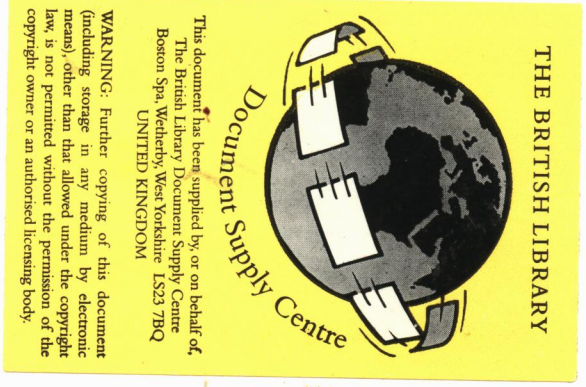

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# Transmission of barley yellow dwarf virus by cereal aphids collected from different habitats on cereal farms

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Cereal aphids were collected from cereal crops, from *Poa annua* within cereal fields, from *Lolium perenne* pastures and from wild grasses in hedge bottoms and around farm buildings. The frequency of barley yellow dwarf virus (BYDV) transmission was assessed by aphid transmission tests. There were differences in transmission rates between aphid species, between host species and between years. The transmission rates of *Rhopalosiphum padi* from the different host species were broadly similar whereas for *Sitobion avenae*, *P. annua* within cereal fields was significantly better than the other host species. Wild grasses other than *P. annua* were relatively poor sources of virus. A large percentage of aphids frequently transmitted more than one strain, suggesting that host plants are often infected with more than one BYDV strain.

## INTRODUCTION

Barley yellow dwarf virus (BYDV) is the most important virus disease affecting cereals in Britain (Thresh, 1980). It is transmitted in a persistent, circulative manner, so that once an aphid has acquired the virus, it is potentially infective for life (Rochow, 1977). *Rhopalosiphum padi* and *Sitobion avenae* are the two main vectors in Britain (Plumb, 1986), although a large number of aphid species have been found to be vectors of BYDV (Irwin & Thresh, 1990).

Three strains of BYDV occur in Britain, their names being acronyms that relate to the aphids that transmit them: RPV transmitted by *R. padi*, MAV by *S. avenae* (formerly *Macrosiphum*), and PAV transmitted by both aphid species. In the field, the RPV and PAV strains are predominantly transmitted by *R. padi*, whereas MAV is transmitted by *S. avenae* (Plumb, 1974). Sometimes, however, PAV is transmitted to crops by *S. avenae* (McGrath & Bale, 1990).

Two of these strains (RPV and MAV) have been described as vector specific (Rochow, 1969) although recent work has shown that vector specificity of designated serotypes is not as clear-cut as has sometimes been assumed (Halbert *et al.*, 1992a). Moreover, in the field, host plants may be infected with two or three BYDV strains. In these circumstances, several phenomena complicate the aphid–virus relationship. Dependent transmission has been found to be a unique feature of aphid–virus relationships. It enables *R. padi* to transmit MAV if its host plant is infected with both RPV and MAV. This involves the process of transcapsidation, which occurs when a virus particle containing a nucleic acid of one virus becomes 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, whereas in *R. padi* it functions like RPV because of the protein coat (Rochow, 1977).

Transmission interference is another phenomenon that confounds the vector specificity of BYDV. Fewer *S. avenae* transmitted the PAV strain if they had first acquired MAV, than if they had previously fed on healthy plants or on plants infected with other BYDV strains. Competition between virus isolates for receptors on aphid salivary glands is the most likely explanation (Gildow & Rochow, 1980).

The transmission efficiency of each strain differs both between aphid species and between host plants for any one aphid species. Both *R. padi* and *S. avenae* are efficient at transmitting their specific strains, whereas PAV is more efficiently transmitted by *R. padi* than by *S. avenae* (Rochow, 1969; Plumb, 1974).

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The main objective of this work was to determine the relative importance of different cereal aphid host species and habitats as reservoirs of infective aphids.

