INTERACTIONS BETWEEN BARLEY YELLOW DWARF VIRUS, APHIDS AND *CLADOSPORIUM* ON CEREALS

by

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ABSTRACT

Field experiments in 1979 revealed that higher populations of *Metopolophium dirhodum* (Wlk.) developed on barley yellow dwarf virus (BYDV)-infected winter wheat and oats than on healthy plants. More *Sitobion avenae* (L.) were similarly recorded in 1980 on BYDV-infected winter wheat, oats and barley.

In both years, foci of BYDV infection attracted more immigrant alates than did healthy plants. This observation was supported by laboratory flight chamber trials in which aphids were simultaneously presented with a choice of targets; both *M. dirhodum* and *S. avenae* alighted more frequently on the leaves of BYDV-infected oats and barley than on those of healthy plants.

The adult size and fecundity of *S. avenae* were increased by feeding on BYDV-infected wheat, oats and barley but *M. dirhodum* was not affected.

Both BYDV infection and aphid honeydew predisposed wheat ears to infection by *Cladosporium*. Individual *M. dirhodum* and *S. avenae* excreted less honeydew on BYDV-infected than on healthy wheat in the laboratory.

The significance of the interactions between BYDV, its aphid vectors and *Cladosporium* is discussed in the light of the foregoing findings.

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GENERAL INTRODUCTION

Background

In 1976 and 1977, the Aerial Photography Unit of the Agricultural Development and Advisory Service (ADAS) detected a prominent and distinctive focal pattern of dark patches in many fields of winter wheat in Essex and parts of East Anglia (Hooper, 1978). On examination, these patches (Figure 1) were found to consist of plants infected with barley yellow dwarf virus (BYDV) and sooty moulds. They averaged about two meters in diameter. The sooty moulds were thought to be growing on aphid honeydew because of the many aphid exuviae found in the patches.

The foci of BYDV infection were restricted to early-sown crops, i.e. before mid-October. This fact was thought to indicate that these particular crops were infected with the virus by aphids flying into the fields in October when the plants would have emerged above ground (A'Brook, 1974, 1979; A'Brook & Dewar, 1980; Plumb, 1976). According to the Rothamsted Insect Survey trap catches, the most prevalent species of aphid at that time of the year are *Rhopalosiphum* spp., especially *R. padi* L. (the bird-cherry aphid) and *R. insertum* (Walker) (the apple-grass aphid) (A'Brook, 1974, 1978, 1979; A'Brook & Dewar, 1980; Plumb, 1981; Taylor & French, 1970-80). Both of these aphids are vectors of BYDV (A'Brook & Dewar, 1980; Oswald & Houston, 1952), and *R. padi* is the most efficient vector of the severe isolate of the virus (Lindsten, 1964; Plumb, 1974; Rochow et al, 1965; Smith, 1963). A varying proportion



Fig. 1A. A field of winter wheat near St Albans, showing yellowish patches of BYDV infection (10.6.81).

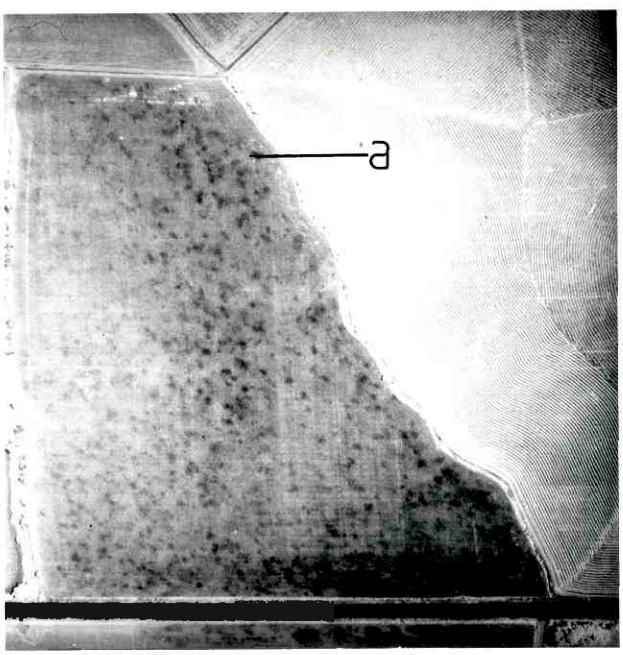


Fig. 1B. Aerial photograph of a field of early-sown winter wheat showing typical dark patches (eg. a.). (Curtesy of the Aerial Photography Unit, ADAS, Cambridge).

of aphids caught alive in suction traps in the autumn at Rothamsted in England and Aberystwyth in Wales are viruliferous (A'Brook, 1978; A'Brook & Dewar, 1980; Plumb, 1974, 1976, 1981). Knowledge of this proportion is being used in attempts to forecast the incidence of BYDV-infection (A'Brook, 1979; A'Brook & Dewar, 1980; Plumb, 1976).

Objective

Of the several relevant questions that needed to be answered about the existence of the patches, this study was aimed at the following:

1. Are there greater numbers of aphids in the patches than in the surrounding crop, and if so, why?
2. Why do the sooty moulds appear to be confined to the virus patches, or at least to be present in these foci in a much higher concentration than in the surrounding crop?

Approach

The approach was to study the complex of interactions between BYDV, its aphid vectors, the plant host and sooty mould development. Cladosporium was chosen because it is one of the predominant grain surface fungi on cereals in the field in most years (Hill, 1977, 1979; Hill & Lacey, 1974; Lacey, 1975).

The study involved extensive laboratory, glasshouse and growth cabinet experimentation. Field trials were also conducted at Rothamsted in 1979 and 1980. In addition, field trips were made to Essex and Cambridge in both years

to see farmers' crops. A flight chamber experiment was conducted at the Insect Physiology Unit of the Imperial College at Silwood Park, Ascot.

The thesis

In the first of five sections, the effects of BYDV infection of winter wheat, oats and barley on the colonization of these crops by cereal aphids, and on the consequent development of aphid populations in the field, are examined.

Section two seeks to verify, using a laboratory insect flight chamber, the field observations concerning the effect of BYDV on the host selection behaviour of cereal aphids.

The third section deals with the effect of the virus on the adult size and fecundity of S. avenae, R. padi and M. dirhodum. Different methods of estimating potential fecundity, and the relationship between adult size and fecundity in these aphids are also investigated.

In section four, the effects of BYDV and aphid honeydew on the incidence of Cladosporium and other phylloplane microflora on winter wheat and barley are described.

Section five reports on the effect of BYDV infection of spring wheat and barley on honeydew production by S. avenae and M. dirhodum under controlled conditions.

The effect of BYDV infection on the grain yield of cereals is described in both sections one and four.

At the end, the overall interactions between BYDV, its aphid vectors and plant hosts, and Cladosporium are discussed together with their implications for each organism in the complex.

REVIEW OF THE LITERATURE

BARLEY YELLOW DWARF VIRUS

Barley yellow dwarf virus (BYDV) was first recognised and named as such in 1951 (Oswald & Houston, 1951), although it is thought to have been a problem much earlier (eg. Bremer, 1965; Bruehl, 1961). The extensive literature that has accumulated thereafter on the virus has been comprehensively reviewed by Bruehl (1961), Rochow (1970), Panayotou (1975) and Pearson (1977).

Distribution and economic importance

The virus is world wide, having been identified in at least one country on every continent. Rochow (1970) considers it the most widely distributed of all cereal viruses. BYDV occurs throughout the British Isles (James, 1969).

The economic importance of BYDV is closely linked with its yield reducing capability. Artificial infections of the virus, especially at the seedling growth stages, can cause yield losses of up to 90% in oats (Endo & Brown, 1957; Gill *et al*, 1969b), wheat (Doodson & Saunders, 1970a,b; Gill, 1967; Gill *et al*, 1969b; Gill, 1980) and barley (Gill *et al*, 1969a; Doodson & Saunders, 1970a,b). Yield losses due to natural infections are complicated by the damaging effects of aphid feeding, other diseases and environmental factors. Not surprisingly, little has been reported on comparing the yields of healthy and naturally BYDV-infected crops. However, Bayon and Ayrault (1977) found that about 63 million francs were lost through BYDV infection of

winter wheat and winter and spring barley in Poitou-Charentes, France in 1975. BYDV also lowered the potential yield of spring wheat by 7% in southern Manitoba, Canada, in 1978 (Gill, 1980). Annual yield losses in cereals in Britain have been estimated at 5 - 10% (Doodson & Saunders, 1969; A'Brook, 1974). Economic losses have also been associated with BYDV in the U.S.A. (eg. Oswald & Houston, 1953a) and New Zealand (Smith, 1963).

Several severe epidemics of BYDV have been reported (eg. Murphy, 1959; Watson, 1959; Gill, 1970). Rochow (1961) considered BYDV to be potentially equally destructive as any other cereal virus while Plumb (1974) described it as the most damaging cereal virus in Britain.

Host Range

The host range varies with the strain of virus, the host preference of the aphid vector and the genetic variability of the host plant. Detailed information on the specific host range of BYDV is available in Oswald and Houston (1952), Bruehl and Toko (1957), Watson and Mulligan (1960), Bruehl (1961), Rochow (1961) and Jones, (1968). About one hundred monocotyledonous species are known to be susceptible to BYDV, including most grasses (Doodson, 1967; Plumb, 1977) and all commercially available cereal cultivars (Plumb, 1974), although several barley varieties from Ethiopia have a high level of tolerance (Schaller *et al*, 1963; Darnsteegt & Bruehl, 1964; Catherall & Hayes, 1966; Jedlinsky, 1972; Jones & Catherall, 1970).

Winter varieties are more susceptible than spring and oats and barley are more susceptible than wheat (Watson & Mulligan, 1960; Doodson & Saunders, 1970).

External symptoms

Some infected plants develop no symptoms (James et al, 1969; Gill, 1970; Catherall, 1963, 1966; Bremer, 1965; Doodson, 1967; Lindsten & Gerhardson, 1969). Depending on the host plant species, cultivar, growth stage at inoculation, physiological and environmental conditions as well as the strain or isolate of the virus, several external symptoms have been associated with BYDV infection. These include stunting of the roots and aerial parts, twisting of leaf blades, death of the apical shoot, increased tillering, narrower and stiffer leaf blades, leaf serrations (Smith, 1959), blasting of the florets (especially in oats), and failure of the ear to emerge (Bruehl, 1961). The earlier infection occurs, the more severe are the symptoms (Watson & Mulligan, 1960; Jenkins, 1966).

Infected leaves may also appear water-soaked and develop chlorotic stripes, blotches or mottles. These developments are often accompanied by drastic colour changes from green to bright yellow in barley and red to purple in oats and wheat. However, some non-cultivated grasses develop no symptoms on infection (Rochow, 1970). Only leaves younger than the one inoculated with the virus show the colour change.

Several authors have pointed out the similarities between these symptoms and those caused by other factors

(eg. Banttari, 1965; Gill et al, 1969b; Rochow & Duffus, 1978; Slykhuis, 1967; Sprague, 1936, 1939; McKinney, 1950; McKinney et al, 1952). It is therefore desirable to eliminate alternative causes of these symptoms and to conduct transmission tests when diagnosing the virus.

Internal symptoms

BYDV infection induces degeneration and eventual necrosis of the phloem, xylem and ground parenchyma tissues of the host plant (Esau, 1957a,b). These effects are more severe in oats and barley than in wheat. Recently, it has been revealed that serologically related variants of the virus induce similar cytopathological alterations in oat cells, and the reverse is the case with serologically unrelated ones (Gill & Chong, 1975, 1976, 1979).

Sugary exudates have been observed on BYDV-infected leaves and Esau (1957b) suggested that these exudates may result from pathological changes in the mesophyll, accumulate in the intercellular spaces and leave the mesophyll via the stomata.

Several metabolic changes have been associated with BYDV-infection of various plant species. It increased respiration and caused an accumulation of soluble carbohydrates and starch (Jensen, 1966, 1968a,b, 1969, 1972; Jensen & Sambeek, 1972; Orlob & Arny, 1961; Goodman et al, 1965; Watson & Mulligan, 1960), and increased the amount of indigestible crude protein (Jensen, 1969; Pearson, 1977) and free amino acids (Markkula & Laurema, 1964). Conversely, transpiration (Orlob & Arny, 1961), chlorophyll content, leaf area and photosynthetic rate were all decreased by BYDV (Jensen, 1966, 1968a, 1969, 1972; Jensen & Sambeek, 1972). Wynd (1943) had suggested that the increases in the amount

of amino acids in a diseased plant may result from either a loss of the ability of the infected plant to synthesize amino nitrogen compounds into more complex molecules, or a lessening of the translocation of intermediate soluble products in diseased plants. The latter view was adopted by Jensen (1972) to explain the accumulation of photosynthates in the leaf blades of BYDV-infected plants. Changes in nitrogen levels (Stubbs & Walbran, 1963; Orlob & Arny, 1961; Jensen, 1969b), deposits of glycogen-like substances in the chloroplasts of barley leaves (Moline & Jensen, 1975), a decrease in catalase activity and an increase in peroxidase activity (Orlob & Arny, 1961) have also been attributed to BYDV infection.

Diagnosis

The diagnosis of BYDV has been hampered by several problems including symptomless infections, the unreliability of symptoms which can resemble those caused by other factors, as well as the cumbersome and time-consuming nature of transmission tests with aphid vectors. In addition, the virus occurs in relatively low concentrations in the plants (Jensen, 1969; Paliwal & Sinha, 1970) and was not detected by commonly used serological tests like tube precipitin, ring interface or microprecipitin, or by "leaf dip" electron microscopy. It is also difficult to distinguish BYDV particles from plant cell constituents in the leaf dip preparations (Paliwal, 1977).

More rapid and reliable techniques have been developed recently. These are serological specific electron microscopy (SSEM) (Paliwal, 1977) and enzyme-linked immuno-

sorbent assay (eg. Lister & Rochow, 1979; Rochow, 1979). Both methods had previously been used to detect other plant viruses (eg. Bar-Joseph et al, 1979; Casper, 1977; Derrick, 1973, 1975; Reeves et al, 1979).

Transmission

By vectors

About eighteen species of aphid vectors of BYDV are known (A'Brook, 1978; A'Brook & Dewar, 1980; Kennedy et al, 1962; Plumb, 1974, 1981), including the grain aphid, Sitobion avenae F., the rose-grain aphid, Metopolophium dirhodum (Walker) and the bird cherry aphid, Rhopalosiphum padi L.. These three aphids, and in some years the apple grass aphid, Rhopalosiphum insertum (Walker) are the most important BYDV vectors in Britain (A'Brook & Dewar, 1980; Plumb, 1981).

Aphids can acquire the virus after several hours of feeding on infected plants (Orlob, 1959; Toko & Bruehl, 1959), and there is usually a latent period when acquisition feeding times are shorter than one day (Rochow, 1963) although transmission readily occurs when acquisition and inoculation feeding times are one to two days (Watson & Mulligan, 1960). Transmission can occur after 15-30 minutes inoculation feeding (Orlob, 1959; Watson & Mulligan, 1960) although longer periods will improve transmission rates. The virus persists in the vector for two to three weeks (Rochow, 1959), is retained during moults, but is not known to multiply in the aphid or to be transmitted transovarially.

Transmission depends on many factors such as aphid species or clone and age (Gill, 1970), virus isolate,

temperature, test plant species, and age of the plant (Rochow, 1969a).

By dodder

BYDV has been recovered by aphids feeding on dodder established on infected barley (Orlob et al, 1961) and it has been transmitted from barley to barley by Cuscuta campestris (Timian, 1964).

By other means

BYDV has not been transmitted mechanically, through seed or soil.

Strains and Vector Specificity

Serological tests have shown that BYDV is a generic name covering many strains or variants (Aapola & Rochow, 1971; Clark et al, 1979). Strains differ in how efficiently they are transmitted by different aphid vectors, the damage they cause and in their geographical distribution in cereals (Plumb, 1977).

Several separate attempts to classify the different variants of BYDV have been based on the degree of virulence (eg. Allen, 1957), host range (eg. Bruehl, 1961), or vector specificity (eg. Toko & Bruehl, 1957, Bruehl, 1958; Rochow, 1969a,b; and Gill, 1967). More recent attempts have been made to base classification on the cytopathological changes induced in the host plant by each strain of the virus (Gill & Chong, 1975, 1976, 1979a & b). The classification in common use is however based on a combination of virulence and vector specifity (Gill, 1969; Plumb, 1974; Rochow, 1969a) (Table I).

Table I: The classification of BYDV

A. American classification (Gill, 1969; Rochow, 1969a)

Variant	Main vector(s)	Virulence	Infrequent/erratic vectors
MAV	*Macrosiphum avenae*	moderate	*R. maidis*, *R. padi*, *S. graminum*
PAV	*Macrosiphum avenae*		
	Rhopalosiphum padi	strong	*R. maidis*, *S. graminum*
RMV	*Rhopalosiphum maidis*	weak	*M. avenae*, *R. padi*, *S. graminum*
RPV	*Rhopalosiphum padi*	weak	*M. avenae*, *R. maidis*, *S. graminum*
SGV	*Schizaphis graminum*	weak	*M. avenae*, *R. maidis*, *R. padi*

B. British classification (Plumb, 1974)

Variant	Main vector(s)	Virulence
MAV	*Macrosiphum (Sitobion) avenae*	mild
MDV	*Metopolophium dirhodum*	
	M (S) avenae	mild
PAV	*M (S) avenae*	
	R. padi	severe
RPV	*R. padi*	severe

Epidemiology

The incidence of BYDV in a crop is closely related to the biology of its aphid vectors. In the U.K., epiphytotics of BYDV are more common on early sown (ie. September to mid-October) cereals (A'Brook, 1974, 1979; Hooper, 1978; Plumb, 1981) which are inoculated with the virus by infective alates, particularly *R. padi* and *R. insertum* (A'Brook & Dewar, 1980; Plumb, 1976) migrating in the autumn from diseased cereals and grasses to their winter hosts. The severity of the epiphytotics depends therefore on the earliness of the crops and the synchronization of crop emergence with aphid migration, the vector species and the isolate of BYDV transmitted, weather factors (eg. A'Brook, 1981; Vickerman, 1977) and the numbers of infective vectors visiting the crop. In the spring and summer months, more virus may be introduced into the crops by alates, especially *R. padi* and *S. avenae* which can overwinter viviparously on grasses in mild winters, but the main sources of BYDV at this time are probably the foci of autumn-introduced virus. Depending on the isolate of BYDV involved, secondary virus spread within the crop probably depends on *S. avenae* and *M. dirhodum* (Plumb, 1976) which are more abundant in crops than *R. padi* in the main growing season (Dean, 1973a).

The effects of BYDV on its vectors

Development and Longevity

Macrosiphum granarium (*Sitobion avenae*) reared on excised leaves of oats (var. Clintland 59) were reported to have an increased rate of development from birth to adult, to live longer and to have a longer reproductive period

(Miller, 1962, Miller & Coon, 1964). The developmental period of M. dirhodum was increased and that of R. padi was unaffected by BYDV infection of young and mature leaves of oats (var. Selma) (Elamin, 1975).

Size and fecundity

The effect of BYDV on aphid size has not been reported previously.

BYDV-infection of oats is known to raise the fecundity of Macrosiphum granarium Kirby (S. avenae) on excised leaves (var. Clinton 59)(Miller, 1962; Miller & Coon, 1964) and that of R. padi on whole plants ((var Selma)(Elamin, 1975) and var. Sisu (Markkula and Laurema, 1964)), and to lower that of M. dirhodum (Elamin, 1975). However, Markkula and Laurema (1964) found that the virus had no effect on the fecundity of S. avenae and M. dirhodum on young oats leaves, and Elamin (1975) showed that the fecundity of S. avenae on young oats was decreased by BYDV. In addition, Bremer (1965) reported that BYDV infection of a BYDV-resistant wild oats host Arrhenatherum elatius had no effect on the number of progeny produced by R. padi after seven days.

Colonies of Rhopalosiphum maidis were smaller on barley plants (cv. DL - 117 and EB - 921) infected with BYDV than on uninfected plants (Gill & Metcalfe, 1977).

In all the studies sited above, fecundity was measured by counting the numbers of progeny produced within a chosen period of time ranging from seven days to the end of the aphids' reproductive life. A comparison of the results is made difficult by differences in experimental procedures, the strains of BYDV used, the age of the plants

at inoculation and the crop variety.

Alate Production

S. avenae and R. padi that had experienced some crowding were more likely to mature as alates when reared on oats (Avena byzantina (Koch)) infected with various isolates of BYDV than were those reared on healthy oats (Gildow, 1980). BYDV could influence aphids during first instar development to mature as alates.

Host Selection

There are no reports on the effect of BYDV on the alighting behaviour of its aphid vectors. Kieckhefer et al (1976) found that flight-active alate Schizaphis graminum, Macrosiphum (Sitobion) avenae and R. padi when exposed to detached healthy and BYDV-infected barley leaves for 16 hours, were equally distributed on both, but the authors did not study the aphids' alightment preferences.

Cytological and Physiological Changes

The virus has been found in various tissues of the vector including connective tissue, the haemolymph and the salivary glands (Paliwal & Sinha, 1970), but unlike some other virus-vector relationships (eg. Littau & Maramorosch, 1956; Maramorosch, 1958), the ingestion of BYDV by Sitobion (Macrosiphum) avenae does not induce any cytological changes in the fat body cells of the aphid (Rutschky & Campbell, 1964).

Miller (1962) and Miller and Coon (1964) found that BYDV infection of oats (var. Clintland 59) reduced the oxygen consumption of M. granarium.

Interactions between BYDV and other micro-organisms.

Interactions between BYDV and several cereal fungal pathogens have been recorded by various workers. Smith (1962) concluded from investigations in New Zealand that BYDV infection predisposed wheat plants to attack by Fusarium and Rhizoctonia root rots and to Gibberella zeae (Schw.) Petch. Cochliobolus sativus (Ito & Kuribay) Drechs. ex Dastur caused more severe root rots in BYDV-infected wheat and oats (Scott, 1968). Prior infection by BYDV similarly increased the susceptibility of wheat plants to Gaeumannomyces graminis (Sacc.) Arx and Oliver (Price, 1970) and of oats to Septoria avenae Frank (Pelletier et al, 1974; Comeau et al, 1976) as well as powdery mildew, Erysiphe graminis DC ex Merat (Potter, 1974). Conversely, BYDV infection either had no obvious effect on (Latch & Potter, 1977) or actually inhibited Puccinia coronata Cda. on oats (Pelletier et al, 1974).

Greenhouse inoculations under conditions of high humidity showed that the ears of BYDV-infected wheat plants were more severely blackened by a combination of Alternaria spp. and Cladosporium spp. (Smith, 1962).

CEREAL APHIDS

The extensive literature on the biology and economic importance of cereal aphids has been reviewed recently by Rautapää (1977), Vickerman and Wratten (1979) and Carter et al (1980). The following aspects were adequately treated and will not be dealt with here: the species complex and their identification; sampling methods; morph determination; life cycles; migration and crop colonization; host plant preference and resistance; feeding site

preferences; reproduction and overwintering survival; natural enemies and abiotic factors; population dynamics; forecasting outbreaks; effects on the host plant; and control measures.

Three species of aphids, Sitobion avenae (F), Metopolophium dirhodum (Walk.) and Rhopalosiphum padi (L.) commonly infest cereals in Britain. In West Wales, Rhopalosiphum insertum (Wlk.) is also of interest as an important vector of barley yellow dwarf virus (A'Brook, 1978; A'Brook & Dewar, 1981).

What follows is a review of certain aspects which, for the purposes of this thesis, were inadequately covered by the earlier reviews.

Höst selection by alatae

The behaviour of insects in selecting their host plants has received much attention as is reflected by the large amount of published work, including reviews by Dethier, (1953), de Wilde (1958) and Thorsteinson (1960). Studies by Müller (1953, 1958, 1962) on Aphis fabae (Scopoli) and Myzus persicae (Sulzer) and by Kennedy (1950) and Kennedy et al (1959a, 1961) on A. fabae, M. persicae and Brevicoryne brassicae (Linnaeus) showed that host selection in these aphids does not occur during the initial approach but only after landing. This conclusion was reached because the aphids tended to alight indiscriminately and in about equal numbers on host and non-host, or on susceptible and resistant varieties alike. Although more aphids thereafter accumulated on the preferred hosts, this was because more had left the less suitable hosts.

Other studies revealed, however, that colour differences could render one plant more attractive to flying aphids than another. For instance, Müller (1964), using direct captures of landing aphids in the field, found that A. fabae and M. persicae landed 3-5 times more frequently on green and yellow-green varieties of lettuce plants than on a dark reddish-brown one. The landing impulse on yellow and green lettuces was increased when their colour contrasted with that of the surroundings. Kennedy et al (1961), similarly reported that in the field, B. brassicae, M. persicae and A. fabae preferentially landed on yellowing leaves of field beans, Vicia faba Linnaeus. Cartier (1963) also found that Acyrthosiphon pisum (Harris) visited a yellowish green variety of pea (Pisum sativum Linnaeus) more frequently and colonized it more heavily than the green varieties.

Several studies using various trapping methods, including water traps (Moericke, 1950, 1951, 1954, 1955; A'Brook, 1973), sticky traps (A'Brook, 1973; Broadbent, 1948) or both (Heathcote, 1957), and coloured cards in a flight chamber (Kring, 1966, 1967; Kennedy, 1976) agree that many aphid species are attracted to yellow. Others (Auclair, 1967, 1969; Cartier, 1965, 1966; Cartier & Auclair, 1964; Moericke, 1950; Kloft, 1956; Kring, 1967, 1969; Wensler, 1962; Rautapää, 1980; also review by Kennedy & Stroyan, 1959) have established that in many aphid species, the alighting and settling behaviour is best elicited by the green-yellow-orange part of the light spectrum, especially yellow.

Cereal aphids in general are less sensitive to yellow than other species that feed on dicotyledonous plants (Adams & Farrell, 1957; Eastop, 1955; Heathcote, 1957; Heathcote et al, 1969; O'Loughlin, 1963). However, on the basis of data from water traps and sticky traps (A'Brook, 1973) and light filters (Kieckchefer et al, 1976), S. avenae, M. dirhodum and R. padi have been classified among the yellow-sensitive species.

The response of aphids to colour changes during flight. Moericke (1955) suggested that post-teneral alatae are initially attracted upwards by the predominantly short-wavelength light from the sky, but after flying for some time, they respond positively only to the longer-wavelength light reflected from the plants and soils below. Kennedy et al, (1961) and Kennedy (1976) have modified this idea by suggesting that throughout its flight, an aphid is simultaneously influenced by a phototactic pull both upwards toward the sky, and downwards toward the earth. At some stage the downward pull increases in strength, relative to the upward one. Rautapää (1980) has also found that the attraction of S. avenae and R. padi to ultraviolet (short-wavelength) radiation relative to green or yellow (long-wavelength) light was high at the immediate post-teneral stage but decreased thereafter.

The influence of plant disease on host selection

The effect of plant diseases on the choice of landing target by flying insects has apparently not been studied. Investigations have been concerned mainly with the distribution of insects after crop infestation in the field (eg. Hull, 1965; Lewis, 1979; Smith, 1939; Ueckert, 1968; Bernays et al, 1977) or of those artificially confined to

healthy and diseased plants or plant parts in a controlled environment (eg. Baker, 1960; Lewis, 1979; Hodgson, 1977, 1981; Kieckhefer *et al*, 1976). Smith (1939), Ueckert (1968), Bernays *et al* (1977) and Lewis (1979) all found that various grasshoppers preferred fungus-infected plant tissues to healthy ones. Hull (1965) observed that percentage infestation by *M. persicae* (Sulz.) in the field was higher on sugar beet yellows virus-infected sugar beet plants than on healthy ones, and that each infected plant had more aphids than a healthy one.

In more controlled conditions, Baker (1960) showed that *M. persicae* (Sulz.), *M. ascalonicus* Doncaster, *Aphis fabae* Scop. and *Aulacorthum solani* Kalt., when caged on sugar beet leaves, all preferred sugar beet yellows virus-infected leaves to healthy ones. Laboratory tests (Lewis, 1979) confirmed the field observations that the grasshopper *Melanoplus differentialis* (Thomas) preferred sunflower (*Helianthus annuus* L.) leaf tissue that had been infected with rust fungus, *Puccinia helianthii*. Hodgson (1977, 1981) showed that infection of turnips (*Brassica rapa* L.) by cabbage black ringspot virus increased the number of leaves suitable for colonization by *M. persicae* (Sulz.) but reduced their number for *B. brassicae* L.. After a 16 hour access period in a cage, the distribution of alate *Schizaphis graminum*, *Macrosiphum* (*Sitobion*) *avenae* and *R. padi* on detached healthy and BYDV-infected leaves of barley was similar(Kieckhefer *et al*, 1976).

Nutrient Requirements

In his review of aphid feeding and nutrition, Auclair (1963) noted that very little was known about the nutritional requirements of aphids. He concluded, however, that the biochemical requirements of aphids were unlikely to differ from those of other insects. Earlier reviews were made by House (1962) on the nutritional requirements of insects in general, and by Friend (1958) on those of phytophagous insects in particular.

Specific information on the nutrient requirements of cereal aphids is similarly not available, but there is no obvious reason why cereal aphids should differ considerably from other aphids in this respect.

Measurement of aphid fecundity

Techniques for measuring the fecundity of individual aphids have been reviewed by Adams and van Emden (1972). Many workers have recorded the total fecundity of aphids by counting the number of progeny at intervals throughout the aphids' life (eg. Adams & Drew, 1964; Markkula & Roukka, 1972; Elamin, 1975). It may sometimes be more meaningful to obtain the rate of reproduction during the first week or during the first few weeks (eg. Müller, 1966; Leather & Dixon, 1981; Rautapää, 1970; Hill, 1971; van Emden, 1966; Dean, 1973b; Lowe, 1977). However, progeny count is both time consuming and gives variable results (Dewar, 1977). An alternative method is to dissect an aphid at the teneral stage and count the embryo content (eg. Honeyborne, 1969; Dewar, 1977; Dharma, 1979; Dixon &

Dharma, 1980a,b; Dixon, 1976; Wellings et al, 1980). A count of embryo number has the merits of speed and low variability (Adams & van Emden, 1972). Embryo number and fecundity are closely related in A. fabae (Dixon & Wratten, 1971; Honeyborne, 1969), and a similar relationship may occur in cereal aphids (Dewar, 1977).

HONEYDEW

Definition and uses

The most recent review on honeydew was made by Auclair (1963) who defined it adequately as "the liquid droplet excretion from the alimentary tract, as released through the anus by aphids, coccids, and many other plant sucking insects."

Honeydew is utilized in various ways by several insect species including bees, ants, insect parasitoids and predators, and others (see Auclair, 1963).

Chemical Composition

Apart from Auclair (1963), the literature on the chemical composition of honeydew has been reviewed by Waterhouse (1957) and Doner (1977). More recent publications on this topic include those by Noda et al (1973), Sidhu & Patton (1970), Hussain et al (1974), Dighton (1978) and Owen (1978).

Rate and frequency of excretion

Measurement

The rate of excretion (the volume of honeydew excreted per aphid in a given period) is usually estimated by multiplying the frequency (the number of honeydew droplets excreted per aphid in a given period) by the average volume of the droplets excreted during that same period (eg.

Auclair, 1957, 1958; Mittler, 1954; Banks & Macaulay, 1964). Mittler (1958) used a more direct technique by determining the time required to fill a 10 or 20 mm glass capillary pipette with the honeydew excreted by a known number of Tuberolachnus salignus (Gmelin) in a colony. A more elaborate method has been described by Adams and van Emden (1972).

The frequency of excretion has been measured by various methods. Maxwell and Painter (1959) collected and counted the droplets produced by single aphids feeding on their host plants. Fisk (1978) modified this by lining the cages with indicator paper impregnated with bromocresol-green in ethyl alcohol or by smoking them with burning magnesium so that the inside was covered with a thin layer of magnesium oxide. Droplets falling on the yellow indicator paper turned blue while those hitting the smoked surfaces left craters which could be counted. Smith (1937) devised a honeydew-clock method which used a circular paper scale rotating under an aphid. This principle was employed later by Mittler (1958) and Auclair (1959) and developed further by Banks and Macaulay (1964). Banks and Macaulay (1964) used chromatography paper stained with bromocresol blue (2 mg/ml ethanol) to record the excretion of individual aphids continuously throughout their life. Aphids were confined on leaves in plastic boxes across the floor of which a strip of stained paper was pulled at a known rate by a 1 rev/h electric motor. Faint or invisible droplets were shown up by heating the paper to caramelize the sugars in the honeydew. Auclair (1958) and Mittler (1958) used a

spray of 0.2% ninhydrin in 95% butanol followed by heating to show up the honeydew by the presence of amino acids. Banks and Macaulay's machine can be used easily to simultaneously measure excretion in many aphids and the duration and rate of run of the record is more flexible than earlier honeydew-clocks.

The volume of individual honeydew droplets was measured by collecting each droplet falling on waxed paper with a micropipette (Auclair, 1958; Paguia et al, 1980). Banks and Macaulay (1964) collected droplets into chemical-free mineral oil (SAE 30 motor car oil, density 0.89) and calculated droplet volume from the diameter of the droplets measured with a micrometer eyepiece. Ehrhardt (1967) also estimated volume by measuring droplet diameter with a micrometer eyepiece. Droplet volume was estimated from the area or weight of honeydew spots on filter paper impregnated with either bromocresol green (2 mg/ml ethanol) (Pathak & Heinricks, 1980) or 0.001% ninhydrin in acetone (Paguia et al, 1980). Known honeydew volumes were spotted on similar indicator paper and the corresponding area measured or weighed to determine the relation between area and weight on one hand and droplet volume on the other. In each case the relationship was linear and significantly positive for the brown planthopper Nilaparvata lugens (Stål), but both methods were reportedly tedious.

Factors affecting the rate and frequency of excretion

The following factors have been known to affect the rate and frequency of honeydew excretion in several species of aphids: the species of aphid; aphid age and form; host

plant species, variety and growth stage; moulting; starvation; temperature; wind; light intensity; and attendance by ants (see Auclair, 1963).

In addition to these factors, the physiological state of the host plant is also important. The frequency of excretion by Hyperomyzus lactucae L. was reduced when feeding on sowthistle (Sonchus oleraceus L.) plants infected with isolates of sowthistle yellow vein virus (Sylvester, 1973). Conversely, Magayarosy et al (1979) apparently recorded a higher rate of excretion from Myzus persicae feeding on Amsinckia douglasiana plants infected with curly top virus than on healthy ones.

Interactions between honeydew and sooty moulds

Several references suggest that the presence of honeydew produced by aphids, coccids and planthoppers increases the incidence of sooty moulds. Meyer (1978) found that the presence of the coccids Icerya purchasi, Coccus hesperidum and Gossyparia spuria on their various hosts was essential for sooty mould (Cladosporium herbarum) growth, and quoted the suggestion by Gardner (1849) and McAlpine (1896) that the insects provide nutrients for the fungus. Parker et al (1956) reported the growth of sooty moulds on honeydew excreted by aphids onto alfalfa plants. The moulds caused a reduction in the yield of alfalfa hay, feed quality and palatability of hay. Tedders and Smith (1976) also found that honeydew produced by large populations of the black-margined aphid, Monellia costalis (Fitch) and Monelliopsis nigropunctata (Granovsky) on the foliage of pecan, Carya illinoensis (Wang K. Koch) supports the growth of sooty

mould fungi. This growth interfers with the functioning of the leaves (Osburn et al, 1966).

Vereijken (1979) and Vereijken and Mantel (1980) have indicated that aphid (S. avenae) honeydew stimulates the development of fungi, especially black (sooty) moulds on cereals. Rabbinge et al (1981) have confirmed this and estimated that of the total yield loss in wheat attributable to aphids and saprophytic fungi, 28% was due to the fungi and 72% was due to the effects of aphid feeding and honeydew. Vereijken (1979) had earlier suggested that damage caused by aphid feeding was as important as that caused by honeydew and saprophytic fungi. Riphagen et al (1979) have also provided experimental evidence that supports the effect of aphid honeydew on fungi. They sprayed honeydew collected from S. avenae onto wheat flag leaves and then monitored the development of phylloplane fungi on the leaves. After 5 days the total population of phylloplane fungi was significantly more on honeydew-sprayed leaves than on control leaves. The growth of all fungal groups including Cladosporium cladosporioides was stimulated to a similar extent.

CLADOSPORIUM

The genus Cladosporium belongs to the dematiaceous hyphomycetes group of filamentous fungi. Some 500 species have been described and keys for some of the common ones are available (eg. Ellis, 1971, 1976). Several other publications include diagnostic descriptions of various Cladosporium species (eg. De Vries, 1952; Brett, 1948; Malone & Muskett, 1964; Barnett & Hunter, 1972).

