# INVESTIGATIONS OF RESISTANCE IN WHEAT, BARLEY, AND OATS TO HETERODERA AVENAE WOLL.



by

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## SUMMARY

Resistance of wheat, barley and oats to different populations of, and the effect of cultivars of wheat on the growth of *H. avenae* were studied.

White females in soil and on roots should both be considered when assessing resistance by the number of females produced on the cultivar. Different results between trials on resistance emphasised the need for uniformity within the accepted methods of assessment, which with the possibility of better methods has been discussed.

Different ratings of resistance occurred between cultivars of the same cereal, suggesting more than a single gene was involved. Two cultivars of wheat (Spring Wheat 12698 and Loros) were resistant. Problems in breeding with the resistant cultivars, and control by using susceptible cultivars have been discussed. Some cultivars reacted differently to the two populations of *H. avenae* used. Loros was resistant to one and susceptible to the other population. Therefore, at least two biotypes of *H. avenae* are in South Australia.

Four growth stages of females of *H. avenae*, separated by three moulting phases, occurred during development on Heron. Growth of the nematode was affected by inherent differences in

growth between cultivars (Heron and Justin) and/or environmental factors affecting growth of cultivars.

(a) Floral initiation occurred earlier in Justin than Heron.

(b) Female growth was slower during the pre-adult stage in Justin.

(c) Early growth of the adult female was similar, but was slower at a later stage when growth in Justin with and without floral initiation was compared.

Growth of H. avenae in resistant cultivars was similar to that in Heron during growth in the second larval stage, but differed in all later stages and few females developed. Infection occurred with all cultivars, and some larvae left the site of infection and reinfected the host at another site. Nematode growth was not retarded in resistant cultivars, but fewer females matured while normal development of the males occurred.

## DECLARATION

I hereby declare that the work presented in this thesis has been performed by myself, except where otherwise stated in the text, and has not been submitted in any other application for a degree.

(Peter C. O'Brien)

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# INTRODUCTION

Cereal root eelworm (Heterodera avenae, Wollenweber 1924, (Filipjev, 1934)), occurs throughout cereal growing regions of the world (Gair, 1965), including the following states of Australia; South Australia (Davidson, 1930), Victoria (Millikan, 1938), Western Australia (Goss, 1967) and New South Wales (McLeod, 1968). Although quantitative assessments are lacking, descriptive accounts of the effects of the disease (Hickinbotham, 1930; Parkin & Goss, 1968; Meagher, 1968 a) and the common use of susceptible cultivars (Brown & Meagher, 1970), indicate the economic importance of the organism in Australia.

H. avenae can apparently inter-act with other pathogenic agents, increase the severity of disease in crops, and cause cereal yield reductions. This was indicated for H. avenae and Rhizoctonia solani on wheat (Meagher & Chambers, 1971). However, for the nematode and "take all" (Ophiobolus graminis) on barley, the inter-relationship was negative, with reduced nematode populations occurring when the "take all" level of infection was increased (Cook, 1969). Therefore, other pathogenic effects could eventually be attributed to H. avenae and it may be of greater importance in cereal disease, although more detailed experimentation is

required to establish the inter-relationship of H. avenae with other organisms. But, an improvement in the control of H. avenae is required to reduce the incidence of the disease in cereal crops.

Effective chemical control of H. avenae in cereals is possible (Williams, 1969; Brown et al, 1970), but uneconomic (Williams, 1969), however the production of cheaper chemicals, lower application rates, or residual effects beneficial to succeeding crops, could make chemical control an economic proposition (Williams, 1969). The development of resistant cereal cultivars suitable for breeding has potential, even though recent attempts to establish resistance in Australia (Brown & Meagher, 1970), especially with wheat cultivars, are not encouraging. Further studies on cereal cultivars resistant to H. avenae in South Australia, examinations of techniques and development of new methods of assessment are presented and discussed within this thesis.

A detailed knowledge of the causal organism (H. avenae) is required to measure, understand and discuss resistance within the cereal cultivars, and so the biology of the causal organism is reviewed. Much of the biological and ecological information is inadequate, and information on other plant pathogenic nematodes, especially Meloidogyne spp.

Heterodera rostochiensis, and Heterodera schachtii, is included, to allow discussion by either comparing the different organisms, or by conjecture with H. avenae when insufficient data is available.

## 1. GENERAL BIOLOGY OF HETERODERA AVENAE

Since the first record of cysts on the roots of cereals by Kühn in 1874, various names have been given to the nematode (Gair, 1965) and so caused confusion until Franklin, Thorne and Oostenbrink (1959) proposed the standardised name of Heterodera avenae Wollenweber, 1924.

Original descriptions of cereal root eelworm morphology and host susceptibility in Australia (Millikan, 1938) differed from Canadian and European descriptions (Franklin 1951; Hesling, 1965). However, observations on morphology (McLeod, 1968) and host susceptibility (Mathison, 1966; Parkin & Goss, 1968) suggested that these differences are minor, and a distinct biotype (Brown, R., 1969) but not a distinct species has probably evolved in Australia.

H. avenae is an obligate parasite (Franklin, 1951) of plant hosts of Gramineae or possibly of certain tribes within that family (Winslow, 1954), although Gill and Swarup (1971) reported a non-graminaceous plant as a host in India.

Commercial cultivars of wheat, barley, oats (Millikan, 1938; Hesling, 1959) and non cultivated species, wild oat (Avena fatua), barley grass (Hordeum murinum) and bromes (Bromus spp.) (Parkin & Goss, 1968), are recognised hosts in Australia. Maize in India (Swarup et al, 1964; Yadav & Verma, 1971), and cereal rye in Australia (Brown & Meagher, 1970) may be important hosts, but the less widely distributed wild oat (Avena sterilis) is not a host (Brown & Meagher, 1970). The use of pasture grasses and leys (Duggan, 1958; Stone, 1960) to control cereal root eelworm was supported by Kort (1964) who established that common pasture grasses were poor hosts in the Netherlands. While this concept is accepted without evidence in Australia, it may not apply since the Australian nematode is a distinct biotype (Brown, R. 1969).

Symptoms of H. avenae in a cereal crop first appear as patches of stunted, discoloured seedlings, which may extend over the whole paddock and resemble symptoms of nitrogen deficiency or waterlogging (Goss, 1967). Usually the plants recover after the initial set back, but remain retarded in development, produce fewer tillers and yield less grain (Banyer, 1966). Severe infections may cause the seedlings to die, leaving bare patches in the field (Hickinbotham, 1930).

The above-ground symptoms can be confused with other conditions and confirmatory identification is obtained by an examination of the plant roots (Banyer, 1966). The primary (seminal) roots are normally infected, root development is hindered or stopped, swelling (galling) occurs at the infection site, and lateral roots develop abnormally from the gall. The laterals become infected and a bunched, matted, restricted, shallow root system forms (Davidson, 1930). Secondary (nodal) root development is delayed, usually allowing these roots to escape serious infection and enabling the plant to recover (Banyer, 1966). Oats often differ from wheat and barley by developing stunted, swollen roots with pronounced swellings, but lacking excessive lateral root growth (Banyer, 1966).

Later in the growing season white, swollen females are easily seen in the swollen or branched areas of the infected roots (Davidson, 1930). The white females provide the best evidence of H. avenae infection in a susceptible cereal host (Banyer, 1966).

## 2. LIFE CYCLE

The life cycle of *H. avenae* (Johnson & Fushtey, 1966) is similar to that of *H. Schachtii* (Raski, 1950; Shepherd, 1965) which is the type species of the genus *Heterodera* (Oostenbrink, 1960). All *Heterodera* spp. are obligate parasites on roots of vascular plant and underground stems (Franklin, 1951) although *H. trifolii* may also develop on leaves of white clover (Ross, 1960).

Most *Heterodera* spp. are heterosexual and show sexual dimorphism; the male is vermiform and free living for most of its adult life, whereas the adult female is sub-spherical or flask shaped and immobile (sedentary), spending its life inside or attached to the root (Shepherd, 1965). Following fertilisation, the female lays embryonated eggs until she dies, and the body wall hardens to form a tough, resistant, brown cyst containing the developing eggs (Shepherd, 1965). Eggs develop into "first stage" larvae, then the larvae moult to the "second stage" which are dormant until just before hatching (Raski, 1950; Franklin, 1951).

During the hot, dry, Australian summer when host plants are unavailable, *H. avenae* larvae survive within the egg inside the brown cyst (Meagher, 1970; Banyer & Fisher, 1971 a). Each cyst usually contains 200-250 eggs, although very full cysts contain over 600 eggs (Andersen, 1961).

A. Hatching

The eggs of some species of Heterodera are stimulated to hatch by exudates from the roots of host plants (Wallace, 1965). With H. avenae, hatching is either not stimulated by root exudates or stimulated by some ephemeral hatching factor (Hesling, 1957 a). Eggs of H. avenae are dormant at the time of cyst maturation and this aids survival by preventing a late hatch (Andersen, 1961; Banyer & Fisher, 1971 a). The break in dormancy appears to be due to environment and not to an inherent capacity (Banyer & Fisher, 1971 a).

H. avenae has one generation per year (Wallace, 1965), whereas H. schachtii can complete 5 generations per year in California (Jones, 1965) and H. rostochiensis develops a partial second generation in Britain (Jones, 1950). The number of generations completed by H. schachtii and H. rostochiensis depends upon the environment and host availability. H. avenae is restricted to a single generation by larval dormancy and the inability of hatching to respond to hatching factors exuded from the host roots.

Hatching studies in Europe and Canada cannot be directly related to the Australian situation because of climatic differences (Wallace, 1965; Meagher, 1970), e.g., the inability of cysts to survive desiccation in airdried

soil in the northern hemisphere (Duggan, 1960) predicts poor survival during Australia's summer, but local observations have established that the cysts are able to survive (Meagher, 1970; Banyer & Fisher, 1971 a).

Dormancy and the subsequent hatching of eggs are indirectly affected by soil texture, structure and moisture which influence oxygen supply to the cyst (Wallace, 1959; 1968 a,b). Low soil temperatures, though not essential, (Banyer & Fisher, 1971 a) will increase the hatching of eggs of H. avenae (Fushtey & Johnson, 1966; Banyer & Fisher, 1971 a).

The simultaneous hatching of large numbers of eggs causes extensive areas of severe infection in the field. This "mass hatch" is caused by the interaction of environmental factors which breaks dormancy and high moisture tension in the soil which restricts hatching until the opening rains (Banyer & Fisher, 1971 a). Therefore, most damage to cereal crops in South Australia could be expected in years with late opening rains (Banyer & Fisher, 1971 a).

B. Infection of and development within the host plant

After hatching the "second stage" larvae migrate to the host root. Movement of the larvae through the soil is affected by soil texture and structure because the larvae

need oxygen, a moisture film and room to move (Wallace, 1963; Fidler & Bevan, 1963), and sub-optimal conditions in the soil can cause an excessive expenditure of energy which limits the ability of the larvae to penetrate the host (Wallace, 1969 b). In Victoria, H. avenae appears to be restricted to the sandy solonised brown soils of the mallee and the friable grey soils of the Wimmera (Meagher, 1968 b). Such restrictions are not evident in South Australia where the nematode occurs in a wide range of soil types, including heavy clay soils (Banyer, 1966). The direction of larval movement through the soil to the host roots may be by chance or by attraction to either chemical stimuli or concentrated gradients induced by the host (Seinhorst, 1961; Klingler, 1965; Shepherd, 1965). When the larvae reach the host they usually penetrate near the growing point of the root (Johnson & Fushtey, 1966).

After penetrating the host root, the larvae move intracellularly, align themselves parallel to the stele with their heads oriented towards the root tip where the host tissue forms syncytia (giant cells) and the roots swell (Johnson & Fushtey, 1966). Evidence with other nematodes (Nusbaum, 1958; Krusberg, 1963; Johnson & Viglierchio, 1969 b; Orion & Minz, 1969) suggests that the larvae secrete either a growth substance or a precursor which stimulates formation of syncytia.

Growth and development continues with four growth stages. Each stage is separated from the previous one by a period of no growth or a moult during which development occurs (Johnson & Fushtey, 1966). Genital primordia develop early in the life cycle; the female larvae contain paired ovaries and the male has a single testis (Shepherd, 1965). Sexes have been distinguished in the third-stage larvae (Shepherd, 1965), although Johnson & Fushtey (1966) could not distinguish sexes with H. avenae on oats until the fourth stage larvae had developed. After the final moult (5th stage), the migratory male emerges from the host root and the sedentary female develops until the vulva either emerges from, or is near, the root epidermis (Johnson & Fushtey, 1966).

The female emits a sex attractant which attracts males of the same and other Heterodera species, there is no cross mating (Green & Plumb, 1970) and H. avenae males probably remain active for 9-10 days as is the case with H. rostochiensis (Evans, 1970). Although parthenogenetic reproduction has occurred within Heterodera spp. (Mulvey, 1958; Netscher, 1969), it has not been observed with H. avenae, and since it is a diploid, amphimictic species reproducing bisexually (Triantaphyllou & Hirschmann, 1964), parthenogenetic reproduction is not expected to occur.

C. Sex ratio

Equal numbers of males and females usually occur with bisexual, cross fertilising species (Triantaphyllou & Hirschmann,1964). However, since variable sex ratios have been reported for H. rostochiensis (Ellenby, 1954; Trudgill, 1967), H. schachtii (Kämpfe & Kerstan, 1964), a similar effect could be expected for H. avenae.

With Meloidogyne incognita, increased nematode populations within the host roots increased the number of males which developed and some males possessed two testes instead of the normal single testis, and this suggested sex reversal had occurred (Triantaphyllou, 1960). Davide & Triantaphyllou (1967), who obtained similar results with other Meloidogyne spp., suggested the majority of larvae were genetically "females", but environments unfavourable to development exercised a masculinising effect. Very few larvae died during development within the host, therefore if sex reversal was discounted, a differential ability between male and female larvae to penetrate the host roots may have occurred, but this was considered improbably by Davide & Triantaphyllou (1967).

There are two possible explanations of variable sex ratios in H. schachtii and H. rostochiensis - sex reversal due

to inadequate food being available to the developing female, and differential survival of larvae because of competition for the food available. The adult sex ratio is determined by the ability of infective second stage larvae to establish syncytia and derive suitable nutrition for normal development (Trudgill, 1967; Kerstan, 1969), and was affected by nutritional stress, due to inter-nematode competition (Ketudat, 1969; Trudgill, 1967), fungal competition (Ketudat, 1969), or lack of plant nutrients (Kämpfe & Kerstan, 1964; Johnson & Viglierchio, 1969 a).

Sex reversal in H. rostochiensis occurred when the host either reduced the food supply to the roots (Trudgill, 1967), or was resistant to development of females (Trudgill & Parrott, 1969). Single larval infections resulted in the majority of larvae developing into females and supported the principle of sex reversal when increased nematode populations infected plant roots (Ross & Trudgill, 1969).

However, it is often difficult to establish sex reversal because at times of nematode competition for space and food, female larval development is restricted and the larvae may die, resulting in a sex-dependent death rate during development which alters the sex ratio (Trudgill & Parrott, 1969 ; Ross & Trudgill, 1969). There is no evidence of sex reversal in H. schachtii, where variable sex ratios can be

explained by differential larval development within the host roots (Kerstan, 1969; Johnson & Viglierchio, 1969 a).

In the absence of published data on sex ratios in H. avenae, one can only assume that the nematode behaves similarly to H. schachtii, as discussed above.

## 3. HOST-NEMATODE RELATIONSHIPS

A plant is a suitable host of H. avenae when the nematode can infect the plant and complete its life cycle, and is "susceptible" when it supports the production of large numbers of prolific females (Shepherd, 1959). However, on some host plants, very few or no females develop, and the host is "resistant" (Andersen, 1961). Resistant plants do become infected, but nematode development is restricted by the plant (Cotten, 1967).

"Host efficiency" depends upon the host's ability to increase, maintain, or decrease the soil population of nematodes (Jones, 1956), while"tolerance" is the host's growth response to infection (Jones, 1956). A tolerant plant is capable of good growth and yield when infected by the nematode, and irrespective of its "efficiency", does not exhibit characteristic symptoms of nematode attack.

Reduced yields have been reported for H. avenae infections on barley cultivars not showing eelworm symptoms (Cotten, 1970 a), and the response of other cereals to infection is variable (Southey, 1955). The host status of cereals not only varies greatly between species and genera, but most importantly, between cultivars within individual species.