## MATERIALS AND METHODS

### Aphid collections

Cereal aphids (*Metopolophium dirhodum*, *M. festucae sensu stricto* (Stroyan), *R. padi*, *R. insertum*, *S. avenae* and *Sitobion fragariae* were collected from farms in a number of different regions of south-west and central Scotland from May 1988 to November 1990. They were collected from identified plants in four habitats: winter barley crops; *Poa annua* within winter barley fields; five species of wild grasses in hedge bottoms and farm lanes (see below); and *Lolium perenne* pastures. The aphid samples were collected randomly at the same time as estimates of aphid abundance (not reported here) were being made; more time was needed to collect aphids from wild grass sources where they were relatively few in number. There were no restrictions on the number of aphids collected from any plant, therefore the infection status of a host plant from which a large number of aphids were collected may have had a large influence on the results.

### Wild grasses

Five grass-weed species that were common on cereal farms along field margins and lanes, and around farm buildings, but not necessarily common within arable fields, were selected: *Alopecurus pratensis*; *Dactylis glomerata*; *Holcus lanatus*; *P. annua* and *L. perenne*. These five species constitute a large proportion of the grass flora in hedge bottoms, on disturbed land at field boundaries and around farm buildings. Aphids were collected during the summer of 1990 from the Scottish Agricultural College's Auchincruive estate and from another farm 8 miles inland.

### Raising of oat seedlings

Oat seedlings were grown in an insect-proofed glasshouse (fine gauze covered all ventilation windows). Four oat varieties were used depending on availability of seed: Coast Black, Maris Tabard, Dula and Pennal. One seed per 7·5-cm pot was sown about 10 days prior to the aphid transmission test.

### Aphid transmission test

The technique used was based on that described by Hill (1984). Aphids were placed individually with a fine paint brush on oat seedlings at the two or three leaf stage (GS 12–13) and were confined by use of a transparent lid with gauze vents. Aphids were allowed to feed for 3 days before the plant was sprayed with Pirimor (ICI, 50% w/w pirimicarb as a water dispersible granule, dilution rate 0·5 g/l). The plants were grown in a glasshouse for 4–6 weeks and then assessed for yellow or red discoloration of the leaves. In 1988, only plants showing any yellow or red discoloration were tested for BYDV using enzyme-linked immunosorbent assay (ELISA). Subsequently, all plants have been tested.

### ELISA

Each oat leaf sample was tested for all three BYDV strains (RPV, PAV and MAV). The method used was based on that given by Clark & Adams (1977) and described in more detail for BYDV by McGrath & Bale (1990). Polyclonal antibodies (supplied by Professor Rochow, Cornell University, Ithaca, NY, USA) were used for coating, while monoclonal antisera (Central Science Laboratory, MAFF, Harpenden, UK) were used after the sample stage. Each sample was represented in duplicate wells, so that the recognized variability of ELISA (Sutula *et al.*, 1986) could be considered in the determination of a positive–negative threshold. Test samples were assayed together with samples known to be virus-free and with samples known to be infected.

A threshold for each BYDV strain was determined using a MINITAB (version 6·2) program that calculates the mean of the virus-free readings, and the mean of the $n$ standard deviations (SD of the two readings per sample) of $n$ test samples. The threshold is the mean of the virus-free absorbance values plus 3·09 × the 'mean SD' of the test samples. The 3·09 corresponds to a probability of 0·002 for one tail of a Gaussian distribution. If both readings of a test sample exceeded this threshold, the BYDV strain under test was considered to be present.

### Analyses

Chi-squared tests were used to compare the number of aphids found to transmit BYDV with the number found not to transmit BYDV.

Comparisons were made between aphid species, between habitats within an aphid species, and between years both within aphid species and within habitats.

## RESULTS

A total of 2271 individuals, comprising five aphid species, were transmission tested for BYDV from May 1988 to November 1990. Tables 1 to 5 show the total number of each species tested and the percentage of aphids that transmitted each BYDV strain, either separately or in mixture, for each of the four habitats from which aphids were collected. Differences in the total number tested mainly reflect the relative abundance of the aphid species in the four habitats. Vector specificity was weaker with the *Rhopalosiphum* spp. than with the *Sitobion* and *Metopolophium* spp. All between-aphid-species differences were significant except that between *R. padi* and *M. dirhodum*.