Occurrence

Some species of Cladosporium are pathogenic to plants but those most frequently encountered are the dark green moulds living saprophytically on decaying vegetable matter. C. herbarum Lk ex Fr. and C. cladosporioides (Fresen.) de Vries are the commonest fungi on dying and dead plant substrates (see Domsch & Gams, 1970), although they also thrive on living aerial surfaces of green plants (Dickinson, 1976; O'Donnell & Dickinson, 1980) and in the soil (see Domsch & Gams, 1970). Their distribution is worldwide and in several investigations on the spore content of the air, Cladosporium, especially C. herbarum, is usually the dominant genus (eg. Harvey, 1967; Hyde & Williams, 1952). Both C. herbarum and C. cladosporioides have a wide range of plant hosts (Domsch & Gams, 1970) including cereal grain, especially wheat.

Economic importance

Together with Alternaria spp., Cladosporium causes a blackening (sooty mould) of the ears and flag leaves of cereals. The leaves, leaf sheaths and stems below the flag leaf contribute only about 15% of the ultimate grain weight. The ears and flag leaves therefore contribute significantly to the final grain weight (Thorne, 1966). The ears alone can contribute between 11 - 40% of the nutrients stored in the grains (see Thorne, 1974). Blackening of these organs by sooty moulds is therefore thought to affect yield by intercepting light and lowering photosynthesis (eg. Rabbinge et al, 1981; Rabbinge & Mantel, 1980; Rabbinge & Vereijken, 1980; Vereijken, 1979; Tedders & Smith, 1976).

Additionally, the blackening affects the appearance and quality of grain. Cladosporium is abundant on freshly harvested grain but is rapidly overshadowed by storage fungi (eg. Hill, 1979).

Although no toxic agent has been identified from the fungus, Cladosporium is strongly allergenic and causes respiratory symptoms in some humans and livestock. It can also cause mycoses in domestic animals (Ainsworth & Austwick, 1955) and when severely infected cereals have been used as fodder (Joffe, 1962; Wogan, 1965).

Isolation

Cladosporium sporulates freely and can be isolated easily by various techniques (Thornton, 1958), including dilution plating (eg. Hill, 1979).

Physical requirements

These requirements have been reviewed by Domsch and Gams (1960). Cladosporium tolerates a wide range of pH from 4.4 up to alkalinity with an optimum around 6. It prefers moist conditions. For C. herbarum, the minimum humidity was found to be 89% for germination, 85% for vegetative growth and 90% for sporulation. Data on optimum temperatures vary between 18 and 28^{o}C. Growth is possible at -6^{o}C and the maximum temperature range lies between 30 and 32^{o}C.

Nutrient requirements

Hawker (1950, 1957) has reviewed and discussed the general nutrition of fungi. Carbohydrates, nitrogen, phosphorus, potassium, magnesium, sulphur and a host of metals such as iron, zinc, copper, manganese etc. in trace amounts

are regarded as essential nutrients for all fungi. The nature, concentration and the total quantity of the food supply are all important in determining growth, development and sporulation in fungi.

The growth of Rynchosporium secalis (Oud.) in culture is affected by the carbohydrate and nitrogen content of the growth medium (Caldwell, 1937; Schein & Kerelo, 1956; Jenkyn & Griffiths, 1976). The susceptibility of barley to the same fungus was reported to be positively correlated with the nitrogen content but negatively so with water-soluble carbohydrates (Jenkyn & Griffiths, 1978). A positive correlation between the susceptibility of cocksfoot genotypes to infection by stripe rust (Puccinia striiformis) and the water-soluble carbohydrate content of leaves is also known (Carr & Catherall, 1964). Freeman (1964) has shown that the severity of Piricularia grisea infection of St. Augustine grass was strongly related with the nitrogen content of leaves. Similar studies have apparently not been made for Cladosporium but its general nutritional requirements are unlikely to differ considerably from those of other fungi.

GENERAL MATERIALS AND METHODS

The glasshouse environment

Each of the glasshouse cubicles used for the experiments measured 3.5 x 2.9 x 2.7m, and was kept at about 20°C under a 16:8 hours light:dark cycle but the temperature fluctuated considerably in the summer months. Lighting was provided by four sodium pressure lamps (400W) hanging at 1.2m above the work benches; they were switched off in the summer.

The aphid cultures

Separate virus-free cultures of *R. padi* L., *M. dirhodum* (Wlk.) and the brown form of *S. avenae* (F.) started from single apterous virginoparae obtained from a field of winter wheat in June 1979, were maintained on seedling wheat (Cappelle Desprez) in the glasshouse. The culture plants were changed fortnightly and the population of aphids was reduced at each plant change in order to avoid overcrowding. Viruliferous cultures of the three aphid species were started with aphids from these virus-free ones but were kept in a separate cubicle to avoid cross-contamination by the virus. To obtain first instar nymphs, alate virginoparae were allowed to feed for a few hours on wheat seedlings and the nymphs were then collected. A fine camel hair brush was used to handle the aphids.

The laboratory plant material

Because of the problems encountered with attempts to vernalize winter cereals, spring varieties of barley (Julia), oats (Manod) and wheat (Highbury) were used throughout the study. Using a separate pot for each crop, twenty seeds

were planted in 12.8cm plastic pots in Eff soil-less (peat) compost. Eight days after planting, at Zadoks growth stage 10 (Zadoks et al, 1974; Tottman et al, 1979), the seedlings were selected for uniformity of size and transplanted, one per pot, into 14cm plastic pots. No supplementary fertilizers were added as the plants grew vigorously. Bayleton (Bayer Ltd.) containing 25% Triadimefon was applied at the rate of 2mg/l of water to control the powdery mildew when necessary.

Inoculation of plants with BYDV

A severe R. padi-specific isolate of BYDV, supplied by Dr R T Plumb of the Plant Pathology Department at Rothamsted, was used in all experiments. Test plants were inoculated with the virus by confining three viruliferous R. padi from the appropriate culture per plant, using cellulose nitrate cages (18 x 4cm diameter) with muslin tops. Control (healthy) plants were infested with three virus-free R. padi L. per plant. Virus-infected and healthy plants were kept in separate cubicles, and the aphids were removed after two days with a spray of pirimicarb (0.41 g ai/l). One day later, the plants were transferred into Saxcil growth cabinets, one cabinet per treatment. The cabinets were exchanged for alternate experiments.

The Saxcil growth cabinets

Each Saxcil growth cabinet (1.3 x 1.3 x 1.5m) was maintained at a constant 20°C and 70% relative humidity with a 16:8 hours light:dark cycle (0500-2100hrs.). Lighting (26,000 lux total radiation at 1.2m from the ceiling) was provided by a bank of incandescent and warm-white

fluorescent lamps which were separated from the working section by a sheet of perspex. Each set of lamps was replaced routinely after 1000 hours of performance. Fresh air was circulated through the cabinet at the rate of 1000 l/min.

Aphid cages

Clip-on cages were avoided because of the dangers associated with their use (eg. Dewar, 1977b). Dialysis tubing (18mm internal diameter, from Medicell International Ltd., London) was therefore used to confine aphids to leaves (7cm long) and ears (15cm long). Each cage was plugged at both ends with cotton wool to prevent the aphids from escaping and for aeration. The dialysis tubing was inflated and exposed in another glasshouse for at least two weeks prior to being used, in order to minimize the risk of toxicity to the aphids and the leaves (Lowe, 1978). A few aphids got caught on the cotton wool but the cages were satisfactory otherwise.

Statistical Analysis

Unless stated otherwise, data were analysed using the variance ratio (F) test and run on the Rothamsted GENSTAT computer program (Nelder *et al*, 1977).

SECTION 1

THE EFFECT OF BARLEY YELLOW DWARF VIRUS ON THE FIELD POPULATION OF CEREAL APHIDS AND GRAIN YIELD

INTRODUCTION

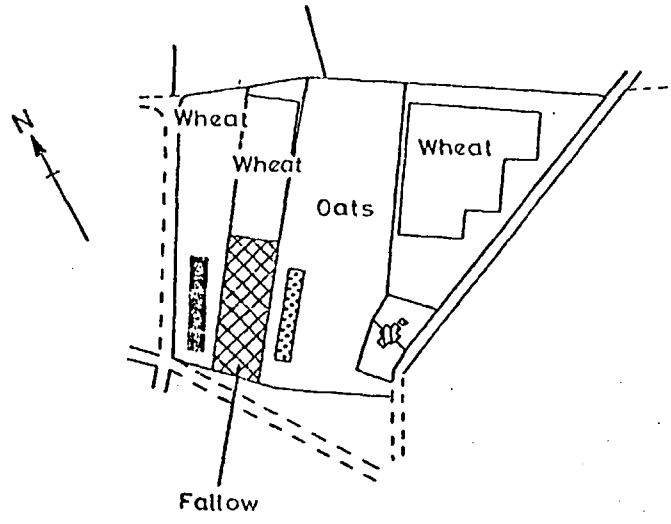
In view of the findings by the Aerial Photography Unit of the ADAS (Hooper, 1978), the trials reported in this section were conducted to establish whether higher aphid populations develop on BYDV-infected plants than on healthy ones in the field. Field experiments were conducted at Rothamsted in 1979 and 1980 in which cereal aphid numbers in healthy and diseased plots of winter cereals were monitored from the time of the spring migration of aphids until crop maturity. Crop yields were also recorded at harvest.

MATERIALS AND METHODS

A. 1979

In fields of winter wheat (cv Flanders, sown on 17.10.78) and winter oats (cv Panema, sown on 27.10.78) in the south-west corner of Stackyard field (Fig.2), plots measuring 0.5m x 0.5m were marked out in two rows The rows were separated by a planted area of 2m and the plots were 5m apart (Fig. 3). Plot boundaries were demarcated by labelled bamboo sticks (Fig. 7). On 17.5.79, when wheat was at growth stage (GS) 18 24 and oats at GS 15 21, ten plots of each crop were artificially infected with a severe *R. padi*-specific isolate of BYDV using viruliferous *R. padi* reared on diseased plants in a glasshouse. Five-centimeter sections of infected leaves,

Plot layout in Stackyard. 1979



Study of aphid populations on:

Winter Wheat (Flanders)
Winter Oats (Panema)

Fig. 2.

Plot layout for studies on the effect of BYDV infection of winter wheat and oats on aphid populations and the incidence of Cladosporium sooty mould, Stackyard 1979

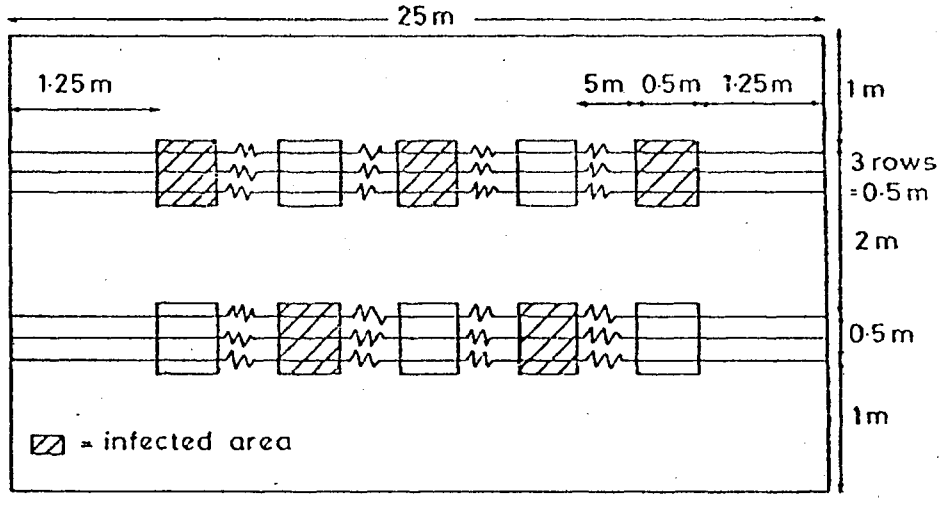


Fig. 3.

each bearing about ten aphids, were distributed within the plots. One leaf section was placed between the youngest leaf and the stem of each tiller. All alates and fourth instar alates were removed in the glasshouse before distribution in the field in order to limit emmigration from the plots. The aphids were confined to each plot with barriers made of wood and cellulose nitrate sheets (similar to Fig.4). Five control plots were similarly infested with virus-free R. padi from a glasshouse culture. All aphids were killed after two days with pirimicarb (0.41 g ai/l) and the cages were removed two days later. Artificial inoculation with BYDV was necessary because the crops had been sown very late and also because natural infection at Rothamsted is rarely widespread in most years (Plumb, 1981).

Thereafter, until crop maturity, weekly counts were made on 5 - 100 tillers per plot on each occasion, depending on aphid density. Aphids were identified to species, and classed as 1, 2, 3 and 4th instar nymphs, adult apterae and alatae.

B. 1980

In the 1980 trials, winter barley (Maris Otter, oats (Panema) and wheat (Flanders) were studied. Barley was included in view of the increasing importance of winter barley in British agriculture (Groves, 1979, Tables 7 & 9). The trials were sited at the south-east corner of Long Hoos field (Fig.5) and the plots were laid out as illustrated in Fig.6. For each crop there were five randomized blocks of two plots (i.e. 10 plots per



Fig. 4.

The location of field studies on the Long Hoos field in 1980

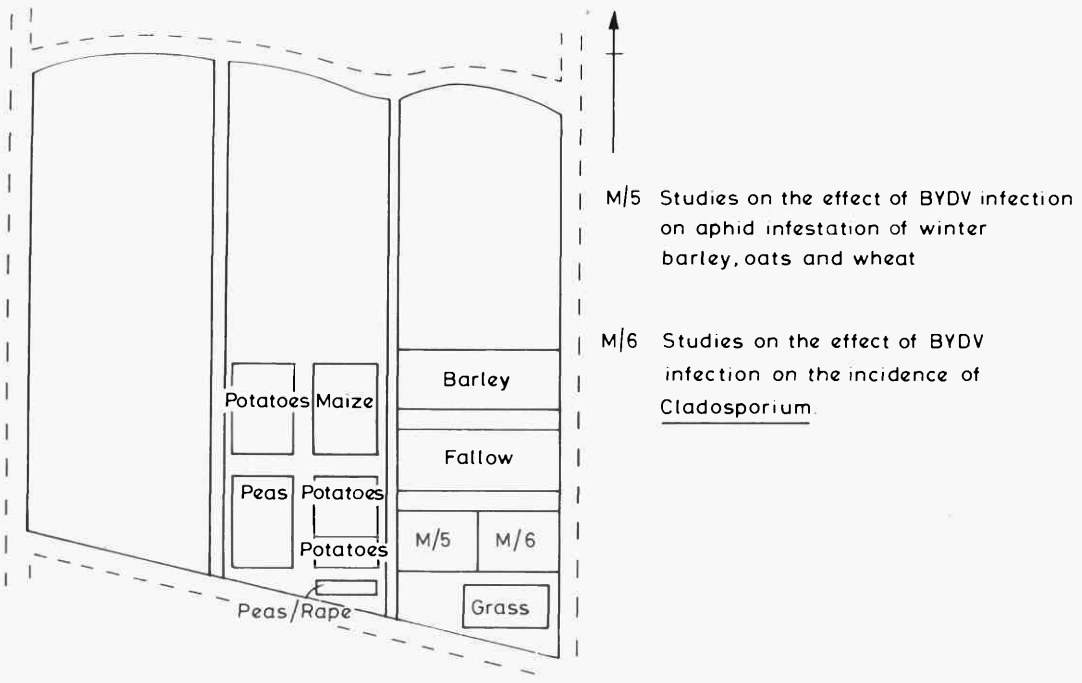
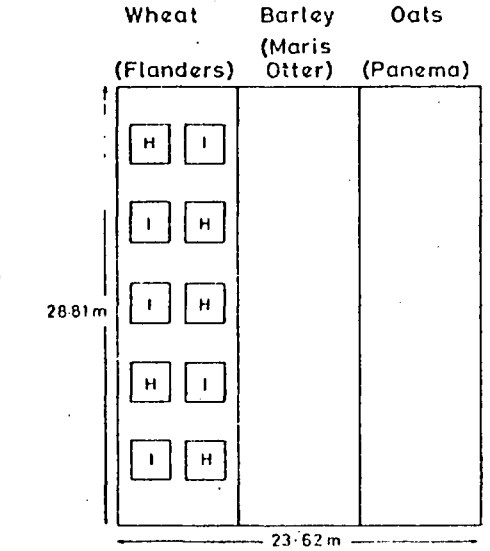


Fig. 5.

Plot layout for studies on the effect of BYDV infection of winter wheat oats and barley on aphid populations

Long Haos 1980



Treatments I = Infected with BYDV

H = Healthy

Relation of plots to discards

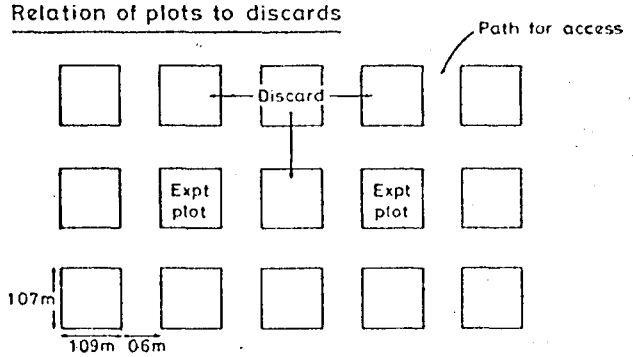


Fig. 6.

crop), each plot measuring approximately 1m x 1m. Adjacent crops were separated by 5.8m consisting of three unsown paths each 0.6m wide plus two discard areas each 2m wide. The whole trial area had a discard surround of adjacent crop 2m wide. This arrangement was chosen in order to minimize interplot interference.

Five plots were infected with BYDV on 21.3.80, using the same virus isolate and procedures as in 1979 except that heavy gauge polythene sheet was used for the barriers. All three crops were at GS 14 22, and the control plants were not infested with virus-free aphids. All aphids were killed after two days with pirimicarb (0.41 g ai/l). Aphid counts were made on 20 randomly chosen tillers per plot on 29.5.80 and weekly thereafter until crop maturity.

Aphids were again identified to species and classed as 1-3 instars, fourth instar apterae and alatae, and adult apterae and alatae.

Yield data

The effect of BYDV on straw length, the length of ears, the number of grains per ear, grain weight, shelling percentage, the weight of grains from 20 ears and the grain yield per plot was measured in each crop. Straw length was measured from soil level to the base of the ear. Shelling percentage was taken as the proportion of the ears that was made up of grain.

RESULTS

Aphid Numbers

All plants within infected plots showed the

characteristic symptoms of BYDV infection before the first aphids were encountered on the crops, and the disease was effectively confined to these plots (Figs. 7 & 8). In 1979 disease symptoms appeared in wheat two weeks later than in oats but in 1980 they appeared at about the same time on all three crops. Diseased leaves were bright yellow on barley, reddish yellow on oats and bright yellow to purple on wheat (Figs. 8, 9 & 10).

Metopolophium dirhodum (Wlk.) was the most abundant aphid species in the crops in 1979 while S. avenae was predominant in 1980. Except on a few sampling dates, the brown form of S. avenae was significantly more common than the green on oats and wheat throughout the sampling period but not on barley (Fig. 11).

The effect of BYDV on the percentage of plants infested by aphids

Percentage infestation was not recorded in 1979. In 1980, significantly more diseased plants were infested by S. avenae (barley $F = 27.24$, $df = 1/32$, $p < 0.001$; oats $F = 74.66$, $df = 1/36$, $p < 0.001$). The difference on wheat was only significant at GS 69 and 71 ($F = 10.91$, $df = 1/4$, $p < 0.05$ and $F = 8.96$, $df = 1/4$, $p < 0.05$ respectively) (Fig. 12). Of the three crops, the level of infestation was initially lower on wheat than on either oats or barley, but at peak infestation and thereafter wheat was the most highly infested and barley the least. However, the difference between healthy and diseased plants was lowest on wheat. The peak percentage infestation occurred at different growth stages on the three crops, 73 on



Fig. 7. A BYDV-infected experimental plot of wheat demarcated in 1979 with bamboo stakes.



Fig. 8. An experimental plot of barley (centre) showing symptoms of BYDV infection (Curtesy of Dr R T Plumb, Rothamsted).



Fig. 9. An experimental plot of oats in 1979 (centre) showing symptoms of BYDV infection.



Fig. 10. Wheat plants in a commercial farm near Cambridge, 1979, showing reddish purple-leaf symptoms of BYDV infection.

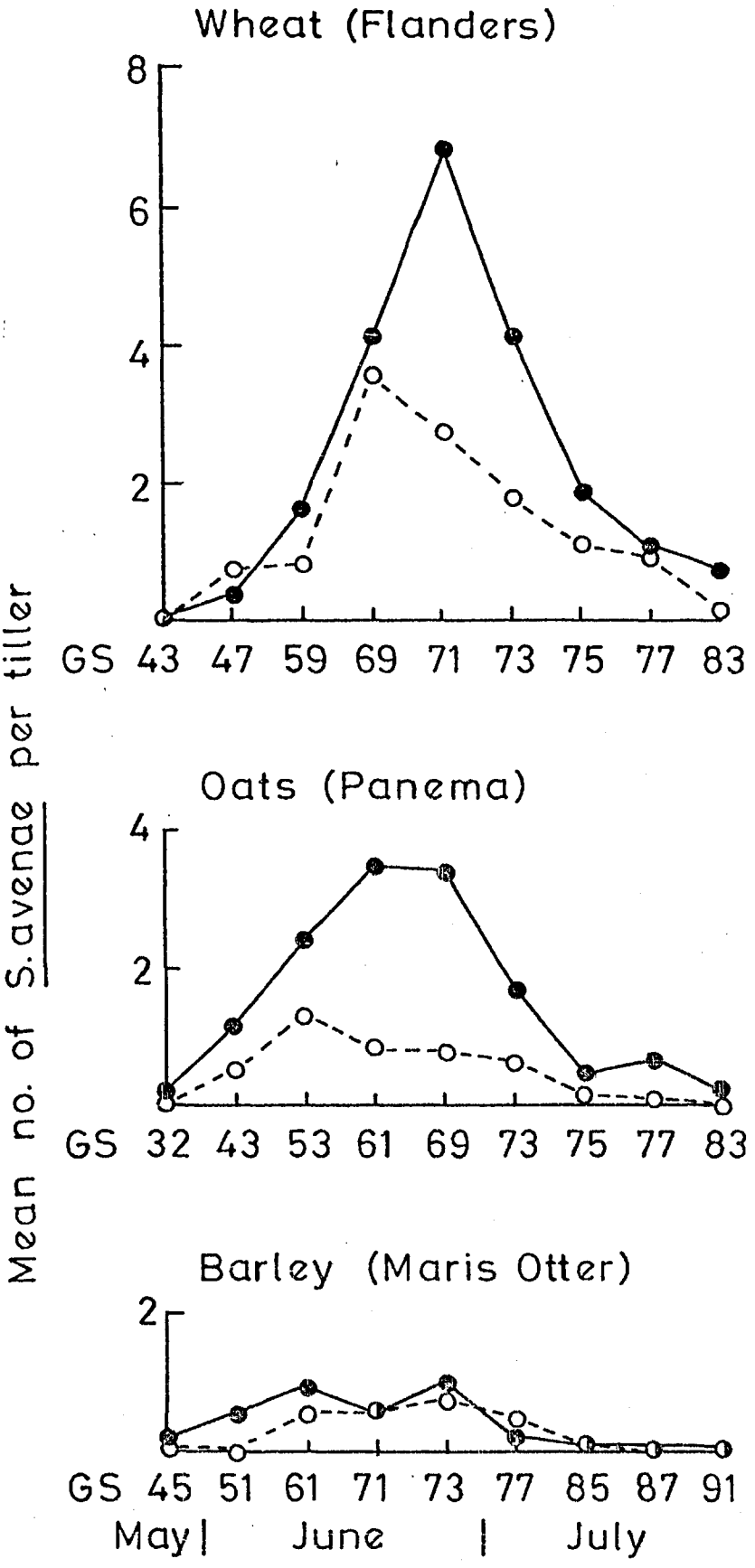


Fig. 11. Numbers of the brown (●) and green (O) forms of S. avenae on wheat, oats and barley in the field, 1980. (Healthy and BYDV - infected combined) (wheat F= 9.47, df = 1/178, $p<0.01$; oats F = 22.47, df = 1/178, $p<0.001$; barley F = 1.49, df = 1/178, NS.).

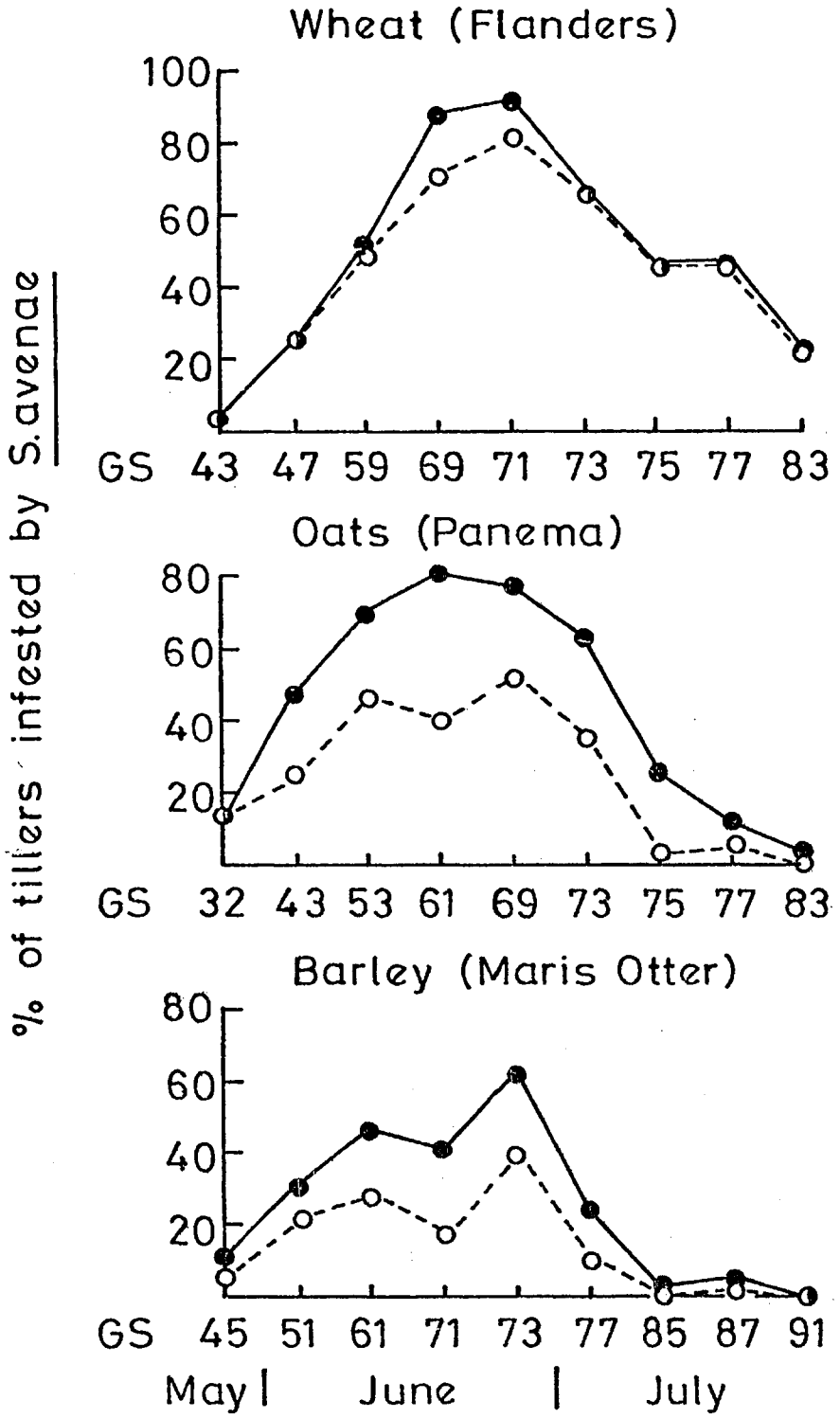


Fig. 12. The percentage of healthy (○) and BYDV - infected (●) wheat, oats and barley infested by S. avenae in the field, 1980.

barley, 61 on oats and 71 on wheat.

The effect of BYDV on the total numbers of aphids

In both 1979 and 1980, the sequence of development of aphid numbers on each crop was similar on healthy and diseased plants (Figs. 13 & 14). Peak populations of M. dirhodum occurred in 1979 at GS 77 on both wheat and oats. In 1980 the numbers of S. avenae peaked at growth stages 61, 61 and 71 respectively on barley, oats and wheat.

In 1979 there were significantly more M. dirhodum on diseased oats ($F = 17.53$, $df = 1/104$, $p < 0.001$) and wheat ($F = 16.80$, $df = 1/62$, $p < 0.001$) than on healthy plants. S. avenae was also significantly more abundant in 1980 on virus-infected barley ($F = 25.24$, $df = 1/32$, $p < 0.001$); oats ($F = 81.19$, $df = 1/36$, $p < 0.001$) and wheat ($F = 24.84$, $df = 1/36$, $p < 0.001$) than on healthy plants. The effect of BYDV infection on the population of aphids was more pronounced on oats than wheat in 1979, strongest on barley and weakest on wheat in 1980 (Table 1).

The effect of BYDV on the population of adult alates

Taken over the eight weeks of sampling in 1979, there were significantly more alate M. dirhodum on BYDV-infected oats than on healthy plants ($F = 6.12$, $df = 1/104$, $p < 0.05$, Fig. 15). BYDV did not affect the numbers of alates on wheat (Fig. 15).

Alates of S. avenae were more abundant in 1980 on diseased barley ($F = 8.53$, $df = 1/32$, $p < 0.01$), oats ($F = 33.62$, $df = 1/36$, $p < 0.001$) and wheat (Fig. 16), but the difference on wheat was not significant.

Table 1: The effect of BYDV on the size of peak populations of M. dirhodum in 1979 and S. avenae in 1980

Crop	Year	Total no. of aphids/ tiller		% increase due to BYDV
		Healthy	BYDV	
Oats	1979	37.64	94.99	152.36
Wheat	1979	53.28	95.67	79.56
Barley	1980	0.46	1.13	145.62
Oats	1980	1.15	3.79	229.57
Wheat	1980	3.40	6.21	82.65

Table 2: The effect of BYDV on the ratio of first instar M. dirhodum nymphs (Li) to adults (Ad) in 1979

	Oats		Wheat	
Crop growth Stage	Li/Ad		Li/Ad	
	Healthy	Diseased	Healthy	Diseased
61	3.04	4.86	-	-
69	4.07	4.47	3.75	3.17
73	7.86	7.21	10.67	8.19
77	4.74	4.70	4.87	6.41
83	-	-	2.72	4.27
87	2.31	4.18	-	4.27
94	0.33	0.00	-	-
Mean	3.73	3.54	5.50	5.26

- = There were no adults

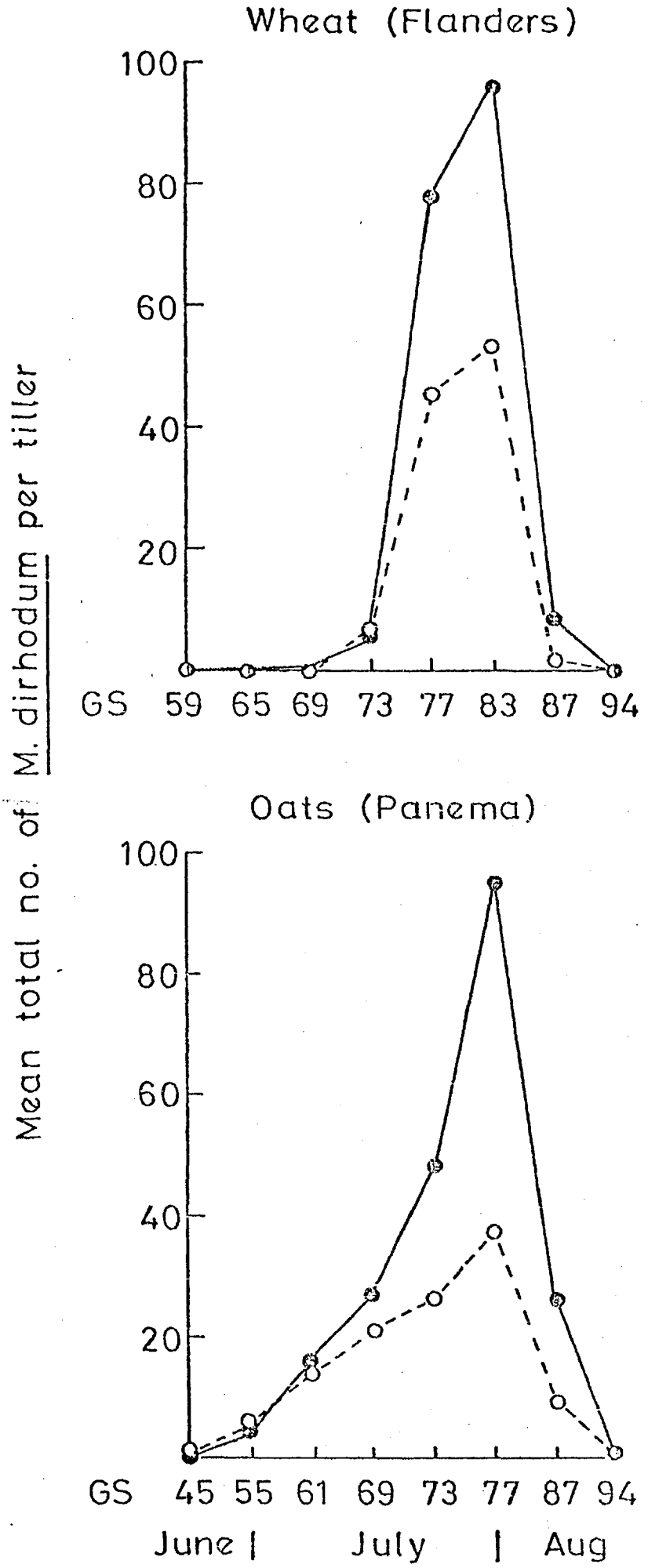


Fig. 13. Numbers of M. dirhodum on healthy (O) and BYDV - infected (●) wheat and oats in the field, 1979.

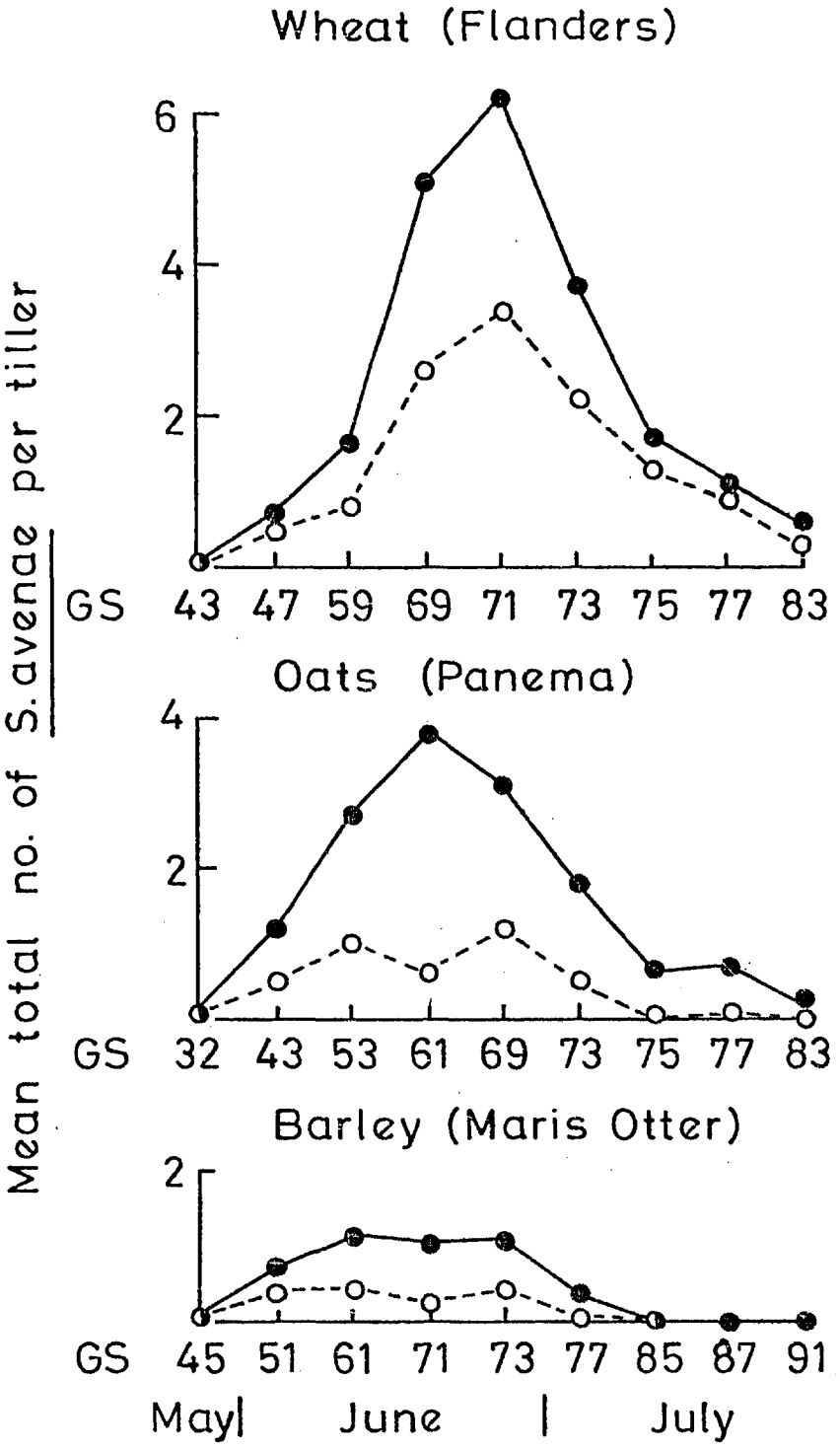


Fig. 14. Numbers of S. avenae on healthy (O) and BYDV - infected (●) wheat, oats and barley in the field, 1980.

