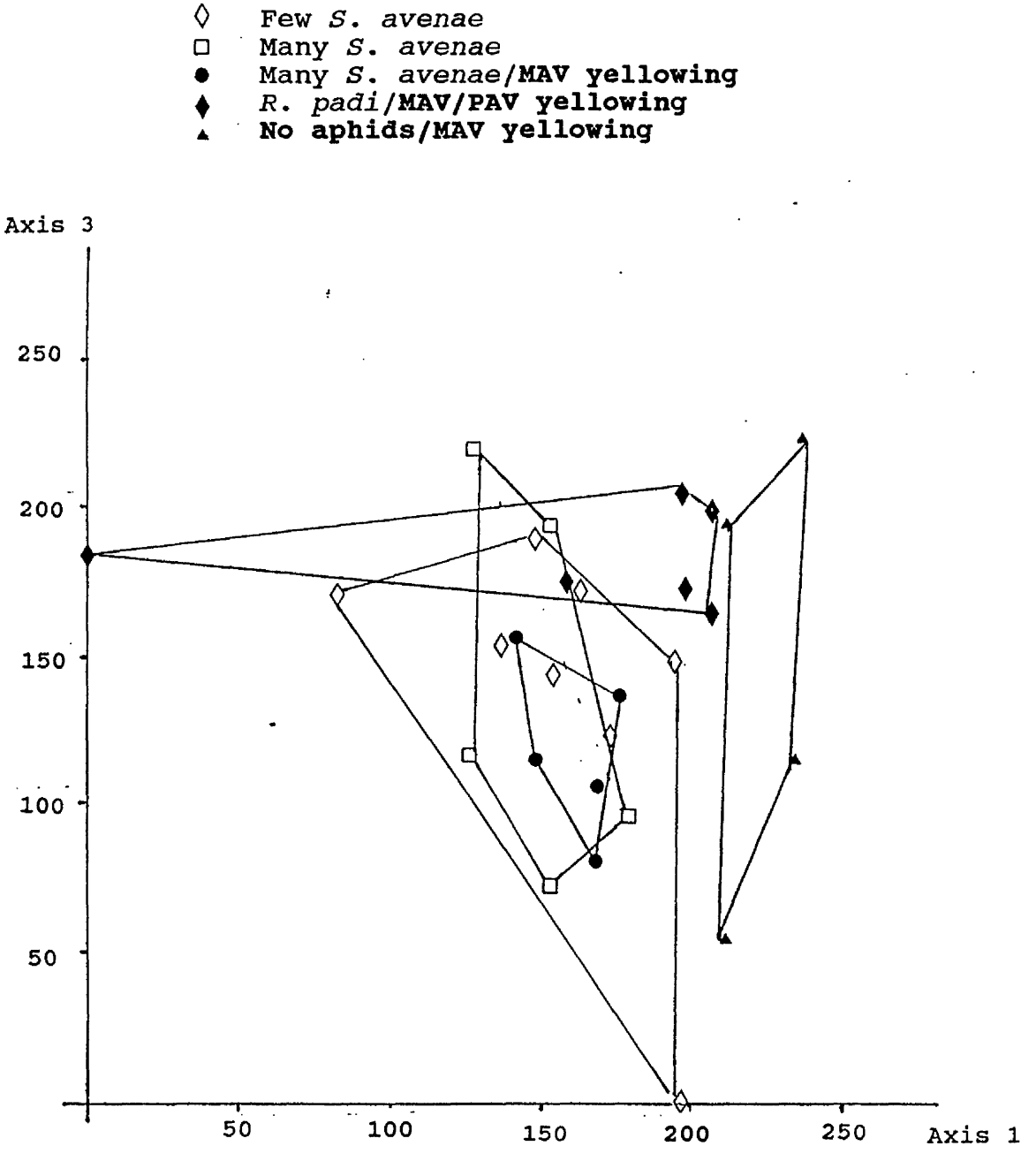


Figure 4.23 DECORANA ordination of BYDV survey 1988/89 data; axis 1 by axis 3 plot of end-groups identified by TWINSPAN.

indicate that fields with large aphid infestations of either species and large crop yellowing estimates were grouped at one end, and the field/farm variable that accounted for most variation of that trend was altitude with a weighted correlation value of 0.802: fields at high altitude were not aphid infested whereas the greatest aphid infestations were found in fields at low altitude.

Table 4.46 Rankings of aphid/BYDV and field/farm variables in the two most significant trends identified in the second run of CANOCO; winter barley, 1988/89.

Trend 1 / Trend 2					
Species rankings		Biplot rankings		Weighted correlation	
Sa	PAVg	Stra	Alt	0.830	0.802
MAVy	PAVy	Cul	Sea	0.398	0.128
Inf	RPVg	Sea	Dri	0.245	0.113
MAVg	RPVy	Moi	Cul	0.177	0.055
Md	MAVy	Dri	Pre	-0.094	0.027
PAVg	Md	Lan	Stra	-0.267	0.007
PAVy	Sa	Asp B	Asp B	-0.303	-0.036
RPVy	Rp	Alt	Lan	-0.330	-0.117
Yel	MAVg	Pre	Moi	-0.351	-0.165
Rp	Yel				
RPVg	Inf				

Table 4.47 Rankings of aphid/BYDV and field/farm variables in the two most significant trends identified in the third run of CANOCO; winter barley, 1988/89.

Trend 1 / Trend 2					
Species rankings		Biplot rankings		Weighted correlation	
Sa	RPVg	Sea	Sea	0.439	0.458
MAVy	Md	Moi	Dri	0.361	0.137
Inf	RPVy	Dri	Lan	-0.183	-0.217
MAVg	PAVg	Lan	Pre	-0.493	-0.304
Md	PAVy	Asp B	Asp B	-0.523	-0.578
PAVg	Rp	Pre	Moi	-0.641	-0.760
Yel	MAVg				
PAVy	Inf				
Rp	Yel				
RPVg	MAVy				
RPVy	Sa				

see Tables 4.39 & 4.40 for explanation of codes.

In the CANOCO, all field/farm variables except the regional weather data and region number were initially included because all fields of a region had the same values. Data from the four fields with wholly negative aphid/BYDV variables were excluded from the analysis. Settings used were the default values. The first CANOCO run with 14 field/farm variables identified that the four types of aspect were highly correlated as were distances from Carlisle, Crieff and Stranraer. Aspect B was selected to be included in further analysis, because wind direction was persistently in the south-west during the winter 1988/89 (Ratcliffe, 1989; Murray, 1991), and so shelter to the

south and west was presumably most relevant. Distance from Stranraer was selected to be included in further analysis, because it was the distance variable most highly correlated with the environmental axis 1. The second analysis therefore included nine field/farm variables (Table 4.46).

In the third run of CANOCO, distance from Stranraer and altitude were excluded, so that less important factors might be identified (Table 4.47). Cultivar was also excluded, because it was correlated with distance from Stranraer.

4.7.2.2 **Discussion of factors affecting the incidence of BYDV in winter barley 1988/89**

The unusual mildness of the winter 1988/89 (Ratcliffe, 1989; Murray, 1991; Figure 4.24) enabled aphids to overwinter in autumn-sown cereals of Scotland in large numbers. It also allowed the regional differences in aphid species incidence present in the autumn of 1988 to develop into different types of BYDV in the spring of 1989. The cumulative value of II for *R. padi* only, measured at Auchincruive (23 September to 4 November) in the autumn of 1988 was 82.

The winter of 1988/89 was $P_5S_5C_2$ (section 2.4), the P value being the highest recorded in the 123 year record. The P index is positively correlated with winter temperature (Murray & Benwell, 1970), and this combination of quints implies that wind direction was in the south-west

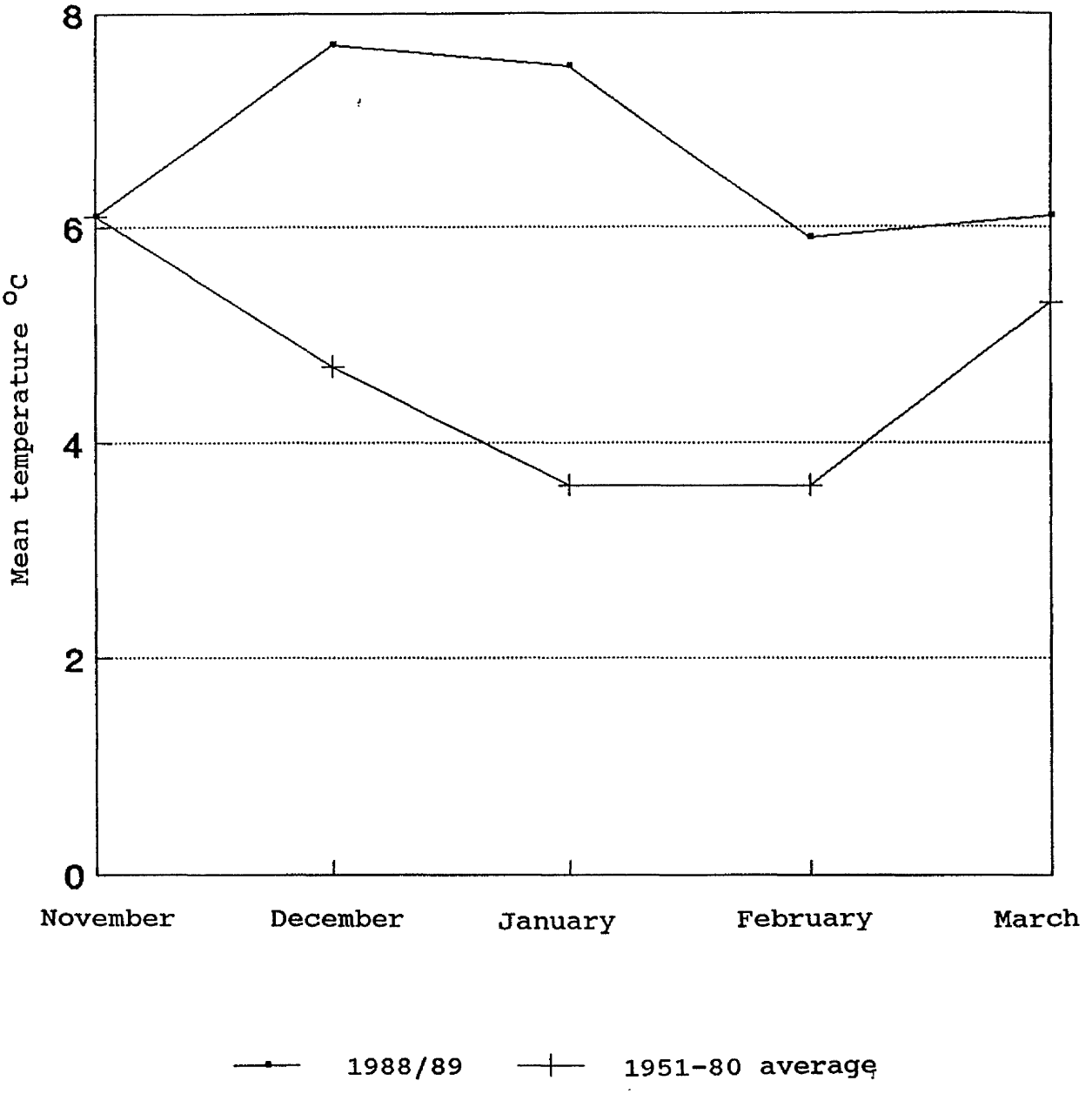


Figure 4.24 Mean temperature at Auchincruive, Ayr, November to March 1988/89 relative to the 1951-80 average.

on more days than average. Scotland experienced milder temperatures than England in this winter (Table 3.16), the mean temperature at Auchincruive relative to the 1951-80 average is shown in Figure 4.24.

TWINSPAN identified one *R. padi*- and four *S. avenae*-transmitted BYDV groups (Tables 4.41 & 4.42). A further group, "No aphids or BYDV" was created to include the fields with wholly negative aphid/BYDV values.

In this season, fields affected by *R. padi*-transmitted BYDV were only found in Wigtownshire and south Ayrshire, therefore CANOCO identified distance from Stranraer as the most important variable affecting the incidence of BYDV: *R. padi*-transmitted BYDV being found near to Stranraer and *S. avenae*-transmitted BYDV elsewhere (Table 4.46). However, *S. avenae*-transmitted BYDV was also present in Wigtownshire, hence the name "*R. padi*/MAV/PAV yellowing", of the group containing Wigtownshire fields.

The second most important factor was altitude, which affected both types of BYDV in a similar manner: no individuals of *R. padi* or *S. avenae* were found in Lanarkshire fields (Table 4.40). After these two factors were removed from the CANOCO analysis (Table 4.47), increasing distance from the sea was found to have a negative influence on both types of BYDV, and high previous cropping type score was positively related to the incidence of *R. padi*-transmitted BYDV.

The DECORANA plot (Figure 4.23) separated "No aphids/MAV yellowing" from the other groups along axis 1 and "*R. padi*/MAV/PAV yellowing" from the other groups along axis 3. Using Table 4.45, it is reasonable to conclude that axis 1 could be altitude and axis 3 either distance from Stranraer, distance from the sea or number of frost days or some other weather variable.

The association of *R. padi* transmitted-BYDV with Wigtownshire is probably owing to relatively large *R. padi* migrations in this region during the autumn 1988. Although winter temperatures were highest in Wigtownshire (Table 4.43), other regions including Lanarkshire had sufficiently mild temperatures to allow the relatively frost-suspectible *R. padi* (Dean, 1974b) to overwinter anholocyclically. Comparison of the September + October 1988 catches of *R. padi* by the two most relevant suction traps supports these theories: Ayr, 2142 and Belfast, 4421. In other regions, *S. avenae*-transmitted BYDV arose, except in Lanarkshire where there may have been few aphids present in the autumn 1988.

Although CANOCO (Table 4.47) and TWINSPAN (Table 4.45) identified that high previous cropping type score was associated with *R. padi*-transmitted BYDV, only one of the three crops that followed grass (W1) was affected by this type of BYDV. One, R10, was severely affected by *S. avenae*-transmitted BYDV, and the other, L1, was hardly affected by BYDV. In the third CANOCO run (Table 4.48), distance from the sea, shelter to the south and west, and soil moisture

were identified as important. The former two variables are related to climate, coastal localities and more sheltered fields experiencing higher temperatures, and perhaps most importantly, fewer frosts. That high values of soil moisture (i.e. freely draining soils) favoured both aphids and crop yellowing is probably spurious. The eight freely draining fields were found in Wigtownshire and Dumfriesshire where aphids and BYDV were most abundant.

In the spring of 1989, winter barley crops had a crisp and spikey appearance. This is considered to be the result of the cold winds and temperatures of April stressing crops following the mild and wet winter which encouraged lush growth.

4.7.3.1 **Season 1989/90**

For each of the 26 winter barley fields, the aphid/BYDV variables and field/farm variables (except regional weather variables, regional distances & region number) are shown in Table 4.48. The "pseudo-species" function of TWINSPAN was set to create five categories (Table 4.49). All other settings used were the default values. The seven groups created by TWINSPAN after three levels of divisions are shown in the dendrogram (Figure 4.25) and the refined-ordination table (Table 4.49). Characteristic "pseudo-species" and field members of the seven TWINSPAN end-groups are shown in Table 4.50. The regional weather data are shown in Table 4.51.

Table 4.48 Aphid/BYDV and field/farm variables of winter barley sampled season 1989/90.

	Aphid/BYDV variables									Field/farm variables												
																			ASPECT			
Field	Rp	Sa	Ins	RPV	PAV	MAV	Yel	Inf	Pat	Dri	Pre	Des	Wee	Moi	Alt	Sea	Lan	A	B	C	T	Cul
Dumfriesshire																						
D1	1	1	-	-	-	-	-	1	1	1	2	-	2	-	40	3	-	1	2	2	5	1
D2	1	2	1	-	-	1	-	1	1	2	-	-	-	1	40	15	-	1	2	1	4	-
D3	1	2	-	-	-	1	-	1	-	2	2	-	-	1	40	15	-	2	3	3	8	1
D4	-	1	1	-	-	-	-	1	-	2	2	h	1	-	40	2	-	1	2	1	4	1
D5	1	-	1	-	1	-	-	1	-	2	2	h	1	-	40	2	-	1	3	1	5	1
D6	-	1	1	-	1	1	-	-	-	1	2	-	1	1	30	4	-	1	3	2	6	-
D7	-	1	1	1	1	-	-	-	-	1	-	-	1	1	20	4	-	2	3	3	8	-
Wigtownshire																						
W1	2	1	1	1	-	1	-	-	1	2	2	-	2	-	20	0.5	1	1	2	3	6	-
W2	4	-	1	1	1	1	-	1	1	1	4	-	2	-	20	0.5	1	1	2	3	6	-
W3	4	2	1	1	-	1	-	1	1	-	4	-	2	1	40	1	1	1	1	3	5	1
W4	3	-	-	-	1	-	1	1	-	1	2	1	-	-	40	1	-	1	3	2	6	1
Ayrshire																						
A1	1	3	-	-	1	1	-	1	1	-	-	e	-	1	50	5	1	3	4	3	10	-
A2	1	2	-	1	1	1	-	1	1	1	-	-	1	1	30	5	1	2	2	2	6	-
A3	-	-	-	-	1	1	-	-	-	1	-	-	-	1	30	4	-	1	2	2	7	-
A4	2	1	1	1	1	-	1	1	1	1	4	-	-	1	60	13	1	3	4	2	9	1
A5	2	-	1	1	1	-	1	1	1	1	4	-	-	1	70	15	1	3	3	4	10	1
Renfrewshire																						
R1	1	4	-	-	-	1	-	1	1	2	2	-	1	1	30	10	-	-	5	1	6	1
R2	1	4	-	-	-	1	-	1	-	2	2	-	-	1	30	10	-	-	5	1	6	0
R3	1	4	-	-	-	1	-	1	1	2	2	-	-	1	30	9	-	2	-	1	3	0
R4	-	1	1	-	-	-	-	-	-	1	2	-	-	1	0	6	-	-	2	2	2	0
R5	-	-	1	1	-	-	-	-	-	1	2	-	-	1	0	6	-	1	3	-	4	0
R6	-	1	1	1	1	1	-	-	-	1	-	h	-	1	10	0.5	-	-	2	3	5	1
R7	1	1	1	-	1	1	-	-	-	1	2	-	1	1	30	0.5	-	2	4	4	10	1
Stirlingshire																						
S1	1	-	1	-	1	1	-	-	-	2	1	-	1	1	50	36	-	3	2	4	9	1
S2	1	1	1	-	1	1	-	1	1	2	1	-	1	1	50	36	-	1	2	3	6	1
S3	2	-	1	-	1	-	1	1	1	2	1	-	-	1	10	25	-	-	-	1	1	1

Key for **Table 4.48**

Rp Score for *Rhopalosiphum* colony incidence on scale 0 to 4.
0 None counted throughout season.
1 Less than five on any visit.
2 More than five on any autumn visit but fewer in summer.
3 More than five on any summer visit but fewer in autumn.
4 More than five on any autumn visit and on any summer visit.

Sa Score for *S. avenae* colony incidence on scale 0 to 4.
0 None counted throughout season.
1 One or two colonies on at least one visit.
2 More than two on every autumn visit but fewer in summer.
3 More than two on every summer visit but fewer in autumn.
4 More than two on every autumn and summer visit.

Ins Autumn application of insecticide (+/-).

RPV Incidence of BYDV strain in leaf samples (+/-).

PAV Incidence of BYDV strain in leaf samples (+/-).

MAV Incidence of BYDV strain in leaf samples (+/-).

Yel Proportion of crop with yellow symptoms (+ if > 0.1%).

Inf Incidence of scattered yellow plants (1 plant / 10 m^2 +).

Pat Incidence of patches of yellow plants (+/-).

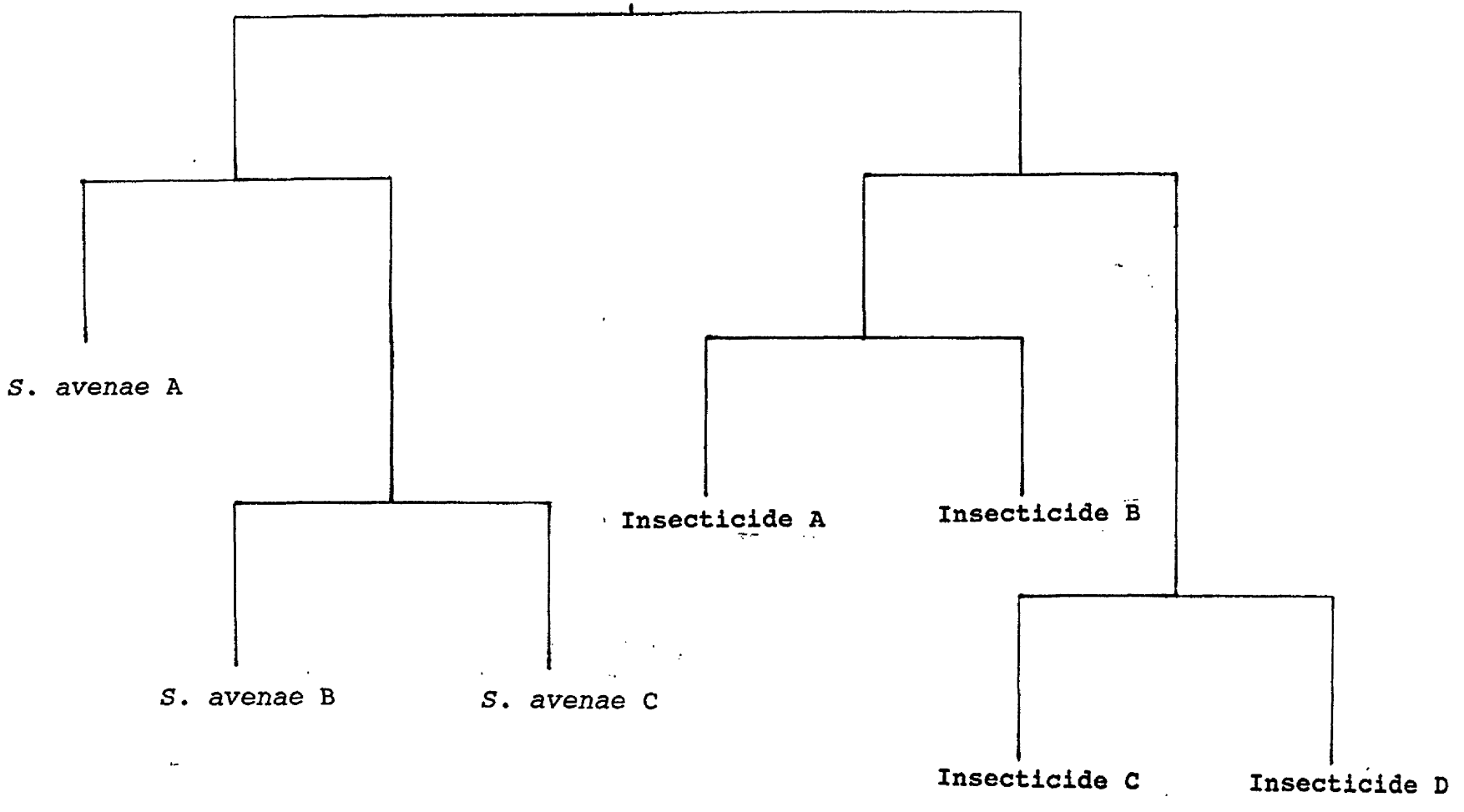


Figure 4.25 Dendrogram showing divisions and end-group names of TWINSPAN classification of BYDV survey 1989/90.

Table 4.49 TWINSPAN refined-ordination table; end-groups of BYDV in winter barley 1989/90.

"Pseudo-species" level

Aphid/BYDV variable	26 fields ordinated to reflect the incidence and levels of abundance of the aphid/BYDV variables																												
Sa	3	2	1	2	2	3	4	4	4	1	1	-	1	1	1	1	-	1	-	-	1	-	-	1	-	2	1		
Pat	1	1	1	1	-	1	1	-	1	-	-	-	-	-	-	-	1	-	-	-	-	1	1	1	1	1	1	1		
MAV	1	1	-	1	1	1	1	1	1	-	-	-	1	-	1	1	1	1	1	-	-	-	-	1	1	1	1		
Inf	1	1	1	1	1	1	1	1	1	-	-	-	-	1	1	1	-	-	-	1	1	1	1	-	1	1	1		
Rp	1	1	1	1	1	2	1	1	1	-	-	-	-	-	-	1	-	1	1	1	2	2	2	2	4	4	01		
RPV	-	1	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-	1	1	-	1	1	1	00		
Yel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	00		
PAV	1	1	-	-	-	-	-	-	-	1	-	-	1	-	1	1	1	1	1	1	1	1	1	-	1	-	00		
Ins	-	-	-	1	-	-	-	-	-	1	1	1	1	1	1	1	-	1	1	1	1	1	1	1	1	1	00		
	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1			
			0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	1	1			
	Gp 1		Gp 2			Gp 3				Gp 4				Gp 5						Gp 6				Gp 7					

"Pseudo-species" levels

- = 0 1 = 1 2 = 2 3 = 3 4 = > 4

Table 4.50 "Pseudo-species" that characterise TWINSPAN end-groups and the group members; BYDV in winter barley 1989/90.

Characteristic "Pseudo-species"						
TWINSPAN end-groups						
1	2	3	4	5	6	7
Sa 2 MAV 1 PAV 1 Ins 0 Pat 1	Sa 2 MAV 1 Ins 0 Pat 1	Sa 4 MAV 1 Ins 0 Pat 1	Rp 0 Ins 1 Pat 0	Rp 1 PAV 1 PAV 1 Ins 1 Pat 0	Rp 2 PAV 1 Ins 1 Pat 1	Rp 4 MAV 1 RPV 1 Ins 1 Pat 1
A1 A2	D1 D2 D3	W4 R1 R2 R3	D7 R4 R5 R6	D4 D6 S2 A3 R7 S1	D5 A4 A5 S3	W1 W2 W3
S. avenae A	*S. avenae* B	*S. avenae* C	Insecticide A	Insecticide B	Insecticide C	Insecticide D

Table 4.51 Winter weather parameters at the climatological stations selected to be representative of the six regions 1989/90.

	November					December					January					February					March				
	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn
Dumfriesshire	9.0	3.0	-5.9	7	0	5.6	0.3	-6.1	12	0	8.8	3.2	-0.7	2	0	8.3	3.7	-2.2	2	1	10.5	4.6	-4.0	4	1
Wigtownshire	9.2	4.9	-2.7	3	0	6.8	1.3	-4.7	10	0	8.4	3.3	-0.4	1	0	8.3	4.4	0.2	0	0	9.7	5.2	-1.0	1	0
Ayrshire	8.8	3.3	-3.2	5	-	6.2	0.8	-4.8	12	0	8.5	3.7	0.2	0	0	8.6	3.4	0.2	0	0	10.0	5.0	-1.0	4	0
Renfrewshire	8.2	2.8	-4.4	7	0	4.8	-0.1	-4.3	15	0	8.1	3.6	0.0	0	3	8.7	3.4	0.2	0	0	10.6	4.9	-1.6	2	2
Stirlingshire	8.5	2.8	-5.5	7	0	5.7	-0.5	-5.0	18	0	8.4	3.3	-0.7	1	0	8.6	3.7	0.3	0	0	10.8	5.1	-2.1	3	0

Mx Mean daily maximum temperature °C

Mn Mean daily minimum temperature °C

Lmn Lowest daily minimum temperature °C

Fr Number of days with air frost

Sn Number of days with snow lying 0900 GMT

The TWINSPAN end-group means of the nine aphid/BYDV variables and the 22 field/farm variables are shown in Tables 4.52 and 4.53 respectively.

Table 4.52 TWINSPAN end-group means of aphid/BYDV variables; BYDV in winter barley 1989/90.

TWINSPAN end-group	Mean values of aphid/BYDV variables						
	Gp 1	Gp 2	Gp 3	Gp 4	Gp 5	Gp 6	Gp 7
Rp	1.0	1.0	1.3	0.0	0.5	1.8	3.3
Sa	2.5	1.7	3.8	0.8	0.7	0.3	1.0
Ins	0.0	0.3	0.0	1.0	1.0	1.0	1.0
Yel	0.0	0.0	0.0	0.0	0.0	0.8	0.0
Inf	1.0	1.0	1.0	0.0	0.3	1.0	0.7
Pat	1.0	0.7	0.8	0.0	0.2	0.8	1.0
RPV	0.5	0.0	0.0	0.8	0.0	0.5	1.0
PAV	1.0	0.0	0.0	0.5	0.8	1.0	0.3
MAV	1.0	0.7	1.0	0.3	0.8	0.0	1.0

Table 4.53 TWINSPAN end-group means of field/farm variables; BYDV in winter barley 1989/90.

TWINSPAN end-group	Mean values of field/farm variables						
	Gp 1	Gp 2	Gp 3	Gp 4	Gp 5	Gp 6	Gp 7
Dri	0.5	1.7	1.8	1.0	1.5	1.5	1.0
Pre	0.0	1.3	2.0	1.0	1.3	2.8	3.3
Moi	1.0	0.7	0.8	1.0	0.8	0.8	0.3
Des	1.0	0.0	0.0	0.5	0.2	0.3	0.0
Wee	0.5	0.7	0.8	0.3	0.8	0.3	2.0
Alt	40	40	33	8	38	45	27
Sea	5	11	8	4	14	14	1
Lan	1.0	0.0	0.0	0.0	0.0	0.5	1.0
Asp A	2.5	1.3	0.8	1.3	1.5	1.8	1.0
Asp B	3.0	2.3	3.3	2.5	2.5	2.5	1.7
Asp C	2.5	2.0	1.3	2.0	2.7	2.0	3.0
Asp T	8.0	5.7	5.3	5.8	7.0	6.3	5.7
Reg	3.0	1.0	3.5	3.3	3.2	3.0	2.0
Stra	76	104	84	119	137	110	5
Carl	127	36	148	123	116	105	140
Crie	110	148	98	92	87	110	182
Cul	0.0	0.7	0.5	0.3	0.7	1.0	0.3
Mx	8.4	8.4	8.2	8.2	8.4	8.4	8.5
Mn	3.2	3.0	3.1	2.9	3.0	3.1	3.8
Lmn	-1.7	-3.8	-2.0	-2.5	-2.8	-2.5	-1.8
Fr	21	27	22	25	26	25	15
Sn	0.0	2.0	3.8	4.3	1.5	0.5	0.0

In the DECORANA, all settings used were the default values. The DECORANA sample scores for axes 1 and 3 (the first and third most significant trends) are plotted as an ordination diagram in Figure 4.26. These two axes were chosen because the TWINSPAN end-groups were separated most using them. Axis 1 (eigenvalue 0.234) accounts for 64% of the variance whereas axis 3 (eigenvalue 0.058) accounts for only 16%.

In the CANOCO, all field/farm variables except the regional weather data and region number were included initially because all fields of a region have the same values. All settings used were the default values. The first CANOCO run with 16 field/farm variables identified that the four types of aspect were highly correlated as were distances from Carlisle, Crieff and Stranraer. One shelter variable, aspect B, was selected to be included in further analysis, because wind direction was persistently in the south during the winter 1989/90 (Ratcliffe, 1990) and so shelter to the south and west was presumably most relevant. One distance variable, distance from Stranraer was selected to be included in further analysis, because it was found to be the most important field/farm variable in the season 1988/89.

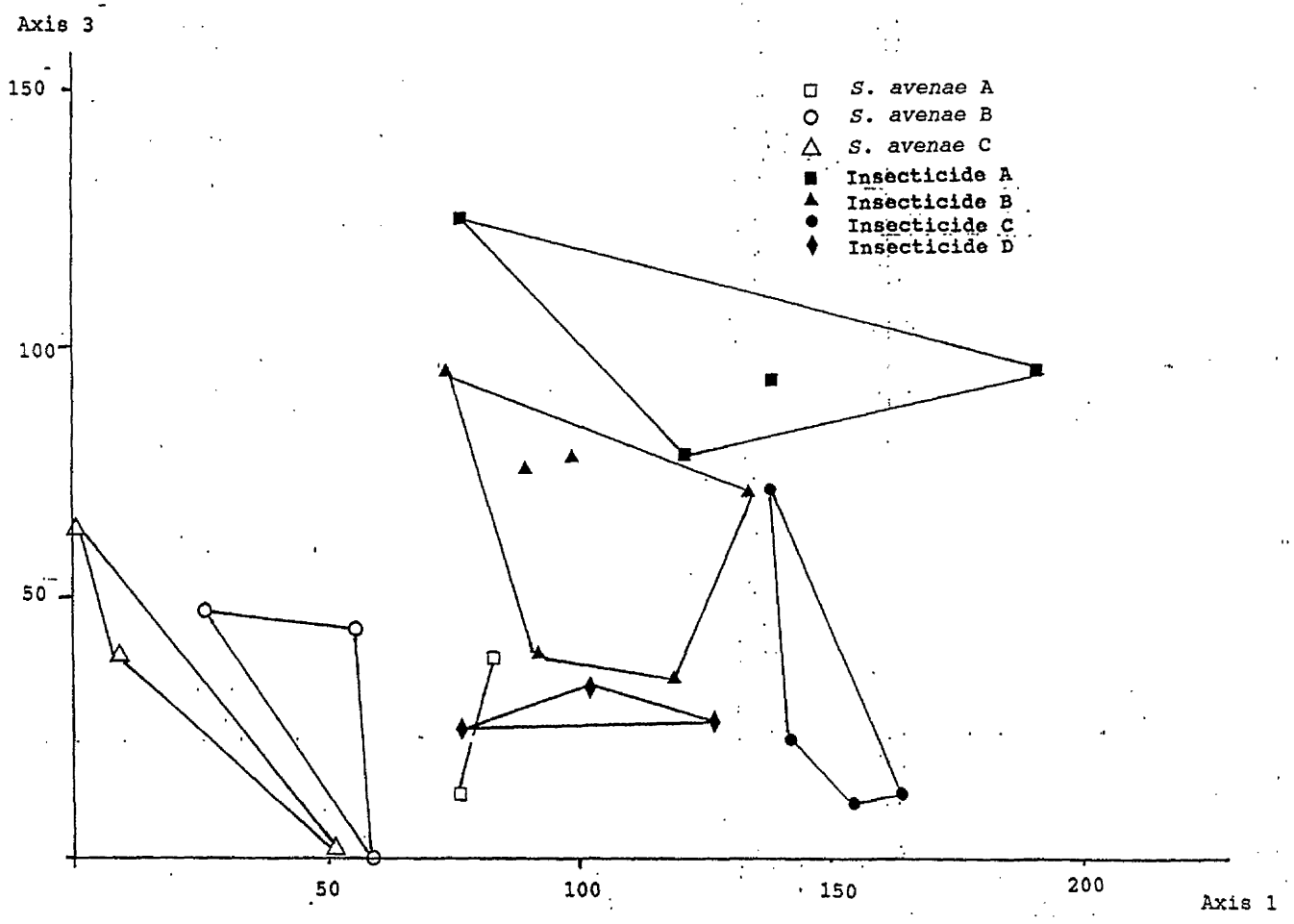


Figure 4.26 DECORANA ordination of BYDV survey 1989/90 data; axis 1 by axis 3 plot of end-groups identified by TWINSPAN.

Table 4.54 Rankings of aphid/BYDV and field/farm variables in the two most significant trends identified in the second run of CANOCO; winter barley, 1989/90.

Trend 1 / Trend 2

Species rankings		Biplot rankings		Weighted correlation	
Sa	Yel	Asp B	Stra	0.336	0.706
MAV	Inf	Des	Sea	0.219	0.390
Inf	PAV	Dri	Alt	0.206	0.346
PAV	Ins	Moi	Dri	0.191	0.313
Ins	Sa	Wee	Des	-0.118	0.174
Pat	Pat	Alt	Moi	-0.187	0.115
RPV	MAV	Stra	Cul	-0.255	0.071
Rp	Rp	Sea	Asp B	-0.267	0.031
Yel	RPV	Cul	Prev	-0.311	-0.144
		Pre	Lan	-0.537	-0.415
		Lan	Wee	-0.578	-0.467

Table 4.55 Rankings of aphid/BYDV and field/farm variables in the two most significant trends identified in the third run of CANOCO; winter barley, 1989/90.

Trend 1 / Trend 2

Species rankings		Biplot rankings		Weighted correlation	
Sa	PAV	Asp B	Stra	0.392	0.755
MAV	Yel	Moi	Des	0.282	0.353
RPV	Inf	Des	Moi	0.217	0.351
PAV	MAV	Alt	Alt	-0.285	0.301
Ins	Pat	Cul	Asp B	-0.336	0.175
Pat	Sa	Stra	Cul	-0.458	0.022
Inf	Ins	Pre	Pre	-0.607	-0.575
Rp	Rp				
Yel	RPV				

see Table 4.39 & 4.48 for explanation of codes.

The second CANOCO run therefore included 11 field/farm

variables (Table 4.54) and showed that moisture and weediness were correlated, as were distance from the sea and drilling date (early drilling being associated with Stirlingshire), landuse and drilling date, and cultivar and altitude. Thus, in the third CANOCO run, weediness, distance from the sea, landuse, drilling date and cultivar were all excluded, leaving a total of seven field/farm variables (Table 4.55).

4.7.3.2 **Discussion of factors affecting the incidence of BYDV in winter barley 1989/90**

As in 1988/89, the mildness of the winter (Ratcliffe, 1990; Figure 4.27) was an important factor in determining BYDV incidence in 1989/90, by allowing anholocyclic overwintering of aphids in autumn-sown cereals. Regional differences in autumn aphid numbers were present, but they were less dramatic than in 1988/89. The cumulative value of II for *R. padi* only, measured at Auchincruive (23 September to 22 October) in the autumn of 1989 was 16.

The winter of 1989/90 was $P_3S_5C_4$ (section 2.4), which implies that there was a greater number of days than average when the wind direction was in the south, but also that were more depressions than usual crossing Britain. These combinations of indices normally suggest milder than average temperatures (Murray, 1972), although in Scotland, a high C index is often associated with cold winter weather (Murray & Benwell, 1970). Only December 1989 was a cold month in Scotland, the mean temperature at

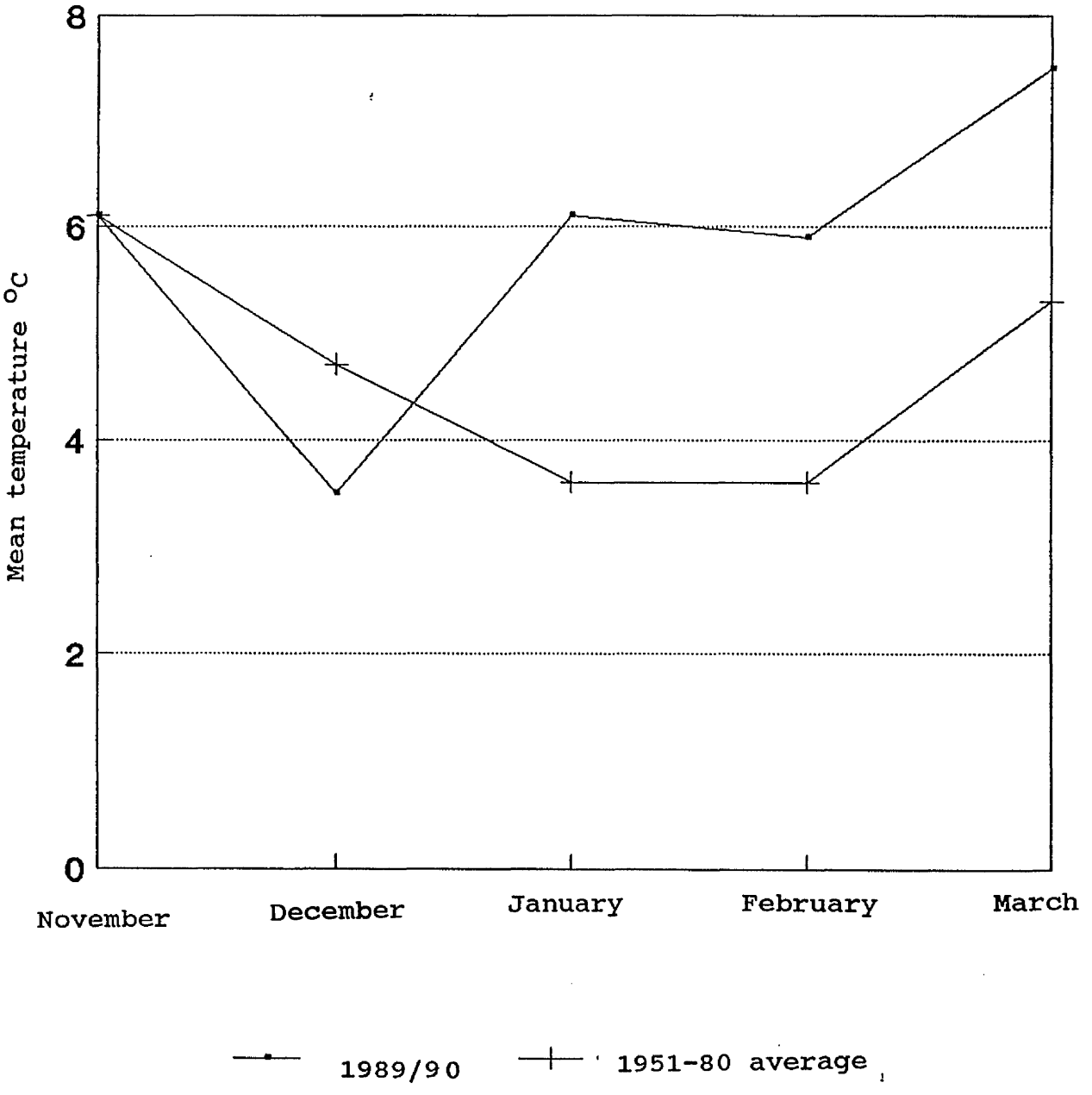


Figure 4.27 Mean temperature at Auchincruive, Ayr, November to March 1989/90 relative to the 1951-80 average.

Auchincruive being 1.2°C below the 1951-80 average. Both January and February 1990 at Auchincruive had mean temperatures more than 2°C above the 1951-80 average. However, in England except the far north, all three winter months were mild (Ratcliffe, 1990).

TWINSPAN identified four groups of *R. padi* and three of *S. avenae*-transmitted BYDV. CANOCO (Tables 4.54 and 4.55) identified high previous cropping type and landuse scores as the main factors determining the incidence of the *R. padi*-transmitted BYDV. The crops with the most yellowing were in regions other than Wigtownshire, therefore increasing distance from Stranraer was associated with greater crop yellowing (Yel). Although more aphids were found in Wigtownshire (Table 4.48), the level of aphid infestation (Inf) was never ranked first or last and negatively associated with distance from Stranraer. Aspect B was positively correlated with higher *S. avenae* numbers, this being the main factor identified by CANOCO affecting the incidence of *S. avenae*-transmitted BYDV.

The DECORANA plot (Figure 4.26) separated the *R. padi*-transmitted BYDV groups from the *S. avenae*-transmitted BYDV groups along axis 1, whilst only the *R. padi* groups were separated along axis 3. Using Table 4.53, it is reasonable to conclude that axis 1 could be either landuse or previous cropping type although "*S. avenae* A" which is nearest to the *R. padi* groups had the lowest previous cropping type mean. Axis 3 could also be either previous

cropping type or landuse, or distance from Crieff (which is similar to region number).

Although Wigtownshire fields had the greatest aphid infestations, the fields with greatest crop yellowing were outside Wigtownshire. Two Ayrshire fields which followed untreated ploughed-in grass leys were affected by *R. padi*-transmitted BYDV as was one Stirlingshire field which followed winter wheat. A common feature of these three fields was that they were on farms with a major livestock component, indicating a predominance of ryegrass pastures. This explains the association of greater crop yellowing with high landuse scores.

4.7.4.1 **Season 1990/91**

For each of the 20 winter barley fields (fields sampled by advisers excluded because these fields had incomplete aphid/BYDV variables), the aphid/BYDV variables and field/farm variables (except regional weather variables, regional distances & region number) are shown in Table 4.56. The "pseudo-species" function of TWINSPAN was set to create three categories (Table 4.57). All other settings used were the default values. The three groups created by TWINSPAN after two levels of divisions are shown in the dendrogram (Figure 4.27) and the refined-ordination table (Table 4.57). Characteristic "pseudo-species" and field members of the seven TWINSPAN end-groups are shown in Table 4.58. The regional weather data are shown in Table 4.59.

Table 4.56 Aphid/BYDV BYDV and field/farm variables of winter barley sampled season 1990/91.

	Aphid/BYDV variables							Field/farm variables											
															ASPECT				
Field	Rp	Sa	Ins	RPV	PAV	MAV	Inf	Dri	Pre	Des	Moi	Alt	Sea	Lan	A	B	C	T	Cul
Dumfriesshire																			
D2	2	2	-	1	1	-	1	1	2	-	-	30	9	-	1	3	2	6	1
D3	2	1	-	-	-	-	-	1	2	h	-	30	3	-	1	2	1	5	1
D4	1	1	-	-	1	1	-	1	2	-	1	10	0.5	-	3	3	3	9	-
D5	2	2	-	1	1	-	1	1	2	-	1	40	1	-	1	1	3	5	-
D6	2	1	-	-	1	1	-	1	-	-	1	20	4	-	2	3	3	8	1
D7	1	1	-	-	-	-	-	1	1	-	1	40	4	-	1	2	-	3	1
Wigtownshire																			
W2	1	1	1	-	1	1	-	1	2	e	-	20	0.5	1	1	2	3	6	-
W3	1	1	1	-	1	1	-	1	2	e	-	20	0.5	1	1	2	3	6	-
W4	1	-	1	-	-	-	1	1	2	-	-	40	1	1	1	1	3	5	1
W5	1	-	1	-	1	-	-	1	1	-	1	60	1	-	1	2	3	6	-
W6	1	1	1	1	1	-	-	-	1	-	1	60	1	-	3	3	2	8	-
W7	1	1	1	-	-	-	-	1	1	-	1	10	-	1	3	5	3	11	-
W8	1	1	1	-	-	-	-	1	1	-	1	10	-	1	4	4	4	12	-
Stirlingshire																			
S1	1	1	-	-	-	1	-	2	-	-	1	10	20	-	1	1	2	4	-
S2	1	2	1	-	1	1	1	2	3	-	1	10	20	-	1	1	2	4	1
S3	1	1	-	-	1	1	-	2	-	-	1	80	30	-	-	2	-	2	-
S4	1	1	-	-	-	1	-	2	-	-	1	60	30	-	3	3	2	8	-
S6	2	1	1	-	1	1	1	2	1	-	1	50	36	-	4	3	5	12	1
S7	1	1	1	-	1	1	-	2	-	-	1	60	34	-	2	3	2	7	1
S9	1	1	-	1	1	1	-	2	2	e	1	10	25	-	-	2	-	2	-

Key for **Table 4.56**

\- denotes zero

Autumn *Rhopalosiphum* spp. and *S. avenae* colony counts transformed to a score on scale 0 to 2.

0 None sampled throughout.
1 Less than ten colonies sampled in whole autumn.
2 Ten or more colonies sampled in whole autumn.

Ins Autumn application of insecticide (+/-).

RPV Incidence of BYDV strain in leaf samples (+/-).
PAV Incidence of BYDV strain in leaf samples (+/-).
MAV Incidence of BYDV strain in leaf samples (+/-).

Inf Incidence of scattered yellow plants
(1 plant / 10 m^2 +) (1 plant / 100 m^2 -).