A. Variations in host response to infection.

Many comparisons of host response to H. avenae infection in various cereals have overlooked the importance of intra-generic variations. Thus Millikan (1938) rated wheat the most susceptible cereal in Australia, while Thomas et al (1946) found oats to be the most susceptible genus in Wales. Results from Western Australia (Parkin & Goss, 1968) establish oats as the most susceptible cereal. These variations in host susceptibility within the same country and between different countries ~~is~~ are due to either different nematode pathotypes or the use of different cereal cultivars.

Intra-species variation in host efficiency for each cereal genus has been established (Millikan, 1938; Brown & Meagher, 1970), and different susceptibility ratings are expected if different host plants are compared. Therefore, conclusions stating that oats is more efficient than barley, which is more efficient than wheat (Hesling, 1959; Stone 1960),

only have meaning when commercial cultivars are compared in a local region to improve control. Variations in H. avenae pathotypes within and between countries (Andersen, 1961; Cotten, 1963), give further evidence of the dangers of comparing cereals between different localities. However, the selection of standard cereal cultivars to compare the nematode pathotypes in different localities is acceptable (Kort et al, 1964; Cotten, 1963; Brown, R. 1969).

Environment will also increase host variations since plant growth, nematode population density and nematode reproduction rate are the end result of a complex ecological situation (Wallace, 1969 a).

B. Effect of nematode density on plant growth

Reduced plant growth and yields due to H. avenae infections of susceptible cereals were established during the first investigations in Australia (Hickinbotham, 1930). Hesling (1957 b) demonstrated the reduction of plant height as the initial nematode populations in the soil increased, but reduction in plant height was not correlated with reduced grain yields, although decreased yields did occur as the nematode population increased (Andersen, 1961). Most data on the effect of different densities of H. avenae on plant yield were determined indirectly after densities were reduced by crop

rotation (Gair et al, 1969) and the use of resistant cultivars (Williams, 1970). When nematode populations were reduced, the host responded with an increase in grain yield.

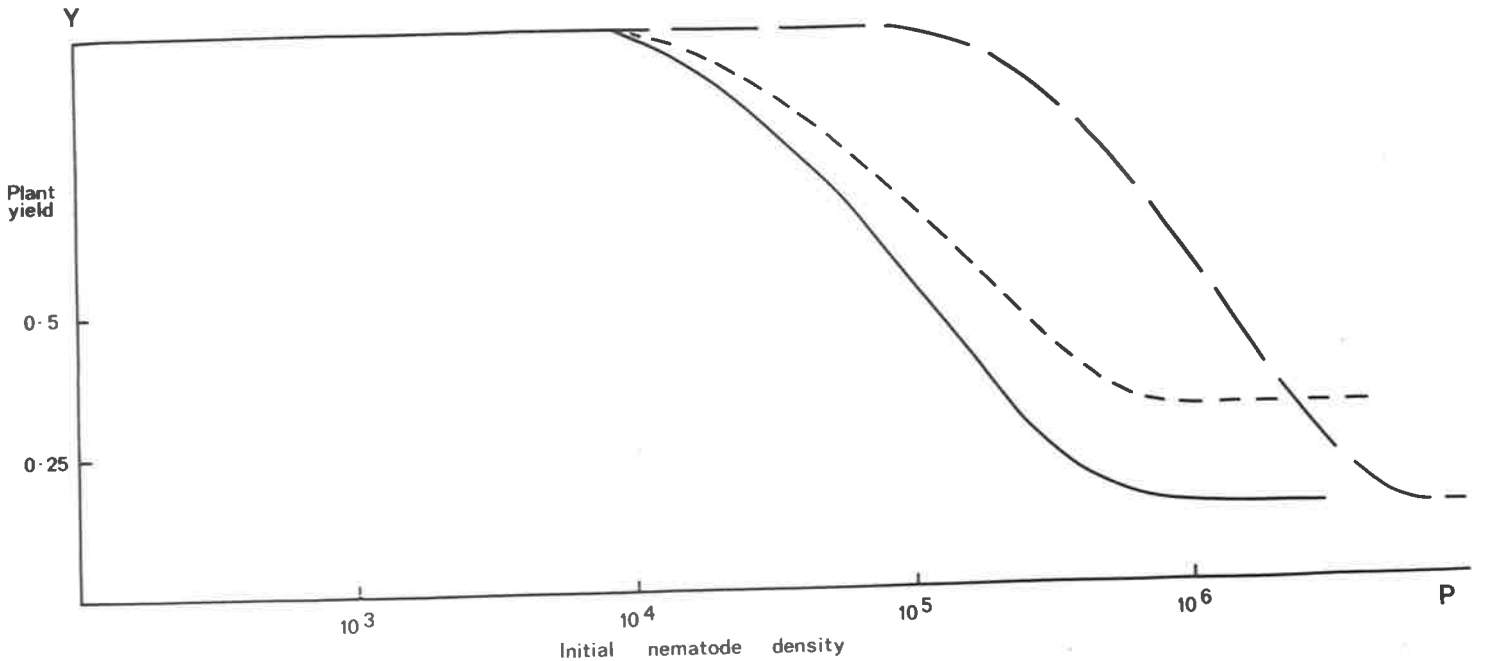
A mathematical relationship between host yield and nematode density (Seinhorst, 1965) has been substantiated with H. rostochiensis (Jones et al, 1967 b; Jones & Parrott, 1969) and H. goettingiana (Jones et al, 1965). The concept of a "tolerance limit" (Seinhorst, 1965) as the greatest nematode density at which no loss of yield occurred, was enlarged by Huijsman et al (1969) to include differences in the minimal yield between cultivars, as indicated in Fig. 1. Brown, E. (1969) observed variations which were independent of soil type and host cultivar, and with the potato cultivar used, he was unable to relate the density of H. rostochiensis to crop performance. However, the morphological response of the host to infection probably explains differences in tolerance to H. rostochiensis between potato cultivars (Huijsman et al, 1969; Seinhorst & Den Ouden, 1971).

Although nematodes are normally expected to reduce the yield of a host (as in Fig. 1), increased growth of a host with low populations of H. rostochiensis (Seinhorst & Den Ouden, 1971) and the stimulation of the growth of various hosts by Meloidogyne javanica (Wallace, 1971) have been reported. While H. rostochiensis may actually stimulate host growth, the

FIGURE 1

Relation between host plant yield and the nematode density (—). A higher tolerance can be obtained by a shift of the limit of tolerance to the right (---) or at a fixed limit of tolerance by a higher minimum yield (...).

(After Huijsman et al, 1969).


Y
Plant yield
0·5
0·25
10 3
10 4
10 5
10 6
P
Initial nematode density

increased yield of the host may be the secondary result of nematodes slowing the growth of the host and thus extending its life, which would allow the host to benefit from higher temperatures and longer days during maturation. Variations in host response to M. javanica infections (Wallace, 1971) are attributed to an inter-action between inhibitory and stimulatory actions of the nematode on the host. Further evidence is required to clarify the variations in host response to nematode infection.

Environmental effects of soil type, nutrients, moisture and host plant also influence the host response to infection (Jones et al, 1965; Wallace 1970), and severe crop losses in the field may be an inter-action between nematode population and the environmental stresses to the plant (Wallace, 1970). The relative importance of nematodes and limiting environmental effects on host yield, stress the need for further ecological studies.

The total ecology of H. avenae and the effect on cereal yield needs thorough investigation. Evidence available suggests that the relationship of H. avenae with cereals is similar to H. rostochiensis with potato, and the limitation of the initial population of nematodes is important in control.

C. Final nematode population

The following empirically based relationship between initial and final populations of sedentary nematodes which do not damage their hosts, has been proposed by Seinhorst (1967 a):

$$Pf = a\,(-\ln q)^{-1}\ (1 - q^{Pi})$$

If the nematode damages the host plant, a different relationship between initial and final nematode populations occurs (Seinhorst, 1967 c):

$$Pf = acz^{Pi}(-\ln q)^{-1}\ (1 - q^{Pi/C_2^{Pi}})$$

Both empirical formulae are supported by experimental data obtained for H. rostochiensis in potato and are presented in Fig. 2.

Departure from the predicted relationship may occur at high and low initial population levels. With low initial populations, the probability of successful female reproduction is reduced due to difficulties of mating between scattered nematodes (Seinhorst, 1968). Less nematode infection of host roots due to restricted root development is unlikely at high initial nematode populations (Seinhorst, 1967 c; Wallace, 1969 a), however either a change in sex ratio caused by inter-nematode

FIGURE 2

(a) Relation between initial and final densities of *Heterodera rostochiensis* (according to Den Ouden & Seinhorst, 1964) when no host damage occurs. Initial and final populations are in eggs per 100 g of soil.
(Modified after Seinhorst, 1967 a).

(b) Relation between initial and final densities of *Heterodera rostochiensis* on potato with host damage (according to Den Ouden, 1966). Initial and final populations are in eggs/g of soil.
(Modified after Seinhorst, 1967 c).

FIGURE 3

Summary of the effects of the cultivation of host and non host crops on final populations of *Heterodera schachtii*.
(Modified after Jones, 1956).

FIGURE 2

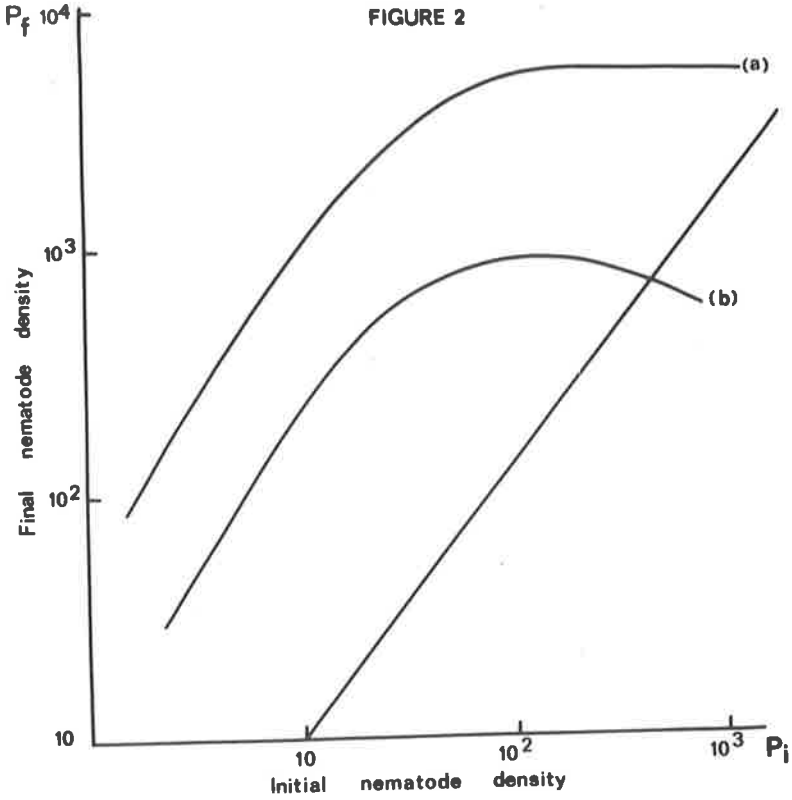
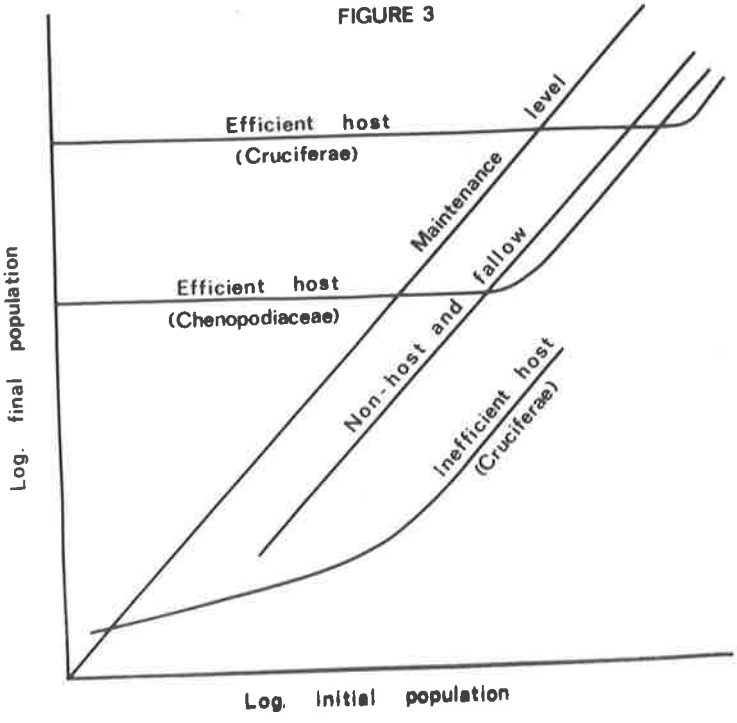



FIGURE 3



competition (Davide & Triantaphyllou, 1967; Kerstan, 1969), or nematode death due to necrotic host tissue associated with severe infections (Seinhorst, 1967 c) may result in either static or reduced populations.

Jones et al (1967 a) computed population changes of H. rostochiensis during growth of resistant cultivars, but guessed many required parameters in lieu of sufficient experimental data. Some of the parameters that influenced final nematode populations were environmental effects on plant root growth, nematode hatch, movement of larvae through soil and infection of the host plant (Wallace, 1969 a). Therefore, the maximum rate of multiplication and highest equilibrium density of nematodes depended upon external conditions as well as the inherent characters of nematodes and host plants (Seinhorst, 1967 b).

Host efficiency has a big effect on the eventual nematode population. When the final population is the same as the initial population a "maintenance" level occurs. Data from H. schachtii infections showed efficient hosts increased the population while either inefficient or non-hosts reduced the final population below the maintenance level (Jones, 1956; Seinhorst, 1967 a). This host effect is presented in Fig. 3. Inefficient hosts reduced H. avenae populations (Hesling, 1959; Stone, 1960), while a population reduction, at a slower rate,

also occurred with the continual cropping of efficient, susceptible hosts (Gair et al, 1969; Cotten, 1970 b). These reductions in the presence of susceptible cultivars have not been explained, and support the probability of other interactions on nematode populations as discussed earlier.

A nematode reaction to increasing populations in the host roots may be limited female development, causing smaller cysts with fewer eggs to form. Production of smaller cysts with fewer eggs as the initial population increased occurred with H. avenae (Hesling, 1957 b), but not with H. rostochiensis (Seinhorst, 1967 a), and the different responses could occur as either a species difference or the development of different pathotypes of H. avenae.

Methods for controlling nematodes include soil fumigants, nematode trapping fungi, and other enemies which reduce nematode populations. With high initial population levels, it is unlikely that such methods reduce the nematode population sufficiently to give good control (Jones et al, 1965). Probably the best chemical control would be a non-phytotoxic systemic poison applied either to the plants, or introduced to the soil near the roots (Jones et al, 1965). Such chemical control methods are effective on H. avenae (Brown et al, 1970), but are not economic (Williams, 1969; Brown et al, 1970). Therefore, improved yield by reducing

populations with resistant cultivars (Cotten, 1970 b; Williams, 1970), appears to be a more profitable method for the future. One danger with resistant cultivars is the breakdown of resistance by increasing the population of resistance breaking pathotypes (Williams, 1970).

## 4. HOST RESISTANCE TO NEMATODE INFECTION

Resistance in barley cultivars to H. avenae increased yield, not only by reducing the nematode population (Cotten, 1970 b; Williams, 1970), but also by increased tolerance over susceptible cultivars when high initial populations of nematodes occurred (Cotten, 1967). However, selection for tolerance had the practical difficulty of recognising degrees of tolerance under field conditions (Cotten, 1970 a).

Some barley cultivars were recognised as resistant to H. avenae by Nilsson-Ehle (1920). Subsequent studies recorded further resistant cultivars (Millikan, 1938; Andersen, 1961; Cotten, 1963), which were restricted to oat and barley cultivars until the Danish spring wheat, cultivar, Loros was reported resistant by Nielsen (1966). Loros was susceptible in Victoria, Australia (Brown & Meagher, 1970).

Cereals having none or very few females on their roots (Andersen, 1961), have been described as resistant. A more

definite criterion for rating cultivars as resistant has been proposed; " a cereal variety is considered to be resistant to the cereal cyst nematode if the total number of newly formed cysts on the roots does not exceed the decisive limit of 5 per cent of the total number of newly-formed cysts on a susceptible comparative variety, under equal conditions of testing. There should be a sufficient replication of numbers to produce a minimum of two hundred newly formed cysts on the susceptible comparative variety" (Brown, R.,1969).

A recently formed International group (Brown, R.,pers. comm.), is attempting to standardise the susceptible comparative cultivars and the methods for testing resistance.