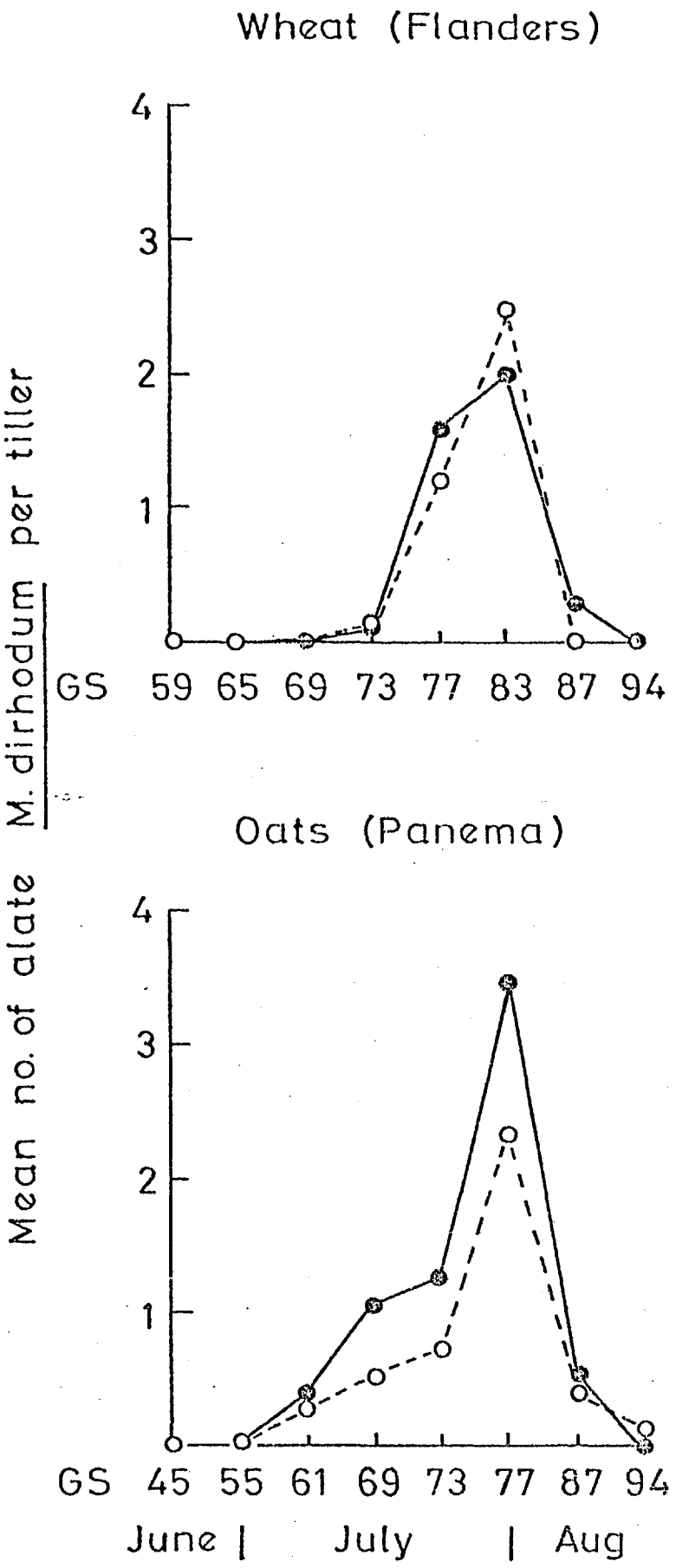
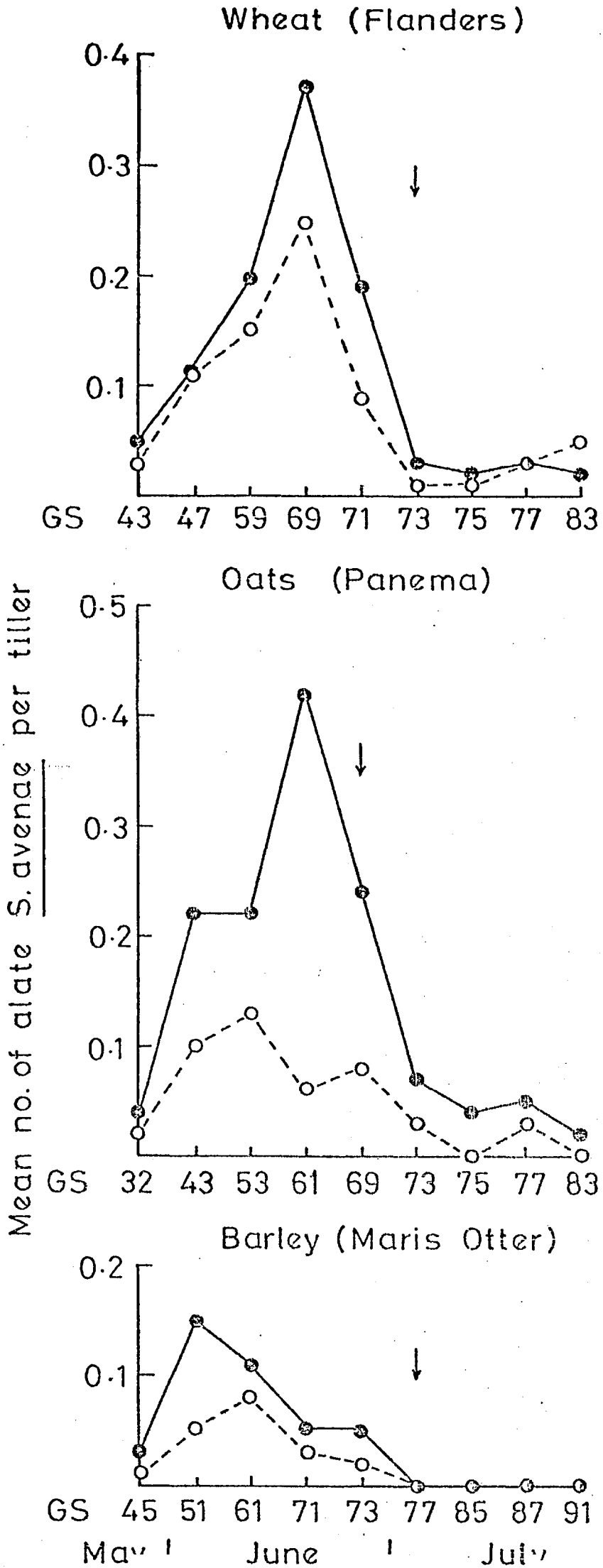


Fig. 15. Numbers of alate M. dirhodum on healthy (O) and BYDV - infected (⊛) wheat and oats in the field, 1979.


Wheat (Flanders)
0·4
0·3
0·2
0·1
GS 43 47 59 69 71 73 75 77 83
Oats (Panema)
Mean no. of alate S. avenae per tiller
0·5
0·4
0·3
0·2
0·1
GS 32 43 53 61 69 73 75 77 83
Barley (Maris Otter)
0·2
0·1
GS 45 51 61 71 73 77 85 87 91
May
June
July

The effect of BYDV on the population of fourth instar alates

Fourth instar alates were not classified in 1979. In 1980, they were encountered in the crops only after the numbers of alate adults had peaked and declined (Fig. 16). BYDV did not affect the populations of alate fourth instars on any of the crops. However, the proportion of fourth instar nymphs developing into alates was significantly larger on diseased oats (10.84%) than on healthy oats (4.86%) (SED = 1.59; $F = 14.10$, df = 1/8, $p < 0.01$).

The effect of BYDV on the population of adult apterae

There were significantly more apterous M. dirhodum on BYDV-infected oats at GS 77 in 1979 ($F = 5.15$, df = 1/13, $p < 0.05$) and consistently more apterae on diseased wheat ($F = 5.77$, df = 1/62, $p < 0.05$) (Fig. 17).

BYDV infection increased the population of apterous S. avenae in 1980 on barley ($F = 4.23$, df = 1/32, $p < 0.05$), oats ($F = 24.78$, df = 1/36, $p < 0.001$) and wheat ($F = 12.00$ df = 1/36, $p < 0.001$) (Fig. 18).

The effect of BYDV on the L1/Ad ratio

The numbers of first instar nymphs (L1) were not recorded in 1980 but in 1979, the ratio of first instar nymphs to adults (L1/Ad) for M. dirhodum was not significantly altered by BYDV infection (Table 2).

The effect of BYDV on the number and size of aphid colonies

Any distinct aggregation of aphids with more than two aphids was considered as a colony. On this basis, there were significantly more colonies of M. dirhodum in 1979 on diseased oats ($F = 11.33$, df = 1/104, $p < 0.001$) and

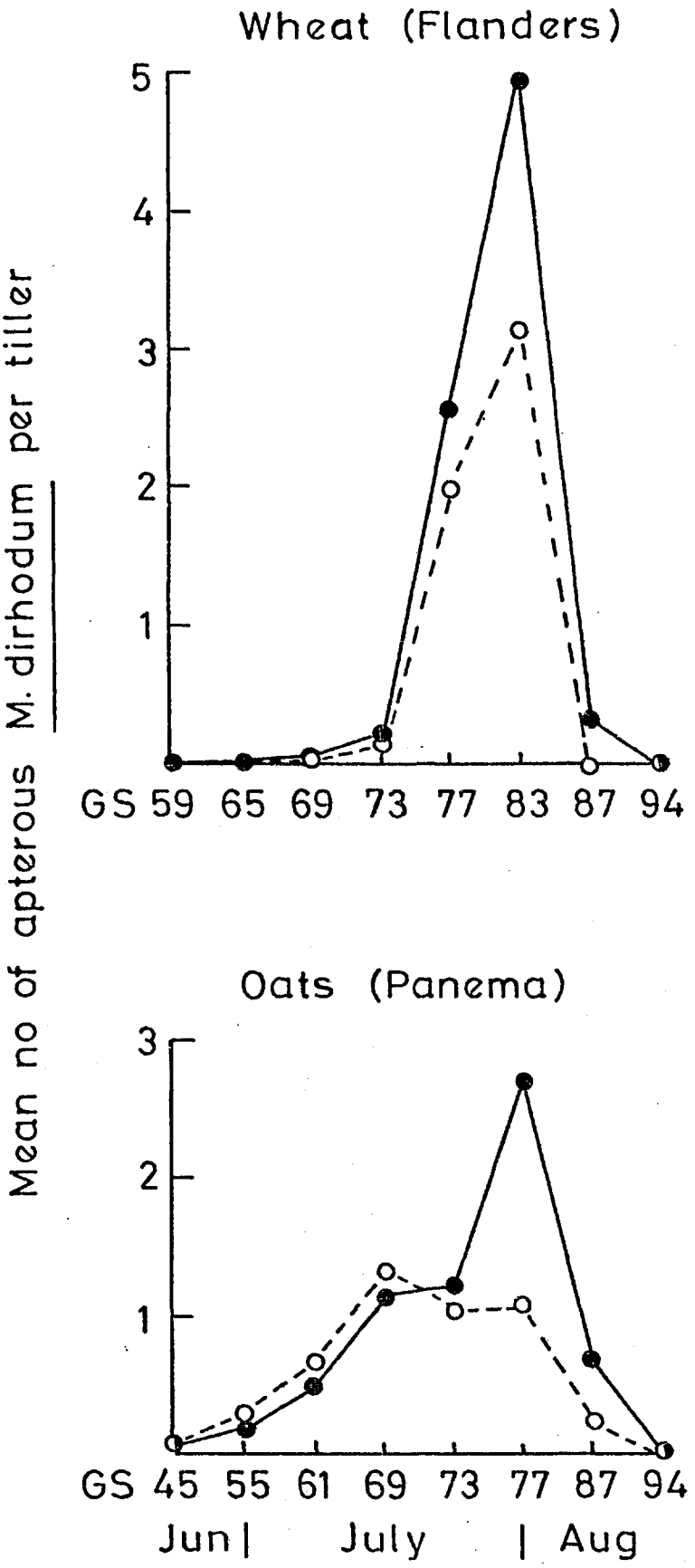


Fig. 17. Numbers of apterous adult M. dirhodum on healthy (O) and BYDV - infected (●) wheat and oats in the field, 1979.

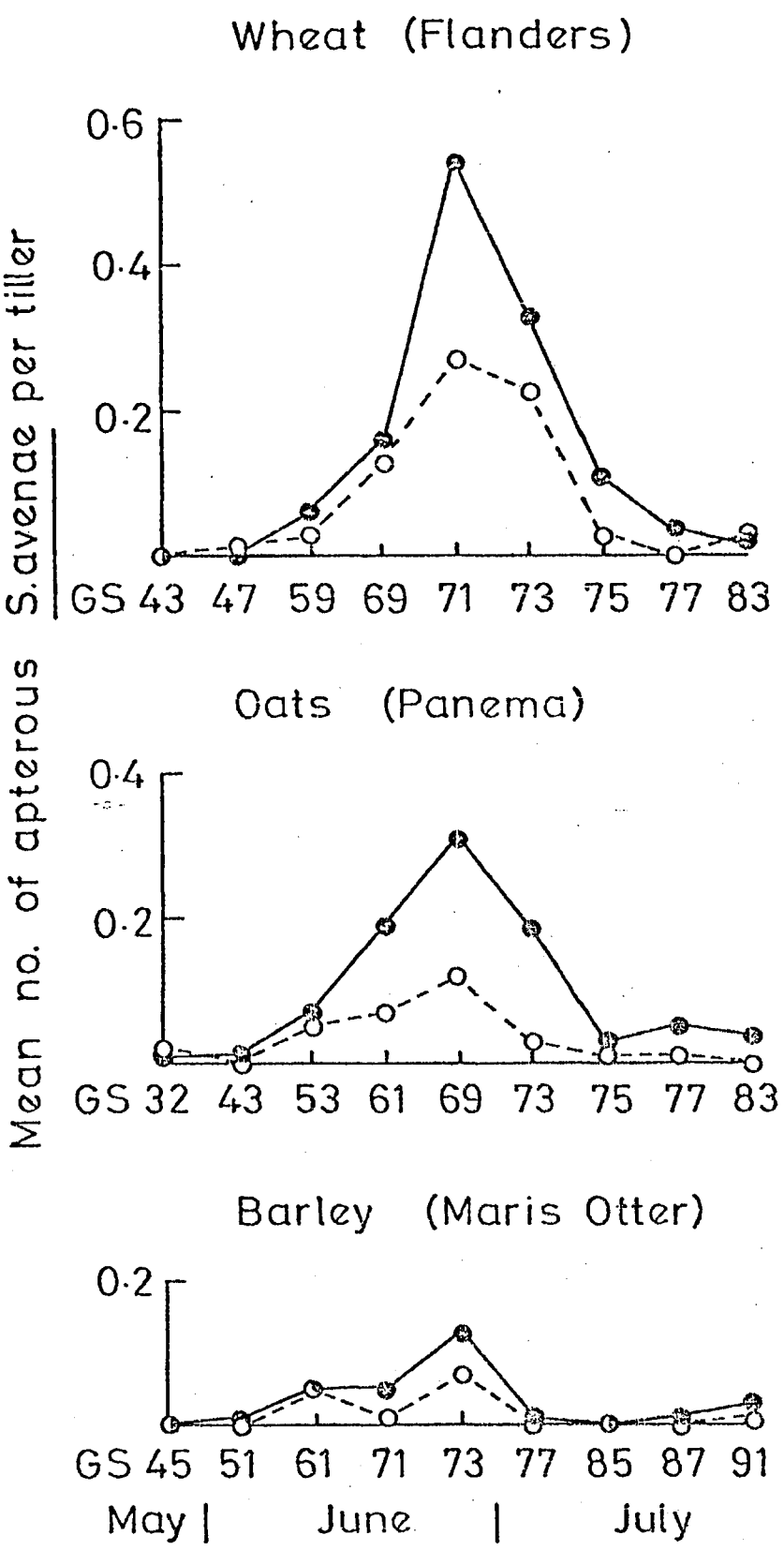


Fig. 18. Numbers of apterous adult S. avenae on healthy (O) and BYDV - infected (⊛) wheat, oats and barley in the field, 1980.

wheat ($F = 10.08$, $df = 1/62$, $p < 0.001$) (Fig. 19), and in 1980 on diseased barley ($F = 4.63$, $df = 1/32$, $p < 0.05$), oats ($F = 53.64$, $df = 1/36$, $p < 0.001$) and wheat ($F = 27.29$, $df = 1/36$, $p < 0.001$) (Fig. 20). Apart from increasing the numbers of aphids per colony on oats in 1979 ($F = 5.80$, $df = 1/118$, $p < 0.05$) (Appendix Table A) BYDV infection did not affect the size of aphid colonies in either year.

The effect of BYDV on yield

Five parameters of yield were measured in 1979 and these were increased to six in 1980 (Table 3). BYDV-infected wheat, barley and oats were shorter and had smaller ears than healthy plants. BYDV decreased the number of grains per ear, the weight of grains from 20 ears and the total grain yield per plot in each crop. Grain weight was reduced by BYDV in all three crops but only significantly in wheat and barley. Shelling percentage was decreased significantly by BYDV only in wheat.

The three crops were ranked according to the severity of the effects of BYDV on their yield in both years (Table 4.). The largest decrease was given a rating of 1. When all the six parameters in Table 4 were considered together, significant differences were found between the crops ($Xr^2 = 63$, $K = 3$, $N = 6$, $p < 0.01$, Friedman's two-way

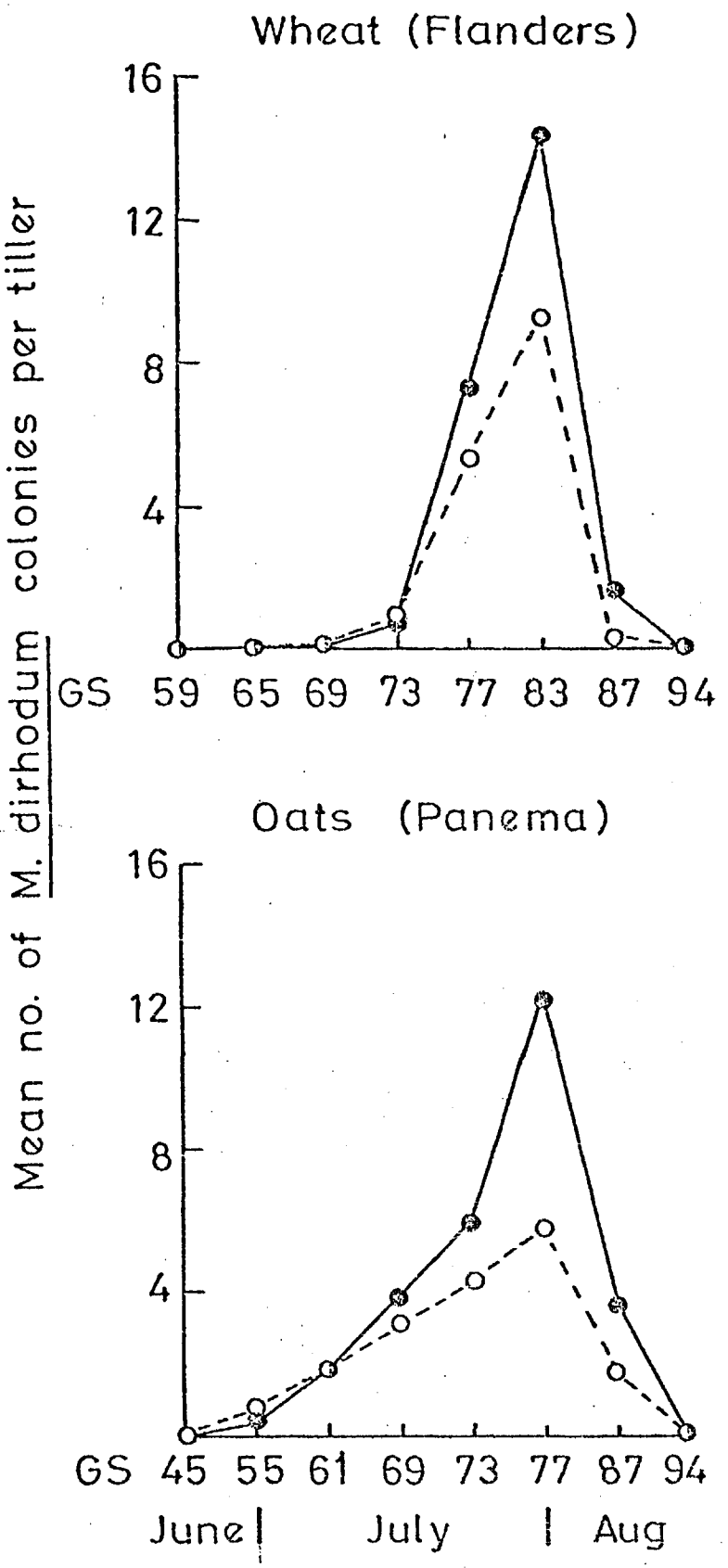


Fig. 19. Numbers of M. dirhodum colonies on healthy (O) and BYDV - infected (●) wheat and oats in the field, 1979.

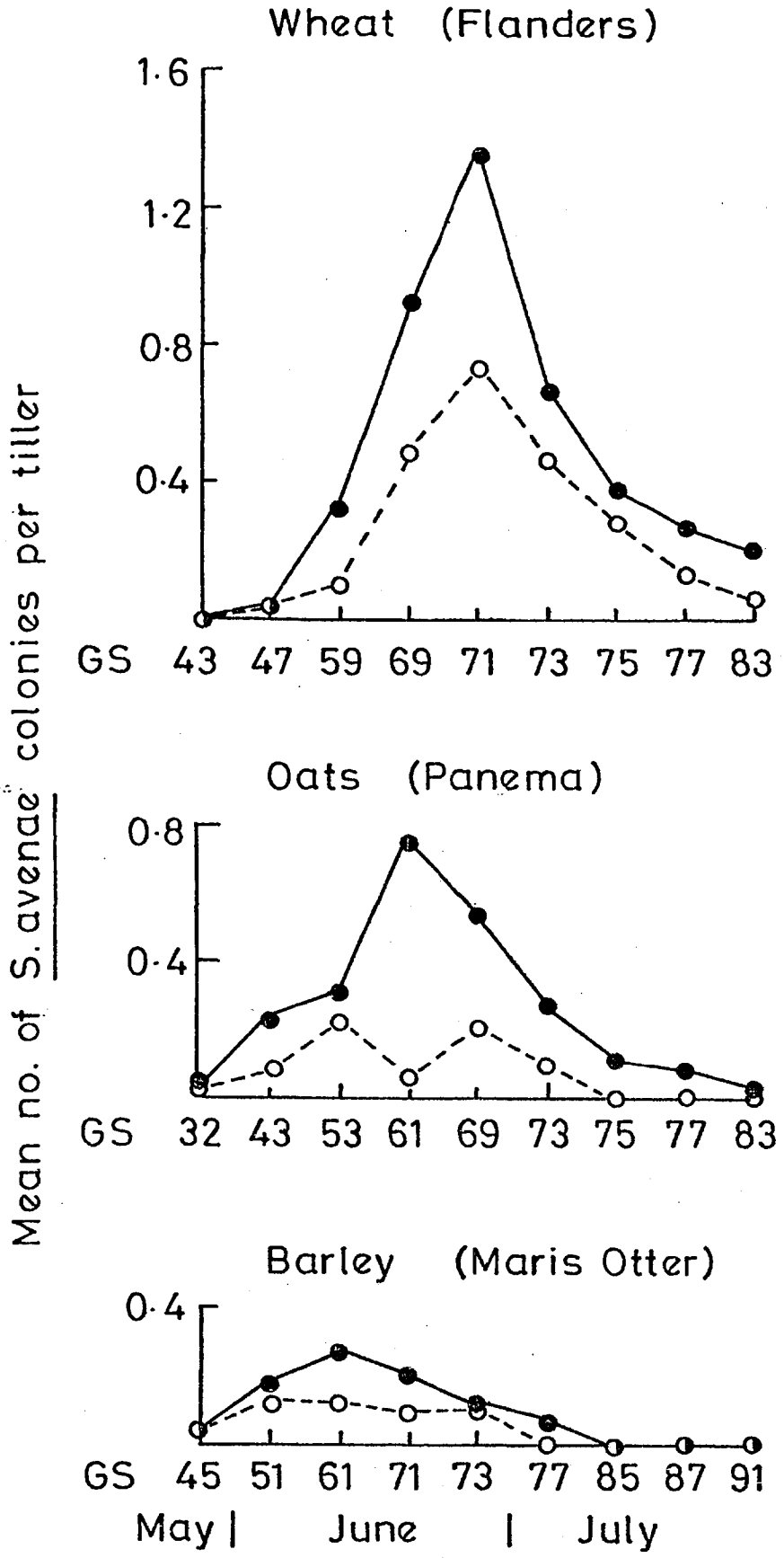


Fig. 20. Numbers of S. avenae colonies on healthy (○) and BYDV - infected (●) wheat, oats and barley in the field, 1980.

Table 3: The effect of BYDV on parameters of yield in winter wheat (Flanders) oats (Panema) and barley (Maris Otter, 1979 and 1980.

Wheat 1979	Straw length (cm) (50 tillers) †	Length of ears (cm) (50 ears)	No. of grains/ear (100 ears)	Shelling % (100 ears)	Grain wt (mg)	Wt of grain (gm) per 20 ears	Grain Yield (gm) plot
Healthy	-	-	33.52±0.73	-	47.61±1.48	31.84±0.51	210.30±1.61
Diseased	-	-	22.85±1.03	-	37.88±1.24	17.55±1.29	69.00±6.42
% reduction	-	-	31.83 ***	-	20.44 ***	44.88 ***	67.19 ***
Wheat 1980							
Healthy	72.61±0.64 ††	9.67±0.30	42.93±1.52	64.71±0.91	45.79±0.93	34.82±1.88	-
Diseased	56.06±1.18	8.21±0.08	25.27±1.72	56.75±1.81	32.27±1.01	14.30±1.28	-
% reduction	22.79 ***	15.10 **	41.14 ***	12.30 *	29.53 ***	58.93 ***	-
Oats 1979							
Healthy	-	-	61.80±3.07	-	27.70±0.36	34.24±1.64	217.50±13.84
Diseased	-	-	27.78±2.27	-	26.01±0.65	15.84±1.91	52.30± 6.50
% reduction	-	-	55.05 ***	-	6.10 NS	53.74 ***	75.95 ***
Oats 1980							
Healthy	88.17±1.58	20.74±0.32	62.13±1.95	63.83±0.44	28.53±0.19	31.92±0.56	-
Diseased	67.55±1.66	15.49±0.31	26.19±2.05	60.86±2.14	25.62±1.08	11.88±1.15	-
% reduction	23.39 ***	25.31 ***	57.85 ***	4.65 NS	10.20 *	62.78 ***	-
Barley 1980							
Healthy	76.04±1.83	9.80±0.31	27.68±0.66	67.00±0.98	46.10±0.42	22.22±0.57	-
Diseased	45.68±0.53	4.77±0.11	13.90±0.55	65.53±0.32	30.03±1.27	6.84±0.34	-
% reduction	39.93 ***	51.33 ***	49.78 ***	2.19 NS	34.86 ***	69.22 ***	-

† Numbers in parentheses represent the sample sizes for each treatment per crop.

†† Values are the means of 5 replicates per treatment per crop ± standard error.

- Not measured

Table 4: The ranking of wheat, oats and barley according to the effect of BYDV on their yield

	Straw length	Length of ears	No. of grains/ear	Shelling %	grain wt	Wt of grains/20 ears	Total
Wheat	3+	3	3	1	2	3	15
Oats	2	2	1	2	3	2	12
Barley	1	1	2	3	1	1	9

Table 5: The parameters of yield ranked according to the effect of BYDV 1980

Parameter	Grain Yield per plot	Wt of grains from from 20 ears	No of grains per ear	Length of ears	Plant Height	Grain wt	Shelling %
Wheat	1	2+	3	6	5	4	7
Oats	1	2	3	4	5	6	7
Barley	1	3	2	4	5	6	7
Total	(3)	(7)	(8)	(14)	(15)	(16)	(21)
Rank	1	2	3	4	5	6	7

+ The most severe effect is given a rating of 1

analysis of variance by ranks, Friedman, 1937). Barley was the most severely affected and wheat the least with oats intermediate. An F-test analysis of the individual indices of yield revealed that straw length, the length of ears and the grain yield per 20 ears were most drastically reduced in barley and least in wheat ($F = 13.09$, $df = 2/24$, $p < 0.001$; $F = 25.89$, $df = 2/24$, $p < 0.001$; $F = 2.67$, $df = 2/24$, NS respectively); the reduction in grain weight was affected most in barley and least in oats ($F = 24.00$, $df = 2/24$, $p < 0.001$); the number of grains per ear was decreased most in oats and least in wheat ($F = 24.00$, $df = 2/24$, $p < 0.001$), while the decrease in the shelling percentage was largest in wheat and lowest in barley ($F = 2.49$, $df = 2/24$, NS).

The seven parameters of yield measured were similarly ranked (Table 5) and they can be arranged in the following order of decreasing severity of the effect of BYDV: grain yield per plot, weight of grains from 20 ears, number of grains per ear, length of ears, straw length, grain weight and the shelling percentage ($Xr^2 = 76.57$, $K = 7$, $N = 3$, $p < 0.001$).

DISCUSSION

Aphid numbers

The different species of cereal aphids were not equally abundant in any one year. *M. dirhodum* survived the very cold winter of 1978/79 better than *S. avenae* and in the absence of natural enemies early in the season (which may have been greatly reduced by low temperatures).

together with other factors (Dean et al, 1980), M. dirhodum developed large populations whose migrations excited the British Press in July 1979 (Cochrane, 1980; Dewar et al, 1980; Schaefer et al, 1979). This enormous increase in numbers probably enhanced the development of large numbers of natural enemies, particularly fungi and parasitoids (Dean et al, 1980), whose activity, though late in the season, must have caused such a decline in the populations of M. dirhodum in 1979 that the latter were unable to fully exploit the milder winter of 1979/80. This may have contributed to the relative scarcity of M. dirhodum in the 1980 growing season. Conversely, S. avenae survived less well than M. dirhodum in 1978/79, attained low numbers in 1979 but overwintered in large enough numbers in 1979/80 to be the predominant species of cereal aphids in the summer of 1980.

The relative abundance of the brown and green forms of S. avenae on crops in 1980 was recorded by other workers in the U.K. For example, Dean (unpublished data) also found proportionately higher numbers of the brown form on virus-free plots of wheat in a different field at Rothamsted. The preponderance of one colour within a crop may depend on the proportions of aphids of each colour that infest a crop initially, but little is known about the factors governing colour form in this species.

The effect of BYDV on the population of aphids

The results clearly show that higher populations of M. dirhodum in 1979 and S. avenae in 1980 developed in the field on BYDV-infected winter cereals, as was reflected by the total numbers of aphids, numbers of adults and colonies, which confirms previous hypotheses. Oswald and Houston (1953) noted that rapidly multiplying colonies of cereal aphids occurred in the well defined foci of BYDV infection in crops, but they did not compare the numbers of aphids on healthy and diseased plants. Hooper (1978), judging from the presence of aphid exuviae, suggested that higher aphid populations might have occurred on the virus-infected patches in winter wheat. The results presented here are therefore probably the first quantitative experimental proof of the effect of BYDV on the populations of cereal aphids in the field.

The observed increases in aphid numbers on BYDV-infected plants may be related to the colour changes accompanying BYDV infection. The yellowish colour induced in the leaves of infected plants may render these plants more attractive to flying aphids which then alight preferentially on them. A higher build up of immigrating alates on diseased plants would contribute substantially to the differences in aphid populations recorded here on healthy and diseased plants. Although cereal aphids are reportedly less sensitive to yellow than species adapted to feeding on dicotyledons (Adams & Farrell, 1967; Eastop, 1955; Heathcote, 1957; Heathcote et al, 1969; O'Loughlin, 1963), both M. dirhodum and S. avenae are known to be

yellow-sensitive (A'Brook, 1973; Kieckhefer et al, 1976). Preferential alightment on plants due to colour differences has been reported for several aphid species (eg. Kennedy et al, 1959; Moericke, 1969; Müller, 1964; Radcliffe & Chapman, 1965). The higher numbers of alate M. dirhodum on virus-infected oats in 1979 and of alate S. avenae on diseased oats and barley in 1980, together with the increase by BYDV in the proportion of aphid-infested plants in 1980, support this hypothesis.

The alates produced within a crop, being potential migrants, are unlikely to remain there long. Most of the alate M. dirhodum found on oats and wheat in 1979 were therefore probably immigrants. However, fourth instar alates were not counted in 1979 to confirm this probability. Most of the alate S. avenae found within the crops in 1980 were immigrants, since fourth instar alates were not encountered on the plants until the numbers of adult alates had peaked and declined. BYDV infection of oats enhances the production of alates in S. avenae that have experienced crowding (Gildow, 1980). This phenomenon was confirmed in the present study but the sequence of occurrence of alate adults and fourth instars suggests that in 1980, most of the colonizing S. avenae must have originated outside the crops.

Thus an increase in the attractiveness of plants to flying aphids due to BYDV infection could explain the observed differences in the field populations of M. dirhodum on oats in 1979 and S. avenae on oats and barley in 1980. But BYDV infection did not significantly affect the

colonization of wheat plants by alatae in either year. In 1979, wheat was at a more advanced growth stage than oats at the time of inoculation with the virus. Symptom expression is most severe in the youngest plants and decreases in intensity as the plant ages (Oswald & Houston, 1953). Although the three crops studied in 1980 were planted at the same time, the virus symptoms that developed on wheat were less pronounced than those on oats or barley, since wheat is less susceptible than the other two crops to BYDV infection (Doodson & Saunders, 1970; Watson & Mulligan, 1960; Jensen et al, 1971). The colour changes in wheat in both years were therefore probably not sufficiently intense to significantly influence the host selection behaviour of alate M. dirhodum and S. avenae.

The larger populations of both aphids which nevertheless developed on diseased wheat are attributable mostly to the greater numbers of apterae on them. Reproduction in the apterae accounts for much of the population growth of an aphid (eg. Rabbinge et al, 1979). BYDV did not affect the L1/Ad ratio of M. dirhodum, suggesting that the fecundity of individual M. dirhodum did not differ on healthy and diseased plants, and confirming thereby that BYDV raised the population of M. dirhodum by increasing the numbers of apterae. In 1980, the population of S. avenae was higher on diseased than on healthy wheat due to a combination of the significantly higher numbers of apterae and the slightly greater numbers of alates on infected plants.