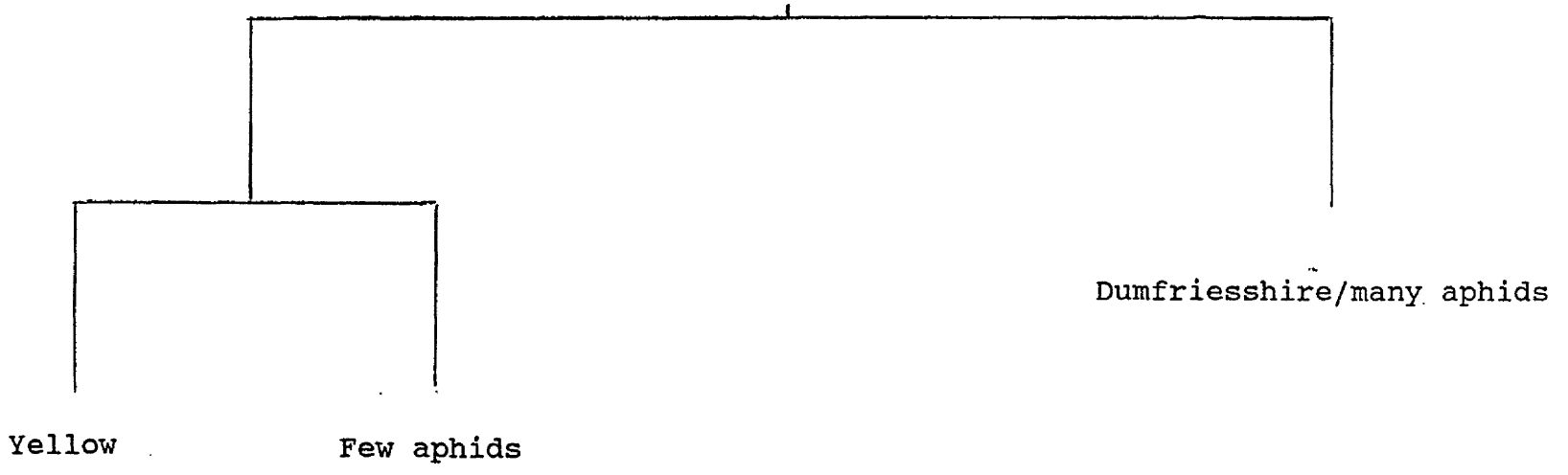


Figure 4.28 Dendrogram showing divisions and end-group names of TWINSPAN classification of BYDV survey 1990/91.

Table 4.57 TWINSPAN refined ordination Table after two divisions; BYDV survey 1991.

	"Pseudo-species" level																					
Aphid/BYDV variable	20 fields ordinated to reflect the incidence and levels of the aphid/BYDV variables																					
Ins	1	1	1	-	-	-	-	-	-	1	1	1	1	1	1	1	-	-	-	-		0
MAV	-	-	1	-	1	1	1	1	1	1	-	-	1	1	1	-	1	-	-	-		0
PAV	-	1	1	-	-	-	1	1	1	1	-	-	1	1	1	1	1	1	-	1		0
Inf	1	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	1		1
Rp	1	1	1	1	1	1	1	1	2	2	1	1	1	1	1	1	1	2	2	2		1
RPV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	1	1
Sa	-	-	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2		1
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1		
	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1					
	Group 1									Group 2								Group 3				

"Pseudo-species" levels

- = 0 1 = 1 2 = 2

Table 4.58 "Pseudo-species" that characterise TWINSPAN end-groups and the group members; BYDV in winter barley 1990/91.

Gp 1	Gp 2	Gp 3
Sa 2	Sa 1	Sa 2
Ins 1	MAV 1	Rp 2
Inf 1		PAV 1
W4	D7	D2
W5	S1	D3
S2	S4	D5
	D4	
	S3	
	D6	
	S5	
	W7	
	W8	
	W2	
	W3	
	S7	
	W6	
	S9	
Yellow/ few aphids	Few aphids	Dumfries/many aphids

Table 4.59 Winter weather parameters at the climatological stations selected to be representative of the three regions 1990/91.

	November					December					January					February					March				
	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn	Mx	Mn	Lmn	Fr	Sn
Dumfriesshire	8.7	2.1	-4.8	7	0	7.2	0.5	-4.0	12	2	5.4	-0.6	-7.1	15	3	5.8	-0.7	-5.4	17	3	-	-	-	-	-
Wigtownshire	9.2	3.7	-2.0	8	0	7.7	2.1	-3.4	6	1	5.9	1.5	-5.1	7	0	5.3	-0.3	-4.6	15	0	-	-	-	-	-
Stirlingshire	8.9	3.3	-3.2	5	0	7.4	1.5	-3.4	8	0	5.7	-0.4	-7.0	14	0	5.9	-0.2	-5.0	16	0	-	-	-	-	-

Mx Mean daily maximum temperature °C

Mn Mean daily minimum temperature °C

Lmn Lowest daily minimum temperature °C

Fr Number of days with air frost

Sn Number of days with snow lying 0900 GMT

The TWINSPAN end-group means of the seven aphid/BYDV variables and the 21 field/farm variables are shown in Tables 4.60 and 4.61 respectively.

Table 4.60 TWINSPAN end-group means of aphid/BYDV variables; BYDV in winter barley 1990/91.

TWINSPAN end-group	Mean values of aphid/BYDV variables		
	Gp 1	Gp 2	Gp 3
Rp	1.0	1.1	2.0
Sa	0.7	1.0	1.7
Ins	1.0	0.5	0.0
RPV	0.0	0.1	0.7
PAV	0.7	0.6	0.7
MAV	0.3	0.7	0.0
Inf	0.7	0.1	0.7

Table 4.61 TWINSPAN end-group means of field/farm variables; BYDV in winter barley 1990/91.

TWINSPAN end-group	Mean values of field/farm variables		
	Gp 1	Gp 2	Gp 3
Dri	1.3	1.4	1.0
Pre	2.0	0.9	2.0
Des	0.0	0.4	0.3
Moi	1.0	0.9	0.3
Alt	37	34	33
Sea	7.3	13.3	4.3
Lan	0.3	0.3	0.0
Asp A	1.0	2.0	1.0
Asp B	1.3	2.7	2.0
Asp C	2.7	2.3	2.0
Asp T	5.0	7.0	5.3
Reg	2.3	2.2	1.0
Stra	66	108	108
Carl	134	123	34
Crie	145	113	161
Cul	0.7	0.3	0.7

In the DECORANA, all settings used were the default values. The ranking of the aphid/BYDV variables produced by DECORANA did not separate *R. padi*-transmitted BYDV variables from those of *S. avenae*-transmitted BYDV, therefore the results were not presented.

In the CANOCO, all field/farm variables except the regional weather data and region number were included because all fields of a region had the same values. The ranking of the aphid/BYDV variables produced by CANOCO did not separate *R. padi*-transmitted BYDV variables from those of *S. avenae*-transmitted BYDV, therefore the results were not presented.

4.7.4.2 **Discussion of the factors affecting the incidence of BYDV in winter barley 1990/91**

The winter of 1990/91 was colder than average (Ratcliffe, 1991c; Figure 4.29), particularly in February (1.1^{o}C below the 1951-80 average at Auchincruive). None of the winter barley crops sampled in the autumn of 1990 was heavily infested with aphids, and the subsequent cold winter may have killed all aphids which attempted to overwinter anholocyclically in winter barley. This is supported by the total absence of aphids found in the spring survey (section 4.5.2). The cumulative value of II for *R. padi* only, measured at Auchincruive (23 September to 4 November) in the autumn of 1990 was 159.

TWINSPAN identified three groups of fields, although none can be associated exclusively with either type of BYDV. In 18 of the 20 fields, both *Rhopalosiphum* spp. and *S. avenae* were observed. Aphids were most numerous in Dumfriesshire during the autumn, but probably because the winter was colder than average (Figure 4.30), BYDV infection was not more extensive in Dumfriesshire than

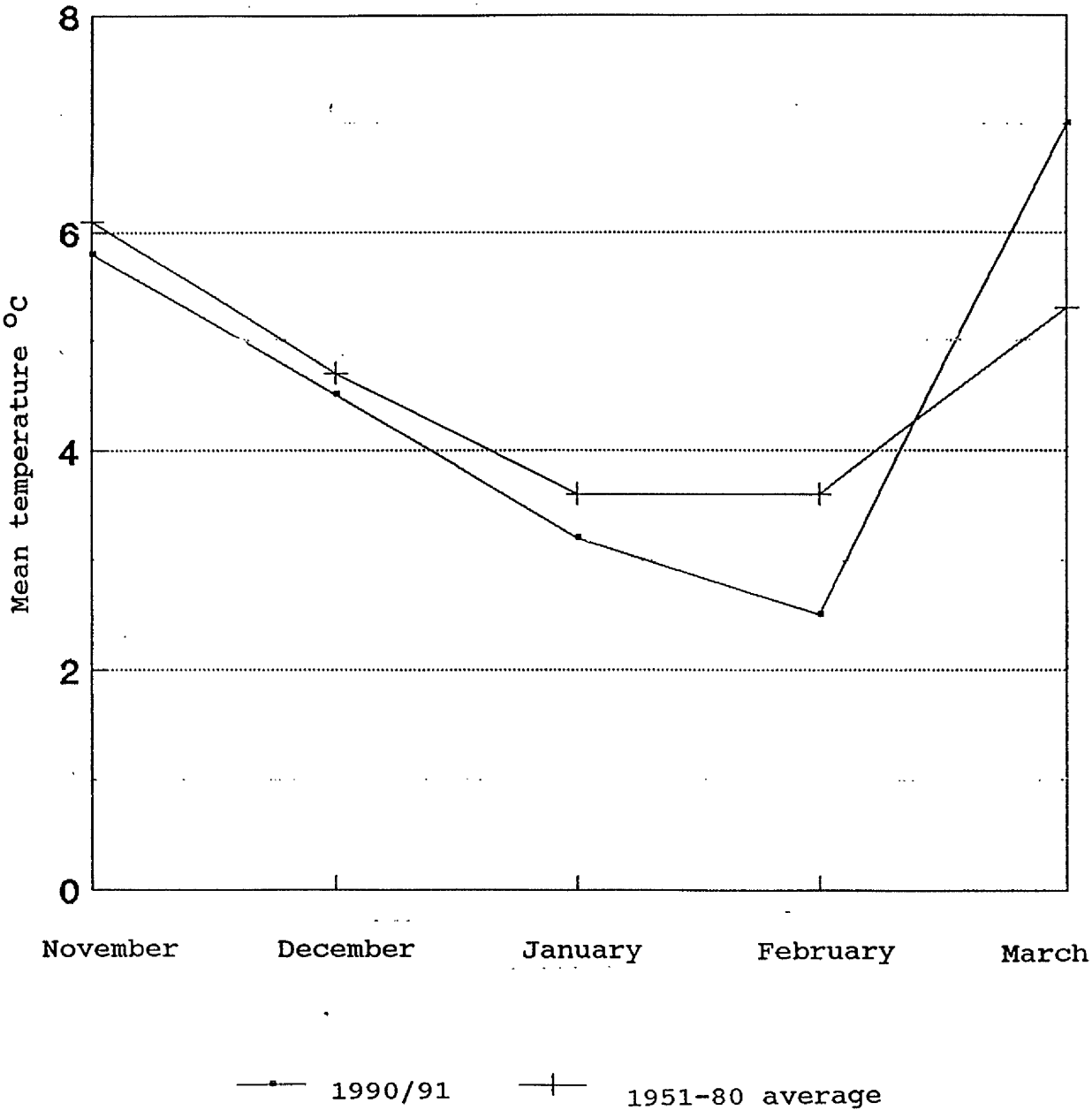


Figure 4.29 Mean temperature at Auchincruive, Ayr, November to March 1990/91 relative to the 1951-80 average.

elsewhere during the spring 1991. Little BYDV infection was found in all regions during the spring. One factor that accounts for the relative absence of BYDV in this season is that fields following untreated ploughed-in grass leys were deliberately not selected during the autumn 1990, because this phenomenon had been studied in the previous two years. The PAV strain was detected in most fields, MAV was mainly confined to Stirlingshire and little RPV was detected in fields of any region.

The three fields of the TWINSPAN end-group, "Dumfriesshire/many aphids" were coastal (Table 4.57), this being the only other factor apart from being in Dumfriesshire that differed from the average field of the other two groups. The distinction between the other two TWINSPAN end-groups was in the abundance of yellow plants. However, in both of the fields with the greater number of yellow plants (W4 & S2), most yellowing was considered to be due to an agent other than BYDV.

4.8 **Discussion**

The monitoring of winter barley crops in three seasons has enabled a critical analysis of II as a forecasting system in Scotland to be made. It has also made possible a study of the factors affecting aphid and BYDV incidence in autumn-sown cereals of Scotland.

The autumn with the greatest II value for *R. padi* was 1990 (23 September to 4 November; 159), whereas 1989 had the lowest (same period; 16). The autumn of 1988 had an intermediate II of 82. Neither *R. padi* or any other aphid species were common in winter barley during the autumn 1990, and little BYDV was detected in the spring 1991. In contrast, in the spring of 1989, both aphids and BYDV were abundant in most winter barley crops.

Meam winter temperature is positively associated with the amount of BYDV infection present in the following springs. Autumn 1988 was followed by a very mild winter (Figure 4.24). Autumn 1989 was followed by a cold December in northern Britain (Figure 4.27) which meant that anholocyclic overwintering in 1989/90 was less extensive than in 1988/89 or in the south of Britain, despite the fact that it too was a very mild winter. Autumn 1990 was followed by a cold winter (Figure 4.29) which prevented anholocyclic overwintering of aphids in cereals.

Clearly, winter temperature was an important factor in BYDV epidemiology in the three years of study as observed

in England (Oakley, 1989). Yet, the regional differences encountered in both aphid species and numbers during the autumns, and in BYDV infection in the springs, indicate that other factors are critical to the disease epidemiology. Attempts were made to identify these factors in each season in sections 4.7.2, 4.7.3 and 4.7.4.

In the following discussion, the field/farm variables are discussed in relation to *R. padi*- and *S. avenae*-transmitted BYDV. The following variables are not discussed:-

1) moisture, because in all three years, fields with freely-draining soils (Tables 4.40, 4.48 & 4.56) were only found in Dumfriesshire and Wigtownshire.

2) weed abundance, because it was only measured in the season 1989/90.

3) desiccant herbicides, because only 8 fields received desiccant applications in the three years of study, and four of these to headlands only.

4) region, because the distances from Stranraer, Carlisle and Crieff are better variables.

5) all climate data variables, because each field does not have its own values.

Most TWINSPAN end-groups were either associated with *R. padi*- or *S. avenae*-transmitted BYDV. A few groups including all those in 1990/91 were of uncertain BYDV identity. The discussion deals with those which are clearly associated with either type of BYDV.

A confounding factor of these analyses was the use of insecticides to control aphids in cereals during the autumn. None of the sampled crops of 1988/89 was treated in the autumn of 1988 although four Wigtownshire crops received applications in the spring of 1989. In the autumns of 1989 and 1990, 65 and 50% of sampled crops respectively were treated with insecticides. These figures are consistent with those in the *Pesticide Usage in Scotland Reports* which show that only 6% of the Scottish winter barley acreage was treated with insecticides in 1988 (Snowden, Bowen & Dickson, 1991a) whereas in 1990, the comparative figure was 43% (Snowden *et al.*, 1991b). The reason for the increase in insecticide use was greater aphid and BYDV problems in Scottish winter barley crops.

Altitude In the season 1988/89, altitude was identified as an important factor in determining BYDV incidence. The fields with the highest elevations above sea level (> 200 m ASL) were in Lanarkshire where no aphids and little BYDV were found. This region is also well inland, distance from the sea probably being just as important as altitude in determining the winter weather figures in Table 4.43. For example, two Wigtownshire fields were quite high (W3 and W4(1988/89), 80 m ASL), but were only 2 km from the sea. Both were affected by *R. padi*-transmitted BYDV, one severely. The climate figures for the nearby town of Whithorn (altitude 50 m ASL, Table 4.43) for Wigtownshire, show that there were only 10 air frosts in the period

November 1988 to March 1989.

In 1989/90 (Table 4.48) and 1990/91 (Table 4.56), all fields sampled were below 100 m. Therefore, this field/farm variable was less important than in 1988/89.

Aspect A, C & T These types of shelter were generally not found to be important during the analyses. However, two *S. avenae*-transmitted BYDV groups, "*S. avenae* C" and "Many *S. avenae*", had the lowest aspect C scores. Given that wind direction was persistently in the south-west and south in the winters of 1988/89 and 1989/90 respectively (Murray, 1991; Ratcliffe, 1989; Ratcliffe, 1990), exposure to the north and east would either be irrelevant to anholocyclically overwintering aphids, or of a disadvantage.

Aspect B Shelter to the south and west was identified as having a positive effect on the incidence of both types of BYDV in 1988/89 and on *S. avenae*-transmitted BYDV in 1989/90. This is not surprising given the south-westerly and southerly wind directions during these two winters (Murray, 1991; Ratcliffe, 1989; Ratcliffe, 1990). Plumb (1988) identified shelter as a cause of greater BYDV risk in certain fields on an individual farm, and examples of this phenomenon were found on some farms in 1988/89. For example, W3 and W4(1988/89) were both affected by *R. padi*-transmitted BYDV, but the more exposed field, W4 had 4% crop yellowing compared with the more sheltered W3 which

had 50% crop yellowing including extensive areas of plant death. Another field R10(1988/89), had large numbers of *S. avenae* in the spring and 50% crop yellowing. This field was very sheltered relative to the other two fields sampled on the same farm which had negligible crop yellowing in comparison. R10 was bounded by mature deciduous woodland on its eastern, southern and western sides, and although it was more exposed to the north, the river Clyde was less than 0.5 km distant.

Cultivar The commonest cultivar of winter barley grown by farmers during the three years of study was *Magie*. No other single cultivar was widely grown. *Magie*'s popularity was not due to characteristics minimising yield loss from BYDV (Anon, 1988), but symptom expression of BYDV does vary between cultivars (Jones & Catherall, 1970). It is possible that that the predominance of *Magie* affected the crop yellowing estimates, because observations suggested that it develops conspicuous chrome-yellow symptoms relative to other cultivars.

In 1988/89, only one Wigtownshire field was sown with *Magie*, therefore cultivar was associated with increasing distance from Stranraer. In 1989/90, *Magie* was associated with increasing altitude. These associations confounded the CANOCOs. Of course, crops which were badly-affected by BYDV during the three years of study were not all of the variety *Magie*, therefore it was not found to be important in any of the analyses.

Drilling date A feature of drilling dates was that they were associated with regions, because crops can only be drilled when soil conditions allow. Weather and therefore, soil conditions, tend to be similar within regions. Thus, in 1989/90 when September weather was fine, many Dumfriesshire, Renfrewshire and Stirlingshire winter barley crops were drilled in early September, whereas in 1990/91, early September drilling was only possible in Stirlingshire.

Thus, the two *S. avenae*-transmitted BYDV TWINSPAN end-groups with the highest drilling date scores, "*S. avenae* B" and "*S. avenae* C", were both from the season 1989/90. Five of the seven fields involved were drilled in early September, relatively large *S. avenae* infestations developed during the autumn, and the MAV strain alone was detected in the barley leaf samples. However, another *S. avenae*-transmitted BYDV group, "*S. avenae* A" from the same season, had the lowest drilling date score. It comprised two crops both drilled about 1 October, but relatively large *S. avenae* infestations nevertheless developed during the autumn.

Eight of the 16 TWINSPAN end-group drilling date means were between 0.8 and 1.2, because most winter barley crops in south-west and central Scotland are drilled in late September. However, in Stirlingshire, there is pressure to drill in early September, so that crops are well-established by December to withstand the hard frosts which

are more characteristic of winters of central Scotland (C.McCombie, personal communication). Thus, in 1989/90 and 1990/91, all the sampled Stirlingshire crops were drilled in the first half of September.

The association between BYDV incidence in autumn-sown cereals and early drilling dates has been known since aerial photography during the summer of 1976 revealed more patches of infected plants in wheat fields of eastern England sown in September 1975, than in crops sown later (Hooper, 1978). Since then, a number of field-trials have reproduced this relationship (Kendall & Smith, 1981a; Plumb, 1986; McGrath & Bale, 1990). This applies to both *R. padi* and *S. avenae*-transmitted BYDV for two reasons: firstly, early drilled crops are exposed to migrating alate aphids for longer, and secondly, larger populations of apterae may build-up in early sown crops, because more time is available before cold weather affects aphid population growth. As a consequence, several workers have recommended delaying drilling until late September or October (A'Brook, 1974; Kendall *et al.*, 1988; Plumb, 1988) as a method of avoiding BYDV infection.

In contrast to the findings of other BYDV workers, only one *R. padi*-transmitted BYDV TWINSPAN end-group was associated with a relatively high drilling date score, Insecticide C with a value of 1.5. This could be because *R. padi* migrations were relatively small in all three autumns

(1988, 1989 & 1990), thus *R. padi*-transmitted BYDV could not express itself in earlier drilled crops. Also, except in Wigtownshire in 1988/89, *R. padi*-transmitted BYDV was not associated with migrating *R. padi*.

Nowadays, drilling dates of winter barley crops in Britain are largely determined by the weather and soil conditions in September, because most farmers aim to finish drilling by the end of September (Carter, 1984). High disease pressure makes drilling prior to 1 September uneconomic, but delaying drilling beyond late September to avoid BYDV infection runs the risk of not being able to drill at all, or of poor crop establishment, because of poor soil conditions. The yield difference between spring and winter barley (Plumb, 1988) ensures that farmers tend to drill winter barley whenever they can in September.

In the three years of study, drilling dates were not found to be the most important factor affecting BYDV incidence. This result is probably partly owing to the fact that few sampled crops were sown late enough to totally avoid BYDV infection. For example, in 1988/89, 74% of sampled crops were drilled in late September.

Distances from Stranraer, Crieff & Carlisle Two *R. padi*-transmitted BYDV groups had the lowest distance from Stranraer scores: "*R. padi*/MAV/PAV yellowing" and "Insecticide D". All except two of the fields involved were in Wigtownshire. Not surprisingly, the same two groups had

the highest distance from Crieff scores. Migrating *R. padi* were the probable cause in the former group, whilst untreated ploughed-in grass leys were the cause in the latter group. Advisory experience has identified Wigtownshire as an area prone to damaging BYDV infection. This is probably only partly due to the mild winter climate of the area (it being coastal), but may also be due to there being higher numbers of aphids moving into crops during the autumn. Therefore, Wigtownshire is another example of a "virus prone" area (Hill, 1982; Plumb, 1988). *S. avenae*-transmitted BYDV groups were not geographically restricted like *R. padi*-transmitted BYDV groups.

Distance from the sea Two *R. padi*-transmitted BYDV groups had the lowest distance from the sea means, and a further two had values of less than 5 km: "*R. padi*/MAV/PAV yellowing" and "Insecticide D", and, "Insecticide A" and "Dumfriesshire/many aphids" respectively. The group, "*S. avenae*/MAV yellowing", also had a low distance from the sea mean (4 km).

The association of BYDV with coastal areas of Britain has led to the establishment of "virus prone" areas in England (Figure 4.30) for advisory purposes in which early drilled winter cereals are likely to be affected by BYDV every year. The cause of this association is thought to be the milder autumn and winter climate of coastal areas which may allow aphids to survive and even multiply during the winter (Hill, 1982; Plumb, 1988). Assuming that this theory

Figure 4.30 The distribution of "virus prone areas" in England identified by ADAS (Anon, 1984).

is correct, both types of BYDV would be more common in coastal areas. In the three seasons studied, *R. padi*-transmitted BYDV was mainly confined to coastal areas of south-west Scotland whereas *S. avenae*-transmitted BYDV was found in all regions and inland. Other regions of Britain where *R. padi*-transmitted BYDV is a frequent problem are also coastal: south and west Wales (A'Brook & Dewar, 1980), and south and south-west England (Figure 4.30). In contrast, *S. avenae*-transmitted BYDV has been more prevalent in the relatively inland cereal growing areas of eastern and northern England (Plumb, 1974; McGrath & Bale, 1989).

Previous crop type Three *R. padi*-transmitted BYDV groups had the highest previous crop type scores: "*R. padi*/MAV/PAV yellowing", "Insecticide C" and "Insecticide D". Six of the 13 fields involved followed untreated ploughed-in grass leys, five followed winter barley, and one each of winter wheat and spring barley. In general, *R. padi* abundance was highest in winter barley crops following grass leys, although in Wigtownshire in 1988/89, *R. padi* infestations were probably due to migrating *R. padi* (4 fields in "*R. padi*/MAV/PAV yellowing" did not follow grass leys).

The association of severe cases of *R. padi*-transmitted BYDV with untreated ploughed-in grass leys is well-known (Plumb, 1988). In the three seasons, seven winter barley crops following untreated ploughed-in grass leys were surveyed for BYDV in the following spring. Except for two

crops, one in Lanarkshire where few yellow plants were observed, and one in Renfrewshire which was severely affected by *S. avenae*-transmitted BYDV, patches of plants affected by the RPV or PAV strains were evident (Figure 4.31), confirming this association. The use of desiccant herbicides to kill the grass leys 10 to 14 days prior to ploughing is the recommended control procedure (Carter, 1984; Kendall *et al.*, 1988). However, observations of *R. padi* infestations in four crops in the autumn of 1989, which followed untreated ploughed-in grass leys, suggest that economic damage can be prevented by insecticide applications during the autumn. Yet, yield measurements were not made, so although severe damage was prevented in these four crops, loss of yield may have been significant. In economic terms, the autumn applied insecticide requires little yield response to pay for itself. In contrast, the use of the more expensive desiccant herbicides will incur a substantial economic loss if few *R. padi* were present in the grass ley. A grass ley that is ploughed up is likely to have been grazed or cut recently, and therefore aphid numbers may not be high (Chapter 5). On the other hand, poor soil conditions may prevent an autumn application of insecticide, thereby risking severe damage from BYDV, which could necessitate re-drilling of the field with spring barley. Thus, the use of a desiccant herbicide is an expensive insurance whereas the use of an autumn applied insecticide which although relatively cheap, is not always an option.

(a)

(b)

Figure 4.32 Spring symptoms of BYDV in a winter barley crop following untreated ploughed-in grass leys which had received an autumn applied insecticide: (a) close-up of an affected patch including plant death, (b) the field view.

Two *S. avenae*-transmitted BYDV groups had the lowest previous crop type means: "*S. avenae* A" and "Many *S. avenae*". Six of the eight fields involved followed spring barley, and one each of winter wheat and winter barley. The group, "Many *S. avenae*/MAV yellowing", had a previous crop type mean of 1.8: three fields followed spring barley, two winter barley, one winter wheat and five oilseed rape.

Winter barley crops following oilseed rape are often early drilled because of the early harvesting date of oilseed rape relative to cereals. However, in this case, the five winter barley crops following oilseed rape were all drilled in late September, so early drilling may not account for the severe *S. avenae*-transmitted BYDV in the fields of this group.

The association of *S. avenae*-transmitted BYDV with low previous cropping type scores may not be directly due to previous cropping type. The farms with winter barley which followed either spring barley or winter wheat crops (previous cropping type scores 0 and 1 respectively) were mainly cereal growing enterprises (landuse score 0). Continuous cropping is known to favour the establishment of plant virus inoculum reservoirs and vector survival: continuous winter barley cropping is considered to be a factor in the rise of the importance of BYDV in Britain in recent years (Hill, 1988). *S. avenae* frequently colonises cereals in the summer (George, 1982), therefore it tends to be associated with cereal growing farms. During late

summer and autumn, grass weeds or volunteers in cereal stubbles can be infested by aphids moving from late maturing cereals such as wheat or spring barley (Plumb, 1988). This explains why destroying grass and stubble regrowth with herbicide prior to drilling can lessen BYDV incidence in succeeding winter cereal crops (Kendall *et al.*, 1988). Alternatively, because farms which specialise in cereals are likely to have a number of stubble fields present during the autumn, alate *S. avenae* may move from grass weeds and volunteers in stubble fields to nearby winter barley crops.

This association of *S. avenae*-transmitted BYDV with farms specialising in cereals may explain the high previous cropping type score of the group "*S. avenae*/MAV yellowing". Five of the fields in this group followed oilseed rape. Oilseed rape is grown as a break crop in cereal rotations and as an entry for winter wheat to minimise the incidence of take-all (Spedding, 1983). Therefore, oilseed rape is associated with farms specialising in cereals.

Landuse Two *R. padi*-transmitted BYDV groups had the highest landuse scores: "Insecticide C" and "Insecticide D". This association was due to the fact that both these groups had high proportions of crops that followed untreated ploughed-in grass leys (50 and 67% respectively). Landuse and winter barley crops following grass leys are positively correlated because winter barley crops grown on farms with a major

livestock component are more likely to follow ploughed-in grass leys than crops grown on a predominantly arable farm.

Advisory experience has shown that *R. padi*-transmitted BYDV can be a problem when winter cereals are adjacent to ryegrass pastures: this being termed a risk factor (Hill, 1982). In the three years of study, there was one case of a crop affected by *R. padi*-transmitted BYDV which was probably associated with *R. padi* moving from adjacent ryegrass pastures. The field of winter barley, S3(1989/90), drilled on 31 August 1989 followed winter wheat. During early October, the scattered yellow plants in the crop were diagnosed as being infected by the MAV strain by the SAC advisory service. An insecticide was applied to control the *S. avenae* infestations on 7 October 1989. By the middle of November, large *R. padi* infestations were observed in the same crop necessitating another insecticide application on 24 November 1989. Numerous patches of yellow plants infected by the PAV strain were observed in the spring. The autumn migration of *R. padi* as measured by Scottish suction traps was small in 1989 (Chapter 11) and problems of *R. padi*-transmitted BYDV associated with migrating *R. padi* were not observed or reported from any region. This field, S3(1989/90), was surrounded on three sides by ryegrass pasture which was the probable source of the *R. padi*.

CHAPTER FIVE

Aphid numbers in ryegrass pasture

5.1 Introduction

Cereal aphids have a wide range of graminaceous hosts on which they breed parthenogenetically (Tatchell *et al.*, 1983). Most studies of cereal aphids in Britain have been concerned with *M. dirhodum* and *S. avenae* on wheat, because of the dramatic early summer outbreaks of 1969 and the late 1970s which caused serious direct damage (Dixon, 1987). Studies of cereal aphids on other host plants are relatively scarce.

Ryegrass pastures as a source of viruliferous aphids All cereal aphids recorded in Britain are known to occur in ryegrass pasture (Hand, 1989). The infection of ryegrass pastures with BYDV (Doodson, 1967; Catherall *et al.*, 1982; Holmes, 1985) and the vast acreages present, particularly in western Britain, suggests that these commercial crops may be important as sources of viruliferous aphids which infest cereals during the autumn.

Ryegrass pastures as a site for overwintering For anholocyclic cereal aphids, grasses or cereals must be the overwintering host plants. Overwintering aphids (*M. dirhodum*, *R. padi* and *S. avenae*) have been observed on cereals (Dean, 1974a; George, 1974; Dewar & Carter, 1984; Hand, 1989), but in colder winters, this habitat probably provides insufficient shelter. This accounts for the widespread BYDV problems in winter cereals after mild winters (Oakley, 1989).

Dean (1974a) observed *M. dirhodum*, *R. padi* and *S. avenae* overwintering in hedgerow grasses and tussocks, and suggested that these sites may be important as overwintering sites, because of the shelter they provide from wind, rain and snow. Ryegrass pastures containing tussocks may be important overwintering sites for cereal aphids.

Hand (1989) sampled both dense and first year leys through three winters in southern England including the severe 1978/79 winter. *R. padi* overwintered successfully in ryegrass pastures in two of the three winters including 1978/79. *Metopolophium festucae cerealium* (Stroyan) and *S. avenae* also successfully overwintered in at least one of the three winters.

Aphids in ryegrass pasture during the spring, summer and autumn Vickerman (1982) studied aphid numbers in grassland from early March to late September, 1972-79 in southern England. Both aphid numbers and species varied with season. Two species attained high densities: *M. festucae* (unspecified sub-species) whose numbers peaked in mid-May, and *R. padi*, whose numbers peaked in late May and early June.

Hand (1989) in his studies, also in southern England, from 1977-80, found *M. festucae cerealium* and *R. padi* to be most abundant. However, only in 1980 did *M. festucae cerealium* show the spring population peak observed by

Vickerman (1982). In the other two years, maximum densities occurred during the autumn/early winter. Numbers of *R. padi* also peaked later, being most abundant in the September to December period.

In both studies, numbers of *M. dirhodum*, *R. insertum*, *S. avenae* and *S. fragariae* were relatively low in ryegrass pastures.

5.2 **Methodology**

Sampling only took place when the pasture was dry or nearly so. Aphids were sampled by sweeping ten times with a flat-bottomed net (aperture 30 x 33 cm) in each sampling area. A sampled area was approximately 1.0-1.5 m^2. In intensively grazed pastures, only lusher areas (usually associated with cowpats) were sampled. In ungrazed and extensively grazed fields, sampled areas were representative of the whole field. A note of the pasture length was made and whether or not it was grazed.

Grass length categories:-

1 = generally short, either the result of intensive grazing or when field is sampled shortly after a silage cut (< 4 cm high).

2 = showing signs of grazing, i.e. a patchwork of closely grazed areas and much lusher patches with long grass associated with cowpats.

3 = essentially long grass, uniform throughout the field. May be ungrazed or extensively grazed. Minimum length is 4 cm.

Season 1988 Between June and August, samples were taken monthly from four fields in Dumfriesshire, Wigtownshire and Stirlingshire and five fields in Ayrshire. A further nine fields were sampled in Ayrshire during the late summer and autumn, five once and the others at least twice. Six areas were sampled in each field, four in the field interior along a diagonal track and two at the field margin. From September, five or ten areas in the field interior were sampled during a circuit of each field but field margins were not sampled. When five areas were sampled, areas 1, 2 and 5 were in one half of the field and areas 3 and 4 in the other half. When ten areas were sampled, there were five areas in each half.

Season 1990 In Ayrshire, 13 fields were sampled between April and September, and six of these were visited on more than two occasions. In Dumfriesshire, Renfrewshire and Stirlingshire, at least one field was sampled monthly from April to June. In Wigtownshire, one field was sampled monthly from April to May. In September, at least one field was sampled once, in each of Dumfriesshire, Wigtownshire and Stirlingshire.

5.3 Results

Prior to analysis, samples were multiplied to be equivalent to 100 m^2 of ryegrass pasture of each field (Appendices 4 & 5), because the sampling methodology changed during the course of the project.

During 1988, perennial ryegrass pastures were sampled for aphids on 98 occasions (an occasion is a sampling visit to one field), a total of 26 fields were visited and on eight occasions, no aphids were sampled. The comparative figures for 1990, were 66, 22 and 18.

In the following analyses, data from the same fields collected on different sampling dates were treated as separate observations, because seasonality was one of the factors to be analysed. Other factors analysed were age of sward at the time of sampling, length of sward (see methodology), region, altitude, distance from sea, and distances from Carlisle, Stranraer and Crieff. These factors are referred to as the "field/farm variables". The first four of these factors were analysed using single factor analysis of variance (ANOVA) on the pooled 1988 and 1990 data. Tables 5.1, 5.6, 5.8 & 5.10 show the mean number of aphids per 100 m^2 of ryegrass pasture for each aphid species in both years and the results of the ANOVA tests, for each level of seasonality, age of sward, length of sward and the region respectively. For the ANOVA tests which were significant, the results are given in Tables 5.2 to 5.5, 5.7, 5.9, 5.11 & 5.12.

Table 5.1 Mean numbers of aphids per 100 m^2 of ryegrass pasture sampled in 1988 and 1990 from April to October.

	Mean numbers of aphids/100 m^2								
	M.d.		M.f.		Rh. spp.		R.i.	S.a.	
Month	1988	1990	1988	1990	1988[a]	1990	1990	1988	1990
April	-	0	-	0	-	0	0	-	0
May	-	0	-	9	-	7	0	-	1
June	15	0	397	58	7	5	0	64	103
July	3	0	70	50	242	187	107	68	30
August	1	3	5	99	160	2607	1111	17	146
September	0	0	0	1	214	221	50	4	1
October	0	20	0	10	243	110	0	3	0
Anova on pooled data	$P < 0.01$		$P < 0.001$		$P < 0.001$ (Rh. spp.)			$P < 0.001$	

a alate *Rhopalosiphum* spp. not separated in 1988.

R.p. *R. padi* Rh. *Rhopalosiphum* M.d. *M. dirhodum*
M.f. *M. festucae* S.a. *S. avenae* R.i. *R. insertum*

Table 5.2 Analysis of Variance Table of $\log_{10}(n + 1)$ numbers of *Rhopalosiphum* spp. per 100 m^2 of ryegrass pasture during April to October.

ANALYSIS OF VARIANCE ON *Rhopalosiphum* spp.

SOURCE	DF	SS	MS	F	P
seasonality	6	111.279	18.546	32.09	0.000
ERROR	157	90.736	0.578		
TOTAL	163	202.015			

INDIVIDUAL 95 PCT CI'S FOR MEAN BASED ON POOLED STDEV

LEVEL	N	MEAN	STDEV	------+---------+---------+---------+
April	9	0.0000	0.0000	(----*----)
May	14	0.3248	0.6489	(---*---)
June	30	0.3694	0.6308	(--*-)
July	19	1.8673	0.8137	(---*--)
August	39	2.0833	1.0739	(--*-)
Sept.	44	2.0268	0.6379	(-*--)
October	9	2.2746	0.2471	(----*----)

POOLED STDEV = 0.7602 ------+---------+---------+---------+ 0.0 1.0 2.0 3.0

Table 5.3 Analysis of Variance Table of $\log_{10}(n + 1)$ numbers of *Metopolophium dirhodum* per 100 m^2 of ryegrass pasture during April to October.

ANALYSIS OF VARIANCE ON *Metopolophium dirhodum*

SOURCE	DF	SS	MS	F	P
seasonality	6	3.548	0.591	3.80	0.001
ERROR	157	24.410	0.155		
TOTAL	163	27.958			

INDIVIDUAL 95 PCT CI'S FOR MEAN BASED ON POOLED STDEV

LEVEL	N	MEAN	STDEV	-+---------+---------+---------+-----
April	9	0.0000	0.0000	(---------*---------)
May	14	0.0000	0.0000	(-------*-------)
June	30	0.4108	0.7094	(----*-----)
July	19	0.1321	0.3958	(------*------)
August	39	0.1000	0.3510	(----*----)
Sept.	44	0.0000	0.0000	(----*----)
October	9	0.1792	0.5376	(---------*---------)

POOLED STDEV = 0.3943 -+---------+---------+---------+----- -0.25 0.00 0.25 0.50

Table 5.4 Analysis of Variance Table of $\log_{10}(n + 1)$ numbers of *Metopolophium festucae* per 100 m^2 of ryegrass pasture during April to October.

ANALYSIS OF VARIANCE ON *Metopolophium festucae*

SOURCE	DF	SS	MS	F	P
seasonality	6	66.323	11.054	20.95	0.000
ERROR	157	82.818	0.528		
TOTAL	163	149.141			

INDIVIDUAL 95 PCT CI'S FOR MEAN BASED ON POOLED STDEV

LEVEL	N	MEAN	STDEV	----------+---------+---------+---------
April	9	0.0000	0.0001	(------*------)
May	14	0.3372	0.6763	(-----*-----)
June	30	1.8008	0.8965	(---*--)
July	19	0.9930	1.0094	(----*----)
August	39	0.6523	0.9172	(--*---)
Sept.	44	0.0301	0.1993	(--*---)
October	9	0.1469	0.4407	(------*------)
				----------+---------+---------+---------

POOLED STDEV = 0.7263 0.00 0.70 1.40

Table 5.5 Analysis of Variance Table of $\log_{10}(n + 1)$ numbers of *Sitobion avenae* per 100 m^2 of ryegrass pasture during April to October.

ANALYSIS OF VARIANCE ON *Sitobion avenae*

SOURCE	DF	SS	MS	F	P
seasonality	6	30.904	5.151	8.50	0.000
ERROR	157	95.091	0.606		
TOTAL	163	125.995			

INDIVIDUAL 95 PCT CI'S FOR MEAN BASED ON POOLED STDEV

LEVEL	N	MEAN	STDEV	----------+---------+---------+---------
April	9	0.0000	0.0000	(--------*--------)
May	14	0.0944	0.3534	(------*-----)
June	30	1.0660	0.9660	(----*---)
July	19	1.1877	0.8871	(-----*-----)
August	39	0.7930	1.0443	(---*---)
Sept.	44	0.1805	0.4637	(---*---)
October	9	0.1469	0.4407	(-------*--------)
				----------+---------+---------+---------

POOLED STDEV = 0.7783 0.00 0.60 1.20

Table 5.6 Mean numbers of aphids per 100 m^2 of ryegrass pasture sampled in 1988 and 1990 in the three grass length categories.

	Mean numbers of aphids/100 m^2								
	M.d.		M.f.		Rh. spp.		R.i.	S.a	
Grass length[a] catagory	1988	1990	1988	1990	1988[b]	1990	1990	1988	1990
1	1.5	0.0	13	0	84	87	67	7	0
2	2.7	2.2	90	24	75	969	301	20	27
3	5.5	0.6	129	43	241	334	207	41	61
Anova on pooled data	N.S.		N.S.		N.S. (Rh. spp.)			P < 0.05	

a 1 - Generally short (< 4 cm high)
2 - Obviously grazed but with lusher areas associated with cowpats
3 - Even, long grass throughout (> 4 cm high)

b alate Rh. spp. not separated in 1988.

Table 5.7 Analysis of Variance Table of $\log_{10}(n + 1)$ numbers of *Sitobion avenae* per 100 m^2 of ryegrass pasture in the three grass length categories.

ANALYSIS OF VARIANCE ON *Sitobion avenae*

SOURCE	DF	SS	MS	F	P
grass length	2	5.936	2.968	3.98	0.021
ERROR	161	120.059	0.746		
TOTAL	163	125.995			

INDIVIDUAL 95 PCT CI'S FOR MEAN BASED ON POOLED STDEV

LEVEL	N	MEAN	STDEV	----+----+----+----
1	15	0.2059	0.5541	(----------*----------)
2	64	0.4460	0.7817	(-----*-----)
3	85	0.7580	0.9591	(-----*----)

POOLED STDEV = 0.8635 0.00 0.35 0.70

All aphid species numbers had significant ANOVA results with seasonality. In the two seasons, *M. dirhodum* was least common (Table 5.1). However, it was observed in both years at a low density, in the June to August period. In contrast, *R. insertum* was mainly observed from July to September 1990, when its abundance (mostly apterae) exceeded 10 per m^2. In 1988, apterous *R. insertum* were not present, and alate *Rhopalosiphum* were much less abundant than in 1990. *R. padi* was the most numerous species in both years, although its population growth started later than the non-*Rhopalosiphum* species. Numbers of *R. padi* remained high relative to other species throughout the autumn, and like *R. insertum*, it had a maximum density of more than 10 per m^2 in August 1990. Both *M. festucae sensu stricto* and *S. avenae* peaked in the June to August period of both 1988 and 1990, at densities of about 1 per m^2.

Table 5.8 Mean numbers of aphids per 100 m^2 of ryegrass pasture sampled in 1988 and 1990 in the four pasture age categories.

	Mean numbers of aphids/100 m^2								
	M.d.		M.f.		Rh. spp.		R.i.	S.a	
Pasture age (years)	1988	1990	1988	1990	1988[a]	1990	1990	1988	1990
< 2	1.1	0.0	12	40	291	2011	328	6	58
2 to 5	4.5	0.0	85	13	90	27	0	25	27
6 to 10	5.0	3.8	132	66	234	739	508	45	70
> 10	3.9	0.0	133	14	61	262	100	29	28
Anova on pooled data	N.S.		N.S.		P < 0.001 (Rh. spp.)			N.S.	

a alate *Rhopalosiphum* spp. not separated in 1988.

Table 5.9 Analysis of Variance Table of $\log_{10}(n + 1)$ numbers of *Rhopalosiphum* spp. per 100 m^2 of ryegrass pasture in the four pasture age categories.

ANALYSIS OF VARIANCE ON *Rhopalosiphum* spp.

SOURCE	DF	SS	MS	F	P
age	3	23.69	7.90	7.08	0.000
ERROR	160	178.33	1.11		
TOTAL	163	202.01			

FOR MEAN — INDIVIDUAL 95 PCT CI'S BASED ON POOLED STDEV

LEVEL	N	MEAN	STDEV	95 PCT CI's
< 2	24	2.063	1.120	(-------*--------)
2 - 5	38	1.107	0.970	(------*------)
6 - 10	51	1.792	1.073	(-----*-----)
> 10	51	1.158	1.068	(-----*-----)

POOLED STDEV = 1.056

1.00 1.50 2.00 2.50

Numbers of *S. avenae* gave a significant ANOVA result with the pasture length categories, increasing abundance being associated with increasing pasture length.

Numbers of *Rhopalosiphum* spp. gave a significant ANOVA result with age of pasture, greatest abundance being associated with pastures less than two years old. However, the relationship was not linear with the four age categories.

Table 5.10 Mean numbers of aphids per 100 m^2 of ryegrass pasture sampled in 1988 and 1990 in the five regions.

	Mean numbers of aphids/100 m^2								
	M.d.		M.f.		Rh. spp.		R.i.	S.a.	
Region	1988	1990	1988	1990	1988[a]	1990	1990	1988	1990
Dumfriesshire	2.6	0.0	32	6	186	22	11	8	23
Wigtownshire	3.2	0.0	33	0	196	212	24	5	0
Ayrshire	6.3	2.0	184	45	178	900	375	56	45
Renfrewshire	-	0.0	-	33	-	0	0	-	200
Stirlingshire	0.0	0.0	40	22	159	34	22	11	32
Anova on pooled data	N.S.		N.S.		$P < 0.001$ (Rh. spp.)			$P < 0.05$	

[a] alate *Rhopalosiphum* spp. not separated in 1988

R.p. *R. padi* Rh. *Rhopalosiphum* spp. M.d. *M. dirhodum*
M.f. *M. festucae* S.a. *S. avenae*

Table 5.11 Analysis of Variance Table of $\log_{10}(n + 1)$ numbers of *Rhopalosiphum* spp. per 100 m^2 of ryegrass pasture in the five regions.

ANALYSIS OF VARIANCE ON Rhopalosipum spp.

SOURCE	DF	SS	MS	F	P
region	4	33.58	8.40	7.92	0.000
ERROR	159	168.43	1.06		
TOTAL	163	202.01			

FOR MEAN

INDIVIDUAL 95 PCT CI'S

BASED ON POOLED STDEV

LEVEL	N	MEAN	STDEV	--+---------+---------+---------+----
Dumfriesshire	26	1.261	1.037	(---*---)
Wigtownshire	26	1.650	1.038	(--*---)
Ayrshire	84	1.786	1.083	(-*-)
Renfrewshire	3	0.000	0.000	(----------*----------)
Stirlingshire	25	0.652	0.847	(----*---)
				--+---------+---------+---------+----
POOLED STDEV = 1.029				-1.0 0.0 1.0 2.0

Table 5.12 Analysis of Variance Table of $\log_{10}(n + 1)$ numbers of *Sitobion avenae* per 100 m^2 of ryegrass pasture in the five regions.

ANALYSIS OF VARIANCE ON Sitobion avenae

SOURCE	DF	SS	MS	F	P
region	4	9.240	2.310	3.15	0.016
ERROR	159	116.755	0.734		
TOTAL	163	125.995			

FOR MEAN

INDIVIDUAL 95 PCT CI'S

BASED ON POOLED STDEV

LEVEL	N	MEAN	STDEV	--+---------+---------+---------+----
Dumfriesshire	26	0.4598	0.7213	(-----*----)
Wigtownshire	26	0.2169	0.5212	(-----*----)
Ayrshire	84	0.7943	0.9705	(--*--)
Renfrewshire	3	0.9263	1.6044	(----------*----------)
Stirlingshire	25	0.3586	0.7539	(-----*-----)
				--+---------+---------+---------+----
POOLED STDEV = 0.8569				0.00 0.60 1.20 1.80

Both *Rhopalosiphum* spp. and *S. avenae* gave significant ANOVA results with region, the former being abundant in Dumfriesshire, Wigtownshire and Ayrshire and rare in Renfrewshire and Stirlingshire. The regional distribution of *S. avenae* was less clear cut with the relatively large number of observations and the high level of abundance in Ayrshire being the main feature.