*R. padi* from *L. perenne* pastures transmitted BYDV (any strain) more frequently (37%) than *R. padi* from winter barley (32%), which transmitted more frequently than *R. padi* from wild grasses (20%; Table 1). *S. avenae* from *P. annua* within cereal fields or from winter barley transmitted BYDV more often (22–23%) than did *S. avenae* from wild grasses (10%; Table 2). There was a significant difference between the four habitats ($\chi^2_{(3)} = 13{\cdot}7$, $P < 0{\cdot}01$), in the case of *S. avenae*, but not in the case of *R. padi*. *M. dirhodum* from winter barley transmitted BYDV more frequently (27%), than *M. dirhodum* from *L. perenne* pastures (8%; Table 3). *R. insertum*, from all four habitats, transmitted BYDV equally frequently (17–18%; Table 4). *M. festucae sensu stricto*, that was abundant only in *L. perenne* pastures, transmitted BYDV less frequently than all other aphid species (7%; Table 5).

*S. avenae* predominantly transmitted MAV in all four habitats. *R. padi* from *L. perenne* pastures and wild grasses transmitted RPV most frequently, while *R. padi* from winter barley transmitted RPV and PAV with equal frequency, and *R. padi* from *P. annua* within cereal fields transmitted RPV and MAV also with equal frequency. The samples of the other three aphid species from some habitats were too small for comparisons.

Thirty per cent of infective *R. padi* transmitted two BYDV strains, whereas only 12% of infective *S. avenae* did so. Only *R. padi* transmitted all three strains simultaneously (6% of infective individuals). MAV was the predominant strain in multiple strain transmissions by *S. avenae*, whereas RPV was the predominant strain in multiple strain transmissions by *R. padi*. Few *Metopolophium* transmitted a strain mixture, whereas 29% of BYDV-transmitting *R. insertum* did so.

Seasonal summaries of the data (Tables 6 and 7) show that there were differences both between seasons and between years in the percentage of *R. padi* and *S. avenae* that transmitted BYDV to oat seedlings. For *R. padi*, approximately 30% of aphids collected from winter barley transmitted BYDV on aggregate. However, in autumn 1989,

**Table 1.** Transmission of barley yellow dwarf virus to oat seedlings by *Rhopalosiphum padi* in four habitats 1988–90

| Habitat | Aphids tested | Aphids transmitting BYDV (%) | Percentage of aphids transmitting[a] each BYDV strain | | |
|---|---|---|---|---|---|
| | | | RPV | PAV | MAV |
| Winter barley | 330 | 106 (32) | 18 | 18 | 10 |
| *Poa annua* within winter barley fields | 17 | 5 (29) | 18 | 0 | 18 |
| Grass weeds in hedge bottoms and farm lanes | 60 | 12 (20) | 12 | 8 | 7 |
| *Lolium perenne* pastures | 405 | 151 (37) | 26 | 13 | 10 |
| Totals | 812 | 274 (34) | 22 | 15 | 10 |

[a] Percentage of the total number of aphids tested that transmitted each BYDV strain either alone or as part of a strain mixture.

**Table 2.** Transmission of barley yellow dwarf virus to oat seedlings by *Sitobion avenae* collected from four habitats 1988–90

| Habitat | Aphids tested | Aphids transmitting BYDV (%) | Percentage of aphids transmitting[a] each BYDV strain | | |
|---|---|---|---|---|---|
| | | | RPV | PAV | MAV |
| Winter barley | 600 | 130 (22) | 2 | 2 | 19 |
| *Poa annua* within winter barley fields | 211 | 48 (23) | 4 | 5 | 19 |
| Grass weeds in hedge[b] bottoms and farm lanes | 156 | 16 (10) | 1 | 1 | 8 |
| *Lolium perenne* pastures | 159 | 24 (15) | 4 | 4 | 9 |
| Totals | 1126 | 218 (19) | 3 | 3 | 16 |

[a] Percentage of the total number of aphids tested that transmitted each BYDV strain either alone or as part of a strain mixture.
[b] Aphid samples from this habitat were comprised of both *S. avenae* and *S. fragariae*.