Yield

Every parameter of yield, except grain size in oats and shelling percentage in oats and barley, was significantly reduced by BYDV infection of the three crops. A decrease in straw length can reduce the surface area exposed to light per plant by increasing mutual shading by the leaves, and thereby lower the amount of photosynthesis (Watson, 1958). The ears of cereals photosynthesize and more than 80% of ear photosynthate is recovered from the grain (Carr & Wardlaw, 1965; Birecka et al, 1968). Ear photosynthesis can contribute between 11 - 40% of nutrients stored in the grains (Birecka et al, 1964; Birecka & Dakic-Wlodkowska, 1964; Birecka et al, 1968). This contribution is especially high in awned crops such as barley and awned varieties of wheat. By reducing the size of ears, BYDV decreases not only the effective photosynthetic area and thereby the amounts of nutrients reaching the grains, but also the numbers of grains per ear. In wheat and barley but not oats, the grains that do develop are smaller than normal. In oats the strong reduction in the number of grains per ear probably compensates for the non effect of BYDV on grain size. In each crop, BYDV decreased the total grain weight per ear more than the weight of the whole ear, the difference being greatest in wheat (Table 4). Thus the increase in chaff production and thereby the decrease in the shelling percentage by BYDV was higher in wheat than in either oats or barley. The ultimate result of all these effects is a lowering of the total grain yield in infected plants,

95.95% and 67.19% in oats and wheat respectively in 1979.

The effects of BYDV on yield parameters have been studied by various workers. These effects differ considerably between crops and between varieties of the same crop, and depend on the virus isolate involved. In this study, the yields of barley and oats were reduced more severely than that of wheat, reflecting the lower susceptibility of wheat to BYDV. BYDV has been found to decrease plant height, ear size, number of grains per ear, grain size and the total grain yield in wheat, oats, barley and maize (eg. Boulton & Catherall, 1980; Burnett et al, 1974; Burnett & Robinson, 1972; Doodson & Saunders, 1970; Endo & Brown, 1957; Panayotou, 1975, 1979; Pearson, 1977). Discrepancies between these earlier studies and the present work in the actual levels of yield reduction are probably due to variations in the severity of BYDV symptoms on different crop varieties, the age of plants at inoculation and the isolate of the virus used.

SUMMARY

The effect of BYDV on the field populations of cereal aphids was studied at Rothamsted in 1979 and 1980 by artificially infecting winter wheat (Flanders), oats (Panema) and barley (Maris Otter) with a severe R. padi-specific isolate of the virus and monitoring the numbers of aphids on the crops. Direct aphid counts were made from the time of the spring migration of alates until the crops were harvested. Seven parameters of yield were also measured. M. dirhodum and S. avenae were abundant on the crops in 1979 and 1980 respectively. BYDV significantly increased the total numbers of aphids and the numbers of alates on diseased plants in both years. The virus also depressed yields on all three crops, but did not affect grain weight in oats and the shelling percentage in oats and barley. The populations of aphids and yields were least severely affected in wheat. The possible reasons for the observed results are discussed in the light of the existing knowledge.

SECTION 2

THE EFFECT OF BARLEY YELLOW DWARF VIRUS ON HOST SELECTION IN CEREAL APHIDS

INTRODUCTION

Having established that higher populations of Sitobion avenae (F.) and Metopolophium dirhodum (Wlk.) developed in the field in plots of wheat, oats and barley infected with barley yellow dwarf virus (BYDV) than in healthy plots (Section 1), it was necessary to investigate the cause(s). The development of larger numbers of aphids on diseased plants could have resulted from a higher initial infestation by immigrant alates. This section describes experiments designed to investigate the effect of BYDV infection of the host plant on host selection by alate S. avenae and M. dirhodum.

MATERIALS AND METHODS

The aphid supply

Alates for the experiment were obtained from crowded glasshouse cultures which were maintained on wheat (Highbury) seedlings (see pages 39-41 for details of glasshouse conditions). About thirty hours before the trial, all adult alates in the culture were removed and discarded. During this thirty hour period the cultures were kept in darkness, in order to inhibit flight by the newly emerging adults (Johnson, 1958).

For the experiment, a pot of wheat seedlings bearing an aphid culture was placed in a non-return take-off box described by Kennedy and Booth (1964). Basically, the arrangement was such that the aphid culture was separated from a source of light by a sloping sheet of glass, a moat

and a vertical glass sheet (Fig. 21) so that aphids could reach the second glass sheet by flight only. Any aphid found on this glass was presumed to have flown for the first time (Kennedy & Booth, 1963). The box was kept at about 19°C and lit by two fluorescent lamps. When an aphid was observed to take off from the plants and land on the vertical glass sheet, it was allowed to walk onto a fine camel hair brush which was promptly transferred to the flight chamber and held at a slight angle until the aphid took off towards the light.

The flight chamber

The flight chamber used has been described in detail by Kennedy and Booth (1963), Laughlin (1974) and Kennedy and Ludlow (1974). Essentially, it is a vertical wind tunnel, the working section of which is lit through the central area of its roof screen so that the aphid flies upwards towards the light but is held below it by the air current blowing downwards (Fig. 22). The walls, floor and the rest of the roof were black. Light was supplied by an ultraviolet lamp. The draught speed, with the valve fully open, was about 25 cm/sec (0.56 m.p.h.) at 15cm below the roof (Kennedy & Booth, 1963). The flight chamber was kept at about 19°C, and the rest of the room containing it was kept dark during each trial.

Each aphid was allowed continuous free flight for 5 minutes while being held at roughly 15cm below the roof. This position was maintained by continually adjusting the rate of downward airflow to balance the aphid's rate of climb toward the light (Kennedy & Ludlow, 1974). Whenever the flying aphid began to sink instead of climbing,

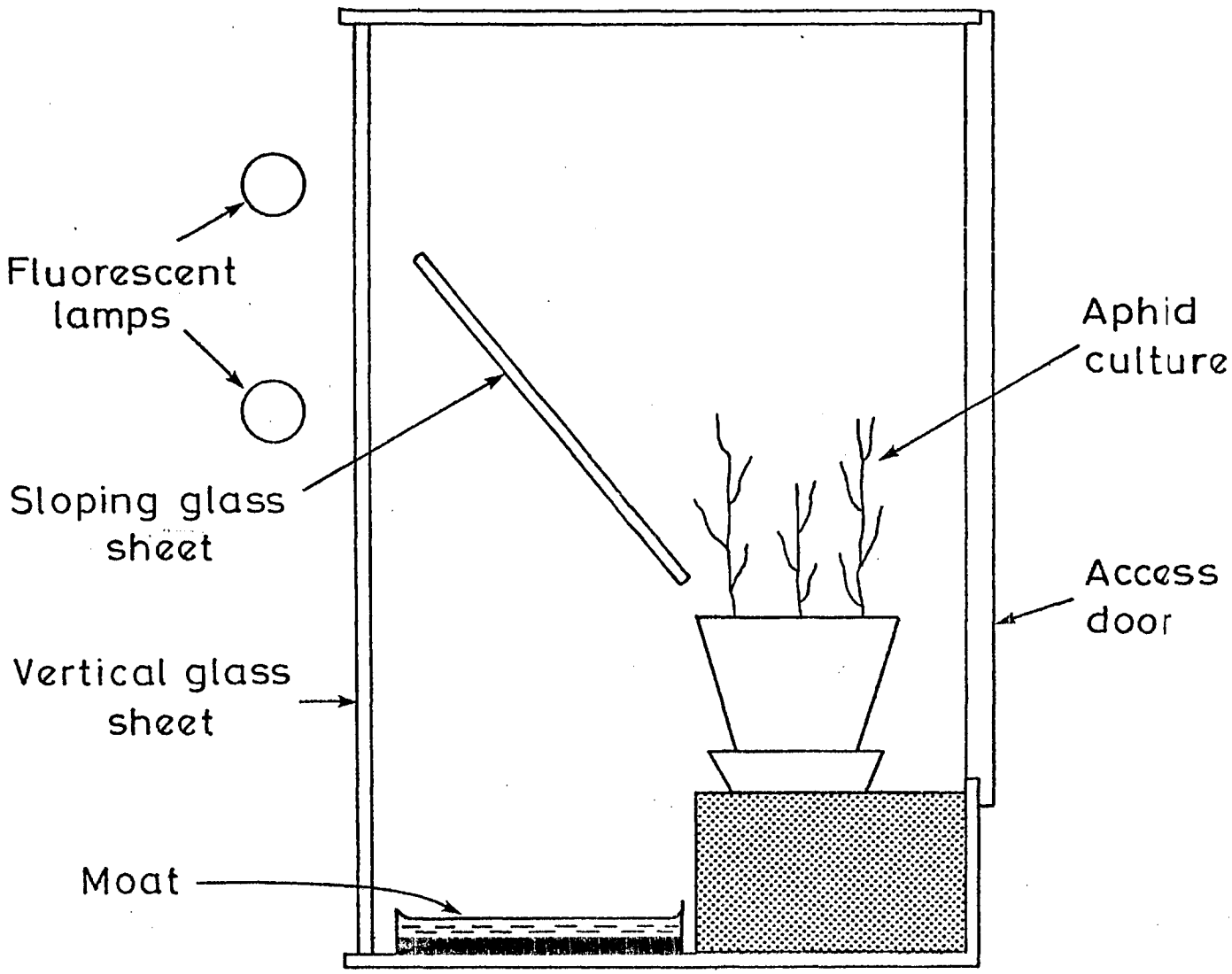


Fig. 21. The non - return take - off box providing a continuous supply of aphids taking flight for the first time (after Kennedy & Booth, 1964

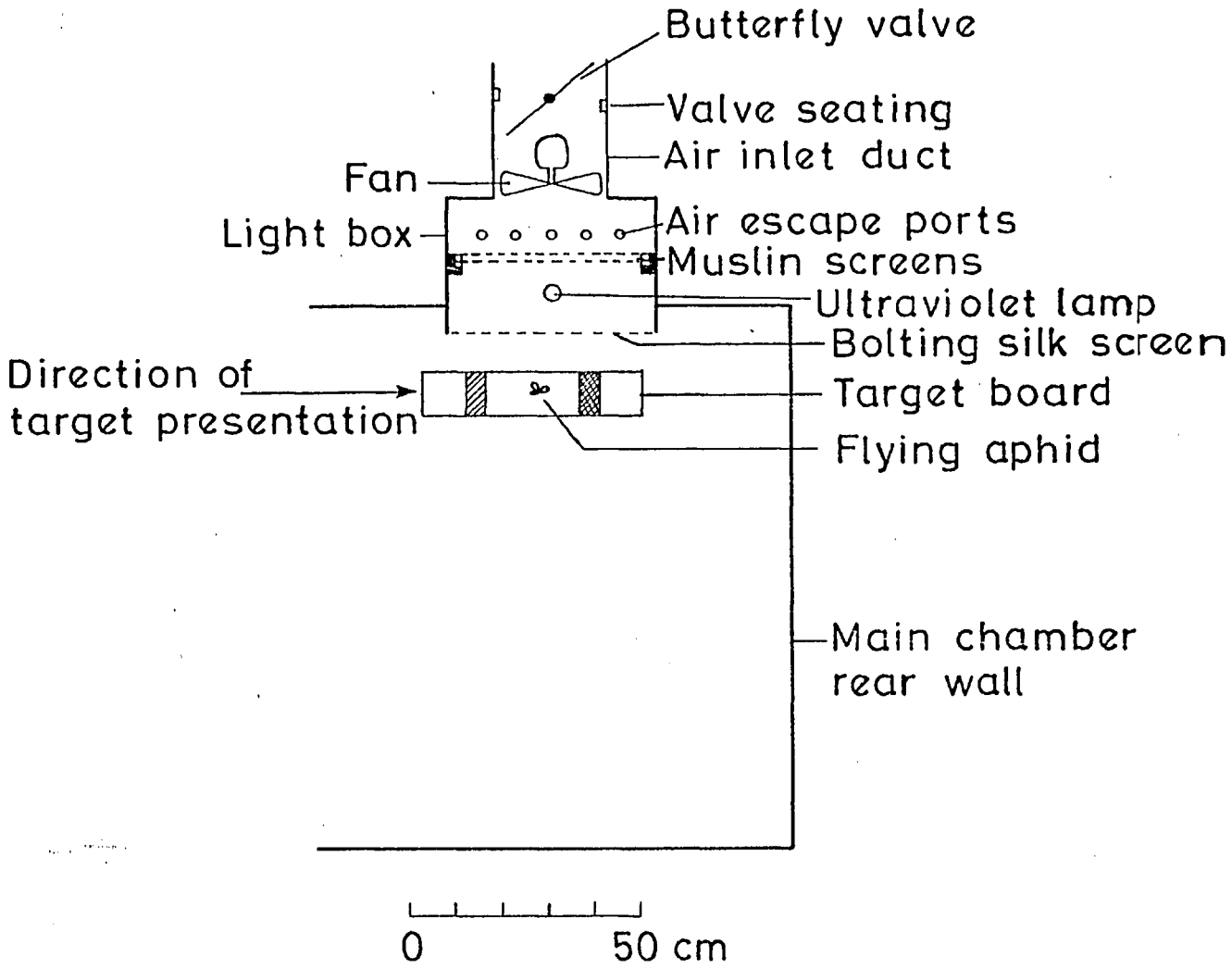


Fig. 22. Diagrammatic vertical section of flight chamber with front opening facing left (adapted from Kennedy & Booth, 1963).

the direction of airflow was reversed from downward to upward.

Target presentation

At the end of 5 minutes, the flying aphid was presented with a choice of landing targets. These were a band each of leaves freshly detached from BYDV-infected and healthy barley (Julia) or oat (Manod) plants, and attached to a black board (Fig. 23). All the leaves from diseased plants showed the colour change characteristic of BYDV infection for that crop - in this case, the barley leaves were bright yellow and the oat leaves were reddish yellow in colour. Leaves from healthy plants were dark green. The 5th leaf on barley (GS 45) and the 4th leaf on oats (GS 32) were used and healthy and diseased leaves were of comparable age.

In preliminary tests, each band was formed with one leaf but, for the actual experiment, three oat or four barley leaves were used to form a band measuring 3 - 4cm across. The bands were separated by a distance of 20cm in order to avoid any edge effects (Kring, 1967). Each set of leaves was replaced every 40 minutes to minimize possible effects of wilting. Preliminary trials had shown that aphids did not respond to the targets before 2 - 3 minutes of flight, so all test aphids were flown for 5 minutes in order to minimize variation in their response.

The targets were presented by the operator wearing a long-sleeved black gown and a black glove. The black board bearing the leaves was suddenly held at about 20cm away from and level with the flying aphid. The initial position of the aphid was always roughly mid-way between

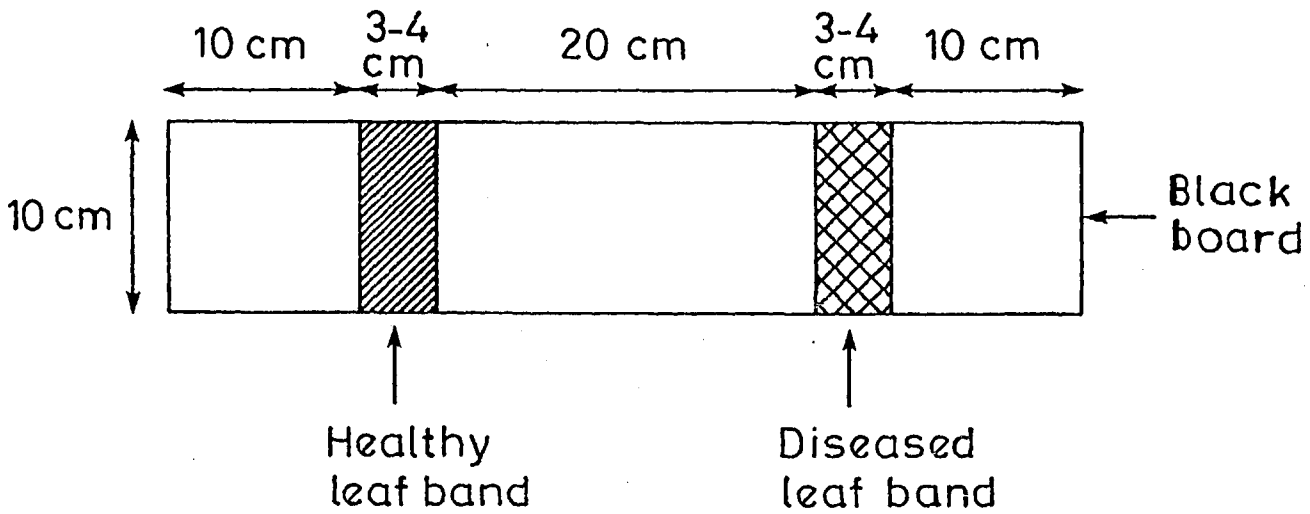


Fig. 23. Diagram of the landing targets presented to flying aphids in the flight chamber.

the two leaf bands whose positions, relative to the operator's hand, were alternated between presentations in order to minimize position effects (Kring, 1967). Only aphids that had settled down to a steady flight within the lighted area were included in the test. Each presentation lasted for one minute and each aphid was tested only once. In the analysis of the results, only the aphids that responded by alighting at the first presentation were considered. The results were subjected to a chi-square analysis.

RESULTS

Significantly more M. dirhodum landed on the leaf targets than on the black background when a wider leaf band was used (Table 6). For both aphid species on both crops, significantly more flying aphids alighted on BYDV-infected leaves than on healthy ones (Table 7). Even when the number of aphids which landed on the background but close to the leaves (0.4 - 3cm away) is included, the effect remains the same (Table 8). Such aphids were observed to promptly walk onto the leaves closest to them.

DISCUSSION

Clearly, flying alates of both S. avenae and M. dirhodum, when simultaneously offered a choice of landing targets, were attracted to BYDV-infected leaves in preference to healthy ones. They responded by alighting. Since the inclusion in the analysis of those aphids that landed on the black background still showed a bias towards infected leaves, it can be concluded that they had

Table 6: The effect of target size on the proportion of *M. dirhodum* landing on the target +

Target size	No. landing on target	No. landing on background	X^2	P	No. of aphids tested
1-leaf band	5	4	0.11	NS	9
4-leaf band	18	8	3.85	<0.05	26

+ Numbers landing on healthy and diseased Barley leaves combined.

Table 7: The numbers of *S. avenae* and *M. dirhodum* alates landing on healthy and BYDV-infected leaves of barley and oats in a laboratory flight chamber

	BYDV-infected	Healthy	X^2	P
S. avenae				
Barley (Julia)	10	1	7.36	<0.01
Oats (Manod)	9	1	6.40	<0.05
M. dirhodum				
Barley (Julia)	18	4	8.91	<0.01
Oats (Manod)	14	1	11.27	<0.001

Table 8: The numbers of S. avenae and M. dirhodum alates that landed on target or within 3cm of healthy and BYDV-infected leaves of barley and oats in a laboratory flight chamber.

	BYDV-infected	Healthy	X^2	P
S. avenae				
Barley	16	4	7.20	< 0.01
Oats	10	1	7.36	< 0.01
M. dirhodum				
Barley	26	7	10.94	< 0.001
Oats	15	5	5.00	< 0.05

actively aimed at but missed their targets for some reason. Although aphids are reportedly unable to discriminate between host and non-host at the initial approach but land on both in about equal numbers (Kennedy et al, 1959 a & b, 1961; Müller, 1958, 1962; Thorsteinson, 1960), the results presented here indicate that they can make a choice where colour differences are involved. As a result of BYDV-infection, the colour of the diseased leaves had changed from dark green to bright yellow and reddish yellow in barley and oats respectively. The attraction was therefore to yellow in preference to green. This attraction to yellowish leaves has also been reported by Müller (1964) who found that Aphis fabae Scop. and Myzus persicae (Sulz.) landed more frequently in the field on yellowish and yellowish-green varieties of lettuce than on a dark reddish-brown one; the attraction to yellowish plants was increased when their colour contrasted with their surroundings. Cartier (1963) also found that a yellowish-green variety of pea (Pisum sativum L.) was visited more frequently and colonized more heavily by Acyrthosiphon pisum (Harris) than green varieties of the same crop. Such a colour attraction also explains the observation by Kennedy et al (1950) that in free infestations by viviparous Myzus persicae and Aphis fabae on sugar-beet plants and spindle bushes, actively growing and senescent leaves were more susceptible to colonization than maturing, mature and drying leaves on the same plant. The growing leaves were pale green, the senescing leaves yellow and the mature leaves dark green. The observations

recorded here also confirm the inclusion of S. avenae and M. dirhodum among the yellow-sensitive aphids (A'Brook, 1973; Kieckhefer et al, 1976), and adequately answer the question raised by Hodgson (1977) as to whether alatae can be attracted to virus-infected plants because of their colour.

The results of laboratory experiments on behaviour are generally difficult to extend without modifications to the situation in the field, since environmental conditions may exert much influence. It may also be argued that detached leaves do not truly represent the whole plant. In this study, however, natural aphid infestations in the field were too low to permit a measurable comparison, particularly of individual aphid species. The age and flight experience of different test aphids could also not be standardised in the field. A flight chamber trial was therefore the only alternative. Foci of BYDV infection in the field can be as big as 3 - 6 metres in diameter (Oswald & Houston, 1951), big enough to create the kind of sharp contrast between infected and healthy leaves which existed in this trial. Lastly, only leaves younger than the one inoculated with BYDV will show the symptoms of colour change (Oswald & Houston, 1951); this indicates that different leaves on the same diseased plant may have a different colouration, and suggests that the comparison of leaves rather than whole plants is justified.

The fact that some of the test aphids did not respond to the targets at the first presentation tends to support

Moericke's (1955) theory, as modified by Kennedy et al (1961), that a migrant aphid was initially more strongly attracted to the predominantly short-wavelength light from the sky, but that after flying for some time, the aphid was more strongly attracted to the longer-wavelength light reflected from the plants and soils below. An ultra violet lamp was used in this study. The reason for the greater attraction of the alighting aphids to yellow as compared to green leaves was not investigated here, but could be due to a difference in the wavelength of light reflected from leaves of either colour. The importance of the effect of such a difference is borne out by the current use of the highly reflective surface of aluminium materials to repel migrant aphids and thereby control aphid-transmitted viruses (Johnson et al, 1967; Kring, 1964, 1970; Smith & Webb, 1969; Smith et al, 1964 a & b).

SUMMARY

The effect of BYDV infection of oats (Manod) and barley (Julia) on the host selection behaviour of S. avenae and M. dirhodum was investigated in a laboratory flight chamber. Individual aphids were flown continuously for five minutes and then simultaneously presented with leaves detached from healthy and BYDV-infected oats or barley. Significantly more aphids of both species alighted on diseased than healthy leaves of both crops, indicating their preferential attraction to the former.

SECTION 3

THE EFFECT OF BARLEY YELLOW DWARF VIRUS ON THE ADULT SIZE, EMBRYO CONTENT AND REPRODUCTIVE RATE OF CEREAL APHIDS.

INTRODUCTION

In addition to the attraction of alates to diseased plants, the possibility remained that the altered physiology of BYDV-infected plants could have increased the fecundity of the aphids feeding on them thereby leading to the development of higher aphid numbers on diseased than on healthy plants. The experiments reported here were designed to investigate the effect of BYDV infection of the host plant on the reproductive physiology of S. avenae, R. padi and M. dirhodum on wheat, oats and barley at various growth stages, using laboratory and field trials.

MATERIALS AND METHODS

A. Laboratory Experiments

Embryo Content

Fecundity was measured by counting the embryo content of teneral adults and by monitoring actual reproduction over a period of 18 - 20 days.

The aphids and test plants used were obtained as described previously (pages 39 - 41). All experiments were conducted in Saxcil growth cabinets under the conditions of temperature, humidity and lighting already described.

At GS 12 (seedling), 22 (tillering), 32 (stem elongation), and 59 (emergence of the inflorescence), two virus-free

first instar nymphs of S. avenae, R. padi or M. dirhodum were confined to the middle portion of the youngest expanded leaf of each plant. At the teneral adult stage, ie. within 24 hours after eclosion, the aphids were removed from the cages, weighed on a microbalance (Beckman LM 800) and dissected in water under a binocular microscope as described by Dewar (1977b). The total number of embryos, the number of embryos with pigmented eyespots and the number of large embryos were recorded. Each swelling of the ovariole was counted as an embryo (Fig. 24). Large embryos were fully developed with distinct appendages (Dharma, 1979). The three measurements were taken to compare their accuracy and suitability for estimating fecundity.

Reproduction

In a parallel set of experiments involving S. avenae and M. dirhodum, the aphids were not dissected but were weighed as teneral adults and recaged onto the youngest expanded leaves of the plants on which they had developed. The daily and total reproduction were then recorded over twenty days, the nymphs being carefully removed daily to avoid overcrowding.

In the case of R. padi, one batch of nymphs was fed continuously on virus-free 5cm wheat leaf segments (Capelle Desprez), while a second group was reared to adult on leaf segments detached from BYDV-infected wheat plants and then transferred as teneral adults onto virus-free

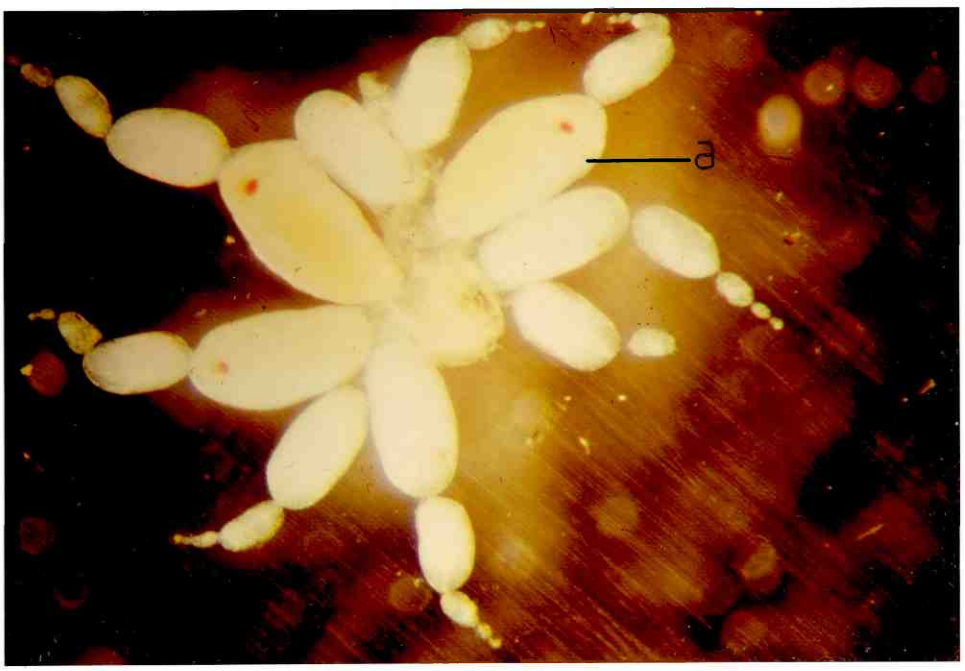


Fig. 24. Embryos dissected from an apterous R. padi. There are 5 embryos with pigmented eyespots (eg. a.).

wheat leaf segments. The leaves were excised at GS 32 and kept inside ventillated perspex boxes (8 x 4.5 x 2cm) containing moistened filter paper.

The aphids were weighed on a microbalance at birth and daily thereafter. Nymphs produced by them at maturity were counted and removed along with the leaf segments which were replaced every two days for 18 days. The filter paper was moistened with water and changed as necessary to avoid contamination by fungi. The experiment using excised leaves was conducted in a constant temperature room which was maintained at 19°C, 70% r.h. with a 16:8h light:dark regime. Lighting was provided by warm white fluorescent lamps.

B. Field Observations

Embryo content

Two virus-free and two BYDV-infected field plots of winter wheat (Flanders) similar to those described in Section 1 were used. At GS 71, ten to twenty tillers per treatment were marked with bamboo stakes. First instar nymphs of *S. avenae*, selected for uniformity of age and size, were confined in pairs on each ear using dialysis tubing cages. Their parents had been collected from symptomless wheat in the field the previous week and allowed to reproduce on seedling wheat in the glasshouse. Each caged ear was secured to the demarcating bamboo stake with some cotton thread to avoid lodging in the wind. The aphids were observed on alternate days until the adult moult when they were removed and dissected.

In addition, at GS 83, five naturally-infested ears of wheat were collected per treatment and taken to the laboratory where they were placed in ventillated perspex boxes. Adults moulting from the fourth instar stage 1 - 2 days later were dissected and their embryo content recorded.

RESULTS

A. Laboratory Experiments

Fecundity Parameters

For each aphid species on each crop, the regression on adult weight of each parameter used to estimate fecundity was calculated by pooling the data for all replications in each treatment, disregarding differences in plant growth stages. In each table of regressions, the displacement term shows the difference in the elevations of the regressionlines for the two treatments, while the degree of parallelism measures differences in the slopes of these lines.

The relationship between aphid size and fecundity

Fecundity as measured by embryo content is significantly positively correlated with teneral adult weight in the three aphids on each crop, for all three parameters used (Tables 9 - 11, Figs. 25 - 27), i.e. larger individuals contained more embryos than smaller ones whichever method of counting them was used. Both the total number of embryos (T) and the number of embryos with pigmented eyespots (P) were better correlated than the number of large embryos (L) with adult weight. "P" was better correlated than "T" in *S. avenae* on wheat and oats, and in *R. padi* on all

Table 9: Regression of embryo content on teneral adult weight - S. avenae (apterae)

Parameter of fecundity			Crop: Wheat	Oats	Barley
Total Embryos	Slope (b)	Healthy	24.16	35.55	34.44
		Diseased	27.12	38.08	37.76
		S.E.	4.64	2.76	4.85
	Intercept	Healthy	33.11	20.40	27.99
		Diseased	33.20	21.87	26.76
	Displacement	(F)	6.10 *	9.45 **	1.07 NS
	Parallelism	(F)	0.26 NS	0.43 NS	0.28 NS
	Regression (He + Di)†	(F)	31.04 ***	131.60 ***	49.71 ***
Embryos with pigmented eyespots	Slope (b)	Healthy	5.99	6.95	8.54
		Diseased	7.59	7.75	8.76
		S.E.	0.94	0.65	0.99
	Intercept	Healthy	6.07	4.50	4.29
		Diseased	4.83	4.43	4.45
	Displacement	(F)	1.78 NS	5.21 *	1.13 NS
	Parallelism	(F)	1.86 NS	0.76 NS	0.03 NS
	Regression (He + Di)	(F)	47.59 ***	92.99 ***	69.24 ***
Large Embryos	Slope (b)	Healthy	1.98	2.46	2.88
		Diseased	3.21	2.62	3.46
		S.E.	0.77	0.47	0.78
	Intercept	Healthy	2.21	1.69	1.67
		Diseased	1.80	2.27	1.85
	Displacement	(F)	15.79 ***	11.69 ***	6.92 **
	Parallelism	(F)	1.63 NS	0.06 NS	0.34 NS
	Regression (He + Di)	(F)	16.55 ***	26.26 ***	19.03 ***

† He - Healthy
Di - Diseased

Table 10: Regression of embryo content on teneral adult weight - *R. padi* (apterae)

Parameter of fecundity			Crop: Wheat	Oats	Barley
Total Embryos	Slope (b)	Healthy	39.99	43.96	29.11
		Diseased	19.12	39.28	36.41
		S.E.	4.73	5.45	6.73
	Intercept	Healthy	30.29	22.55	33.84
		Diseased	45.56	27.77	34.08
	Displacement	(F)	0.27 NS	1.87 NS	16.06 ***
	Parallelism	(F)	7.91 **	0.46 NS	0.73 NS
	Regression (He + Di)	(F)	22.53 ***	57.54 ***	38.92 ***
Embryos with pigmented eyespots	Slope (b)	Healthy	14.69	19.05	16.07
		Diseased	16.22	5.11	13.56
		S.E.	1.40	1.56	2.02
	Intercept	Healthy	6.62	-2.21	4.21
		Diseased	4.26	11.77	5.08
	Displacement	(F)	10.78 ***	1.81 NS	6.43 *
	Parallelism	(F)	0.49 NS	49.42 ***	0.97 NS
	Regression (He + Di)	(F)	70.78 ***	84.95 ***	51.83 ***
Large Embryos	Slope (b)	Healthy	4.46	10.46	6.20
		Diseased	7.91	1.63	6.56
		S.E.	0.94	1.05	1.53
	Intercept	Healthy	3.24	1.24	0.71
		Diseased	0.17	3.75	-0.21
	Displacement	(F)	6.18 *	29.40 ***	3.27 NS
	Parallelism	(F)	5.44 *	43.95 ***	0.03 NS
	Regression (He + Di)	(F)	29.14 ***	59.11 ***	15.53 ***

Table 11: Regression of embryo content on teneral adult weight - M. dirhodum (apterae)

Parameter of fecundity			Crop: Wheat	Oats	Barley
Total Embryos	Slope (b)	Healthy	30.11	27.11	28.46
		Diseased	41.52	37.22	30.82
		S.E.	2.52	2.59	3.18
	Intercept	Healthy	36.06	38.41	37.80
		Diseased	24.73	28.94	38.08
	Displacement	(F)	0.02 NS	2.44 NS	13.12 ***
	Parallelism	(F)	7.04 **	6.48 *	0.31 NS
	Regression (He + Di)	(F)	115.67 ***	99.27 ***	79.20 ***
Embryos with pigmented eyespots	Slope (b)	Healthy	9.40	5.34	4.74
		Diseased	11.46	7.71	7.93
		S.E.	1.55	1.43	1.85
	Intercept	Healthy	4.90	7.86	8.18
		Diseased	1.26	4.80	4.09
	Displacement	(F)	10.24 **	1.18 NS	3.57 NS
	Parallelism	(F)	0.61 NS	1.16 NS	0.98 NS
	Regression (He + Di)	(F)	29.07 ***	15.88 ***	9.10 **
Large Embryos	Slope (b)	Healthy	4.68	2.53	37.92
		Diseased	6.14	4.73	24.91
		S.E.	1.02	0.96	2.85
	Intercept	Healthy	0.90	2.51	30.24
		Diseased	-1.68	-0.21	43.86
	Displacement	(F)	11.74 ***	1.19 NS	0.29 NS
	Parallelism	(F)	0.72 NS	2.22 NS	6.68 *
	Regression (He + Di)	(F)	20.75 ***	12.06 ***	55.38 ***

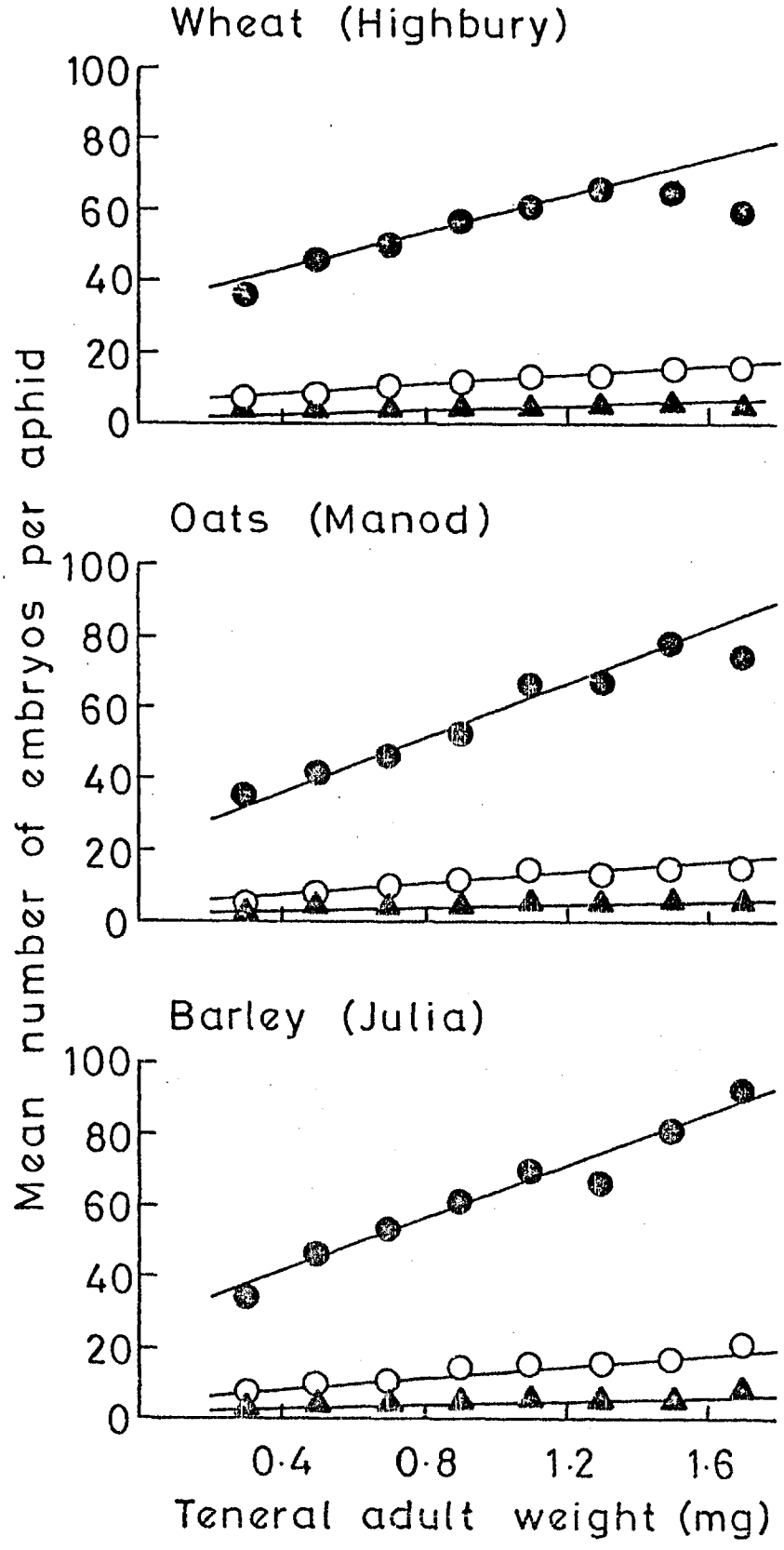


Fig. 25. Regression of embryo content on teneral adult weight in S. avenae. (●) = total no. of embryos; (○) = no. of embryos with pigmented eyespots; (▲) = no. of large embryos.