The importance of all nine field/farm variables was tested using multivariate analysis on the pooled 1988 and 1990 data.

TWINSPAN The "pseudo-species" settings were set to create six categories (Table 5.13). The refined-ordination table after two divisions is shown in Table 5.13 and the dendrogram of divisions in Figure 5.1. Further divisions were not included because of the small number of species involved. The characteristic "pseudo-species" of each group are shown in Table 5.14.

The mean number of aphids per 100 m^2 of ryegrass pasture for each aphid species in each TWINSPAN end-group are shown in Table 5.15 along with the field/farm variable means of each TWINSPAN end-group and of a fifth group comprised of observations when no aphids were sampled ("No aphids").

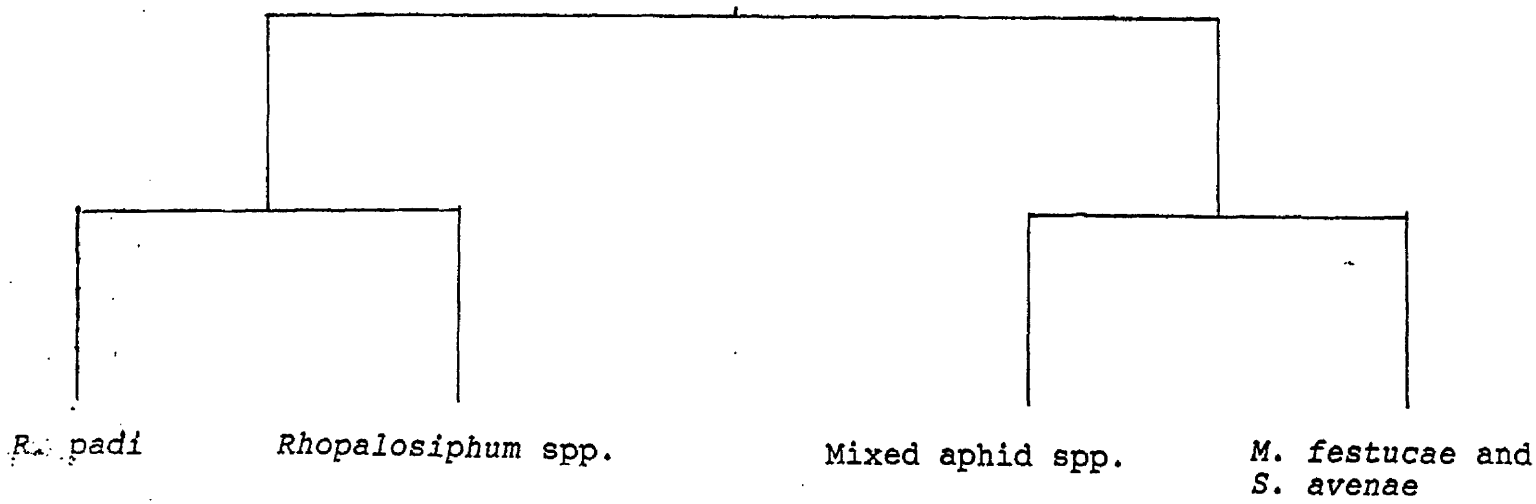


Figure 5.1 Dendrogram showing divisions and end-group names of TWINSPAN classification of aphid numbers per 100 m^2 of ryegrass pasture in 1988 & 1990.

Table 5.13 TWINSPAN refined-ordination table after two divisions; aphids per 100 m^2 of ryegrass pasture 1988 & 1990.

"Pseudo-species" level

Aphid species	138 occasions of sampling ryegrass pastures ordinated to reflect the incidence and abundance of the five aphid species

```
RHOPINE 1----------------------------------------------------------2---------3112433333455435135 3----------------------------------------- 0
RHOPADI 11111111111111111332252333323332323333332333332323322233343233332455533433352-22233311-55534531423122111332 11----111----11-1-1------------ 0
MEDRDOR ----------------------1-------------------------------------------------------------1---4-1-112---1-------------------1---22211------ 1
MEDPAES ----------------111-----------------------------------------------113221-1-------3131-332355512221-------1133333333333533233311222 12 1
STOBION ---------------------------------------------------------11111-1--2212113------1-2---333331331333323133111113---4322111212---1-11-----11 1
```