77% of aphids transmitted BYDV to oat seedlings. Transmission by *S. avenae* collected from winter barley was more variable. Only 5% of the 135 aphids tested in autumn 1988 transmitted BYDV, whereas in the autumns of both 1989 and 1990 (the latter volunteer cereals), more than 50% transmitted BYDV. These annual differences (data for summer and autumn pooled) were significant for both *R. padi* $\chi^2_{(2)} = 15{\cdot}0$, $P < 0{\cdot}001$) and *S. avenae* $\chi^2_{(2)} = 36{\cdot}9$, $P < 0{\cdot}001$). There were also annual differences in the BYDV transmission rates for aphids collected from *L. perenne* pastures (Table 6), but these were significant only in the case of *R. padi* $\chi^2_{(2)} = 15{\cdot}9$, $P < 0{\cdot}001$). Again, the prevalence of MAV transmission by *S. avenae* and multiple BYDV strain transmission by *R. padi* were evident.

The results of the transmission tests on aphids collected from wild grasses (Table 8) show large differences between host plants for both aphid species. No *R. padi* collected from *D. glomerata*,

**Table 3.** Transmission of barley yellow dwarf virus to oat seedlings by *Metopolophium dirhodum* in four habitats 1988–90

| Habitat | Aphids tested | Aphids transmitting BYDV (%) | Percentage of aphids transmitting[a] each BYDV strain | | |
|---|---|---|---|---|---|
| | | | RPV | PAV | MAV |
| Winter barley | 48 | 13 (27) | 4 | 4 | 21 |
| *Poa annua* within winter barley fields | 13 | 2 (15) | 0 | 8 | 8 |
| Grass weeds in hedge bottoms and farm lanes | 51 | 11 (22) | 0 | 0 | 22 |
| *Lolium perenne* pastures | 13 | 1 (8) | 8 | 0 | 0 |
| Totals | 125 | 27 (22) | 2 | 2 | 18 |

[a] Percentage of the total number of aphids tested that transmitted each BYDV strain either alone or as part of a strain mixture.

**Table 4.** Transmission of barley yellow dwarf virus to oat seedlings by *Rhopalosiphum insertum* in four habitats 1988–90

| Habitat | Aphids tested | Aphids transmitting BYDV (%) | Percentage of aphids transmitting[a] each BYDV strain | | |
|---|---|---|---|---|---|
| | | | RPV | PAV | MAV |
| Winter barley | 59 | 9 (17) | 5 | 2 | 12 |
| *Poa annua* within winter barley fields | 28 | 5 (18) | 7 | 11 | 7 |
| Grass weeds in hedge bottoms and farm lanes | 6 | 1 (17) | 0 | 17 | 0 |
| *Lolium perenne* pastures | 28 | 5 (18) | 7 | 11 | 4 |
| Totals | 121 | 21 (17) | 6 | 7 | 7 |

[a] Percentage of the total number of aphids tested that transmitted each BYDV strain either alone or as part of a strain mixture.

or *S. avenae* collected from *A. pratensis*, transmitted BYDV. *P. annua* was the wild grass from which both these aphid species transmitted BYDV most often.

## DISCUSSION

The transmission rates of aphids collected from the four habitats will be influenced by differences in the BYDV infection of the host species. Moreover, the BYDV infection of cereal crops (A'Brook, 1974) and of *P. annua* within cereal fields changes, to a large extent from year to year. This probably accounts for the large differences in the percentages that transmitted BYDV to oat seedlings in different years and seasons (Table 7). However, some of the variability evident in the data is probably due to small sample sizes: BYDV transmission rates exceeding 50% were confined to samples below 100 aphids whereas the maximum percentage for samples of more than 100 aphids was 37%.