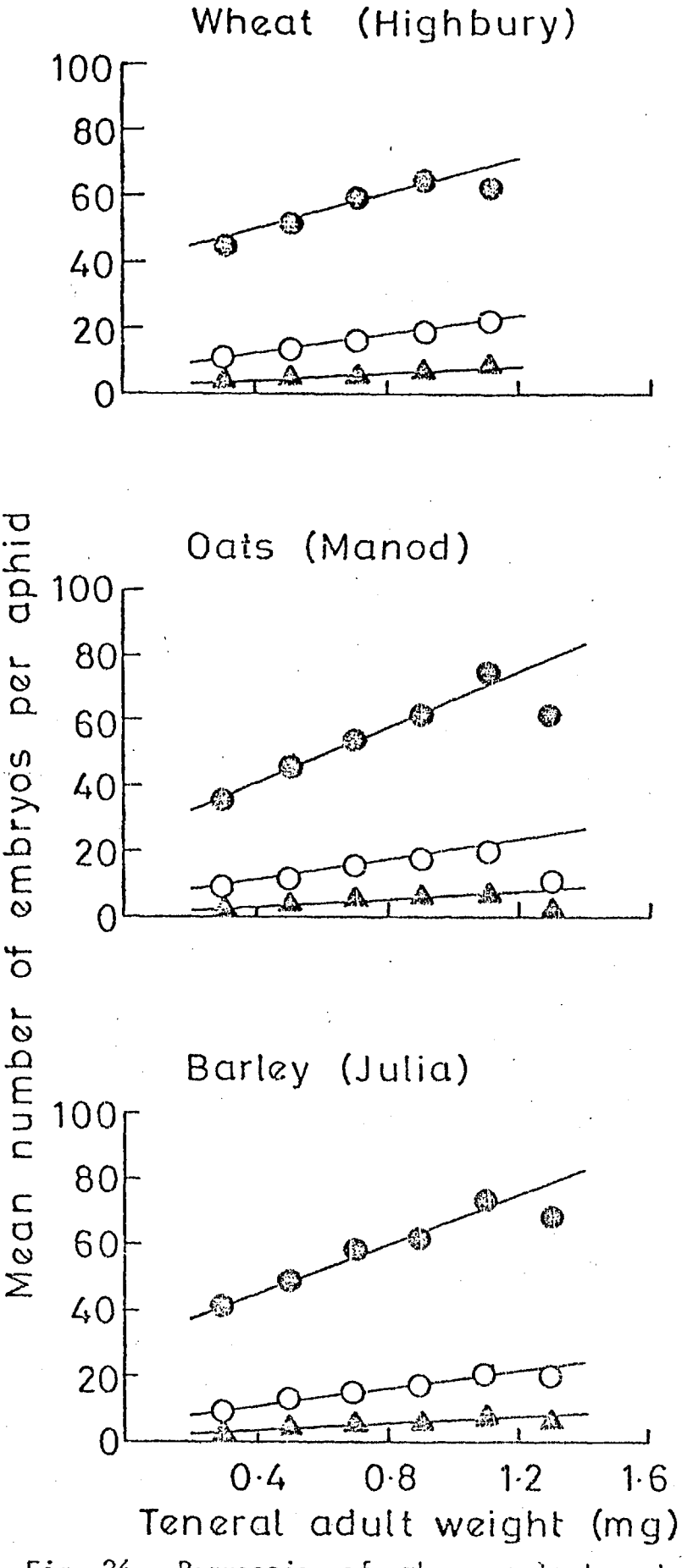


Fig. 26. Regression of embryo content on teneral adult weight in *R. padi*. (●) = total no. of embryos; (○) = no. of embryos with pigmented eyespots; (▲) = no. of large embryos.

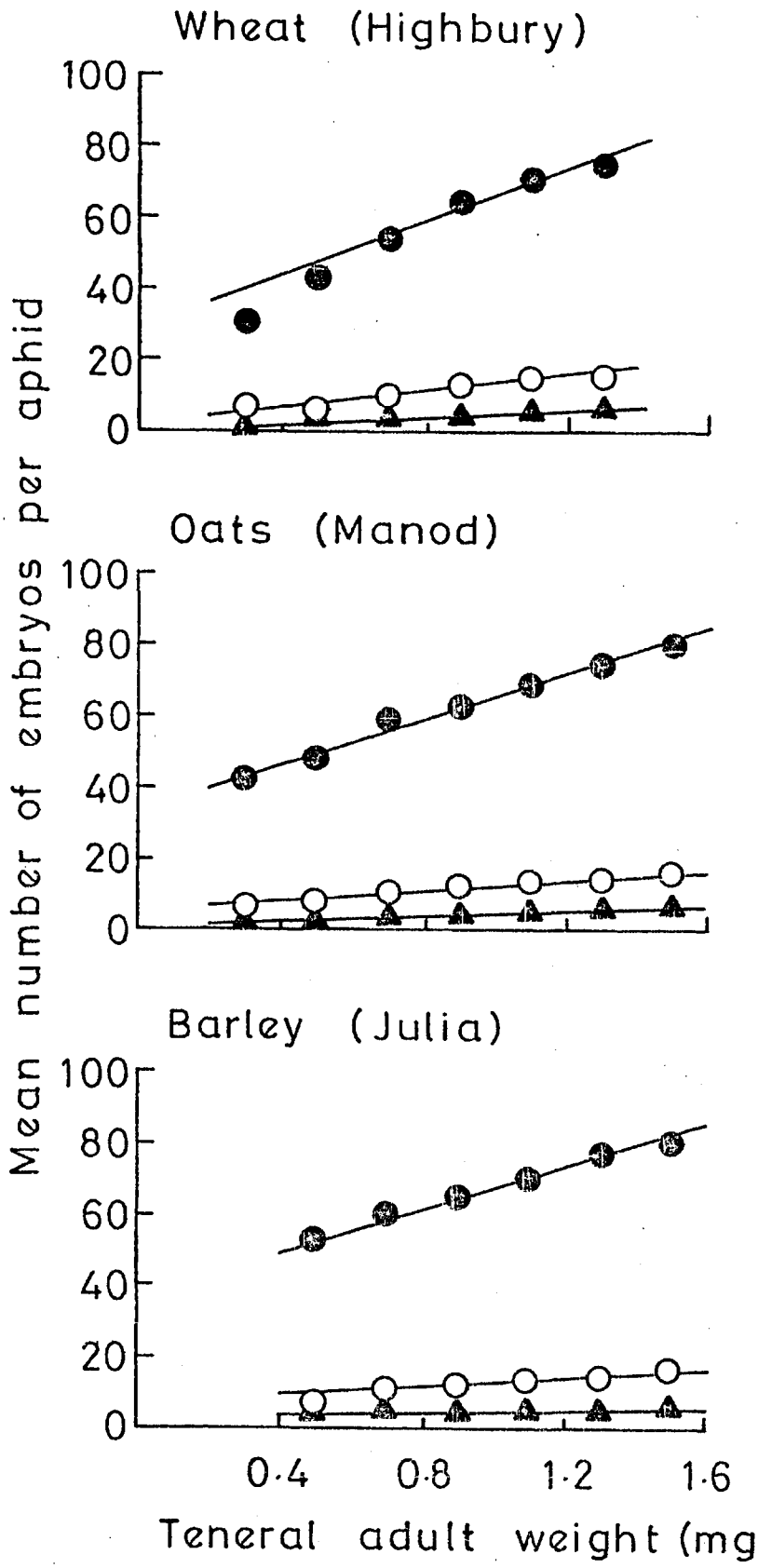


Fig. 27. Regression of embryo content on teneral adult weight in M. dirhodum. (●) = total no. of embryos; (○) = no. of embryos with pigmented eyespots; (▲) = no. of large embryos.

the three crops, but the reverse was the case in S. avenae on oats and in M. dirhodum on the three crops. As it was relatively easier and quicker to identify and count the number of embryos with pigmented eyespots than the total number of embryos, the former was consequently used to measure fecundity, except where otherwise indicated.

The effect of BYDV on aphid size

Individual R. padi fed as nymphs on BYDV-infected excised wheat leaf segments were consistently larger than those fed continuously on virus-free leaves (Fig. 28). The difference in weight became significant at the teneral adult stage ($F = 9.52$, $df = 1/18$, $p < 0.01$) and thereafter ($F = 61.86$, $df = 1/24$, $p < 0.001$). In both sets of aphids, aphid weight increased considerably during the nymphal stages but changed much less after the adult moult, although adult weight fluctuated to a certain extent (Fig. 28).

The size of S. avenae and R. padi was significantly increased overall by BYDV infection of wheat, oats and barley (Tables 12A & B and Figs. 29 & 30), although the differences were not significant at every growth stage. The adult weight of M. dirhodum was significantly increased overall by BYDV on barley, decreased on oats but was unaffected on wheat (Table 12C and Fig. 31). The differences for M. dirhodum were however not significant at any one growth stage.

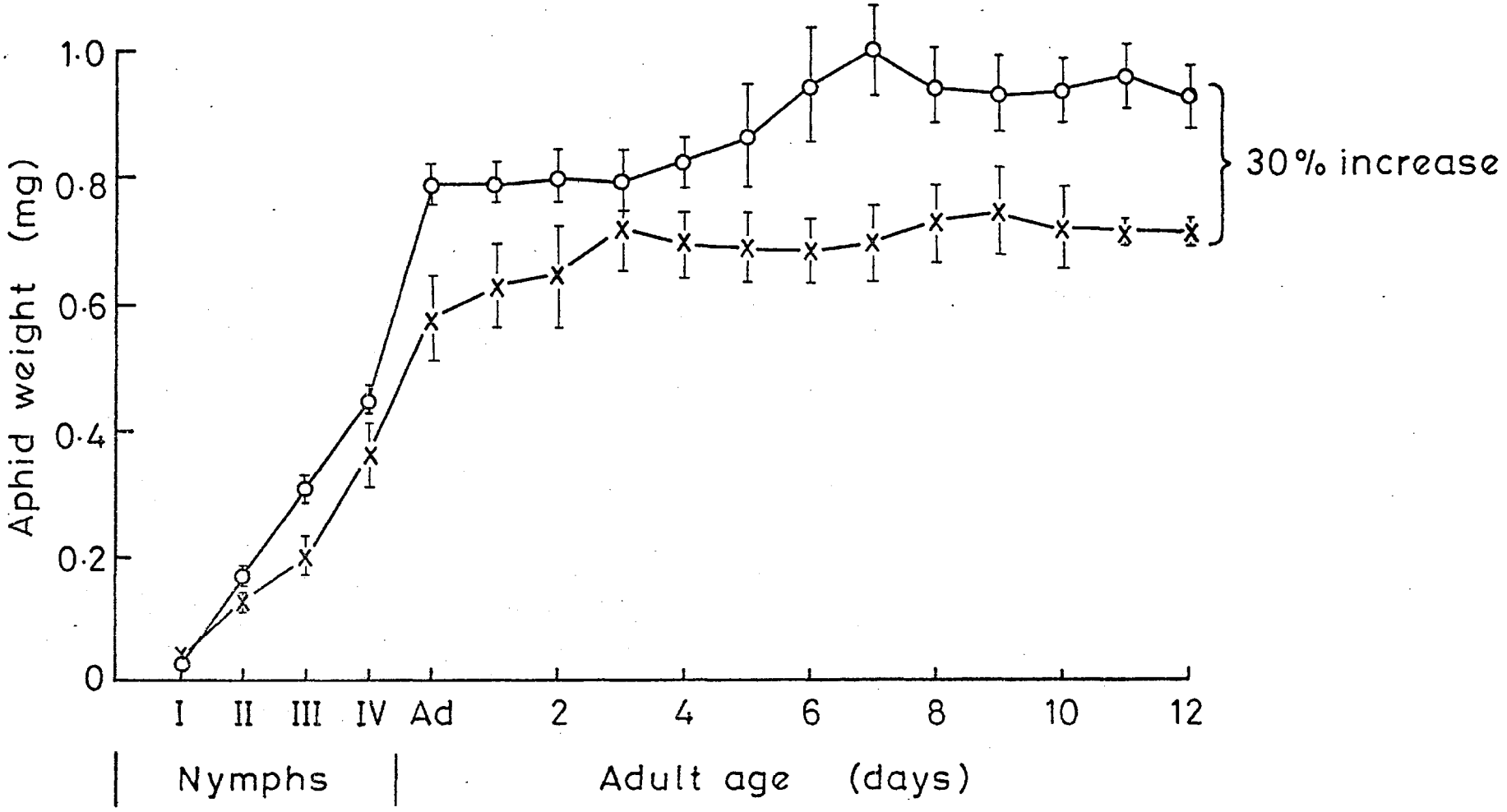


Fig. 28. Nymphal and adult weight of *R. padi* on healthy (×) and BYDV - infected (○) excised wheat leaves.

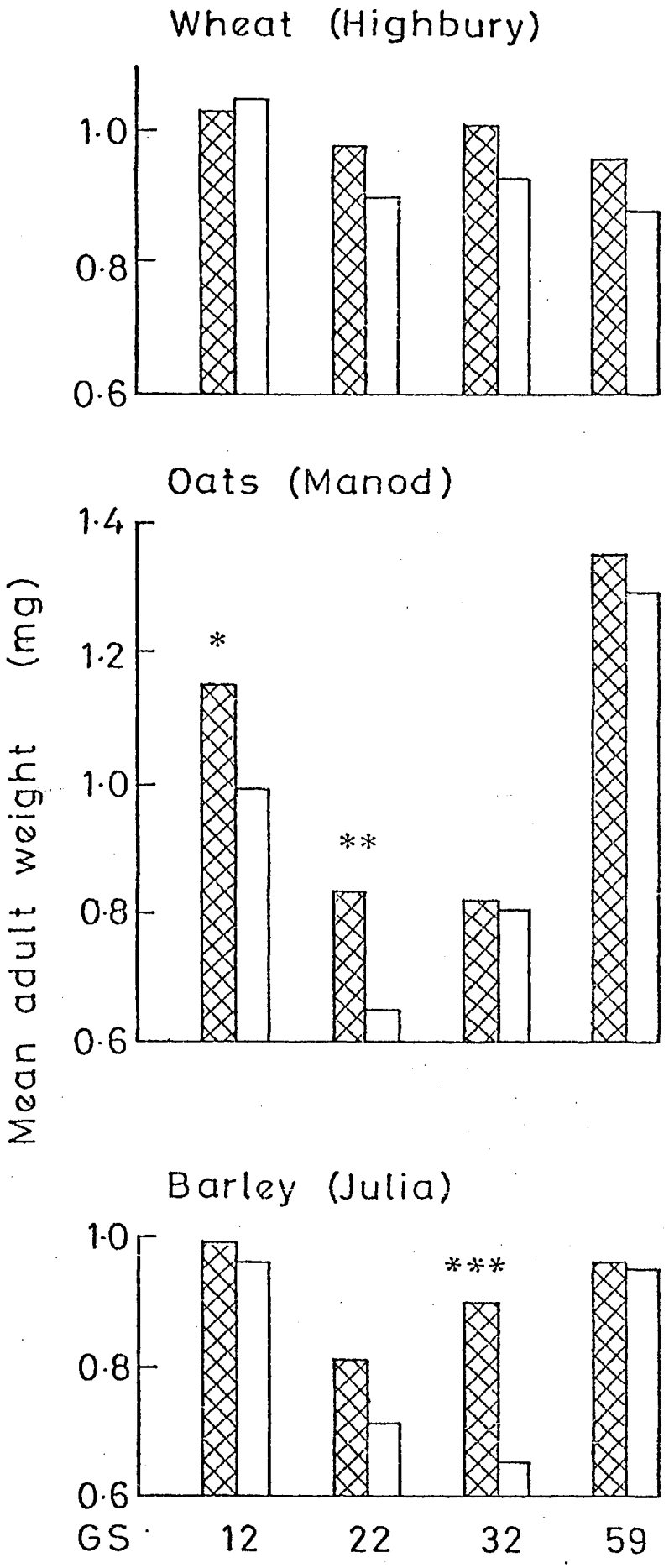


Fig. 29. The teneral adult weight of S. avenae on healthy (□) and BYDV - infected (⊠) plants.

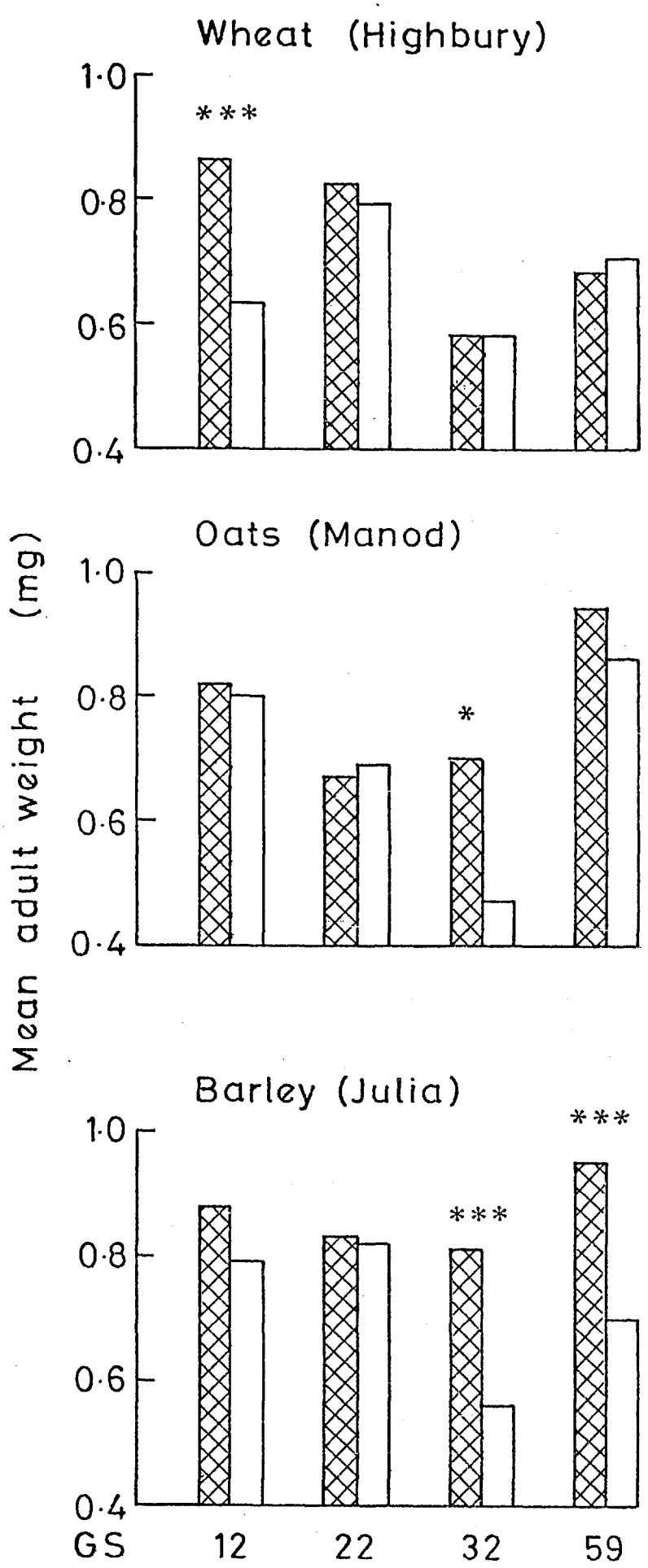


Fig 30. The teneral adult weight of R. padi on healthy (☐) and BYDV - infected (☒) plants.

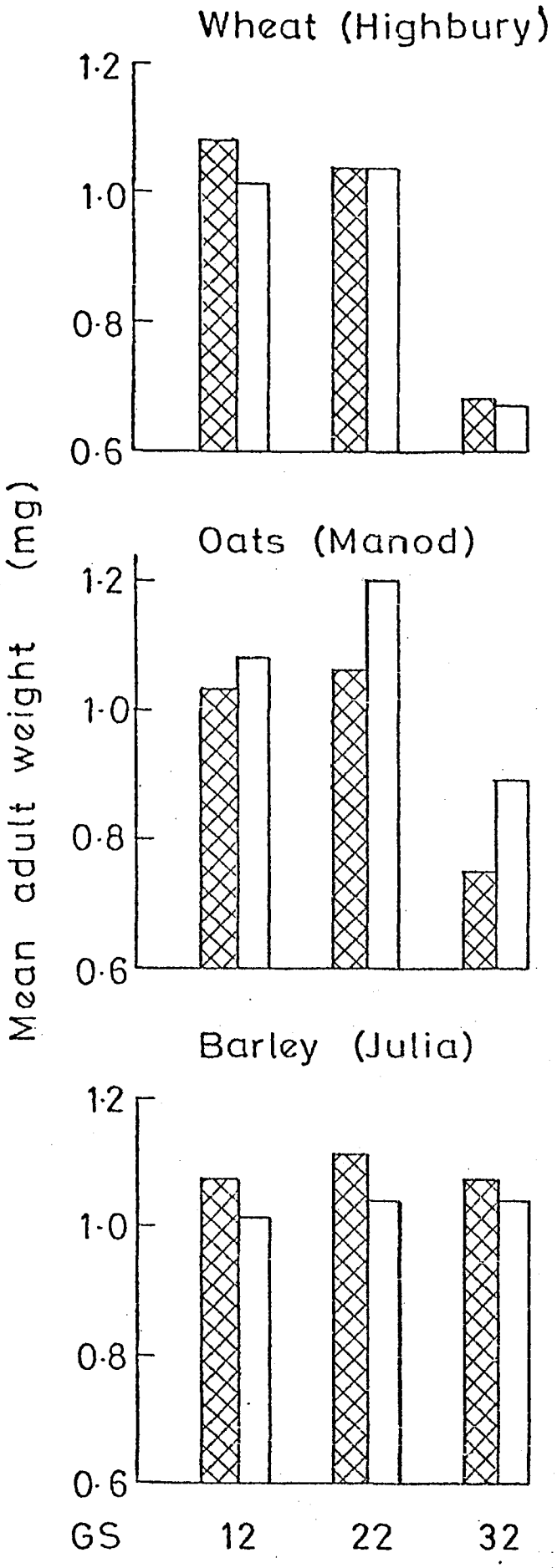


Fig. 31. The teneral adult weight of M. dirhodum on healthy (□) and BYDV - infected (⊠) plants.

The effect of BYDV on fecundity

BYDV infection of the host plant significantly increased the fecundity of S. avenae overall on the three crops (Table 12A and Fig. 32), and that of R. padi on oats and barley but not on wheat (Table 12B and Fig. 33). Virus infection did not alter the fecundity of M. dirhodum on wheat or barley, but decreased it overall on oats (Table 12C and Fig. 34). However, for each aphid species on the three crops, the differences in fecundity attributable to BYDV were not significant at every growth stage.

S. avenae of the same weight contained significantly more embryos with pigmented eyespots when reared on BYDV-infected oats than on healthy oats ($F = 5.21$, $df = 1/236$, $p < 0.05$; Table 13A). Equal sized R. padi were significantly less fecund on diseased wheat and barley than on healthy plants ($F = 10.78$, $df = 1/282$, $p < 0.001$; $F = 6.43$, $df = 1/256$, $p < 0.05$ respectively; Table 13B). Similar sized M. dirhodum had significantly fewer embryos with pigmented eyespots on diseased wheat than on healthy wheat ($F = 10.24$, $df = 1/108$, $p < 0.01$; Table 13C). In all other cases, equal sized aphids of all species were equally fecund on healthy and diseased plants.

The influence of plant growth stage

Except for the weight of M. dirhodum on barley (Table 12C and Fig. 31), teneral adult weight and fecundity in the three aphid species varied significantly between plant growth stages (Tables 12A - C and Figs. 29 - 34).

Table 12: Summary of the analysis of variance - F values

Parameter		Crop		
		Wheat	Oats	Barley
A. S. avenae (apterae)				
Aphid weight	Plant GS	3.91 **	61.56 ***	12.03 ***
	Treatment †	5.24 *	9.50 **	7.67 **
	Interaction	0.68 NS	1.82 NS	2.52 NS
No. of embryos with pigmented eyespots	Plant GS	24.22 ***	25.78 ***	24.76 ***
	Treatment	14.07 ***	21.81 ***	4.87 *
	Interaction	6.83 ***	8.94 **	2.83 *
B. R. padi (apterae)				
Aphid weight	Plant GS	28.13 ***	42.77 ***	19.33 ***
	Treatment	17.18 ***	24.83 ***	71.17 ***
	Interaction	11.87 ***	11.65 ***	8.20 ***
No. of embryos with pigmented eyespots	Plant GS	57.09 ***	100.53 ***	59.82 ***
	Treatment	0.47 NS	9.59 **	23.25 ***
	Interaction	0.82 NS	11.31 ***	5.00 **
C. M. dirhodum (apterae)				
Aphid weight	Plant GS	43.69 ***	14.38 ***	0.68 NS
	Treatment	1.85 NS	7.27 **	4.19 *
	Interaction	0.44 NS	0.80 NS	0.10 NS
No. of embryos with pigmented eyespots	Plant GS	118.23 ***	40.60 ***	39.96 ***
	Treatment	1.05 NS	6.23 *	0.04 NS
	Interaction	0.90 NS	0.71 NS	2.87 NS

† Treatment = the effect of BYDV infection

Table 13: The effect of BYDV on the embryo content of S. avenae, R. padi and M. dirhodum on wheat, oats and barley.

Aphid + crop species	Treatment	No. of embryos with pigmented eyespots/aphid Size of aphid (mg)		
A. S. avenae (apterae)		0.5	1.0	1.5
Wheat	Healthy	9.07	12.06	15.06
	Diseased	8.63	12.42	16.22
Oats	Healthy	7.98	11.45	14.93
	Diseased	8.31	12.18	16.06
Barley	Healthy	8.56	12.83	17.10
	Diseased	8.83	13.21	17.59
B. R. padi (apterae)				
Wheat	Healthy	13.97	21.31	28.66
	Diseased	12.37	20.48	28.59
Oats	Healthy	7.32	16.84	26.37
	Diseased	14.33	16.88	19.44
Barley	Healthy	12.25	20.28	28.32
	Diseased	11.86	18.64	25.42
C. M. dirhodum (apterae)				
Wheat	Healthy	9.60	14.30	19.00
	Diseased	6.99	12.72	18.45
Oats	Healthy	7.03	13.20	15.87
	Diseased	8.66	12.51	16.37
Barley	Healthy	10.55	12.92	15.29
	Diseased	8.06	12.02	15.99

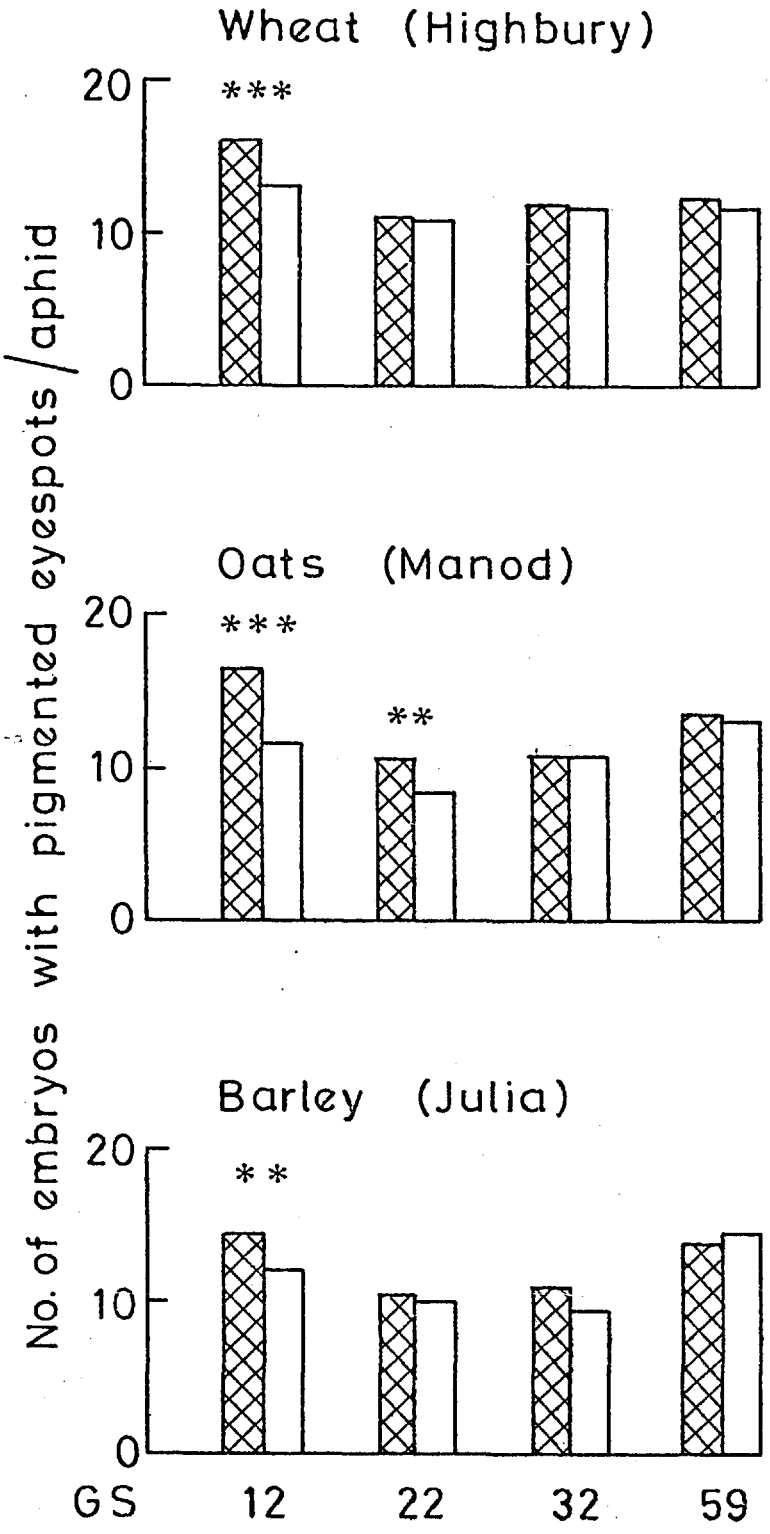


Fig. 32. The number of embryos with pigmented eyespots in S. avenae on healthy (□) and BYDV - infected (⊠) plants.

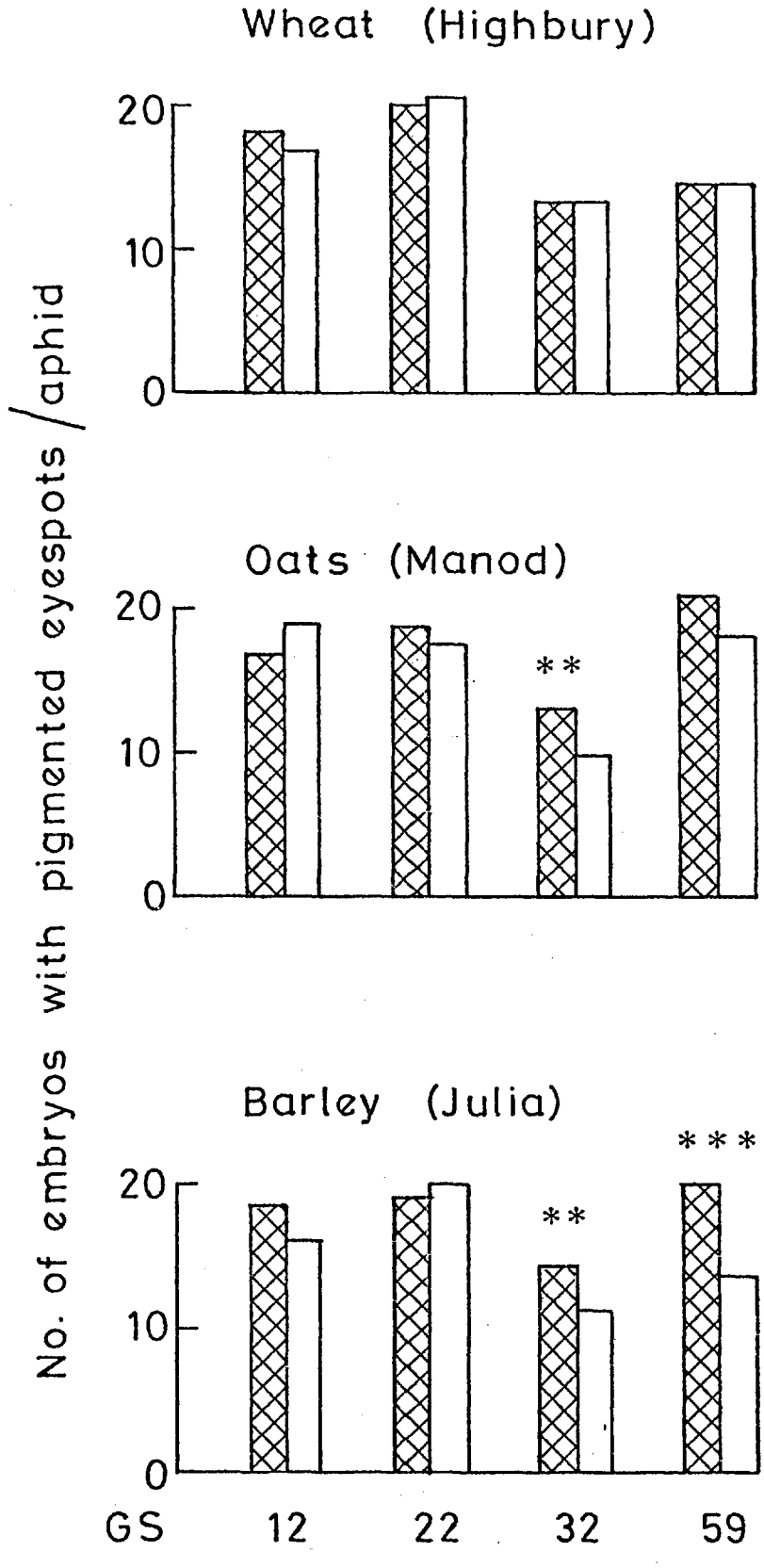


Fig. 33. The number of embryos with pigmented eyespots in R. padi on healthy (□) and BYDV - infected (▨) plants.