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00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000011111111111111111111111111111111111111111111111111
00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000111111111111111100000000000000000000011111111111111111111111
```

"Pseudo-species" levels (number of aphids per 100 m^2 of ryegrass pasture).

-	= 0	1 = 1 to 49	2	=	50 to 99
3	= 100 to 449	4 = 500 to 999	5	=	> 999

Table 5.14 Group names and characteristic "pseudo-species" of TWINSPAN end-groups; aphids in ryegrass pasture 1988 & 1990.

End-group[a]	Group name	Characteristic "pseudo-species"	
00	*R. padi*	RHOPPADI	3
01	*Rhopalosiphum* spp.	RHOPPADI	3
		RHOPINSE	3
10	Mixed aphid spp.	RHOPPADI	3
		SITOBION	3
		METOPFES	3
11	*M. festucae* and *S. avenae*	RHOPPADI	0
		METOPFES	3
		SITOBION	1

[a] End-groups names from bottom of Table 5.13.

Table 5.15 Mean aphid numbers per 100 m^2 of ryegrass pasture and the field/farm variables of the TWINSPAN end-groups.

	Mean values of aphid numbers & field/farm variables				
TWINSPAN end-group	R.p.	Rh. spp.	Mixed aphid aphid spp.	M.f./ S.a.	No aphids
M. dirhodum	0.5	1.3	7.4	9.3	0
M. festucae	5	52	117	162	0
Rh spp.	275	1704	299	6	0
S. avenae	7	62	137	51	0
Ratio of[a] 1988:1990	60:15	0:16	11:9	19:8	8:18
Grass length	2.4	2.1	2.6	2.6	2.4
Pasture age	2.6	2.7	3.0	3.0	3.0
Season	5.6	5.1	4.1	3.0	2.5
Region[b]	2.6	2.9	3.0	2.9	3.3
Carlisle	58	114	84	75	103
Crieff	130	111	108	113	92
Stranraer	69	83	86	90	116
Altitude	51	57	56	45	41
Distance from sea.	8	13	10	12	21

[a] ratio of the number of observations sampled in 1988 to the number sampled in 1990.

[b] Regions numbered as follows: Dumfriesshire 1
Wigtownshire 2
Ayrshire 3
Renfrewshire 4
Stirlingshire 5

The "*R. padi*" and the "*Rhopalosiphum* spp." groups had low pasture age and pasture length means and the highest seasonality means. Only the "*R. padi*" group was associated with the southernmost regions, and it also had the lowest "distance from the sea" mean.

The "mixed aphid spp." and the "*M. festucae* and *S. avenae*" groups had the same pasture age mean as the group "No aphids" but seasonality means intermediate between "No aphids" and the other two groups. Grass length means were greatest in these two groups and they had similar distances from Carlisle, Crieff and Stranraer as "*Rhopalosiphum* spp."

"No aphids" had an intermediate pasture length mean, the lowest seasonality mean, the highest region mean and the highest "distance from the sea" mean. Thus, this group contained two types of field observations: firstly, observations collected in the spring and secondly, observations collected from Renfrewshire and Stirlingshire. Altitude did differ between groups but the lowest mean belonged to the "No aphids" group, contrary to expectation.

The TWINSPAN end-group ratios of the number of observations from the years 1988 and 1990 differed. The "*Rh spp.*" group was comprised entirely of 1990 observations, the "*R. padi*" and the "M.f./S.a." groups mainly of 1988 observations, the group "No aphids" mainly of 1990 observations, and the "Mixed aphid spp." group an equal number of observations from each year.

DECORANA and CANOCO Due to the small number of species, these analyses failed to differentiate between many of the observations. Their results were therefore deemed invalid.

5.4 Discussion

Aphid species incidence differed from the observations made in southern England. The *M. festucae* individuals sampled by Hand (1989) were mostly the subspecies *cerealium* (Vickerman (1982) did not specify the subspecies) whereas in Scotland, they were *sensu stricto*. *S. fragariae* was found by Hand (1989) in dense ryegrass in large numbers on a few occasions, but *Sitobion* sampled in ryegrass pasture in Scotland were mainly *avenae*. Most *R. insertum* sampled by Hand (1989) were alatiform and confined to the autumn period, suggesting that they were feeding on roots in those summers. In Scotland, apterous *R. insertum* were present on aerial parts of ryegrass in densities greater than 10 per m^2 during August 1990, although in 1988, they were apparently feeding on roots only. The presence of large numbers of apterous *R. insertum* feeding on the aerial parts of ryegrass has not been observed before in Britain, the species being a rootfeeder during the summer months (Blackman & Eastop, 1984).

The seasonality trends and the relative numbers of each species were generally similar to those found by Vickerman (1982) and Hand (1989), with *Metopolophium* spp. and *S. avenae* peaking in the summer months at lower

densities than *Rhopalosiphum* spp. which were most common during late summer and autumn.

The interactions of pasture length, pasture age and region with aphid species abundance were confounded by the seasonality of aphid numbers. Nevertheless, significant interactions were found.

Mean numbers of *S. avenae* were approximately 2 per 100 m^2 of ryegrass pasture at pasture length category 1 compared with approximately 6 per 100 m^2 of ryegrass pasture at pasture length category 3. Hand (1982) also found that grazing reduced aphid numbers, and suggested that farmers could use grazing to reduce aphid abundance at certain times of year, e.g. during the late winter/early spring to lessen the size of the overwintering population in ryegrass.

Mean numbers of *Rhopalosiphum* spp. varied non-linearly with pasture age, which suggests the relationship may be the result of the seasonality factor confounding the data. *M. festucae* numbers increased with pasture age, although the relationship was non-significant. Hand (1989) sampled first year leys and older ryegrass pastures. He found that *S. avenae* numbers were greatest on first year leys but that *M. festucae cerealium* and *Rhopalosiphum* spp. were most common in older swards.

Most aphid sampling in ryegrass pasture took place in Ayrshire, and very little in Renfrewshire. However,

Dumfriesshire, Wigtownshire and Stirlingshire were sampled on an approximately equal number of occasions. The higher numbers of *Rhopalosiphum* spp. in Dumfriesshire, Wigtownshire and Ayrshire relative to Renfrewshire and Stirlingshire is consistent with the association of *R. padi*-transmitted BYDV with coastal areas of southern and western Britain (Plumb, 1974). Apart from the three Renfrewshire observations, *S. avenae* numbers were highest in Ayrshire. There is no obvious reason for Ayrshire having the greatest numbers of *S. avenae*, therefore, the result may be due to seasonality confounding the data.

The TWINSPAN classification also identified the seasonality of the different species, and the absence of all species early in the year. It also identified the association of *R. padi* with the more southernmost regions, and the relative scarcity of aphids in the northernmost regions. Non-*Rhopalosiphum* spp. were associated with greater grass length and pasture age, which is partially consistent with the observations of Hand (1989). The low distance from the sea mean of the *R. padi* group, and the large mean of the "No aphids" group is consistent with the aphid data obtained from winter barley crops (Chapter 4). An odd result is the low altitude mean of the group "No aphids", this probably owing to the relatively few sampling observations early in the season when aphids were absent.

CHAPTER SIX

Aphid infestation and the BYDV infection of, wild grasses in hedge bottoms and farm lanes

6.1 **Introduction**

Many weeds and grasses are reservoirs of virus diseases which can be transmitted to agricultural crops by insects (van Emden, 1965). The wide host ranges of both BYDV (Oswald & Houston, 1953; Guy *et al.*, 1986; Kurppa *et al.*, 1989) and cereal aphids (Smith *et al.*, 1984a; Tatchell *et al.*, 1983) suggest that wild grasses could be important as sources of viruliferous aphids.

6.2 **Methodology**

6.2.1 **Aphid infestation of wild grasses**

Five grass weed species that were common on cereal farms, but not necessarily common within arable fields, were selected: *Alopecurus pratensis* (L.), *Dactylis glomerata* (L.), *Holcus lanatus* (L.), *Poa annua* (L.) and *Lolium perenne* (L.) These five species constitute a large proportion of the grass flora in hedge bottoms, on disturbed land at field boundaries and around farm buildings. Two estates in Ayrshire were sampled to the following schedule in 1990:-

	Dates in month when sampling took place				
Estates	May	June	July	Aug	Sept
Auchincruive	30	6	18	6	4
Barskimming	30	10	14	4/5	3/4

On each date, aerial parts of ten individuals of each grass weed species were examined *in situ* at the specified estate. Within an estate, different sites in which wild grasses occur were sampled. These sites were re-visited on each occasion at Barskimming, however, at Auchincruive, weed control destroyed some sites necessitating the selection of new ones for further sampling. No special attempt was made to re-sample the same plants. Each plant chosen bore at least one inflorescence in any stage of development. Numbers of colonies (section 4.4.1) of each aphid species on either leaves/stems or inflorescences were noted.

6.2.2 **BYDV infection of wild grasses**

The five species of grass sampled for aphids were tested for BYDV incidence. Samples were collected from various sites on six farms during May and June 1990: two farms in Ayrshire, and one in each of Dumfriesshire, Wigtownshire, Renfrewshire and Stirlingshire. In Ayrshire, samples of each grass species were collected on two occasions, elsewhere on one occasion. Samples were taken from plants in hedge bottoms, along farm lanes and around farm buildings. Five 1 g leaf samples of each species from each farm was the intended sample. Samples were tested for BYDV by ELISA (Mortar and Pestle method). Healthy *L. perenne* comprised the healthy samples.

6.3 Results

6.3.1 Aphid infestation of wild grasses

Table 6.1 shows the total numbers of plants on which at least one aphid colony of any cereal aphid species was observed on either leaves/stems or inflorescences for each of the five grass weed species examined during the summer of 1990. One hundred individuals of each grass weed species were examined. The highest infestation level was observed on *D. glomerata* inflorescences: 18% were aphid infested. The lowest infestation level was found on *L. perenne* inflorescences: 2% were infested.

Table 6.1 Total number of plants (leaves/stems or inflorescences) with at least one aphid colony for each grass species after 100 plants were examined (pooled from both sites); summer 1990.

	Number of aphid-infested plants		
Grass weed	Leaves/stems	Infloresences	Totals
Alopecurus pratensis	7	6	13
Dactylis glomerata	3	18	21
Holcus lanatus	2	13	15
Lolium perenne	3	2	5
Poa annua	11	8	19
Totals	26	47	73

Twenty-nine per cent of the total 73 aphid infested plant parts belonged to *D. glomerata*, compared with 26, 21, 18 and 7% for *P. annua*, *H. lanatus*, *A. pratensis* and *L. perenne* respectively. Sixty-four per cent of these 73 aphid infestations were situated on inflorescences.

The site of aphid infestions differed significantly between grass weed spp. (*A. pratensis* and *L. perenne* [pooled], and *D. glomerata* and *H. lanatus* [pooled], $x^2_{(2)} = 14.6$, $P < 0.001$). *D. glomerata* and *H. lanatus* were similar in that most aphid infestation of these spp. occurred on inflorescences with few on leaves/stems. Aphid infestation of the other three grass weed species occurred approximately equally on the leaves/stems and inflorescences.

Table 6.2 shows for three cereal aphid genera, the total numbers of plants on which at least one aphid colony was observed on either leaves/stems or inflorescences at each site, for each of the five grass weed species during the summer of 1990. One hundred grass weed individuals were examined.

Table 6.2 Numbers of plants infested (either leaves/stems or inflorescences) by aphids for each grass weed species at each site.

Metopolophium spp.

	Auchincruive estate		Barskimming estate	
Grass weed	lves/stems	inflores	lves/stems	inflores
A. pratensis	1	0	0	0
D. glomerata	1	0	0	0
H. lanatus	0	0	0	0
L. perenne	0	0	1	0
P. annua	3	0	1	0
Totals	5	0	2	0

Rhopalosiphum spp.

	Auchincruive estate		Barskimming estate	
Grass weed	lves/stems	inflores	lves/stems	inflores
A. pratensis	0	0	0	0
D. glomerata	2	2	0	0
H. lanatus	1	1	1	0
L. perenne	1	1	0	0
P. annua	3	0	3	0
Totals	7	4	4	0

Table 6.2 continued.

Sitobion spp.

	Auchincruive estate		Barskimming estate	
Grass weed	lves/stems	inflores	lves/stems	inflores
A. pratensis	5	3	1	3
D. glomerata	0	14	0	2
H. lanatus	0	12	0	0
L. perenne	1	1	0	0
P. annua	0	4	1	4
Totals	6	4	2	9

lves leaves inflores infloresences

The highest number of colonies on individual plants was in excess of ten (hundreds of individuals), on leaves/stems of one *D. glomerata* and on both leaves/stems and inflorescences of one *L. perenne*. *R. padi* was the aphid involved in both cases.

Metopolophium infested 0.7% of the 1000 plant parts. All seven colonies counted were *dirhodum*. Fifty-seven per cent of *Metopolophium* infested plant parts belonged to *P. annua* and only single individuals of three other grass weed species were infested. *M. dirodum* did not infest *H. lanatus* or inflorescences of any grass species. All *M. dirhodum* colonies were apterous and occurred singly on *M. dirhodum* infested plants.

Rhopalosiphum infested 1.5% of the 1000 plant parts. Affected plants were infested by either single alate individuals, either *insertum* or *padi*, or multiple colony populations of apterous *padi*. *Rhopalosiphum* showed no strong preference for any of these five grass weed species although *A. pratensis* was never infested. The 11 colonies counted on leaves/stems compared with four colonies on inflorescences perhaps suggests a preference for the former plant part.

Sitobion infested 5% of the 1000 plant parts. Seventy per cent of all plant part infestations were *Sitobion*. Both *avenae* and *fragariae* were common. Nine per cent of the inflorescences of the 500 grass weeds examined were infested by *Sitobion*. Eighty-four per cent of *Sitobion* infested plant parts involved inflorescences, and 60% of these were either on *D. glomerata* or *H. lanatus*. Thirty-one *Sitobion* infested plant parts involved single colonies, compared with 17 plant parts which had multiple *Sitobion* colony infestations (both leaves/stems and inflorescences of some plants were infested).

There was no difference between the three aphid genera, in the total number of aphid-infested leaves/stems of all five grass species, compared with the total number not aphid-infested ($x^2_{(2)} = 1.1$, N.S). In contrast, the comparative test for the inflorescences gave a significant result ($x^2_{(2)} = 85.4$, $P < 0.001$), due to the relatively

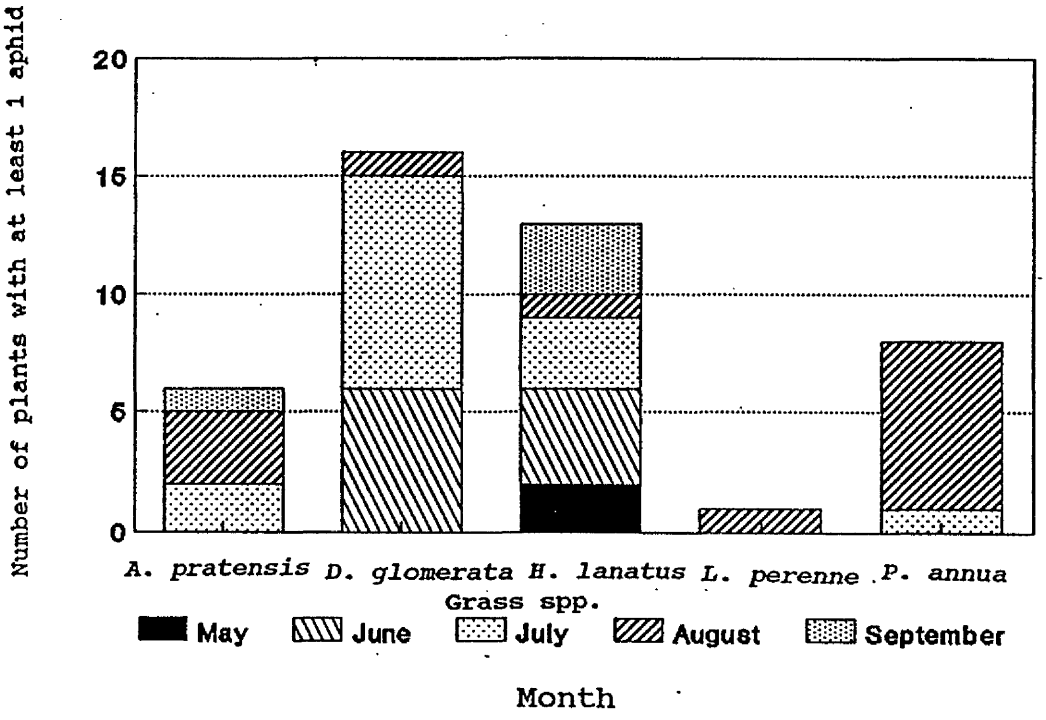
high number (9%) of inflorescences infested by *Sitobion* spp.

There was no difference between the aphid-infested:not aphid-infested ratios of the leaves/stems and infloresences (all grass weed species pooled) for the *Rhopalosiphum* ($x^2_{(1)}$ = 3.53, N.S.) genus. However, there was a significant difference for *Metopolophium* ($x^2_{(1)}$ = 7.25, $P < 0.01$, 2 expecteds < 5), because of the total absence of infestations on inflorescences, and for *Sitobion* ($x^2_{(1)}$ = 32.2, $P < 0.001$), because of the greater number of infestations on the inflorescences.

Figure 6.1 shows the number of plants with *Sitobion* infestation of the inflorescences for the five grass weed spp. and how this changes during the progression of the summer. *H. lanatus* was infested during all five months, whereas *D. glomerata* was not infested in September when its inflorescences were dead. *Sitobion* infestations of *A. pratensis* and *P. annua* occurred in the latter half of the summer.

Four-times as many *Sitobion* infested plants were observed at the Auchincruive estate relative to the Barskimming estate. Overall, aphid infested plants were three times as numerous at Auchincruive.

A few plants infested by vagrant aphids were encountered, such as a *D. glomerata* infested by *Euceraphis punctipennis* underneath a *Betula* spp. at Auchincruive.



N.B. Twenty plants of each grass weed spp. examined each month.

Figure 6.1 Monthly numbers of five grass weed spp. sampled in hedge bottoms whose inflorescences were infested by *Sitobion* spp. summer 1990.

6.3.2 BYDV infection of wild grasses

Table 6.3 shows the BYDV strain incidence in each of the five grass weed species (data from all regions pooled). The percentage infection of each grass weed species with each strain is shown in Figure 6.2. There was a significant difference in the incidences of the three BYDV strains in the five grass weed species ($x^2_{(8)} = 21.7$, $P < 0.01$).

All *D. glomerata* sampled were infected, usually with more than one strain. In contrast, 43% of *H. lanatus* were infected, and only this species was infected with predominantly one strain alone, MAV. In *L. perenne* and *D. glomerata*, all three strains were found in at least 30% of samples. In *A. pratensis*, *H. lanatus* and *P. annua*, at least one strain occurred in less than 15% of samples. Scarcity of RPV was a characteristic of both *H. lanatus* and *P. annua*, whilst scarcity of PAV was a characteristic of both *H. lanatus* and *A. pratensis*.

MAV was the commonest strain, being present in 52% of samples compared with 37 and 27% for RPV and PAV respectively. In *P. annua*, PAV was the predominant strain, although overall this strain was least common.

6.4 Discussion

6.4.1 Aphid infestation of wild grasses

Metopolophium and *Rhopalosiphum* were found on a small percentage of the 500 examined plants. Although the five grass species were examined in a variety of sites on the

Table 6.3 BYDV strain incidence in five species of wild grass, summer 1990.

Grass species	No of samples	Percentage infected	Number of positive tests for BYDV strain		
			RPV	PAV	MAV
Alopecuris pratensis	28	61	11	4	12
Dactylis glomerata	38	100	34	21	33
Holcus lanatus	40	43	2	3	17
Lolium perenne	33	82	16	10	22
Poa annua	39	49	3	11	10
Total	178		66	49	94

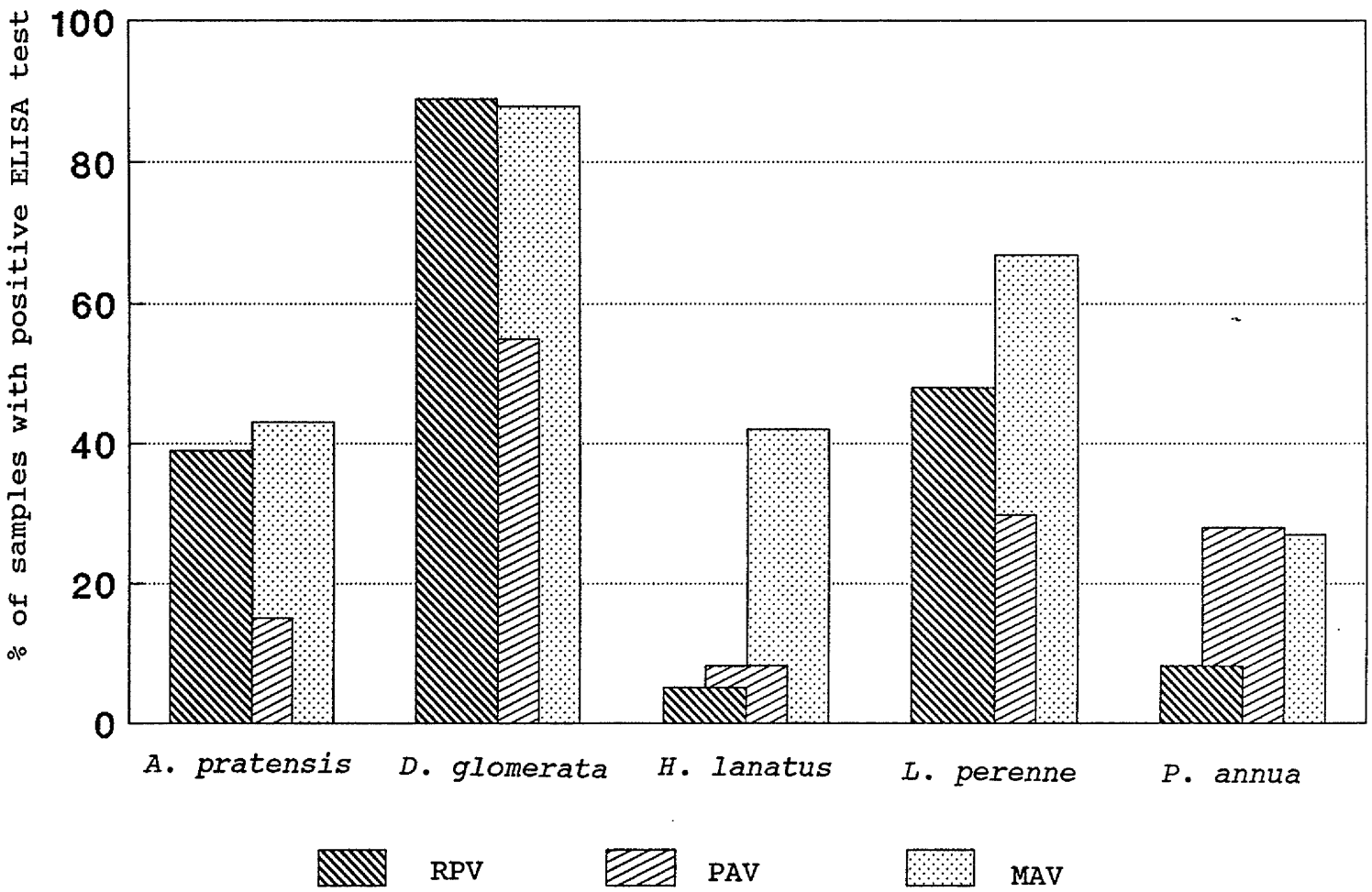


Figure 6.2 Percentage of the five grass weed spp. sampled in hedge bottoms infected with each BYDV strain; summer 1990.

two Ayrshire estates, the scarcity of these aphids may have been due to the year. However, Orlob (1961) in Canada and Guy *et al.* (1987) in Tasmania found aphids to be rare on wild grasses. Furthermore, studies of individuals on marked wild grasses in the field showed that most alatae moved from the plant within 1 to 2 days (Orlob, 1961). Contrary to this work, other field studies of cereal aphids on wild grasses found *R. padi* to be the most abundant species, and to infest the widest range of wild grass species (Orlob, 1961; Orlob & Medler, 1961; Guy *et al.*, 1987).

There have been several laboratory studies of the host plant preferences of cereal aphids. Coon (1959) compared the reproductive potential and the survival of *R. padi* and *S. avenae* on 59 grass species in 30 genera. In terms of these two characteristics, *Festuca* spp. and *Lolium multiflorum* (L.) were the best hosts for *S. avenae* whereas *Festuca* spp. and *L. perenne* were the best for *R. padi*. In contrast to the findings of this work, *P. annua* or *H. lanatus* were relatively poor hosts for both aphid species.

Dean (1973) compared the intrinsic rates of increase (r) of *M. dirhodum*, *R. padi* and *S. avenae* on barley and several species of wild grass. Only *R. padi* could maintain a comparable r on the other wild grasses to that on barley. He also examined the host plant preferences of cereal aphids by giving them a free choice of grass species in a large cage outdoors. Most *M. dirhodum* were

found on *D. glomerata*, *Poa pratensis* (L.) and *Festuca pratensis* (L.). Most *R. padi* were found on *F. pratensis* and *L. perenne*. Most *S. avenae* were found on *D. glomerata* and *L. perenne*. These results contrast with the scarcity of aphids on *L. perenne* found in this study.

Tatchell *et al.* (1983) reviewed the host plants of 30 species of pest aphid included in the RIS *Aphid Bulletin*. The preferred grass hosts of *M. dirhodum* are listed as *Bromus* spp., which are rare in Scotland, and *Phalaris arundinacea*. For *R. padi*, only *P. annua* is listed as a preferred host, whereas for *S. avenae*, *Glyceria fluitans*, *Holcus spp.* and *Carex sylvatica* are listed.

Smith *et al.* (1984b) screened 39 grass weed species for their susceptibility to *R. padi* and *S. avenae*. Both aphid species reproduced well on *D. glomerata* and *L. perenne* whereas on *H. lanatus*, their reproduction was intermediate. *P. annua* was found to be one of the best host plants for both spp. (Smith *et al.*, 1984a).

In this study, *P. annua* was colonized by aphids of all three genera. Most *Metopolophium* and *Rhopalosiphum* infested plants were *P. annua*, and all these infestations were found on the leaves/stems. *Sitobion* were mainly found on the infloresences of *P. annua*, but a smaller proportion of the 100 *P. annua* examined was infested than *D. glomerata* and *H. lanatus*.

The presence of *Sitobion* spp. on infloresences of *D. glomerata* and *Holcus* spp. has been observed before in southern England (Watt, 1981; Loxdale & Brooks, 1990), and like in this study, *fragariae* as well as *avenae* was found. While Watt (1981) mostly observed *avenae* on *D. glomerata*, Loxdale & Brookes (1990) found *fragariae* to be predominant on this grass weed. Two of the years in which Watt (1981) studied *S. avenae* on wild grasses were years when this aphid was numerous on winter wheat (1976 & 1977). He observed the highest densities on *D. glomerata* in the field margin of a winter wheat crop heavily infested by *S. avenae*, and concluded that wild grasses normally support aphid populations lower than their maximum carrying capacity, and that the highest densities are found in years when large populations build up in agricultural crops.

The findings of Loxdale & Brooks (1990) suggest that *D. glomerata* may not be as important as a source of *S. avenae* as its high levels of *Sitobion* infestation in Ayrshire might suggest. The large numbers of *Sitobion* nymphs on *D. glomerata* and *H. lanatus* infloresences, and the difficulty of identifying these morphs to species, prevented accurate determination of the relative abundance of these two species. It is considered that they were approximately equally abundant.

The seasonality of wild grass infestation by *S. avenae* has also been observed in southern England (Watt, 1981; Loxdale & Brooks, 1990). Aphid density rose during and

shortly after flowering, and fell sharply as the grass hosts matured, as it does in cereals (Watt, 1981). However, because grasses in different growth stages are present at the same time, this seasonality factor may not be important over large areas. Nevertheless, on the scale of wild grasses in a field margin, growth stage may be more synchronous, because plants in the same field margin grow in similar soil and experience a similar climate. Therefore, because *S. avenae* may disperse short distances, and because movements of many *S. avenae* individuals from local senescing *D. glomerata* or *H. lanatus* inflorescences may occur, adjacent winter cereals may become heavily colonised early in the autumn. This theory could explain why a few fields drilled during early September developed large *S. avenae* infestations, and why early drilled crops in general suffered more from *S. avenae*-transmitted BYDV rather than *R. padi*-transmitted BYDV in the three years of study (Chapter 4).

The difference in aphid infestations between the two Ayrshire estates is another example of aphid numbers varying between sites. Also, greater aphid numbers were found at the more coastal site, Auchincruive. In cereals, Dewar (1984) found large differences in aphid numbers between regions, and the highest densities were found in a field near the Essex coast.

6.4.2 **BYDV infection of wild grasses**

The BYDV infection of a grass weed could be dependent on both its longevity and attractiveness to viruliferous cereal aphids. Clearly, a perennial weed such as *D. glomerata* is more likely to be BYDV infected than an annual or short-lived perennial such as *P. annua*. The percentage BYDV infection of these two grass weed species (Table 6.3) support this theory.

BYDV infection in many wild grasses is symptomless (Oswald & Houston, 1953; Kurppa *et al.*, 1989), thus uninfected and BYDV infected grass weeds are probably equally attractive to viruliferous and aviruliferous aphids alike. Therefore, the attractiveness of a grass weed to viruliferous aphids probably depends on the aphid species.

The relationships between the different aphid species and the three BYDV strains (Plumb, 1974) means that the BYDV infection of the five grass weed species is likely to depend to some extent, on their relative attractiveness to the different cereal aphid species, assuming that all three strains can replicate in all five grass weed species. Thus, the data suggest that *D. glomerata* and *L. perenne* are more attractive to *R. padi* than the other three grass weed species, whereas *H. lanatus* is only attractive to *Sitobion* spp. (and possibly *Metopolophium* spp.). This MAV infection of *H. lanatus* is consistent with the predominance of *Sitobion* infestation on this grass weed found in section 6.3.1

The occurrence of BYDV in wild grasses is well known (Oswald & Houston, 1953; Guy *et al.*, 1986; Kurppa *et al.*, 1989), and the incidence of the different BYDV strains in different grass weed species is perhaps expected given the knowledge of the host plant preferences of the different aphid species outlined above (section 6.4.1). Guy *et al.* (1987) tested 2077 grass plants for BYDV using ELISA. BYDV was found in 25 of the 56 grass species. Four per cent of the 250 *D. glomerata* tested for BYDV were infected, mostly with the RPV strain. Seven per cent of the 28 *H. lanatus* tested for BYDV were infected, also with the RPV strain. However, 27% of the 200 *L. perenne* tested for BYDV were infected, mostly with PAV alone. None of the ten *P. annua* tested for BYDV was infected.

In Finland, 599 samples of wild grasses were collected from field margins in July 1986, and tested for BYDV using ELISA (the B & F antisera). Seventy-eight per cent of the 54 *Alopecurus pratensis* tested for BYDV were infected, mostly with the PAV strain. Forty-five per cent of the 38 *Poa* spp. tested for BYDV were infected, also mainly with the PAV strain. The highest infection levels (92%) were found in the 159 *Agropyron repens* which were tested for BYDV, and the PAV and MAV strains occurred approximately equally. This species is a common weed in cereal fields of Finland (Kurppa *et al.*, 1989).

The percentage BYDV infection of wild grasses found in this study is similar to that found in Finland but higher

than that found in Tasmania. However, in all studies, there were marked species differences in both the percentage infection and in the BYDV strains involved.

Although the age of sampled plants was unknown, the existence of these differences in BYDV infection between the perennial grass weed species (*P. annua* excluded) probably indicates that the preference of cereal aphids for a grass species is more important in the determination of the BYDV infection of an individual plant, than the plant's age. The explanation for this may lie in the method of host plant selection by aphids and the manner of BYDV transmission.

Many aphids select host plants by alighting on any green plant, and then probe to identify whether or not it is a host plant. On a host plant, an aphid will normally remain to feed and/or reproduce, whereas an aphid will normally fly from a non-host plant. Aphids therefore, accumulate on their preferred host plants (Taylor, 1973). To transmit BYDV, the aphid stylet must penetrate the phloem tissue, and for the transmission of MAV by *S. avenae*, a minimum probe time (access period) of 17 minutes was found to be necessary (Scheller & Shukle, 1986). Given this host plant selection process of aphids, and the different BYDV infections of the five grass weed species, it is reasonable to conclude that duration or depth of probe necessary for an aphid to identify a plant as a non-

host is insufficient for the transmission of BYDV.

An interesting paradox of this Chapter is the absence of aphid infestations on *L. perenne* (Table 6.1) and the high levels of BYDV infection of this grass weed (Table 6.3). In *L. perenne* pastures (Chapter 5), aphids were sometimes very abundant. Evidently, aphids do feed on *L. perenne* in the hedge bottom situation, but they may not reproduce on it. However, Leather & Dixon (1982) found that *R. padi* preferred *L. perenne* to other grass species and cereals.

The host plant preferences of cereal aphids found by other workers and summarised in section 6.4.1 are somewhat variable. This variability may be due to the existence of "biotypes" in different areas which are adapted to specific host plants. These biotypes may change over a number of years, in response to the changing agriculture and weather (Taylor, 1982).

Finally, the predominance of MAV in the wild grasses, and the greater numbers of *Sitobion* spp. on grass weeds in hedge bottoms and farm lanes, relative to aphids of other genera could be associated.

CHAPTER SEVEN

Transmission of BYDV by field-collected aphids

7.1 Introduction

BYDV belongs to a virus group known as Luteoviruses. The characteristics of this group are that they are transmitted by aphids in a persistent, circulative manner, they cannot be transmitted mechanically and they are confined to phloem tissue in low concentrations (Rochow, 1977).

Vector relationships The existence of vector-specific strains of BYDV has been established for isolates collected in different parts of the world (Rochow, 1958; Toko & Bruehl, 1959; Watson & Mulligan, 1960), and their relationships with their vectors form the basis of current strain classification system. In Britain, isolates transmitted specifically by *R. padi* are classified as RPV, isolates transmitted specifically by *S. avenae* (formerly *Macrosiphum*) as MAV, and isolates that can be transmitted by aphids of both genera (hence, non-specifically), as PAV (Plumb, 1974). However, in recent years, more aphid species have been found to be vectors of BYDV, and this has weakened the plausibility of classifying BYDV strains by their supposedly specific aphid vectors (Irwin & Thresh, 1990).

There are several phenomena which obscure vector-specific relationships. For example, *R. padi* is able to transmit MAV regularly from plants infected with both the RPV and MAV strains. This loss of vector-specificity by MAV is known to be an example of the phenomenon, dependent

transmission, of which there are several types. This one is of the type termed transcapsidation. This is when a virus particle containing nucleic acid of one virus is enclosed in a complete protein coat of a second virus (e.g. MAV nucleic acid in RPV protein coat) during virus replication within the plant. In the plant, such a transcapsidated particle functions like MAV (because of the nucleic acid), but in *R. padi*, it functions like RPV (because of the protein coat).

Transcapsidation enables *R. padi* to transmit MAV indefinitely in the presence of RPV (termed the "helper" virus), whereas *R. padi* transmitting MAV alone is a rare event (Rochow, 1977). This may have several important implications for BYDV epidemiology in Britain. Firstly, *R. padi* may spread MAV in the field in the absence of *S. avenae*. Secondly, mixed infections of BYDV may be characteristics of virus spread by *R. padi*. Thirdly, *R. padi* may be responsible for transmitting MAV to host plants that are not preferred by *S. avenae* or *M. dirhodum*.

Transmission interference is another phenomenon that confuses the vector-specific relationships of BYDV. Fewer *S. avenae* transmitted the PAV strain if they had first acquired MAV, than if they had previously fed on healthy oats or on oats infected with other BYDV strains. Competition between virus isolates for receptors on aphid salivary glands is considered to be the most likely

explanation (Gildow & Rochow, 1980). Thus, unlike *R. padi*, *S. avenae* in the field is associated with a single strain, MAV (Plumb, 1974), because it will select out MAV from mixed BYDV infections.

Transmission efficiency This is the ability of a group of aphids to transmit BYDV from an infected plant to indicator plants. It is determined experimentally in the laboratory and is expressed as the percentage of individuals that transmit BYDV to indicator plants.

Transmission efficiency of BYDV is aphid-specific (Rochow, 1969). Both *R. padi* and *S. avenae* are efficient at transmitting their specific strains whereas PAV is more efficiently transmitted by *R. padi* than *S. avenae* (Rochow, 1969; Plumb, 1974). However, transmission efficiency within an aphid species may depend on the host plant on which the aphid fed: *R. padi* fed on infected ryregrass transmit BYDV less efficiently than from infected oats (Plumb *et al.*, 1982).

The differing BYDV transmission efficiency of aphids feeding on different host plants may have important implications for BYDV epidemiology. The number of viruliferous alatae entering a cereal crop during the autumn may be influenced not only by the total number of alatae, but also by the relative proportions of the different host plants on which these aphids fed. This may be the unspecified thesis of II.

7.2 **Methodology**

Aphids were collected from the field to determine whether or not they contained BYDV and whether or not they could transmit the isolate(s) to an oat seedling. Because it was unknown whether or not these aphids had fed on a BYDV infected plant, transmission efficiency could not be measured. The results of these tests are therefore termed BYDV transmissibility.

Aphids which were tested for BYDV transmissibility were collected from identified plants in four habitats: winter barley crops, grass weeds in winter barley fields, wild grasses in hedge bottoms and farmlanes, and ryegrass pastures. Aphids were normally collected when they were found to be numerous during aphid number assessments, although special visits to the "wild grasses in hedge bottoms" habitat were made solely for aphid collection. Restrictions on the number of aphids collected from one plant were not made, and there was no attempt to collect aphids from all fields or to collect similar numbers from each region. Most individuals were apterous, because apterous aphids were predominant on these host plants.

Raising of indicator plants Oat seedlings were grown in an "insect-free" glasshouse (fine gauze covering all the ventilation windows) to prevent the risk of the plants being infected with BYDV prior to the tests for BYDV transmission. Four oat varieties were used in succession, mainly because further stocks became unobtainable during

the course of the BYDV project: Coast Black, Maris Tabard, Dula and Pennal. One seed per 7.5 cm pot was sown about ten days prior to the BYDV transmission test. From October to March, the glasshouse was heated, and artificial lighting was used to provide conditions of continuous daylight.

The BYDV transmission tests The technique used was based on that described by Hill (1984). On the same day as collection (section 2.1.2), aphids were placed individually with a fine paint brush on oat seedlings at the two or three leaf stage (GS 12-13). The use of conventional plastic plant labels (Rainbow) was found unsatisfactory, because frequent watering of the plants rendered them illegible. Self-adhesive paper labels (Blick) were attached to the side of the 7.5 cm pots, where they were sheltered from watering. The label gave details of the aphid's identity, previous host plant, and place and date of collection. Aphids were confined by use of a transparent lid with gauze vents. Aphids were allowed to feed for three days before the plant was sprayed with Pirimor (ICI, 50% w/w pirimicarb as a water dispersible granule - dilution rate 0.5 g/l). A check was carried out on each of the three days to determine whether the aphid was alive or dead, whether or not it had produced offspring and whether or not it had left the plant. Wandering aphids were returned to the plants.

The plants were grown on in a glasshouse for four to

six weeks and then assessed for yellow or red leaf discolouration. In 1988, only plants showing any yellow or red leaf discolouration were tested for BYDV using ELISA. Subsequently, all plants have been tested.

Analysis A BASIC program was written which stored the details of each aphid tested, and the result of the BYDV transmission test. It enabled the summaries presented in section 7.3 to be quickly produced without errors.

7.3 **Results**

A total of 2271 aphids, of five species, were tested for BYDV transmission from May 1988 to November 1990. Relative numbers tested of each species approximately reflect the relative abundance of the five species in the four habitats because aphid collections for BYDV transmission testing were representative of aphid infestations in the four habitats. Fifty per cent of aphids tested for BYDV transmissibility were *S. avenae* compared with 35, 6, 6 and 4% for *R. padi*, *M. festucae*, *M. dirhodum* and *R. insertum* respectively.

The total numbers of the five aphid species tested for BYDV transmission and the number and percentage which transmitted BYDV in each habitat are shown in Tables 7.1 to 7.5 which pool data from all regions and all three years. The frequency of single BYDV strains and strain mixtures in the oat plants detected by ELISA, which were infected by

aphids collected from the four habitats are shown and a grand total for each aphid species is given.

Annual or seasonal totals of the number of the three most numerous aphid species (*R. padi*, *S. avenae* and *M. dirhodum*), which were tested for BYDV transmission, and the number and percentage which transmitted BYDV, and the percentage of aphids which transmitted each BYDV strain either singly or as part of a strain mixture are shown in Tables 7.6 to 7.9 for each of the four habitats.

Table 7.1 Transmission of BYDV to oat seedlings by *Sitobion avenae* collected from four habitats; 1988-1990.

Habitat	*Sitobion avenae*		No of aphids transmitting BYDV strain or strain mixture to oat seedling						
	No tested	No transmitting BYDV to oats (%)	RPV	PAV	MAV	RP	RM	PM	RPM[a]
Winter barley	600	130 (22)	5 (*14*	7 *13*	106 *115*)	3	6	3	0
Grass weeds in winter barley	211	48 (23)	2 (*8*	4 *10*	32 *40*)	2	4	4	0
Grass weeds in[b] hedge bottoms	156	16 (10)	2 (*3*	2 *3*	10 *12*)	0	1	1	0
Ryegrass pastures	159	24 (15)	6 (*7*	2 *5*	13 *15*)	1	0	2	0
Totals	1126	218 (19)	15 (*32*	15 *31*	161 *182*)	6	11	10	0

a Mixed infections of BYDV strains R = RPV; P = PAV; M = MAV.

b Both *avenae* and *fragariae* were collected.

Italicised figures in brackets are the total numbers of aphids transmitting each BYDV strain alone or as part of a mixture.

Table 7.2 Transmission of BYDV to oat seedlings by *Rhopalosiphum padi* collected from four habitats; 1988-1990.

Habitat	*Rhopalosiphum padi*		No of aphids transmitting BYDV strain or strain mixture to oat seedling						
	No tested	No transmitting BYDV to oats (%)	RPV	PAV	MAV	RP	RM	PM	RPM[a]
Winter barley	330	106 (32)	28 (*60*	28 *59*	16 *33*)	17	3	2	12
Grass weeds in winter barley	17	5 (29)	2 (*3*	0 *0*	2 *3*)	0	1	0	0
Grass weeds in hedge bottoms	60	12 (20)	3 (*7*	3 *5*	2 *4*)	2	2	0	0
Ryegrass pastures	405	151 (37)	71 (*104*	22 *53*	16 *40*)	18	11	9	4
Totals	812	274 (34)	104 (*174*	53 *117*	36 *80*)	37	17	11	16

[a] Mixed infections of BYDV strains R = RPV; P = PAV; M = MAV.

Italicised figures in brackets are number of aphids transmitting a BYDV strain either alone or as part of a mixture.

Table 7.3 Transmission of BYDV to oat seedlings by *Metopolophium dirhodum* collected from four habitats; 1988-1990.

Habitat	*Metopolophium dirhodum*		No of aphids transmitting BYDV strain or strain mixture to oat seedlings						
	No tested	No transmitting BYDV to oats (%)	RPV	PAV	MAV	RP	RM	PM	RPM[a]
Winter barley	48	13 (27)	1 (*2*	1 *2*	10 *10*)	1	0	0	0
Grass weeds in winter barley	13	2 (15)	0	1	1	0	0	0	0
Grass weeds in hedge bottoms	51	11 (22)	0	0	11	0	0	0	0
Ryegrass pastures	13	1 (8)	1	0	0	0	0	0	0
Totals	125	27 (22)	2 (*3*	2 *3*	22 *22*)	1	0	0	0

[a] Mixed infections of BYDV strains R = RPV; P = PAV; M = MAV.

Italicised figures in brackets are number of aphids transmitting a BYDV strain either alone or as part of a mixture.

Table 7.4 Transmission of BYDV to oat seedlings by *Rhopalosiphum insertum* collected from four habitats; 1988-1990.

Habitat	*Rhopalosiphum insertum*		No of aphids transmitting BYDV strain or strain mixture to oat seedling						
	No tested	No transmitting BYDV to oats (%)	RPV	PAV	MAV	RP	RM	PM	RPM[a]
Winter barley	59	9 (17)	2	1	6	0	1	0	0
Ryegrass pastures	28	5 (18)	1	3	0	0	1	0	0
Grass weeds in winter barley	6	1 (17)	0	1	0	0	0	0	0
Ryegrass pastures	28	5 (18)	1	3	0	0	1	0	0
Totals	121	21 (17)	4	8	6	0	3	0	0

[a] Mixed infections of BYDV strains R = RPV; P = PAV; M = MAV.

Table 7.5 Transmission of BYDV to oat seedlings by *Metopolophium festucae* collected from four habitats; 1988-1990.

Habitat	*Metopolophium festucae*		No of aphids transmitting BYDV strain or strain mixture to oat seedling						
	No tested	No transmitting BYDV to oats (%)	RPV	PAV	MAV	RP	RM	PM	RPM[a]
Winter barley	2	0	0	0	0	0	0	0	0
Ryegrass pastures	129	9 (7)	1	2	5	0	1	0	0
Totals	131	9 (7)	1	2	5	0	1	0	0

[a] Mixed infections of BYDV strains R = RPV; P = PAV; M = MAV.

Table 7.6 Transmission of BYDV to oat seedlings by aphids collected from winter barley; 1988-1990.

Season	No tested	No transmitting BYDV to oats (%)	% of aphids which transmitted BYDV strain to an oat seedling		
			RPV	PAV	MAV
R. padi					
Summer 1988	16	0	0	0	0
Autumn 1988	55	14 (26)	18	2	7
Summer 1989	107	36 (34)	18	24	5
Autumn 1989	31	24 (77)	61	32	39
Summer 1990	32	10 (31)	3	25	6
Autumn 1990 (volunteers in stubble fields)	47	16 (34)	11	23	15
Autumn 1990	42	6 (14)	7	7	7
S. avenae					
Summer 1988	39	4 (10)	3	0	8
Autumn 1988	135	6 (5)	1	1	3
Summer 1989	287	75 (26)	4	4	22
Autumn 1989	15	8 (53)	0	0	53
Summer 1990	75	23 (31)	0	1	31
Autumn 1990 (volunteers in stubble fields)	9	5 (56)	0	0	56
Autumn 1990	40	9 (23)	0	0	23
M. dirhodum					
Summer 1988	10	2 (20)	10	0	10
Summer 1989	34	11 (32)	3	6	27
Summer 1990	4	0	0	0	0

Table 7.7 Transmission of BYDV to oat seedlings by aphids collected from grass weeds (mostly *Poa annua*) in winter barley fields; 1988-1990.

Season	No tested	No transmitting BYDV to oats (%)	% of aphids which transmitted BYDV strain to an oat seedling		
			RPV	PAV	MAV
R. padi					
Summer 1989	4	1 (25)	25	0	0
Autumn 1989	9	4 (44)	22	0	33
Summer 1990	4	0	0	0	0
S. avenae					
Summer 1989	77	17 (22)	3	8	14
Autumn 1989	9	7 (78)	56	0	67
Summer 1990	112	21 (19)	0	4	19
Autumn 1990	13	3 (23)	8	0	15
M. dirhodum					
Summer 1989	3	0	0	0	0
Summer 1990	10	1 (10)	0	10	10

Table 7.8 Transmission of BYDV to oat seedlings by aphids collected from four species of wild grasses in hedge bottoms at two farms in Ayrshire; summer 1990.

Season	No tested	No transmitting BYDV to oats (%)	% of aphids which transmitted BYDV strain to an oat seedling		
			RPV	PAV	MAV
R. padi					
A. pratensis	1	0	0	0	0
D. glomerata	26	0	0	0	0
P. annua	33	12 (36)	21	15	12
S. avenae					
A. pratensis	13	0	0	0	0
D. glomerata	41	4 (10)	2	2	7
H. lanatus	51	3 (6)	0	2	4
P. annua	51	9 (18)	4	2	14
M. dirhodum					
A. pratensis	3	0	0	0	0
D. glomerata	4	0	0	0	0
P. annua	44	11 (25)	0	0	25

Table 7.9 Transmission of BYDV to oat seedlings by aphids collected from ryegrass pastures; 1988-1990.

Season	No tested	No transmitting BYDV to oats (%)	% of aphids which transmitted BYDV strain to an oat seedling		
			RPV	PAV	MAV
R.padi					
Summer and autumn 1988	213	66 (31)	26	8	1
Summer and autumn 1989	61	36 (59)	36	20	25
Summer and autumn 1990	131	49 (37)	21	18	16
S. avenae					
Summer and autumn 1988	75	7 (9)	8	1	1
Summer and autumn 1989	23	8 (35)	4	13	22
Summer and autumn 1990	61	9 (15)	0	3	15
M. dirhodum					
Summer and autumn 1988	8	0	0	0	0
Summer and autumn 1989	3	1 (33)	33	0	0
Summer and autumn 1990	2	0	0	0	0

In all habitats except ryegrass pasture, *S. avenae* was the most numerous aphid. Compared with the other aphid species, *S. avenae* abundance was at a population level at which it was evident during habitat sampling for a greater part of the year. This factor contributed to the larger number of *S. avenae* collected. In ryegrass pasture, *R. padi* was the most numerous species although it was highly seasonal.

Chi-squared tests compared the BYDV transmissibility of aphids between species, within species and between habitats, and within species and habitats and between years (Table 7.10). The frequency of single BYDV strains and strain mixtures in the oat plants infected by aphids differed significantly ($P < 0.001$) between *R. padi* and *S. avenae*. *R. padi* transmitted RPV alone most frequently although strain mixtures were transmitted by 31% of BYDV transmitting aphids. No other aphid species transmitted all three strains together. In contrast, *S. avenae* transmitted MAV alone most frequently and strain mixtures were transmitted by 13% of BYDV transmitting aphids. *M. dirhodum* and *M. festucae* were similar to *S. avenae* in mostly transmitting the MAV strain alone, with 81 and 55% of BYDV transmitting aphids respectively transmitting this strain alone. A Chi-squared test comparing the transmission of all three strains (either alone or as part of a mixture of strains) by *S. avenae* with *Metopolophium* spp. gave a non-significant result. *R. insertum* (based on a

sample size of 121) transmitted all three strains fairly equally.

Differences in the transmission of any BYDV strain between habitats within species were tested, for *R. padi*, *S. avenae* and *M. dirhodum*. BYDV transmission by *R. padi* did not differ between habitats but the test for *S. avenae* was significant at the 1% level. This result was due to the lower number of aphids which transmitted BYDV relative to the number of aphids that did not, in the "grass weeds in hedge bottoms" habitat. When data from this habitat were excluded, a non-significant result was obtained. BYDV transmission by *M. dirhodum* also did not differ between habitats.

The "wild grasses in hedge bottoms" habitat was sub-divided into its constituent species and within aphid species between grass weed species differences in transmission of any BYDV strain were tested, for *R. padi* and *S. avenae*. There was a significant difference in the transmissibility of *R. padi* on *D. glomerata* and *P. annua* due to the absence of BYDV transmission on the former grass weed (this being notable for a sample of 26 *R. padi*). For *S. avenae*, the test comparing the transmission of any BYDV strain on three of the grass weed species gave a non-significant result.

Table 7.10 Results of Chi-squared tests to compare the BYDV transmissibility of aphids between species, within species and between habitats, and within species and habitats and between years.

Null hypotheses	
BYDV transmissibility[a] of aphids does not differ between *R. padi* and *S. avenae*.	$x^2_{(6)} = 205$ P < 0.001
BYDV transmissibility[b] of aphids does not differ between *R. padi* and *M. dirhodum*.	$x^2_{(2)} = 50.4$ P < 0.001
BYDV transmissibility[b] of aphids does not differ between *S. avenae* and *Metopolophium* spp.	$x^2_{(2)} = 0.3$ N.S[d]
BYDV transmissibility[c] of *R. padi* does not differ between the four habitats.	$x^2_{(3)} = 7.2$ N.S.
BYDV transmissibility[c] of *S. avenae* does not differ between the four habitats.	$x^2_{(3)} = 13.7$ P < 0.01
Same test for *S. avenae* excluding wild grasses habitat.	$x^2_{(2)} = 3.9$ N.S.
BYDV transmissibility[c] of *M. dirhodum* does not differ between the three habitats (ryegrass pastures and grass weeds in winter barley were pooled).	$x^2_{(2)} = 3.9$ N.S.
The ratio of the RPV:PAV:MAV strains transmitted by *R. padi* does not differ between the three habitats (grass weeds in winter barley and grass weeds in hedge bottoms were pooled).	$x^2_{(2)} = 7.1$ P < 0.05

Table 7.10 continued.

The ratio of the RPV+PAV strains to the MAV strain transmitted by *R. padi* does not differ between the winter barley and ryegrass pasture habitats.	$x^2_{(1)} = 0.1$	N.S.
The ratio of the RPV:PAV:MAV strains transmitted by *S. avenae* does not differ between the three habitats (grass weeds in winter barley and grass weeds in hedge bottoms were pooled).	$x^2_{(2)} = 4.6$	N.S.
BYDV transmissibility[c] of *R. padi* collected from winter barley does not differ between the three years (data from summer and autumn of each calendar year were pooled).	$x^2_{(2)} = 15.0$	P < 0.00:
BYDV transmissibility[c] of *S. avenae* collected from winter barley does not differ between the three years (data from summer and autumn of each calendar year were pooled).	$x^2_{(2)} = 36.9$	P < 0.001
BYDV transmissibility[c] of *S. avenae* collected from grass weeds in winter barley fields does not differ between 1989 and 1990 (data from summer and autumn of each calendar year were pooled).	$x^2_{(1)} = 2.2$ using Yates' correction	N.S.
BYDV transmissibility[c] of *R. padi* collected from *D. glomerata* and *P. annua* does not differ.	$x^2_{(1)} = 11.8$	P < 0.001
BYDV transmissibility[c] of *S. avenae* collected from *D. glomerata* *H. lanatus* and *P. annua* does not differ.	$x^2_{(2)} = 3.7$	N.S.[e]

Table 7.10 continued.

BYDV transmissibility[c] of *R. padi* collected from ryegrass pastures does not differ between three years.	$x^2_{(2)} = 15.9$	$P < 0.001$
BYDV transmissibility[c] of *S. avenae* collected from ryegrass pastures does not differ between three years.	$x^2_{(2)} = 0.9$	N.S.

[a] no of aphids transmitting each BYDV strain alone and strain mixtures to oat seedling.

[b] no of aphids transmitting each BYDV strain, either alone or as part of a mixture.

[c] number of aphids transmitting BYDV compared with number not transmitting BYDV.

[d] Two expecteds marginally less than five, 4.58 and 4.71 but total Chi-square value is very low.

[e] Expected for number of infective *S. avenae* on *D. glomerata* was slightly less than five (4.6) but total Chi-square value was 1.3 less than the P = 0.05 figure.

Differences in the transmission of the three BYDV strains between habitats within species were tested, for *R. padi* and *S. avenae*. The test for *R. padi* was significant at the 5% level, due to the dissimilar transmission of the RPV and PAV strains in ryegrass pastures. In the other habitats, there was similar transmission of the RPV and PAV strains. Another test for *R. padi* comparing transmission of the RPV+PAV strains with the MAV strain in ryegrass

pastures and winter barley gave a non-significant result. Transmission of the three BYDV strains did not differ between habitats for *S. avenae*.

Differences in the transmission of any BYDV strain between years within species and habitats were tested, for *R. padi* and *S. avenae*. In winter barley, significant differences were found between the number of aphids transmitting any BYDV strain and the total number of aphids not transmitting BYDV for both species. This was because in 1988, there were fewer aphids which transmitted BYDV.

Only *S. avenae* was common on grass weeds in winter barley fields, and the test for differences in BYDV transmission of any strain between years gave a non-significant result.

In ryegrass pastures, significant between years differences in the transmission of any BYDV strain were found for *R. padi*, due to the relatively high number which transmitted BYDV in 1989. The test for *S. avenae* was non-significant.

A feature of these aphid BYDV transmissibility data is that percentage BYDV transmission exceeding 50% was confined to sample sizes below 100 tested aphids, whereas the maximum percentage for sample sizes above 100 aphids tested was 37% (e.g. see Table 7.9, *R. padi* in ryegrass pastures).

7.4 Discussion

The randomness of the collection methodology and the ignorance of BYDV infection status of the host plants confer an unknown degree of variability to the data. Although general BYDV infection of ryegrass pasture may not have changed between years, it is known that the BYDV infection of winter barley and *P. annua* in winter barley fields does change between years and within regions in the same year (Chapter 4). So although the strains transmitted by, and the transmission efficiency of an aphid species on a certain host plant are to some extent predictable, a collection of aphids of a species from the field have an unpredictable status of BYDV transmission.

These facts may explain why percentage BYDV transmission exceeding 50% was confined to sample sizes below 100 tested aphids whereas the maximum percentage for sample sizes above 100 aphids tested was 37%. This suggests that the percentage BYDV transmission values obtained for groups of less than 100 aphids should be regarded with suspicion.

Vector relationships Twenty-two, 15 and 10% of field-collected *R. padi* transmitted the RPV, PAV and MAV strains respectively, to oat seedlings. The comparative figures for *S. avenae* and *M. dirhodum* were 3, 3 and 16%, and, 2, 2 and 18% respectively. These data are consistent with the vector relationships outlined in section 7.1. The percentage transmission is, of course, much lower than those obtained

when transmission efficiency is measured in the laboratory, because not all aphids feed on BYDV infected plants in the field. For example, Plumb (1974) found that the B strain (which reacts to both RPV & PAV isolates) was transmitted by *R. padi* with an efficiency of 87% whereas *S. avenae* transmitted the F strain (which reacts to both PAV & MAV isolates) with an efficiency of 96%.

The transmission of all three strains simultaneously by 16 *R. padi*, and the transmission of strain mixtures by 31% of BYDV transmitting *R. padi* suggests that transcapsidation is common in BYDV infected plants in the field.

The transmission of PAV by 15% of field-collected *R. padi* compared with 3% of *S. avenae* might suggest that for the latter species, transmission interference of PAV by MAV is occurring (clearly, PAV is present in the field).

Transmission differences between habitats For *R. padi*, a difference in the transmission of the RPV and PAV strains was found between habitats. In all three years of aphid collections from ryegrass pasture, transmission of RPV was more common than that of PAV, whereas in winter barley, there was no consistent trend. Both these strains are termed "severe" (Plumb, 1974), therefore infection of winter barley by either strain is a matter of concern. However, in winter barley crops in general (Chapter 4), PAV

was much more common in the leaf samples than RPV. This might indicate that ryegrass pasture is not the main source of *R. padi* entering the crops in the autumn. However, most *Rhopalosiphum* in crops during the autumns were alate *insertum* (Chapter 4).

Ten per cent of *S. avenae* collected from the "wild grasses in hedge bottoms" habitat transmitted BYDV, compared with 22 and 23% in winter barley and grass weeds in winter barley fields respectively (Table 7.1). Of the four species of grass from which *S. avenae* was collected (Table 7.8), the highest percentage BYDV transmission was found for individuals collected from *P. annua*. This figure of 18% is closer to the 23% infectivity of *S. avenae* collected from grass weeds in winter barley fields, which were mainly *P. annua*. Grasses are regarded as being poor sources of BYDV relative to cereals (Plumb *et al.*, 1982), but *P. annua* appears to be an exception (Table 7.8).

For *R. padi* too, a lower percentage (20%) of individuals collected from the "wild grasses in hedge bottoms" habitat transmitted BYDV relative to individuals collected from winter barley (32%), grass weeds in winter barley fields (29%) and ryegrass pastures (37%). Thirty-six per cent of the *R. padi* collected from *P. annua* transmitted BYDV compared with 0% of individuals from *D. glomerata*. Twenty of the *R. padi* collected from *D. glomerata* were from the leaves and stems of one plant. ELISA tests for BYDV on leaf samples from this plant indicated that it was BYDV

infected. *R. padi* was rare on *D. glomerata* during the summer of 1990 (section 6.3.1), so although 100% of *D. glomerata* were BYDV infected (section 6.3.2), the scarcity of the aphid on this plant, and its inability to transmit BYDV from it, might indicate that *D. glomerata* is not important to *R. padi*-transmitted BYDV epidemiology in autumn-sown cereals.

Transmission differences between years For *R. padi*, there was a significant difference in BYDV transmissibility between years in both winter barley and ryegrass pastures (data from summer and autumn in each calendar year pooled). The highest percentage BYDV transmissions in both winter barley and ryegrass pasture were found in 1989 with 43 and 59% respectively. In 1988 and 1990, the comparative figures were 20 and 31%, and, 26 and 37%, respectively. Except in winter barley in 1988 (71), and in ryegrass pasture in 1989 (61), the sample sizes exceeded 100 aphids. Given that the percentage transmission was always highest in ryegrass pasture, there is some evidence that the percentage of field-collected *R. padi* that transmits BYDV does vary between years.