A. Biotypes

Barley cultivars resistant to one population of H. avenae were susceptible to other populations within Denmark, and two distinct races or biotypes of the nematode were recognised (Andersen, 1959). Standard test plants were used in other European countries and several biotypes of H. avenae were diagnosed (Cotten, 1963; Kort et al, 1964; Neubert, 1966).

When the European test plants were used in Victoria, one biotype which differed from the European biotypes was established, and additional biotypes may be recognised when

the number of indicator plants is extended (Brown, R.,1969). Although resistance testing throughout Victoria was reported to support the conclusion of one biotype present (Brown & Meagher, 1970), variations in host response to nematode infection occurred, which may have been an effect of either different biotypes or changes in environment. Further information on biotypes within Australia is lacking.

B. Inheritance of resistance

Variations in the pathogenicity of isolated H. avenae populations and the occurrence of different biotypes can be explained by the gene-for-gene hypothesis (Hayes & Cotten, 1970), which proposes that the genes for resistance within the host are matched by genes for virulence within the nematode. By comparing the reported responses of barley cultivars to different nematode races, Hayes & Cotten (1970) have tentatively predicted the minimum number of genes governing host resistance and nematode virulence as six for each organism.

Barley resistance in Denmark was due to single dominant genes (Andersen, 1961), and two genes for resistance on different loci, either on the same chromosome without linkage or on different chromosomes, were established (Andersen & Andersen, 1968). Cotten & Hayes (1969) identified three

genes and confirmed the existence of another, one gene was independent of the other three which were closely linked on the same chromosome.

Due to difficulties in isolating pure H. avenae populations, no positive information is available on the genes for nematode virulence. However, virulence appears to be dominant (Anderson, 1965).

C. Response of plants resistant to infection

Host genotypes will express resistance by either limiting the penetration of nematode larvae or preventing normal growth and development of female nematodes after infection.

Resistance in barley cultivars to H. avenae had no effect on larval penetration (Cotten, 1967, 1970 a), although host effects on penetration occurred with H. schachtii (Shepherd, 1959). Retarded female development and decreased numbers of nematodes occurred within host roots resistant to H. avenae (Cotten, 1970 a), H. schachtii (Shepherd, 1959), and H. glycines (Ross, 1962). The reduced nematode numbers were due to a higher death rate with H. schachtii (Shepherd, 1959). All larvae of Meloidogyne incognita acrita migrated out of the roots of resistant alfalfa plants after successful

penetration, because there was no host response to infection (Reynolds & Carter, 1969). Both these effects of death and movement could explain lower female numbers of H. avenae in resistant cultivars.

Cytological changes occurred in the roots of corn (Zea mays L. variety, Pride 5)when infected by H. avenae, and these inhibited mating and reduced egg production (Johnson & Fushtey, 1966). Further evidence of cytological reactions with H. avenae infections is lacking.

Thus, very little is known of the response of plants resistant to H. avenae infection. A better understanding of the responses and the biochemistry of resistant host reactions is required and may allow the development of better techniques for assessing plant resistance.

## D. Techniques in assessing plant resistance

The use of a standard criterion to determine resistance, (Brown, R.,1969) while desirable, is difficult due to the wide variations in the numbers of females produced on genetically homozygous, susceptible genotypes (Cotten & Hayes, 1969). Such variations occurred under a uniform environment and made it impossible to determine a numerical limit for resistance (Cotten & Hayes, 1969). Therefore, techniques are

needed to restrict variation. This could be achieved by either more precise control over the present techniques or the development of new methods of evaluation.

With current techniques, the plant growth container, soil mixture, methods of inoculation and female counting, cause variations which can be minimised.

When different soil containers were used under uniform test conditions, the female count was changed (Andersen, 1963). Inoculation was by using infected soil and may have altered infection levels, although changes in the soil environment due to the different containers were probably the main cause of variation. Infected soil with a known cyst content (Andersen, 1961), is commonly used as the inoculum to test responses of hosts to infection. Therefore, when different soil mixtures are used to test for biotypes, the host-nematode relationships will vary as previously reviewed.

Inoculations with infected soil are expected to have a normal distribution of cysts, but large variations in hatching can occur (Banyer & Fisher, 1971 a, b) and cause large differences in nematode infection between treatments. Therefore, by using motile, second stage larvae as the inoculum, it may be possible to limit variation in infection. Such inoculations have been successful (Shepherd, 1959;

Endo, 1964) and the number of larvae infecting the host roots have been measured (Shepherd, 1959; Cotten, 1970 a) in other studies.

Counting the number of white females on an entire root system after careful washing (Andersen, 1961) is often used to assess host resistance. However, the development of dense root systems by plants have prevented accurate counts (Kort et al, 1964). More accurate counts were made by Cotten (1963) when the white females were washed from the bulky roots and counted from the soil.

Therefore, variability can be reduced by modifying current techniques, and although fewer cultivars will be tested at one time, simpler techniques can be used in the initial selection. The recommendations of an International group (Brown, R., pers. comm.) appear to be self-defeating, since a standard criteria is suggested without uniform testing methods.

When the resistant mechanisms of cereals to H. avenae infections are clearer, new techniques may develop from either life cycle studies of the nematode or biochemical tests. However, the fluctuating environments associated with field trials induce variations unsuitable in evaluating resistance. Once resistance is established, the cultivar must be tested in the field to test its suitability for breeding.

## E. Breeding for resistance

Resistant cultivars of cereals with commercial agronomic characters are needed for practical control. Current commercial cultivars of wheat and barley have insufficient resistance (Brown & Meagher, 1970), and although oat cultivars can be used (Mathison, 1966), they are not generally grown. Therefore, when suitable resistance is recorded it will need to be introduced into the commercial cultivars of Australia. Present techniques of assessment of resistance are destructive of plants and prevent seed development. Since plant generations are propagated by seeds, new, non-destructive techniques are required in plant breeding.

Monogenic or vertical resistance is broken more quickly than polygenic or horizontal resistance, and the rate of breakdown depends mainly upon the virulence of the pathogen (Van der Plank, 1968). Although horizontal resistance is difficult to assess and transfer between cultivars, it has potential in future breeding programmes. Therefore, the development of vertical resistance and the rotation of resistant and susceptible crops as recommended by Jones et al (1967 a) would give earlier benefit. But, more information is needed on the virulence of H. avenae before recommendations are made for the use of resistant cultivars.

## 5. AIM OF EXPERIMENTAL WORK

Because of the importance of *H. avenae* in limiting yields of wheat in South Australia, and the possible improvement of control by using resistant cultivars, an investigation of host resistance to the nematode was undertaken.

Cereal cultivars, especially wheat, were screened for resistance to *H. avenae*, and critically tested to determine the degree of resistance.

The life cycle of the nematode in susceptible and resistant hosts was examined, and comparisons under uniform and different environments made.

Attempts were made to evaluate certain aspects of resistance testing, develop new evaluation methods, and suggest further studies to utilise the resistance cultivars reported herein.

## RESISTANCE WITHIN WHEAT, BARLEY AND OAT CULTIVARS TO HETERODERA AVENAE

H. avenae causes one of the most important diseases affecting cereals in South Australia. This is due partly to the use of susceptible cereal cultivars and partly to ineffective control by crop rotation in farm management. Certain oat cultivars effectively reduce soil populations of the nematode (Mathison, 1966), but they usually follow susceptible wheat and barley crops when grown. The crop rotation is completed by either one or two years of pasture. Wild oats (Avena fatua) and barley grass (Hordeum murinum ~~marinum~~) are the dominant grasses of many pastures in S.A., they are efficient hosts of H. avenae (Parkin & Goss, 1968), and are not effectively controlled by cultural practices. Therefore, the influence of inefficient oat cultivars on H. avenae is lost with present farming methods.

Although the organism can be effectively controlled by chemical means, such control is uneconomical at this time (Brown et al, 1970) and the development of suitable resistant varieties needs to be explored. Certain barley (Hordeum sativum) and oat (Avena sterilis and Avena strigosa) cultivars are resistant, while several oat (Avena sativa) cultivars are moderately resistant to H. avenae in Victoria (Brown & Meagher,

1970). The Danish spring wheat cv. Loros was reported as resistant in Europe (Nielsen, 1966), but was subsequently found to be susceptible under Victorian conditions (Brown & Meagher, 1970). No wheat (Triticum aestivum) cultivars have been reported as resistant to H. avenae in Australia.

Different biotypes of H. avenae occur throughout Europe (Andersen, 1959; Cotten, 1963; Kort et al, 1964; Neubert, 1966) and a distinct biotype (Brown, R., 1969) but not a distinct species has probably evolved in Australia. Different biotypes may occur in Australia, but they cannot be identified until a test assortment of resistant cultivars is established. Therefore, the recognition of cereal cultivars with resistance to H. avenae will aid the identification of different biotypes and improve the control of the organism.

## 1. MATERIALS AND METHODS

The results of resistance of cereal cultivars to H. avenae were determined from four separate trials conducted during 1967, 1969, 1970 and 1971. Each of the last three trials was designed in January of the year of the trial as a sequel to the one preceding it, after a revision of aims, techniques and cultivars used previously had been made.

## A. Selection of cereal cultivars

### (i) Wheat cultivars

During January, 1967, 790 cultivars were selected at random from the Waite Agricultural Research Institute (W.A.R.I.) wheat cultivar collection, and included cultivars from 44 different countries and several cultivars of unknown origin (Appendix 1). Additional cultivars included for testing during 1969 were two new cultivars released from Roseworthy Agricultural College (R.A.C.), six cultivars which produced a good yield on a nematode infected site during 1968 (Rathjen, pers. comm.), and the Danish cv. Loros (Appendix 2).

### (ii) Barley and oat cultivars

The barley and oat cultivars tested during 1967 were the complete cultivar collections at R.A.C. The collections contained 31 barley and 81 oat cultivars (Appendix 3). Four new barley cultivars developed at the W.A.R.I., one barley cultivar (Esperance) and one oat cultivar (Saia) reported resistant to *H. avenae* in Victoria (Brown & Meagher, 1970) were included in the cultivars to be tested for resistance during 1969 (Appendix 4).

(iii) Selection of control cultivars

Heron, Prior and Early Kherson were selected as the wheat, barley and oat control cultivars respectively and were retained as controls throughout the experiments, irrespective of alterations in seasonal cultivar recommendations. All the control cultivars selected were susceptible to H. avenae, widely grown throughout South Australia and recommended as commercial cultivars during 1967.

The susceptible oat cultivar (Sun II) recommended by an International group (Brown, R., pers. comm.) was included in the 1971 pot trial to compare with the susceptible oat cultivar, Early Kherson.

B. Preliminary selection of resistant cultivars

Cereal cultivars selected during 1967 (Appendices 1,3) were tested for resistance to H. avenae in a field trial at R.A.C. in 1967.

(i) Site of trial

An area of wheat cv. Heron infected with H. avenae during 1966 at Roseworthy Agricultural College was examined for the distribution of the nematode in February, 1967. The area was divided into smaller units of 16 $m^2$, and from each

sub-unit the number of cysts in the soil around the roots of five stubble plants selected at random was assessed. Each soil sample was thoroughly dried and the cysts collected from a Fenwick can (Goodey 1963). The organic material collected was remixed with water, aliquots were filtered through Whatman No. 1 filter paper, and the number of new cysts counted under a dissecting microscope.

A trial site of 40 m x 170 m was selected for the trial. Throughout the site, each sub-unit averaged 5 or more new cysts per stubble plant and the soil was a Mallee loam.

(ii) Experimental design

Cereal cultivars tested for resistance (Appendices 1,3) were grown in single rows. Each row was 11.5 m long and the seeding rate was designed to give a seed spacing of 0.15 m. The rows were spaced 0.45 m apart. The seeding rate and row spacing were designed to reduce competition between cultivars and facilitate the assessment of resistance on individual plants.

(iii) Field management

The trial site was cultivated with a disc plough, combine tynes and harrows to prepare a good seed bed. Prior

to seeding, the area was fertilised with a 3 to 1 mixture of superphosphate to sulphate of ammonia at a rate of 30 kg/ha. Seeding was on the 27th July, 1967, and was done with a modified Finlay seeder (Finlay, 1963).

(iv) Assessment of resistance

The cultivars were examined for resistance either just prior to or at ear emergence. Five plants were randomly selected per cultivar, and each plant was carefully removed from the soil to retain as much of the root system as possible. The roots were gently agitated to remove loose soil, carefully washed in water and examined for white females of the nematode. The cultivars with no females were selected as being resistant and these cultivars were tested again in the field during 1969, either to confirm or negate this resistant classification.

C. Further evaluation of resistance and tolerance

Some additional cereal cultivars and the cultivars selected as resistant from the 1967 field trial (Appendices 2,4) were tested for resistance in a field trial during 1969 at Watchman. Information was also sought on cultivar tolerance by comparing the growth of each cultivar in infected and non-infected soil.

(i) Site of trial

The year 1967 was a drought year and the effect of drought on yields at R.A.C. is shown in Table 1. Reduced growth and yields due to the drought conditions masked the effect of H. avenae in all crops, and no selection of sites with H. avenae infections could be made in 1967 for the 1968 season. During 1968, a site was selected at Watchman as no suitable site was available at R.A.C.

Two trial areas were selected and these differed by the presence and absence of H. avenae infection assessed by reduction in crop growth during 1968. Both sites were on a sandy loam soil in the same field. The density and distribution of H. avenae cysts in each site was determined from 2.5 cm x 2.5 cm x 15.0 cm soil core samples taken at the intersecting points of a 1.5 m x 2.0 m grid pattern. The number of cysts in each sample was assessed by the method described in Methods B (i).

An area of 30 m x 40 m with a nematode cyst population greater than 30 cysts per 100 g of topsoil was selected for the nematode infected trial site. A similar area with no cysts recorded from the soil was selected as the nematode free area.

TABLE 1

Average grain yields of wheat, barley and oats at R.A.C. from 1966-1971 and total rainfall from April to October inclusive.

Only yields of crops after a period of leyland are given because all field trials for resistance were after a period of leyland. The rainfall represents rainfall during the normal growing period of crops at R.A.C.

| Year | Rainfall (mm) | Cereal grain yield (kg/ha) | | |
|---|---|---|---|---|
| | | Wheat | Barley | Oats |
| 1966 | 255.5 | 1614 | 1667 | 1748 |
| 1967 | 162.1 | 1055 | 1033 | 412 |
| 1968 | 473.1 | 2865 | 2431 | 1968 |
| 1969 | 292.6 | 2556 | 1711 | 1430 |
| 1970 | 317.8 | 1923 | 2361 | 1613 |
| 1971 | 413.0 | 3100 | 2507 | 2362 |

(ii) Experimental design

A randomised split-plot design with 3 blocks at each of two sites was used, with whole plots of wheat, barley and oats within each block and the treatments randomised within each whole plot.

Each treatment contained two test cultivar rows with a control row on each side. The rows were 4 m long, 0.2 m apart, and the seed spacing within rows was approximately 0.04 m. Row spacings were selected to comply with normal farming practice, and the seed spacings complied with the normally recommended seeding rates of 44.8 kg/ha to 67.3 kg/ha for wheat, barley and oats.

(iii) Field management

Seed bed preparation was the same as described in Methods B (iii) and prior to seeding, superphosphate fertiliser was applied at the rate of 30 kg/ha. The trial was sown on the 27th May, 1969, with a modified Finlay seeder (Finlay 1963). On the 31st July, sulphate of ammonia was applied at the rate of 44.8 kg of N. per ha and later, on the 4th August, the plots were sprayed with a prometryne/2.4 D ester mixture to control weeds. Both applications were part of the normal crop management programme for the district.

(iv) Assessment of tolerance and resistance

Originally, the grain yield of each treatment was to be used in the assessment of tolerance. However, plant density was reduced up to 70 percent by a field mice plague following seeding and this made yield evaluations impractical. Therefore, tolerance was assessed on a visual appraisal of growth compared with the susceptible control cultivar.

Resistance was assessed by a modification of the method described in Methods B, (iv). Three plants per treatment in the infected site were examined on 10th September, and the white females per root system were counted. When the female count was less than 10 for the three plants within a treatment, three plants from each of the two adjacent control rows, (Methods A, (iii)) were examined to confirm infections of H. avenae and three additional plants were examined within the test cultivar rows.

The standard error was calculated for all cultivars with less than 50 females per root system and the remainder were recorded as having more than 50 females per root system. A resistance rating was given to each cultivar according to Table 2 which was a modification of the criteria used by Brown & Meagher (1970).

TABLE 2

The number of females of H. avenae produced on a cereal cultivar expressed as a numerical rating and a descriptive reaction of resistance.

| Females/root system | Rating | Reaction |
|---|---|---|
| 0 | 1 | Resistant (R) |
| 1 - 10 | 2 | Moderately resistant (M.R.) |
| 11 - 50 | 3 | Susceptible (S) |
| 50 | 4 | Very susceptible (V.S.) |

Each cultivar was placed in the highest rating possible after considering the mean number of females per root system and the standard error of all plants tested for that cultivar.