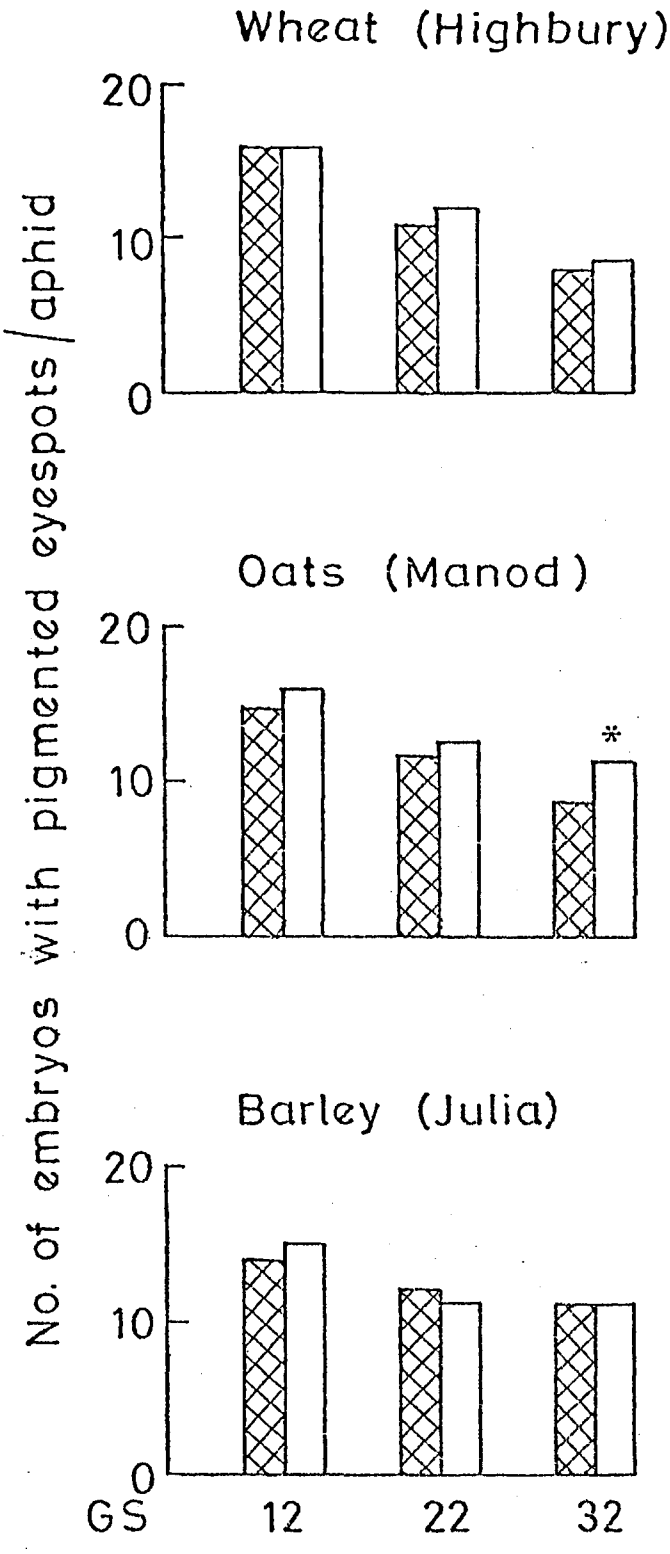


Fig. 34. The number of embryos with pigmented eyespots in M. dirhodum on healthy(□) and BYDV- infected (▨) plants.

The aphids were heaviest and most fecund mainly at the seedling (GS 12) and earing (GS 59) growth stages, while the lowest weights and fecundity were achieved either at tillering (GS 22) or stem elongation (GS 32).

The effect of BYDV on the rate of reproduction

After twenty days the cumulative reproduction of S. avenae was higher on BYDV-infected wheat ($F = 7.76$, $df = 7$, $p < 0.05$) and barley ($F = 20.56$, $df = 7$, $p < 0.01$) than on healthy plants (Fig. 35A). Aphids feeding on diseased wheat plants had 4.17% of their total embryo content still unborn after twenty days, compared with 10.60% on healthy wheat. On diseased barley, S. avenae had 3.05% of their total complement of embryos left unborn compared with 16.15% on healthy barley ($F = 5.97$, $df = 7$, $p < 0.05$). The sum of progeny and unborn embryos was significantly higher on infected wheat ($F = 8.89$, $df = 7$, $p < 0.05$) and barley ($F = 17.13$, $df = 7$, $p < 0.01$) than on healthy plants.

The cumulative reproduction of M. dirhodum after 20 days was not significantly altered by BYDV infection of wheat ($F = 1.17$, $df = 19$, NS) or barley ($F = 0.01$, $df = 25$, NS) (Fig. 35B). The data for oats were not analysed due to the poor survival of the test aphids, but they did not indicate any significant effect of virus on the reproduction of M. dirhodum.

Until the seventh day of adult life, BYDV did not affect the reproduction of R. padi on excised leaves but thereafter, aphids that fed as nymphs on BYDV-infected leaves produced more progeny (Fig. 35C), although the difference was not significant even after 18 days.

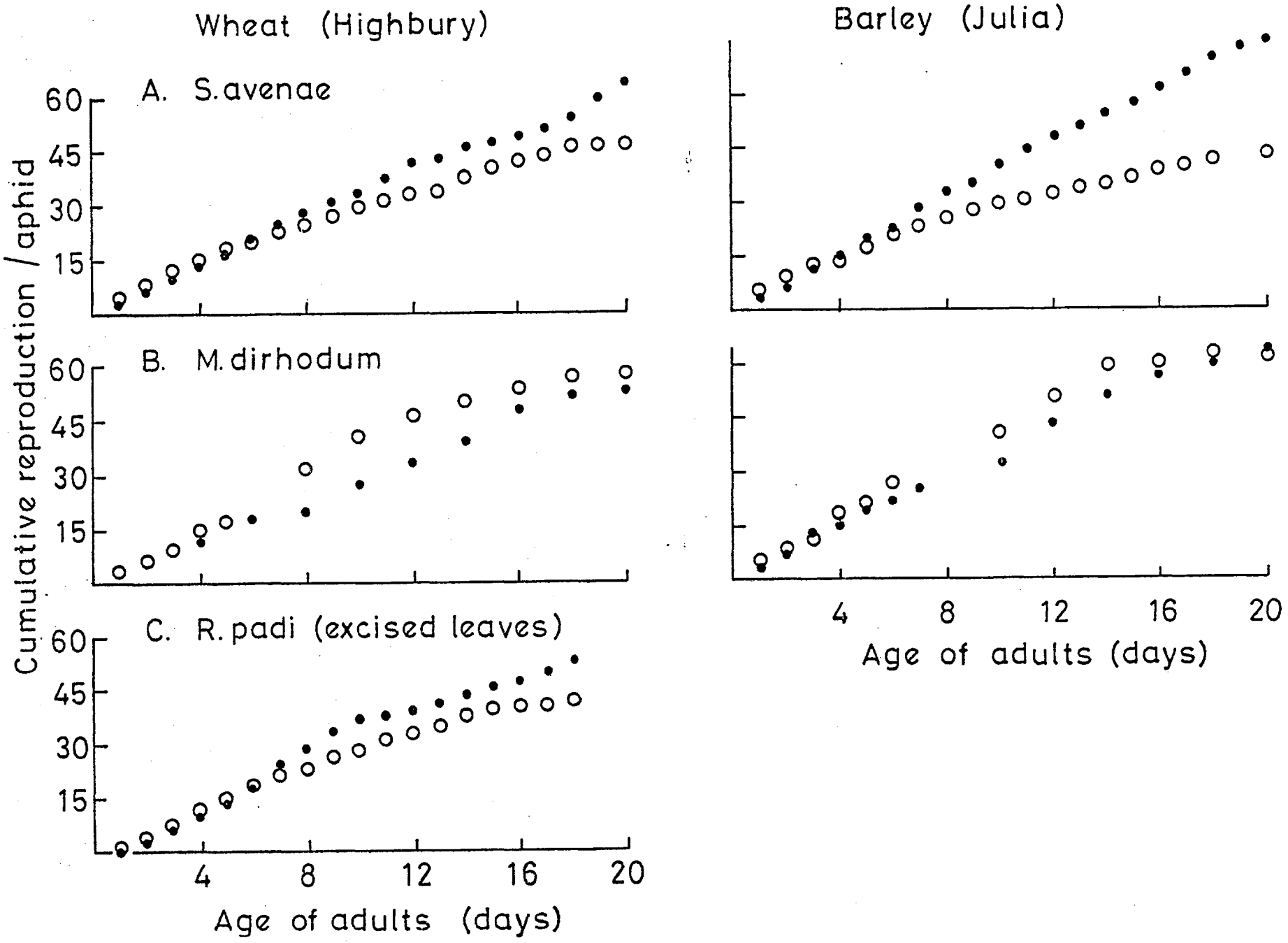


Fig. 35. The reproduction of S. avenae, M. dirhodum and R. padi on healthy (○) and BYDV - infected (●) tissue.

B. Field Observations

Caged apterous S. avenae contained significantly more (total) embryos on virus-infected wheat than on healthy wheat ($F = 11.84$, $df = 1/8$, $p < 0.01$). All the aphids collected on naturally-infested ears were alates. They too had more total embryos ($F = 10.48$, $df = 1/32$, $p < 0.01$), embryos with pigmented eyespots ($F = 4.38$, $df = 1/32$, $p < 0.05$), and large embryos ($F = 6.42$, $df = 1/32$, $p < 0.05$) on diseased than healthy wheat (Table 14).

Table 14: The embryo content of S. avenae on wheat (Flanders) in the field.

	Total		With pigmented eyespots		Large	
	Di	He	Di	He	Di	He
Apterae	93.40± 1.78	79.50± 1.85	-	-	-	-
Alatae	64.71± 0.97	60.06± 1.00	16.00± 0.78	11.13± 0.83	5.47± 0.49	3.82± 0.40

DISCUSSION

Aphid size and fecundity

The fecundity of S. avenae, R. padi and M. dirhodum was found to be highly positively correlated with teneral adult weight on both healthy and BYDV-infected plants irrespective of the crop species or plant growth stage. Similar significant correlations between adult weight and fecundity have been recorded previously for S. avenae (Watt, 1979; Wratten 1977), R. padi (Dewar, 1977; Dixon, 1976; Wellings et al, 1980), M. dirhodum (Dewar, 1977; Wratten, 1977) and several other aphid species (Dixon, 1970; 1971; Dixon & Dharma, 1980 a,b; Dixon & Wratten, 1971; Murdie, 1969; Taylor, 1975). This has prompted Dewar (1977) to suggest the use of teneral adult weight to predict an aphid's subsequent reproductive performance. However, Vickerman and Wratten (1979) have pointed out that the use of aphid weight is valid only if the age of the aphid can be precisely determined. This study has shown that althoygh much of the changes in weight occurred during the nymphal stages in R. padi, adult weight also increased and fluctuated to some degree (Fig. 28). Weight has been shown to increase after the teneral adult stage in other aphids such as Drepanosiphum platanoides (Schr.) (Dixon, 1975) and Acyrthosiphon pisum (Harris) (Mackay & Downer, 1979) and this may be of general occurrence in aphids. As a reliable index, the teneral adult weight would therefore be more appropriate than any other weight measurement as it can be more accurately determined. In view of the

difficulty in ascertaining the precise age of an aphid in the field, however, the use of teneral aphid weight would be more suited for laboratory studies, such as those reported here.

The effect of BYDV on the size of aphids has not previously been reported. BYDV was found in this study to increase the adult weight of S. avenae and R. padi on wheat, oats and barley, and to increase that of M. dirhodum on barley while decreasing it on oats. It has been established that aphids can discriminate between variations in dietary amino acids and carbohydrates, and select the concentrations optimum for their growth and development (see review by Auclair, 1963; also Auclair, 1965). BYDV infection increases the concentrations of these substances in the tissues of infected plants relative to healthy ones (Goodman et al, 1965; Jensen, 1969, 1972; Markkula & Laurema, 1964; Orlob & Arny, 1961; Watson & Mulligan, 1960). Aphids feeding on diseased plants should therefore be better nourished and attain a larger adult size than those on healthy plants. However, it is not clear why BYDV affected the three aphid species differently, or why it increased the adult weight of M. dirhodum on barley but decreased it on oats. It is possible that the aphids prefer different optimal concentrations of nutrients or that different substances are limiting to their biological performance. It is equally possible that the increases by BYDV infection in the concentrations of individual amino acids and

carbohydrates vary between the crops thereby affecting the proportional balance of the nutrients. However, information is not available to clarify these possibilities.

Progeny counting is both time consuming and prone to large variability mostly resulting from poor survival of test individuals. Embryo counting has the advantages of speed and low variability (Adams & van Emden, 1972). Although a count of the total embryo content, the number of embryos with pigmented eyespots or the number of large embryos could adequately indicate the potential reproductive capacity of these aphids, it was much easier and quicker to identify and count embryos with pigmented eyespots than other categories. In addition, the total number of embryos can only be counted on a perfect dissection. Dixon and Dharma (1980b) have also hinted at the difficulty in identifying and counting embryos, especially the smallest ones, in Aphis fabae.

The findings in this study that BYDV increased the embryo content of S. avenae and R. padi on oats confirms the earlier reports by Miller (1962), Miller and Coon (1964) and Elamin (1975) for S. avenae, and by Markkula and Laurema (1964) and Elamin (1975) for R. padi. The results also agree with Elamin's (1975) report that BYDV decreases the fecundity of M. dirhodum on oats. Conversely, Markkula and Laurema (1964) found that the virus had no effect on the fecundity of S. avenae and M. dirhodum on young oats leaves, and Elamin (1975) showed that the fecundity of S. avenae on young diseased oats leaves was decreased.

The apparent discrepancies have probably arisen from differences in the varieties of oats studied (eg. Elamin, 1975), the nature of the virus isolates used, the method of assessing fecundity, and the growth stages of the test plants both at inoculation and during the fecundity studies. As this study shows, the effect of BYDV on the adult weight and fecundity of the aphids varied considerably between growth stages.

Fecundity was increased overall in S. avenae on wheat and barley, but on barley alone in R. padi. Whereas R. padi is known to prefer barley to wheat or oats (Adams & Drew, 1964; Dean, 1972; Îto, 1960; Rautapää, 1976; Rautapää & Uoti, 1976), the host preference of S. avenae is less clear. Dean (1972), Orlob and Medler (1961) and Rautapää (1970) found that S. avenae performed best on barley under controlled conditions whereas, in the field, it was more common on wheat and oats than on barley (Dean & Luuring, 1970). In addition, S. avenae was reportedly more successful on wheat than on barley (Îto, 1960) or showed no preferences between barley, oats and wheat (Apablaza & Robinson, 1967). It therefore appears that S. avenae does well on the three crops, although there might be varietal differences (eg. Bruehl, 1961; Kolbe, 1969; Latteur, 1976; Rautapää, 1970).

From the results presented here, it is apparent that the nutritional changes induced by BYDV infection do not affect the order of preference of the aphids for the three crops. Elamin (1975) similarly detected no significant alteration in the susceptibility of oats and wheat varieties to S. avenae, R. padi and M. dirhodum following infection with BYDV, and Gill and Metcalfe (1977) showed that BYDV infection did not change the relative resistance of several barley varieties to Rhopalosiphum maidis.

The results indicate that BYDV raises the fecundity of cereal aphids by increasing their adult weight, since increases in adult weight were almost always accompanied by increases in embryo content and since aphids of the same weight were not always more fecund on diseased plants. However, in certain cases such as with R. padi on wheat and M. dirhodum on barley, weight increases did not confer higher fecundity on the aphid. In the case of R. padi, the milder symptoms of BYDV on most wheat varieties relative to oats and barley (Jensen et al, 1971) could cause less severe biochemical changes, insufficient to alter significantly the aphid's fecundity. Conversely, although BYDV symptoms are quite severe on barley, either the balance of nutrients consequent on BYDV infection does not affect the fecundity of M. dirhodum, or the response of M. dirhodum to the nutritional changes induced in

plants by the virus probably differs from those of R. padi and S. avenae. In neither case is there appropriate information for clarification.

It is important that the field results confirmed the laboratory observation that BYDV infection of wheat increased the embryo content of S. avenae, in view of the usual and justified criticism of the applicability of the results of laboratory experiments to the field situation (eg. Vickerman & Wratten, 1979).

Reproduction

In the progeny count studies, S. avenae gave birth to more progeny and a higher proportion of their total embryo content within 20 days on diseased than on healthy wheat and barley, thereby indicating a more rapid rate of maturation of embryos on the diseased plants. Neither the reproductive rate of M. dirhodum on wheat and barley nor that of R. padi on excised wheat leaf segments was altered by BYDV after 20 and 18 days respectively. The progeny count and embryo count methods of estimating the effect of BYDV on reproductive performance in these aphids are therefore in agreement. This fact further validates the counting of embryos instead of progeny to indicate the aphids' potential reproductive capacity as discussed earlier. Positive correlations between embryo content and reproduction have previously been recorded in S. avenae and M. dirhodum (Wratten, 1977) and in Aphis fabae (Dixon & Wratten, 1971; Honeyborne, 1969).

Leaf excision did not alter the effect of BYDV infection of wheat on the reproductive rate of R. padi as may be expected since detached leaves are in general more

acceptable than undetached leaves to aphids (eg. Farkas et al, 1964; Kennedy, 1958; Mackinnon, 1961). Excised leaves resemble senescing tissue physiologically and senescing leaf tissue is more acceptable to aphids than mature foliage. Although excised leaves would also show differences in aphid fecundity following BYDV infection (eg. Miller, 1962; Miller & Coon, 1964, and this study), several factors discouraged its use in the present study. The physiological changes that occur in excised leaves may actually reverse the susceptibility for aphids of the tissue as part of the whole plant (eg. Müller, 1966). Secondly, special care was needed to minimize contamination of the filter paper and leaf segments by fungi. In addition, the excision and routine changing of the latter may affect the performance of the aphids (Adams & van Emden, 1972).

SUMMARY

Laboratory and field experiments were conducted to investigate the effect of BYDV infection of wheat, oats and barley on the adult weight and fecundity of S. avenae, R. padi and M. dirhodum. Fecundity was measured by counting the number of embryos in teneral adults and by recording the aphids' rate of reproduction for three weeks. Both methods gave similar results but embryo counting was preferred for its speed and low variability.

Large individuals of each aphid species contained more embryos than smaller ones whichever method of counting them was used, but counting the number of embryos with pigmented eyespots was preferred for ease of identification and counting.

BYDV infection of the host plant increased teneral adult weight in S. avenae and R. padi on the three crop species. In M. dirhodum, adult weight was increased on barley, decreased on oats but was unaffected on wheat.

BYDV increased fecundity in S. avenae on the three crops and in R. padi on oats and barley but not on wheat. The fecundity of M. dirhodum was unaffected by BYDV infection of barley and wheat but it was decreased on oats. Aphids of equal weight were rarely more fecund when reared on BYDV-infected plants than on healthy plants.

SECTION 4

THE EFFECTS OF BARLEY YELLOW DWARF VIRUS AND APHID HONEYDEW ON CLADOSPORIUM

INTRODUCTION

Observations by the Aerial Photography Unit of the Agricultural Development and Advisory Service (ADAS) in 1976 indicated that plants in the foci of BYDV infection in early-sown winter wheat were more heavily blackened (Fig. 36) by mould fungi than the surrounding virus-free crop (Hooper, 1978). It was not certain, however, if this enhanced blackening was due to the honeydew produced by the higher population of aphids in these foci, or to some other effect connected with the virus.

Alternaria and Cladosporium are among the most common species of sooty mould fungi which colonize the ears of some cereal crops (Lacey et al, 1972; Lacey, 1974; Lacey & MaClean, 1978; Mehrotra & Dwivedi, 1980), and in most years, Cladosporium is the predominant species (Hill, 1979; Hyde,1951; Lacey, 1974; Lacey & MaClean, 1978; Mais, 1979). BYDV-infected plants support higher populations of aphids in the field than healthy ones (Section 1) and are probably also covered with more aphid honeydew. The experiments reported here were conducted to investigate the interactions between BYDV, aphid honeydew and Cladosporium and certain other microflora on cereals.

MATERIALS AND METHODS

Field Experiments.

1979

The plots of winter wheat (Flanders) in which aphid



A B

Fig. 36. Ears of wheat (Flanders)
Set A are from BYDV-free plants
Set B are from BYDV-infected plants



Fig. 38. Potato dextrose agar (PDA) plates showing greenish/black colonies of Cladosporium spp. Dilution rates were:

10^{-7} 10^{-4}

10^{-3} 10^{-2}

populations were monitored in 1979 (Section 1) were also used in this study.

At the milky growth stage (GS 73) in July, 1979, all the ten plots were sprayed with a suspension of Cladosporium spores in sterilized water at the rate of 2,000 spores/ml, using a hand-operated sprayer. Each plot received approximately 10^4 spores.

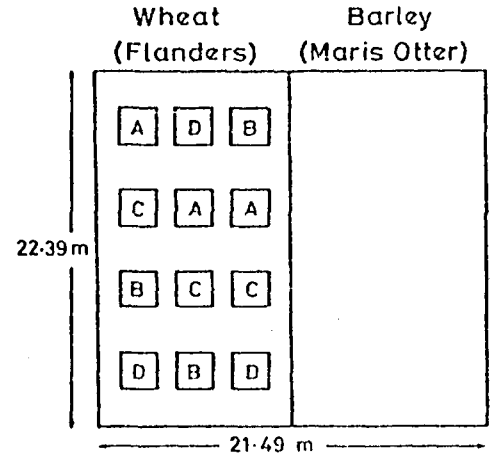
Starting one week after inoculation and thereafter until harvest, random weekly samples of 5 - 10 ears were taken from each plot and placed carefully inside polythene bags. These were sealed and kept in a cold room (-8°C) until examination. Sampling was done at the same time (0900 hrs) on each occasion and the ears were cut with at least five inches of the stem for ease of handling and to minimize cross-contamination between samples during weighing operations.

1980

Plots of winter wheat (Flanders) and barley (Maris Otter), whose location, dimensions and layout were similar to those described in Section 1 (1980 experiments), were used in 1980 (Fig. 37). The experimental design was randomized blocks, and there were four treatments as follows:

1. Weekly sprays with pirimicarb (0.41 g ai/l) from stem elongation (GS 30) until crop ripening (GS 94) (Aphids and BYDV absent).
2. Weekly sprays with pirimicarb from GS 30 until the earing stage (GS 55) then infested with approximately 5 S. avenae per ear (Aphids present, BYDV absent).
3. Inoculated with BYDV at the seedling stage (GS 14) and sprayed weekly with pirimicarb from GS 30 until

Plot layout for studies on the effect of BYDV infection of winter wheat and barley on the incidence of Cladosporium sooty mould. Long Hoos. 1980



Treatments
- A No BYDV; Weekly aphicide
- B No BYDV; Aphids introduced
- C BYDV introduced; Weekly aphicide
- D BYDV and aphids introduced

Relation of plots to discards

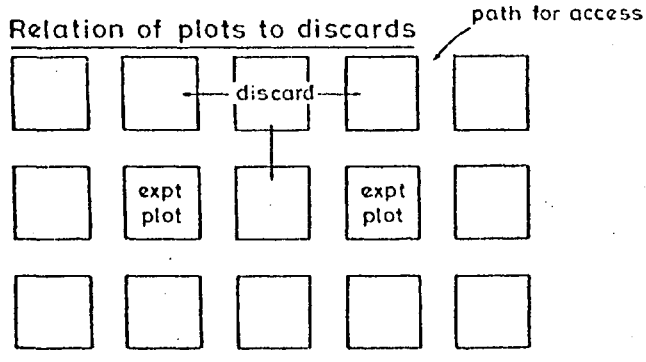


Fig. 37.

GS 94 (Aphids absent, BYDV present).

4. As in 3 but also infested with 5 S. avenae per ear at GS 55 (Aphids and BYDV present).

Artificial inoculations with BYDV were done as described earlier (Section 1). Infestation at GS 55 was achieved by attaching aphid-bearing leaf segments of wheat or barley onto the ears. The aphids were obtained from glasshouse cultures which had been started with virginoparae collected from the field in 1980. All the plots were sprayed with equal amounts (4.8×10^9 spores/plot) of a suspension of Cladosporium spores (2.4×10^9 spores/ml) in sterilized water on 18.6.80 (wheat GS 69, barley GS 71). Weekly samples of ears were taken from each plot beginning on 25.6.80 (one week after inoculation) and thereafter until 13.8.80 (GS 94), stored inside polythene bags in a cold room at $-8^{\circ}C$, and examined in the laboratory within 24 hours of sampling.

Examination in the laboratory

The fungus content of the ears was assessed in the laboratory by the dilution plating technique. Potato dextrose agar (PDA) containing benzyl penicillin (20 units/ml) and streptomycin sulphate (40 units/ml) was used throughout the study. From each plot, 10g of ear material was added to 90ml of 0.1% tap water agar in a Stomacher bag, allowed to soak for 20 minutes and then comminuted in a Colworth Stomacher (A.J. Seward Ltd., London). From this initial suspension, tenfold dilutions were made down to 10^{-7} in a sterile culture room, using McCartney bottles, an automatic pipette (Gilson, France) and disposable 1ml pipette tips.

The contents of each bottle were shaken vigorously for 15 seconds before the next dilution. At each transfer, the pipette tip was flushed three times with the suspension in order to minimize discrepancies in the volume transferred (Hornby, 1969; Wieringa, 1958).

Beginning with the most dilute, 0.2ml of each test dilution was placed onto three plates of PDA which had solidified overnight in 9cm plastic petri dishes. The suspensions were spread out evenly over the plates with bent pasteur pipette spreaders which were disposed of after each sample. Sufficient time was allowed for the suspensions to be absorbed onto the surface of the agar (about 12 hrs) and the plates were inverted and incubated at 25^{o}C for 5 days. The numbers of colonies of Cladosporium and, in 1980 only, other microflora growing on each plate were then counted under a binocular microscope. From this the number of viable propagules of each micro-organism per gram of ear material was calculated for each plot.

The microflora were identified with the aid of the Illustrated genera of imperfect fungi (Barnett & Hunter, 1972) and Dematiaceus Hyphomycetes (Ellis, 1971).

Yield Measurements

At harvest (18.8.80), measurements were made on six parameters of yield (see Table 20) in all the plots. Straw length was measured from the soil to the base of the ear.

Glasshouse Experiment.

The effect of aphid honeydew on the infection of wheat plants by Cladosporium was further tested under

controlled conditions in a glasshouse. The brown form of S. avenae and potted spring wheat (Highbury) plants obtained from glasshouse cultures (see pages 39 - 41) were used for the experiment. Glasshouse conditions were as described earlier. There were four treatments as follows:

1. Wheat plants were protected from aphids by soil application of a systemic insecticide (Aldicarb granules) at ear emergence (GS 55) (No aphid or aphid honeydew).
2. As in 1 but plants were attached to aphid-infested plants to collect honeydew shooting off the aphids (Honeydew without aphids).
3. Wheat ears were infested at ear emergence with 1 apterous virginoparous S. avenae per ear without a cage (Honeydew from a low aphid infestation).
4. Wheat ears were infested at ear emergence with 5 apterous virginoparae of S. avenae per ear without a cage (Honeydew from a high aphid infestation).

There were 40 fertile tillers per treatment. Plants in each treatment were sprayed at the beginning and end of flowering (GS 61 & 69) and at the early milky stage (GS 75) with equal amounts (20 ml) of a suspension of Cladosporium spores in sterilized distilled water (2×10^9 spores/ml). The plants were also sprayed with equal amounts (20ml) of distilled water, 24 hours after the second inoculation with Cladosporium, in order to encourage the germination and development of the fungus. At crop ripening (GS 94), the ears were removed and their content of Cladosporium was enumerated by the dilution plating technique. Flag leaf samples from each

treatment were similarly examined for the incidence of Cladosporium.

RESULTS

Some dilution rates (eg. 10^{-2}) contained too many and others (eg. 10^{-5} - 10^{-7}) too few colonies for reliable counting (Fig. 38). With experience all counts were therefore made at 10^{-4} (1979) or 10^{-3} (1980) dilution rates which gave the most consistent results.

Micro-organisms isolated

Apart from Cladosporium spp, (C. herbarum and C. cladosporioides), other microflora colonizing the plates included Aureobasidium sp. Hyalodendron sp., Verticillium sp, pink yeasts and white yeasts. Colonies of Alternaria were rarely observed and then only at the lowest dilution rates.

The effect of BYDV on Cladosporium

In 1979, although the overall difference was not statistically significant ($F = 2.01$, $df = 1/148$, NS) (Table 15), there was consistently more Cladosporium on the ears of BYDV-infected wheat plants than on healthy ones, except on 31.7.79 (Fig. 39A). More Cladosporium was recovered from the ears in 1980 than in 1979 possibly because of the lower fungal inoculum applied in 1979 and also due to the dry spell that occurred around the time of inoculation in 1979 (Fig. 39B).

In 1980, significantly more Cladosporium developed on the ears of BYDV-infected wheat ($F = 45.26$, $df = 1/48$, $p < 0.001$) (Fig. 40A) and barley ($F = 40.13$, $df = 1/48$, $p < 0.001$) (Fig. 40B) than on healthy plants over the 8 weeks of sampling.

Table 15: The effect of BYDV on Cladosporium on wheat in the field, 1979

Treatment	Mean no. (Log_e +0.5) of viable propagules/g ear		SED (148 df)
	Healthy control	BYDV	
	3.58	5.17	1.13

Table 16: The effect of BYDV on the total microflora on wheat and barley in the field, 1980

Treatment	Mean no. (Log_e +0.5) of viable propagules/g ear		SED (30 df)
	Healthy control	BYDV	
A. Wheat			
Sampling date			
9.7.80	14.27	14.03	0.24
16.7.80	13.83	14.15	
23.7.80	13.79	14.40	
7.8.80	14.28	15.22	
14.8.80	14.54	15.06	
B. Barley	14.32	14.85	0.14

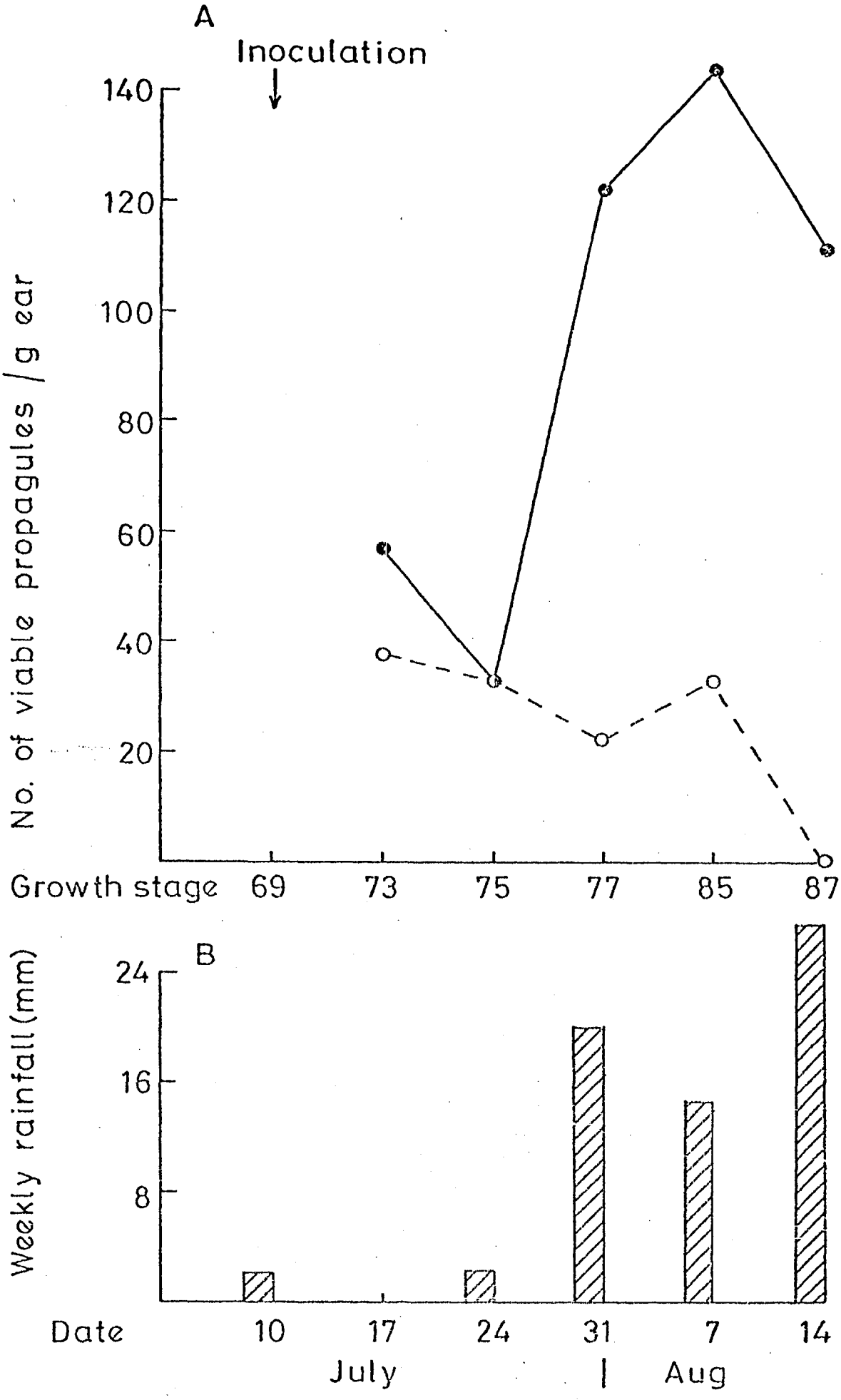
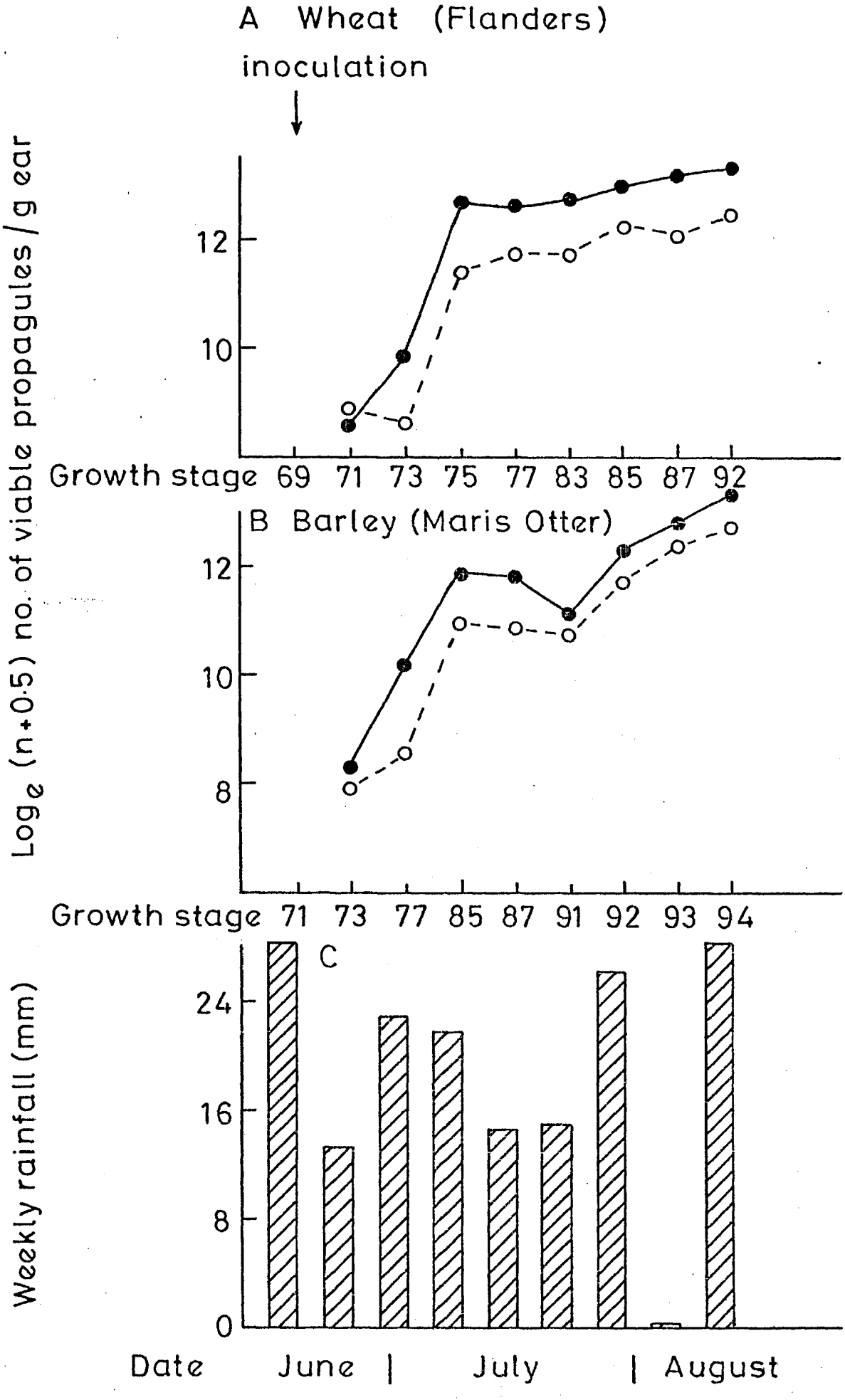


Fig. 39A. Effect of BYDV infection on the incidence of Cladosporium on wheat ears in the field, 1979.

B. Rainfall at Rothamsted during the sampling period.

(●) = BYDV - infected; (○) = Healthy.


A Wheat (Flanders)
inoculation
12
10
Growth stage 69 71 73 75 77 83 85 87 92
B Barley (Maris Otter)
12
10
8
Growth stage 71 73 77 85 87 91 92 93 94
Log e (n+0·5) no. of viable propagules / g ear
C
24
16
8
0
Weekly rainfall (mm)
Date June | July | August

The effect of BYDV on other microflora in 1980

BYDV infection significantly increased the abundance of the total microflora, including *Cladosporium*, on the ears of wheat ($F = 16.37$, $df = 1/30$, $p < 0.001$) (Table 16A) and barley ($F = 14.48$, $df = 1/30$, $p < 0.001$) (Table 16B). With wheat, there was a BYDV x date interaction which was absent in the case of barley.