For *S. avenae* collected from winter barley, there were significant differences in BYDV transmission between years, but not for aphids collected from ryegrass pasture (all samples in ryegrass pasture were below 100 aphids). The percentage of aphids collected from winter barley that

transmitted BYDV (data from summer and autumn pooled) increased from 6% in 1988, to 27% in 1989 to 30% in 1990. The higher percentages of 1989 and 1990 were associated with large numbers of *S. avenae* in winter barley crops during the spring, following the milder winters of 1988/89 and 1989/90. Therefore, there was extensive infection of most crops with the MAV strain in the spring of 1989, and some crops in 1990 (Chapter 4) which would have increased the likelihood of an individual *S. avenae* feeding on an infected barley plant, and therefore of the collection of an infective *S. avenae* in those years. A similar phenomenon was found in the USA. It was concluded that in years when aphid infestations and incidence of BYDV in cereals were low, the percentages of aphids that transmitted BYDV were also low, and *vice versa* (Kieckhefer & Stoner, 1967).

S. avenae reaches its highest densities on cereals (Hand, 1989) and it reaches outbreak numbers on winter wheat in some summers in England (George & Gair, 1979). The percentages of *S. avenae* that transmitted BYDV in the autumns of 1989 and 1990 were also greater than those of 1988. Although the cereal crop is absent between cereal harvest in late summer and the next barley crops emerging during the autumn, barley volunteers and grass weeds are often present in cereal stubble fields. The maintenance of the high percentages of *S. avenae* that transmitted BYDV, during the autumns of 1989 and 1990 perhaps indicates that *S. avenae* infestations on grass weeds or volunteers

infected with MAV, in adjacent stubble fields, or on untreated ploughed-in stubbles, are the major source of *S. avenae* that infest barley during the autumn.

Only *S. avenae* was present in large numbers on grass weeds (mostly *P. annua*) in winter barley fields during the summers of 1989 and 1990. In both years, approximately 20% transmitted BYDV, compared with 26 and 31% of *S. avenae* collected from winter barley in 1989 and 1990 respectively.

CHAPTER EIGHT

Pre-harvest sampling: a method of measuring the risk of BYDV to autumn-sown cereals posed by local aphids

8.1 Introduction

8.1.1 Aphid migration and dispersal

An important feature of insect lifecycles is the migratory flight made by most winged insects during the first part of their adult life, prior to mating and breeding. This serves to transfer the next generation of the insect population to a new breeding ground. Migration has perhaps become an integral part of the life of adult insects for two main reasons. Firstly, the adults may only live for a few days, and a migratory flight at the beginning of their adult life enables them to find a new breeding ground quickly. Secondly, the breeding ground of many insects is ephemeral, thus a population is doomed to extinction unless it leaves (Johnson, 1969).

Although insect migration has no strict definition, migratory aphids are generally regarded as holocyclic species that alternate between primary host plants on which they overwinter as eggs and secondary host plants on which they reproduce parthenogenetically in summer. In these species, there is a mass movement of alate individuals at one time, in response to an environmental variable such as shortening daylength (Johnson, 1969).

Less dramatic movements of alate aphid populations also occur which are a result of the actions of individual or groups of aphids to different and more localized environmental stimuli, such as a crowded or desiccated foodplant. If the aphid ignores stimuli such as a new host

plants or oviposition sites for a period of time after flying from its original host plant, then the aphid is said to migrate. Alternatively, if it is sensitive to such stimuli throughout its flight, it is said to disperse.

All these movements can result in new host plants being colonised, but with migration, the distance between the old and new host plants may be great (many kilometres). In contrast, a dispersing aphid may theoretically settle on the first host plant it lands on (Johnson, 1969).

In North America, cereal aphid migrations of hundreds of kilometres have been recorded in association with strong winds which persist in the same direction in a region for several days (Johnson, 1969). In Britain, frequent wind direction changes are characteristic of the weather and the cool summer nights prevent aphid flight (Taylor, 1963). Each days aerial aphid fauna is considered to be composed of different individuals, and migrations of hundreds of kilometres are not thought to occur (Johnson, 1969; Vickerman & Wratten, 1979).

However, the RIS data show that at certain times of year, large numbers of cereal aphids may be found at 12.2 m (Taylor, 1982), suggesting that long distance flight, at least exceeding the boundaries of individual farms, might occur. Nevertheless, this does not necessarily imply that most cereal aphids that colonise autumn-sown cereals come from distant sources.

Vickerman and Wratten (1979) stated that it was unkown whether alatae that colonise cereals in summer have migrated long distances or have moved from more local sources such as hedgerows. In the epidemiology of the virus diseases of sugar beet and potato (sections 1.5 & 1.6), local, not distant sources of viruliferous aphids were found to be important.

Each suction trap is intended to sample the aerial aphid fauna above wide tracts of land, many kilometres across (Taylor, 1973). Crop colonisation not monitored by suction traps was encountered during the suction trap validation exercise described in section 1.7, when *M. dirhodum* probably dispersed from local overwintering sources (Taylor, 1973).

S. avenae is another aphid which may disperse locally rather than migrate long distances. The numbers of *S. avenae* in suction trap samples in autumn are usually much smaller than those of *R. padi* (Tatchell *et al.*, 1988) which are mainly comprised of the gynoparae and males that are seeking *P. padus*. The 12.2 m suction traps are efficient at monitoring aphid migrations such as the autumn *R. padi* migration of males and gynoparae to *Prunus padus*, because these morphs fly at a relatively high altitude. However, in crop samples, the differences in the total numbers of these two species are much less (Tatchell *et al.*, 1988) indicating that *S. avenae* may fly locally. In south-west

and central Scotland (Chapter 4), *S. avenae* was more common than *R. padi* in winter barley crops from 1988 to 1990, although the reverse was true in the suction traps.

8.1.2 **Natural enemies of cereal aphids**

Natural enemies are one of a number of biotic factors that control cereal aphid populations in cereals and grassland (Dixon, 1973). They have been studied in cereal fields during the spring and early summer to assess their role in determining whether or not *M. dirhodum* or *S. avenae* achieve population levels that can cause direct damage (Dean, 1974b; Chambers *et al.*, 1983; Holmes, 1984). They can be divided into three main groups: aphid-specific predators, polyphagous predators and aphid parasitoids.

Aphid-specific predators Aphids are the only, or a major component in the diet of these predators in at least one stage of the predator's lifecycle.

Coccinellids or ladybirds (Coleoptera: Coccinellidae) are the most evident members of this group, and *Coccinella 7-punctata* (L.), commonly known as the seven spot ladybird, is largely responsible for this high profile. *C. 7-punctata* is most prevalent in years when *S. avenae* and *M. dirhodum* are sufficiently numerous to cause direct damage to cereals in England and its abundance has caused annoyance to holidaymakers on the east coast of England (Heathcote, 1978). There are two other species whose habitats are described as diverse and so may include cereal fields

(Majerus and Kearns, 1989) and whose distribution was found to include south-west and central Scotland in the Coccinellidae Distribution Mapping Scheme 1984-89 (Majerus *et al.*, 1990): *Adalia 2-punctata* (L.) and *Propylea 14-punctata* (L.).

Adult and larval ladybirds feed on aphids, both stages having a voracious appetite. For example, Rautapaa (1976) found that *C. 7-punctata* (a large species) adults consumed on average 48.2 *R. padi* and *S. avenae* a day and larvae 71.7 aphids per day between the second and eighth day after hatching. However, this species will only settle in crops when aphid densities reach $10/m^2$, and begin to develop eggs at aphid densities of 1 per 200-400 cm^2 of leaf area (Honek, 1980). As a result, coccinellids are only abundant in cereals in years when cereal aphids are numerous in cereals during the spring (Heathcote, 1978). Therefore, it is unlikely that ladybirds prevent aphid outbreaks on cereals in summer. Nevertheless, they can be very important and effective at reducing aphid numbers after the population has peaked (Holmes, 1984).

Holmes (1984) studied the predation of *S. avenae* in two years (1981 and 1982) when coccinellids were not numerous, and evidence was found that syrphids and *Tachyporus* larvae were keeping the aphid populations in check.

Syrphids or hoverflies (Diptera: Syrphidae), of the

sub-family Syrphinae are aphidophagous in the larval stage and may eat up to 1200 aphids during the course of their development. They feed mainly at night, hiding in leaf axils or at the base of plants during the day, and this has probably resulted in their role being underestimated (Vickerman and Wratten, 1979; Holmes 1984). In contrast, syrphid adults feed on nectar and pollen (Gilbert, 1986) and the females must feed on pollen prior to egglaying, and may obtain this from the crop, weeds within the crop or weeds in hedge bottoms. They can retain their eggs for several weeks if aphids are not present, and may lay eggs when aphid densities are as low as 0.4 to 0.5 per tiller (Chambers, 1987). Syrphid lifecycles are shorter than those of ladybirds (Holmes, 1984) and there may be several generations per year (Gilbert, 1986). All these factors suggest that syrphids could be more important natural enemies of cereal aphids than coccinellids, not least because the adults may usually be present in the crop prior to aphid immigration in the summer (Holmes, 1984).

Another group of aphid-specific predators are chrysopids or lacewings (Neuroptera: Chrysopidae). Several studies in southern England revealed the presence of these predators in cereal fields in summer but their role as natural enemies is not considered to be important (Dean, 1974b; Holmes, 1984; Chambers *et al.*, 1983; Chambers *et al.*, 1986).

Polyphagous predators Aphids are one invertebrate component in the diet of these predators, although they may be the major food when aphid populations are large.

Although a range of polyphagous predators such as beetles (Coleoptera), earwigs (Dermaptera), harvestmen (Opiliones), mites (Acari) and spiders (Araneida), are known to feed on aphids (Sunderland and Vickerman, 1980), studies have generally identified beetles as being most important (Dean, 1974b; Sunderland, 1975; Vickerman and Sunderland, 1975; Chambers *et al.*, 1983). Species of Cantharidae, Carabidae and Staphylinidae can be found in cereal fields, they are predatory both as larvae and adults and they are able to climb barley plants (Sunderland and Vickerman, 1980; Holmes, 1984).

Feeney (1984) using pitfall traps, investigated the beetle fauna of cereal fields in Ireland from 1979-83. It was found that not only were some species of carabids and staphylinids numerous, but that different species were most abundant in the autumn and winter compared with the spring and summer. Some species were trapped in numbers throughout the winter. Several studies have revealed that *Tachyporus* species (Staphylinidae) are abundant in cereal fields (Feeney, 1984; Holmes, 1984; Vickerman and Sunderland, 1975) and that they feed on aphids (Sunderland, 1975; Sunderland and Vickerman, 1980).

Sunderland and Vickerman (1980) dissected the guts of

12,000 predators collected from winter wheat fields from May to September 1972-77. They found that when species were considered separately, the proportion containing aphid remains increased with aphid density, although there was no relationship between the amount of aphid feeding (all species) and aphid density in different years.

Aphid parasitoids These are parasites (Hymenoptera: Braconidae) whose larval stages feed on the internal tissues of aphids. They are capable of host-seeking during the winter months, and so can parasitise overwintering populations of anholocyclic aphids in cereals during mild winters (Chambers *et al.*, 1986). Dean (1974b) concluded that parasitoids may be more important than predators at controlling cereal aphid populations, because their short lifecycle means that they are more likely to synchronise with the aphids.

Later studies have revealed that in early autumn-sown cereal crops where aphids overwinter, parasitoids appeared to significantly reduce aphid numbers in the following spring (Chambers *et al.*, 1986). However, in the more usual situation when aphids migrate into and infest cereal crops during the spring, little parasitism was detected until after the aphid population had peaked. This suggests that parasitoids do not normally play a significant role in controlling the growth of aphid populations in the spring (Chambers *et al.*, 1983).

Field work has shown that the parasites that attack cereal aphids are mainly *Aphidius* spp. which are able to parasitise *M. dirhodum*, *R. padi* and *S. avenae* (Dean, 1974b; Vickerman, 1982; Chambers *et al.*, 1983). Adult parasitoids are highly mobile, being caught in the 12.2 m suction traps (Dean, 1974a). Vickerman (1982) in a study from 1972-79, found a positive relationship between the number of adult parasitoids in winter wheat fields in June with the number in nearby grass fields in the preceding month.

The population dynamics of aphid parasitoids are complicated by hyperparasites whose larvae parasitise the parasitoid larvae (Dixon, 1973). Dean (1974b) found hyperasites to be more numerous than parasitoids, and Carter *et al.* (1980) discovered that hyperparasitism to be significant in late summer, probably reducing the effectiveness of parasitoids as natural enemies of cereal aphids.

8.1.3 **The theories behind pre-harvest sampling**

Methods of measuring the risk to autumn-sown cereals from local aphids have not been developed, but the importance of more local sources of viruliferous aphids to BYDV epidemiology is increasingly suspected (Carter, 1984; Kendall *et al.*, 1988; McGrath & Bale, 1990; Tatchell *et al.*, 1988; Irwin & Thresh, 1990).

Pre-harvest sampling was devised as a method of

measuring the potential transfer of BYDV inoculum by local aphids from the winter barley crops of one season to the crops of the next in the same region. Sampling on a regional basis is required because advisory experience has shown that BYDV risk differs between regions of south-west and central Scotland.

The importance of weeds as reservoirs of plant viruses is well known (van Emden, 1965; Thresh, 1981). Both *R. padi* and *S. avenae* are able to reproduce on a wide range of wild grasses (Smith *et al.*, 1984b) which can harbour BYDV (Oswald and Houston, 1953; Kurppa *et al.* 1989). Therefore, the extent of grass weed infestation of winter barley fields in July could influence the amount of BYDV inoculum and the number of aphids present on a farm in July and later in the year. *Poa annua* (L.) is a common grass weed in cereal fields and on disturbed land characteristic of farms (Hubbard, 1968; Chancellor & Froud Williams, 1984). Laboratory work has shown this grass to be a good host plant for both *R. padi* and *S. avenae* (Smith *et al.*, 1984b). It was observed during the course of field sampling (Chapter 4) that *P. annua* was the commonest grass weed in winter barley fields of south-west and central Scotland, sometimes infesting entire fields. The only other grass weed species commonly encountered was *Lolium perenne*, but this was much less abundant. Because of this, it was decided that an assessment of the extent of infestation of winter barley fields with *P. annua* gave a good assessment

of the extent of grass weed infestation in winter barley fields.

The abundance of *P. annua* in winter barley fields enabled the extent of infection by each of the three BYDV strains to be measured in both barley leaves and *P. annua*. A relationship between the BYDV infection of these two types of plant material was tested.

Aphid species incidence was assessed by examining both leaves/stems and infloresences of barley plants and *P. annua*. Cereal aphids are not usually common in Scotland (Sparrow, 1974), therefore a thorough examination of a set number of plants would normally yield zero aphids unless a large number of plants were examined. In this situation, an assessment made by cursory examinations of hundreds of plants during a circuit of a field is more likely to yield aphids. The strains transmitted by field-collected aphids were assessed by removing aphids to the laboratory and performing BYDV transmission tests.

The studies of natural enemies of cereal aphids undertaken in southern England were concerned with assessing their importance in controlling aphid population growth on cereals during the summer. The importance of natural enemies to BYDV infection of autumn-sown cereals may be twofold. Firstly, they may affect the survival on, or prevent the colonisation of, grass weeds and/or volunteers in stubble fields by cereal aphids during the

summer, thereby influencing the amount of BYDV inoculum and the number of aphids, both above and below ground, on a farm during the autumn when winter barley emerges. Secondly, they may affect the extent of colonisation and subsequent survival of cereal aphids in winter barley during the autumn.

Sparrow (1974) during a study of spring cereals in Scotland from 1969-72 when aphid numbers were small, observed few polyphagous predators, isolated syrphid larvae, and parasitism at a low level. Because pre-harvest sampling involved only one visit to each field, pitfall trapping to assess predator incidence and abundance was not an option. Furthermore, because cereal aphids are seldom abundant in Scottish cereals, the natural enemies that vary most between years are probably those that are associated with large aphid populations on Scottish cereals in the summer: ladybirds (*C. 7-punctata*) and parasitoids. The assessments aimed to determine whether or not these two types of natural enemy were active in a region rather than to obtain an accurate estimate of their abundance.

Both *C. 7-punctata* adults and larvae are conspicuous and can be assessed in the field. As with aphids, a cursory assessment of hundreds of plants during a circuit of each field is more likely to detect an animal than the thorough examination of a set number of plants.

There are several different methods of assessing

percentage aphid parasitism by parasitoids (Dean, 1974b). However, because the purpose is to assess the presence/absence of parasitoids rather than to obtain an accurate estimate of the percentage parasitism, it was decided that the observation of aphid mummies (either eclosed or uneclosed) on plants would probably be satisfactory.

8.1.4 **The aims of pre-harvest sampling**

BYDV infection of winter barley crops may be the result of virus spread by apterae moving from ploughed-in grass/grass weeds/volunteers, and by alatae flying long-distance, and by alatae flying from local host plants (Irwin & Thresh, 1990). For local aphids, the BYDV infection in the barley leaves and grass weeds of the previous season's winter barley acreage could be important, either as ploughed-in weeds and volunteers leading to direct transfer via the "green bridge", or in the form of adjacent stubble fields from which alate aphids may disperse locally. By assessing the abundance of *P. annua*, ladybirds and aphid parasitoids, the importance of these factors in determining the abundance of local aphids in a region in late summer and early autumn might be determined.

In this Chapter, the pre-harvest sampling data are analysed to determine the relative importance of local and migrating aphids in introducing BYDV into crops in the autumns of 1989 and 1990, and to assess the efficiency of the methodology used in achieving its objectives.

8.2 **Pre-harvest sampling methodology**

Sampling took place during the first half of July in both 1989 and 1990. This time of year was selected for pre-harvest sampling, because it is late enough for aphids to have colonised cereals, but not so late that green barley leaves are unobtainable. Sampling in three fields per region was considered sufficient to give a regional measurement. There were three criteria for field selection. Firstly, the crop should have or be suspected of having, a degree of BYDV infection, thereby ensuring that samples of BYDV in a region are obtained. Secondly, selected fields should be widely separated, so that the sample is representative of the region. Thirdly, the previous cropping of the field should not have been a grass ley, because of the associated high risk of *R. padi* transmitted BYDV.

During a circuit of each field using tramlines, seven assessments were made. No more than two barley leaf or *P. annua* samples (one from each headland) were taken from headlands. These samples were taken from a swath one metre either side of the tramlines.

1) **BYDV strain incidence in barley leaf samples.** In 1989, 50 leaves which were at least partly green were collected, and tested for BYDV by ELISA (Mortar and Pestle method) in five batches of ten. In 1990, ten single leaves, at least partly green, were collected and tested for BYDV by ELISA (Seam-roller method).

2) **BYDV strain incidence in** *P. annua*. Ten well-established *P. annua* plants were collected from tramlines and tested for BYDV by ELISA (Mortar and Pestle method).

3) **Transmissibility of aphids on cereals.** Ten aphids that were representative of aphid infestations on barley plants were collected (section 2.1.2) and tested for BYDV transmission (section 7.2).

4) **Transmissibility of aphids on** *P. annua* **and/or other grasses.** Ten aphids that were representative of aphid infestations on grass weeds were collected (section 2.1.2) and tested for BYDV transmission (section 7.2).

5) **Extent of infestation by** *P. annua* **and/or other grasses.** After a visual assessment of grass weed infestation, the field was allocated to one of three categories:

Category 1:- Scattered plants in tramlines.

Category 2:- Appreciable proportion of tramlines infested (at least 1-5%).

Category 3:- Extensive areas of field infested.

6) **Abundance of ladybirds.** After a visual estimate of the abundance of ladybird larvae and/or adults, the field was allocated to one of three categories:

Category 1:- No ladybirds.

Category 2:- Few ladybirds.

Category 3:- Many ladybirds.

7) **Abundance of aphid parasitoids.** After a visual estimate of the abundance of aphid mummies, the field was allocated to one of three categories:

Category 1:- No aphid mummies.

Category 2:- Few aphid mummies.

Category 3:- Many aphid mummies.

8.3 Results

8.3.1 Pre-harvest sampling results 1989

Data were collected in 14 winter barley crops in five regions of the west of Scotland from 11 to 24 July 1989. In Ayrshire, two fields were sampled, in other regions three fields. Tables 8.1 to 8.5 show the results for each assessment on a regional basis.

Assessments 1 and 2 BYDV in barley leaves and *P. annua*

All three BYDV strains were present in the barley leaf samples of Dumfriesshire, Wigtownshire, Ayrshire and Stirlingshire (Table 8.1), and were common in the *P. annua* samples of Dumfriesshire, Wigtownshire and Ayrshire (Table 8.2).

Table 8.1 Assessment 1; number of barley leaf samples infected with each BYDV strain in each region; July 1989.

Region	No of samples		No of positive ELISA tests for BYDV strain RPV	PAV	MAV
Dumfriesshire	15		2	1	8
Wigtownshire	5		2	5	2
Ayrshire	10		3	6	6
Renfrewshire	10		0	0	7
Stirlingshire	15		2	1	8
Totals	55		9	13	31
		%	16	24	56

Table 8.2 Assessment 2; number of *Poa annua* infected with each BYDV strain in each region; July 1989.

Region	No of samples		No of positive ELISA tests for BYDV strain RPV	PAV	MAV
Dumfriesshire	25		12	14	25
Wigtownshire	29		21	24	9
Ayrshire	19		10	11	6
Renfrewshire	29		0	3	22
Stirlingshire	30		1	5	19
Totals	132		44	57	81
		%	33	43	61

Test of $\beta = 0$ $t = 3.53$, df 13, $P < 0.01$

Test of $\beta = 1$ $t = -1.38$, df 13, N.S.

$$y = 0.719x + 4.521$$

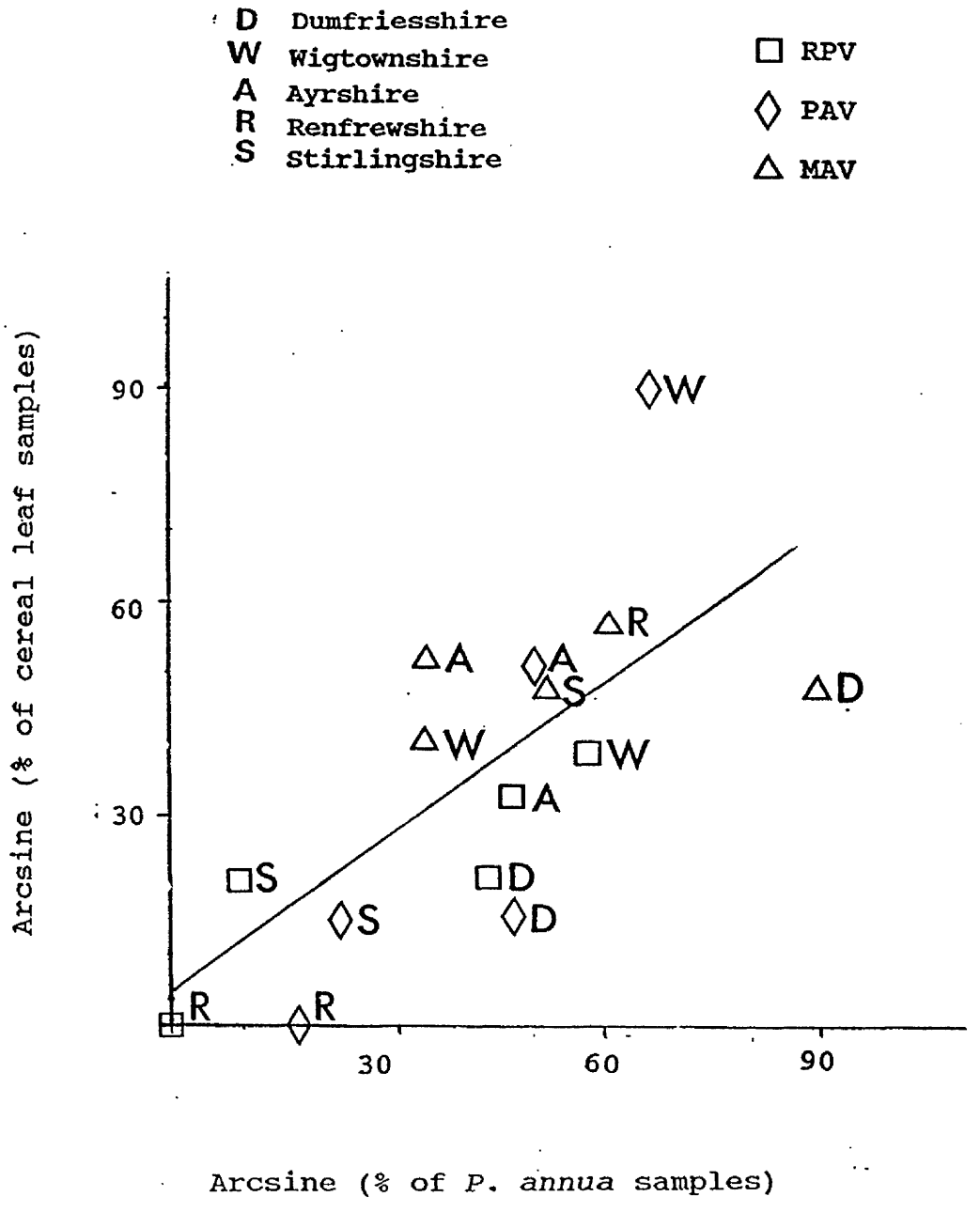


Figure 8.1 Relationship between the arcsine (% of cereal leaf samples) and arcsine (% of *Poa annua* samples) infected with each strain of BYDV; pre-harvest sampling 1989.

A Chi-squared test between the "all regions" BYDV strain ratios of the barley leaf (Table 8.1) and the *P. annua* (Table 8.2) samples ($x^2_{(2)}$ = 3.3, N.S.) indicated that the BYDV strain incidence was similar in these two plant sample types. There was a relationship between the regional percentage BYDV infection in the barley leaf and in the *P. annua* samples collected in July 1989 (arcsine transformation, linear regression on data for separate strains, Figure 8.1), indicating that the extent of infection of barley leaf samples with a particular BYDV strain was related to the extent of infection of *P. annua* samples with that particular strain.

Assessments 3 and 4 Aphids on barley plants and *P, annua*.

Only *S. avenae* was common in winter barley crops, being present in 11 of the 14 fields. In two Wigtownshire fields, a few *R. padi* alone were observed, whereas no aphids were observed in one Dumfriesshire field. In another Dumfriesshire field, *R. padi*, *M. dirhodum* and *S. avenae* were present, although only the latter species was common. Numbers of aphids collected from cereal plants were low relative to numbers on *P. annua*.

The sample of ten aphids representative of aphid infestations of each host plant type in each crop could not be achieved in most fields. Table 8.3 shows the number of aphids tested, the number transmitting each BYDV strain for the 53 and 68 aphids collected from barley plants and *P. annua* respectively. Ninety-three per cent of aphids

Table 8.3 Assessments 3 & 4; the number of aphids tested and the number of positive BYDV transmission tests for the aphid samples collected from barley plant and *Poa annua* host plants in each region in 1989.

		Number of positive tests for BYDV strain						
		Aphids on barley plants				Aphids on *P. annua*		
Region	No tested	RPV	PAV	MAV	No tested	RPV	PAV	MAV
Dumfriesshire	8	0	0	0	6	0	0	4
Wigtownshire	24	4	1	1	0	0	0	0
Ayrshire	0	0	0	0	26	2	2	2
Renfrewshire	9	0	1	1	22	0	1	4
Stirlingshire	12	1	0	3	23	1	2	1
Totals	53	5	2	5	77	3	5	11
	%	9	4	9		4	6	14

collected were *S. avenae*.

Assessment 5 Grass weed abundance.

Table 8.4 lists the number of fields in each region allocated to each grass weed abundance category. Grass weed infestation in most cereal fields was extensive in July 1989, thus ten of the 14 fields were allocated to the higher two grass-weed abundance categories. However, two Stirlingshire and one Renfrewshire field were relatively weed-free (abundance category 1).

Table 8.4 Assessment 5; extent of field infestation with *Poa annua* or *Lolium perenne* in each region July 1989.

	No of fields in each category		
Region	1	2	3
Dumfriesshire	1	2	0
Wigtownshire	0	1	2
Ayrshire	0	2	0
Renfrewshire	1	1	1
Stirlingshire	2	1	0
Totals	4	7	3

Category 1 Scattered plants in tramlines.

Category 2 Appreciable proportion of tramlines infested (at least 1-5%).

Category 3 Extensive areas of crop infested.

Assessments 6 Abundance of ladybirds.

Table 8.5 lists the number of fields in each region allocated to each ladybird abundance category. Ladybirds were found in all fields except one in Renfrewshire. However, many ladybirds were observed in the other two Renfrewshire fields. Fifty-seven per cent of fields were allocated to the intermediate ladybird abundance category (i.e few ladybirds).

Table 8.5 Assessment 6 regional abundance of ladybirds; July 1989.

	No of fields in each category		
Region	None (1)	Few (2)	Many (3)
Dumfriesshire	0	2	1
Wigtownshire	0	2	1
Ayrshire	0	2	0
Renfrewshire	1	0	2
Stirlingshire	0	2	1
Totals	1	8	5

Assessment 7 No data collected in 1989.

8.3.2 Pre-harvest sampling results 1990

Data were collected in nine winter barley crops in three regions of the west of Scotland from 2 to 12 July 1990. Three fields were sampled in each region. Tables 8.6 to 8.11 show the results for each assessment on a regional basis.

Assessments 1 and 2 BYDV in barley leaves and *P. annua*.

All three BYDV strains were present in the barley leaf samples of Dumfriesshire, compared with almost no BYDV of any strain in the Wigtownshire and Stirlingshire samples (Table 8.6). In contrast, MAV alone was detected in the Dumfriesshire *P. annua* samples compared with the Wigtownshire and Stirlingshire samples which contained all three strains (Table 8.7). In both sample types, MAV was the commonest strain.

Table 8.6 Assessment 1; number of barley leaf samples infected with each BYDV strain in each region July 1990.

		No of positive ELISA tests for BYDV strain		
Region	No of samples	RPV	PAV	MAV
Dumfriesshire	27	5	1	11
Wigtownshire	20	0	0	1
Stirlingshire	20	1	0	0
Totals	67	6	1	12
	%	9	1	18

Table 8.7 Assessment 2; number of *Poa annua* infected with each BYDV strain in each region July 1990.

Region	No of samples		No of positive ELISA tests for BYDV strain RPV	PAV	MAV
Dumfriesshire	26		0	0	3
Wigtownshire	30		2	2	24
Stirlingshire	30		1	2	6
Totals	86		3	4	33
		%	3	5	38

A Chi-squared test between the "all regions" BYDV strain ratios of the barley leaf and the *P. annua* samples ($x^2_{(2)}$ = 2.7, N.S., 1 expected marginally less than five) indicated that the BYDV strain incidence was similar in these two plant sample types. However, there was no relationship between the percentage BYDV infection in the barley leaf and the *P. annua* samples collected in July 1990 (arcsine transformation, linear regression on data for separate strains, r = 0.07, N.S.), indicating that extent of infection of barley leaf samples with a particular BYDV strain was not related to the extent of infection of *P. annua* samples with that particular strain.

Assessments 3 and 4 Aphids on barley plants and *P. annua*.

S. avenae was observed in all fields, except one in Wigtownshire. *M. dirhodum* was observed in two Stirlingshire and one Dumfriesshire field. A couple of *R. padi* were observed in one Stirlingshire field. Aphids were found on cereal plants, wheat volunteers and *P. annua,* but were common only on the latter. Aphids were not easily found on barley plants of any region. Nineteen of the 24 aphids tested from this host plant type were collected from Dumfriesshire fields. None were collected from barley in Wigtownshire.

The sample of ten aphids representative of aphid infestations of each host plant type could not be achieved in most fields. Table 8.8 shows the number of aphids tested, the number transmitting each BYDV strain for the 24 and 65 aphids collected from barley plants and *P. annua* respectively. Ninety-eight per cent of aphids collected were *S. avenae*.

Assessment 5 Grass weed abundance.

Table 8.9 lists the numbers of fields in each region allocated to each grass weed abundance category. Grass weed infestation was greatest in Wigtownshire where all three fields were allocated to the highest category. However, two Dumfriesshire fields were relatively weed-free (abundance category 1). Overall, 66% of fields were allocated to the two higher categories, indicating that many fields had large grass weed infestations in July 1990.

Table 8.8 Assessments 3 & 4; the number of aphids tested and the number of positive BYDV transmission tests for the aphid samples collected from barley plant and *Poa annua* host plants in each region in 1990.

		Number of positive tests for BYDV strain						
		Aphids on barley plants				Aphids on *P. annua*		
Region	No tested	RPV	PAV	MAV	No tested	RPV	PAV	MAV
Dumfriesshire	19	0	0	1	15	0	0	0
Wigtownshire	0	0	0	0	18	0	1	9
Stirlingshire	5	0	0	1	32	0	3	5
Totals	24	0	0	2	65	0	4	14
	%	0	0	8	%	0	6	22

Table 8.9 Assessment 5; extent of field infestation with *Poa annua* or *Lolium perenne* in each region July 1990.

	No of fields in each category		
Region	1	2	3
Dumfriesshire	2	0	1
Wigtownshire	0	0	3
Stirlingshire	1	2	0
Totals	3	2	4

Category 1 Scattered plants in tramlines.

Category 2 Appreciable proportion of tramlines infested (at least 1-5%).

Category 3 Extensive areas of field infested.

Assessment 6 and 7 Abundance of ladybirds and aphid mummies.

Table 8.10 and 8.11 list the number of fields in each region allocated to each ladybird and aphid mummie abundance category.

Ladybirds were not observed in 55% of fields, and no field was allocated to the highest abundance category.

Aphid mummies were observed in seven fields. Two Wigtownshire and one Stirlingshire field were allocated to the highest aphid mummie abundance category. Both parasitised *S. avenae* and *M. dirhodum* were observed.

Table 8.10 Assessment 6; regional abundance of ladybirds July 1990.

	No of fields in each category		
Region	None	Few	Many
Dumfriesshire	2	1	0
Wigtownshire	1	2	0
Stirlingshire	2	1	0
Totals	5	4	0

Table 8.11 Assessment 7; regional abundance of aphid mummies July 1990.

	No of fields in each category		
Region	None (1)	Few (2)	Many (3)
Dumfriesshire	0	3	0
Wigtownshire	1	0	2
Stirlingshire	1	1	1
Totals	2	4	3

8.4 Relationships between pre-harvest sampling measurements and aphid/BYDV incidence in the winter barley crops of the succeeding season

In this section, the relative importance of migrating and local aphids in introducing BYDV into winter barley crops during the autumns of 1989 and 1990 was investigated. To assess the importance of local aphids, aphid and BYDV data obtained during pre-harvest sampling in July 1989 and 1990, was compared with aphid data collected in winter barley crops during the succeeding autumns, and BYDV data collected in the springs of 1990 and 1991 respectively. Suction trap data were used to assess the importance of migrating *Rhopalosiphum* spp. during the autumns of 1989 and 1990.

Incidence of BYDV strains Incidence and extent of BYDV infection in both *P. annua* and barley leaf samples was measured in several regions in early July 1989 and 1990. These measurements were compared with incidence and extent of BYDV infection in barley leaf samples in the same regions in May 1990 and 1991 respectively. The regional differences in BYDV incidence, in the springs of 1990 and 1991 have already been studied (Chapter 4).

The percentage BYDV infection for each strain in barley leaf and *P. annua* samples in July 1989, and in barley leaf samples in May 1990 are shown in Table 8.12. The data from winter barley crops sampled in May 1990, which followed untreated ploughed-in grass were excluded, because *R. padi*-transmitted BYDV was common in these

fields: two fields in each of Wigtownshire and Ayrshire. Such fields may be at risk from *R. padi*-transmitted BYDV spread by local aphids via the "green bridge" every year irrespective of migrant aphid pressure.

In July 1989, all three strains were present in the barley leaf and *P. annua* samples of Dumfriesshire, Wigtownshire and Ayrshire. From July 1989 to May 1990, there was a decrease in the percentage of samples infected with the RPV and PAV strains, so that MAV was the commonest strain in the barley leaf samples of these three regions in May 1990. In contrast, in Renfrewshire and Stirlingshire, there was an increase in the percentage of the plant samples infected with the PAV strain compared with a decrease for the MAV strain. In Renfrewshire, MAV was the commonest strain at both times, but in Stirlingshire, although MAV was predominant in July 1989, PAV was more common in May 1990. In Wigtownshire, Ayrshire and Stirlingshire, the differences in the incidence of the different strains between July 1989 (data of the BYDV strain incidence in barley leaf and *P. annua* samples were pooled) and May 1990 were significant (Table 8.13).

Table 8.12 Percentage of the barley leaf and *P. annua* samples collected in July 1989 and the barley leaf samples collected in May 1990 infected with each BYDV strain.

Region	% of samples with BYDV strain		
	RPV	PAV	MAV
Dumfriesshire			
July barley leaves	13	7	53
July *P. annua*	48	56	100
May barley leaves	9	18	26
Wigtownshire			
July barley leaves	40	100	40
July *P. annua*	72	83	31
May barley leaves	10	0	70
Ayrshire			
July barley leaves	30	60	60
July *P. annua*	53	58	32
May barley leaves	8	23	69
Renfrewshire			
July barley leaves	0	0	70
July *P. annua*	0	10	76
May barley leaves	6	14	51
Stirlingshire			
July barley leaves	13	7	53
July *P. annua*	4	17	63
May barley leaves	0	54	31

Table 8.13 Chi-squared tests (using Yates' correction) on the ratios of the incidence of the RPV + PAV strains to the MAV strain in the July 1989 samples (barley leaf and *P. annua* samples added together) compared with the May 1990 barley leaf samples.

Region	Value	Significance
Dumfriesshire	$x^2_{(1)} = 0.13$	N.S.
Wigtownshire[a]	$x^2_{(1)} = 17.2$	$P < 0.001$
Ayrshire	$x^2_{(1)} = 6.9$	$P < 0.01$
Renfrewshire[a]	$x^2_{(1)} = 3.4$	N.S.
Stirlingshire[a]	$x^2_{(1)} = 5.4$	$P < 0.05$

[a] one expected less than five.

The percentage BYDV infection for each strain in barley leaf and *P. annua* samples in July 1990 and in barley leaf samples in May 1991 are shown in Table 8.14. In July 1990 in all three regions, RPV and PAV were present in no more than 11% of barley leaf or *P. annua* samples compared with greater percentages for the MAV strain in either sample type. In May 1991, MAV remained the commonest strain in Wigtownshire and Stirlingshire whilst PAV and MAV were equally common in Dumfriesshire. In all three regions, the percentage of plant samples infected with the PAV strain more than doubled from July 1990 to May 1991 whereas the percentages for the RPV strain changed relatively little. In Wigtownshire, these differences in the incidence of the different strains between July 1990 and May 1991 were significant (Table 8.15).

Table 8.14 Percentage of the barley leaf and *P. annua* samples collected in July 1990 and the barley leaf samples collected in May 1991 infected with each BYDV strain.

Region	% of samples with BYDV strain		
	RPV	PAV	MAV
Dumfriesshire			
July barley leaves	11	4	41
July *P. annua*	0	0	5
May barley leaves	8	24	24
Wigtownshire			
July barley leaves	0	0	5
July *P. annua*	7	7	80
May barley leaves	3	16	30
Stirlingshire			
July barley leaves	5	0	0
July *P. annua*	3	7	20
May barley leaves	2	22	42

Table 8.15 Chi-squared tests (using Yates' correction) on the ratios of the incidence of the RPV + PAV strains to the MAV strain in July 1990 samples (barley leaf and *P. annua* samples added together) compared with the May 1991 barley leaf samples.

Region	Value	Significance
Dumfriesshire	$x^2_{(1)} = 2.6$	N.S.
Wigtownshire[a]	$x^2_{(1)} = 3.9$	$P < 0.05$
Stirlingshire[a]	$x^2_{(1)} = 0.2$	N.S.

[a] one expected less than five.

The introduction of the RPV and PAV strains into winter barley crops by migrating *Rhopalosiphum* spp. during

the autumn can be measured to some extent by the size of the suction trap catches during the autumn (Plumb, 1988). Ten year averages (1981-90) of the pooled September and October catches of *R. padi* and *R. insertum* at Ayr, Belfast and Dundee are shown in Table 8.16 along with the autumn catches of 1989 and 1990. These three suction traps are perhaps the most relevant ones to south-west and central Scotland. Catches of *R. padi* were below the ten-year average at all three sites in both 1989 and 1990. *R. insertum* was well above average at Dundee but below average at the other two sites in 1989, and near average at all three sites in 1990. Although the 1989 *R. insertum* grand total was greater, the grand total of 1990 was distributed more equally between sites.

Table 8.16 The 1981-90 average number of *Rhopalosiphum padi* and *R. insertum* caught during September and October at Auchincruive, Belfast and Dundee by 12.2 m suction traps, and the figures for 1989 and 1990.

Suction trap catches during September and October

	R. padi			*R. insertum*		
Site	Average	1989	1990	Average	1989	1990
Ayr	3236	254	1044	1494	991	1515
Belfast	4537	249	2377	1589	183	1012
Dundee	12090	1512	1163	1780	3640	1377
Grand totals	19863	2015	4584	4863	4814	3904

Aphid species incidence and BYDV transmission by field-collected aphids

Aphids in cereals during July Pre-harvest sampling assessments 3 and 4 were the collection of ten aphids from both barley and *P. annua* plants in each winter barley field for BYDV transmission tests. Although *S. avenae* was unusually abundant in Scottish cereal crops (Sparrow, 1974) in the springs of 1989 and 1990 (Chapter 4), aphids were relatively scarce by July in both years. Time spent in each field had to be limited to 60 to 75 minutes, and there was mortality of field-collected aphids in transit to the laboratory. Therefore the intended sample was achieved in only a few fields. In Ayrshire July 1989 and Wigtownshire July 1990, no aphids were found on barley plants whereas in Wigtownshire July 1989, no aphids were found on *P. annua*. In both years, only *S. avenae* was common, and most aphids were found on inflorescences rather than leaves or stems, and on *P. annua* rather than barley. The numbers of fields infested with *M. dirhodum*, *R. padi* and *S. avenae* during pre-harvest sampling 1989 and 1990 are shown in Table 8.17. *S. avenae* was found in all fields of a region on five of the eight occasions (an occasion is a visit to a region), whereas *M. dirhodum* and *R. padi* were only present in small numbers in a minority of fields.

Table 8.17 Number of fields in which *Metopolophium dirhodum*, *Rhopalosiphum padi* and *Sitobion avenae* were observed during pre-harvest sampling 1989 and 1990.

		Number of fields with aphid species		
Region	n	*M. dirhodum*	*R. padi*	*S. avenae*
1989				
Dumfriesshire	3	1	1	2
Wigtownshire	3	-	2	1
Ayrshire	2	-	-	2
Renfrewshire	3	-	-	3
Stirlingshire	3	-	-	3
1990				
Dumfriesshire	3	1	-	3
Wigtownshire	3	-	-	2
Stirlingshire	3	2	1	3

N.B. Three fields per region except Ayrshire July 1989 when two fields were sampled.

\- no fields with aphid spp.

Aphids in cereals during the autumn Aphid variables (Table 8.18) were created from the aphid colony counts per metre length obtained during the autumns of 1989 (Table 4.23) and 1990 (Table 4.34). Few *M. dirhodum* were encountered during autumn sampling in either year, therefore only *Rhopalosiphum* and *S. avenae* variables were produced. These aphid variables (Table 8.18) were chosen

because they are less sensitive to the differences in aphid sampling frequency between the autumns of 1989 and 1990 than aphid colony totals or means. It was desirable to lessen the importance of data collected during late autumn visits, because few aphids are present at this time. The values of these aphid variables in the autumns of 1989 and 1990 are shown in Table 8.20.

Table 8.18 Definitions of the aphid variables created from the aphid colony counts obtained during the autumns of 1989 and 1990.

Regional variable	Definition
Rhopalosiphum proportion	Number of *Rhopalosiphum* colonies observed divided by the total number of aphid colonies observed.
S.avenae proportion	Number of *S. avenae* colonies observed divided by the total number of aphid colonies observed.
Rhopalosiphum[a] metre lengths	Percentage of metre lengths of drill infested by *Rhopalosiphum* during the autumn up to and including the first sampling visit in November.
S. avenae[a] metre lengths	Percentage of metre lengths of drill infested by *S. avenae* in during the autumn up to and including the first sampling visit in November.

[a] Few aphids are caught by suction traps after the first few days of November, so early November can be regarded as the end of alate aphid migration.

Table 8.19 Total numbers of aphid colonies and the values of the aphid variables (Table 8.18) for the autumns of 1989 and 1990: *Rhopalosiphum* spp. and *Sitobion avenae*.

	Total no of colonies		Proportion of total colonies		% of metre lengths	
Region	Rh. spp.	S.a	Rh. spp.	S.a	Rh. spp.	S.a
1989						
Dumfriesshire	9	18	0.30	0.67	6	10
Wigtownshire[a]	11	7	0.61	0.39	12	8
Ayrshire[a]	9	23	0.28	0.72	8	14
Renfrewshire	7	45	0.13	0.87	3	14
Stirlingshire	14	1	0.93	0.01	9	0
1990						
Dumfriesshire	71	51	0.58	0.42	15	8
Wigtownshire	36	17	0.68	0.32	8	3
Stirlingshire	33	40	0.45	0.55	7	7

[a] fields following untreated ploughed-in grass leys were excluded.

Rh. spp. *Rhopalosiphum* spp. S.a. *Sitobion avenae*

There were more metre lengths infested by *S. avenae*, relative to *Rhopalosiphum* spp. in three regions in the autumn 1989, which correlates with the preponderance of *S. avenae* in cereals in July 1989. However, just one *S. avenae* colony was observed in the three Stirlingshire fields during the entire autumn. In 1990, more metre lengths were infested by *Rhopalosiphum* than *S. avenae* in Dumfriesshire

and Wigtownshire, and an equal number of metre lengths were infested by these two aphid groups in Stirlingshire.

The differences between these two autumns are that in 1990, *Rhopalosiphum* spp. constituted a greater proportion of the aphid colony totals, and *S. avenae* infested a lower percentage of the metre lengths, than in 1989. The greater suction trap totals of *Rhopalosiphum* spp. in the autumn 1990 than in 1989 (Table 8.16) are consistent with the aphid colony totals (Table 8.19).

The BYDV transmission data for both years (Tables 8.3 and 8.8), show that the MAV strain was most commonly transmitted by aphids collected during pre-harvest sampling, this being associated with the fact that most aphids collected were *S. avenae*. The exception was Wigtownshire in 1989 where *R. padi*, which subsequently transmitted RPV, was collected. This preponderance of MAV transmission for aphids collected during both Julys, corresponds with the predominant MAV infection present in winter barley crops in the succeeding autumns.

The relative importance of the factors assessed in pre-harvest sampling and the autumn aphid variables, in determining the BYDV infection of barley leaves in the following spring was assessed using multiple regression. The percentage BYDV infection of the barley leaf samples from different regions during the springs of 1990 and 1991 was regressed on the percentage BYDV infection of the

barley leaf and *P. annua* samples of the previous Julys, the abundance of grass weeds and ladybirds in winter barley fields during the previous Julys, and the aphid variables (the proportion and metre lengths variables, Table 8.19) of the previous autumns. The percentage of barley leaf samples collected in the spring which was infected with the RPV strain was added to the percentage infected with the PAV strain, to form the "spring RPV/PAV" variable whereas the percentage of barley leaf samples collected in the spring which was infected with the MAV strain was named the "spring MAV" variable.

The regional variables other than the aphid variables, which were used as predictors, are shown in Table 8.20. Each variable was tested individually and in combination with other variables although no more than one aphid variable was included in any one equation. *Rhopalosiphum* and *S. avenae* variables were included in the regression equations for the "spring RPV/PAV" and "spring MAV" variables respectively.

There were two significant relationships involving two regional predictor variables which explained the variation of the "spring RPV/PAV" variable: the weed abundance variable and the proportion *Rhopalosiphum* variable. There were no significant relationships for the "spring MAV" variable.

Table 8.20 Regional predictor variables used to explain the variation in BYDV infection in winter barley during the springs of 1990 and 1991.

Variable	Description
July RPV/PAV	Percentage of barley leaf and *P. annua* samples infected with RPV and those with PAV all added together.
July MAV	Percentage of barley leaf and *P. annua* samples infected with MAV added together.
Weed abundance	A mean weed category score was calculated for each region by multiplying the number of fields in each category by the value of the category, and adding all 3 totals together, and dividing that total by the number of fields in each region.
Ladybird abundance	Calculated as for weed abundance.

Table 8.21 Significant relationships identified by multiple regression between the "spring RPV/PAV" variable and the regional predictor variables (Table 8.20).

Predictor	Coefficient	R-sq	F-stat	Significance
1) Weed abundance	-17.0	54.7%	7.26	P = 0.036
2) Weed abundance	-17.3	54.7%		
Proportion of metre lengths	23.6	23.3%		
		76.7%	8.21	P = 0.026

Summary Common features of winter barley fields sampled during pre-harvest sampling in July 1989 and July 1990 were: the prevalence of MAV in barley leaf and *P. annua* samples, the presence of *S. avenae*, the absence of other aphid species, high levels of *P. annua* infestation and the presence of ladybirds. A noticeable difference between these two Julys was in the abundance of ladybirds: 36% of fields in the highest abundance category in 1989 compared with 0% in 1990 whereas the comparative figures for the intermediate abundance category were 57% and 44% respectively.

From the above summary of the pre-harvest sampling data, it is reasonable to hypothesise that local populations of *S. avenae* could introduce MAV into winter barley crops emerging during the autumns of 1989 and 1990. High levels of *P. annua* in both years could favour aphid survival whereas the abundance of ladybirds, particularly in 1989, may compromise the potential of local aphids to persist in stubble fields during late summer. In July 1990, aphid parasitoids were assessed, and were present in seven fields. This factor also could lessen the possibility of aphid populations persisting in winter barley stubbles during late summer 1990.

In the springs of 1990 and 1991, BYDV infection was detectable in most fields although the percentage of each crop affected was less than 1% in 48 of the 51 fields surveyed. Two of the fields with 1% or more crop yellowing

followed untreated ploughed-in grass leys. The MAV strain was predominant on six occasions (4 regions in May 1990 and 2 in May 1991) and equally predominant with PAV on one occasion (Tables 8.12 and 8.14).

This provides some evidence for the spread of BYDV (MAV) by local aphids from the winter barley crops of one season to the winter barley crops of the next, although it was not sufficient to cause widespread economic damage.

8.5 Discussion

8.5.1 The importance of local and migrant aphids

The autumns of 1989 and 1990 had low *Rhopalosiphum* suction trap totals at Ayr, Belfast and Dundee (Table 8.16). This was reflected in both the low percentage infection of the yellow barley leaf samples with the RPV and PAV strains in the springs of 1990 and 1991, and in the low extent of BYDV infection in each sampled field.

Infestation by *S. avenae* and MAV infection were characteristics of winter barley crops of all regions in both Julys, and the MAV strain was detectable in the barley leaf samples of all regions during the following springs. However, this does not prove local spread but could be indicative of long distance migration, except that few *S. avenae* are caught by suction traps during the autumn (Plumb, 1986). At Ayr, during the autumns (September and October) of 1989 and 1990, five and four *S. avenae* respectively, were caught in the suction trap. The

comparative figures for the Dundee trap were 25 and 3 *S. avenae*.

Aphids that fly higher will migrate further on the stronger winds present at greater altitudes (Tatchell *et al.*, 1988). The low numbers of *S. avenae* at 12.2 m and the greater numbers of *S. avenae* colonies on crops relative to *Rhopalosiphum* colonies in these two autumns might suggest that most *S. avenae* moved into winter barley crops from local sources.

The larger *Rhopalosiphum* suction trap catches at Dundee in the autumn 1989 relative to the catches at Ayr and Belfast (Table 8.16) could explain the increase in the PAV infection of the barley leaf samples of Renfrewshire and Stirlingshire from July 1989 to May 1990 (Table 8.12). More *Rhopalosiphum* were caught at Ayr and Belfast in 1990 compared with 1989, and this may account for the PAV increasing in all three regions from July 1990 to May 1991 (Table 8.14). Although the *Rhopalosiphum* catches at Dundee were less in 1990 than in 1989, they were larger than the catches at Ayr and Belfast in 1989. Each region does not have its own suction trap, therefore it was not possible to confirm these associations using regression.

In both 1989 and 1990 at Ayr and Dundee (Table 8.16), *insertum* comprised a much greater proportion of the autumn alate *Rhopalosiphum* suction trap totals than *padi*. In sampled crops too, *R. insertum* predominated the alate

Rhopalosiphum on barley plants. *R. insertum* removed to the laboratory and placed on oat seedlings for BYDV transmission tests did not reproduce, and apterous *R. insertum* were not observed in winter barley crops during these two autumns. Thus, little secondary spread of the RPV and PAV strains occurred which is reflected in the following two facts. Firstly, no regions in either autumn had *Rhopalosiphum* totals exceeding 100 colonies (having excluded fields following untreated ploughed-in grass leys in 1989). Secondly, no more than 15% of one-metre lengths of drill were infested by *Rhopalosiphum* in any region (Table 8.19).

8.5.2 The importance of the factors assessed in pre-harvest sampling

BYDV infection was not generally extensive in crops of any region in the springs of 1990 and 1991 (Chapter 4). Therefore, regression was only possible with the percentage of samples infected data and not the percentage of crops comprised of patches of yellow plants. The factors found to be important using regression should be interpreted in the light of these facts. Also, firm conclusions cannot be drawn from two years data.

BYDV infection of barley leaves and P. annua The percentage infection of the yellow barley leaf and the *P. annua* samples did not feature in the significant relationships (Table 8.21). However, it is a plausible hypothesis that the amount and strain(s) of BYDV inoculum present in barley

the amount and strain(s) of BYDV inoculum present in barley leaves and *P. annua* of a region in July may increase the risk of that BYDV strain(s) occurring in winter cereals in the following autumn. However, *S. avenae*, which mainly transmits the MAV strain in the field (Plumb, 1974), was the only common aphid species in all regions in both Julys, except for Wigtownshire in 1989. The infection of barley leaves and *P. annua* with RPV and PAV in addition to MAV in Dumfriesshire, Wigtownshire and Ayrshire in July 1989 (Table 8.12) was academic, because an aphid species that transmits these strains (i.e *R. padi*) was generally absent. This confirms the need for aphid species assessments in pre-harvest sampling, in addition to collections of plant material for BYDV testing by ELISA.

Weed abundance Both the significant relationships found for the "spring RPV/PAV" variable involved the weed abundance predictor, which in both cases explained more than 50% of the variation. Contrary to theories expressed in section 8.4, increasing weed abundance was negatively associated with the percentage RPV + PAV infection of the spring barley leaves. However, these relationships are probably the result of the low levels of RPV and PAV in Wigtownshire in both springs where *P. annua* infestation was greatest in both Julys, and where these two strains were most common (Table 8.12). It has already been suggested that the increased PAV infection in Renfrewshire and Stirlingshire in the spring of 1990 and in all regions in 1991 is

Rhopalosiphum species.

Ladybird abundance Ladybird abundance did not feature in either of the two significant relationships (Table 8.21). In both years, ladybirds were active in cereal fields during July, where presumably they had contributed to the decrease in aphid numbers from the spring to the early summer.

Ladybirds were more abundant in July 1989, but there were more metre lengths of drill infested by *S. avenae* in the autumn of 1989 than in 1990. However, the important point may be that ladybirds (mostly *C. 7-punctata*) were active in all regions in both Julys and large aphid infestations did not generally develop in winter barley crops of any region during the following autumns. Ladybirds may possibly have limited populations of local aphids in stubble fields between July and the emergence of the following winter barley crops. Nevertheless, they were not observed in winter barley crops during the autumn. Further analysis with more years data is required to fulfil the aims outlined in section 8.1.4.