D. Critical evaluation of resistance

The resistance of cereal cultivars selected from the 1969 field trial was assessed in two separate pot trials during 1970 and 1971.

(i) Experimental design

Cultivars with a resistance rating of 1 or 2 were selected from the 1969 field trial and tested for resistance and tolerance in a pot trial during 1970. A randomised block design was used and contained four blocks with three sub-plots in each block. Cultivars were grown in infected soil to evaluate resistance, in infected and non infected soil to measure tolerance, and the three treatments constituted the sub-plots. The sub-plots were completely randomised with one another within each block.

A further selection of cultivars with a resistance rating of 1 or 2 was made from the first pot trial, and with the commercially recommended oat varieties, were tested again for resistance during 1971. The trial contained six blocks in a randomised block design.

Throughout both trials, 0.002 $M^3$ (2 litre) polystyrene pots were used to grow a single test plant. Each block contained pots of the same colour and the treatments were randomised within each block at weekly intervals.

(ii) Collection of inoculum

Partly due to difficulties in collecting and isolating large numbers of cysts from Watchman, and partly due to an attempt to gain some information on biotypes, the inoculum of

H. avenae cysts for the pot trials was obtained from a sandy soil at Mannum. Inoculum was collected during February 1970 and 1971 from the same site, and after infected barley (cv. Clipper) had been grown during the previous year. Soil was removed to a depth of 15 cm , sieved through a coarse sieve and roots and debris retained by the sieve were placed in air-tight polythene bags with a limited quantity of soil.

(iii) Inoculation and management of trials

Cyst material collected during 1970 was stored at ambient temperature until mid-May. The roots were separated from the soil with a 2.38 mm sieve, shredded and remixed with the soil. A soil mix of 2 parts inoculum, 4 parts sand, 4 parts loam and organic fertiliser was thoroughly mixed by coning and quartering. Due to the size of the trial, two mixes of inoculated soil were required. A nematode free soil mix was prepared by replacing the infected soil component with sand.

Soil was added to within 2 cm of the top of the pots and they were stored in a damp condition at ambient temperature for two weeks. A single germinated seed of a test cultivar was planted at a depth of 2 cm in each pot. The pots remained at ambient temperature for an additional two weeks, and then they were transferred to the glasshouse.

Half the cyst material for the 1971 trial was stored at ambient temperature, and the other half at 5°C. The pots were prepared, inoculated and seeded during mid-May in a similar manner to the 1970 trial. However, the inoculated soil in the mix was made up from equal proportions of cysts stored at ambient temperature and 5°C. The final cyst content was 3.6± 0.4 cysts per 100 gms of soil (Methods B, (i)). Only one soil mix was prepared and the pots were moved immediately to the glasshouse.

Management of the pots was the same for both trials. Pots were checked daily, dusted with Sulphur to control powdery mildew, sprayed with "rogor"* insecticide to control green aphid, and watered when required.

(iv) Assessment of tolerance and resistance

During the 1970 pot trial, tolerance was assessed by comparing the growth and yield of each cultivar grown under inoculated and non-inoculated conditions.

The resistance of cultivars to H. avenae was assessed in both trials on the number of females produced per plant. At ear emergence, the plant was removed from the pot and the excess soil gently washed from the roots. The remaining

* 40% w/v dimethoate (o,o-dimethyl S-(N-methylcarbamoylmethyl) phosphorodithioate).

soil was removed by more vigorous agitation and collected in a large beaker. Fine soil particles were removed by washing through a 0.149 mm sieve, and the females counted by spreading the remaining soil evenly over a flat tray with a black base. The root material was macerated in a Waring blender, washed with a fast jet of water through a 1.68 mm sieve and collected in a 0.149 mm sieve. Counts of females were made by the same method used for the soil count. The total female count was the addition of the soil and root counts.

(v) Statistical analysis

The results for wheat, barley, oats in the 1970 trial, and wheat, oats and commercial oats in the 1971 trial were transformed to log (x + 2). An analysis of variance was made on each and the L.S.D. at 5% was determined when significance was present.

Because both trials were designed to test resistance, the results of cultivars common to both trials were analysed as a 5 x 2 factorial for wheat, and a 12 x 2 factorial for oats to test for the presence of cultivar x trial interactions.

## 2. RESULTS

Severe drought conditions (Table 1) during the preliminary field trial for resistance (Methods B) prevented 58 wheat cultivars from growing and caused poor growth in all other cultivars. Although assessment of resistance was difficult, 13 wheat, 8 barley and 22 oat cultivars were selected for further testing. These selected cultivars and additional cultivars, when tested at Watchman in 1969, (Methods C) showed a range of reactions from resistant to very susceptible (Table 3). All of the barley cultivars tested were tolerant whether they were rated as susceptible or moderately resistant while few of the wheat or oat cultivars were tolerant (Table 3). The cultivars rated resistant or moderately resistant were selected for further pot trials for resistance.

Results of the pot trial in 1970 to examine resistance are shown in Table 4. All barley cultivars were rated as susceptible, but when the numbers of females developed by each barley cultivar were compared on the basis of the L.S.D., (Figure 4), three distinct levels of susceptibility became apparent. The reactions of wheat and oat cultivars, (Table 4), showed considerable variation. When the resistance of cultivars tested in the pot trial (Table 4) were compared with the reaction from the field trial

(Table 3), marked differences occurred within certain cultivars, especially Loros, Freja, Avon, Irwin and Swan. No assessment of tolerance (Method D (iv)) was made from the 1970 pot trial as no significant differences in growth occurred between infected and non infected cultivars.

When the resistant and moderately resistant wheat and oat cultivars were examined in the further pot trial, significant variations in the number of females per plant occurred between cultivars (Figure 5), and three indistinct levels of resistance could be noted for both wheat and oat cultivars.

Both of the pot trials to test the resistance of cultivars to H. avenae produced significant results, but when cultivars of oats common to the two trials were compared (Figure 6), a cultivar x trial interaction became apparent. A factorial analysis of variance (Table 5) confirmed a cultivar x trial interaction for both oats and wheat.

In the method used to assess cultivar resistance in the second pot trial, females in soil and on roots were counted. A significant correlation ($R_{(104)} \doteq 0.78$) occurred between numbers of females in the soil and from roots when all treatments were compared, i.e., for a range of numbers of females on roots from 0 to 264 (Figure 7).

The slope of the regression line for this correlation was 0.76. But when treatments with five or less females on the roots were compared, the correlation ($r_{(26)} = 0.27$) was not significant.

Good resistance to H. avenae was recorded for two wheat cultivars. Spring wheat 12698, which originated from Afghanistan, produced less than five females per plant in all trials, while the Danish cultivar (Loros) produced less than seven females per plant in both of the pot trials. The latter cultivar was rated susceptible when grown at Watchman (Table 3).

TABLE 3

Reaction of wheat, barley and oat cultivars to H. avenae at Watchman.

Resistance was rated on the number of females per root system (Table 2) and the reaction described as resistant (R), moderately resistant (M.R.), susceptible (S), or very susceptible (V.S.). The tolerance reaction (Methods C (iv)) was a visual assessment of cultivar growth as being either very poor (-) or substantially better than the controls with no symptoms of discolouration (+).

| Cultivar | Resistance | | Tolerance Assessment | Cultivar | Resistance | | Tolerance Assessment |
|---|---|---|---|---|---|---|---|
| | Rating | Reaction | | | Rating | Reaction | |
| WHEAT | | | | | | | |
| Arawa | 3 | S. | - | Trabut | 3 | S. | + |
| Daphne | 2 | M.R. | - | Trabut 38 | 3 | S. | + |
| Ford 617 | 3 | S. | - | Trebli | 2 | M.R. | + |
| Glaive | 4 | V.S. | - | WI 2137 | 4 | V.S. | + |
| Halberd | 3 | S. | - | OATS | | | |
| Heron | 4 | V.S. | - | | | | |
| Joppa | 3 | S. | + | Adios | 1 | R. | - |
| Loros | 3 | S. | - | Algerian | 2 | M.R. | - |
| Medeah | 3 | S. | - | Avon | 1 | R. | - |
| Negroz 1145 | 2 | M.R. | + | Bathurst 4 | 3 | S. | - |
| Portugal 120 | 2 | M.R. | - | Blythe | 1 | R. | - |
| Portugal 131 | 2 | M.R. | - | Boone | 3 | S. | - |
| Portugal 143 | 3 | S. | - | Boppy | 1 | R. | - |
| Salonica 14 | 3 | S. | - | Cocker Fulgrain | 4 | V.S. | - |
| Spring Wheat 12698 | 2 | M.R. | + | Dale | 2 | M.R. | - |
| Turvey | 4 | V.S. | - | Dawn | 3 | S. | - |
| Van Hoek | 3 | S. | + | Early Kherson | 4 | V.S. | - |
| Waratah | 3 | S. | - | Fulmark | 4 | V.S. | - |
| Yanward | 3 | S. | - | Fulton | 4 | V.S. | - |
| BARLEY | | | | Gidgee | 1 | R. | - |
| | | | | Guyra | 2 | M.R. | - |
| Barbless | 2 | M.R. | + | Irwin | 1 | R. | - |
| Bussell | 3 | S. | + | Kent | 2 | M.R. | - |
| CI 3576 | 2 | M.R. | + | Mortgage Lifter | 1 | R. | + |
| Clipper | 4 | V.S. | + | Mulga | 1 | R. | - |
| Esperance | 4 | V.S. | + | N.Z. Cape | 1 | R. | + |
| Freja | 2 | M.R. | + | Saia | 2 | M.R. | - |
| Palestine x Yala | 3 | S. | + | Smyrna | 4 | V.S. | - |
| Prior | 3 | S. | + | Sunrise | 2 | M.R. | - |
| | | | | Swan | 1 | R. | - |

TABLE 4

Resistance rating to H. avenae of wheat, barley and oat cultivars selected from Table 3 and tested in a pot trial.

Resistance of cultivars to H. avenae collected from Mannum was assessed as in Table 3.

| | Resistance | | | Resistance | |
|---|---|---|---|---|---|
| Cultivar | Rating | Reaction | Cultivar | Rating | Reaction |
| WHEAT | | | OATS | | |
| Daphne | 3 | S. | Adios | 2 | M.R. |
| Heron | 4 | V.S. | Algerian | 2 | M.R. |
| Loros | 2 | M.R. | Avon | 3 | S. |
| Negroz 1145 | 3 | S. | Blythe | 2 | M.R. |
| Portugal 120 | 2 | M.R. | Boppy | 2 | M.R. |
| Portugal 131 | 1 | R. | Dale | 3 | S. |
| Spring Wheat 12698 | 2 | M.R. | Early Kherson | 4 | V.S. |
| BARLEY | | | Gidgee | 2 | M.R. |
| Barbless | 3 | S. | Guyra | 2 | M.R. |
| CI 3576 | 3 | S. | Irwin | 3 | S. |
| Freja | 4 | V.S. | Kent | 3 | S. |
| Prior | 4 | V.S. | Mortgage Lifter | 2 | M.R. |
| Trebli | 4 | V.S. | Mulga | 2 | M.R. |
| | | | N.Z. Cape | 2 | M.R. |
| | | | Saia | 3 | S. |
| | | | Sunrise | 3 | S. |
| | | | Swan | 3 | S. |

TABLE 5

Test of significance of the effect of cultivar and experimental conditions on the resistance of cereal cultivars to H. avenae tested in two pot trials.

| | WHEAT | | OAT | |
|---|---|---|---|---|
| Independent variable | df | M.S. | df | M.S. |
| Cultivars | 4 | 4.3421** | 11 | 1.2112*** |
| Trials | 1 | 1.4629 | 1 | 14.2712*** |
| Cultivars x Trials | 4 | 0.1970* | 11 | 0.2357*** |
| Error | 30 | 0.0590 | 72 | 0.0658 |

* Significance at 5%

** Significance at 1%

*** Significance at 0.1%

FIGURE 4

Degrees of resistance of certain barley cultivars to H. avenae.

Cultivars (varieties) of barley were tested for resistance in a pot trial during 1970. Cultivars were graded for resistance on the mean log (x + 2) transformation of four replicates.

| Cultivar (Variety) | |
|---|---|
| 1 | Barbless |
| 2 | CI 3576 |
| 3 | Prior |
| 4 | Trebli |
| 5 | Freja |

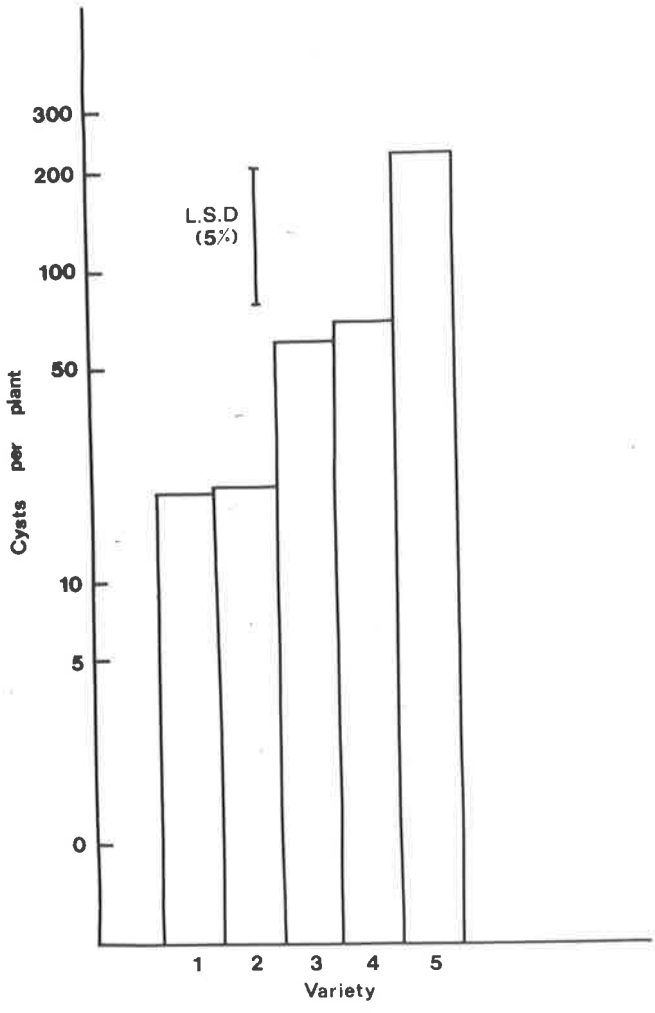

300
200
100
50
10
5
0
Cysts per plant
L.S.D
(5%)
1
2
3
4
5
Variety

FIGURE 5.

Degrees of resistance of certain wheat and oat cultivars to H. avenae.

Resistant and moderately resistant cultivars from Table 3, commercially recommended oat cultivars, and Sun II oats were tested for resistance in a pot trial during 1971. Cultivars were graded for resistance on the mean log (x + 2) transformation of six replicates.