Individual microflora on wheat other than *Cladosporium* were not significantly increased by BYDV, although there were consistently more *Verticillium* propagules on virus-infected wheat ears from 16.7.80 onwards ($F = 3.18$, $df = 1/30$, NS) (Table 17A). On barley the incidence of *Verticillium* only was significantly greater on BYDV-infected ears ($F = 23.91$, $df = 1/30$, $p < 0.001$) (Table 17B).

The effect of aphid honeydew on Cladosporium

Field experiments

The effect of aphid honeydew on *Cladosporium* was tested only in 1980 when the grain aphid, *Sitobion avenae* was the predominant species. The presence of aphid honeydew significantly increased the abundance of *Cladosporium* on wheat ($F = 6.682$, $df = 1/48$, $p < 0.05$) (Fig. 41A), the increase being greatest on 25.6.80 (GS 73) one week after the attainment of peak aphid numbers. (SED with 30 df = 0.35).

Honeydew had no significant effect on the incidence of *Cladosporium* on barley ears (Fig. 41B) on which there were relatively few aphids.

Table 17: The effect of BYDV on Verticillium on wheat and barley, 1980

Treatment	Mean No. (Log_e + 0.5) of viable propagules/g ear: Healthy	BYDV	SED (30 df)
A. Wheat			
Sampling date			
9.7.80	6.61	2.89	2.44
16.7.80	2.91	9.43	
23.7.80	6.76	11.54	
7.8.80	11.63	13.20	
14.8.80	12.52	13.11	
B. Barley			
Sampling date			
9.7.80	1.04	6.66	2.40
16.7.80	4.77	10.52	
23.7.80	2.89	11.03	
7.8.80	11.21	11.67	
14.8.80	5.25	11.50	

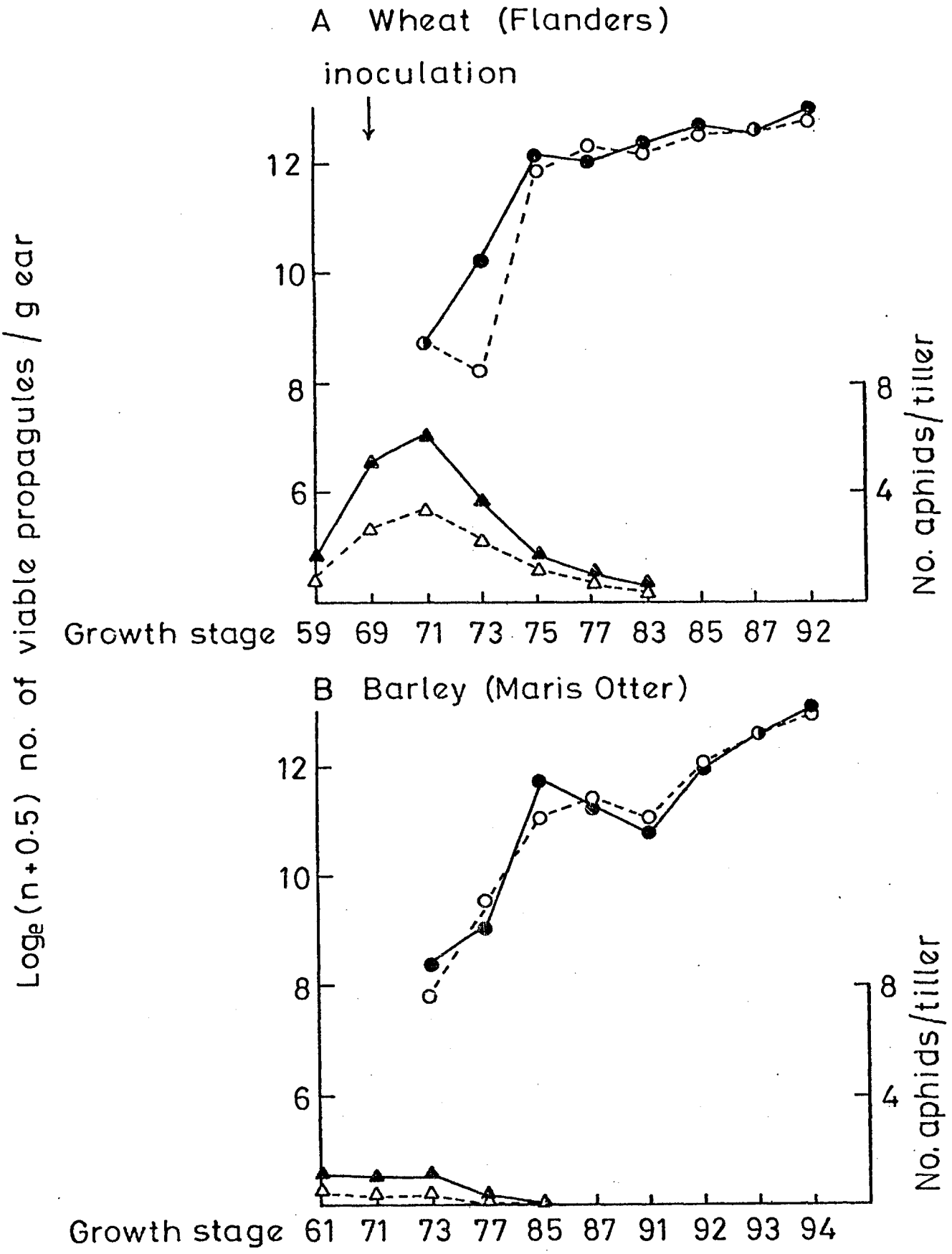


Fig. 41. The effect of aphid numbers and aphid honeydew on the incidence of Cladosporium on the ears of wheat (A) and barley (B) in the field, 1980. (●) = Honeydew present; (○) = Honeydew absent; (▲) = BYDV - infected; (△) = Healthy.

Glasshouse Experiment

Very large numbers of *S. avenae* developed on the ears of plants in treatments 3 and 4 (about 400 and 300 aphids per ear respectively at peak infestation), but plants in treatment 1 remained free of aphids throughout the experiment. Some aphids moved onto plants in treatment 2 while these were in contact with aphid-infested plants but they died within 24 hours because of the insecticide treatment. The honeydew deposited on these plants therefore came mostly from aphids feeding on neighbouring plants.

There were significant differences between the treatments in the populations of *Cladosporium* on the ears ($F = 38.49$, $df = 3/24$, $p < 0.001$) and on the flag leaves ($F = 598.87$, $df = 3/8$, $p < 0.001$) (Table 18). The ears of aphid-infested plants contained significantly more *Cladosporium* than those of non-infested plants and there were significant differences between the "high" and the "low" aphid-infested plants. The plants which had aphid honeydew without aphids had more *Cladosporium* on the ears and flag leaves than those without aphids or honeydew, but the difference was significant only on the leaves.

The ears were almost completely free of other microflora other than *Cladosporium* and the leaves had so few that they were not included in the analyses.

The effect of aphid honeydew on other microflora in the field.

The presence of aphid honeydew on the ears of wheat did not significantly affect either the total microflora or the abundance of individual microflora other than *Cladosporium*.

On barley, honeydew significantly increased total microflora ($F = 9.18$, $df = 1/30$, $p < 0.01$)(Table 19) but did not alter the incidence of each species of micro-organism.

Interactions between BYDV and aphid honeydew

There was no significant interaction between BYDV and aphid honeydew on wheat or barley.

The influence of rainfall on Cladosporium.

In 1979, there was very little rainfall in the weeks immediately before and after the inoculation of wheat ears with Cladosporium (Fig. 39B). There was a corresponding decrease in the incidence of Cladosporium on the ears during this period, followed by a sharp increase after the onset of rainfall. In 1980, however, there was much rainfall throughout the study period except in early August (Fig. 40C). Slight increases and decreases in the incidence of Cladosporium corresponded with periods of high or low rainfall but these fluctuations were smaller than in 1979. It therefore appears that rainfall was critical for Cladosporium in the early stages of infection and had little effect after the fungus was well established on the crops.

Yield

Except for the shelling percentage in barley, all the six parameters of yield were significantly depressed by BYDV infection of wheat and barley (Table 20). The reduction ranged from 10.11 - 63.51% in wheat and 3.42 - 60.30% in barley. The effect of aphids on these indices of yield was not significant in either crop. Interactions between BYDV and aphid feeding significantly reduced grain weight in barley ($F = 8.10$, $df = 1/6$, $p < 0.05$)(Table 21) but were otherwise insignificant.

Table 18: The effect of aphid honeydew on the incidence of Cladosporium on the ears and leaves of wheat (Highbury) in the glasshouse.

Treatment	Mean No (Log_e + 0.5) of viable propagules/g plant material+					
Aphid	NO	NO	YES(low)	YES(High)	SED	Df
Honeydew	NO	YES	YES	YES		
Ears	9.48	10.30	13.12	14.30	0.558	3/24
	a	a	b	c		
Leaves	8.92	11.40	13.35	11.03	0.105	3/8
	a	b	c	d		

+ Values with the same letter do not differ significantly at the 5% level.

Table 19: The effect of aphid honeydew on the total microflora on barley in the field, 1980.

Treatment	Control	Honeydew	SED (30 df)
	14.38	14.79	0.14

Table 20: The effect of BYDV on parameters of yield in wheat, oats and barley.

Parameter	Straw length (cm)	Length of ears (cm)	No. of grains per ear	Shelling % †	Grain wt (mg)	Wt of grains per 20 ears (gm)(Dry)
Wheat						
Healthy	72.16	9.32	44.36	64.30	39.26	31.05
Diseased	56.05	7.84	22.57	57.80	29.18	11.33
% reduction	22.33**	15.88**	49.12***	10.11**	25.67**	63.51***
SED (6 df)	3.34	0.39	3.04	1.13	1.70	2.24
Barley						
Healthy	81.15	9.13	25.34	68.06	38.53	17.33
Diseased	49.07	4.98	14.55	65.73	28.80	6.88
% reduction	42.00***	45.45***	42.58***	3.42	25.25**	60.30***
SED (6 df)	2.17	0.26	1.06	1.22	1.69	0.58

† transformed into angles

Table 21: The combined effects of BYDV and aphid feeding on grain size in barley.

	Grain weight (mg)		SED(6 df)
Treatment	- aphids	+ aphids	
- BYDV	37.92	39.15	2.39
+ BYDV	32.99	24.62	

DISCUSSION

The seven micro-organisms identified in this study are characteristic of ripening grain at Rothamsted (eg. Hill, 1979; Mais, 1979). Alternaria was encountered less frequently than the other microflora possibly because it sporulates less readily than eg. Cladosporium and may therefore be underemphasized by the dilution plating method (Hill, 1979).

In both years, more Cladosporium developed on the ears of BYDV-infected plants than on healthy ones. In 1979, when the leaf-feeding Metopolophium dirhodum was abundant, the ears were free of aphids and aphid honeydew. In 1980, the ears in some plots were protected from the grain aphid, Sitobion avenae, with an insecticide. The differences in the levels of Cladosporium on the ears of healthy and infected plants in such plots were therefore attributable to the effect of the virus alone. BYDV is known to increase the concentration of nutrients such as carbohydrates (Goodman et al, 1965; Orlob & Arny, 1961 ; Watson & Mulligan, 1960) and free amino acids (Markkula & Luurema, 1964) in the tissues of infected plants. This would enhance the suitability of the infected plants as substrates for fungal growth by improving their nutritive value, since carbohydrates and nitrogen are among the nutrients essential for all fungi (Hawker, 1950, 1957). Although Cladosporium is predominantly a saprophytic phylloplane fungus (Dickinson, 1976; Dickinson & Bottomley, 1980; Dickinson & O'Donnell, 1977), O'Donnell and Dickinson (1980) have shown that some isolates of C. cladosporioides and C. herbarum can penetrate and

grow inside living plant tissues. They can thereby benefit from a favourable change in the nutritive value of their host plant.

In addition, many plants have been found to leach chemical substances onto surfaces such as the leaves, flowers and developing grains (Tukey & Morgan, 1964, and reviews by Tukey, 1970, 1971). The substances leached include large amounts of free sugars and all the amino acids found in plants (Morgan, 1963; Morgan & Tukey, 1964), although organic substances, principally carbohydrates, account for the majority. The tissues of healthy and vigorously growing plants are much less prone to leaching than are those of plants which are injured, no matter whether injury is induced by micro-organisms, adverse climate, nutritional and physiological disorders or by mechanical means (Tukey & Morgan, 1963). Any factor which will raise the nutrient status of the plant will result in higher levels of leaching (Arens, 1934; Schoch, 1955). Sugary exudates have been observed on the leaves of BYDV-infected oats and barley (Esau, 1957b) and must occur on the ears too, since enzyme-linked immunosorbent assay (ELISA) tests indicate high levels of the virus in the ears of wheat (Hill & Merriman, unpublished data). No attempt was made in this study to compare the quantities and chemical composition of the exudates on healthy and diseased plants, but it is likely that the ears of BYDV-infected plants contained more exudates than those of healthy plants. This could explain the greater development of total microflora, Cladosporium, and Verticillium on the ears of diseased plants.

The relationship between the concentration of nutrients and the growth of various other fungi has been well documented (see Literature review). Although the optimum amounts of these nutrient components necessary for the growth and development of Cladosporium were not investigated here, it does seem likely that the altered physiology of BYDV-infected plants predisposed them to infection by Cladosporium. Smith (1962) had found that when the ears of wheat were kept under conditions of high humidity in a greenhouse and sprayed with spores of Alternaria and Cladosporium species, the ears of BYDV-infected plants were more severely blackened than those of healthy plants. He did not attempt, however, to separate the effect of the virus on the two fungi or to explain the cause of the increased blackening. The results presented here confirm his observation in the greenhouse and that of Hooper (1978) in the field. Similar interactions between BYDV and several other fungi eg. Erysiphe graminis DC ex Merat (powdery mildew) and a variety of root-rotting fungi, on cereals have been recorded by various workers (Comeau & Pelletier, 1976; Pelletier et al, 1974; Potter, 1974, 1980; Price, 1970; Scott, 1968; and Smith, 1962). The effect of BYDV on Verticillium recorded here may be due to a combination of the changed physiology of the host plant, and the fact that this fungus can parasitize Cladosporium (Lacey, pers. comm.). The additive nature of these two effects is supported by the finding that aphid honeydew increased the abundance of Cladosporium but not that of Verticillium.

In the field, the influence of aphid honeydew on Cladosporium, though significant on wheat, was unimportant on barley. On wheat, the effect was strongest on the second sampling occasion, about one week after the attainment of peak aphid numbers on the ears. The effect of honeydew decreased thereafter as the density of aphids declined. The numbers of S. avenae on barley ears were much lower than on wheat. It therefore appears that the effect of honeydew on Cladosporium is dependent on the numbers of aphids present and that it is short-lived in the absence of aphids. There was much rainfall during this period and rain could have removed honeydew from the ears. The relationship between aphid honeydew and Cladosporium was confirmed by the glasshouse experiment in which the presence or absence of aphids and differences in the populations of aphids on the ears of wheat were reflected in the incidence of Cladosporium. The glasshouse study also casts some doubt on the possibility that aphid feeding per se and not honeydew might be responsible for increasing the infection of wheat plants by Cladosporium, for differences in the incidence of Cladosporium between treatments 1 (aphid and honeydew absent) and 2 (honeydew present) were significant not on the ears but on the flag leaves, indicating that more honeydew from aphids on the ears of neighbouring plants must have fallen on the flag leaves than on the ears of plants in treatment 2.

Honeydew contains large amounts of sugars, amino acids and amides (see review by Auclair, 1963). It is known from experimental work quoted earlier that the concentrations of

these compounds influence the growth and development of various fungi. There is some evidence in the literature that the presence of honeydew produced by aphids or coccids favours the incidence of sooty moulds, including Cladosporium (eg. Bushing & Burton, 1974; Gardner, 1849; Jamil Khan & Sultana, 1974; McAlpine, 1896; Meyer, 1978; Parker et al, 1956; Riphagen et al, 1979; Stover, 1975; Tedders & Smith, 1976).

On the basis of the results presented here, it is obvious that infection of the host plant by BYDV predisposes the plant to infection by Cladosporium. It probably affects Alternaria, another sooty mould fungus of common occurrence on cereals, in a similar manner. However, in this study, Alternaria was observed at dilution rates lower than those at which fungal colonies were counted. The relatively smaller effect of honeydew on Cladosporium in the field was probably due to the low numbers of aphids in 1980. In years when populations of S. avenae are high, as exemplified by the glasshouse study, honeydew will no doubt exert a greater effect than was recorded here. It is therefore premature to speculate on the relative importance of BYDV and aphid honeydew in enhancing the infection of cereals by Cladosporium.

The decline in the incidence of Cladosporium in the first two weeks of sampling in 1979 was probably due to the long dry spell which extended from late June to late July. The decline may have started immediately after artificial innoculation but sampling was not done early

enough to detect this. Micro-organisms are known to be adversely affected by hot dry weather and to grow more rapidly in warm wet conditions (eg. Hyde & Galleymore, 1950). The development of Cladosporium herbarum on wheat was correlated with moist, warm weather (Bennett, 1928), and the germination of several isolates of C. herbarum and C. cladosporioides was found to be strikingly influenced by humidity (Dickinson & Bottomley, 1980). Cladosporium is therefore a wet weather fungus and the environmental conditions appear to have been adequate for its growth and development in 1980.

Yield

The yield losses caused by BYDV in this experiment confirm the findings in Section 1 and the explanations for the differences between crops have been discussed in that section. Aphid feeding damage did not significantly affect yield in this trial probably due to the low populations of S. avenae on the ears in 1980. Heavy aphid infestations are known to cause serious yield losses in both wheat and barley (eg. Ba-Angood & Stewart, 1980a,b; George & Gair, 1979; Lowe, 1974; Wratten, 1978 and Rautapaa, 1966, 1968a,b).

Summary

The ears of winter wheat (Flanders) and barley (Maris Otter), artificially infected with a severe R. padi-specific isolate of barley yellow dwarf virus (BYDV) and healthy ones, were inoculated after flowering in the field with spores of Cladosporium. Levels of Cladosporium infection in the two treatments were monitored by weekly samples from which the numbers of viable propagules per gram of ear material were assessed by the dilution plating method.

The effect of aphid honeydew was similarly tested on winter wheat and barley in the field and on spring wheat (Highbury) in the glasshouse. The results showed that prior infection of both wheat and barley by BYDV predisposed them to infection by Cladosporium and Verticillium. Aphid honeydew increased the incidence of Cladosporium on wheat ears and flag leaves but not on barley ears, and this was attributable to the higher numbers of aphids on wheat. BYDV significantly depressed the yield of winter wheat and barley as measured by several parameters.

SECTION 5

THE EFFECT OF BARLEY YELLOW DWARF VIRUS ON HONEYDEW PRODUCTION BY THE CEREAL APHIDS, SITOBION AVENAE F. AND METOPOLOPHIUM DIRHODUM WLK.

INTRODUCTION

Field experiments in 1979 and 1980 showed that significantly more Cladosporium grew on the ears of wheat plants infected with a severe Rhopalosiphum padi-specific strain of barley yellow dwarf virus (BYDV) than on healthy plants in neighbouring plots (Section 4). This was true in the presence or absence of aphids on the ears but aphid infestation of the ears further increased infection with the sooty mould fungus. It was thought that BYDV infection of the plants increased the production of honeydew by aphids feeding on them, thereby encouraging the growth and development of mould fungi which thrive on honeydew. Such an increase in honeydew excretion could be due either to a larger aphid population or to more honeydew being excreted per aphid, or both. Field observations revealed that larger aphid populations developed on BYDV-infected than on healthy plants - Metopolophium dirhodum Wlk. in 1979 and Sitobion avenae F. in 1980 (Section 1), confirming the first hypothesis. This section describes experiments, in which the second hypothesis, that BYDV infection of the host plant increases the amount of honeydew produced per aphid, was investigated.

MATERIALS AND METHODS

The insects, plants, glasshouse and Saxcil growth cabinets

The insects and plants used for this experiment were

obtained from glasshouse cultures as described previously, but the aphids were maintained on wheat (Highbury) and barley (Julia). The glasshouse and Saxcil growth cabinets have also been described (pages 39 - 41).

The Honeydew Recording Machine

Two honeydew recording machines similar to that described by Banks and Macaulay (1964) were used (Fig. 42). They differed from the earlier version in having only one horizontal steel rod which wound up five strips of indicator chromatography paper (Whatman No. 1, 4cm wide). Holes, which were covered with muslin cloth, were made in the lids of the transparent boxes for ventilation and to eliminate condensation which may have obliterated honeydew spots. The potted plants and unused rolls of indicator paper were arranged on the side of the machine opposite the rod the level of which could be adjusted to suit the height of the experimental plants. Separate machines were used for BYDV-infected and control plants but were exchanged for alternate experiments.

Measurement of frequency and volume of honeydew production.

Post-teneral alate virginoparae of comparable size and maturity were obtained from the cultures and allowed to feed and reproduce on the undersurface of the youngest leaf of the main stem of each plant above each strip of indicator paper within each box. When all the alates had each produced at least one nymph, they were removed with all but the youngest nymphs, using a fine camel hair brush. In this way the age and size of the experimental nymphs were standardised as much as possible.



Fig. 42A. Modified Banks and Macaulay's (1964) honeydew recording apparatus, set up with 4 strips of indicator paper and a potted wheat plant.

Diagram of honeydew recording apparatus

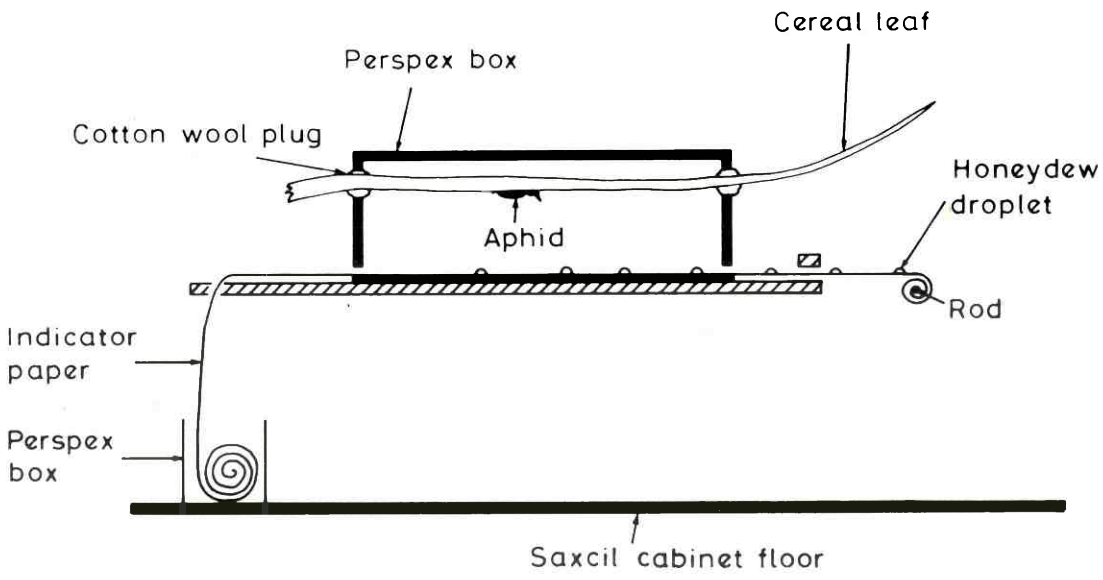


Fig. 42B.

The honeydew droplets excreted by each aphid made distinct spots on the moving paper which was replaced every 24 hours. The number of droplets per 24 hours was counted and the mean diameter of each was measured and used to calculate its area. Droplet diameter was the mean of two measurements taken at right angles to each other using an ocular micrometer.

To calibrate the relationship between spots and droplet volume, known honeydew volumes of 0.7, 1, 2, 3, 4, 5, and 6 µlitres were collected separately from S. avenae and M. dirhodum colonies with microcapillaries and spotted onto a strip of indicator paper and their area measured.

RESULTS

The effect of BYDV on the frequency of honeydew excretion.

Both S. avenae and M. dirhodum were tested on the flag leaf of healthy and BYDV-infected wheat (GS 55-60) (Zadoks et al, 1974). S. avenae was further tested on wheat leaves at the tillering stage (GS 32) and on the ears at flowering (GS 65). M. dirhodum was not tested on the ears due to its reluctance to feed there, but was tested on barley leaves at growth stage 32. A maximum of ten aphids per treatment was studied where possible, although some S. avenae were very restless and did not allow recordings to be made beyond five days. The results for S. avenae at the three growth stages were pooled before analysis because of the consequent lack of replication.

The frequency of excretion was not constant throughout the aphids' development in either species. On wheat, the number of droplets excreted on healthy plants increased

from birth to a peak on the third day in M. dirhodum and on the fourth day in S. avenae and then decreased thereafter (Fig. 43). M. dirhodum feeding on diseased wheat plants produced significantly less honeydew on all days except the fourth and fifth when plants in both treatments were not watered. The difference for S. avenae was significant on the first and fourth days only. On barley, M. dirhodum excreted significantly more frequently on healthy plants on all except the ninth day. The rate of excretion in both treatments peaked on the third day.

The cumulative number of droplets excreted by M. dirhodum was consistently and significantly higher on healthy than on diseased wheat and barley from the first day (Fig. 44). On the ninth day after birth, M. dirhodum excreted 41% fewer droplets ($F = 14.13$, $df = 11$, $p < 0.01$) on diseased wheat and 29% fewer droplets ($F = 19.33$, $df = 18$, $p < 0.001$) on diseased barley than on healthy plants. The cumulative number of droplets excreted by S. avenae on healthy wheat was also consistently higher than on diseased wheat but the significance of this difference was not tested because there were insufficient replications on most days. On the fifth day after birth S. avenae excreted 23% fewer droplets on diseased plants. The corresponding values for M. dirhodum were 32% on wheat ($F = 5.22$, $df = 11$, $p < 0.05$) and 26% on barley ($F = 12.06$, $df = 18$, $p < 0.01$).

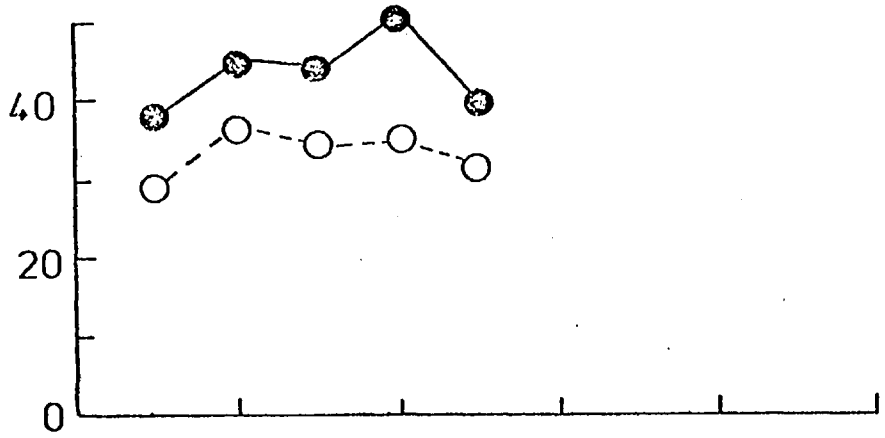
The relationship between the area and volume of honeydew droplets.

The volume of honeydew droplets excreted by S. avenae and M. dirhodum is highly correlated with the area of their

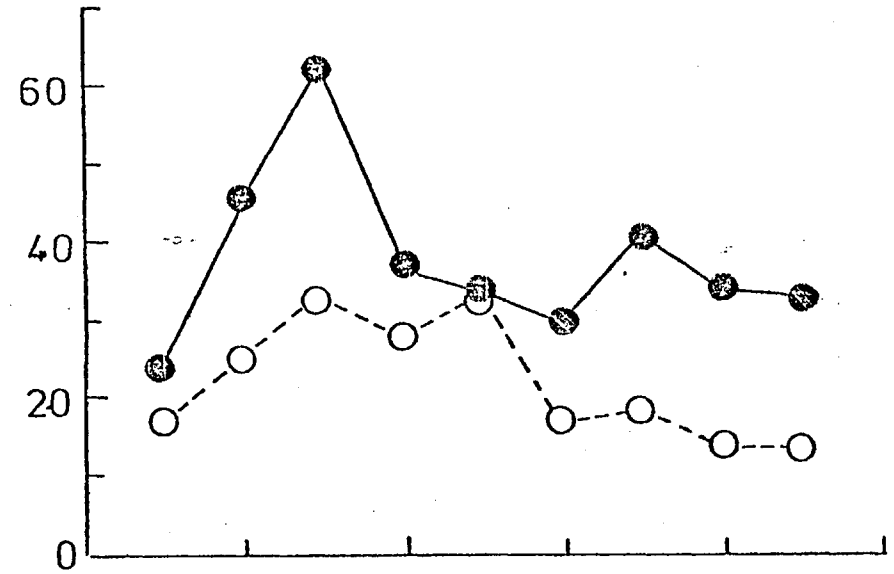
Fig. 43. The effect of BYDV infection on the frequency of honeydew excretion by S. avenae and M. dirhodum feeding on wheat and barley.

● = healthy; ○ = BYDV-infected.

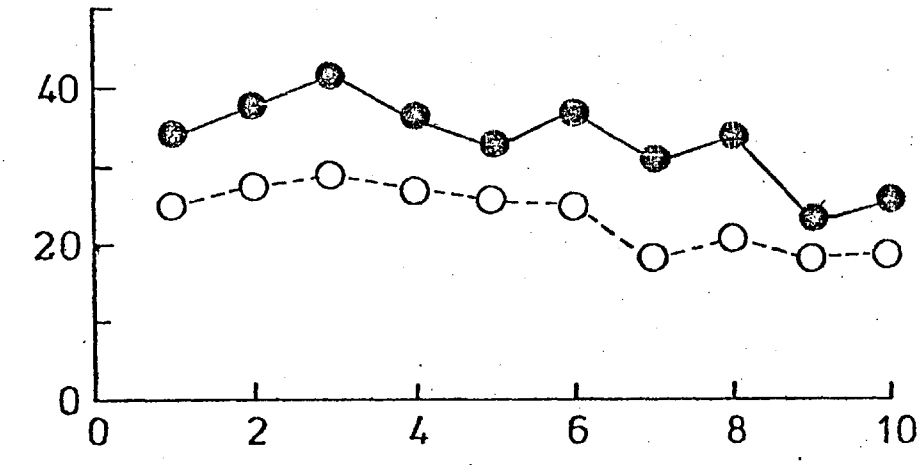
S. avenae on wheat leaves and ears, G.S. 32-69.



M. dirhodum on wheat flag leaves, G.S. 65.



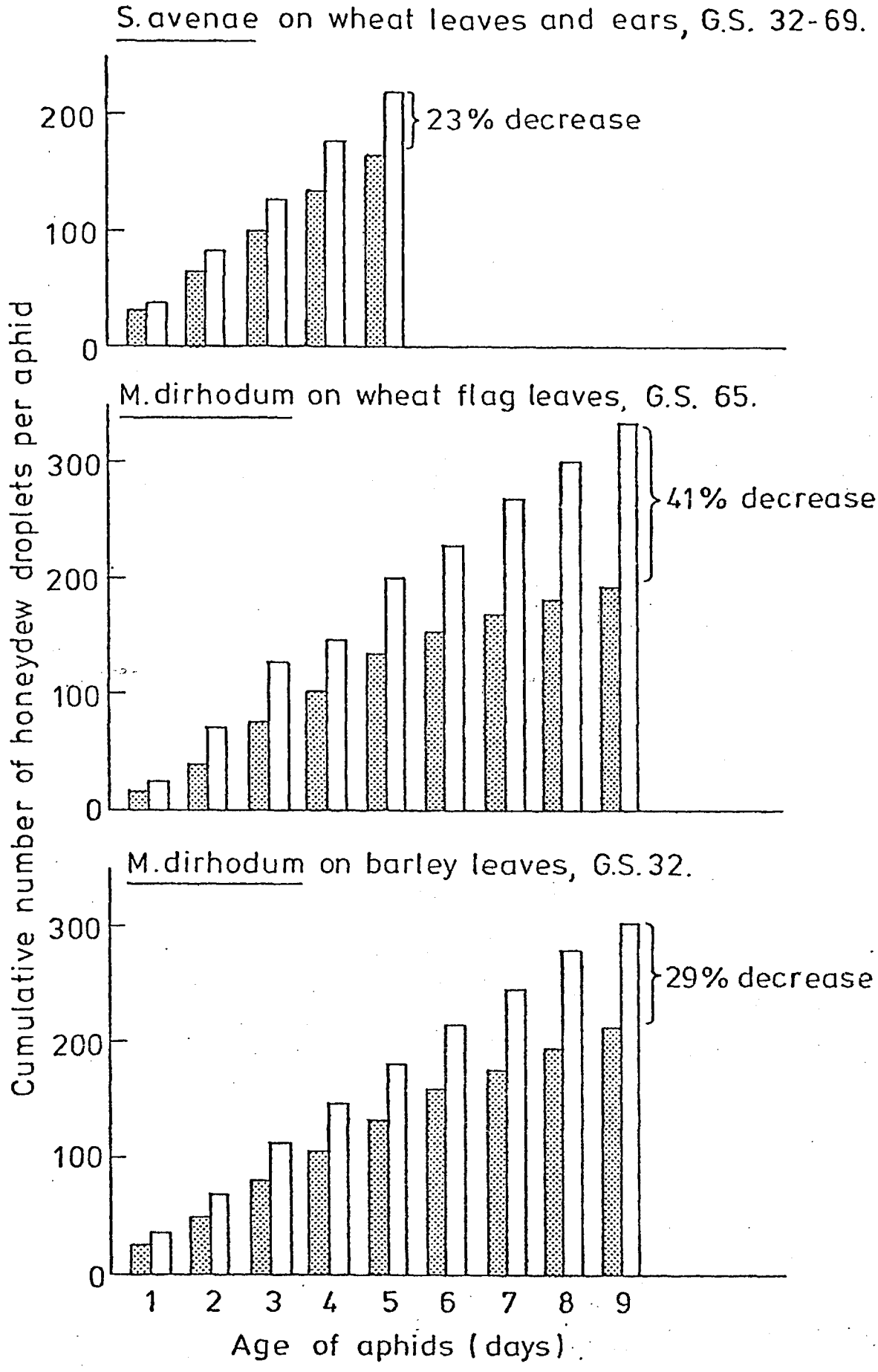
M. dirhodum on barley leaves, G.S. 32.



Mean number of honeydew droplets per aphid / day

Fig. 44. The effect of BYDV infection of wheat and barley on the cumulative number of droplets produced by *S. avenae* and *M. dirhodum*.

□ = healthy plants; ▨ = BYDV-infected plants.


S. avenae on wheat leaves and ears, G.S. 32-69.
200
100
0
23% decrease
M. dirhodum on wheat flag leaves, G.S. 65.
300
200
100
0
41% decrease
M. dirhodum on barley leaves, G.S. 32.
300
200
100
0
29% decrease
Cumulative number of honeydew droplets per aphid
1 2 3 4 5 6 7 8 9
Age of aphids (days)

spots on indicator paper (Fig. 45). The regression equation for this relationship is $y = 0.076x + 0.289$, ($r = 0.985$, $p < 0.001$) compared with $y = 0.057x + 0.149$, ($r = 0.998$, $p < 0.001$) for water. The regression for aphid honeydew was subsequently used to calculate the volume of honeydew produced.

The effect of BYDV and the age of aphids on the volume of honeydew excreted.

The volume of individual honeydew droplets produced by both species increased greatly from birth to the adult ($r = 0.964$, $p < 0.001$ and 0.988, $p < 0.001$ for M. dirhodum and S. avenae respectively) but there was no significant difference between treatments (Fig. 46). M. dirhodum excreted larger droplets than S. avenae (F slope = 1.86, df = 1/30, N.S.; F elevation = 34.65, df = 1/30, $p < 0.001$).

Both species of aphid produced a larger cumulative volume of honeydew when feeding on healthy plants than on BYDV-infected plants (Fig. 47). The magnitude of the differences between treatments was similar to that reported above for the cumulative number of droplets produced (Table 22).

The effect of BYDV and plant growth stage on honeydew excretion by S. avenae.