The parasitoid abundance categories were not included in the regression equations because data were not collected in July 1989. However, they were observed parasitising *S. avenae* in both Julys and unlike ladybirds, they were encountered in aphid populations collected from winter barley crops during both autumns. For example, in the

autumn of 1990, nine of the 40 *S. avenae* tested for BYDV transmission became mummies compared with none of the 42 *R. padi*. Therefore, for *S. avenae* at least, parasites may have been limiting population growth in autumn-sown cereals during the autumns of 1989 and 1990, and therefore the spread of BYDV.

Rhopalosiphum variables The proportion variable featured in one significant relationship in which it was positively associated with the "spring RPV/PAV" variable (Table 8.21). Since most *Rhopalosiphum* colonies observed in these two autumns were alate (excluding 4 fields in 1989 which followed untreated ploughed-in grass), it is reasonable to conclude that migrating *Rhopalosiphum* spp. introduced much of the PAV into winter barley during these two autumns. In 1990, none of the alate *Rhopalosiphum* placed on oat seedlings for BYDV transmission tests produced nymphs. Most were *R. insertum* and probably gynoparae. The suction trap catches of Ayr, Belfast and Dundee support this theory (Table 8.16).

8.5.3 Efficiency of pre-harvest sampling methodology

At a collaborative meeting with a colleague from the Queen's University of Belfast in June 1991, the pre-harvest sampling methodology was discussed and alterations made:-

BYDV was detected by testing of both barley leaves and *P. annua*. Overall, the percentage infection of *P. annua*

was higher despite symptomless material being collected. The "all regions" BYDV incidence was similar in barley leaves and *P. annua* although within a region, differences in BYDV strain ratios between the two sample types were found. These differences could perhaps be reduced by increasing the sample sizes. A decision was made to double to 20 the number of single barley leaves to be collected from each field, and to collect a hundred leaves from a few fields.

The sample of ten aphids representative of aphid infestations on both barley leaves and *P. annua* was seldom achieved in either 1989 or 1990, both years when *S. avenae* was numerous on cereals. The senesced state of these crops was probably a major factor which was reflected in the greater numbers present on *P. annua* rather than barley. It has been established that the strains transmitted by an aphid mainly depend on the aphid species (Chapter 7), therefore, it was decided to discontinue aphid collection for BYDV transmission tests. The aphid species incidence assessments were extended to include an examination of ten one-metre lengths of drill, so that the success of this more precise measurement could be compared with the cursory visual examination of hundreds of plants, both barley and *P. annua*.

The method of assessing the extent of *P. annua* infestation was considered satisfactory, and was unaltered.

The methodology used to assess ladybird and parasitoid incidence successfully detected these natural enemies in winter barley fields during both Julys. However, it was decided that a comparison should be made with assessments of ladybird and parasitoid incidence made during the examination of 10 x 1 m lengths of barley drill for aphids.

CHAPTER NINE

Cereal stubble surveying as a method of measuring the risk of BYDV to autumn-sown cereals

9.1 **Introduction**

The relatively short time between stubble surveying in late August and crop emergence in the autumn makes this method of forecasting BYDV risk to autumn-sown cereals more rational and attractive than pre-harvest sampling. However, this short period of time also prevents the use of techniques such as testing of aphids for BYDV transmission, or the testing of large numbers of plant samples for BYDV (by ELISA). Currently, both approaches are being examined and comparison of their results in the same summer, and with the subsequent aphid and virus situation in autumn-sown cereals will determine their relative merits.

In 1990, aphid species assessments were made in a number of cereal stubbles in late August and early September.

9.2 **Methodology**

In late August and early September 1990, a range of cereal crop stubbles were examined for aphid species incidence. Three winter barley stubbles were sampled in Dumfriesshire, five in Wigtownshire, two in Ayrshire and two in Stirlingshire (one Stirlingshire field was a winter wheat stubble). Two spring barley stubbles were sampled in Dumfriesshire, and one in both of Wigtownshire and Stirlingshire (three of these fields were undersown with perennial ryegrass). Five winter barley stubbles were sampled twice, all other fields once.

In each field, aerial parts of five grass weeds that represented the dominant grass weed species were examined during a circuit of the field. In winter barley stubble fields, five groups of ten barley volunteers (each group adjacent to a selected grass weed) were also examined. In a few fields during late August, groups of fewer than ten barley volunteers had to be selected. Volunteers were absent in spring barley stubbles.

9.3 **Results**

The mean number of infested plants in each field for each plant type (grass weed or volunteer group) in each region is shown for each cereal aphid species in Table 9.1. A Chi-squared test on the total number of plants infested (all regions pooled) by each species (except *M. dirhodum*) on the two plant types, gave a non-significant result ($x^2_{(2)} = 0.94$, N.S.), indicating that the ratios of the three aphid species infestations did not differ between the two plant types.

R. padi was the most numerous aphid species on both sample types. It was observed in 11 winter barley stubble fields, in contrast to both *S. avenae* and *M. dirhodum* which were observed in six and *R. insertum* in four fields. Overall, 27% of grass weed plants examined were aphid infested compared with 54% of volunteer barley groups.

Both *R. padi* and *S. avenae* were twice as common on groups of volunteers as on grass weeds. *R. insertum* was

Table 9.1 Aphid infestation of grass weeds and barley volunteers in winter barley stubble fields 1990.

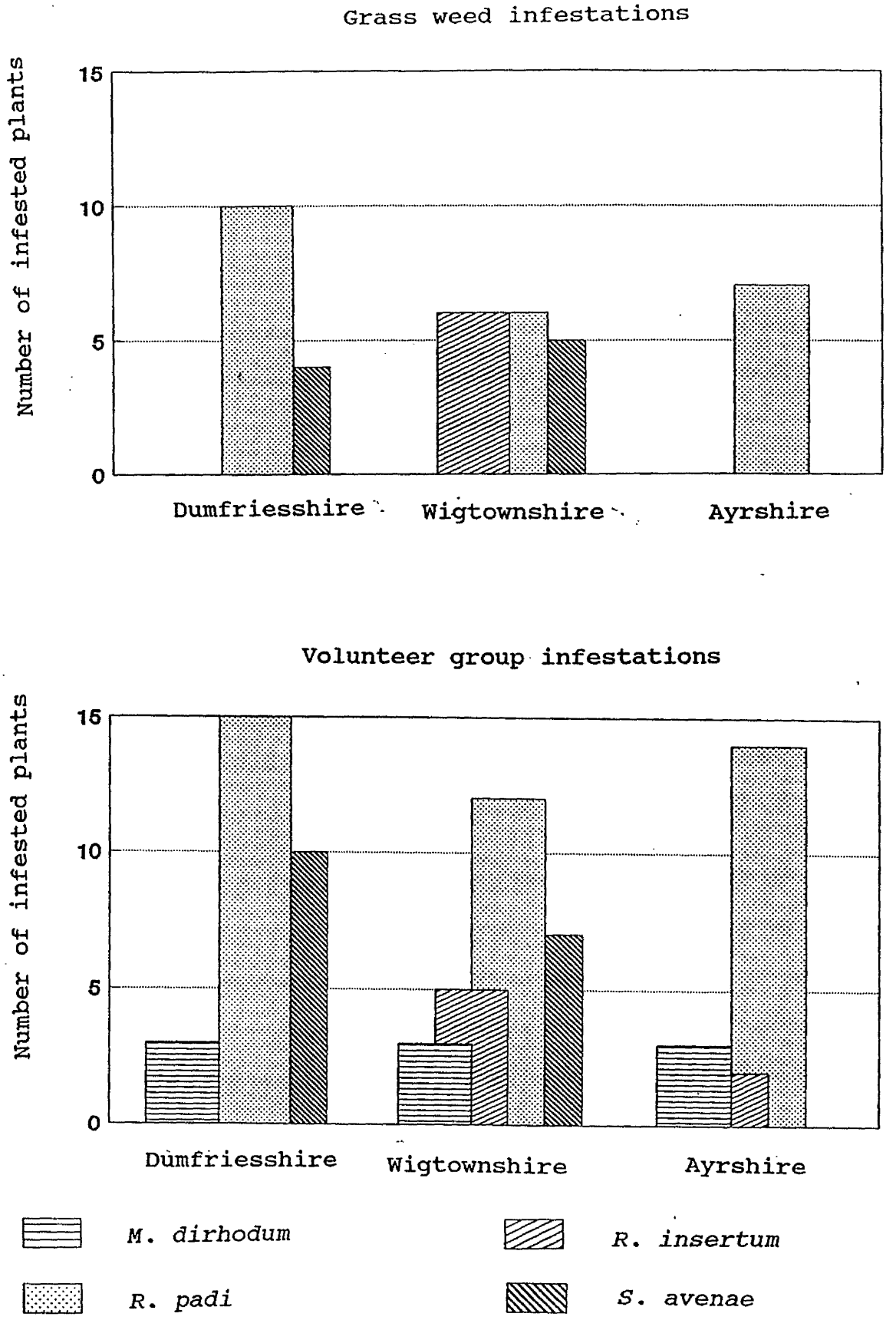
Region	No of samples	Mean number of plants infested per field: Grass weeds M.d.	R.i.	R.p.	S.a.	Volunteers M.d.	R.i.	R.p.	S.a.
Dumfriesshire	25	-	-	0.3	0.1	0.1	-	0.4	0.3
Wigtownshire	35	-	0.2	0.2	0.1	0.1	0.1	0.3	0.2
Ayrshire	15	-	-	0.2	-	0.1	0.1	0.4	-
Stirlingshire	10	-	-	-	-	-	-	-	-
Total number of samples infested.		-	6	16	8	6	6	29	15

Key

M.d. *M. dirhodum.* R.p. *R. padi.*

R.i. *R. insertum.* S.a. *S. avenae*

Grass weeds were either *L. perenne* or *P. annua* in every field except the Stirlingshire field in which case all weeds were *H. lanatus.*



N.B. Number of samples differs between regions (Table 10.1).

Figure 9.1. Numbers of grass weeds and volunteer groups infested by each cereal aphid species in each region.

observed on both six grass weeds and six volunteer groups. *M. dirhodum* was only observed on volunteers (Figure 9.1).

No aphids were observed in Stirlingshire and no aphids were observed on grass weeds in the four spring barley stubbles examined.

It was a conspicuous feature of these infestations that many were comprised of single individuals. Heavily infested plants by any species were not encountered.

9.4 **Discussion**

In all regions during pre-harvest sampling 1990 (Chapter 8), *S. avenae* was the predominant aphid species. Post-harvest, *R. padi* was more abundant (Table 9.1) in three regions, whereas in Stirlingshire, no aphids at all were observed. Thus, changes in aphid species incidence had occurred and these differed between regions.

In the autumn of 1990 (Table 4.34), apterous *S. avenae* and alate *Rhopalosiphum* (mostly *insertum*) were both encountered in many winter barley fields. The incidence of apterous *R. padi* on "would-be" ploughed-in grass weeds and volunteers (Table 9.1) did not translate into apterous *R. padi* colonies in barley crops in the autumn of 1990.

The fact that many of the aphid infestations in stubble fields were comprised of single individuals might suggest that natural enemy pressure was high, preventing heavy infestations to develop. Presumably, this high natural

enemy pressure could have persisted into the autumn, preventing the apterous *R. padi* moving locally from ploughed-in grass weeds and volunteers from thriving. The lower percentage of metre lengths infested by *S. avenae* in autumn 1990, relative to 1989 (Table 8.19), may also be due to this high natural enemy pressure, although a stubble survey was not carried out in late summer 1989 to prove this.

CHAPTER TEN

Prediction of the size of the autumn migration of *R. padi*

10.1 **Introduction**

A logical development was the desire to predict the numbers of *R. padi* caught by suction traps during the autumn in advance, in addition to monitoring the event using II. Accurate forecasts give a range of personnel in the agricultural industry the two following advantages: information useful for decision making and time in which to organise the appropiate materials.

A'Brook (1981) identified relationships between the numbers of *Rhopalosiphum* spp. caught during September and October at Aberystwyth (1969-79), and summer rainfall and autumn temperature. Wet summers and warm autumns favouring large migrations and *vice versa*. He further explored these relationships with regressions between autumn aphid numbers and the available soil moisture (mm) in the upper 91 cm of soil, 1969-79, and between autumn aphid numbers and dry matter yields (t/ha) from grass trials, 1976-79. The implications of these analyses too, was that high summer rainfall is important, particularly in July and August.

However, II takes a monitoring approach to the autumn migration of *R. padi*, partly because a late autumn application of an insecticide is an effective treatment (Plumb, 1986). Advocates of II question the value of a forecast of the size of the autumn migration on two points. Firstly, what advantages does a forecast confer to a farmer if he can effectively protect his crops later in the autumn, regardless of the size of the autumn migration.

Secondly, because variation in the infectivity of aphids is also important, the forecast is unlikely to be accurate.

Aims of analyses

1) To produce mathematical models to predict the size of the autumn catch of *R. padi* by the Ayr suction trap, using conventional meteorological data recorded at Auchincruive (section 10.2.1).

2) To explain variations between years and between regions in the numbers of *R. padi* caught by UK suction traps, using PSC indices (section 10.2.2).

3) To assess the numbers of *R. padi* in ryegrass pastures during August, as a method of predicting the size of the autumn migration of *R. padi* (section 10.2.3).

10.2 Methodology and Results

10.2.1 Mathematical modelling

The intention was to produce a number of models which can predict the total numbers of *R. padi* caught by the Ayr suction trap during September & October, on 1 September of that autumn. This prediction could then be used as an indicator of the risk posed to autumn-sown cereals by migrating *R. padi* in south-west & central Scotland. A lower limit had to be imposed on the time period from which weather data was analysed, in relation to the autumn suction trap catches at Ayr from 1975-89. A logical lower

limit was considered to be 1 year previous to the date on which the prediction would be made (i.e weather data from the previous September to August period).

Using common sense, the following monthly weather parameters were chosen as candidate predictors for the models: total rainfall (T, mm), number of rain days (RD, > 0.2 mm), average rainfall per rain day (T/RD, mm day^{-1}), total sunshine (S, hours), mean daily maximum temperature (Tmax, ^{o}C), mean daily minimum temperature (Tmin, ^{o}C), mean daily temperature ([Tmean (Tmax + Tmin)/2], ^{o}C) and mean daily grass minimum (Tgmin, ^{o}C).

Relationships were first examined by correlation between the log (autumn aphid totals) and all sequential combinations of the monthly weather parameters from the previous September to August period (78 combinations x 8 parameters). Of the 624 correlations, 70 were significant: 19 rainfall parameters, 18 sunshine parameters and 33 temperature parameters. Using the STEPWISE facility of MINITAB, the number of weather parameters was further reduced. Four rainfall parameters in the September to February period each accounted for 67-75% of the autumn aphid total variation. Four sunshine parameters in the February to August period each accounted for 69-72% of the autumn aphid total variation. Six temperature parameters in the November-January period each accounted for 68-77% of the autumn aphid total variation.

Two variables from each of these three groups were selected, so that eight regression analyses, each containing one rainfall, one sunshine and one temperature parameter could be achieved. An important factor in the selection process was to avoid having more than one weather variable from the same time period, because many weather variables are correlated over short time periods. The following two rainfall parameters were selected: average rainfall per rain day from September to October and average rainfall per rain day from September to December, because they accounted for most variation in the autumn aphid data. The following two sunshine parameters were selected: total sunshine from February to August and total sunshine from March to August, because they avoided the winter period when sunshine totals are relatively small which would therefore reduce the sensitivity of the variable. They are also more negatively correlated with summer rainfall (section 10.1) than periods including the winter. The following two temperature parameters were selected: mean daily grass minimum from November to February and mean daily maximum temperature from January to February, because they explained most variation in the aphid data apart from maximum daily temperature in January (which was excluded because there is is no biological evidence for a cold January being more important than any other cold winter month - therefore selection of a variable with a longer timespan is preferable).

At first, each regression contained only three predictors (one rainfall, one sunshine and one temperature variable). However, severe winter weather can markedly reduce anholocyclic overwintering by *R. padi* (Dewar & Carter, 1984), and numbers of eggs laid on *P. padus* varies between autumns (Leather, 1981). Therefore, in some summers, the summer build-up of *R. padi* could be delayed owing to the relatively few individuals present early in the season. Thus, it was postulated that the inclusion of a variable representing the size of the previous autumn migration of *R. padi* (as measured by the Ayr suction trap) might improve the regressions. The scoring system for the size of the previous autumn *R. padi* migration is shown below (Table 10.1):

Table 10.1 Scoring system for previous years September & October *R. padi* total caught by the Ayr suction trap.

Score	Number of *R. padi* caught by the Ayr Tower trap in September & October.
1	0 - 1999
2	2000 - 3999
3	4000 - 5999
4	> 6000

Table 10.2 Coefficients, percentage of variation in autumn aphid accounted for, and the significance of the relationship for each of the eight regressions with & without the variable representing the size of the previous year's autumn *Rhopalosiphum padi* migration.

		Without aphid variable			With aphid variable		
Predictors		Coef.	R-sq	P	Coef.	R-sq	P
Model 1		4.23			4.05		
T/RD	Sep-Dec	0.0278	70.2	0.003	0.0078	80.2	0.002
S	Feb-Aug	-0.00172			-0.00142		
Tgmin	Nov-Feb	-0.578			-0.0463		
Aphid	score	-			0.199		
Model 2		3.94			3.69		
T/RD	Sep-Dec	0.283	67.4	0.005	0.0095	77.5	0.003
S	Mar-Aug	-0.0155			-0.00119		
Tgmin	Nov-Feb	-0.0575			-0.0465		
Aphid	score	-			0.202		
Model 3		4.31			4.07		
T/RD	Sep-Dec	0.056	70.2	0.003	0.034	78.1	0.002
S	Feb-Aug	-0.00116			-0.00108		
Tmax	Jan-Feb	-0.089			-0.0643		
Aphid	score	-			0.184		
Model 4		3.97			3.69		
T/RD	Sep-Dec	0.058	68.2	0.004	0.0367	76.1	0.004
S	Mar-Aug	-0.00089			-0.000764		
Tmax	Jan-Feb	-0.0929			-0.0690		
Aphid	score	-			0.184		
Model 5		4.74			4.16		
T/RD	Sep-Oct	0.0346	72.0	0.002	0.0178	80.9	0.001
S	Feb-Aug	-0.00199			-0.00154		
Tgmin	Nov-Feb	-0.0504			-0.0413		
Aphid	score	-			0.189		
Model 6		4.49			3.86		
T/RD	Sep-Oct	0.0343	69.2	0.004	0.0169	78.1	0.002
S	Mar-Aug	-0.00187			-0.00134		
Tgmin	Nov-Feb	-0.0496			-0.042		
Aphid	score	-			0.192		

Table 10.1 continued.

		Without aphid variable			With aphid variable		
Predictors		Coef.	R-sq	P	Coef.	R-sq	P
Model 7		5.37			4.70		
T/RD	Sep-Oct	0.0514	72.3	0.002	0.0347	79.5	0.002
S	Feb-Aug	-0.00172			-0.00143		
Tmax	Jan-Feb	-0.0776			-0.057		
Aphid	score	-			0.175		
Model 8		5.13			4.44		
T/RD	Sep-Oct	0.0505	69.8	0.003	0.0338	77.1	0.003
S	Mar-Aug	-0.00158			-0.00121		
Tmax	Jan-Feb	-0.0788			-0.0603		
Aphid	score	-			0.177		

The percentage of variation in the autumn aphid data accounted for, and the significance of the relationship are shown for each regression with and without the variable representing the size of the previous autumn migration in Table 10.2. All the regressions were significant and the inclusion of the aphid variable improved the percentage of variation accounted for in all eight cases. The signs of the coefficients were consistent with the relationships identified using correlation: rainfall predictors were positively related to aphid numbers, sunshine and temperature predictors were negatively related to aphid numbers and the score for the previous year's aphid migration was positively related to aphid numbers.

Testing of models Autumn suction trap data from the Queen's University of Belfast, Newforge Lane (DANI), and weather data from Aldergrove airport, for 1977-90, were obtained for the testing of the eight models. Grass minimum was not measured at Aldergrove, but since 1982, it has been measured at Newforge Lane, therefore, only half the models could be tested on Belfast data prior to 1982. Both Aldergrove & Newforge Lane weather data are henceforth referred to as the Belfast weather data.

The Belfast data used to test the models are compared with the Auchincruive data used to produce the models in Table 10.3. Important differences are that most weather variables in Belfast have greater coefficients of variation, and that the rainfall predictors at the two sites are unrelated.

The use of a good model would be to provide an indication of the likely size of the migration, therefore, studying model predictions in terms of the aphid number scores (Table 10.1) is sensible. The predicted scores are shown for the models with and without the variable representing the size of the previous years autumn migration (Tables 10.4 & 10.5).

All models had a tendency to underestimate autumn aphid numbers (large negative bias). Clearly, inclusion of the scores representing the previous year's autumn migration in the eight regression equations improves the

Table 10.3 Comparison of the values of model predictors of Belfast & Auchincruive.

	Belfast / Auchincruive									
	Rainfall per rain day				Total sunshine				Temperature ^{o}C			
	mm/day^{-1}				hours				Mean maximum		Grass minimum	
Year	Sep - Oct		Sep - Dec		Feb - Aug		Mar - Aug		Jan - Feb		Nov - Feb	
1975	-	7.1	-	18.0	-	1310	-	1193	-	16.2	-	3.7
1976	-	10.1	-	18.3	-	1087	-	1047	-	15.1	-	1.4
1977	16.8	16.7	24.8	25.5	1118	1177	1069	1096	11.4	11.8	-	-7.5
1978	7.5	16.3	14.2	25.9	854	967	787	882	11.2	10.9	-	-4.8
1979	6.2	9.5	20.6	19.8	865	947	794	858	7.9	7.9	-	-8.6
1980	8.2	8.0	18.0	20.3	869	997	817	955	12.6	12.2	-	-3.8
1981	9.8	13.8	17.0	24.8	862	960	810	885	13.8	13.9	-	-2.8
1982	13.1	17.2	18.7	24.7	1025	1065	971	997	13.9	13.4	-	-6.8
1983	9.7	11.8	20.0	25.4	886	944	811	860	13.1	14.0	-2.8	-2.5
1984	7.9	12.8	15.7	20.5	1087	1116	1035	1063	12.3	12.3	0.2	1.2
1985	7.9	13.6	15.9	24.1	856	925	780	826	10.2	11.0	-7.1	-4.9
1986	10.1	16.8	17.8	26.4	935	923	856	840	9.1	8.6	-12.6	-7.3
1987	15.3	10.5	13.1	23.8	840	879	764	816	11.3	11.5	-5.4	-0.5
1988	10.9	9.7	18.4	20.7	942	996	872	938	14.1	14.2	1.8	-0.3
1989	8.8	10.4	16.4	20.3	1165	1083	1076	1024	17.6	17.8	7.2	5.6
1990	7.8	6.5	15.3	14.7	924	920	868	884	16.9	17.1	3.2	-0.5
mean	10.0	12.4	17.6	22.6	945	993	879	923	12.5	12.6	-2.0[a]	-3.1
cv	0.31	0.28	0.17	0.15	0.12	0.09	0.13	0.10	0.22	0.22	3.2	1.3
r	0.381		0.190		0.870***		0.914***		0.988***		-	

[a] 1983-1990 mean. All other means for 1977-90.

r correlation coefficients between Auchincruive & Belfast data. *** = $P < 0.001$

accuracy of the models, as indicated by the percentage of variation in the aphid data accounted for by the models (Table 10.2). None of the eight models is clearly superior: all models grossly underestimated in 1977, 1984 & 1988, and grossly overestimated in 1979.

Table 10.4 Predictions of models without the score for the previous years autumn migration, expressed as scores (Table 10.1), when tested on the Belfast weather data 1977-1990.

	Score for size of *R. padi* migration								
	Model number								Observed at
Year	1	2	3	4	5	6	7	8	Belfast
1977	-	-	2	2	-	-	2	2	4
1978	-	-	1	1	-	-	2	2	4
1979	-	-	3	3	-	-	2	2	1
1980	-	-	1	1	-	-	2	1	2
1981	-	-	1	1	-	-	2	1	1
1982	-	-	1	1	-	-	1	1	2
1983	2	2	1	1	2	2	2	2	2
1984	1	1	1	1	1	1	1	1	3
1985	3	2	1	1	3	2	2	2	4
1986	4	4	2	2	4	4	2	2	4
1987	2	2	1	1	2	2	2	1	2
1988	1	1	1	1	1	1	1	1	3
1989	1	1	1	1	1	1	1	1	1
1990	1	1	1	1	1	1	1	1	2

Table 10.5 Predictions of models including the score for the previous years autumn migration, expressed as scores (Table 8.1), when tested on the Belfast weather data 1977-1990.

	Score for size of *R. padi* migration								
	Model number								Observed at
Year	1	2	3	4	5	6	7	8	Belfast
1977	-	-	1	1	-	-	1	1	4
1978	-	-	3	2	-	-	4	4	4
1979	-	-	4	4	-	-	4	4	1
1980	-	-	1	1	-	-	1	1	2
1981	-	-	2	1	-	-	2	2	1
1982	-	-	1	1	-	-	1	1	2
1983	2	2	2	1	2	2	2	2	2
1984	1	1	1	1	1	1	1	1	3
1985	4	4	3	3	4	4	4	4	4
1986	4	4	4	4	4	4	4	4	4
1987	4	4	3	2	4	4	3	3	2
1988	1	1	1	1	1	1	1	1	3
1989	1	1	1	1	1	1	1	1	1
1990	1	1	1	1	1	1	1	1	2

Sensitivity analyses The population dynamics of *R. padi* are not fully understood. However, A'Brook (1981) found an association between autumn numbers and preceding summer rainfall. Therefore, if there is any justification for any parameter in the models being more important, that variable would be summer sunshine, which is negatively correlated with summer rainfall.

The results of sensitivity analyses for the eight models including the variable representing the size of the previous year's *R. padi* migration, are shown in Table 10.6, for the approximate range of observed values of the predictors at Auchincruive 1975-90. In these sensitivity

Table 10.6 Sensitivity analyses for the eight models including the predictor for the size of the previous year's *Rhopalosiphum padi* migration.

Model predictions obtained when predictors[a] are varied to the extent observed at Auchincruive 1975-90

	Rainfall		Grass minimum		Sunshine		Score	
Ranges[b]	*18*	*27*	*-9*	*6*	*950*	*1350*	*1*	*4*
Model 1	**1755**	**2063**	**3772**	**762**	**4681**	**658**	**1193**	**4716**
Ranges	*18*	*27*	*-9*	*6*	*750*	*1250*	*1*	*4*
Model 2	**1439**	**1752**	**3149**	**632**	**3363**	**855**	**986**	**3980**
Ranges	*18*	*27*	*8*	*18*	*950*	*1350*	*1*	*4*
Model 3	**1328**	**2686**	**3642**	**829**	**2205**	**815**	**1189**	**4238**
Ranges	*18*	*27*	*8*	*18*	*750*	*1250*	*1*	*4*
Model 4	**1140**	**2439**	**3373**	**689**	**2607**	**1082**	**1046**	**3730**

[a] Predictors not being varied at that stage had values close to the average observed at Auchincruive 1975-90.

[b] The first italicised value is similar to the lowest observed value of the predictor at Auchincruive 1975-90 whereas the second italicised value is similar to the highest value.

Table 10.6 continued.

Model predictions obtained when predictors[a] are varied to the extent observed at Auchincruive 1975-90

	Rainfall		Grass minimum		Sunshine		Score	
Ranges	*7*	*17*	*-9*	*6*	*950*	*1350*	*1*	*4*
Model 5	**1523**	**2295**	**3469**	**833**	**2465**	**597**	**1210**	**4464**
Ranges	*7*	*17*	*-9*	*6*	*750*	*1350*	*1*	*4*
Model 6	**1230**	**1815**	**2801**	**657**	**3522**	**753**	**960**	**3616**
Ranges	*7*	*17*	*8*	*18*	*950*	*1350*	*1*	*4*
Model 7	**1256**	**2792**	**3470**	**934**	**2421**	**649**	**1252**	**4192**
Ranges	*7*	*17*	*8*	*18*	*750*	*1250*	*1*	*4*
Model 8	**1049**	**2285**	**2974**	**742**	**3360**	**834**	**1030**	**3499**

[a] Predictors not being varied at that stage had values close to the average observed at Auchincruive 1975-90.

[b] The first italicised value is similar to the lowest observed value of the predictor at Auchincruive 1975-90 whereas the second italicised value is similar to the highest value.

analyses, the values of the other predictors that were not being varied at that stage, were close to the average observed at Auchincruive 1975-90.

The predictor that least affected model outcomes in each case, was the autumn rainfall parameter. Models 1 & 6 were most sensitive to changes in the sunshine predictor whereas all other models were most sensitive to the score for the size of the previous year's autumn migration. All eight models were quite responsive to changes in the winter temperature predictor, there being little difference between the two types.

The results of the sensitivity analyses indicate that these models are plausible. Of the four predictors, the rainfall in the preceding autumn should perhaps be viewed as least effective, because it is the weather variable most distant in time from the date of the prediction. However, A'Brook (1981) commented that both air temperature and rainfall during the late autumn and early winter influence the reproduction, mobility and mortality of aphids in cereal crops, but the sign of the relationship with rainfall was not specified. On the basis of the work of A'Brook (1981) who found summer rainfall to be important, models 1 & 6 appear to be best because summer sunshine, which is negatively correlated with summer rainfall, was the most effective predictor in these two models. Nevertheless, the score for the size of the previous years autumn migration improved all eight models. Therefore the

importance of this variable relative to summer sunshine, needs to be established before any of these models can be singled out as superior.

There are no *a priori* reasons for altering these models. The imperfect predictions made for the Belfast suction trap do not neccessarly imply that the same inaccuracy will be associated with future predictions using weather data recorded at Auchincruive. This inaccuracy must in part be due to the fact that the Belfast suction trap normally catches greater numbers of *R. padi* than the Ayr trap (Table 10.7), and therefore, the models had a negative bias.

In 1990, the models predicted aphid number score 1 correctly. In 1991, the models predicted either score 1 or 2 when the numbers caught by the Ayr suction trap lay in score 3

The importance of topography to suction trap catches When comparing the size of catch of two suction traps, it is important to be aware of any large differences in the siting of the two traps, so that any variations in trap catches between sites that are due to dissimilar local topography are recognized.

The Ayr suction trap is sited 2 miles east of the west coast of Scotland (the Firth of Clyde coast) on an exposed slope. In contrast, the Belfast suction trap is sited close

to the east coast of Northern Ireland in a more sheltered location. Evidently, trap catches at Ayr are likely to be limited when the wind is from a westerly point and favoured when from an easterly point (see A'Brook, 1975) whereas at Belfast, the opposite situation will probably apply.

The greatest differences in the sizes of the *R. padi* catches of these two traps (Table 10.7) occur in autumns (September + October) when large catches occur at both Ayr and Belfast. In years with relatively low suction trap catches at both sites, more *R. padi* are sometimes caught at Ayr.

Table 10.7 Suction trap catches of *Rhopalosiphum padi* at Ayr & Belfast during September & October 1977-90, and the number of days with any of the westerly and easterly Lamb daily weather types in the same periods.

	R. padi suction trap catches			Lamb weather types	
Year	Ayr	Belfast	Differences[a]	All westerly	All easterly
1977	3743	10284	-6541	30	12
1978	2456	10153	-7697	36	1
1979	1726	1404	322	20	9
1980	3491	3277	214	32	4
1981	1767	631	1136	26	1
1982	2306	2695	-389	19	2
1983	1494	2822	-1328	27	3
1984	1916	5952	-4036	26	0
1985	13739	38982	-25243	15	6
1986	6059	7765	-1706	28	4
1987	2536	2396	140	17	7
1988	2142	4421	-2279	19	10
1989	255	259	-4	-	-
1990	1143	2377	-1234	-	-

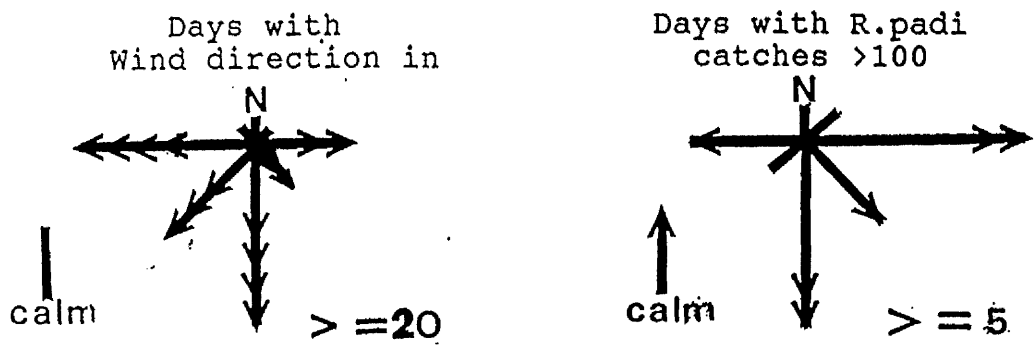
[a] Belfast catch subtracted from Ayr catch.

Daily trap catches at Ayr were analysed to test whether autumn catches of *R. padi* are limited by the incidence of westerly winds. It was found that days during the autumns of 1977-88 with trap catches greater than 100 *R. padi* were significantly associated with days when the wind direction at 0900 GMT was in the east or south (Figure 10.1) as at Aberystwyth (A'Brook, 1975).

In Britain for most of the year except the winter, winds directly off the sea are cool relative to winds from inland. The prevailing westerly winds on low ground are normally strongest on southern & western coasts of Britain which are more exposed to the west. Therefore, the higher temperatures and lighter winds associated with wind directions from the south & east at Ayr, relative to the prevailing westerly winds, could be as critical as the fact that westerly winds come directly off the Firth of Clyde where there are presumably relatively few aphids, if the possibility of aphids from the Isle of Arran is considered. These facts may explain why the *R. padi* catches at Belfast are normally greater than those at Ayr.

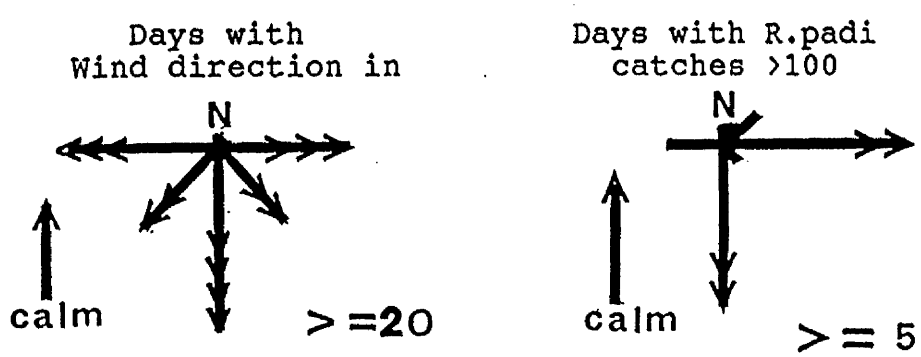
The Lamb daily weather types (Lamb, 1950; section 2.4) relate to the surface airstream over the whole British Isles, and unlike wind direction measurements made at climatological stations at specific times, they refer to the average synoptic type in the full 24 hours. Because westerly winds limit trap catches at Ayr and easterly winds may limit trap catches at Belfast, the number of days with

SEPTEMBERS 1977-1988



$x^2_{(7)} = 29.4, \quad P < 0.01$

OCTOBERS 1977-1988



$x^2_{(7)} = 22.9, \quad P < 0.001$

Figure 10.1 Comparison of the distribution of daily wind direction measurements made at 0900 GMT at Auchincruive in September & October 1977-88 with the distribution of daily wind direction measurements on days when the Ayr suction trap caught 100 or more *Rhopalosiphum padi*.

the nine westerly and nine easterly Lamb daily weather types were noted for each September to October period 1977-88 (Table 10.7). These were compared with the differences in the *R. padi* catches between the Ayr and Belfast suction traps.

Clearly, the westerly and easterly Lamb daily weather types do not explain a large proportion of the variation. However, in 1977 & 1978, high incidences of westerly winds were associated with large aphid catch differences between Ayr and Belfast, many more being caught at Belfast. Two of the three years with larger trap catches at Ayr (1979 & 1987) had relatively high incidences of easterly types, although the two years with the highest incidence of the Lamb easterly types (1977 & 1988) had much larger trap catches at Belfast.

The importance of wind direction to the size of *R. padi* trap catches at Ayr reduces the value of predictions made using the eight models (Table 8.2). It also a good illustration of the site-specific factors that may affect the catch size of individual suction traps.

10.2.2 **Variation of the size of the autumn migration of** *R. padi* **between years and between regions of Britain**

R. padi-transmitted BYDV is associated with southern and western coastal areas of Britain (Plumb, 1974; Figure 4.30). The size of the autumn migration of *R. padi* is considered to be a factor in the risk of *R. padi*-transmitted BYDV in autumn-sown cereals (Plumb, 1986).

This hypothesis is partially supported by the generally larger numbers of *R. padi* caught by suction traps in the west of Britain (Table 10.8).

Table 10.8 Comparison of the mean number of *Rhopalosiphum padi* caught by suction traps in western and eastern England 10 September to 7 October 1976-88.

	Numbers of *R. padi*			
Year	Preston	Hereford	Rothamsted	Brooms Barn
1976	860	55	160	333
1977	11519	2826	1113	864
1978	8401	3646	966	1878
1979	2568	2887	752	881
1980	8338	3704	1842	2942
1981	972	114	43	71
1982	22707	6609	1611	1274
1983	2699	513	174	221
1984	8463	1045	204	447
1985	26194	9172	2446	3366
1986	9899	2974	705	1211
1987	16144	3892	562	948
1988	5727	680	420	1901
mean	9576	2932	846	1257
cv	0.83	0.91	0.87	0.81

However, the north-south axis of Britain may also be important to *R. padi* suction trap catches during the autumn.

For this analysis, one trap from the west of each of England & Scotland and two traps from the east were selected, and meteorological data from a climatological station nearby to each trap were obtained from the *Monthly Weather Report* (Table 10.9). The number of *R. padi* caught

Table 10.9 Details of the six climatological stations which relate to six 12.2 m suction traps.

Climatological station	Altitude	Latitude	Longitude	National grid reference	Suction trap site
Auchincruive	48	55 28N	04 34W	NS 379233	Ayr
Dundee	45	56 28N	02 56W	NO 422313	Dundee
East Craigs	61	55 57N	03 19W	NT 183735	East Craigs
Brooms Barn	75	52 16N	00 34E	TL 753657	Brooms Barn
Rothamsted	128	51 48N	00 21W	TL 132134	Rothamsted
Starcross	9	50 38N	03 27W	SX 972821	Starcross

from 10 September to 4 November 1976-90 (data obtained from Part II of Rothamsted Reports) is shown for each suction trap in Table 10.10.

Table 10.10 Numbers of *Rhopalosiphum padi* caught by the six suction traps 10 September to 4 November 1976-90.

	Numbers of *R. padi*					
Year	D	A	E	S	R	B
1976	1646	680	1527	394	414	851
1977	8809	3742	3840	2317	1942	1418
1978	11531	1955	2778	9972	2514	4514
1979	12411	1284	6251	6001	1575	1924
1980	4531	3449	3966	696	2240	3384
1981	11300	764	4451	78	66	115
1982	3332	2965	3480	3758	2537	2708
1983	6188	1530	1804	972	338	469
1984	4568	1322	3097	2063	707	1382
1985	60924	12843	18353	6650	4888	6394
1986	20917	6022	10516	7836	1384	2822
1987	2570	2635	4501	937	1007	2007
1988	3686	2061	3449	1056	628	2533
1989	1480	242	474	1648	495	1100
1990	1052	1043	1076	558	683	780
mean	10330	2836	4638	2996	1428	2160
cv	1.45	1.11	0.97	1.04	0.88	0.77

cv coefficient of variation (sd/mean)

t-tests between Scottish & English sites:

mean t = 1.62, df 4, N.S.

cv t = 1.72, df 4, N.S.

In most years, larger numbers of *R. padi* are caught by the Scottish suction traps during the autumn, relative to those of England although at least one English trap catch

exceeded that at Ayr in 8 of the 15 years: see section 10.2.1 for an explanation of the relatively low catches at Ayr. However, if the period of the autumn migration is split in half, the difference between England & Scotland is seen to be more apparent in the first half of the autumn, although it is not significant (Tables 10.11 & 10.12).

Table 10.11 Numbers of *Rhopalosiphum padi* caught by the six suction traps 10 September to 7 October 1976-90.

	Numbers of *R. padi*					
Year	D	A	E	S	R	B
1976	924	439	715	180	160	333
1977	7189	2425	1433	1302	1113	864
1978	7691	694	1823	2566	966	1878
1979	4931	773	4355	1107	752	881
1980	3697	2700	3496	648	1842	2942
1981	11073	698	4296	28	43	71
1982	2828	1471	3063	2877	1611	1274
1983	5086	1034	1112	268	174	221
1984	2651	966	2023	654	204	447
1985	52230	10778	14108	3421	2446	3366
1986	18380	5726	9635	4927	705	1211
1987	2070	2058	3957	602	562	948
1988	2091	614	2331	680	420	1901
1989	1237	227	344	390	137	610
1990	490	461	636	341	21	76
mean	8171	2071	3555	1333	744	1135
cv	1.60	1.34	1.05	1.08	0.98	0.88

t-tests between Scottish & English sites:

mean t = 1.91, df 4, N.S.

cv t = 2.07, df 4, N.S.

Scotland
D Dundee
A Ayr
E East Craigs

England
S Starcross
R Rothamsted
B Brooms Barn

Table 10.12 Numbers of *Rhopalosiphum padi* caught by the six suction traps 8 October to 4 November 1976-90.

	Numbers of *R. padi*					
Year	D	A	E	S	R	B
1976	722	241	812	214	254	518
1977	1620	1317	2407	1015	829	554
1978	3840	1261	955	7406	1548	2636
1979	7480	511	1896	4894	823	1043
1980	834	749	470	48	398	442
1981	227	66	155	50	23	44
1982	504	1494	417	881	926	1434
1983	1102	496	692	704	164	248
1984	1917	356	1074	1409	503	935
1985	8694	2065	4245	3229	2442	3028
1986	2537	296	881	2909	679	1611
1987	500	577	544	335	445	1059
1988	1595	1447	1118	376	208	632
1989	243	15	130	1258	358	490
1990	562	582	440	217	662	704
mean	2158	765	1082	1663	684	1025
cv	1.21	0.79	0.99	1.27	0.90	0.83

t-tests between the Scottish & English sites:

mean t = 0.41, df 4, N.S.

cv t = -0.02, df 4, N.S.

Scotland
D Dundee
A Ayr
E East Craigs

England
S Starcross
R Rothamsted
B Brooms Barn

The relationship between the size of the early (Table 10.11) and late (Table 10.12) autumn catches of *R. padi* was examined by correlation and by subtraction of the late autumn catches from the early autumn catches (Table 10.13).

Table 10.13 Differences between the numbers of *Rhopalosiphum padi* caught from 10 September to 7 October and the numbers caught from 8 October to 4 November at the six sites 1976-90.

	Numbers of *R. padi*[a]					
Year	D	A	E	S	R	B
1976	202	198	-97	-34	-94	-185
1977	5569	1108	-974	287	284	310
1978	3851	-567	868	-4840	-582	-758
1979	-2549	262	2459	-3787	-71	-162
1980	2863	1951	3026	600	1444	2500
1981	10846	632	4141	-22	20	27
1982	2324	-23	2646	1996	685	-160
1983	3984	538	420	-436	10	-27
1984	734	610	949	-755	-299	-488
1985	43536	8713	9863	192	4	338
1986	15843	5430	8754	2018	26	-400
1987	1570	1481	3413	267	117	-111
1988	496	-833	1213	304	212	1269
1989	994	212	214	-868	-221	120
1990	-72	-121	196	124	-641	-628
mean	6013	1306	2473	-330	60	110
cv	1.89	1.93	1.27	5.52	8.38	7.43
r	0.709**	0.517*	0.651**	0.530*	0.735**	0.620*

[a] late autumn catches subtracted from early autumn catches.

t-tests between Scottish & English sites:

mean t = 2.33 df 4, N.S.

cv t = -6.24 df 4, P = 0.0034

r correlation coefficient between the numbers of *R. padi* caught from 10 September to 7 October and the numbers caught from 8 October to 4 November at that site. * P < 0.05 ** P < 0.01

All six correlations between early and late autumn migrations were positive and significant indicating that the differences between the size of the early & late autumn catches were greater when the early autumn catch was larger.

The greatest differences were found in Scotland where early autumn catches of *R. padi* are largest. In England, not only were the differences smaller, but negative values were almost as common as positive values, indicating that late autumn catches greater than early autumn catches are nearly as frequent as early autumn catches greater than late autumn catches.

Although the t-test between the mean difference of the English & Scottish suction traps gave a non-significant result, the significant result between the coefficients of variation identifies the greater variability between the early and late autumn catches of *R. padi* in England.

Winter temperature data and summer rainfall data are presented, along with the PSC quints (section 2.4) of the winter and summer seasons preceding the autumns of the aphid catches in Table 10.14. In the following analyses, evidence to support the weather parameters identified as important in the mathematical modelling (section 10.2.1) was looked for.

TWINSPAN was used to group years with similar distributions of autumn *R. padi* catches between the six suction traps (3 in England and 3 in Scotland). Three separate analyses were carried out because of the differences revealed by Table 10.13: the early autumn, Table 10.15; the late autumn, Table 10.16; and the whole autumn, Table 10.17),

Table 10.14 Winter temperature data (from Table 3.16), summer rainfall data (using data from climatological stations in Table 10.9) and the PSC quints of the the winter and summer preceding the autumn of the aphid catches.

	Mean winter °C temperature		Total summer (June to Aug) rainfall mm		Quints					
					Winter			Summer		
Year	Scotland	England	Scotland	England	P	S	C	P	S	C
1976	4.9	4.4	236	170	4	2	1	1	3	1
1977	2.2	3.2	578	529	1	3	5	1	1	2
1978	2.6	3.6	552	492	2	4	4	2	1	2
1979	1.6	1.5	541	364	1	4	4	5	3	3
1980	3.5	4.4	856	607	1	3	5	2	3	5
1981	4.0	3.9	418	335	4	1	1	3	2	1
1982	2.2	2.2	469	575	1	5	3	2	4	3
1983	3.4	4.1	354	245	4	2	2	1	3	1
1984	3.6	4.0	295	369	2	5	4	1	3	1
1985	3.2	2.3	913	538	1	3	2	4	5	5
1986	2.5	2.7	518	541	1	3	5	1	2	3
1987	3.1	3.0	769	615	1	3	2	1	1	4
1988	4.4	5.0	742	626	2	5	3	2	4	4
1989	6.3	5.9	519	354	5	5	2	4	4	1
1990	4.4	6.3	-	-	3	5	4	3	5	5
mean	3.5	3.8	554[a]	454[a]						
cv	0.35	0.35	0.37	0.32						

[a] 1976-89 mean - data for 1990 not available

Table 10.15 TWINSPAN refined-ordination table after 3 divisions; totals of *Rhopalosiphum padi* 10 September to 7 October 1976-90.

"Pseudo-species" level

	Autumn														
Year	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
	8	7	8	8	9	7	8	8	8	7	7	8	8	8	8
	1	6	4	9	0	7	0	3	7	8	9	8	2	5	6
AYR	2	2	2	2	2	3	3	3	3	2	2	2	3	4	3	1
EAST CRAIGS	3	2	3	2	2	3	3	3	3	3	3	3	3	4	3	01
DUNDEE	4	2	3	3	2	3	3	3	3	3	3	3	3	4	4	01
STARCROSS	1	2	2	2	2	3	2	2	2	3	3	2	3	3	3	00
ROTHAMSTED	1	2	2	2	1	3	3	2	2	2	2	2	3	3	2	00
BROOMS BARN	1	2	2	2	1	2	3	2	2	3	2	3	3	3	3	00
	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	
	0	0	0	0	0	1	1	1	1	1	1	1				
	0	1	1	1	1	0	0	0	0	1	1	1				
	A					B				C			D			

"Pseudo-species" levels

1	=	1	-	99
2	=	100	-	999
3	=	1000	-	9999
4	=		>	10000

Table 10.16 TWINSPAN refined-ordination table after 3 divisions; totals of *Rhopalosiphum padi* 8 October to 4 November 1976-90.

"Pseudo-species" levels

	Autumn														
Year	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
	8	8	7	8	8	9	8	8	8	7	8	7	7	8	8
	2	7	6	0	1	0	3	6	9	8	5	7	9	4	8
AYR	4	3	3	3	2	3	3	3	2	4	4	4	3	3	4
BROOMS BARN	4	4	3	3	2	3	3	4	3	4	4	3	4	3	3
DUNDEE	3	3	3	3	3	3	4	4	3	4	4	4	4	4	4
EAST CRAIGS	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4
ROTHAMSTED	3	3	3	3	2	3	3	3	3	4	4	3	3	3	3
STARCROSS	3	3	3	2	2	3	3	4	4	4	4	4	4	4	3
	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1
	0	0	1	1	1	1									
	A						B			C					

"Pseudo-species" levels

2	=	10	-	99
3	=	100	-	999
4	=	1000	-	9999

Table 10.17 TWINSPAN refined-ordination table after 3 divisions; totals of *Rhopalosiphum padi* 10 September to 4 November 1976-90.

"Pseudo-species" levels

	Autumn															
Year	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
	7	8	8	9	8	8	8	7	8	8	8	7	7	8	8	
	6	1	3	0	4	8	9	7	0	2	7	8	9	5	6	
AYR	3	3	4	4	4	4	3	4	4	4	4	4	4	5	4	
BROOMS BARN	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	
DUNDEE	4	5	4	4	4	4	4	4	4	4	4	5	5	5	5	
EAST CRAIGS	4	4	4	4	4	4	3	4	4	4	4	4	4	5	5	
ROTHAMSTED	3	2	3	3	3	3	3	4	4	4	4	4	4	4	4	
STARCROSS	3	2	3	3	4	4	4	4	3	4	3	4	4	4	4	
	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	
	0	0	0	0	1	1	1	1	1	1	1					
					0	0	0	1	1	1	1					
	A				B			C				D				

"Pseudo-species" levels

2	=	10	- 99
3	=	100	- 999
4	=	1000	- 9999
5	=		> 10000

Using contingency tables which showed the distribution of PSC quints in the preceding winters and summers of years in each TWINSPAN end-group, or in new groups derived from the TWINSPAN end-groups, similarities in preceding winter and summer weather were sought for years with high or low aphid catches during the autumn (Tables 10.18 to 10.20). For clarity, PSC quints of the previous spring were not provided, although weather in this season must also be of relevance.

PSC indices & early autumn *R. padi* **numbers** (Table 10.18) Groups A & B (Table 10.15) were comprised of autumns with fewer *R. padi* relative to those in groups C & D.

Autumn 1981 was clearly different because of the very low numbers caught by the English suction traps. The quints of the previous winter and summer seasons of this year were $P_4S_1C_1$ and $P_3S_2C_1$ respectively. The inferences of these quints are that the winter was mild (Murray, 1972) and the summer dry, although wetter in the north than in the south (Murray & Benwell, 1970). The winter was milder than average and the summer was drier than average in both the north and the south, albeit wetter in the north (Table 10.14). Furthermore, the difference between the summer rainfall in Scotland & England was not large, whereas the difference in *R. padi* numbers was (Table 10.11).

Autumns in group A (Table 10.15) tended to have high P quints in the preceding winter and low C quints in the

preceding summer (Table 10.18). In other words, these autumns were all preceded by drier than average summers which followed mild winters (Murray & Benwell, 1970).

Table 10.18 Contingency tables examining the distribution of PSC quints in each group; totals of *Rhopalosiphum padi* from 10 September to 7 October (Table 10.15).

P quint in winter

Gp	1	2	3	4	5
A	-	1	1	2	1
B	3	-	-	1	-
C	1	2	-	-	-
D	3	-	-	-	-

P quint in summer

Gp	1	2	3	4	5
A	2	-	2	1	-
B	3	1	-	-	-
C	-	2	-	-	1
D	1	1	-	1	-

S quint in winter

Gp	1	2	3	4	5
A	1	1	-	-	3
B	-	1	3	-	-
C	-	-	-	2	1
D	-	-	2	-	1

S quint in summer

Gp	1	2	3	4	5
A	-	1	2	1	1
B	2	-	2	-	-
C	1	-	1	1	-
D	-	1	-	1	1

C quint in winter

Gp	1	2	3	4	5
A	2	1	-	2	-
B	-	2	-	-	2
C	-	-	1	2	-
D	-	1	1	-	1

C quint in summer

Gp	1	2	3	4	5
A	4	-	-	-	1
B	1	1	-	1	1
C	-	1	1	1	-
D	-	-	2	-	1

Gp Groups equal to or derived from TWINSPAN end-groups (Table 10.15)

\- denotes zero

Groups B & C (Table 10.15) had intermediate *R. padi* migrations. Autumns in these two groups tended to be preceded by winters with a low P quint indicating that they were colder than average (Murray & Benwell, 1970). The preceding summers had low P quints and variable C quints. This suggests that these summers had variable rainfall (Murray & Benwell, 1970). Only one autumn of groups B & C was preceded by a dry summer in both countries; 1983 (Table 10.14). The remaining autumns of groups B & C were preceded by summers with greater rainfall in Scotland than in England, and summer rainfall was average or above average in both countries (except 1979 in England).

Autumns in group D had high *R. padi* totals in both England & Scotland, particularly in the latter country; 1982, 1985 & 1986. These autumns had low P quints in the preceding winter and average or above average C quints in the preceding summer. As suggested by PSC quints (Murray & Benwell, 1970; Murray, 1972), all three winters were colder than average and in neither country in any of the three years was the summer rainfall much below average. However, the mean summer rainfall at the three English sites was greater than that of Scottish in two of the three years.

PSC indices & late autumn ***R. padi*** **numbers** (Table 10.19) The ordination of late autumn *R. padi* totals (Table 10.16) differs considerably from that of early autumn *R. padi* totals (Table 10.15). The three autumns on the far right of

the "early autumn" ordination (i.e. 1982, 1985 & 1986 - large early autumn migrations) were well separated in the late autumn ordination.

Table 10.19 Contingency tables examining the distribution of PSC quints in each group; totals of *Rhopalosiphum padi* from 9 October to 4 November (Table 10.16).

P quint in winter

Gp	1	2	3	4	5
A	3	-	1	2	-
B	1	-	-	1	1
C	3	3	-	-	-

P quint in summer

Gp	1	2	3	4	5
A	2	2	2	-	-
B	2	-	-	1	-
C	2	2	-	1	1

S quint in winter

Gp	1	2	3	4	5
A	1	1	2	-	2
B	-	1	1	-	1
C	-	-	2	2	2

S quint in summer

Gp	1	2	3	4	5
A	1	1	2	1	1
B	-	1	1	1	-
C	2	-	2	1	1

C quint in winter

Gp	1	2	3	4	5
A	2	1	1	1	1
B	-	2	-	-	1
C	-	1	1	3	1

C quint in summer

Gp	1	2	3	4	5
A	2	-	1	1	2
B	2	-	1	-	-
C	1	2	1	1	1

Gp Groups equal to or derived from TWINSPAN end-groups (Table 10.16)

\- denotes zero

In contrast to early autumns, late autumns with low *R. padi* totals (group A in Table 10.19) were not associated with preceding winters with a high P quint. Both cold & mild winters preceded autumns in group A. The preceding summers mostly had low P & high C quints which are often wetter and cooler than average (Murray & Benwell, 1970; Murray, 1972). The preceding summers of this group (Table 10.14) were a mixture of dry ones (1976 & 1981) and wet ones (1980 & 1987).

Late autumns with intermediate *R. padi* migrations (group B) had no associations with winter PSC quints. In the preceding summers, none had a high P or C index indicating that they were not wetter than average (Murray & Benwell, 1970). This is confirmed by the rainfall totals in Table 10.14, except for England in 1986 which was wetter than average.

Late autumns with large *R. padi* migrations (group C in Table 8.16) were preceded by winters with low P, and high S & C quints indicating that they were colder than average (Murray, 1972; Murray & Benwell, 1970). Four of the six preceding winters were colder than average (Table 10.14). These autumns were preceded by summers with variable S & C quints but low P quints. P is more positively related to summer rainfall in Scotland than England. This fact in combination with the variable C quints suggests that many of these summers were not wetter than average (Murray & Benwell, 1970). Rainfall in three of these summers (1977,

1978 & 1979) was near average, one was very dry (1984) and the other two (1985 & 1988) were much wetter than average (Table 10.14).

PSC indices & *R. padi* numbers in the whole autumn (Table 10.20) A repercussion of the different TWINSPAN ordinations of the early & late autumn *R. padi* numbers is that the TWINSPAN ordination of the pooled data is different again (Table 10.17).

The autumns with fewest *R. padi* (group A), were preceded by winters with high P quints indicating that they were milder than average. The preceding summers of group A had low or average P quints and low C quints indicating that they were hot dry summers (Murray & Benwell, 1970, Murray, 1972), which is supported by the rainfall figures in Table 10.14.

Autumns with intermediate *R. padi* migrations (groups B & C) were preceded by winters with a low P quint (i.e cold winters; Murray, 1972), and the preceding summers had low P quints and variable C quints. Therefore, these summers were not associated with high rainfall (Murray & Benwell, 1970): some were dry (1984 & 1989) and others wet (1980, 1987 & 1988).

Table 10.20 Contingency tables examining the distribution of PSC quints in each TWINSPAN end-group; totals of *Rhopalosiphum padi* for the whole autumn (Table 10.17).

P quint in winter

TW	1	2	3	4	5
A	-	-	1	3	-
B	-	2	-	-	1
C	4	1	-	-	-
D	3	-	-	-	-

P quint in summer

TW	1	2	3	4	5
A	2	-	2	-	-
B	1	1	-	1	-
C	2	2	-	-	-
D	1	1	-	1	1

S quint in winter

TW	1	2	3	4	5
A	1	2	-	-	1
B	-	-	-	-	3
C	-	-	3	-	1
D	-	-	2	2	-

S quint in summer

TW	1	2	3	4	5
A	-	1	2	-	1
B	-	-	1	2	-
C	2	-	1	1	-
D	1	1	1	-	1

C quint in winter

TW	1	2	3	4	5
A	2	1	-	1	-
B	-	1	1	1	-
C	-	1	1	-	2
D	-	1	-	2	1

C quint in summer

TW	1	2	3	4	5
A	3	-	-	-	1
B	2	-	-	1	-
C	1	1	1	-	1
D	-	1	2	-	1

TW TWINSPAN end-group - denotes zero

Autumns with large *R. padi* migrations (group D) were preceded by winters with a low P quint (i.e cold winters [Murray, 1972]), but the summers showed little affinity for either P, S or C indices, suggesting that there is no

link between large *R. padi* migrations in the whole autumn (i.e. 10 September to 4 November) and summer rainfall greater than average. Both 1985 & 1986 were wet summers, but 1978 & 1979 had summer rainfall closer to average.

The Lamb daily weather types and *R. padi* numbers Quintile boundaries of PSC indices have only been calculated for months or meteorological seasons. For *R. padi*, consideration of rainfall in the May-August period is perhaps biologically more meaningful than rainfall in the summer months (June-August) alone. Therefore, for each of 1976-88, the number of days in May-August with the cyclonic, anticyclonic and straight westerly Lamb daily weather types was calculated in addition to the total rainfall in the same periods (Table 10.21).

High incidences of cyclonic days or straight westerly days are indicative of wet summers, whereas high incidences of anticyclonic days are indicative of dry summers. Dual combinations of these Lamb weather types provide more information. High incidences of both cyclonic days & straight westerly days are indicative of a wet summer in both the north & south of Britain. High incidences of both anticyclonic days & straight westerly days are indicative of a wetter summer in the north of Britain than in the south.

Table 10.21 The number of days in May-August 1976-88 with the cyclonic (C), anticyclonic (A) and straight westerly (W) Lamb daily weather types and the total rainfall (same period) of England & Scotland (calculated from the six sites).

	Number of days May-August			Total summer (May to August) rainfall mm	
Year	C	A	W	Scotland	England
1976	11	41	6	448	256
1977	19	23	12	689	662
1978	11	27	14	633	648
1979	29	25	15	705	636
1980	32	14	6	910	680
1981	18	27	10	603	631
1982	24	21	22	613	780
1983	23	43	7	590	548
1984	10	39	10	389	580
1985	36	14	21	1074	708
1986	22	20	17	803	718
1987	23	18	12	907	772
1988	27	28	16	877	801
mean	22	26	13	711	648
cv	0.37	0.37	0.40	0.28	0.22

It has been established that large *R. padi* migrations in early autumn (Table 10.18) are associated with high rainfall in the preceding summer more than large late autumn migrations (Table 10.19). Therefore, the annual values of C, A & W were pooled (Table 10.22) according to the groups derived from the TWINSPAN end-groups of early autumn migrations (Table 10.15). The relevance of these three Lamb daily weather types to *R. padi* numbers in the early autumn was examined by Chi-squared tests on the pooled data (Table 10.22).

Table 10.22 Group (from Table 10.15) total values of the incidences of the cyclonic (C), anticyclonic (A) and straight westerly (W) Lamb daily weather types May-August 1976-88.

		Number of days May-August		
Group	n	C	A	W
A	3	39	107	26
B	4	97	98	37
C	3	67	80	45
D	3	82	55	60

All	$x^2_{(6)} = 52.3$,	$P < 0.001$
A & W	$x^2_{(3)} = 32.4$,	$P < 0.001$
C & W	$x^2_{(3)} = 7.5$,	N.S.
C & A	$x^2_{(3)} = 33.6$,	$P < 0.001$

All three Lamb daily weather types vary as expected in relation to to the *R. padi* groups. High incidences of cyclonic & westerly Lamb weather types being associated with groups C & D and high incidences of the anticyclonic Lamb weather type being associated with groups A & B. However, there were no significant differences between groups when the combination of cyclonic & westerly days was tested. The combination of anticyclonic & westerly days was significant indicating that this combination could be important in determining the distribution of sizes of *R. padi* suction trap catches in Britain during the autumn, via influencing the distribution of May to August rainfall.

10.2.3 **Predicting the size of the autumn migration of** *R. padi* **by assessing** *R. padi* **numbers in ryegrass pasture in late August**

Methodology This was based on that described in section 5.2. Five areas in each field were sampled.

1989 Assessments took place in three of the regions in which pre-harvest sampling took place in July (section 8.3.1). Two fields were sampled in each of Wigtownshire & Stirlingshire, and one field in Ayrshire. Numbers in excess of 100 per m^2 were sampled in one Wigtownshire field and both Stirlingshire fields. In contrast, few aphids were found in the one sampled field of Ayrshire.

Each sampled region was allocated to one of three categories

(Table 10.23):

Category 0:- No *R. padi*.

Category 1:- Low numbers of *R. padi* (< 10 per m^2).

Category 2:- High numbers of *R. padi* (> 10 per m^2).

Table 10.23 Regional *Rhopalosiphum padi* abundance in ryegrass pastures during late August 1989.

Region	Abundance
Wigtownshire	2
Ayrshire	1
Stirlingshire	2

1990 Assessments took place in the same three regions in which pre-harvest sampling took place in July (section

8.3.2). Three fields were sampled in each region. Table 10.24 shows the numbers of *R. padi* sampled in each of the five areas per field. Numbers in excess of 100 per m^2 were sampled in one Wigtownshire field. The maximum abundance observed in other fields was 19 per m^2 at Beoch, another Wigtownshire field.

Table 10.24 Numbers of *Rhopalosiphum padi* in ryegrass pasture during late August 1990 in five sampling areas.

	Number of *R. padi*					
Field	1	2	3	4	5	Totals
Dumfriesshire						
Charlesfield	1	3	1	6	2	13
Dryfeholme	3	7	3	8	5	26
Spitalridding	1	2	3	2	2	10
Wigtownshire						
Beoch	10	10	19	9	5	53
Kirkmabreck[a]	100	200	50	100	100	550
Kirranrae	5	1	1	7	2	16
Stirlingshire						
East third	5	3	9	9	0	26
Shearerston	7	4	17	14	5	47
Westwood	2	0	1	3	0	6

[a] estimates

The data in Table 10.24 (log(n + 1) transformation) were analysed using Analysis of Variance. Table 10.25 shows the significant result obtained when the 15 observations per region were compared, indicating that there were regional differences in the numbers of *R. padi* in ryegrass pasture during late August 1990.

Table 10.25 Analysis of Variance; log (n + 1) *Rhopalosiphum padi* numbers sampled in ryegrass pasture in three regions during late August 1990.