(a) All oat cultivars (Varieties)

1. Guyra
2. Mortgage Lifter
3. Avon
4. N.Z. Cape
5. Blythe
6. Swan
7. Boppy
8. Algerian
9. Kent
10. Sun II
11. Irwin
12. Mulga
13. Early Kherson

(b) Commercial oat cultivars (Varieties)

1. Avon
2. Swan
3. Kent
4. Irwin
5. Early Kherson

(c) Wheat cultivars (Varieties)

1. Spring Wheat 12698
2. Loros
3. Portugal 131
4. Portugal 120
5. Heron

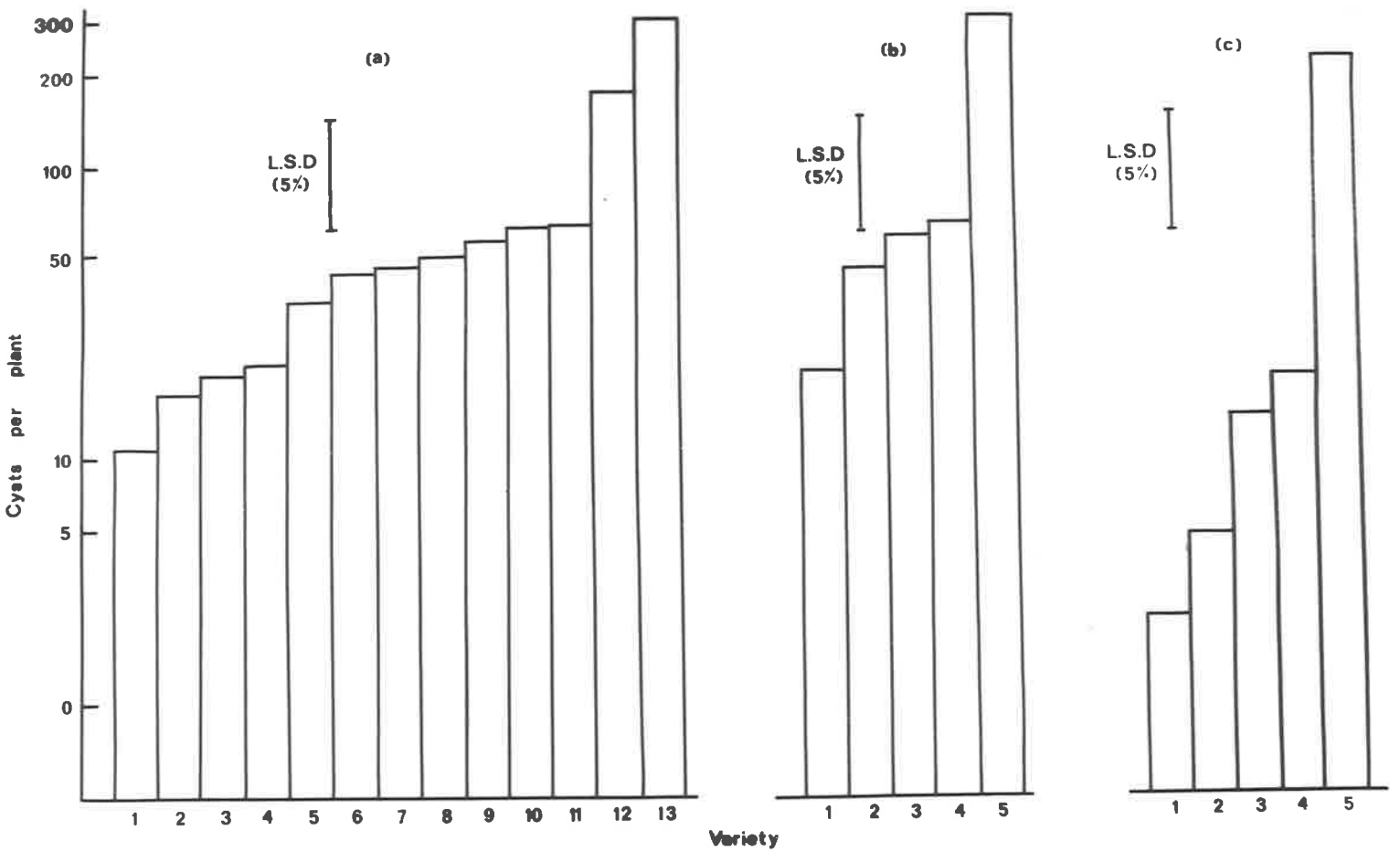

300
200
100
50
10
5
0
Cysts per plant
(a)
L.S.D
(5%)
1 2 3 4 5 6 7 8 9 10 11 12 13
(b)
L.S.D
(5%)
1 2 3 4 5
(c)
L.S.D
(5%)
1 2 3 4 5
Variety

FIGURE 6.

Effect of cultivar and experimental conditions on the degree of resistance of oat cultivars to H. avenae.

Comparison of the number of females per root system of oat cultivars tested in two different pot trials. Each result is the mean log (x + 2) transformation of total females per root system of each cultivar.

 First pot trial

 Second pot trial

Oat cultivars (varieties)

| | | |
|---|---|---|
| 1. Guyra | 5. Blythe | 9. Kent |
| 2. Mortgage Lifter | 6. Swan | 10. Irwin |
| 3. Avon | 7. Boppy | 11. Mulga |
| 4. N.Z. Cape | 8. Algerian | 12. Early Kherson |

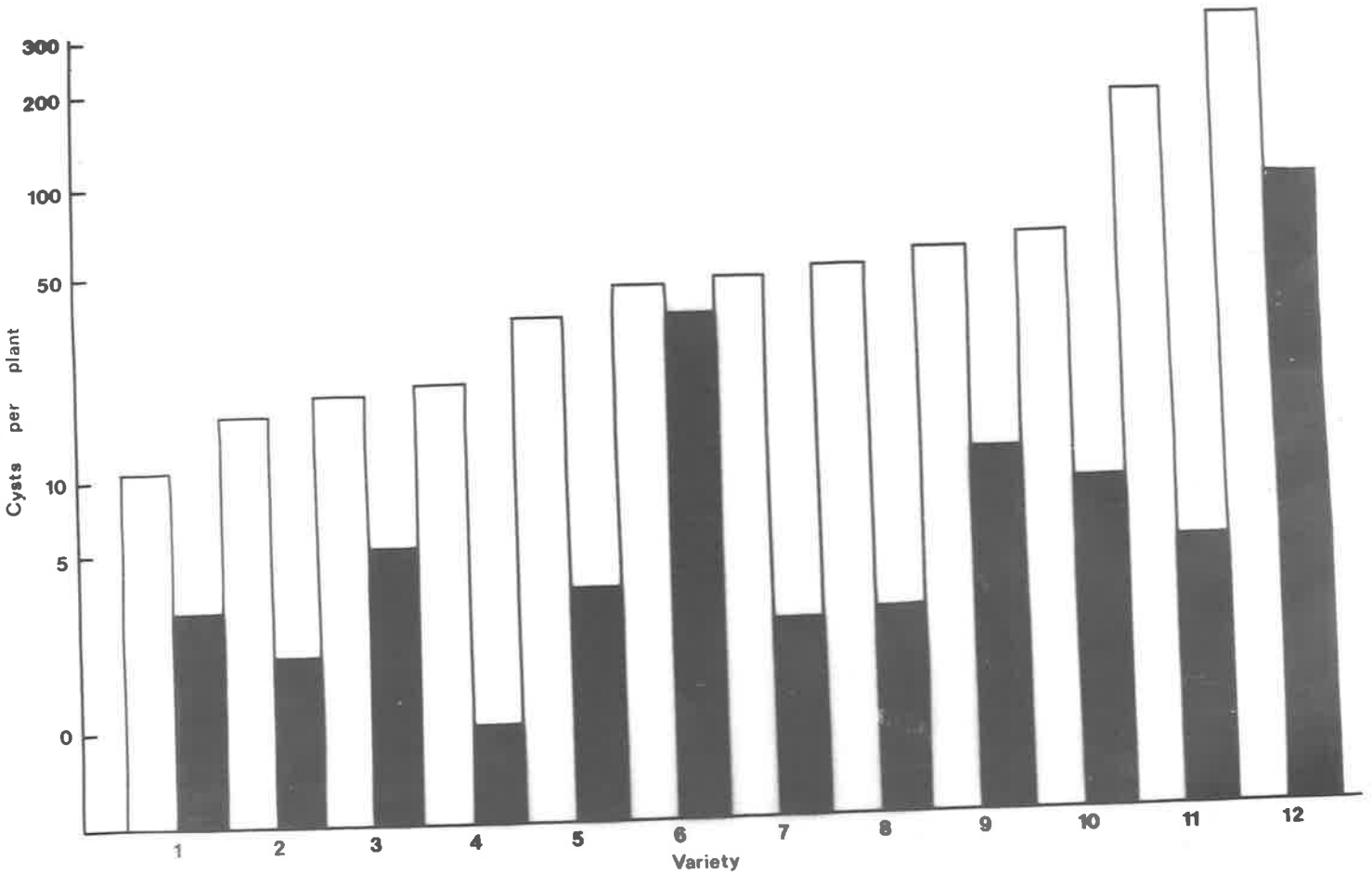
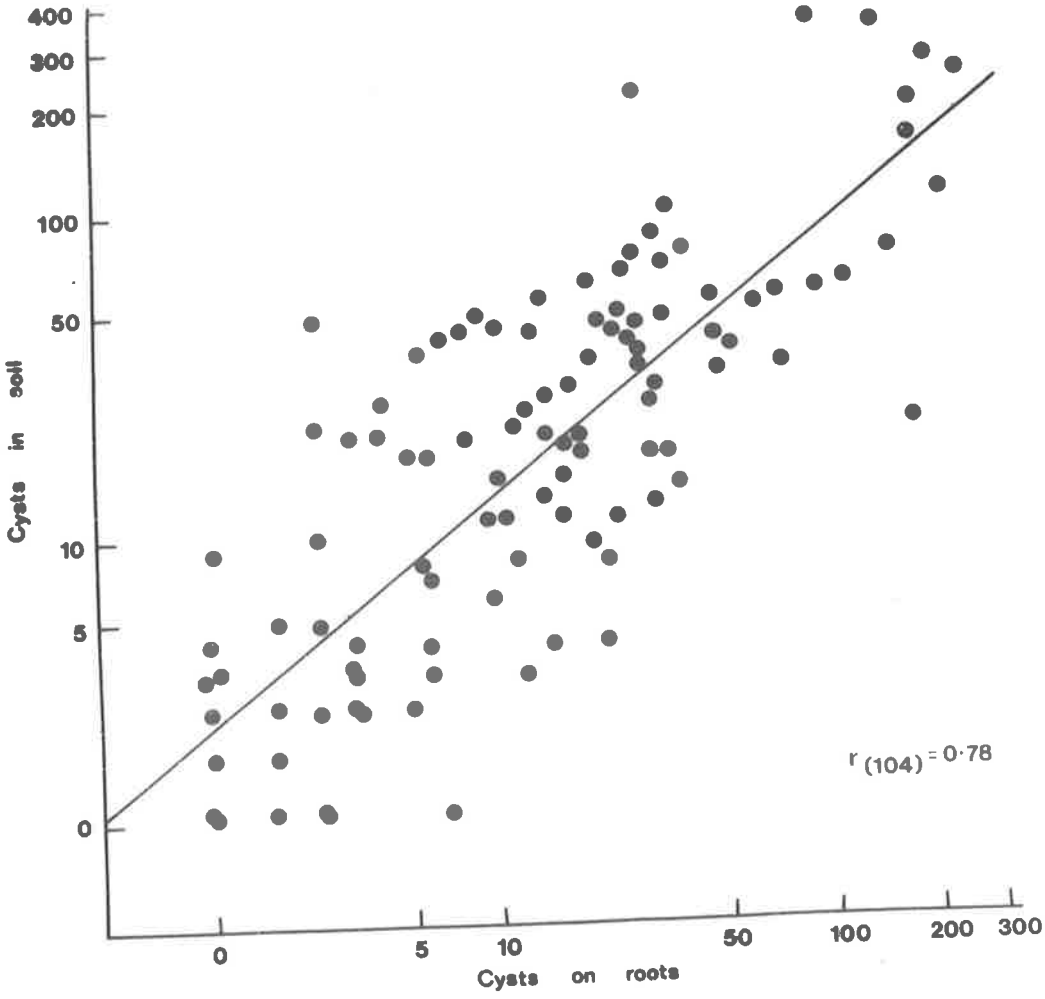

300
200
100
50
10
5
0
Cysts per plant
1
2
3
4
5
6
7
8
9
10
11
12
Variety

FIGURE 7

Scatter diagram showing the relationship between white cysts of H. avenae counted from soil and host roots.

The number of females per root system used to assess the resistance of cultivars from pot trials was the sum of females counted in soil and on roots (Methods D, (iv)). The relationship between the two counts was plotted as the log (x + 2) transformation of all treatments from the 1971 pot trial.


400
300
200
100
50
10
5
0
Cysts in soil
0
5
10
50
100
200
300
Cysts on roots
r (104) = 0·78

## 3. DISCUSSION

Wheat is the major cereal grown in South Australia (Aitchison, 1971), but barley and oats are often grown within a crop rotation system. Therefore, the reduction of populations of H. avenae on all crops is important in controlling the nematode. Heron, Insignia 49, Gamenya and Gabo for wheat; Prior for barley; and Avon, Kent and Early Kherson for oats, were the prominent cultivars of each cereal type grown during 1969 (Aitchison, 1971. Since then, new cultivars of Glaive and Halberd for wheat; Clipper for barley; Swan, Irwin and Coolabah for oats, have been released and recommended as replacements for some of the previously recommended cultivars (Heard, 1972).

All the recommended, commercial cultivars that have been tested for resistance to H. avenae were susceptible. However, the reactions of many of the cultivars were different when tested in the field or in pots, and often both were different from the reactions recorded in Victoria (Brown & Meagher, 1970). These differences must result from one or more of the following reasons; variations in methods of assessment, different initial population densities, or the existence of different biotypes.

A. Methods of assessment

With most cultivars, the improved method of counting the white females per root system used in the pot trials resulted in an increased number of females from that found in the field. Only portion of the root system could be sampled from the field, whereas the entire root system was recovered from pots. The portion of the root system sampled in the field was variable due to differences in the pattern of root growth between different cultivars, and differences in root growth within a cultivar growing in different soil environments (Troughton, 1962). In the field, unless plants were widely spaced, roots of neighbouring plants overlapped, were included in the sample, and were difficult to remove without removing the roots of the test plant. These variables could only be compensated for by sampling a greater number of plants as was done in the field trial at Watchman, where only the number of females per root system was assessed. This method of assessment was similar to that used by Andersen (1961) and Brown & Meagher (1970) but it suffers from some inaccuracies.

A reliable assessment of numbers can only be made when the females are mature, protruding from the roots and are easily seen. But these requirements also mean that the

females may be easily dislodged when soil is being removed from the root system. Thus, when hosts with a wide range of reaction to nematode infection were used, a good correlation between numbers of females on roots and in soil was obtained. This suggests that a correlation factor might be used to transform root counts to total counts, but two problems prevent this; the difficulty of counting females from entire root systems (Kort et al, 1964) and the fact that no correlation could be obtained for hosts with a small number of females on the roots. Thus, the most reliable method of assessment must be based on the number of females in soil and on roots, and the latter count may be obtained by washing all the females from roots (Cotten, 1963), or by root maceration in a Waring blender. Total numbers of females (from both roots and soil) were counted in both my pot trials, and the greater number of females obtained (compared with my field results and those of Brown & Meagher (1970)), probably reflects the increased accuracy of the method.

While field trials provide the most convenient method of testing large numbers of cultivars for resistance to H. avenae, the cultivars selected must be critically evaluated by a pot trial in which the variables associated with counting the total numbers of females per root system can be minimised. The final evaluation is then made in another field trial to

test the reactions of the selected cultivars to infection under natural environmental conditions and to evaluate other agronomic features of the cultivars. For this field trial, the number of cultivars tested should be reduced to a number small enough so that ample replication can be made for a realistic assessment of resistance.

B. Effect of initial nematode density.

Improved methods of assessment probably explain part of the variation in the reactions of wheat and barley cultivars in the field and pot trials (Tables 3 and 4), but the complete resistance of several oat cultivars in the field is more likely to be an effect due to the initial nematode density. When the same method of assessment was used in both pot trials, a significant cultivar x trial interaction occurred (Table 5), and this was more significant in oats due to the wider range of cultivars tested. Since the source of nematode, pot size and soil mix were also similar in both trials, the cause of the interaction was partially due to differences in the initial nematode density.

(i) Effect on field trial

Oats are generally regarded as being less tolerant of H. avenae than either wheat or barley (Gair, 1965), and barley

cultivars are very tolerant (Table 3). Differences in tolerance are probably due partly to differences in the rate of root growth and development, where the rate of root growth with the tolerant plant is slowed to a lesser extent following infection by the nematode than the intolerant plant, and unless the plant is genetically resistant to H. avenae, the nematode is more likely to develop normally as competition is also less between nematodes in the roots. Therefore, following the initial infection of the oat cultivars in the field trial by the nematode, the growth and development of the roots was slower and this probably reduced the total number of larvae penetrating the plants. Even so, enough may have penetrated to cause either severe competition between larvae or a host reaction as a result of the number of larvae infecting the limited root system and this may have prevented normal development of the female nematodes. The effect of nematode density on root growth would be more marked in a field trial than a pot trial because of the added effect of the environment, which is very variable in the field.

Many questions remain unanswered, and more information is needed on the effect of different nematode densities on the resistance of host plants, as a plant resistant at one density may not be resistant at another. Reduced numbers of females could be a nematode-induced effect rather than a host effect,

and this is demonstrated by the ability of susceptible crops to reduce nematode populations (Gair et al, 1969; Cotten, 1970 b; Williams 1970).

(ii) Effect on pot trials.