Multiple BYDV strain transmissions were characteristic of *R. padi* whereas *S. avenae* was generally MAV specific. Overall 10% of *R. padi* transmitted MAV. This suggests that transcapsidation is common within BYDV-infected plants in the field, enabling *R. padi* to transmit MAV. Although 15% of *R. padi* transmitted PAV, only 3% of *S. avenae* did so, suggesting that transmission interference with PAV by MAV may be occurring in field populations of *S. avenae*. These observations also suggest that BYDV infections of host plants in the field usually consist of more than one strain. While BYDV-transmitting *R. padi* will produce further

**Table 5.** Transmission of barley yellow dwarf virus to oat seedlings by *Metopolophium festucae* in four habitats 1988–90

| Habitat | Aphids tested | Aphids transmitting BYDV (%) | Percentage of aphids transmitting[a] each BYDV strain | | |
|---|---|---|---|---|---|
| | | | RPV | PAV | MAV |
| Winter barley | 2 | 0 | 0 | 0 | 0 |
| *Lolium perenne* pastures | 129 | 9 (7) | 2 | 2 | 5 |
| Totals | 131 | 9 (7) | 2 | 2 | 5 |

[a] Percentage of the total number of aphids tested that transmitted each BYDV strain either alone or as part of a strain mixture.

**Table 6.** Transmission of barley yellow dwarf virus to oat seedlings by *Lolium perenne* pastures 1988–90

| Habitat | Aphids tested | Aphids transmitting BYDV (%) | Percentage of aphids transmitting[a] each BYDV strain | | |
|---|---|---|---|---|---|
| | | | RPV | PAV | MAV |
| *Rhopalosiphum 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 |
| *Sitobion avenae* | | | | | |
| Summer and autumn 1988 | 75 | 7 (9) | 8 | 1 | 1 |
| Summer and autumn 1989 | 23 | 8 (35) | 4 | 13 | 2 |
| Summer and autumn 1990 | 61 | 9 (15) | 0 | 3 | 15 |

[a] Percentage of the total number of aphids tested that transmitted each BYDV strain either alone or as part of a strain mixture.

**Table 7.** Transmission of barley yellow dwarf virus to oat seedlings by aphids collected from winter barley crops 1988–90

| Habitat | Aphids tested | Aphids transmitting BYDV (%) | Percentage of aphids transmitting[a] each BYDV strain | | |
|---|---|---|---|---|---|
| | | | RPV | PAV | MAV |
| *Rhopalosiphum padi* | | | | | |
| Spring 1988 | 16 | 0 | 0 | 0 | 0 |
| Autumn 1988 | 55 | 14 (26) | 18 | 2 | 7 |
| Spring 1989 | 107 | 36 (34) | 18 | 24 | 5 |
| Autumn 1989 | 31 | 24 (77) | 61 | 32 | 39 |
| Spring 1990 | 32 | 10 (31) | 3 | 25 | 6 |
| Autumn 1990 (volunteers in cereal stubble fields) | 47 | 16 (34) | 11 | 23 | 15 |
| Autumn 1990 | 42 | 6 (14) | 7 | 7 | 7 |
| *Sitobion avenae* | | | | | |
| Spring 1988 | 39 | 4 (10) | 3 | 0 | 8 |
| Autumn 1988 | 135 | 6 (5) | 1 | 1 | 3 |
| Spring 1989 | 287 | 75 (26) | 4 | 4 | 22 |
| Autumn 1989 | 15 | 8 (53) | 0 | 0 | 53 |
| Spring 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 |

[a] Percentage of the total number of aphids tested that transmitted each BYDV strain either alone or as part of a strain mixture.

**Table 8.** Transmission of barley yellow dwarf virus to oat seedlings by aphids collected from four species of wild grasses from two farms in Ayrshire during summer 1990

| Habitat | Aphids tested | Aphids transmitting BYDV (%) | Percentage of aphids transmitting[a] each BYDV strain | | |
|---|---|---|---|---|---|
| | | | RPV | PAV | MAV |
| *Rhopalosiphum padi* | | | | | |
| *Dactylis glomerata* | 26 | 0 | 0 | 0 | 0 |
| *Poa annua* | 33 | 12 (36) | 21 | 15 | 12 |
| *Sitobion* spp.[b] | | | | | |
| *Alopecurus pratensis* | 13 | 0 | 0 | 0 | 0 |
| *Dactylis glomerata* | 41 | 4 (10) | 2 | 2 | 7 |
| *Holcus lanatus* | 51 | 3 (6) | 0 | 2 | 4 |
| *Poa annua* | 51 | 9 (18) | 4 | 2 | 14 |

[a] Percentage of the total number of aphids tested that transmitted each BYDV strain either alone or as part of a strain mixture.
[b] Aphid samples were comprised of both *S. avenae* and *S. fragariae*.

multiple BYDV infections, *S. avenae*, by selecting MAV from multiple infections, will tend to produce new, single-strain MAV infections.