```
ANALYSIS OF VARIANCE ON R. padi numbers
SOURCE        DF        SS         MS         F         P
Region         2     3.475      1.737      7.98     0.001
ERROR         42     9.140      0.218
TOTAL         44    12.614

                                        INDIVIDUAL   95 PCT  CI'S
FOR MEAN
                                        BASED  ON  POOLED  STDEV
 LEVEL              N       MEAN       STDEV    ---------+---------+---------+-------
Dumfriesshire      15     0.5800      0.2124    (-------*-------)
Wigtownshire       15     1.1964      0.6600                              (-------*-------)
Stirlingshire      15     0.6381      0.4148       (-------*-------)
                                                 ---------+---------+---------+-------
    POOLED  STDEV  =    0.4665                          0.60      0.90      1.20
```

To judge the relevance of these assessments to the size of the *R. padi* migration in the following autumns, the *R. padi* catches of the Ayr, Belfast & Dundee suction traps are shown for 1989 & 1990 along with the 10 year average (Table 10.26).

Table 10.26 The 1981-90 average number of *Rhopalosiphum padi* caught during September and October at Ayr, Belfast and Dundee by 12.2 m suction traps, and the figures for 1989 and 1990.

R. padi suction trap catches
September to October

Site	Average	1989	1990
Ayr	3236	254	1044
Belfast	4537	249	2377
Dundee	12090	1512	1163

R. padi catches of the Dundee suction trap can be viewed as representative of the aerial aphid fauna of Stirlingshire, whereas trap catches of Belfast & Ayr representative of Wigtownshire & Ayrshire respectively. Dumfriesshire cannot be reasonably related to any suction trap. The following is a crude attempt to compare the relative magnitudes of the *R. padi* samples in ryegrass pasture in late August, with the relative magnitudes of the three suction trap catches in the succeeding autumn.

In 1989, the Dundee trap catch and Stirlingshire ryegrass samples, and the Ayr trap catch and the Ayrshire ryegrass samples were consistent, whereas those of Belfast and Wigtownshire were not.

In 1990, the Dundee trap catch and Stirlingshire ryegrass samples and the Belfast trap catch and the Wigtownshire ryegrass samples were consistent (Dumfriesshire ignored).

10.3 **Discussion**

10.3.1 **Mathematical modelling** The identification of preceding winter temperature and the size of the previous year's *R. padi* migration as critical factors in the size of the autumn migration, is a new contribution to knowledge of *R. padi* population dynamics. A'Brook (1981) did not find winter temperature to be important and he did not include the size of the previous year's autumn migration in the analyses. However, the fact that air temperature and

rainfall in the late autumn period was found by A'Brook (1981) to influence the survival & mobility of *R. padi* in crops during the autumn, suggests that these variables might reflect the number of virginoparae that enter the winter. This could be the biological significance of the autumn rainfall predictors included in the eight models, wet (or the associated mild temperatures) autumns & early winters favouring virginoparae survival.

The importance of cold winters in delaying the spring date of crop colonisation by an aphid species is well-established (Turl, 1982; Walters & Dewar, 1986; Harrington *et al.*, 1990). It is reasonable to assume that cold winters can delay all aphids irrespective of the time of year at which their numbers peak.

The importance of cold winters identified both by mathematical modelling using Auchincruive data, and by use of PSC indices on *R. padi* data from both the north & south of Britain, suggests three things. Firstly, the unfavourable effects that cold winters have on aphids overwintering anholocyclically can affect the population growth of *R. padi* in the succeeding summer & autumn, presumably because of the relatively few that survive cold winters. Secondly, in spite of the greater abundance of the primary host of *R. padi*, *Prunus padus*, in northern Britain (Perring & Walters, 1976), migrants derived from holocyclic clones on *P. padus* are of no consequence to *R. padi*

population dynamics during the summer and the autumn, relative to those from anholocyclic clones. If migrants from holocyclic clones were important, cold winters would probably not be a factor favouring large migrations at Auchincruive. Thirdly, the scarcity of aphids in general in springs following cold winters (Walters & Dewar, 1986), and the associated scarcity of natural enemies relative to their abundance after milder winters (Chambers *et al.*, 1986), may be a factor in the development of large *R. padi* migrations during the autumn.

The improvement to the models engendered by the inclusion of the scores of the size of the previous year's *R. padi* migration (Table 10.2), implies that in autumns following preceding small autumn migrations, the size of the aerial population can be limited. Conversely, a high previous autumn migration can boost the size of the following autumn migration. The sensitivity analyses (Table 10.6) show that this predictor is important to model outcomes. This can be taken to indicate that large autumn migrations occur in years when the largest population peak of *R. padi* in grassland occurs in the autumn.

Wiktelius (1987) found a negative correlation between the sizes of the summer & autumn migration, and concluded that the size of the autumn migration is mainly dependent on aphid population growth in grasslands during late summer & autumn. If other model predictors are favourable for a large autumn migration, the size of the previous year's

migration can either lead to an earlier population peak in grassland or to a later one. Thus, the size of the autumn migration of *R. padi* may be a compromise between the weather in the previous winter & summer, and the number of virginoparae (the size of the previous year's autumn migration is likely to be related to this) that enter the previous winter.

The greater importance of a summer (Feb-Aug) sunshine variable than a summer rainfall variable (which are negatively correlated) found during the modelling, may be because sunshine increases the contrast between standard air temperature at 1.25 m, as measured by thermometers in Stevenson screens, and air temperature recorded within a crop canopy (Broadbent, 1950b). The population growth of *R. padi* in grassland may be slowed in a wet cloudy summer because of the relatively low temperatures in the grass canopy, whereas in a dry sunny summer, the much higher temperatures within the grass canopy will lead to short generation times. A summer sunshine variable, therefore includes good information on the rate of aphid population growth in addition to information on rainfall amount, compared with a summer rainfall variable. Also, a pitfall of rainfall data is that they can be boosted by heavy showers or thunderstorms irrespective of whether the summer is warm & sunny, or cool & cloudy. The non-existence of a relationship between autumn rainfall at Ayr & Belfast 1977-90 (Table 10.3) illustrates the dangers of rainfall data.

10.3.2 Variation of the size of the autumn migration of *R. padi* between years and between regions of Britain

The importance of crop drilling date to the incidence of BYDV in autumn-sown cereals is well established (Kendall & Smith, 1981a; Plumb, 1986; McGrath & Bale, 1990). In the north of Britain, not only is the whole autumn migration of *R. padi* usually larger (Table 10.10), but a much greater proportion of the migration occurs from 10 September to 7 October than from 8 October to 4 November (Table 10.13). In contrast, in southern Britain, the autumn migration is distributed more equally between the two halves, such that, quite often, more *R. padi* are caught in the second half of the migration than in the first half (Table 10.13).

At Rothamsted, studies have revealed that most *R. padi* caught live at 1.2 m after early September, are a mixture of gynoparae & males seeking *P. padus* (Tatchell *et al.*, 1988). Walters *et al.* (1984) found that *R. padi* gynoparae do not feed, even if starved for 48 hrs. This suggests that they would be unlikely to transmit BYDV to autumn-sown cereals, but it does not imply that these morphs do not settle in autumn-sown cereals. At first, gynoparae feed on Gramineae, but later, their host preferences change to *P. padus* (Dixon, 1971). However, the extent of this physiological switch in gynoparae varies between individuals, so that a number will settle and produce oviparae on barley seedlings (Tatchell & Parker, 1990). Thus, during the autumn, some gynoparae and presumably

males, may settle in autumn-sown cereals, although they will not produce viable progeny. Sampling of winter barley crops during three autumns (Chapter 4) identified the presence of large numbers of *Rhopalosiphum* alatae (both *padi* & *insertum*) which did not produce nymphs, suggesting that many were gynoparae. Furthermore, there was evidence that they introduced detectable quantities of BYDV inoculum into crops (Chapter 8).

Currently, BYDV workers are altering the methods of calculation of II, to remove the holocyclic component (gynoparae & males) of the autumn migration (McGrath & Bale, 1989; Gillet *et al.*, 1990; Kendall & Chinn, 1990), whose contribution to BYDV spread is uncertain (Kendall & Chinn, 1990). This effectively reduces the importance of *R. padi* catches in the second half of the autumn, and increases those of early autumn.

The above shows that there is evidence that migrant *R. padi* in late autumn are of less importance to the epidemiology of BYDV, relative to early autumn migrants. Therefore, it is reasonable to focus our attention on the meteorological factors that determine the size of the early autumn *R. padi* migration.

Both 1985 & 1986 had large early autumn migrations (Table 10.11). These autumns were both preceded by cold winters (Table 10.14) and May to August periods with above average rainfall (Table 10.21). Both these years had above

average incidence of the straight westerly Lamb daily weather type and below average incidence of anticyclonic weather type in the May to August period (Table 10.21).

In 1982, there were large numbers of migrant *R. padi* in England, but unexceptional numbers in Scotland (Table 10.11). Again, the winter was colder than average (Table 10.14), but the summer was drier than average in Scotland and wetter in England, with a higher than average incidence of westerly days and lower than average incidence of anticyclonic days (Table 10.21).

Another two years with relatively high early autumn totals in both England & Scotland were 1978 & 1980 (Table 10.11). Although the preceding winter in 1978 was colder than average, in 1980, Scotland had average temperatures whereas England was warmer than average (Table 10.14). The summer rainfall of 1978 was close to average, whereas in 1980, the summer was very wet in both England & Scotland (Table 10.14). In 1980 (May-August), there were very few days with the straight westerly Lamb weather type, but there was a high incidence of cyclonic days (second only to 1985) and a low incidence of anticyclonic days (equal with 1985, Table 10.21).

Thus, it would seem that a very wet summer can compensate for a milder than average winter to some extent, although the largest autumn migrations require both meteorological pre-conditions.

The smallest early autumn migrations of *R. padi* were in 1976, 1989 & 1990 (Table 10.11). These three autumns were preceded by exceptionally mild winters (Table 10.14) and dry anticyclonic summers (at least in England, Tables 10.14 & 10.21). In these years, large numbers of *R. padi* would probably have survived the winter anholocyclically, and the high temperatures encountered by aphids in the grass canopy in the following hot, dry summer, would oblige the main population peak to occur well before the autumn.

This theory can be tested by comparing the July to August catches of *R. padi*, with the 10 September to 7 October catches, at Ayr in years of large early autumn *R. padi* catches (1985 & 1986) and small early autumn *R. padi* catches (1976, 1989 & 1990, Table 10.27).

Table 10.27 Comparison of the number of *Rhopalosiphum padi* caught at Ayr in July to August with the number from 10 September to 7 October in years with contrasting numbers in the latter period.

	Numbers of *R. padi*	
Year	July & August	10 September to 7 October
1976	2758	439
1989	749	227
1990	1225	461
1985	73	10778
1986	543	5726
r (log transformation),	-0.788, df 3,	N.S.

All three, small early autumn *R. padi* migrations were preceded by larger suction trap catches during July & August. Both large early autumn migrations were preceded by smaller suction trap catches during July & August. Although the relationship was not significant, the observations are similar to those of Wiktelius (1987) in Sweden.

There was one year with large early autumn *R. padi* migrations in Scotland, but tiny (< 100 *R. padi*) migrations in England. This autumn, 1981, was preceded by a milder than average winter and drier than average summer in both England & Scotland (Tables 10.14 & 10.21). The factor that lead to the greater than average numbers in Scotland is unknown. In 1980, there were generally larger *R. padi* migrations than average, but the mild winter and dry summer were unfavourable for a large autumn in migration in 1981. This highlights the limitations of predicting aphid numbers on weather alone.

10.3.3 **Predicting the size of the autumn migration of *R. padi* by assessing *R. padi* numbers in ryegrass pasture in late August**

Although there appeared to be some association between the numbers of *R. padi* in grassland in late August, and the numbers caught by the nearest suction trap in September & October, the high numbers encountered in some fields in both years were followed by lower than average suction trap catches. In both 1989 & 1990, more *R. padi* were caught in

July & August than in early autumn (Table 10.27). Ryegrass sampling in late August is probably more a reflection of the former suction trap catches, because an alate generation that will migrate out of ryegrass pastures could be imminent.

At a joint meeting between colleagues at Auchincruive & the Queen's University of Belfast in May 1991, it was decided that delaying the ryegrass sampling until early September would increase the relevance of the samples to the impending autumn migration.

Summary The size of the autumn migration of *R. padi* is associated with the timing of the largest population peak of *R. padi* in grassland. Large autumn migrations happen when the largest population peak occurs during the autumn. Low temperatures in the preceding winter and summer favour large migrations, but the size of the previous year's migration can affect the timing of the population peak: large previous migrations lead to an earlier population peak and *vice versa*.

CHAPTER ELEVEN

Infectivity indexing as a method of forecasting the risk of BYDV to autumn-sown cereals

11.1 **Introduction**

The background to Infectivity Indexing (II) has already been outlined in Chapter 1. Its purpose is to assess the risk to autumn-sown cereals posed by BYDV during the migration of aphids in September and October, and to use this assessment as the basis to apply an appropiate pesticide (Plumb, 1986). The cornerstone of II is the finding of research done in the 1970s that established that the proportion of captured aphids that transmit BYDV to indicator plants varies both between years, and between regions in the same year. The factors determining these variations have not been defined but the two following aspects of aphid-transmitted virus diseases of plants indicate possible causes.

(a) **Abundance of infected host plants** Nymphs do not inherit BYDV from their parents (Plumb, 1974) so an aphid can only become viruliferous by feeding on a BYDV infected plant. In summer, cereals or grasses are the host plants of cereal aphids. It is known that the autumn BYDV infection of winter cereals varies between years, but by harvest, high levels of virus are present in many cereal crops (A'Brook, 1974). This is due to immigration into and colonisation of cereal crops by alate aphids during the spring, which spread the virus. BYDV is also widespread in wild grasses, although levels of infection in eastern England may be lower than those observed in western Scotland (see section 6.3). Thus, the varying proportion of Gramineae infected

with BYDV could be a factor in the differing proportion of aphids that are viruliferous, either between years or between regions.

(b) **Aphid activity** The probability of an aphid acquiring BYDV from an infected plant depends to some extent, on the activity of the aphid (i.e. the number of plants on which it feeds) assuming the aphid has not acquired virus from the host plant on which it was born. Because aphids are poikilotherms, their activity is dependent on temperature. Aphid behaviour and therefore aphid activity, also depends on a number of other environmental stimuli including other facets of weather. Furthermore, the environmental stimuli that elicit different aphid behaviours are subtle, involving different hues of green of host plants, the visual contrast between a host plant and its surroundings, and the growth stage and amino acid status of the host plant (Dixon, 1973). Thus, the weather and other aspects of the environment in which an aphid lives, may be factors in the differing proportion of aphids that are viruliferous, either between years or between regions.

Other approaches to measuring virus spread The relative importance of factors determining the spread of plant viruses by insect vectors has been investigated by a few workers using mathematical modelling. Often, information on the amount and rate of build-up of virus in a crop is required. The effects of different sizes of vector population, its transmission efficiency and different

levels of host plant resistance on the yield of a crop can be simulated. However, because the system is a three-cornered one, that is, host plant-virus-vector, it is more complex than the other systems to which mathematical modelling has been applied: predator-prey; herbivore-plant; and plant-fungus (Carter, 1986). For this reason, and because the relationship between the insect vector and the host plant is complex and little understood, success with mathematical modelling has been limited (Irwin & Ruesink, 1986).

Use of mathematical models involves the setting of state variables including how many vectors are present, how many of these are carrying the virus, and how many of the plants in a given field are already infected and how many are not (Irwin & Ruesink, 1986). Such data even for a single field are difficult and expensive in man hours to obtain. To provide virus spread forecasts for a region, modelling spread within individual fields is perhaps not the best approach.

The II proposed by Plumb (1986) is not a model, but is a measure of the risk of BYDV to autumn-sown crops in a region (not a specific field) posed by migrating aphids, made at a site remote from crops. II simplifies the host plant-virus-vector relationship by confining the determinants of the amount of virus spread to just two factors: numbers of migrating aphids and the proportion

that are viruliferous. It is known that at the beginning of the season, all plants in a crop are uninfected because seed transmission doesn't occur (Rochow, 1970; Eweida *et al.*, 1988). The purpose of II is to estimate the amount of primary infection of BYDV present at the end of the aphid migration in early November.

In this Chapter, the II data collected at Auchincruive 1984-90 were analysed to ascertain the following:-

1) the relative magnitudes of variation of the numbers of *Rhopalosiphum* spp. that are caught at 12.2 m during September and October, and the percentage of them caught at 1.2 m that transmit BYDV to indicator plants (% infectivity).

2) whether the numbers of migrating *Rhopalosiphum* spp. that are viruliferous can be estimated using the total numbers caught at 12.2 m.

Using infectivity data collected at Aberystwyth and Rothamsted in addition to Auchincruive, it was investigated whether or not the percentage of migrating *Rhopalosiphum* spp. that are viruliferous, depends on air temperature, either current, seasonal or annual measurements.

11.2 Methodology at Auchincruive

Traps Aphids were sampled at 12.2 m by a Rothamsted suction trap (Macaulay *et al.*, 1988) which was emptied daily by

Auchincruive staff. Catches were sorted and identified at the Scottish Office Agriculture and Food Department, Scientific Services, East Craigs, Edinburgh. Live aphids were caught at 1.2 m using "commode" traps (one 1984-87, two subsequently) with a nominal airflow of 5090 m^3/hr. These low-level traps were operated on the Auchincruive campus during September and October each year, being emptied 2 or 3 times each day.

Testing of aphids for BYDV transmission The technique used was that described in section 7.2.

Testing of indicator plants All indicator plants were tested for BYDV by ELISA (Mortar & Pestle method), except in 1985 when only plants showing yellow or red leaf discolouration were tested. In 1984 and 1985, polyclonal B and F antisera (IACR, Rothamsted) were used. Since then, monoclonal antibodies to the RPV, PAV and MAV strains (Central Scientific Laboratory, MAFF, Harpenden) have been employed.

Calculation of weekly II Live trapping of aphids took place during week days, therefore dates of trapping weeks differ between years. Also, trapping commenced on 11 August in 1985 whereas not until 3 September in 1989. Few *Sitobion* were caught by either the suction trap or the "commode" traps in any year, therefore weekly infectivity indices for *S. avenae* were not calculated. Weekly infectivity indices (section 1.7) were calculated for every

week in which trapping took place in the seven autumns, for both *R. insertum* and *R. padi*.

11.3 Results

11.3.1 Auchincruive The number of *Rhopalosiphum* spp. tested, the number which transmitted BYDV to oat seedlings and the number caught by the Ayr suction trap during each week of operation, are shown for each year in Tables 11.1 to 11.7, along with the BYDV infectivity index (Plumb, 1986).

A weekly index value has been calculated separately sixty-seven times, for *R. padi* and *R. insertum*. The average value of the indices were 44 and 33 respectively, based on a weekly average of 17 and 7 aphids tested respectively. The number of *R. padi* and *R. insertum* tested was above zero and below 10 during 39 and 55% of weeks respectively. In a further 6 and 21% of weeks respectively, the number of aphids tested was zero.

The relationships between the infectivity index and the number of aphids tested for BYDV transmission, the number of aphids that transmitted BYDV to the oat seedlings, the % of aphids tested that transmitted BYDV to indicator plants, and the number of aphids caught by the Ayr suction trap, are best studied by pooling the weekly data in each year and analysing the annual data, because of the small numbers of aphids involved in one week. Also, the infectivity index

Table 11.1 Numbers of *Rhopalosiphum* spp. tested, number infective, total number caught in suction trap, and the weekly infectivity index at Auchincruive; autumn 1984.

Week ending	Number of aphids				Suction trap catches		Index	
	Tested		Infective					
	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.
9.9	12	5	1	0	81	6	7	0
16.9	0	1	0	0	87	1	0	0
23.9	3	4	0	0	93	3	0	0
30.9	11	6	1	0	514	35	47	0
7.10	25	9	2	0	162	55	13	0
14.10	2	0	0	0	160	48	0	0
21.10	10	7	1	0	77	52	8	0
28.10	0	0	0	0	55	0	0	0
4.11	5	4	0	0	20	0	0	0

R.p. *R. padi* R.i. *R. insertum*

Table 11.2 Numbers of *Rhopalosiphum* spp. tested, number infective, total number caught in suction trap, and the weekly infectivity index at Auchincruive; autumn 1985.

Week ending	Number of aphids				Suction trap catches		Index	
	Tested		Infective					
	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.
18.8	2	1	0	0	24	8	0	0
25.8	2	0	1	0	13	1	7	0
1.9	7	1	1	0	41	1	6	0
8.9	0	0	0	0	791	0	0	0
15.9	5	1	1	0	374	2	75	0
22.9	34	3	11	0	2337	7	756	0
29.9	26	2	5	0	7727	214	1486	0
6.10	11	3	1	1	427	40	39	13
13.10	25	1	0	0	366	5	0	0
20.10	15	0	0	0	1021	79	0	0

R.p. *R. padi* R.i. *R. insertum*

Table 11.3 Numbers of *Rhopalosiphum* spp. tested, number infective, total number caught in suction trap, and the weekly infectivity index at Auchincruive; autumn 1986.

Week ending	Number of aphids				Suction trap catches		Index	
	Tested		Infective					
	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.
31.8	5	0	5	0	29	43	29	0
7.9	4	0	1	0	10	18	3	0
14.9	15	0	1	0	80	252	5	0
21.9	9	0	0	0	79	169	0	0
28.9	43	3	0	1	2711	2126	0	709
5.10	34	7	0	1	2059	5192	0	742
12.10	32	2	3	0	937	1052	88	0
19.10	40	3	0	1	166	764	0	255
24.10	0	0	0	0	1	10	0	0
2.11	11	1	0	0	17	42	0	0

R.p. *R. padi* R.i. *R. insertum*

Table 11.4 Numbers of *Rhopalosiphum* spp. tested, number infective, total number caught in suction trap, and the weekly infectivity index at Auchincruive; autumn 1987.

Week ending	Number of aphids				Suction trap catches		Index	
	Tested		Infective					
	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.
30.8	4	8	0	0	34	37	0	0
6.9	27	5	3	1	24	15	3	3
13.9	30	7	4	1	16	3	2	1
20.9	23	3	0	1	258	119	0	40
27.9	18	0	1	0	33	73	2	0
4.10	38	30	2	3	1448	868	76	87
11.10	49	12	1	0	466	138	10	0
18.10	44	14	0	0	127	28	0	0
25.10	60	10	1	0	138	69	3	0
1.11	33	18	2	0	37	66	2	0
8.11	18	24	0	0	18	21	0	0

R.p. *R. padi* R.i. *R. insertum*

Table 11.5 Numbers of *Rhopalosiphum* spp. tested, number infective, total number caught in suction trap, and the weekly infectivity index at Auchincruive; autumn 1988.

Week ending	Number of aphids				Suction trap catches		Index	
	Tested		Infective					
	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.
2.9	1	0	1	0	12	17	12	0
9.9	42	1	3	0	69	5	5	0
16.9	23	5	3	0	46	143	6	0
23.9	25	33	4	1	167	248	27	8
30.9	20	45	0	2	156	176	0	8
7.10	42	17	3	0	247	355	18	0
14.10	27	34	1	0	679	443	25	0
21.10	54	4	1	0	639	583	12	0
28.10	38	28	0	0	133	165	0	0
4.11	5	6	0	0	18	17	0	0

R.p. *R. padi* R.i. *R. insertum*

Table 11.6 Numbers of *Rhopalosiphum* spp. tested, number infective, total number caught in suction trap, and the weekly infectivity index at Auchincruive; autumn 1989.

Week ending	Number of aphids				Suction trap catches		Index	
	Tested		Infective					
	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.
10.9	3	0	3	0	13	33	13	0
17.9	1	0	0	0	19	53	0	0
24.9	3	6	0	1	93	440	0	73
1.10	4	5	0	0	84	180	0	0
8.10	14	10	7	2	31	134	16	27
15.10	1	3	0	1	1	78	0	26
22.10	10	9	0	3	10	63	0	21

R.p. *R. padi* R.i. *R. insertum*

Table 11.7 Numbers of *Rhopalosiphum* spp. tested, number infective, total number caught in suction trap, and the weekly infectivity index at Auchincruive; autumn 1990.

Week ending	Number of aphids				Suction trap catches		Index	
	Tested		Infective					
	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.
2.9	2	1	0	0	188	122	0	0
9.9	3	2	1	0	22	16	7	0
16.9	5	5	0	1	120	82	0	16
23.9	1	1	0	0	23	52	0	0
30.9	8	10	2	1	301	369	75	37
7.10	4	17	1	1	17	42	4	2
14.10	13	15	1	4	161	308	12	82
21.10	3	7	0	0	279	557	0	0
28.10	22	35	6	7	156	117	43	23
4.11	1	1	1	1	25	12	25	12

R.p. *R. padi* R.i. *R. insertum*

was developed to measure BYDV inoculum pressure which was considered to differ annually (Plumb, 1986). Table 11.8 shows the annual data for *Rhopalosiphum* spp.

Relationships between the annual infectivity index (pooled weekly values) and the pooled aphid data were tested using linear regression (Table 11.9). The annual *R. padi* infectivity index was unrelated to all four aphid variables whilst the *R. insertum* infectivity index was positively related to the number of *R. insertum* caught by the Ayr suction trap.

Differences in the value of the infectivity index between weeks may be more influenced by one or other of the variables used to calculate it, because of the relative variability of these two variables. Clearly (Table 11.8), the variability of the weekly suction trap catches of both aphid species is greater than that of the weekly percentage infective variable. However, both variables show large between week differences (large coefficients of variation), and therefore both of them would have made major contributions to differences of the index between weeks. As a result, the weekly index has a very large coefficient of variation.

Table 11.8 Annual totals of *Rhopalosiphum* species and the infectivity index at Auchincruive, 1984-90.

Year	Number of aphids						Suction trap catches		Cumulative weekly index	
	Tested		Infective		% infective					
	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.	R.p.	R.i.
1984	68	36	5	0	7	0	1249	200	75	0
1985	127	12	20	1	16	8	13121	357	2639	13
1986	197	16	10	3	5	19	6089	9668	125	1706
1987	344	131	14	6	4	5	2599	1437	98	131
1988	277	173	16	3	6	2	2166	2152	105	16
1989	36	33	10	7	28	21	251	981	29	147
1990	62	94	12	15	19	16	1292	1677	166	172
mean[a]	16.5	7.4	1.3	0.5	13.2	7.2	400	246	44.3	32.6
cv	0.95	1.35	1.54	2.4	1.88	2.20	2.63	2.82	4.55	3.91

[a] mean of weekly values from which indices are calculated.

Correlation coefficients between weekly values:

R.p. tested and R.p. caught by suction trap, $r = 0.496$, $P < 0.001$

R.i. tested and R.i. caught by suction trap, $r = 0.349$, $P < 0.01$

cv coefficient of variation (sd/mean).

Table 11.9 Results of tests for linear regression between the (log (n + 1) infectivity index totals) and the total numbers of *Rhopalosiphum* spp. caught by commode and suction traps, and the number which transmitted BYDV to oat seedlings, during the infectivity indexing period 1984-90.

Aphid parameter	Significance	
	R.p.	R.i.
Number of aphids tested	N.S.	N.S.
Number of aphids tested which transmitted BYDV to oat seedling. (Log (n+1))	N.S.	N.S.
% infectivity of aphids	N.S.	N.S.
Number of aphids caught in suction trap.	N.S.	P = 0.022

R.p. *R. padi* R.i. *R. insertum*

Given that after early September, gynoparae and males comprise the major proportion of the *R. padi* alatae caught by traps at either 1.2 or 12.2 m (Tatchell *et al.*, 1988), it is pertinent to examine whether or not there is a trend in the percentage of aphids that transmit BYDV to indicator plants during the autumn. The weekly *R. padi* data from the seven years were pooled, so that this could be achieved (Table 11.10).

Table 11.10 Weekly *Rhopalosiphum padi* infectivity indexing data from 1984-90, pooled to test for a trend in the percentage of aphids that transmit BYDV to indicator plants during the autumn

Week ending	Number of *R. padi* tested	infective	% infective
9.9	91	12	13.2
16.9	79	9	11.4
23.9	98	15	15.3
30.9	130	9	6.9
7.10	168	16	9.5
14.10	149	6	4.0
21.10	176	2	1.1

t-test between % of *R. padi* infective data

September cf October t = 2.31, df 5, N.S.

9.9 - 23.9 cf 30.9-21.10 t = 3.38, df 5, P = 0.02

correlation between number of *R. padi* tested and number infective.

r = -0.474, df 5, N.S.

Significantly higher (P = 0.02) percentages of *R. padi* caught prior to 23 September transmitted BYDV to indicator plants, relative to those caught after this date. The lack of a relationship found by correlation, between the number tested and the number found to be infective is further evidence that a change has occurred in the percentage of *R. padi* that transmitted BYDV to indicator plants.

11.3.2 Analysis of percentage infectivity data at Auchincruive, Aberystwth and Rothamsted with mean air temperature

Percentage infectivity data for *R. padi*, September to October 1984-90 at Auchincruive (Table 11.8), May to November 1970-79 at Aberystwyth (A'Brook & Dewar, 1980), and May to October 1969-73 at Rothamsted (Plumb, 1976, (Table 11.11)), were regressed on mean air temperature of single meteorological seasons and consecutive combinations of current and preceding seasons up to one year previous. Single months, or other consecutive monthly combinations were not considered. This was because an aphid must acquire BYDV from an infected host plant, therefore temperature acting through aphid activity over long periods might increase the number of infected plants in a region, but a warm single month would be of less importance.

Table 11.11 Percentage of *Rhopalosiphum padi* that transmitted BYDV to indicator plants at Aberystwyth and Rothamsted.

	% infectivity	
Year	Aberystwyth	Rothamsted
1969	-	9.5
1970	9.5	2.3
1971	11.1	1.1
1972	13.4	2.6
1973	13.2	11.5
1974	14.0	-
1975	39.0	-
1976	12.8	-
1977	18.5	-
1978	12.0	-
1979	3.7	-

Table 11.12 Sign and significance of regressions between percentage infectivity of *Rhopalosiphum padi* and mean air temperature of single meteorological seasons and consecutive combinations of current and preceding seasons up to one year previous.

	Sign and significance of regressions		
Season(s)	Auchincruive	Aberystwyth	Rothamsted
Winter (W)	+, P = 0.014	+, P = 0.02	N.S.
Spring (SP)	N.S.	N.S.	N.S.
Summer (SM)	N.S.	N.S.	N.S.
Autumn (A)	N.S.	N.S.	N.S.
W + SP	N.S.	N.S.	N.S.
W + SP + SM	N.S.	N.S.	N.S.
W + SP + SM + A	N.S.	N.S.	N.S.
SP + SM	N.S.	N.S.	N.S.
SP + SM + A	N.S.	N.S.	N.S.
SM + A	N.S.	N.S.	N.S.

At both Auchincruive and Aberystwyth, significant relationships were found between mean air temperature in the preceding winter and percentage infectivity of *R. padi*: high percentage infectivities occurring in autumns following mild winters (Table 11.12).

11.4 Discussion

11.4.1 Auchincruive

In the seven years of infectivity indexing at Auchincruive, the percentage infectivity of *R. padi* (pooled

weekly data) has varied between 4 and 28%, but the number of infective *R. padi* has only varied between 5 and 20 individuals. The high variability of the weekly infectivity index value is due to the large weekly variations of both the percentage infective and the number of aphids caught by suction traps (Table 11.8). Because the number of aphids tested for transmission of BYDV to indicator plants is correlated with the number caught by suction traps (Table 11.8), one infective individual in weeks when few are tested can give a high index even though the number of aphids flying is relatively low. Examples of this phenomenon are 15 September, 1985 (Table 11.2), 14 October, 1990 (Table 11.7) and 4 November, 1990 (Table 11.7). This imperfection is due to the calculation of the index on a weekly basis. Longer time periods would reduce incidences of this phenomenon and lessen the large variability of the index. This might help to elucidate what an index value represents.

The fact that the annual index of *R. padi* (pooled weekly values) is independent of all four aphid parameters (Table 11.9), indicates that the annual value is insensitive to the differing sampling sizes in each year, and is not determined largely by either of the two variables used to calculate it: the percentage infectivity and the number of aphids caught by suction trap. However, the index of *R. insertum* is determined by the number caught by the Ayr suction trap.

The significantly diminishing percentage of *R. padi* that transmitted BYDV to indicator plants during the autumns 1984-90 (Table 11.10) is perhaps further evidence of the predominance of gynoparae and males over alate exules after early September (Tatchell *et al.*, 1988), because they do not feed (Walters *et al.*, 1984).

11.4.2 Analysis of percentage infectivity data at Auchincruive, Aberystwth and Rothamsted with mean air temperature

Comparison of the percentage infectivity of *R. padi* at Auchincruive, Aberystwyth and Rothamsted shows that there is both variation between sites in the same year (Aberystwyth & Rothamsted, 1970-73, Table 11.11), and large between years differences at all three sites. Furthermore, the percentage infectivities at Rothamsted were generally lower than those of Auchincruive, and those of Auchincruive were generally lower than those of Aberystwyth. The existence of these between site differences (Plumb, 1976) has spawned difficulties in the application of cumulative index thresholds above which insecticide treatments are considered necessary, at sites other than Rothamsted (Carter, 1984; McGrath & Bale, 1989)

The positive and significant relationship found at both Auchincruive and Aberystwyth between mean air temperature in the preceding winter and the percentage of aphids that transmitted BYDV to indicator plants suggests two things. Firstly, that the number of aphids overwintering

anholocyclically affects the percentage that transmit BYDV to indicator plants in the following autumn. Secondly, that percentage infectivity may depend on the number of previous generations passed on Gramineae, the relatively large number after mild winters favouring high percentage infectivities, perhaps acting through greater BYDV infection of Gramineae. However, this latter theory is not supported by the absence of a relationship between winter temperature and percentage infectivity at Rothamsted.

The relationship between percentage infectivity and mean air temperature in the preceding winter at both Auchincruive and Aberystwyth, coupled with the relationship between autumn suction trap catches of *R. padi* and weather in the preceding winter and summer (Chapter 10), brings into question the plausibility of II in the west of Britain. After a mild winter, the size of the *R. padi* migration is usually small, but a high percentage transmit BYDV to indicator plants. After a cold winter, the migration is often large, but the percentage infectivity is low, although summer rainfall is also important to the numbers of *R. padi* caught by suction traps (Chapter 10).

The two factors used to calculate II are therefore negatively correlated in the west of Britain (Auchincruive 1984-90, $r = -0.535$, df 5, N.S.), although because the index is calculated weekly, and because of the variable contribution of percentage infectivity during the autumn (Table 11.10), the index has large fluctuations between

years (Table 11.8).

11.4.3 **Limitations of II**

II is intended to measure the amount of primary BYDV spread by alate aphids, but not to measure the amount of secondary spread by the apterous progeny of the alatae that introduced the BYDV (Plumb, 1986). If the alatae are exules, the secondary spread is likely to be positively related to the amount of primary spread. If the alatae are gynoparae & males, then little or no secondary spread will occur. For this reason, adjustments to II have been proposed (McGrath & Bale, 1989; Gillet *et. al.*, 1990; Kendall & Chinn, 1990) so that the alate exules which are a minority after early September are given greater weighting in the calculation of the index. It may be that spatial and temporal variations in the proportion of different aphid morphs in migrant populations result in differences in BYDV transmission to autumn-sown cereals between regions and years respectively (Kendall & Chinn, 1990).

The numbers of *S. avenae* caught by suction traps are normally much smaller than those of *R. padi*, although in crops, the differences between these two species are much smaller (Tatchell *et. al.*, 1988). In Scotland, autumn suction trap catches of *S. avenae* are very small (section 8.5.1), although in winter barley crops, *S. avenae* was more common and widespread from 1988-91 than *R. padi*. Thus, II does not monitor primary spread by *S. avenae*, at least in

Scotland.

BYDV may be introduced into crops by apterous aphids walking from ploughed-in grass leys (Carter, 1984; Plumb, 1988), ploughed-in weeds or volunteers (Plumb, 1988), or by alatae flying locally from adjacent stubble fields. II does not measure primary spread by these methods of virus introduction.

11.4.4 **The importance of aphid infectivity**

In other aphid-transmitted virus diseases of British crops, percentage infectivity of aphids is not considered to be a critical factor in determining the extent of virus infection in an area (sections 1.5 & 1.6). Nevertheless, on a field scale, it was observed that similar levels of aphid infestation did not produce equal levels of virus incidence in crops, and the percentage infectivity was suggested as one of a range of factors such as aphid activity and proximity of sources of alate aphids that might account for the differing extents of virus infection (Broadbent, 1950a).

Also, it is common knowledge that apparently few aphids can cause noticeable BYDV damage. This would not be the case if percentage infectivity was an important factor limiting BYDV infection. In springs following mild winters, BYDV infection is widespread in autumn-sown cereals (Oakley, 1989). This is because mild winters allow aphids

to overwinter anholocyclically in cereal crops, but not because mild winters allow a greater percentage of aphids to transmit BYDV.

Clearly, the probability of an aphid in a cereal crop acquiring BYDV will depend to some extent on the BYDV infection of the crop (Irwin & Thresh, 1990). If few plants are infected, the chances of an individual aphid feeding on an infected plant are remote, in contrast to the probability when a high proportion of crop plants are infected. Therefore, percentage infectivity of an aphid population is a response to the percentage infection of their host plants.

In France, maize is considered to be the major source of *R. padi* infesting autumn-sown cereals. From 1983-85, a high and constant proportion of alate aphids landing on the barley plots transmitted BYDV compared with in 1986-87. Maize crops from 1983-85 had much greater levels of BYDV infection than in the latter two years when cold winters killed aphids overwintering on most Gramineae (Gillet *et al.*, 1990).

This demonstrates that not only is the host plant species important to percentage infectivity of alate aphid populations, but so too is the BYDV infection status of the host plants. Although host plant variations, such as the abundance of maize crops, can be described on a regional scale, variations in the BYDV infection status of host

plants from which alate aphids have just left are probably not regionally based, but vary on a much smaller scale. This is because BYDV infection of host plants is influenced by aphid infestations (Chapter 6).

Aphid populations continually redistribute themselves, having no fixed population centre (Taylor, 1973). During the summer and autumn, aphid infestations wax and wane on cereal crops (Chapter 4), ryegrass pastures (Chapter 5), grass weeds and volunteers in stubble fields (Chapters 8 & 9) and wild grasses in hedge bottoms and farm lanes (Chapter 6). The percentage infectivity of alatae on any particular day will probably depend to a large extent on the BYDV infection status of the host plants these alatae have just left. The value of percentage infectivity of alate cereal aphid populations probably varies from day to day, and between sites small distances apart on the same day. If sufficient numbers of aphids could be tested in one day, and if aphids moved locally, such a percentage infectivity value might have relevance to autumn-sown cereals in a locality. The meaning of a percentage infectivity value derived weekly by testing small and differing numbers of aphids each day is a little uncertain.

CHAPTER TWELVE

General Discussion

12.1 Introduction

In a recent review (Irwin & Thresh, 1990), BYDV epidemiology was described as a study in ecological complexity. This complexity is comprised of three types of interaction: plant/virus, virus/vector and plant/vector. However, because the virus is widespread in several crop and perennial plant species, has a number of distinct variants, which are themselves transmitted specifically or non-specifically by a number of different vector species, the pathosystem is more convoluted than implied by the three interactions.

In Britain, the classification of the disease into two types *R. padi*- and *S. avenae*-transmitted BYDV (McGrath & Bale, 1990) helps to simplify the complexity, and it draws attention to a fundamental aspect of the disease. BYDV is associated with aphids, the duality in Britain being the result of species-specific relationships between aphids and virus strains. The ubiquity of BYDV in Gramineae of a region such as Britain, and the worldwide distribution of the virus (Plumb, 1988) suggest that in the field, the associations between aphids and the specific strains are strong and are normally unconstrained. Therefore, it is the movement of vectors which is responsible for BYDV epidemics in cereals by influencing spatial and temporal patterns of infection in fields, and determining which fields become infected (Irwin & Thresh, 1990).

This Discussion attempts to contribute to our

understanding of why cereal aphids move into autumn-sown cereals and cause damaging BYDV spread in some years, whereas in most, they do not. It also discusses the possibilities for forecasting BYDV risk to autumn-sown cereals.

12.2 *R. padi*- and *S. avenae*-transmitted BYDV

In the spring of 1989 (section 4.4.4), the difference in damage to winter barley crops affected by *R. padi*- and *S. avenae*-transmitted BYDV was enormous, endorsing the distinction between these two types of BYDV introduced by McGrath & Bale (1990). Monoclonal antibodies (MAFF, Central Scientific Laboratory, Harpenden) enable this distinction to be easily applied to discoloured field-collected plant material. As a result, it has been possible to distinguish between the factors that affected the incidence and extent of these two types of BYDV in the three years of study (sections 4.7.2.2, 4.7.3.2 and 4.7.4.2). This was achieved using multivariate analysis which enabled several measured aphid/BYDV variables from a number of fields to be explained on the basis of several measured field/farm variables from the same fields, in the one analysis. This cannot be achieved with conventional statistics. A summary of the results of these analyses is shown below:-

***R. padi*-transmitted BYDV** The association of this type of BYDV with preceding untreated ploughed-in grass leys (Carter, 1984; Plumb, 1988) was re-affirmed in both 1988/89

and 1989/90. The occurrence of this type of BYDV only in Wigtownshire in 1988/89 where there was a relatively large migration of *R. padi* in the autumn of 1988 (as measured by the Belfast suction trap) also re-affirms the association of this type of BYDV with the number of migrant *R. padi* (A'Brook & Dewar, 1980; Plumb, 1986).

***S. avenae*-transmitted BYDV** This type of BYDV was more widespread than *R. padi*-transmitted BYDV, MAV being the most common strain in the leaf samples collected from winter barley in the three years of study. Infestation of crops by *S. avenae* almost seemed inevitable, whereas *R. padi* infestations apparently required specific preconditions.

Factors that enhanced *S. avenae* infestations and therefore *S. avenae*-transmitted BYDV were the nature of the farm enterprise, cereal enterprises increasing the risk (Hill, 1988), and climate-related factors such as distance from the sea, altitude and shelter from the prevailing wind (Plumb, 1988). Fields, which for topographical reasons, would have lower incidences of frost and conditions of high wind-chill, had greater infection with the MAV strain, presumably because vector movement and survival were favoured in such fields. Early-sowing date (Plumb, 1986; McGrath & Bale, 1990; Table 4.53) may have increased the risk of *S. avenae*-transmitted BYDV in 1989/90, and studies of aphids on wild grasses in hedge bottoms and farm lanes provided a possible reason for this (Chapter 6):

synchronised movements of *S. avenae* from senescing infloresences of *D. glomerata* and *H. lanatus* in hedge bottoms and field margins.

12.3 Where do aphids that colonise autumn-sown cereals come from? (i.e. Where are cereal aphids during late summer?)

Vector movement is one area that Irwin & Thresh (1990) considered to be inadequately studied. They identified four types of virus spread: enlarging of existing foci; developing new foci within the same field; in nearby fields; or distant fields. The issue of where aphids that colonise crops come from, or more specifically whether or not they come from nearby hedge bottoms, field margins, nearby fields, or from more distant sources, is contentious (Johnson, 1969; Taylor, 1973; Vickerman & Wratten, 1979).

The use of suction traps to monitor aphids may have tended to bias the consensus in favour of more long-distance flight, but evidence in support of such flight being the norm for aphids colonising autumn-sown cereals is lacking. For example, in Scotland, the *S. avenae* that colonise winter barley are not monitored by suction traps (Chapters 4 & 8). The gynoparae and males of *Rhopalosiphum* spp. that are caught in large numbers by Scottish suction traps during the autumn may introduce some virus inoculum (Chapter 8), but they do not give rise to apterous progeny which leads to the damaging secondary spread (Tatchell *et al.*, 1988).

In this thesis, evidence for local sources of aphids being important to BYDV epidemiology was sought. A range of different Gramineae on farms was sampled for both aphids and BYDV: winter barley crops, grass weeds within winter barley fields, ryegrass pasture (aphids only) and wild grasses in hedge bottoms and farm lanes. The questions of whether or not aphids from these sources colonise local autumn-sown cereals, and whether or not aphids from these different sources are viruliferous, are discussed below:-

Winter barley stubbles Aphids from this habitat may colonise autumn-sown cereals either by walking from ploughed-in grass weeds or volunteers (Plumb, 1988) if winter barley was the previous crop, or by flying from grass weeds or volunteers in the stubble field during the autumn.