Whether both trials were inoculated with the same density of nematode cysts or eggs was minor, as the density of nematodes available to infect the plants depended upon the number of larvae hatching from the cysts. Hatching is a complex process (Banyer & Fisher, 1971 a, b), with a better hatch occurring when the cysts are stored at 5°C than at ambient temperature. Therefore, more larvae were available to infect the host in the second trial, and if the interaction was simply an effect of different nematode densities, a proportional decrease in the number of females produced and the same relative resistance rating between cultivars would be expected. No such relation was obtained (Figure 6). With small numbers of infective larvae distributed in the soil, the probability of infection was reduced unless the host roots permeated the soil. Therefore the more rapid growth of roots of the barley cultivars probably permitted good infection of the roots and the eventual development of female nematodes, but variations in the growth of roots within wheat and oat cultivars probably caused variations in infection and in the number of females which developed. Different environments

used in each trial, especially the delay in placing pots in the glasshouse for the first trial, further accentuated this variation in cultivar root growth and the eventual level of infection.

Therefore, if results of trials used to assess the resistance of cereals to H. avenae are to be compared, methods of assessment must be uniform and the degree of variation between treatments minimised. The main problem is in ensuring a uniform density of nematodes capable of infection for each cultivar. Information is required on the relationship between growth characteristics of different cultivars and density of infective nematodes, so that a range of nematode densities which are effective in inoculating all cultivars can be determined and used when cultivars are tested for resistance to the nematode. The results presented for barley cultivars in Figure 4 and for wheat and oat cultivars in Figure 5, provide a realistic grading of the cultivars for resistance to H. avenae as satisfactory levels of nematode infection were achieved within the respective pot trials.

C. Evidence for biotypes

In the evaluation of resistance of cultivars to H. avenae, two populations of the nematode were used to

indicate the possibility of different biotypes occurring in S.A., and these were selected from geographically isolated areas (Figure 8). The reaction of Loros, Freja and Trebli to nematode populations at Watchman (Table 3) and Mannum (Table 4) differ sufficiently to suggest a biotype affect, rather than a difference in either assessment or nematode density. However, further testing with selected cultivars is required to confirm the presence of different biotypes of H. avenae in S.A.

D. Selection of resistant cultivars

Complete resistance of cereal cultivars to H. avenae has rarely been observed, and a cultivar rated as resistant has produced a few females (Andersen, 1961), but variations in the number of females produced on genetically, homozygous genotypes occur which make a numerical limit of resistance difficult to determine (Cotten & Hayes, 1969). Recently, a criterion of a resistant cultivar producing 5% or less of the number of females on a comparative susceptible cultivar was proposed (Brown, R., 1969), and although the limit of resistance would vary with the comparative cultivar selected, i.e., wide variations in the reactions of cultivars to H. avenae occur (Figure 4, 5), it would have the advantage of compensating for different densities of nematode inoculum

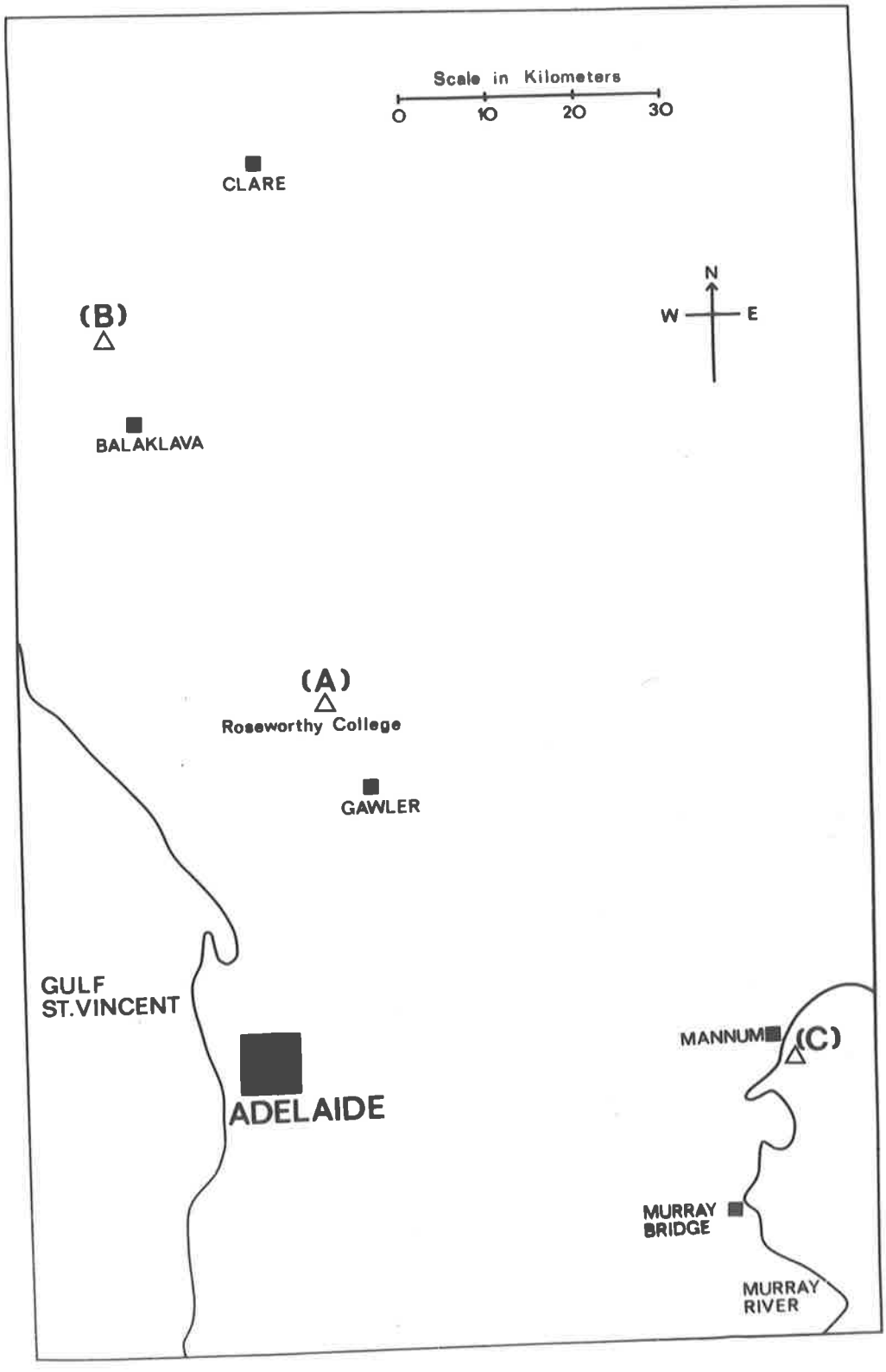
FIGURE 8

Section map of South Australia showing the location of H. avenae populations used in testing cereal cultivars for resistance.

(A) Site of 1967 preliminary selection trial (R.A.C.)

(B) Site of 1969 field trial (Watchman)

(C) Site of cyst collections for pot trials.


Scale in Kilometers
0
10
20
30
CLARE
N
W
E
(B)
BALAKLAVA
(A)
Roseworthy College
GAWLER
GULF
ST.VINCENT
ADELAIDE
MANNUM
(C)
MURRAY
BRIDGE
MURRAY
RIVER

occurring between trials, provided a comparative range of nematode densities was used. If the comparative susceptible cultivar produced 500 females, a cultivar producing 25 females would be rated as resistant to H. avenae by the latter criterion, and although it is significantly more resistant than the comparative cultivar, a rating of resistance to H. avenae is doubtful. Therefore, numerical limits for resistance which are based on female counts are flexible and depend upon the degree of resistance required.

Immediate benefits in the control of H. avenae may be obtained by using the recommended cultivar with the best degree of resistance. Such cultivars may be susceptible, and produce many females and so improved control could not be predicted unless information is available on the effects of different nematode populations on cereal yields. This information is not available for South Australia, however, Mathison (1966) reported Avon oats as sufficiently resistant to reduce the nematode population and increase the yield of a wheat crop in the following season. From the results of the degrees of resistance of commercial oat cultivars (Figure 5 b), Avon oats would be the recommended cultivar and so supports the principle of immediate benefits being obtained by using cultivars with the best resistance. No suitable commercial cultivars are available for wheat, but if the new cultivar

(CI 3576) of barley is released as a suitable commercial cultivar it would give better control than either Prior or Clipper (Figure 4). Although the introduction of wheat quotas throughout Australia has resulted in increased areas of barley and oats being sown (Roberts, 1971), the increase in oats is only slight and it remains a minor crop. This limits the use of oat cultivars in the control of H. avenae in S.A.

In the absence of suitable resistance in the commercial cultivars of wheat and barley, suitable resistant cultivars are needed to breed resistance into these cultivars. From all the cultivars of wheat, barley and oats that were tested for resistance, only two wheat cultivars, Spring Wheat 12698 and Loros, were rated as resistant to H. avenae populations from Mannum. The resistant cultivars averaged less than five females per plant and no plant produced more than seven females in either pot trial, while all other cultivars produced an average of between 20 and 365 females per plant in the pot trial used to assess resistance to H. avenae (Figure 4, 5). Further information on the reaction of both resistant cultivars to different inoculation densities, different nematode populations and the field environment is needed before they can be considered suitable for breeding resistance into other cultivars.

E. Inheritance of resistance.

A knowledge of the inheritance of resistance within cultivars is required for an efficient breeding programme. Results presented in Figure 4 and Figure 5 clearly demonstrate more than a single gene is operative throughout the cultivars tested. Any further conclusions with regards to the inheritance would be conjecture, but the few cultivars presented for wheat (Figure 5 c) and barley (Figure 4) indicate a similar type of inheritance could occur in both, and could be similar to that described for barley by Hayes & Cotten (1970). The degrees of resistance present throughout oat cultivars (Figure 5 a) suggests several genes are involved in determining the resistance reactions (Andersen, 1961). Assuming several genes control resistance in oat cultivars, the reactions of Avon, Swan, Kent and Irwin (Figure 5 b) demonstrate the difficulty in breeding for, and selecting a cultivar line with uniform resistance from polygenic parents as these cultivars have been developed from the same parental lines. However, polygenic resistance may be preferred to monogenic resistance as it delays the development of resistance-breaking biotypes (Van der Plank, 1968), and information is required on the type of inheritance within individual cultivars, the distribution of nematode biotypes and the suitability of the techniques being used to assess resistance during a breeding programme.

F. Resistance-breaking biotypes

A danger in breeding resistant cultivars is the possibility of developing resistance-breaking biotypes (Williams, 1970), and this underlines the need to test for, and to test resistant cultivars against different biotypes. A different biotype to any previously recorded in Europe occurs in Victoria (Brown, R., 1969) and results suggest two possible biotypes within S.A. Further testing is required to confirm and determine the range of biotypes present throughout Australia. An International group (Brown, R., pers. comm.) is attempting to standardise the methods of determining and coding biotypes in different countries. This may be possible throughout Europe where much information on biotypes has already been gained, but to standardise the coding of biotypes between Europe and Australia the same test range of cultivars which includes both susceptible and resistant cultivars must be used. Results show a significant difference between the susceptible cultivars of Sun II and Early Kherson (Figure 5) and that no suitable cultivars with resistance (Brown, R., 1969) are available from the test assortment range recommended by an International group (Brown, R., pers. comm.). Therefore, due to the geographical isolation of Australia, the procedures adopted in the classification of different strains of stem rust (Watson & Luig, 1961) are appropriate, and supports

the need for the development of standard test plants for Australia, but combined with some international standards to maintain international co-ordination. The first stage is to select cultivars with suitable resistance to one nematode population, then these cultivars are tested against different populations in carefully controlled trials to ensure that the variations recorded are a biotype effect and not a technique difference. A comparison of the rating of resistance between cultivars tested at Watchman (Table 3) and in a pot trial (Table 4), suggests Spring Wheat 12698, Loros, Freja, Trebli and a susceptible comparative cultivar (Early Kherson or Heron) could be used as test plants until other cultivars become available as a result of further testing for resistance to H. avenae.

G. Tolerance assessment of cultivars

Attempts to measure the tolerance of cultivars to H. avenae were thwarted by environmental conditions, supporting the conclusions of Cotten (1970 a) and preventing the coupling of this character with resistance at this time. However, a study of the agronomic features of cultivars known to be tolerant may provide a suitable method of assessing tolerance during a breeding programme.

## GROWTH OF H. AVENAE IN WHEAT

In the assessment of resistance of cereals to H. avenae, a stage of growth in the host plant was used as a guide to determine the best time to count the females present on the host roots. General observations suggested floral initiation and floral development within the host were the stages most likely to affect nematode development, and this was checked by determining a growth curve for H. avenae growing within different cultivars of wheat. During this study a different method of evaluating resistance within cultivars was suggested, and further testing of wheat cultivars resistant to H. avenae, Spring Wheat 12698 and Loros, not only supported this possibility but also gave an indication of the mechanism of resistance operating within the cultivars.

### 1. MATERIALS AND METHODS

Similar methods were used throughout the three experiments to measure the effect of different wheat cultivars on the growth of H. avenae.

A. Source of material

Four wheat cultivars were used to measure the effect of the host on the growth of the nematode, two were the susceptible cultivars of Heron and Justin, while the other two, Spring Wheat 12698 and Loros, were the cultivars selected as resistant to H. avenae in the previous study. The susceptible cultivars were selected to provide differences in the time of floral initiation, both between different cultivars and within the same cultivar, to determine the effect of floral initiation on nematode growth. These comparisons were possible because Justin not only initiated floral development earlier than Heron when both cultivars were grown in the same controlled environment of 16 hours of continuous incandescent light per day, but also failed to initiate floral development when grown in a controlled environment of eight hours of continuous incandescent light per day.

In all experiments, the larvae used to inoculate the plants were from cysts of H. avenae collected from Mannum during February, 1971, and stored at 5°C in airtight polythene bags.

B. Inoculation of seedlings

(i) Germination of seeds

Seeds selected for each experiment were soaked in water for 24 hours, sterilised in a 1:1,000 Mercuric Chloride solution for two minutes, and germinated on moist cotton wool in a petri dish which was incubated at 20°C. Germinated seeds at a similar stage of growth were selected, and three germinated seeds were placed in each 90 mm petri dish on the surface of a 1% nutrient agar medium which contained 0.1% Streptomycin Sulphate to suppress the growth of bacteria. These petri dishes were incubated at 20°C until three roots with a minimum length of 20 mm had developed, when the seedlings were either inoculated or stored at 5°C until they could be inoculated.

(ii) Collection of larvae

Root material containing nematode cysts was separated from soil with a 2.38 mm sieve, and washed with a fast jet of water in a 1.68 mm sieve to remove nematode cysts which were collected in a 0.25 mm sieve with other organic material. The nematode cysts, with the organic material, were placed on a cloth of fine mesh, covered by a thin layer of water in a flat dish and stored at ambient temperature. At daily

intervals the number and species of nematodes which had emerged into the water was examined and the water replaced. The collection was discarded unless larvae of H. avenae dominated the population of nematodes; the number of larvae of H. avenae was assessed from aliquots of the solution in a Doncaster dish (Goodey, 1963). The larvae of H. avenae were stored in water at 5°C until sufficient numbers of larvae were collected to inoculate the wheat seedlings. A preliminary experiment showed no loss of ability of larvae after storage at 5°C over a period of seven days to infect the roots of wheat seedlings. Therefore, only larvae which had been stored at 5°C for up to seven days were used in inoculating the seedlings.

(iii) Inoculation of seedlings

All larvae were thoroughly mixed in water, and diluted until an average count of 40 larvae per drop from a pasteur pipette was obtained from ten separate samples. The same pipette was used throughout each experiment and all drops were assumed to be approximately the same volume. Since a preliminary experiment showed sufficient numbers of larvae penetrated seedlings in 12 hours at 15°C when a single drop containing 40 larvae was placed on the root tip growing on agar, all inoculations were done by this method.

C. Management of infected plants

Following inoculation, the seedlings were carefully removed from the agar and washed in running water to remove larvae which had failed to penetrate the roots. Three seedlings were transplanted into a cylindrical, polythene container of an internal diameter of 5 cm and depth of 25 cm, which was open at the bottom to allow free drainage of water. A soil mixture of six parts sand to four parts loam with added organic fertiliser was used to fill the containers to within 2 cm of the top. All pots were placed in environmental cabinets and watered regularly to maintain a consistent moisture content throughout the experiments.

D. Measurement of growth of nematodes

At each harvest for measuring the growth of the nematode, two growth containers were selected at random, and the nematodes within the roots of the six plants were stained with lactophenol cotton blue (Goodey, 1963) so that the nematodes could be dissected from the roots and mounted in 0.0025% lactophenol cotton blue. The longitudinal sectional area of a random sample of twenty nematodes was used as the measure of nematode growth, and was obtained from the magnified outline of a nematode projected onto drawing

paper which was traced and measured with a planimeter. In each case, the nematode was magnified 200 times.