This is the first published example of a large number of field-collected *R. padi* showing dependent transmission of MAV with RPV as the helper virus. These observations support laboratory work by Rochow (1977), who noted the stability and reproducibility of this phenomenon. Dependent transmission by *R. padi* appears to have more influence on the selection of BYDV strains transmitted than does *R. padi*'s specificity for the RPV strain. However, in studies of BYDV in winter barley crops from 1988 to 1990, *R. padi* infestations were generally associated with the PAV strain, although in spring 1989, crops that were infested by both *R. padi* and *S. avenae* were infected with all three strains. Collections of *R. padi* from winter barley crops in the spring of 1989 only transmitted MAV at 5% (Table 7) compared with an aggregate of 10% (Table 1). This variability in the transmission rates of MAV by *R. padi* (Tables 1 and 7) is confusing, but the results are similar to those of other workers who have found *R. padi* to be an efficient BYDV vector (Rochow, 1969; Plumb, 1976; A'Brook & Dewar, 1980; Halbert *et al.*, 1992b).

Habitat influenced both the strains transmitted and the efficiency of BYDV transmission (Tables 1–5). During the autumn, most alate *R. padi* originate from *L. perenne* pastures (Plumb, 1988; Hand, 1989). The high percentage (37%) of infective *R. padi* from this habitat relative to that from wild grasses (20%) provides a possible explanation for the variability in the infectivity of *R. padi* in different years at specific suction traps (Plumb, 1976; A'Brook & Dewar, 1980). The percentage of *R. padi* that are infective is thought to be one of the major determinants of BYDV infection in autumn-sown cereals. Its measurements forms part of Infectivity Indexing (II) that has been used to forecast BYDV in eastern England (Plumb, 1986) and Scotland (Foster *et al.*, 1993). Annual variations in the number of *R. padi* that migrate from each of the different host species during the autumn, may account for much of the variation in aphid infectivity.

For *S. avenae*, habitat also influenced BYDV transmission rates, with cereals producing the most infective *S. avenae* populations. This might partially explain the increase in the BYDV transmission rates of *S. avenae* collected from winter barley from 1988 to 1990 (Table 7). The more efficient a vector is in a specific habitat, the greater its sensitivity to changes in the level of infection of its host plant. The higher-than-average temperatures experienced in Britain in the late 1980s (Auchincruive mean annual temperature: 1951–1980 average 8·8°C; 1988, 9·3°C; 1989, 9·2°C; 1990, 9·5°C) have favoured cereal aphid infestations and BYDV infection in cereals (Oakley, 1989). This resulted in a build-up

of MAV infection on cereal farms during this period with an associated rise in the incidence of infective *S. avenae* (Table 8).

A reduction of BYDV was transmitted both by *R. padi* and by *S. avenae* from wild grasses than by aphids from other habitats (Table 8). In France, collections of *R. padi* from four species of wild grass transmitted BYDV at mean rates of 14% and 25% in 1985 and 1986, respectively, while the equivalent figures for *S. avenae* were 7% and 0% (Henry, 1988). The reason for this is unknown, but virus titre in the phloem sap could be important.

For both *R. padi* and *S. avenae*, *P. annua* was the wild grass from which BYDV was transmitted most often, with transmission rates similar to those of aphid populations collected from *P. annua* within cereal fields (Tables 1 and 2). Studies that have assessed the reproduction and growth of cereal aphids on different grass-weed species have given conflicting results. Smith *et al.* (1984) showed *P. annua* to be a good host plant both for *R. padi* and for *S. avenae*, whereas Tatchell *et al.* (1983) listed it as a preferred host only for *R. padi*, and Coon (1959) showed it to be a poor host for both aphid species. Our data suggest that much *P. annua* is infected with BYDV. The high infectivity of aphids of both species collected from *P. annua* indicates that this grass weed may play a major role in the epidemiology of BYDV in autumn-sown cereals.