In Chapter 4, an association between *S. avenae*-transmitted BYDV and farms with mainly cereal growing enterprises was found. The explanation for this was considered to be that continuous winter barley growing may have increased the local *S. avenae* population, thereby increasing the incidence of BYDV. This phenomenon is considered to be a factor in the rise in the importance of BYDV in recent years (Hill, 1988). *S. avenae* was observed on winter barley and grass weeds pre-harvest (Chapter 8) and on both grass weeds and volunteers post-harvest (Chapter 9). Both methods of movement outlined above may

have contributed to the incidence of *S. avenae*-transmitted BYDV in autumn-sown cereals on farms with mainly cereal growing enterprises. If the latter type of movement occurred, it suggests that alatae flying from stubble fields do not move far.

The highest percentages of *S. avenae* which transmitted BYDV (the MAV strain) to indicator plants (Table 7.1) were associated with aphid collections from winter barley (22%) and grass weeds in winter barley fields (23%). In 1989 and 1990, high percentage infectivities of *S. avenae* collected from cereal fields were maintained from the summer to the autumn suggesting that cereal stubbles may be the major source of *S. avenae* that colonise autumn-sown cereals (section 7.4). During pre-harvest sampling of both years, MAV was common in both cereal leaves and *P. annua* collected from winter barley fields (Chapter 8).

R. padi was scarce during pre-harvest sampling in both years (Chapter 8). However, in late August 1990, it was common on grass weeds and volunteers in cereal stubble fields (Chapter 9). Nevertheless, unequivocal evidence of local movement into emerging cereal crops was not detected in the autumn of 1990.

Percentage infectivities of *R. padi* collected from winter barley and grass weeds in winter barley fields which transmitted BYDV to indicator plants (Table 7.2) were around 30%, and strain mixtures were transmitted often.

Ryegrass pasture Plumb (1988) considers ryegrass pasture to be the principal source of both aphids and BYDV. The two types of movement outlined above in the section on winter barley stubbles, also apply to aphids from ryegrass pasture.

With respect to *R. padi*, movement of apterae from untreated ploughed-in ryegrass leys is well documented (Carter, 1984; Plumb, 1988) and its potential to cause extensive damage to autumn-sown cereals was witnessed on several occasions during this study (Chapter 4). The equivalent phenomenon for *S. avenae* has not been proven.

Numbers of *S. avenae* in ryegrass pasture tend to peak in mid-summer, in contrast to *R. padi* which peaks in late summer and early autumn, and they are low relative to numbers of *Rhopalosiphum* spp. (Vickerman, 1982; Hand, 1989; Chapter 5). However, the extensive acreage of this crop (Plumb, 1988) could mean that relatively low numbers flying from ryegrass pasture results in epidemiologically important numbers colonising autumn-sown cereals, particularly if they do not fly far (i.e. they do not disperse themselves over a wide area).

For *R. padi*, local flights from ryegrass pastures (Hill, 1982) and maize (Plumb, 1988) into autumn-sown cereals is well-known: adjacent ryegrass pastures being termed a risk factor in England (Hill, 1982). It is interesting to note that the one probable case of movement

of alate *R. padi* from a ryegrass pasture into an adjacent autumn-sown cereal in the three years of study occurred late in the autumn, but the movement did involve large numbers of exules (section 4.8).

The high densities attained by this aphid in ryegrass pasture (Hand, 1989; Chapter 5) could translate into large primary infection of nearby autumn-sown cereals. If the alatae are exules, massive secondary spread by apterous progeny may follow (Tatchell *et al.*, 1988).

S. avenae collected from ryegrass pasture had lower than average percentage infectivity (Table 7.1) whereas *R. padi* collected from this habitat had its greatest percentage infectivity (Table 7.2).

Wild grasses in hedge bottoms and farm lanes From this habitat, flying is presumably the main method of movement into autumn-sown cereals, although walking (Ferrar, 1968) into field margins could conceivably be important. Except for *Sitobion* spp., aphids were scarce on these wild grasses (Chapter 6). However, other workers have found *R. padi* to be abundant on wild grasses (Orlob, 1961; Orlob & Medler, 1961; Guy *et al.*, 1987). The coincidence of senescence of grass weeds in hedge bottoms with the emergence of early-sown cereals nearby in September, might be a further explanation for the association of BYDV with early drilling dates, particularly for *S. avenae* which mainly infest

inflorescences (Kendall & Smith, 1981a; Plumb, 1986; McGrath & Bale, 1990). The spatial differences of grass weeds within and between farms might account for the varying risk of BYDV between fields of a farm and between farms respectively.

Aphids collected from grass weeds in hedge bottoms and farm lanes had the lowest percentage infectivities for both *R. padi* (20%; Table 7.2) and *S. avenae* (10%; Table 7.1). Grass has been identified as a poor source of virus by other workers (Plumb *et al.*, 1982). This was the only habitat in which aphid infectivity appeared to be constrained, although BYDV infection was common in these weeds (Table 6.3).

Some evidence for local movement of aphids into autumn-sown cereals has been presented above. The approach used in this thesis to gather evidence of local movement of aphids, was to establish the location of aphid infestations and BYDV inoculum on farms of different regions during the summer, both pre- and post-harvest. These data were then compared with aphid data collected from cereals of that region during the following autumn, and BYDV data collected from the same crops in the following spring (Chapter 8). Both the autumns of the "local aphid" study had low *R. padi* migrations which did not mask possible evidence of local spread. In both years, detectable quantities of MAV may have been carried from stubble fields to winter barley crops of the next season,

by local *S. avenae* (Chapter 8). However, severe damage to crops was not observed.

For the "local aphid" study, no attempt to identify the previous host plants of individual aphids found in autumn-sown cereals was made. The ELISA technique (Clark & Adams, 1977) could be utilised for this purpose by preparing monoclonal antibodies to host plant proteins. To estimate how far an aphid has travelled prior to landing in a cereal crop, "lipid depletion" studies (Liquido & Irwin, 1986) could be employed to determine the length of time an aphid has flown.

To resolve the question, "Where do infective *S. avenae* that colonise autumn-sown cereals come from?", the employment of such techniques is perhaps necessary. With information on the locations of *S. avenae* on farms in the preceding summer, these techniques may enable the spatial and temporal distribution of *S. avenae* during the summer and autumn months to be elucidated. Scottish suction traps cannot be used to achieve this, because they catch few *S. avenae* during the autumn (Dewar, 1982; Plumb, 1986).

12.4 The importance of natural enemies to aphids in cereals during the summer and autumn

Aphids in cereals during the spring and aphids in cereals during the following autumn are likely to be related to some extent. This is because aphid numbers and their associated natural enemies present in cereal

ecosystems during the spring, must have repercussions for aphid and natural enemy numbers later in the summer and autumn. One of the purposes of pre-harvest sampling (Chapter 8) is to measure aphid and natural enemy numbers in July, to assess the possibility of using these data as part of a forecast of BYDV risk to autumn-sown cereals.

In cereals during the autumn and winter, parasitoids are known to be active in anholocyclic aphid populations (Chambers *et al.*, 1986). *S. avenae* collected from cereals during the autumn by the author were sometimes parasitised. This may have been associated with the large numbers of *S. avenae* in cereals during the springs of 1989 & 1990.

Kendall *et al.* (1988) and Kendall & Smith (1991) using field trials found that both BYDV infection and aphid numbers were greater after conventional ploughing and drilling than after direct drilling. Pitfall trapping in October revealed greater numbers of beetles (both Carabidae and Staphylinidae) and money spiders (Linyphiidae) in direct drilled plots than in ploughed plots, suggesting that more drastic soil cultivations (i.e ploughing) may have greater adverse effects on natural enemy numbers than direct drilling. Incorporating straw instead of removing it from the field also reduced BYDV incidence and increased yields, possibly for the same reasons.

It is reasonable to assume that aphid/BYDV problems in cereals during the autumn are no less independent of

natural enemies than aphid problems in cereals during the spring (Dewar, 1982; Entwistle & Dixon, 1989). This is an area of BYDV epidemiology that requires more research.

12.5 **The importance of aphid morph**

The predictability of the size of the autumn migration of *R. padi* (as measured by suction traps) using weather data of the preceding winter and summer (Chapter 10), and the percentage infectivity (Chapter 11), might suggest that the levels of *R. padi*-transmitted BYDV caused by migrant *R. padi* are predictable to some extent, if Plumb's (1986) II is correct. However, the suggestion by Kendall & Chinn (1990) that it may be the spatial and temporal variations in the proportion of different aphid morphs in migrant populations that result in differences in BYDV transmission to autumn-sown cereals between regions and years respectively casts doubt on this assertion. Recent work at IACR, Rothamsted has also highlighted the importance of aphid morph to damaging BYDV spread: only alate exules colonise Gramineae during the autumn (Tatchell *et al.*, 1988; Blake, 1991).

In the three years of study, most alate *Rhopalosiphum* observed in cereals during the autumns had not reproduced on the plants on which they were found (Chapter 4), and the few removed to the laboratory also failed to reproduce on the oat seedlings on which they were placed. Many of these *Rhopalosiphum* were *insertum* which does not prefer cereals,

but the failure to reproduce was probably also due to the "morph" factor: only exules can give birth to viable progeny on cereals (Tatchell *et al.*, 1988) whereas gynoparae and males cannot give birth to viable progeny and any progeny respectively. Therefore, there is a need to measure the proportion of the different morphs in the migrant population each year, and to establish whether or not there is a relationship between the size of the migrant population and the relative proportions of the different morphs.

A plausible hypothesis would be that larger autumn migrations of *R. padi* are comprised of a greater proportion of alate exules. Large autumn migrations follow cold winters and summers (Chapter 10), and under these conditions of relatively low temperature, the appearance of gynoparae and males is likely to be delayed.

Assuming this hypothesis to be correct, regional differences in the proportion of the autumn migration of *R. padi* comprised of alate exules, could be explained on the basis of winter and summer weather. Such analyses would be more challenging than those concerned with a number of years data at one site, because there would be less variation in the weather data. New daily weather variables might have to be created, such as the product of the addition of sunshine hours to air temperature, not only to overcome this reduced variability, but also to increase the

biological relevance of the standard weather measurements to variations in aphid numbers, and the proportion comprised of alate exules. The key to success might be in creating a weather variable whose units closely correspond with the number of aphid generations.

However, during late summer and early autumn, the problem is complicated by the the change in host plant preference of individual *R. padi* (Dixon & Glen, 1971). The relationship between current weather and this change might be an important factor governing regional variations.

Recent work at IACR Rothamsted has shown that *R. padi* clones collected from different latitudes of Britain are adapted to the seasonal shortening of daylength at that latitude, such that clones from further north will produce gynoparae and males at longer daylengths than those collected further south (Tatchell, G. M., personal communication). This is supported by suction trap catches which show that in the north, greater numbers of *R. padi* are caught from 10 September to 7 October than from 8 October to 4 November, whereas in the south, numbers are more equally distributed in this period (Table 10.13). After early September, most *R. padi* caught by suction traps are comprised of gynoparae and males (Tatchell *et al.*, 1988). The later occurrence of the physiological switch from alate exules to gynoparae and males (Dixon & Glen, 1971) in the south, may explain why *R. padi*-transmitted BYDV is more common than in the north (Plumb, 1974).

In south & west Wales (A'Brook & Dewar, 1980) and south west England (Kendall & Chinn, 1990), *R. padi*-transmitted BYDV is a regular problem. A reliable weather singularity in Britain is the return of the westerlies as the commonest weather type (section 2.4) around the end of June after their relative absence in spring (Lamb, 1950). Therefore, in most western areas of Britain, the July-August period is much wetter and cloudier than the May-June period (Lamb, 1964). The susceptibility of south & west Wales and south-west England to *R. padi*-transmitted BYDV may be owing to both the later physiological switch from alate exules to gynoparae and males, relative to *R. padi* in the north, and to their exposure to the westerly weather types which normally further delay the physiological switch, such that colonisation of autumn-sown cereals by alate exules is normal.

12.6 **The effects of September weather on BYDV incidence**

One factor that may affect the incidence of BYDV in autumn-sown cereals, but that is independent of farm and field history, topography and aphids, is the weather during September. This is because early sowing date increases BYDV incidence in autumn-sown cereals (George, 1982; Carter, 1984; Plumb, 1986; McGrath & Bale, 1990). Nowadays, drilling dates of winter barley crops in Britain are largely determined by the weather and soil conditions

in September, because most farmers aim to finish drilling by the end of September (Carter, 1984; Plumb, 1988). A study of the variability of September weather and its likely effects on crop drilling dates is therefore relevant to a study of the factors affecting the incidence of BYDV.

The occurrence of occasional long spells of weather, marked by the persistence of one or another easily recognised and definable type, is a well-known feature of Britain's climate. Such spells commonly determine the prevailing character of a season. Lamb (1950) catalogued long spells of weather (at least 25 days) with any of the following seven weather types in the period 1898-1947: anticyclonic AC; cyclonic C; westerly W; north-westerly NW; northerly N; easterly E; and southerly S. Interruptions of weather type not exceeding 3 days were not considered as ending a spell, because such interruptions are a natural part of the sequence of some weather patterns: for example, between two Atlantic depressions.

It was discovered that in this period, the annual minimum of long spells of weather of any type occurred in September. With respect to cyclonic spells of weather, a marked trough was observed in September between the main peaks of cyclonicity in late summer and autumn. This latter fact is probably related to the high incidence of anticyclonic days in September approaching 20/50 years in the middle of the month, although long spells of anticyclonic weather did not occur (Lamb, 1950). In other

words, September weather is a very changeable.

The Lamb daily weather types for the period 1976-88 were examined to see whether or not the weather of September was very changeable today (Figure 12.1). There was a sharp peak of anticyclonic days from 18 to 20 September (peak of 5/13 years) and another sharp peak of cyclonic days from 20 to 21 September (peak of 5/13 years), confirming the absence of long spells of weather in September and showing that strong singularities of weather type do not occur in September, as noted by Lamb (1950).

A striking feature of Figure 12.1 is the significant decrease in the incidence of westerly days from the first half of September (from a peak of 7/13 years on 8 September) to the second half, and a corresponding significant increase in the number of southerly days (Table 12.1). Lamb (1950) noted a marked decrease in rainfall in many parts of Britain in the two weeks after 27 August to 3 September associated with the decrease in the incidence of cyclonic days. Although there was not a significant decrease in cyclonic days during September 1976-88, the decrease in westerly days suggests that more days with settled weather suitable for drilling may be found in late September than in early September.

However, drilling is only possible after three main pre-conditions have been satisfied: firstly, the ground has

Weather type	Lamb daily weather types
A	A
C	C
W	CW, ACW, W
S	CS, AS, S, CSW, ASW, SW, CSE, ASE, SE

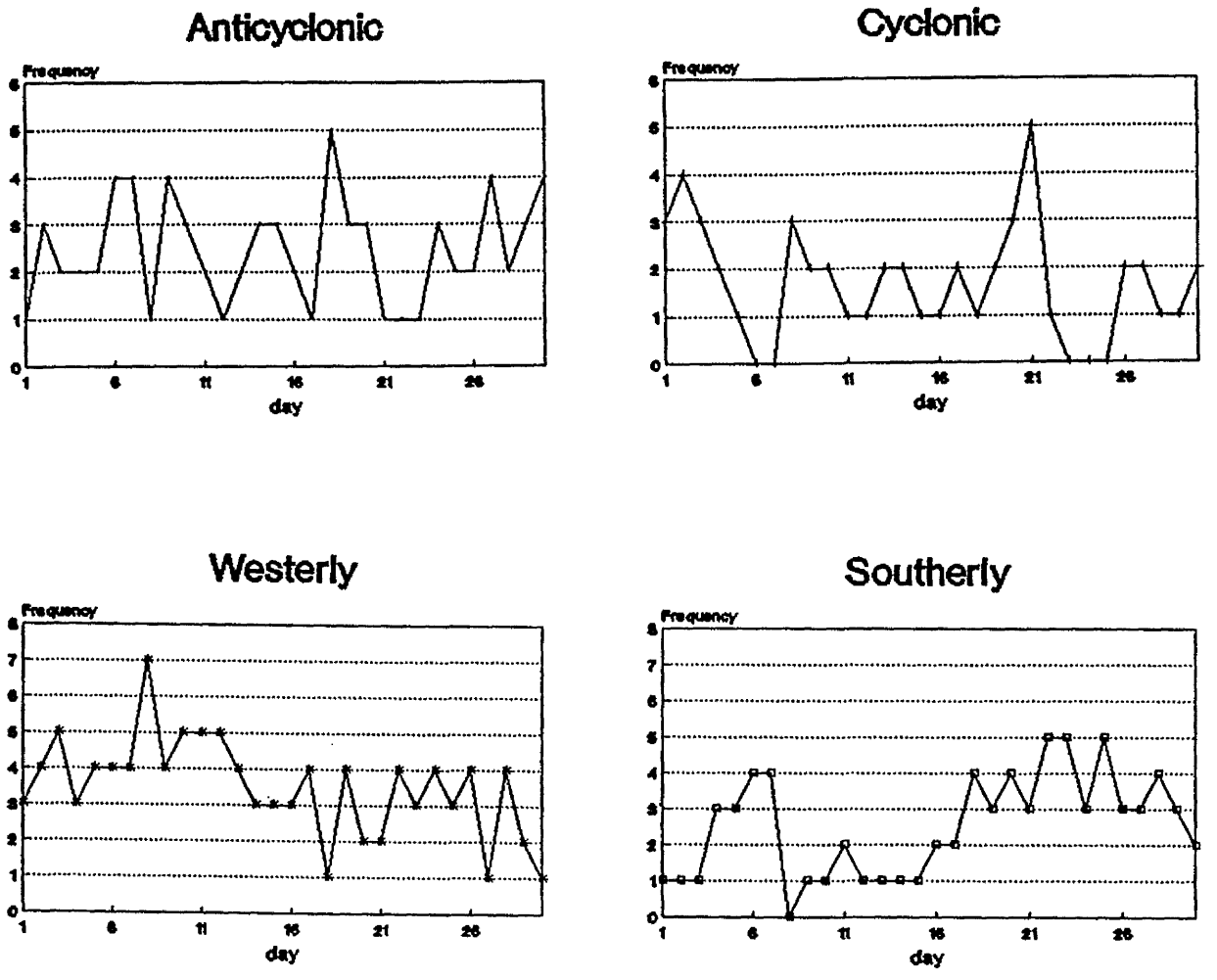


Figure 12.1 Daily frequencies of the four most frequent weather types during September 1976-88.

been prepared (i.e. ploughed in Scotland); secondly, the soil conditions are suitable for drilling (i.e. not too wet); and thirdly, the current weather will not deteriorate soil conditions during drilling. Therefore, the incidence of favourable drilling weather in early September does not necessarily mean that crops can be drilled.

Table 12.1 The number of days with weather types (defined in Figure 12.1) in each half of September 1976-88.

	Number of days 1976-88	
	September	
	first half	second half
Anticyclonic	37	39
Cyclonic	27	23
Westerly	63	42
Southerly	25	51

Chi-squared tests:-

all $x^2_{(3)} = 13.4$, $P < 0.01$

AC vs C $x^2_{(1)} = 0.34$, N.S.

AC vs W $x^2_{(1)} = 2.3$, N.S.

AC vs S $x^2_{(1)} = 3.9$, $P < 0.05$

C vs W $x^2_{(1)} = 0.5$, N.S.

W vs S $x^2_{(1)} = 13.0$, $P < 0.001$

C vs S $x^2_{(1)} = 5.5$, $P < 0.05$

Nevertheless, in the few autumns when early September weather is relatively dry in the west of Scotland, some crops are likely to be drilled at this time. In a more average September, the westerly weather types probably prevent early September drilling for many crops except those on light land. Thus, September weather may well augment the variability in the incidence of BYDV in autumn-sown cereals, through influencing crop drilling dates.

12.7 **The importance of mild winters**

In the three years of study, winter temperature was positively associated with the extent of BYDV incidence in autumn-sown cereals (section 4.8). Mild winters are known to be important to the epidemiology of many aphid-transmitted virus diseases of crops in Britain (Harrington *et al.*, 1990). However, in the spring of 1989, *R. padi*-transmitted BYDV arose only in Wigtownshire whereas *S. avenae*-transmitted BYDV arose in all regions except Lanarkshire (section 4.3.4). Therefore, mild winters may be more important to the incidence of the latter type of BYDV, because the former type requires specific pre-conditions (Chapter 10).

Mild winters are important to BYDV epidemiology because viviparous aphids are not frost-hardy (Bale, 1989). That serious BYDV problems arise after mild winters (Oakley, 1989) suggests that many autumn-sown cereals are infested by aphids during the autumn. Normally, many of these are

killed by low temperatures before they establish large populations of apterae which are able to cause damaging BYDV spread. Therefore, mild winters enable low numbers of autumn colonisers, which are insufficient to cause damage during the autumn, to survive and to multiply, so that damaging BYDV spread occurs subsequently.

Using the technique of seasonal forecasting (Ratcliffe, 1991b), a prediction of the temperature of each winter in Britain is presented in the "Letters to the Editor" page of each December issue of *Weather* (magazine of the Royal Meteorological Society). This forecast has been correct in three of the last four winters. In Britain, the majority of winter barley is drilled in September (Carter, 1984; Plumb, 1988). Therefore, it is likely that the majority of winter barley is infested by low numbers of aphids during the autumn, which might lead to damaging BYDV spread during a mild winter. Oakley (1989) stated that in future mild winters, control can be obtained with December- or January-applied sprays. A forecast of an impending mild winter could therefore be of use to both farmers and the agrochemical industry.

In the three years of study, a succession of mild winters (1987/88, Ratcliffe, 1988; 1988/89, Ratcliffe, 1989; 1989/90, Ratcliffe, 1990) may have accounted for the unusual abundance (Sparrow, 1974) of *S. avenae* in Scottish cereals. In the Vale of York (McGrath & Bale, 1990), *S. avenae*-transmitted BYDV problems followed the two mild

winters of 1982/83 and 1983/84 (Table 3.16). A preceding mild winter, in contrast to *R. padi*-transmitted BYDV (Chapter 10), may be a pre-condition of *S. avenae*-transmitted BYDV in autumn-sown cereals.

12.8 What aspects of BYDV can be forecast?

Theoretically, in years of high grass weed populations in stubble fields, heavy late summer infestation by *R. padi* could lead to severe BYDV damage similar to that obtained when untreated ploughed-in grass leys are followed by an autumn-sown cereal (Carter, 1984; Plumb, 1988), but on a regional scale. Monitoring stubbles (Chapter 9) in late summer could identify this situation, and advice to treat stubbles with desiccants issued in early September.

When data from a number of years has been collected, the assessments made during pre-harvest sampling will enable the pre-conditions of damaging local spread of BYDV to be identified. At present, there are many unknowns:-

(a) How damaging can BYDV spread by local aphids be (untreated ploughed-in ryegrass leys apart)?

(b) Is the phenomenon preceded by large numbers of aphids in cereals during the previous summer, or by an absence of aphids?

(c) Are the conditions that favour large aphid populations in stubble fields in summer, the same as those

that favour large *R. padi* migrations (Chapter 10)?

Once these questions have been answered, accurate forecasts of whether or not treatment of stubbles with desiccants is required may be available.

Forecasting the size of the autumn migration of *R. padi* is an immediate possibility given the agreement between the mathemátical models and the explanation of the groupings of the six British suction trap catches of *R. padi* using PSC indices (Chapter 10). The predictions can be tested to some extent each year prior to being used as forecasts, by sampling for aphids in ryegrass pasture during early September. The scarcity of *R. padi* in habitats other than ryegrass pasture during the three years of study engenders confidence in forecasting this aphid species: ryegrass appears to be the major source of *R. padi*. However, until variations in the alate exule component of *R. padi* migrations (Tatchell *et al.*, 1988; Kendall & Chinn, 1990) can be explained, annual and regional differences in the risk from *R. padi*-transmitted BYDV will not be accurately identified.

Forecasting the percentage infectivity of *R. padi* in western Britain is possible using winter temperature data. Reservations about its meaning have been expressed in Chapter 11. Also, its importance relative to that of aphid morph is probably small.

12.9 Use of suction trap data

Suction trap samples only record events in that part of an aphid's life cycle which involve migration (section 8.1), and this is sometimes but not always related to the density of aphids on crops or other host plants (Dewar, 1982). Interpretation of suction trap samples depends on an understanding of, and the relationships between aphid biology and ecology and crop development throughout the year (Tatchell, 1982). Weather is also important to suction trap catches in a number of ways (Chapter 3; Dewar, 1982; Walters & Dixon, 1984), and is a necessary factor for the interpretation of samples: both between traps on the same day or season (Chapter 3); and also between years at the same trap (Turl, 1980; Walters & Dewar, 1986; Harrington *et al.*, 1990).

Taylor (1973) compared the catches from suction traps of varying distances apart over varying lengths of time. The stronger between trap correlations at sites closer together is probably owing not only to the more similar aerial insect fauna at sites closer together, but also to the more similar weather at sites closer together. Similar weather will contribute to between trap correlations of aphid catches, because, for example, during May and June at Rothamsted from 1965-79, high wind speeds and low temperatures on 48% of the days were unsuitable for cereal aphid flight (Walters & Dixon, 1984). Suction traps closer together are more likely to have weather unsuitable for

aphid flight on the same days, than traps further apart.

Taylor (1973) also noted that seasonal cycles of population density were in phase at sites close together, but were sometimes out of phase as distance increased, especially with increasing latitude difference. Table 3.1 illustrates the marked temperature gradient with latitude in Britain during the spring and summer months which is likely to account for latitudinal differences in the seasonal cycles of aphid population density.

The RIS database represents a long and continuous record of the sizes of a number of pest's alate generations. If the relationship between the aerial and plant populations is known, suction trap catches can be related to the pest's population levels on crops (Tatchell, 1982). When this condition is satisfied, RIS data can contribute to pest forecasting systems, by providing information on the number of aphids in crops. It can also be used to construct a historical record of the numbers of aphids in crops. This latter use may be desirable, because crop sampling for aphids tends to be sporadic.

With respect to BYDV, analysis of RIS data has revealed new knowledge of *R. padi* population dynamics (Chapter 10). This can be used to predict the numbers of *R. padi* caught by suction traps during the autumn, thereby providing early warning in potentially high risk years.

12.10 **The importance of aphid monitoring**

Aphid monitoring in cereals during the autumn is a desirable approach to assessing the risk of BYDV to autumn-sown cereals for three reasons:

1) Few *S. avenae* are caught by suction traps during the autumn (Dewar, 1982; Plumb, 1986; McGrath & Bale, 1989).

2) Damaging BYDV spread is normally associated with apterous aphid populations, whose development may be affected more by weather than by the number of migrants (Kendall & Smith, 1981b).

3) With respect to *R. padi*, apterous populations only occur in cereal crops if the migrants are exules: this morph is a minority in the migrant population measured by British suction traps (Tatchell *et al.*, 1988; McGrath & Bale, 1989; Kendall & Chinn, 1990).

In the Rennes basin, experiments from 1983-87 showed that the extent of aphid infestation of barley seedlings placed near to a suction trap gave a better prediction of the extent of BYDV infection of the same barley seedlings than the number of *R. padi* caught by the suction trap. However, the number of *R. padi*, and the number of *R. padi* less males caught by suction traps, were also significantly correlated with the BYDV infection of the barley seedlings (Gillet *et al.*, 1990).

In Britain, Kendall & Chinn (1990) have found that a

variable (the crop vector index) which is derived from the numbers of vectors caught by a suction trap, the number of these which are viruliferous, and the numbers of aphids in crops, is more correlated with virus infection and yield loss in experimental winter barley plots, than either Plumb's (1986) index, or a modified index (aerial vector index) which excludes the holocyclic component of the *R. padi* migration.

These results suggest that a new scheme should include some crop monitoring. A number of conclusions have been drawn from the author's experience of aphid monitoring:-

1) It is better to count colonies of aphids rather than individuals. A colony is defined as a group of aphids numbering one or more. Noting colonies avoids the need for counting to large numbers, and it provides an epidemiological meaningful measure of aphid numbers, because it relates to the number of potential sites of BYDV infected plants (section 4.4.1).

2) Aphids do not seek shelter on the approach of the aphid monitor, although alatae can easily be dislodged from their host plant. Nor do they necessarily seek shelter in wet, windy or frosty conditions, as feeding individuals have frequently been observed in such weather conditions. Indeed, the unprecedented aphid and BYDV problems in Scottish cereals in the spring of 1989, were preceded by the wet and windy winter of 1988/89 (Ratcliffe, 1989). The

winter of 1989/90 was exceptionally wet and windy in southern Britain (Ratcliffe, 1990), and BYDV was widespread in autumn-sown cereals of England in the spring of 1990 (Kendall & Smith, 1991).

3) In contrast to the experience of other workers (George, 1982; Anon, 1984) *R. padi* was not cryptic, it being very conspicuous in the fields affected by *R. padi*-transmitted BYDV. This was because both leaves and stems were heavily infested by adults and nymphs, giving barley plants a blackened appearance, evident from a distance of several metres. This was observed in several fields in both autumn and spring.

4) During the autumn, alate *Rhopalosiphum* can be very numerous (> 1 per metre length of drill) in winter barley crops, as noted by Kendall & Smith (1981c). However, most observed during the three years of study had not reproduced on the plants on which they were found. The samples of *Rhopalosiphum* alatae that were removed to the laboratory for aphid transmission tests rarely reproduced either, suggesting that they were gynoparae and males (some were identified as males).

5) The variations in aphid infestation within fields appeared to be adequately sampled by the ten x one-metre lengths of drill examined in each field. As each one-metre length of drill was examined, adjacent drills were inevitably also scanned for aphid infestations. Some pest's

require a monitoring approach involving many fields and many samples per field (Taylor, 1973). This is apparently not the case for aphids in cereals during the autumn.

6) The discovery of individual aphids, either alatae or apterae, is common when undertaking aphid monitoring. Damaging BYDV spread occurs when apterous colonies build-up in small areas of the crop. The purpose of aphid monitoring is to detect these localized aphid infestations, so that insecticides are applied only when necessary.

6) For *R. padi*, many aphid colonies on one or a few plants in one metre length, is symptomatic of the development of damaging BYDV spread (George, 1982). For *S. avenae*, several colonies distributed between a number of plants (McGrath & Bale, 1990) in each of several one-metre lengths is symptomatic of the development of damaging BYDV spread.

12.11 **Regional variations in Britain's climate**

In Chapters 3, 10 and 11, aphid data from different regions of Britain were compared. Analyses with climate data from these different regions tested whether or not climate accounted for variations in the aphid data.

In Chapter 3, the difference in the mean daily maximum temperature in the spring was identified as an important factor in determining the size of spring suction trap catches of cereal aphids in the north and south of Britain (Table 3.26). However, a difference in the variability of

late winter temperature between the north and south of Britain was suggested as a reason for the greater number of significant relationships between date of first aphid catch and winter temperature obtained for the south.

Therefore, knowledge of differences in both the means and the variability of weather variables of different regions of Britain may be required.

The climate of Scotland differs from that of England in several respects:

1) Rainfall is significantly and positively correlated with the P index in all months in Scotland in contrast to only three months in England. The C index is significantly and positively correlated with rainfall in both countries in all months (section 2.4; Murray & Benwell, 1970).

2) Scotland experiences a different frost regime to that of England. The synoptic conditions which produce anomalously large or small numbers of frosts over England and Wales do not necessarily have the same effect in Scotland (Tout, 1987).

3) The decrease in mean monthly temperature with height is greater in Scotland than in England (Manley, 1953).

4) The climate of Scotland is less continental than that of England: both long hot spells in summer and long cold spells in winter are more frequent in the more south-eastern parts of Britain (Lamb, 1964).

12.12 The importance of weather patterns to BYDV epidemiology

A good illustration of the importance of weather patterns to BYDV problems in cereals was an outbreak in California in the spring of 1951 (Oswald & Houston, 1952). Continuous winter rains in the winter 1950-51 favoured both rank grass growth and large populations of grass aphids. Rain delayed the planting of spring crops until after March 1. A long drought then commenced, such that grasses died, and by March 20, aphids were leaving the grasses and moving into the young cereal crops. By mid-April, BYDV was widespread in spring cereals.

In Britain, BYDV in autumn-sown cereals may largely be the result of weather patterns in the previous year, because aphid populations, whose movement introduces to, and spreads the virus within crops (Irwin & Thresh, 1990), are very sensitive to weather. Figure 12.2 summarises the weather in the preceding year which was found to be important to BYDV incidence in autumn-sown cereals in the three years of study. However, more data are required, particularly pre-harvest sampling data, to consolidate this thesis.

	Cold winter	Mild winter
	Average or wet cool summer	
	Late August/early September weather suitable for ploughing and drilling	Late August/early September weather suitable for ploughing and drilling
Crop drilled	Mild autumn	Mild autumn
	Mild winter	Mild winter
	***R. padi*-transmitted BYDV**	***S. avenae*-transmitted BYDV**

BYDV risk to autumn-sown cereals increases with each of the above weather pre-conditions being satisfied.

Figure 12.2 Weather pre-conditions considered to be important to BYDV incidence in autumn-sown cereals.

12.13 **The Major Conclusions of the research**

1) BYDV occurs as two main types: *R. padi*- and *S. avenae*-transmitted BYDV. The former type has a much greater propensity to cause yield-loss in autumn-sown cereals.

2) *R. padi*-transmitted BYDV is likely when an autumn-sown cereal follows an untreated ploughed-in grass ley. It is probably more likely to affect crops on a regional scale in autumns which are preceded by both a cold winter and a cool wet summer.

3) *S. avenae*-transmitted BYDV is more likely to cause yield-loss in autumns which are preceded by a mild winter.

4) Current mild winters dramatically increase the risk of both types of BYDV by allowing anholocyclic overwintering in autumn-sown cereals.

5) *S. avenae*-transmitted BYDV was common in cereals both during pre-harvest sampling assessments in July 1989 & 1990, and during the springs of 1990 & 1991. Local movement by *S. avenae* is the likely explanation.

6) The following factors specific to farms or fields were found to affect BYDV incidence:- farm type; distance from the sea; distance from Stranraer; previous crop type; crop drilling date; shelter; and altitude.

7) Aphid infestations in ryegrass pasture were highly seasonal and *Rhopalosiphum* spp. attained high densities (> $100/m^2$) for short periods of time.

8) Aphid infestations on wild grasses were less rampant than those in cereals and ryegrass pasture, but BYDV infection was common.

9) BYDV-transmission by field-collected aphids was largely consistent with laboratory observations: characteristic vector-specificity and vector-efficiency were encountered, and transcapsidation and transmission interference were common.

10) Differences both between years and habitats were found in the percentage transmission of BYDV to indicator plants by field-collected aphids.

11) A significantly diminishing percentage of *R. padi* tested during Infectivity Indexing work 1984-90, transmitted BYDV to indicator plants during the autumn.

12) Spring weather is more critical to the differences in the size of spring suction trap catches of cereal aphids between the north and south of Britain, than winter weather.

13) The size of the autumn suction trap catch of *R. padi* at Ayr and other British sites is largely determined by the temperature of the preceding winter and rainfall of the preceding summer.

12.14 **Future work**

1) To maintain aphid and BYDV assessments in winter barley crops of different regions of Scotland to extend the aphid and BYDV incidence record.

2) To continue pre-harvest sampling to assess its value, not only in identifying aphid and BYDV incidence in cereals during summer, but also as a predictive tool.

3) To obtain data of the proportion of migrant *R. padi* population that is comprised of exules in different regions of Scotland during several autumns, and to explain this on the basis of the weather during the preceding winter and summer.

4) To establish whether cereal stubbles, wild grasses or ryegrass pastures, are the chief source of viruliferous *S. avenae*.

5) To clarify the issue of how far the aphids that colonise autumn-sown cereals fly: short local flights or flights exceeding the boundaries of individual farms.

6) To discover to what extent aphid colony establishment in autumn-sown crops is impaired by weather conditions and natural enemies, or whether the numbers of colonists, and the aphid morph are the critical factors.

7) To discover the the factors that lead to large numbers of *S. avenae* in fields and to establish whether or not the extent of aphid parasitism is the critical factor.

8) Given the relationships between weather and suction trap catches of aphids, it may be desirable to study the effects of weather singularities on suction trap catches.

APPENDIX 1

Mean winter (December to February) temperature °C at the six sites (Table 3.2).

	L	D	EC	BB	R	W
1976	4.9	4.8	5.0	4.5	4.3	4.4
1977	2.1	2.3	2.1	3.2	3.0	3.5
1978	2.6	2.8	2.4	3.3	3.6	3.9
1979	2.0	1.7	1.1	1.5	1.1	1.8
1980	3.4	3.5	3.6	4.4	4.1	4.7
1981	4.0	4.1	4.0	4.0	3.7	4.1
1982	2.4	2.2	1.9	2.2	2.0	2.4
1983	3.2	3.5	3.4	3.9	4.0	4.3
1984	3.6	3.6	3.7	3.9	3.7	4.3
1985	3.4	3.4	2.9	2.3	2.1	2.5
1986	2.4	2.7	2.4	2.8	2.3	3.1
1987	3.1	3.1	3.0	3.1	2.8	3.2
1988	3.8	4.7	4.6	5.1	4.7	5.3
1989	6.1	6.3	6.4	6.0	5.7	5.9
1990	3.8	4.6	4.7	6.3	5.9	6.7
Mean	3.4	3.6	3.4	3.8	3.5	4.0
sd	1.09	1.20	1.38	1.36	1.35	1.33

Key

Scotland		*England*	
L	Lossiemouth	BB	Brooms Barn
D	Dundee	R	Rothamsted
EC	East Craigs	W	Writtle

APPENDIX 2

Mean spring (April to June) daily maxima temperature ^{o}C at the six sites.

	L	D	EC	BB	R	W
1976	14.4	15.1	15.0	17.8	17.7	18.9
1977	12.0	13.6	13.3	14.1	13.9	14.7
1978	13.0	13.6	13.3	14.6	14.6	15.1
1979	12.4	13.5	13.2	15.3	15.0	15.7
1980	13.8	14.9	15.0	15.9	15.5	16.3
1981	13.6	14.1	14.1	14.7	14.4	15.3
1982	13.6	14.7	14.6	16.5	16.4	16.9
1983	11.7	12.2	12.2	14.7	14.6	15.6
1984	13.3	14.5	14.4	14.8	15.1	15.7
1985	12.7	13.4	13.3	14.7	14.6	15.7
1986	13.4	13.1	13.1	15.2	14.7	15.7
1987	12.7	13.5	13.5	15.2	15.2	16.1
1988	13.8	14.3	14.5	15.4	15.3	16.3
1989	13.8	14.5	14.6	16.2	16.3	17.2
1990	13.9	14.5	14.5	16.5	16.3	17.3
Mean	13.2	14.0	14.0	15.4	15.3	16.2
sd	0.77	0.78	0.83	0.98	0.99	1.05

Key

Scotland		*England*	
L	Lossiemouth	BB	Brooms Barn
D	Dundee	R	Rothamsted
EC	East Craigs	W	Writtle

APPENDIX 3

The following data are from the RIS aphid bulletin. The number of cereal aphids caught in April, May and June 1976-90 is shown for each of the six suction traps (Table 3.2).

Numbers of aphids caught by Elgin suction trap

	May				June			
	Rp	Sa	Sf	Md	Rp	Sa	Sf	Md
1976	4	0	0	1	3	5	30	4
1977	0	0	0	0	0	0	0	0
1978	0	0	0	0	2	0	0	1
1979	0	0	0	0	0	0	0	0
1980	0	0	0	0	8	0	1	0
1981	2	3	0	1	1	3	3	2
1982	0	0	0	0	25	1	0	4
1983	0	0	0	0	1	0	0	0
1984	0	0	0	0	14	2	0	0
1985	0	0	0	0	2	1	0	0
1986	0	0	0	0	12	2	0	1
1987	0	0	0	0	1	0	0	0
1988	1	0	0	0	0	2	1	0
1989	43	34	0	52	574	884	3	45
1990	0	0	0	0	17	7	8	7

No aphids were caught in April in each year.

Rp *Rhopalosiphum padi* Sa *Sitobion avenae*

Sf *Sitobion fragariae* Md *Metopolophium dirhodum*

Numbers of aphids caught by Dundee suction trap

	May				June			
	Rp	Sa	Sf	Md	Rp	Sa	Sf	Md
1976	1	0	0	0	17	42	9	51
1977	1	0	0	0	2	1	0	0
1978	3	0	0	0	3	0	2	0
1979	0	0	0	0	2	0	0	0
1980	0	3	1	1	4	14	6	6
1981[a]	3	4	0	1	16	9	5	5
1982	8	0	0	0	15	1	0	31
1983	1	0	0	0	0	2	0	0
1984	2	1	0	0	43	9	0	0
1985	0	0	0	0	9	0	0	0
1986	0	0	0	1	10	1	0	3
1987	1	0	0	0	1	0	0	0
1988	4	2	0	0	502	44	13	73
1989	1	96	0	14	301	2834	3	29
1990	53	0	0	1	84	11	6	54

[a] No aphids caught in April except in 1981 when one *R. padi* was caught.

Rp *Rhopalosiphum padi* Sa *Sitobion avenae*

Sf *Sitobion fragariae* Md *Metopolophium dirhodum*

Numbers of aphids caught by East Craigs suction trap

	May				June			
	Rp	Sa	Sf	Md	Rp	Sa	Sf	Md
1976[a]	5	2	2	2	41	51	7	28
1977	0	0	0	0	5	0	0	0
1978	4	1	0	1	60	2	2	1
1979	0	0	0	0	37	0	1	1
1980	77	3	1	6	82	2	6	22
1981[b]	22	5	0	14	7	4	2	9
1982	14	0	0	1	20	1	3	13
1983	0	0	0	0	14	6	4	0
1984	4	1	0	0	128	11	2	0
1985	0	0	0	0	25	0	5	1
1986	0	0	0	0	17	9	5	3
1987	46	0	0	1	135	5	4	4
1988	0	3	1	5	39	68	15	22
1989[c]	141	73	2	50	1814	1684	32	213
1990	128	1	1	2	214	15	8	46

[a] One *R. padi* caught April 1976.

[b] One *R. padi* and one *S. fragariae* caught April 1981.

[c] One *R. padi* caught April 1989.

Rp *Rhopalosiphum padi* Sa *Sitobion avenae*

Sf *Sitobion fragariae* Md *Metopolophium dirhodum*

Numbers of aphids caught by Brooms Barn suction trap

	April				May				June			
	Rp	Sa	Sf	Md	Rp	Sa	Sf	Md	Rp	Sa	Sf	Md
1976	0	0	1	0	66	13	6	2	643	2840	0	590
1977	0	0	0	0	3	4	0	1	22	61	11	11
1978	0	0	0	0	2	0	0	3	90	2	6	1
1979	0	0	0	0	6	0	0	0	47	0	6	2
1980	0	0	0	0	5	8	0	2	16	226	9	13
1981	0	0	0	0	31	72	0	6	122	117	8	2
1982	0	0	0	0	16	1	0	5	28	30	2	160
1983	0	0	0	0	2	2	0	0	60	294	16	21
1984	0	0	0	0	0	1	0	0	12	310	9	52
1985	0	0	0	0	2	1	0	0	3	12	11	8
1986	0	0	0	0	0	0	0	0	2	1	0	2
1987	0	0	0	0	10	2	0	1	1	37	3	12
1988	1	0	0	0	27	205	15	4	881	1178	62	84
1989	0	0	0	1	305	97	20	62	1202	635	69	976
1990	12	5	1	8	228	37	8	66	74	55	9	386

Rp *Rhopalosiphum padi*

Sa *Sitobion avenae*

Sf *Sitobion fragariae*

Md *Metopolophium dirhodum*

Numbers of aphids caught by Rothamsted suction trap

	April				May				June			
	Rp	Sa	Sf	Md	Rp	Sa	Sf	Md	Rp	Sa	Sf	Md
1976	1	0	0	0	31	33	1	1	539	1924	24	939
1977	0	0	0	0	2	6	1	1	6	30	1	0
1978	0	0	2	0	0	0	0	0	4	2	13	11
1979	0	0	0	0	0	0	0	1	5	0	10	0
1980	0	0	0	0	0	17	3	1	15	241	15	9
1981	0	0	1	0	13	18	10	3	30	20	14	5
1982	0	0	0	0	6	14	2	2	3	68	4	63
1983	0	0	0	0	3	8	0	0	51	302	27	26
1984	1	0	0	0	1	0	0	0	17	830	20	50
1985	0	0	0	0	14	1	1	1	10	23	14	10
1986	0	0	0	0	0	0	0	0	3	1	4	6
1987	0	0	0	0	4	4	0	4	1	79	8	30
1988	0	0	0	0	18	122	12	7	145	421	48	40
1989	0	1	0	4	365	205	10	81	1287	310	30	236
1990	17	4	0	1	345	42	3	70	55	120	10	469

Rp *Rhopalosiphum padi*

Sa *Sitobion avenae*

Sf *Sitobion fragariae*

Md *Metopolophium dirhodum*

Numbers of aphids caught by Writtle suction trap

	April				May				June			
	Rp	Sa	Sf	Md	Rp	Sa	Sf	Md	Rp	Sa	Sf	Md
1976	3	0	0	0	56	64	6	17	1306	5258	58	4917
1977	0	0	0	0	6	4	0	0	7	28	4	9
1978	0	0	0	0	0	0	0	0	3	14	11	11
1979	0	0	0	0	0	0	0	2	0	0	12	5
1980	0	1	0	0	2	63	11	2	9	964	32	6
1981	1	0	0	0	31	44	19	6	59	21	39	7
1982	0	0	0	0	10	37	4	8	6	202	25	109
1983	0	0	1	0	5	30	0	5	158	441	31	91
1984	0	0	0	0	1	5	1	0	162	791	18	180
1985	0	0	0	0	1	5	0	1	8	49	21	33
1986	0	0	0	0	0	0	0	0	6	12	13	25
1987	0	3	0	0	5	19	3	4	11	163	10	80
1988	2	0	0	2	118	174	48	15	456	413	63	38
1989	13	5	0	4	1076	278	53	162	1285	616	37	634
1990	16	7	2	13	266	71	17	143	121	156	20	584

Rp *Rhopalosiphum padi*

Sa *Sitobion avenae*

Sf *Sitobion fragariae*

Md *Metopolophium dirhodum*

APPENDIX 4

Numbers of aphids per 100 m^2 of ryegrass pasture in 1988 for each field on each sampling occasion.

			Numbers of aphids per 100 m^2			
Field	Date	gsleng	Rh spp.	Md	Mf	Sit
Dumfriesshire						
D1	14/6	2	17	0	100	17
D1	4/8	2	67	0	0	0
D1	15/8	1	33	0	0	0
D1	21/9	3	480	0	0	0
D2	14/6	3	17	0	100	0
D2	18/7	3	1899	0	0	33
D2	4/8	3	250	0	0	0
D2	15/8	3	117	0	0	0
D2	21/9	3	80	0	0	0
D3	14/6	2	0	50	83	17
D3	19/7	2	116	0	50	17
D3	4/8	2	183	0	0	0
D3	15/8	2	17	0	0	0
D3	21/9	3	80	0	0	0
D4	14/6	2	0	0	166	17
D4	18/7	2	33	0	100	50
D4	4/8	2	17	0	0	0
D4	15/8	2	0	0	0	0
D4	21/9	2	120	0	0	0
Wigtownshire						
W1	9/6	3	0	67	250	0
W1	2/8	2	17	0	0	0
W1	18/8	2	100	0	0	0
W1	7/9	3	10	0	0	0
W1	26/9	3	220	0	0	0
W1	10/10	2	280	0	0	0
W1	24/10	2	440	0	0	20

gsleng code for grass length (section 5.2).

Rh spp. *Rhopalosiphum* spp. Md *Metopolophium dirhodum*

Mf *Metopolophium festucae* Sit *Sitobion* spp.

Appendix 4 continued.

			Numbers of aphids per 100 m^2			
Field	Date	gsleng	Rh spp.	Md	Mf	Sit
W2	9/6	3	0	0	50	33
W2	2/8	3	1400	0	0	0
W2	18/8	3	133	0	0	0
W2	7/9	2	100	0	0	0
W2	26/9	2	60	0	0	0
W2	10/10	2	160	0	0	0
W2	24/10	2	220	0	0	0
W3	9/6	2	0	0	0	0
W3	2/8	3	17	0	0	0
W3	26/9	3	333	0	0	0
W4	9/6	3	0	0	350	33
W4	2/8	1	384	0	33	17
W4	7/9	2	200	0	0	0
W4	26/9	2	50	0	0	0
Ayrshire						
A1	9/6	1	0	17	34	0
A1	2/8	3	133	0	0	33
A1	7/9	1	0	0	0	0
A2	9/6	3	0	0	17	0
A2	2/8	1	17	0	0	0
A2	7/9	2	33	0	0	0
A3	16/6	3	17	17	1149	166
A3	12/7	1	17	0	67	67
A3	1/8	2	150	0	0	0
A4	16/6	3	0	84	150	17
A4	12/7	3	17	17	50	100
A4	1/8	2	50	0	0	0
A5	16/6	3	0	0	1699	0
A5	12/7	3	383	17	549	283
A5	26/7	3	184	0	0	50
A5	1/8	3	450	0	33	200
A5	5/9	3	80	0	0	0
A5	11/9	3	140	0	0	0
A5	14/9	3	430	0	0	20
A5	15/10	3	200	0	0	0

Rh spp. *Rhopalosiphum* spp. Md *Metopolophium dirhodum*

Mf *Metopolophium festucae* Sit *Sitobion* spp.

Appendix 4 continued.

			Numbers of aphids per 100 m^2			
Field	Date	gsleng	Rh spp.	Md	Mf	Sit
A6	5/9	2	80	0	0	0
A7	28/6	3	50	67	1300	400
A7	1/8	3	450	0	0	50
A7	5/9	3	80	0	0	0
A7	11/9	3	340	0	0	20
A7	14/9	3	510	0	0	10
A7	17/9	3	400	0	0	0
A7	20/9	3	1540	0	0	0
A8	20/7	3	66	0	0	283
A9	28/6	2	50	0	1699	467
A9	15/10	1	280	0	0	0
A10	26/7	3	150	0	0	67
A10	5/9	3	40	0	0	40
A10	11/9	3	60	0	0	20
A10	14/9	3	220	0	0	0
A10	20/9	3	640	0	0	0
A10	15/10	1	120	0	0	0
A11	27/6	2	17	17	366	66
A12	27/6	2	0	0	300	0
A12	20/7	2	150	17	117	33
A13	27/6	2	0	17	167	33
A14	27/6	2	0	0	183	0
A14	1/8	1	117	0	17	0
Stirlingshire						
S1	21/6	1	0	0	0	0
S1	27/7	3	84	0	33	0
S1	9/8	3	17	0	0	33
S1	22/8	3	0	0	0	0
S1	12/9	1	0	0	0	0

gsleng code for grass length (section 5.2).

Rh spp. *Rhopalosiphum* spp. Md *Metopolophium dirhodum*

Mf *Metopolophium festucae* Sit *Sitobion* spp.

Appendix 4 continued.

			Numbers of aphids per 100 m^2			
Field	Date	gsleng	Rh spp.	Md	Mf	Sit
S2	21/6	3	0	0	200	50
S2	27/7	2	0	0	0	0
S2	22/8	2	17	0	0	0
S2	12/9	2	20	0	0	0
S2	27/9	2	20	0	0	0
S3	21/6	3	0	0	367	83
S3	27/7	3	33	0	0	0
S3	22/8	3	50	0	0	0
S4	27/7	1	34	0	0	0
S4	27/7	2	0	0	0	0

gsleng code for grass length (section 5.2).

Rh spp. *Rhopalosiphum* spp. Md *Metopolophium dirhodum*

Mf *Metopolophium festucae* Sit *Sitobion* spp.

APPENDIX 5

Numbers of aphids per 100 m^2 of ryegrass pasture in 1990 for each field on each sampling occasion. Field names don't relate to those of 1988.

			Numbers of aphids per 100 m^2				
Field	Date	gsleng	Rp	Ri	Md	Mf	Sit
Dumfriesshire							
D1	18/4	3	0	0	0	0	0
D1	16/5	3	0	0	0	0	0
D1	14/6	3	0	0	0	40	40
D2	18/4	3	0	0	0	0	0
D2	16/5	3	0	0	0	0	0
D2	14/6	3	0	0	0	0	120
D2	11/9	2	80	80	0	0	0
Wigtownshire							
W1	12/4	3	0	0	0	0	0
W1	14/5	3	0	0	0	0	0
W1	10/9	2	60	0	0	0	0
W2	10/9	3	320	60	0	0	0
W3	10/9	2	560	60	0	0	0
A1	1/5	3	0	0	0	0	0
A1	16/6	3	0	0	0	60	0
A1	31/7	3	40	160	0	180	40
A1	13/8	3	1080	3020	0	240	200
A2	16/6	3	20	0	0	200	20
A2	13/8	3	2000	2400	20	280	340
A3	31/7	2	0	280	0	60	0
A3	13/8	3	360	880	0	40	0
A3	13/10	2	160	0	0	20	0
A4	1/5	3	0	0	0	0	20

gsleng code for grass length (section 5.2).

Rp *Rhopalosiphum padi* Ri *Rhopalosiphum insertum*

Md *Metopolophium dirhodum* Mf *Metopolophium festucae*

Sit *Sitobion* spp.

Appendix 5 continued.

			Numbers of aphids per 100 m^2				
Field	Date	gsleng	Rp	Ri	Md	Mf	Sit
A5	21/5	3	40	0	0	20	0
A5	13/7	3	40	0	0	40	100
A6	13/7	2	360	0	0	20	20
A6	13/10	2	60	0	40	0	0
A7	1/5	3	0	0	0	0	0
A7	21/5	3	40	0	0	0	0
A7	31/7	1	40	200	0	0	0
A7	13/8	2	560	3720	20	140	240
A7	7/9	2	100	0	0	0	0
A8	24/4	3	0	0	0	0	0
A8	15/5	3	20	0	0	40	0
A9	1/8	2	40	200	0	0	80
A9	14/8	2	2580	760	0	0	0
A10	7/9	2	180	0	0	0	0
A10	1/8	2	60	40	0	60	0
A10	14/8	3	360	840	0	20	220
A10	30/9	2	40	20	0	0	0
A11	24/4	3	0	0	0	0	0
A11	21/5	3	0	0	0	0	0
A11	15/6	1	20	0	0	0	0
A11	8/7	3	0	0	0	0	20
A11	7/9	3	200	0	0	0	0
A11	30/9	2	40	0	0	0	0
A12	1/8	3	60	100	0	80	180
A12	14/8	2	2680	1120	0	0	0
A12	7/9	2	80	20	0	20	0
A13	15/6	2	0	0	0	0	40
A13	1/8	2	960	300	0	300	240
A13	14/8	2	8700	1060	0	20	100
A13	7/9	2	220	0	0	0	0
A13	30/9	2	400	240	0	0	0

Rp *Rhopalosiphum padi* Ri *Rhopalosiphum insertum*

Md *Metopolophium dirhodum* Mf *Metopolophium festucae*

Sit *Sitobion* spp.

Appendix 5 continued.

			Numbers of aphids per 100 m^2				
Field	Date	gsleng	Rp	Ri	Md	Mf	Sit
Renfrewshire							
R1	10/4	1	0	0	0	0	0
R1	8/5	3	0	0	0	0	0
R1	4/6	3	0	0	0	100	600
Stirlingshire							
S1	9/4	3	0	0	0	0	0
S1	9/5	2	0	0	0	0	0
S1	5/6	3	0	0	0	60	0
S1	14/9	2	120	100	0	0	20
S2	9/4	2	0	0	0	0	0
S2	9/5	2	0	0	0	0	0
S2	14/9	2	0	120	0	0	0
S3	9/4	3	0	0	0	0	0
S3	9/5	3	0	0	0	60	0
S3	6/7	3	0	0	0	100	300

gsleng code for grass length (section 5.2).

Rp *Rhopalosiphum padi* Ri *Rhopalosiphum insertum*

Md *Metopolophium dirhodum* Mf *Metopolophium festucae*

Sit *Sitobion* spp.

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