E. Experimental design

Two environmental cabinets were used throughout the experiments, both were set to provide a constant temperature of 20°C and eight hours of intensive, fluorescent lighting, within each 24 hour period but one cabinet simulated long day conditions for floral initiation by providing 16 hours of incandescent light within each 24 hour period, while the other simulated short day conditions and only provided eight hours of incandescent light. All individual plant growth containers used throughout an experiment were randomised within the cabinet and were re-randomised at regular intervals.

In the first experiment, infected plants of Heron and Justin were grown under long day conditions to compare the effect of cultivars with different times of floral initiation on nematode growth. Time of initiation was calculated for 20 plants of each cultivar by the scoring system used by Friend et al. (1963). Nematode growth in Heron was measured at intervals of two or three days, and in Justin was measured at intervals of six or seven days, until the adult female stage was reached; after which the interval of growth

measurement was similar for both cultivars.

Due to a failure in the cabinet set to simulate short day conditions, growth of the nematode in Justin without floral initiation was not measured in the first experiment. Growth of the nematode in Justin growing under long and short day conditions was measured in a separate experiment. A comparison was made of the growth of the nematode at both 34 and 41 days after floral initiation to ascertain the effect of such initiation on the rate of development of the adult female of the nematode.

A further experiment was used to determine the effect of host plants resistant to H. avenae on the growth of the nematode. Infected plants of Heron, Spring Wheat 12698, and Loros were grown under long day conditions, and growth of the nematode measured at four times, i.e., 5, 14, 20 and 34 days after inoculation. These times, selected from the results of the first experiment with Heron, were chosen to give measurements for each of the larval stages and mature females.

Results of the first two experiments were analysed by determining the standard error of each treatment, and since two treatments were being compared in all instances, a t-test of significance between the two means was made. In the final

experiment, the three cultivars at each sample period were subjected to an analysis of variance.

## 2. RESULTS

From the measurement of growth of H. avenae on Heron wheat at regular intervals, a continuous growth curve for females was obtained by drawing in the curve of best fit (Figure 9). Females were smaller on day 22 than either day 20 or day 24 because it was difficult to dissect entire females from the roots of the host when the nematode was moulting, and developing females within the original cuticle were measured. When the growth of the nematode was compared with that on Justin wheat (Figure 9), significant differences occurred on days 13, 20 and 27. Because of the longer intervals between sampling times on Justin wheat, fitting a growth curve to the data was more difficult. If it was assumed that a similar pattern of growth of the nematode occurred on Justin as was found on Heron, then the growth curve would appear as in Figure 9. Significant differences in sizes of the nematodes from the two wheats occurred on days 13, 20, and 27, but not before or after these times. However, floral initiation was earlier in Justin than in Heron (Figure 9).

Floral initiation did not occur in Justin grown under

simulated conditions of short days, but occurred at 25±0.6 days following inoculation when Justin was grown under conditions of long days. Obvious differences in plant growth occurred between the two environments, with tall plants, in which the stem had elongated and few tillers were produced, developed under conditions of long days while short plants, in which no elongation of the stem occurred and many tillers were produced, developed under conditions of short days. Although the growth of females of the nematode was similar in both environments at 34 days, they were smaller in the plants grown under conditions of short days following 41 days of growth (Table 6).

Results on the effect of cultivars of wheat with resistance to H. avenae on the growth of the nematode showed no effect during the first stage (day 5), but reduced growth during the second (day 14) and third (day 20) stages of the nematode (Table 7). No females (fourth stage) had developed on Spring Wheat 12698, and only two developed on Loros after 34 days of growth (Table 7).

To examine uniformity of development of the nematodes on Heron wheat, the frequency distribution of the sizes of the nematodes in each sample was plotted (Figure 10). The percentage of nematodes within a particular size range was

plotted for all samples where the number of nematodes measured was twenty or more. At day 6 (Figure 10), sizes showed a narrow, normal distribution and this broadened with time till day 22 when a double peak occurred, followed by a single peak at day 29. A similar distribution was obtained in the second experiment with Heron (Figure 11).

When the resistant cultivar, Spring Wheat 12698, was compared, a single peak with little variation was obtained at all times, although the size at which the peak occurred gradually increased with time (Figure 11).

FIGURE 9

Mean area of females of *H. avenae* in Heron and Justin wheat.

No distinction was made between male and female larvae during the first 15 days of growth, but potential or actual females were selected by both size and shape at later times. The standard error for each mean for Heron and the means for Justin which differed significantly from Heron at the same age are given.

■——■ Heron  □– – –□ Justin

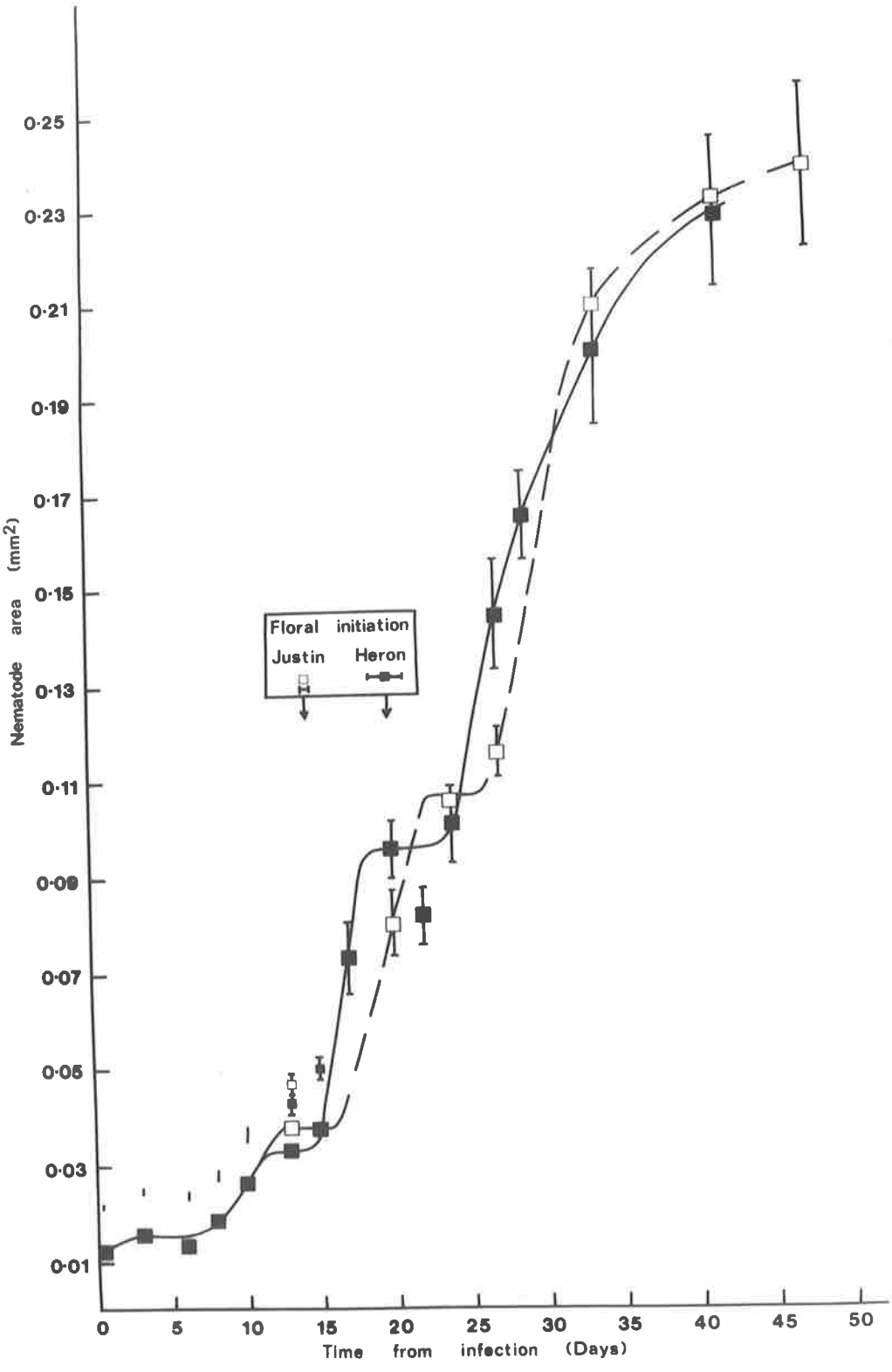

0·25
0·23
0·21
0·19
0·17
0·15
0·13
0·11
0·09
0·07
0·05
0·03
0·01
Nematode area (mm²)
Floral initiation
Justin
Heron
0
5
10
15
20
25
30
35
40
45
50
Time from infection (Days)

TABLE 6. Size of H. avenae measured at two different times in Justin wheat grown under long and short days.

| | Nematode area ($mm^2 \times 10^2$) | | | |
|---|---|---|---|---|
| Days from infection | 34 | | 41 | |
| Growth condition | Mean | S.E. | Mean | S.E. |
| Long day | 20.0 | 1.5 | 24.1 | 1.2 |
| Short day | 19.5 | 1.1 | 22.5 | 1.3 |
| | N.S. | | *** | |

TABLE 7.

Size of H. avenae measured at four different times in a susceptible and two resistant wheat cultivars. Experiment done under long day lighting.

| Cultivar | Nematode area ($mm^2 \times 10^3$) Days from infection | | | |
|---|---|---|---|---|
| | 5 | 14 | 20 | 34 |
| Heron | 15.2 | 31.0 | 46.4 | 222.4(1) |
| Spring Wheat 12698 | 14.7 | 24.5 | 29.7 | Nil |
| Loros | 15.0 | 23.4 | 28.7 | 251.3(2) |
| L.S.D. (5%) | N.S. | 4.0 | 10.5 | - |

(1) Mean of 12 nematodes

(2) Mean of 2 nematodes.

FIGURE 10.

Variation in size of H. avenae in Heron wheat at eight different times.

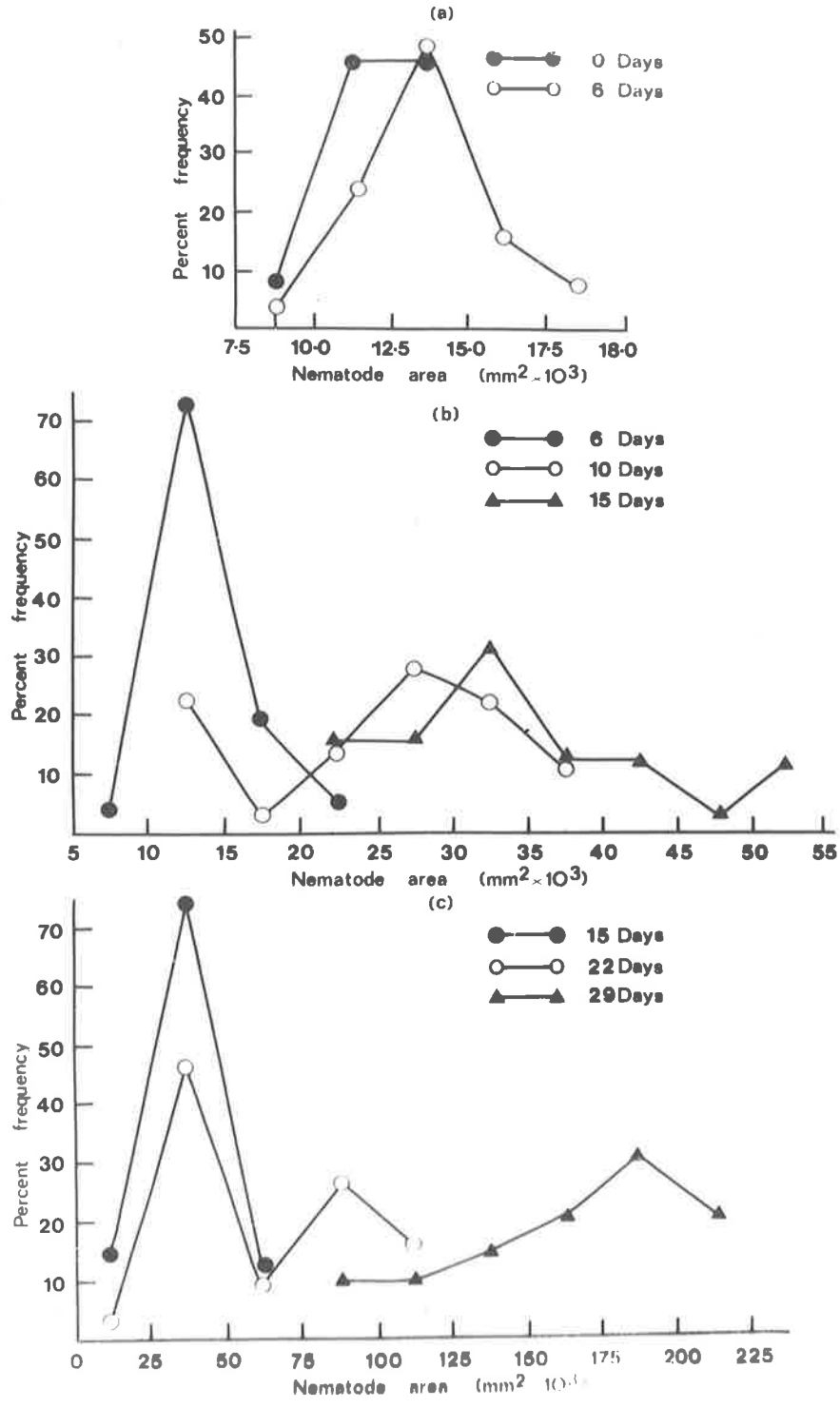
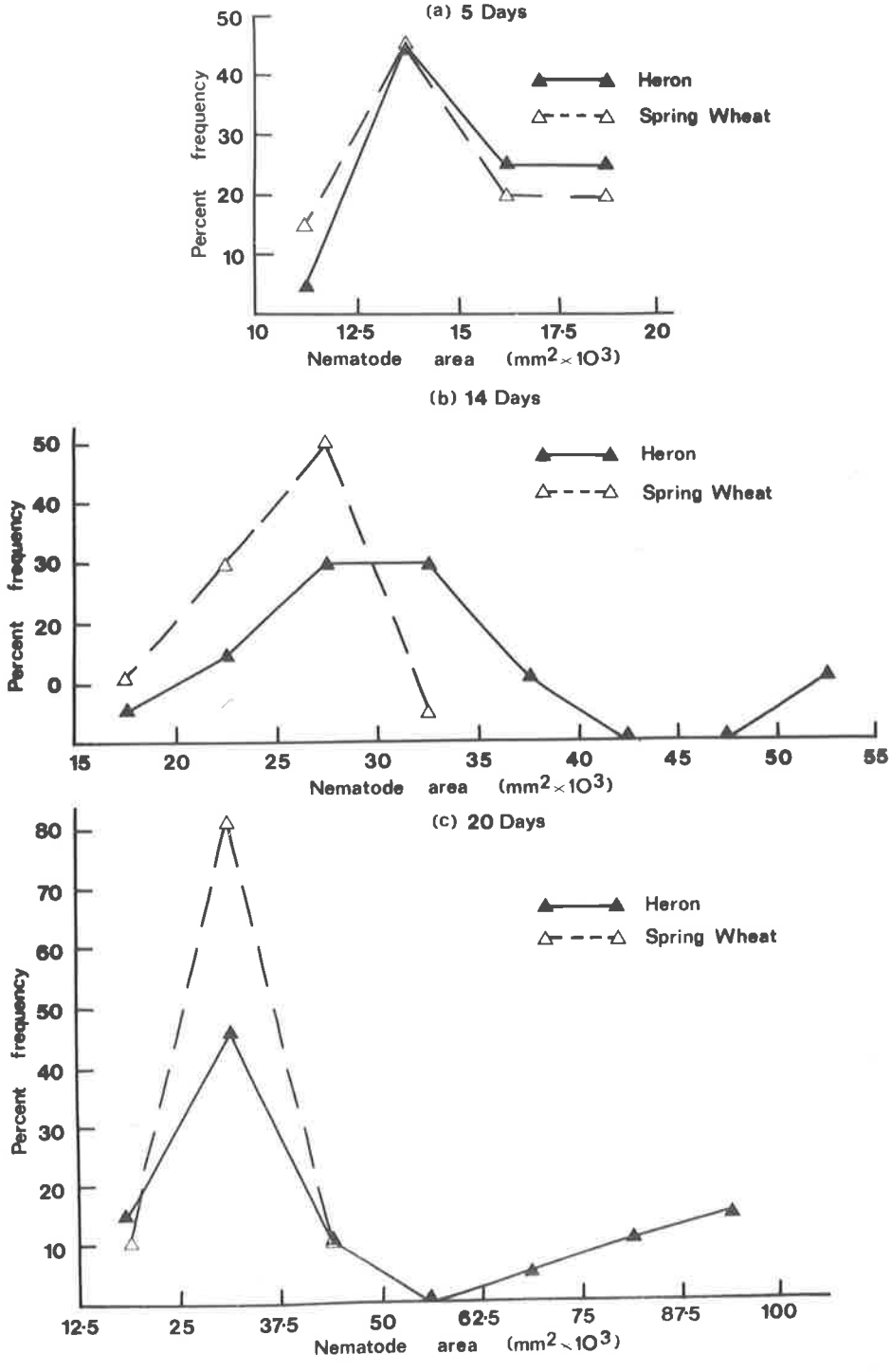

(a)
0 Days
6 Days
Percent frequency
50
40
30
20
10
7·5
10·0
12·5
15·0
17·5
18·0
Nematode area (mm2 ×10³)
(b)
6 Days
10 Days
15 Days
Percent frequency
70
60
50
40
30
20
10
5
10
15
20
25
30
35
40
45
50
55
Nematode area (mm2 ×10³)
(c)
15 Days
22 Days
29 Days
Percent frequency
70
60
50
40
30
20
10
0
25
50
75
100
125
150
175
200
225
Nematode area (mm2 10³)

FIGURE 11.