The BYDV transmission rates observed in this study are high in relation to those reported by some other workers (Plumb, 1976; Halbert *et al.*, 1992b), but A'Brook & Dewar (1980) at another western UK site found similarly high levels. The occurrence of cereal aphids in different habitats, and the associated variation in BYDV transmission rates, together with these regional variations in transmission rates, are aspects of BYDV epidemiology that require more research. The approach of this work, collecting aphids from identified host plants, is practical and provides new data that can be used in the development of improved methods of forecasting BYDV high-risk conditions in autumn-sown cereals.

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# The role of *Poa annua* in the epidemiology of barley yellow dwarf virus in autumn-sown cereals

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Studies of cereal aphids and barley yellow dwarf virus (BYDV) from 1989 to 1992 revealed that *Poa annua* is an abundant weed of commercial winter barley crops during the summer months. *P. annua* was frequently infected with BYDV, and there were usually similarities with the BYDV infection of the surrounding barley crop. These *P. annua* weeds were often infested by cereal aphids both in July (pre-harvest) and in September (in cereal stubble fields). *Poa*-infested cereal stubbles may be major local sources of viruliferous aphids, increasing the risk of BYDV in nearby winter cereals. *P. annua* plays an important role in the epidemiology of *S. avenae*-transmitted BYDV.

## INTRODUCTION

Barley yellow dwarf virus (BYDV) is the most important virus disease affecting cereals in Britain (Thresh, 1980). The two main aphid vectors are *Rhopalosiphum padi* and *Sitobion avenae* (Plumb, 1986). Correspondingly, two types of BYDV can be recognized: *R. padi*- and *S. avenae*-transmitted BYDV (McGrath & Bale, 1990).

Three strains of BYDV occur in Britain, their names being acronyms that relate to the aphids that transmit them: RPV transmitted by *R. padi*, MAV by *S. avenae* (formerly *Macrosiphum*) and PAV transmitted by both aphid species (Plumb, 1974). In the field, RPV and PAV are predominantly transmitted by *R. padi* whereas MAV is transmitted by *S. avenae* (Plumb, 1974). Sometimes, however, PAV is transmitted to crops by *S. avenae* (McGrath & Bale, 1990).

Many weeds and grasses are reservoirs of virus diseases that can be transmitted to agricultural crops by insects (van Emden, 1965). Both BYDV (Oswald & Houston, 1953; Kurppa *et al.*, 1989) and cereal aphids (Smith *et al.*, 1984; Tatchell *et al.*, 1983) have wide host ranges suggesting that grass weeds could be important sources of viruliferous aphids.

This paper examines whether or not *Poa annua* within cereal fields plays an important role in the epidemiology of BYDV in autumn-sown cereals. *P. annua* is an annual or short-lived perennial grass. It does not compete strongly with established plants but because germination is rapid and seed production is prolific, *P. annua* is characteristic of unstable and disturbed situations. Therefore it is one of the most common arable weeds (Hubbard, 1968; Hutchinson & Seymour, 1982).

*P. annua* normally germinates in late summer or early autumn from seed produced one or 2 months earlier. The young seedlings grow rapidly during the autumn but are capable of limited growth during the winter. Compared with most other grasses, *P. annua* resumes active growth and begins flowering earlier in the spring. Flowering continues throughout the summer and the autumn. Annual ecotypes die after flowering while perennial types begin a phase of secondary tiller formation that markedly increases the density of the sward (Wells, 1974).

In Scotland, ploughing is the standard method of preparing the ground for autumn-sown cereals. Therefore, *Poa* infestations present in autumn-sown cereals in summer are comprised of plants that germinated in the preceding autumn and spring. All infected *P. annua* within a barley crop must have acquired the virus after the emergence of the crop because BYDV is not seed-transmitted (Eweida *et al.*, 1988).

## MATERIALS AND METHODS

All sampling was carried out in commercial winter barley crops of south-west and central

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