S. avenae excreted less honeydew on the ears than on the leaves, and more on the flag leaves than on leaves at the tillering stage (Fig. 48). This effect of plant growth stage on honeydew excretion was significant on all but the first day of the aphids' life. Whereas the daily rate of excretion increased with time on the flag leaf, it decreased

* $y = (12.703 + 0.729)x - 2.628 + 2.268$,

** $y = (17.510 + 0.571)x - 2.267 + 3.321$

Fig. 45. The relationship between the volume and area of honeydew droplets:
(1) S. avenae and M. dirhodum honeydew:
$y = (12.703 + 0.729)x - 2.628 + 2.268$ $(r = 0.985, p < 0.001)$
(2) water droplets; $y = (17.510 + 0.571)x - 2.267 + 3.321$
$(r = 0.998, p < 0.001)$.

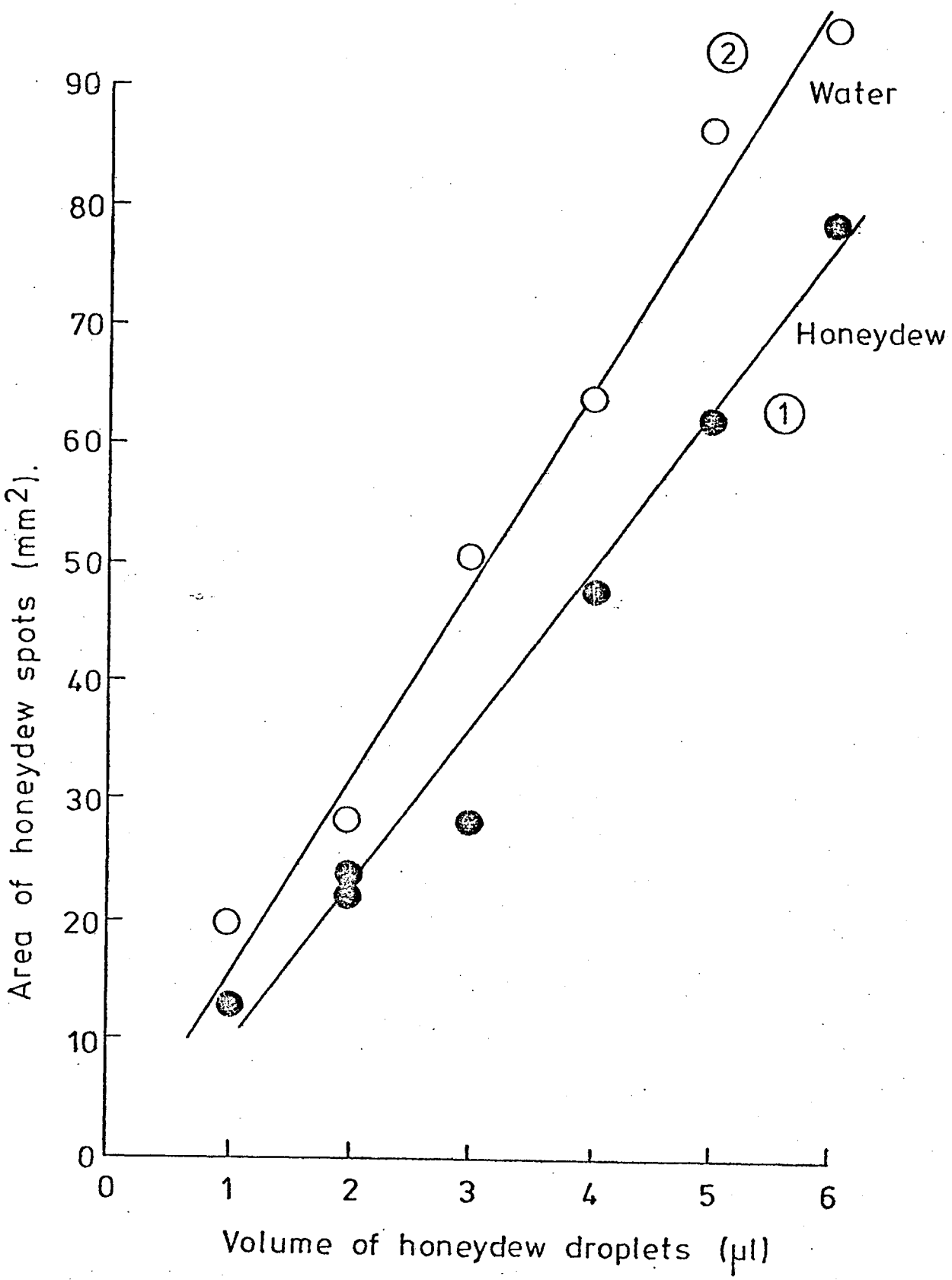

Area of honeydew spots (mm2).
Volume of honeydew droplets (µl)
Water
Honeydew
1
2
0
10
20
30
40
50
60
70
80
90
0
1
2
3
4
5
6

Fig. 46. The effect of age on the size of honeydew droplets excreted by M. dirhodum and S. avenae feeding on healthy (○ △) and BYDV-infected (● ▲) wheat. Regression equations are:

M. dirhodum - $y = (0.026 + 0.002)x + 0.321 + 0.010$ ($r = 0.964$, $p < 0.001$);
S. avenae - $y = (0.022 + 0.001)x + 0.301 + 0.004$ ($r = 0.988$, $p < 0.001$).

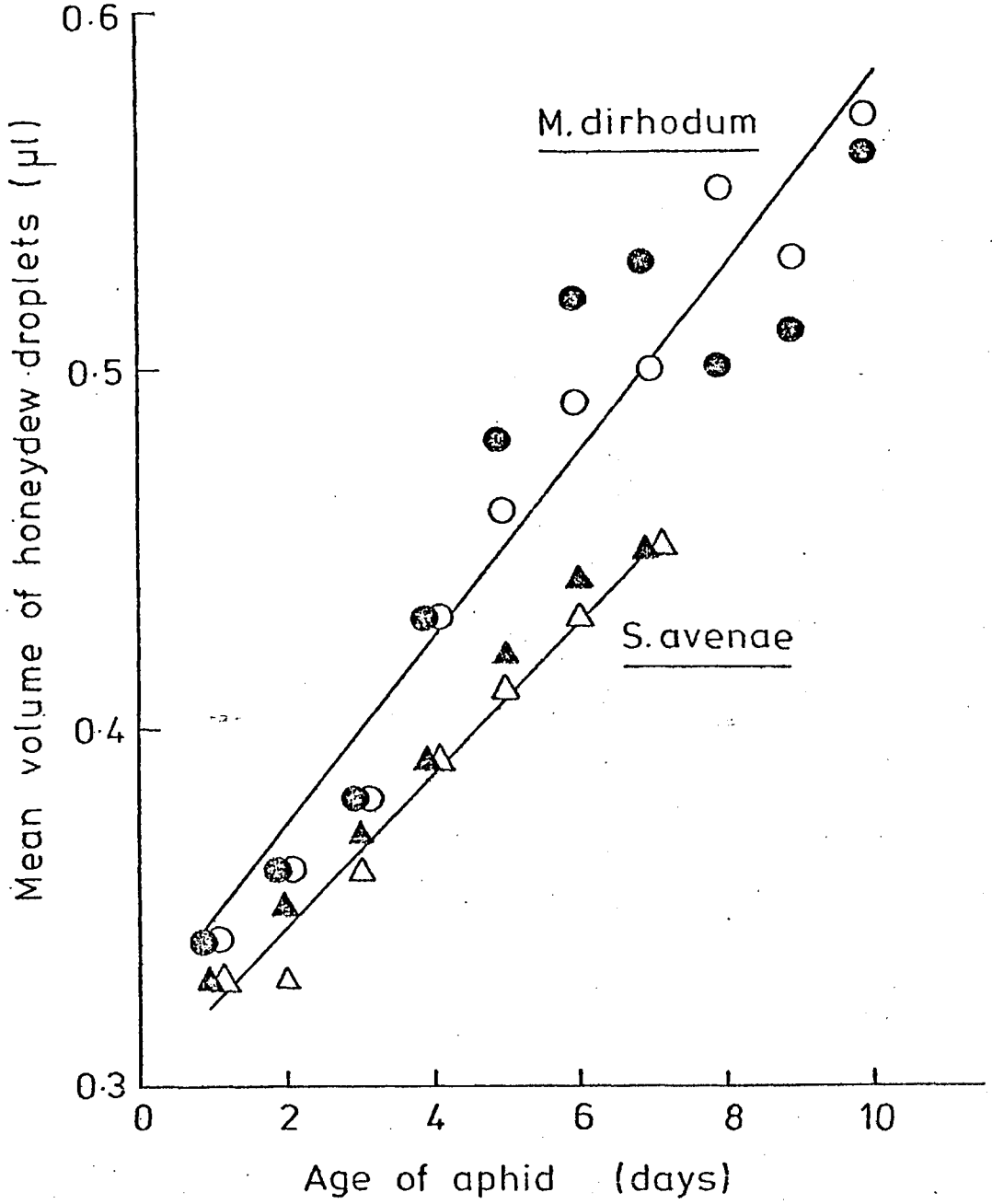

0·6
0·5
0·4
0·3
Mean volume of honeydew droplets (µl)
M. dirhodum
S. avenae
0
2
4
6
8
10
Age of aphid (days)

Fig. 47. The effect of BYDV infection on the cumulative volume of honeydew excreted by *S. avenae* and *M. dirhodum* feeding on wheat and barley.
□ = healthy plants; ▨ = BYDV-infected plants.

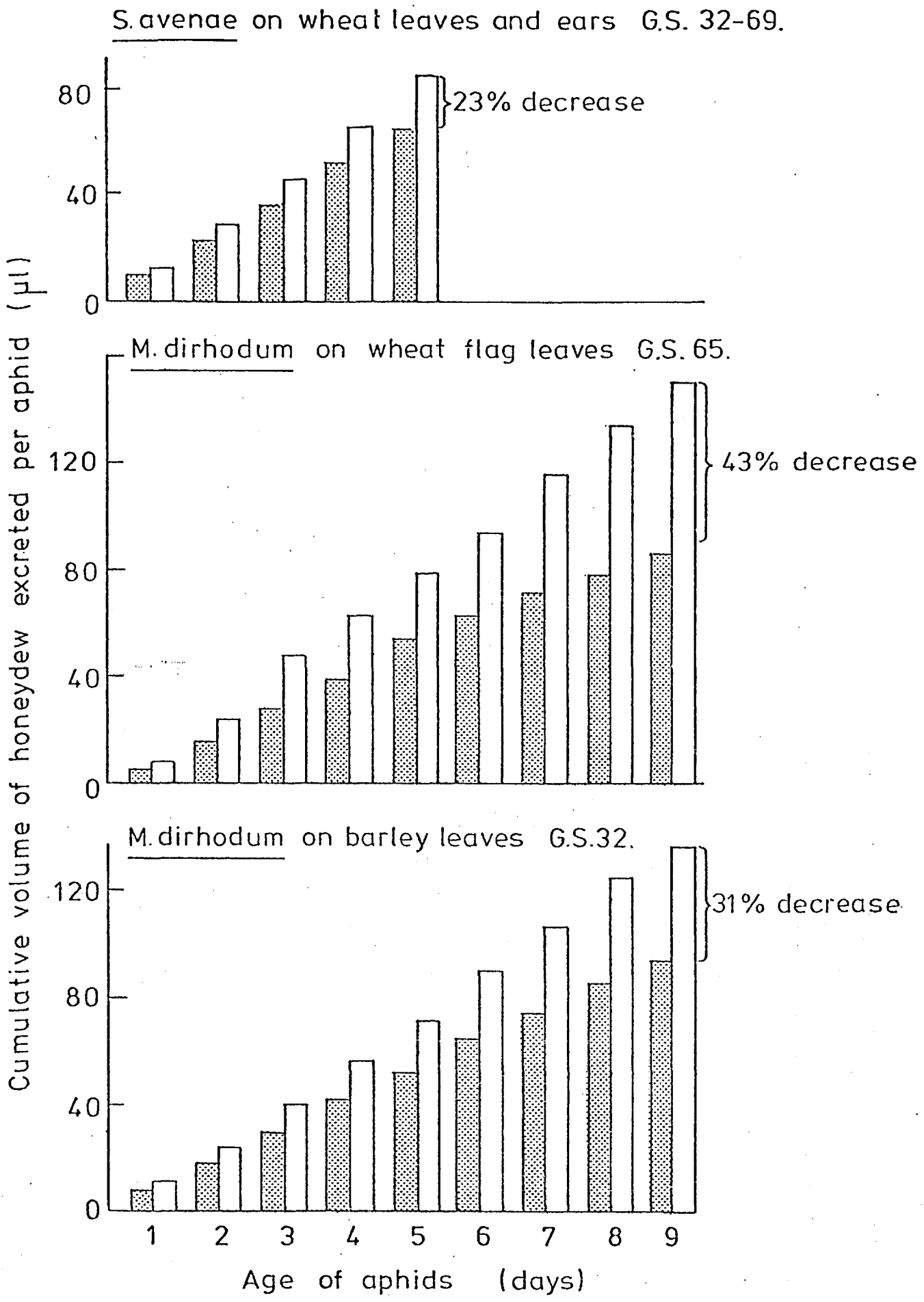
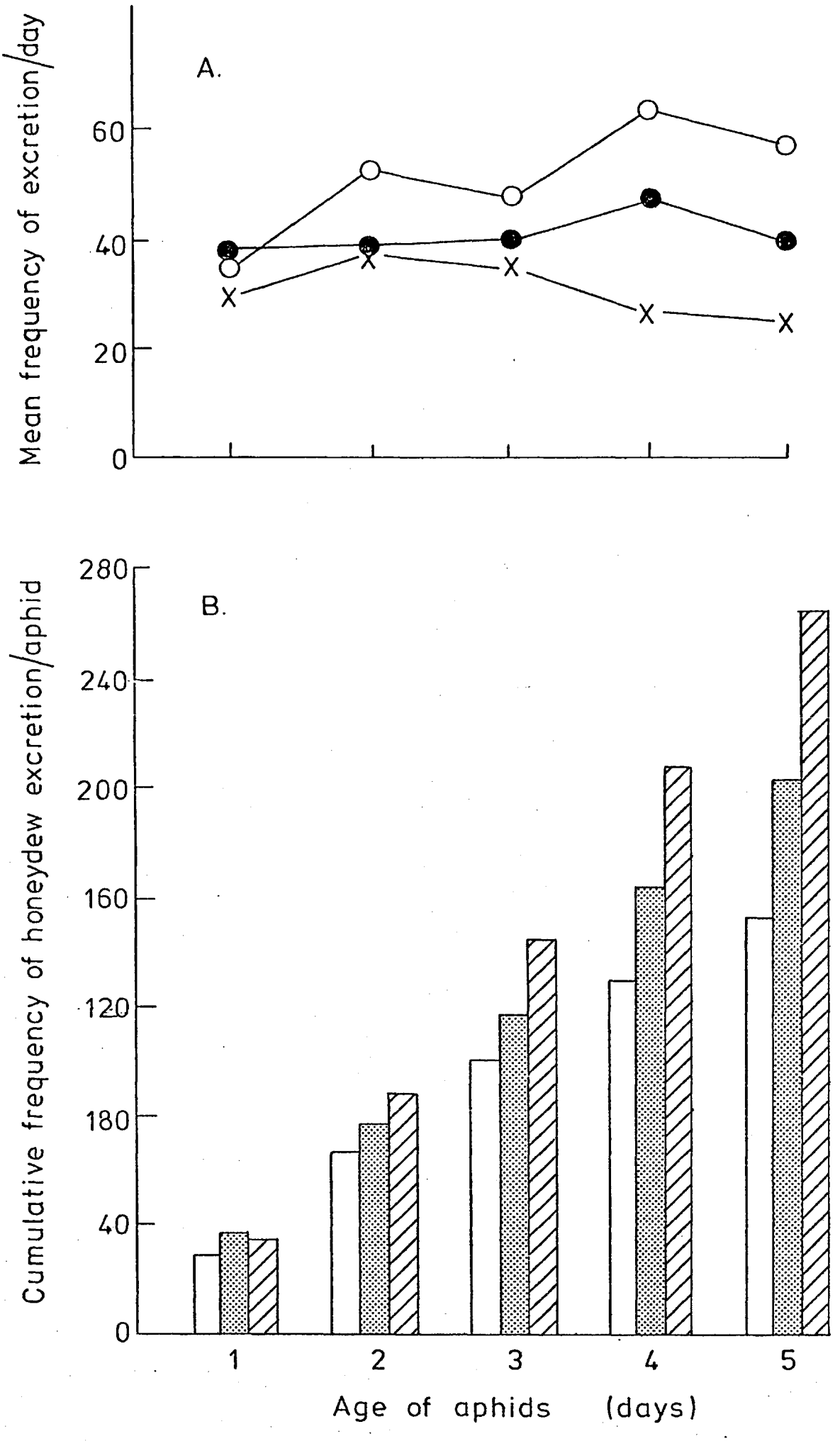

S. avenae on wheat leaves and ears G.S. 32-69.
80
40
0
23% decrease
M. dirhodum on wheat flag leaves G.S. 65.
120
80
40
0
43% decrease
M. dirhodum on barley leaves G.S.32.
120
80
40
0
31% decrease
1 2 3 4 5 6 7 8 9
Age of aphids (days)
Cumulative volume of honeydew excreted per aphid (µl)

Fig. 48. The effect of plant growth stage on (A) daily frequency and (B) cumulative number of droplets produced by S. avenae feeding on wheat.

X □ = Ears (GS 65); ● ▩ = Leaves (GS 32);

○ ▨ = Flag leaves (GS 65).


A.
Mean frequency of excretion/day
60
40
20
0
B.
Cumulative frequency of honeydew excretion/aphid
280
240
200
160
120
180
40
0
1
2
3
4
5
Age of aphids (days)

with time on the ears (Fig. 48A). Although BYDV infection lowered the rate of excretion by S. avenae (Figs. 44 and 47), there was no significant interaction between the disease and plant growth stage.

Comparison of the amount of honeydew excreted by S. avenae and M. dirhodum.

The cumulative frequency and volume of honeydew excreted in five days for S. avenae and M. dirhodum are compared in Table 22. S. avenae excreted less honeydew on the ears but more on the leaves than M. dirhodum on the leaves.

DISCUSSION

BYDV infection of the host plant resulted in a decrease of the total volume of honeydew excreted by individual S. avenae and M. dirhodum by lowering the frequency of excretion since it did not affect the size of droplets. Since much of the plant sap ingested by an aphid (sometimes up to 90% (Banks and Macaulay, 1964) is excreted as honeydew, the frequency and volume of excreted honeydew are acceptable indices of the feeding rate and of the total amount of food ingested (Auclair, 1959, 1963; Banks & Macaulay, 1964; Fisk, 1978; Mittler, 1958; Mittler & Sylvester, 1961; Smith, 1937). The results of these studies reveal therefore that S. avenae and M. dirhodum ingest less sap when feeding on BYDV-infected wheat and barley.

It is unlikely that the nutrient requirements of aphids feeding on diseased and healthy plants differ. A reduction of the volume of sap ingested could result from a better utilization of the ingested food by the aphid or from an improvement of the quality of the plant sap as a

Table 22: Comparison of the amount of honeydew excreted in five days by S. avenae and M. dirhodum

Species of aphid	Crop and growth stage	Cumulative no. of honeydew droplets per aphid		Cumulative volume (µl) of honeydew per aphid	
		Healthy	BYDV	Healthy	BYDV
S. avenae	Wheat flag leaf GS 69	285.71 ± 24.47	223.27 ± 29.17	107.64 ± 9.32	81.77 ± 10.91
S. avenae	Wheat leaf GS 32	226.52 ± 20.40	181.60 ± 12.76	79.77 ± 4.52	66.12 ± 4.36
S. avenae	Wheat ear GS 65	173.15 ± 23.37	134.25 ± 23.39	61.84 ± 7.31	46.09 ± 8.55
M. dirhodum	Wheat flag leaf GS 55	199.00 ± 25.57	135.13 ± 12.57	78.95 ±10.98	54.36 ± 5.19
M. dirhodum	Barley leaf GS 32	180.00 ± 11.53	132.60 ± 5.89	71.31 ± 4.33	51.79 ± 2.48

result of virus infection. The first hypothesis would indicate a direct effect of the virus on its vector as was suggested by Miller (1962) and Miller & Coon (1964) who reported a lower oxygen consumption in viruliferous compared with healthy Macrosiphum granarium (Kirby) (Sitobion avenae F.). However, contrary to earlier observations with some virus-vector relationships (see reviews by Carter, 1962; Jensen, 1963; Maramorosch & Jensen, 1963), BYDV does not induce any cytological changes in the fat body cells of this aphid (Rutschky & Campbell, 1964). In addition, while the fecundity of Rhopalosiphum padi (L.) is higher on BYDV-infected than on healthy susceptible oat plants (Markkula & Laurema, 1964) it is not altered on an infected immune wild oat (Bremer, 1965). A direct effect of the virus on the aphids is therefore doubtful.

A more plausible explanation for a decrease in the amount of sap ingested following BYDV infection lies in changes in the nutritional status of infected plants, and in the consequent effect of these changes on the rate of feeding of the aphids. BYDV infection induces an accumulation of carbohydrates (Goodman et al, 1965; Orlob & Arny, 1961; Watson & Mulligan, 1960) and free amino acids (Markkula & Laurema, 1964) in infected plants. It is possible, therefore, that to obtain the desired quantity of essential nutrients, S. avenae and M. dirhodum must ingest more of the relatively less nutritious sap provided by healthy plants and consequently excrete more honeydew. No work has been done on the nutrient requirements of cereal aphids to test this hypothesis.

A similar effect of differences in the physiological condition of the host plant on honeydew excretion in aphids

was observed by Mittler (1954) who showed that Tuberolachnus salignus (Gmelin) excreted less honeydew on actively growing plants than on mature plants because the sap of the former was more nutritious. Vereijken (1979) and Vereijken & Mantel (1980) reported too that S. avenae excreted 2 - 3 times as much honeydew and 1.7 times more honeydew dry matter per gram aphid on the flag leaf than on the wheat ear. The ear had about twice the concentration of essential nutrients in the flag leaf. In the same study, Vereijken (1979) also found that extra nitrogen dressing at stem elongation increased the amount of nitrogen and phosphorous in the grain and in the phloem sap, and resulted in a sharp decrease in honeydew production. In the present study, the cumulative amount of honeydew produced by S. avenae in the first five days of its life on the wheat flag leaf was 1.7 times that on the ear and 1.3 times that on the leaves at the tillering stage (Fig. 48). This suggests that, from the nutritional point of view, the ears of wheat are a more suitable feeding site for S. avenae than the leaves, and explains why this aphid shows a marked preference for feeding on the ears of its host plants (Latteur, 1971; Phillips, 1916; Watt, 1979).

S. avenae excreted less honeydew on the ears and more on the leaves of wheat than M. dirhodum on the leaves. Watt (1979) had found that S. avenae was more fecund on the ears of wheat in the field but less so than M. dirhodum on the leaves. Since S. avenae feeds predominantly on the ears and M. dirhodum almost entirely on the leaves (Dean,

1974b; Latteur, 1976; Wratten, 1975, 1978), the observed differences in their excretion of honeydew reflect how well each one is adapted to its preferred feeding site. Since the ear contains more aphid nutrients than the leaves, S. avenae probably requires a more nutritious diet than M. dirhodum.

The frequency of honeydew excretion by S. avenae decreased with time on the ears and increased with time on the flag leaves (Fig. 47). This difference was probably a consequence of the relocation of nutrients from the flag leaves into the ear for grain filling (Austin & Jones, 1976).

There was no interaction between BYDV and plant growth stage. All the infected experimental plants had been inoculated with BYDV at the seedling stage and the effect of the virus must have stabilized by the youngest growth stage used. Later infection may have resulted in interactions since the stage of development of the plant at infection is known to modify the effect of the virus (Oswald & Houston, 1953).

M. dirhodum excreted larger honeydew droplets than S. avenae. It is possible that individual M. dirhodum were larger than S. avenae but this was not tested because of the need to maintain the continuity of honeydew recordings without disturbing the aphids.

SUMMARY

Individual S. avenae and M. dirhodum excreted significantly fewer droplets of honeydew on plants infected with BYDV than on healthy plants. S. avenae excreted less honeydew on the ears than on the leaves of wheat. M. dirhodum excreted less than S. avenae on the leaves. The size of honeydew droplets increased with the age of aphids but was not affected by BYDV infection.

GENERAL DISCUSSION

The results show that both crop species and growth stage influenced the effects of BYDV on its vectors. The effects were more severe on oats and barley than on wheat. The embryo count and progeny count methods were in agreement and the results of laboratory and field trials were similar. As might be expected due to factors outlined on page 116, the results presented here confirm some of the earlier studies but differ from others. In particular, they confirm the increase in the fecundity of S. avenae and R. padi on oats and the decrease in that of M. dirhodum on oats due to BYDV. The results on wheat and barley are new and reveal that whereas S. avenae was more fecund on virus-infected wheat and barley, R. padi contained more embryos on diseased barley only, while M. dirhodum was not affected by the virus.

Unlike fecundity, the effect of BYDV on honeydew excretion by aphids has not previously been investigated. The honeydew study shows quite clearly that BYDV infection of the host plant decreased honeydew excretion in both S. avenae and M. dirhodum. This compares well with the reduction in the frequency of excretion by Hyperomyzus lactucae L. on sowthistle by the sowthistle yellow vein virus (Sylvester, 1973).

Aerial suction trap and crop sampling over many years indicate that in the U.K., R. padi, and in West Wales also R. insertum, is mostly responsible for introducing BYDV into early winter-sown cereal crops in the autumn. The subsequent spread of the virus within a crop in the

spring and summer months is less well understood. However, since R. padi is less abundant than S. avenae and M. dirhodum on the crops during that time of the year, the latter two species are probably the main agents of virus spread in the spring and summer, although this will depend largely on weather conditions and the strain of BYDV involved (Plumb, 1976). S. avenae can transmit both severe and mild strains of the virus while M. dirhodum is associated with a mild one only (Plumb, 1974). In addition, S. avenae overwinters mostly viviparously on Gramineae, whereas M. dirhodum does so mainly as eggs on Rosaceae which are non-hosts to BYDV. S. avenae is therefore probably better suited to the role since most grasses are reservoirs of the virus, and since it would normally take longer for eggs than viviparous individuals to establish large populations from which alates would colonize cereals.

In any case, by the time of the main spring immigration of alates from winter hosts into cereal crops, and of inter- and intra-crop migration, symptoms of virus infection would usually have become apparent (Plumb, 1976). These symptoms include a change in the colour of the leaves from green to various shades of yellow-orange-purple. This study shows that these alates are preferentially attracted to the infected plants due to the colour of their leaves. The progeny of the colonizing aphids are enabled to attain a larger adult size on diseased plants due to the altered physiology of the latter following virus infection. Consequently aphids

contain more embryos which mature faster on BYDV-infected than on healthy plants, as is borne out by their greater numbers of embryos with pigmented eyespots at eclosion and by the fewer embryos still unborn after twenty days of reproduction. The virus thus enables the aphids to optimize their reproduction (Dixon & Dharma, 1980b) by producing more progeny earlier in their lives than those on healthy plants. Ultimately, larger populations of aphids develop on diseased plants than on healthy plants in the field.

The relative importance of the two mechanisms, increased attraction of alates to and increased fecundity of their progeny on diseased plants, is not easily defined since it would depend on the strain of the virus, the species of aphid and the species and variety of the crop. Thus, although both S. avenae and M. dirhodum are attracted to diseased plants, the fecundity of the former alone is higher on such plants. The larger numbers of S. avenae that develop on BYDV-infected plants must therefore be due to a combination of both effects of the virus. Preferential attraction alone apparently accounts for the increased populations of M. dirhodum on diseased relative to healthy plants. This hypothesis is supported by the greater numbers of alate M. dirhodum on infected oats in 1979.

There was no significant difference in the populations of alate S. avenae or M. dirhodum found on healthy and diseased wheat, contrary to the situation on oats and barley. This is attributable to the lower susceptibility

of wheat to BYDV infection, relative to oats and barley. The colour change induced in wheat by the virus was less intense than in the other two crops, and was probably not sufficient to show up significant differences in the numbers of alates found on healthy and diseased plants. However, there were significantly more apterae of both species on diseased plants (Figs. 17 & 18). It is possible that more alates landed on BYDV-infected plants, deposited some nymphs which later developed into apterae, but moved on again and did not remain long enough to be counted. Larger differences in alate populations might have been detected if the interval of sampling had been shorter than one week, but this was impracticable under the conditions of the experiments.

In his review of the role of aphids in the ecology of plant viruses, Swenson (1968) stated that viruses must maintain their populations by a dependable means of transfer among susceptible hosts, and the relationship between a virus and its vectors must ensure the necessary frequency of transfers. Aphids are the only known vectors of BYDV. This study indicates that BYDV enhances its own propagation among its plant hosts by enabling the aphid vectors to attain larger populations and, in the case of S. avenae on oats, by increasing the proportion of aphids that develop into alates on diseased relative to healthy plants (Page 54, and Gildow, 1980). Both effects are conducive to the increased movement of aphids within a crop and between different fields, and thereby to virus spread.

The relationship between BYDV and its aphid vectors is therefore mutually beneficial to both. By contrast it appears that the host plant is merely being exploited to the advantage of both virus and aphids. Firstly, virus infection of wheat, oats and barley caused considerable grain losses in grain yield (Table 3) through its effects on plant size, photosynthetic activity, and possibly also the translocation of nutrients from the leaves to the grains. Secondly, BYDV infection increased the population of aphids on virus-infected plants. Direct aphid feeding can cause serious yield losses especially if large aphid numbers are involved at the right plant growth stage.

Thirdly, although honeydew production by individual aphids is lower on infected than on healthy plants, this is more than compensated for by the significantly larger populations of aphids that develop on the former. Calculations using laboratory data on the rate of honeydew production and field data on aphid populations in 1979 and 1980 (see Appendix for formula) indicate that over a period of six weeks in 1979, M. dirhodum would have excreted 4.7% more honeydew on BYDV-infected (41.53 µl/tiller/day) than on healthy (39.68 µl/tiller/day) wheat plants in the field. Corresponding values for S. avenae over a nine-week period in 1980 were 22.5% more on infected wheat (5.00 µl/tiller/day) than on healthy wheat (4.08 µl/tiller/day).

Finally, both the mere presence of BYDV in the host plants in 1979 and 1980, and the higher aphid infestation

of infected plants in 1980 increased the growth of Cladosporium on the ears of wheat (Figs. 39, 40 & 41). Honeydew and Cladosporium, together with other sooty mould fungi, are thought to interfere with the functioning of the stomata and of the photosynthetic surfaces of cereals (eg. Rabbinge et al, 1981; Vereijken, 1979).

Therefore, although direct aphid feeding, honeydew and sooty mould growth are in themselves yield depressants, the influence of BYDV infection of the host plant is to aggravate their effects.

The questions asked at the beginning of this thesis can now be answered on the basis of the results presented. Greater numbers of both S. avenae and M. dirhodum develop in the field on BYDV-infected than on healthy wheat, oats and barley. This is attributable to the preferential colonization, by immigrant alates of both species, of diseased plants in the spring and summer on account of the colour of their leaves. In addition, S. avenae is more fecund and reproduces faster on infected plants than on healthy.

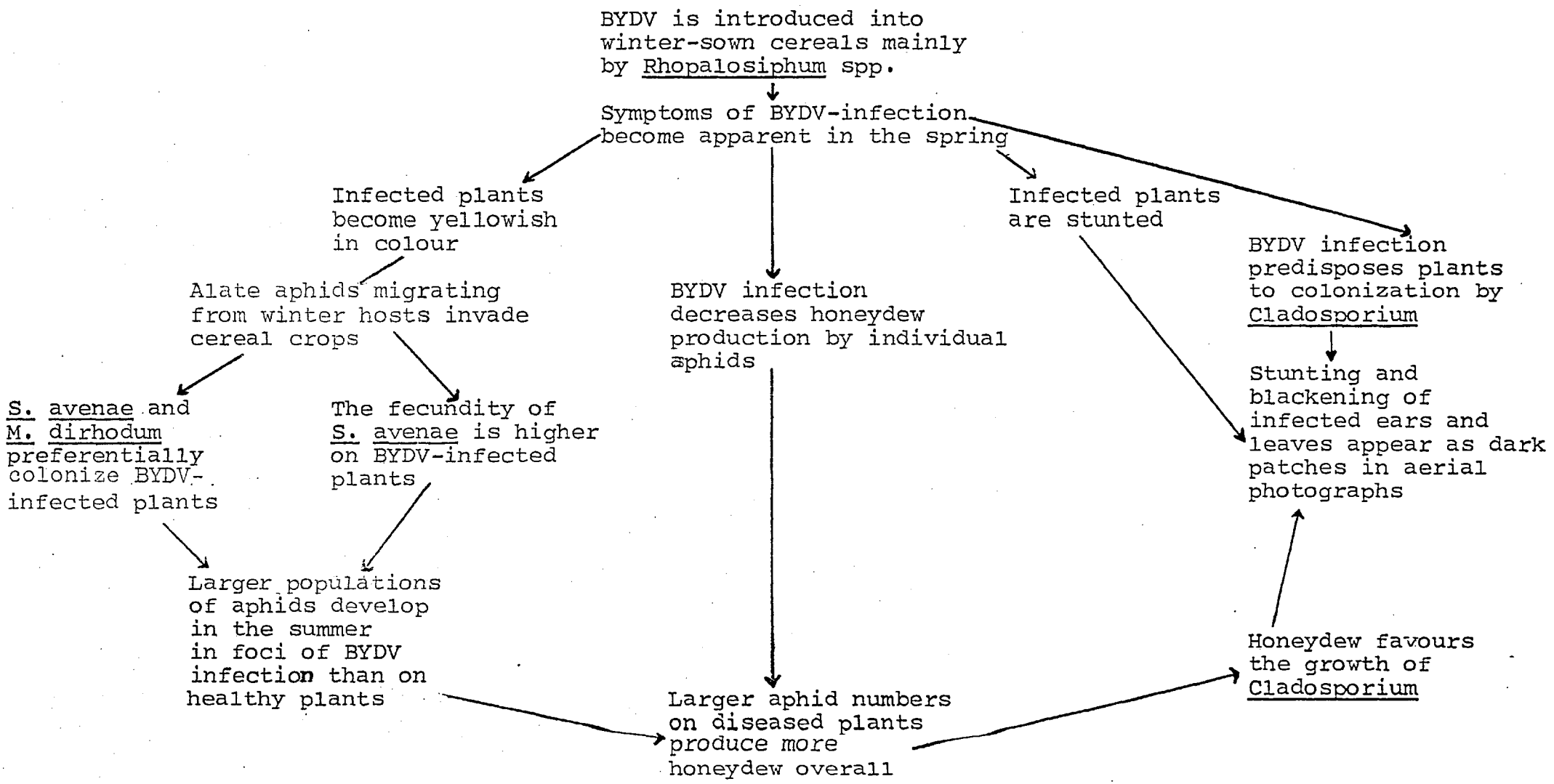
BYDV infection by itself predisposes wheat plants to colonization by Cladosporium and possibly other sooty mould fungi. In addition, the larger aphid numbers that develop on diseased plants produce more honeydew which favours the growth of Cladosporium on the ears and/or leaves.

The stunting of infected plants by BYDV together with the blackening of the ears and leaves by sooty mould growth produces the dark patches that

were recorded on the ADAS aerial photographs (Fig. 1).

The complex interactions between BYDV, its aphid vectors and plant hosts, and Cladosporium is illustrated diagrammatically overleaf.

Diagrammatic representation of the interactions between BYDV, its aphid vectors, and *Cladosporium*



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APPENDIX A

Table A: The effect of BYDV on the numbers of *M. dirhodum* per colony on oats, 1979.

Crop growth stage	Mean no. of aphids/colony	
	Healthy	Diseased
45	8.24	7.83
55	7.28	8.60
61	7.66	8.55
69	6.97	6.97
73	6.14	8.06
77	6.53	7.86
87	5.48	7.18
94	0.00	4.10
Seasonal Mean	6.04 ± 0.45	7.39 ± 0.47*

APPENDIX B

The following formula was used to estimate the quantity of honeydew excreted by *S. avenae* and *M. dirhodum* on wheat plants in the field:

$$a = b \times c \times d$$

Where

a = mean total volume (µl) of honeydew excreted/tiller/day

b = mean number of aphids/tiller/day

c = mean number of honeydew droplets/aphid/day

d = mean volume (µl) of each honeydew droplet.

Data for b were obtained from field counts of aphids in 1979 and 1980 (Section 1). The data for c and d came from laboratory studies on honeydew excretion by *S. avenae* and *M. dirhodum* on wheat (Section 5) and took into account the excretory capacities of the different age groups.