Variation in size of H. avenae in Heron and Spring Wheat 12698 at three different times.


(a) 5 Days
Percent frequency
50
40
30
20
10
Heron
Spring Wheat
10
12·5
15
17·5
20
Nematode area (mm2×10³)
(b) 14 Days
Percent frequency
50
40
30
20
0
Heron
Spring Wheat
15
20
25
30
35
40
45
50
55
Nematode area (mm2×10³)
(c) 20 Days
Percent frequency
80
70
60
50
40
30
20
10
Heron
Spring Wheat
12·5
25
37·5
50
62·5
75
87·5
100
Nematode area (mm2×10³)

## 3. DISCUSSION

The development of females of H. avenae on Heron (Figure 9) was similar to the growth and development of females of H. schachtii (Raski, 1950). Although the growth of females of H. avenae should be similar on different susceptible hosts, differences might occur if the growth of the host influences the nematode, and resistant cultivars should have a drastic effect on the growth of the nematode.

### A. Nematode growth in susceptible hosts.

Resistance of cultivars was assessed in all trials when the inflorescence of the host had or nearly had emerged from "the boot". That all cultivars, irrespective of their time of maturity, were assessed at the same stage suggests a relationship between growth of the nematode and the host, i.e., that the physiological development of the host as influenced by its genetic constitution and/or the environment controls the growth of the nematode. But growth of the nematodes on Heron and Justin, grown under the same environmental conditions, was similar except for one period of time - growth of the nematode was slower in each cultivar at the time of floral initiation so that eventually the same size of females was produced at the same time. When the

genetic constitution was left constant but the environment was altered (Justin grown under short and long days) the females reached a larger size under long days than under short days, and floral initiation did not occur under short days. Thus a direct effect of floral initiation on growth of the nematode is untenable and an indirect effect, such as increased competition for metabolites between the host and nematode at this time, seems more likely.

B. Nematode growth in resistant hosts.

Barley cultivars with resistance to H. avenae did not affect the number of larvae penetrating the roots, but growth of the nematode was delayed and very few females developed (Cotten, 1969; 1970 a). A similar effect occurred with resistant cultivars of wheat, except that there was no effect on the growth of the nematode, and the nematode did restrict growth of the root but no galls and very few lateral roots developed. The development of lateral roots from the site of infection is likely to be a result of the successful formation of syncytia and galls by the nematode in the host, especially if the larvae secrete either a growth substance or a precursor to stimulate formation of syncytia as occurs with other nematodes (Nusbaum, 1958; Krusberg, 1963; Johnson & Viglierchio, 1969 b; Orion & Minz, 1969). Therefore,

the absence of lateral roots and galls on the resistant plants suggested a mechanism of resistance in which the host prevented the formation of suitable syncytia for female growth. Further to this, secondary infections by larvae were noted with Heron which appeared to result in the development of females and a failure to form galls and lateral roots also occurred at some of the infection sites. Since inter-nematode competition has affected the ability of larvae to establish syncytia (Trudgill, 1967; Ketudat, 1969), the movement of larvae to another site, and their eventual development into females was probably an effect of over population of nematodes in the original site of infection.

Therefore, resistance in Spring Wheat 12698 and Loros was probably due to the prevention of larvae establishing suitable syncytia for female growth and the larvae left the root, died or developed into males, but the latter possibility of sex reversal appears unlikely with larvae of H. avenae. However, similar results with Heron demonstrate a possible effect of nematode density on growth of females and before the mechanism of resistance can be clarified, the effect of different densities of nematodes on both nematode and plant growth must be determined.

# GENERAL DISCUSSION

Soil pests and diseases are notoriously difficult to control, and H. avenae is no exception due to the distribution in the soil and the protection of dormant larvae by the cyst wall, egg shell and larval cuticle. Although control of H. avenae has been obtained with soil fumigants (Williams, 1969) and non-phytotoxic systemic poisons (Brown et al, 1970), it was not economic and undesirable effects on the ecology of the soil could be expected. Thus, in the absence of effective and economic methods of killing H. avenae before planting, reliance has been placed on crop rotation, which has not been effective in Australia due to the use of susceptible cereal cultivars and the prevalence of susceptible, volunteer grasses in the pastures. Predictions of changes in farming practices throughout Australia as a result of the introduction of wheat quotas is difficult (Roberts, 1971), but longer rotations, the introduction of non-host plants as alternative crops, or the regular use of cultivars of oats which can give some control as previously discussed, are possibilities which could give improved control. However, improved yields by reducing populations of H. avenae with resistant cultivars appears to be the most profitable method for the future.

A major problem in the use of resistant cultivars is the development on, and the increase in population of biotypes of the nematode which can multiply on the resistant host. This difficulty has been experienced with H. rostochiensis on potato, and from computed population changes of the nematode an alternation of resistant and susceptible potatoes in a crop rotation programme was suggested (Jones et al, 1967 a). Biotypes of H. avenae do occur throughout Europe and results from experiments presented here indicate that they occur in Australia, but as the virulence of the nematode appears to be dominant (Andersen, 1965) rather than recessive, as appears likely with H. rostochiensis (Jones & Parrott, 1965), the problem may not be as serious with H. avenae. Also, resistance in cereals can be due to more than a single gene, which suggests that better resistance to the biotypes of H. avenae could be obtained than is available for H. rostochiensis at present (Howard, 1969). To overcome a similar problem in breeding wheat cultivars with resistance to stem rust in wheat (Puccinia graminis tritici), a continuous breeding programme has been maintained to develop new cultivars with resistance to the new races of the fungus, and a continual coding of races of rust with a test assortment range has been necessary. A similar approach will be needed for H. avenae, and although the development of suitable techniques of assessment are more

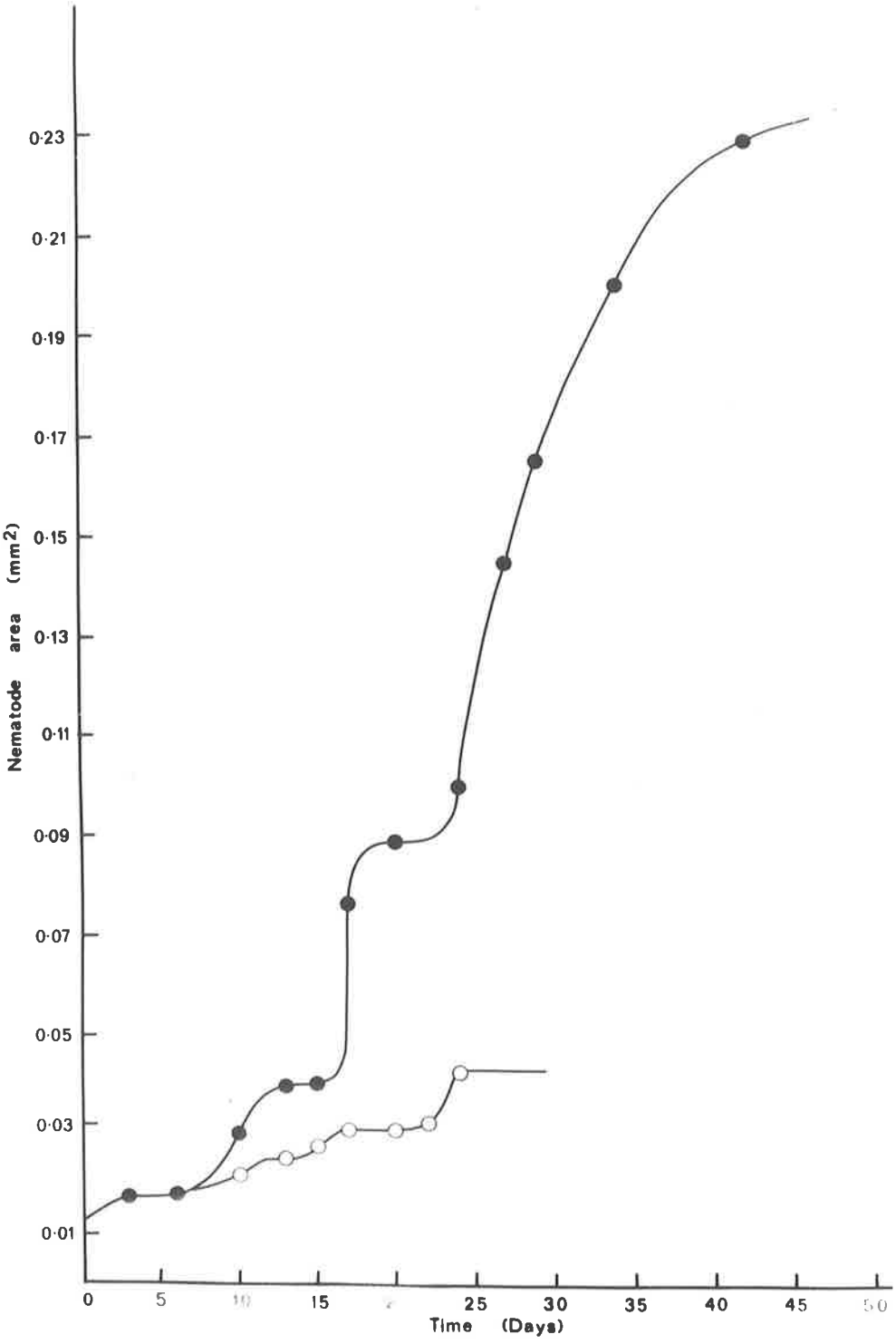
difficult with a soil pathogen, there is an advantage of fewer new biotypes developing and a slower spread of such a biotype if it does develop. Therefore, once the present biotypes have been identified, they are likely to be stable and cultivars resistant to them are likely to remain resistant for a long period.

Spring Wheat 12698 and Loros have been assessed as resistant to H. avenae, and Spring Wheat 12698 was the better cultivar as it was resistant to the two probable biotypes. During the assessment of resistance in both field and pot trials, problems were encountered with the methods used and deficiencies in other methods that have been used were suggested, both of which have been discussed previously. However, while studying the development of the nematode in wheat cultivars, a possibility of developing a new method of assessment became apparent.

Results on the growth of H. avenae on Heron (Figure 9) suggested that potential females could be identified after a short period of growth. Since sex reversal is unlikely in H. avenae and few females are produced on resistant hosts (Table 7), a hypothetical growth curve for males and females (Figure 12) was obtained by calculating the probable mean size of each. This was done by assessing the likely size distribution

FIGURE 12.

Hypothetical growth of H. avenae in wheat


0·23
0·21
0·19
0·17
0·15
0·13
0·11
0·09
0·07
0·05
0·03
0·01
Nematode area (mm²)
0
5
15
25
30
35
40
45
50
Time (Days)

of males and females from the variations in size obtained at each stage of growth on resistant and susceptible hosts. From this curve (Figure 12), a differentiation of males and females is possible after only ten days growth, but since morphology is still similar, differentiation after 20 days growth is more practical. Therefore, the inoculation of the roots of seedlings on agar with a measured number of larvae, growth in controlled conditions of environment, and assessment of resistance on either the number of potential females or probable sex ratio after 20 days growth, is suggested as a method of determining resistance of cultivars to H. avenae.

Before such a method could be used with confidence, much more information is required on plant and nematode relationships, especially the effect of different nematode densities on nematode and plant growth. Observations on the development of galls and lateral roots at the site of infection suggested that the morphological development of the host could possibly be used to eliminate susceptible plants, thereby eliminating the need to either examine or measure the nematodes in the roots of all plants being tested. Once again, more information is required before plant morphology following infection could be used as a preliminary means of selection or rejection of cultivars in the method described. Advantages in developing the method are, the reduced time required to test

cultivars, control over the density of inoculation, uniform measurement of nematodes, an indication of the mechanism of resistance, and independence of the effect of the agronomic characters of individual plant growth. Unless some biochemical test of plants becomes available to assess resistance, it will be difficult to assess resistance without the destruction of the plant, but perhaps the growth of excised roots which have been infected by the nematode in tissue culture may provide an alternative in future years.

Throughout all this work, it has been apparent that much more information is required on the biology of H. avenae before resistance of cultivars can be fully utilised. Some of the additional information required includes: presence of and distribution of biotypes, virulence of the nematode and its ability to break resistance, effect of nematode density on plant and nematode growth, mechanisms of resistance, sex ratios and the possibilities of sex reversal.

# APPENDIX

## APPENDIX 1. Wheat cultivars selected to test for resistance to H. avenae at R.A.C. during 1967.

Cultivars were selected at random from the cultivar collection at the Waite Agricultural Research Institute in 1967. Since that time, the collection has been transferred to the Australian Wheat Collection at Tamworth, N.S.W. All named cultivars that were screened for resistance are listed under their country of origin, and those with an "Aus. No." are available from the Australian Wheat Collection. Cultivars with only a catalogue number and cultivars which failed to grow during the trial have been omitted.

| Aus. No. | Cultivar |
|---|---|
| | ABYSSINNIA |
| 4040 | Abyssinnia 1 |
| 4041 | " 10 |
| 4044 | " 21 |
| 4047 | " 24 |
| 4050 | " 28 |
| 4054 | " 37 |
| | AFGHANISTAN |
| 4065 | Afghanistan 6 |
| 4070 | " 19 |
| | " 21 |
| 4074 | " 25 |
| 4076 | " 29 |
| 4078 | " 32 |
| | " 41 |
| 4091 | " 52 |
| | " 56 |
| 4107 | " 100 |
| 4109 | " 108 |
| 10843 | Fettiorci 12693 |
| 2908 | Lutescens 12681 |
| 10894 | Spring Wheat 12698 |
| | ARGENTINE |
| 1778 | American 8 |
| | Gaboto |
| | Klein Rendidor |
| 2885 | Litoral Precoz |
| | Magnif |
| | Sinvalocho |
| | AUSTRALIA |
| | ATP 163 |
| 1924 | Bencubbin |
| | Beacon |
| 11404 | Canberra x Hope |
| 2117 | Charter |
| 2172 | Comeback |
| 157 | Dirk |
| 9929 | Dural |
| | Eureka 2 |
| 218 | Federation |
| 11393 | Fed. x Webster |
| 2406 | Festival |
| 10414 | Florence |
| 2441 | Free Gallipoli |
| | Gabo |
| 250 | Gabo 56 |
| 2501 | Gluyas |
| 322 | Heron |
| 2662 | Javelin |
| 410 | Kings White |
| | K.F. Heron |
| 438 | Koala |
| 2859 | Leatherhead |
| 506 | Marathon |
| 2984 | Mayquad |
| 10429 | Minflor |
| 669 | Nabawa |
| 719 | Noongaar |
| 3117 | Olympic |
| 3168 | Pinnacle |
| 799 | Pioneer |
| 3182 | President |
| 884 | Purple straw |
| 3213 | Quadrat |
| 10446 | Rajah |
| 1192 | Scimitar |
| 10408 | Seafoam |
| 1196 | Seewari |
| 3358 | Sepoy |
| | Spica |
| 1317 | Stockade |
| 1335 | Sunset |
| 1381 | Thew |
| 3451 | Totadgin |
| | Triple Dirk |
| 3466 | Turvey |
| 3485 | Union |
| | Wallace |
| 1612 | Waratah |
| 1634 | Warigo |
| 1676 | Wongoondy |
| 1678 | Woodie |
| 1686 | Yalta |
| 3555 | Yandilla king |
| | BRAZIL |
| 701 | Negroz 11 45 |
| 1086 | Rio Negro |
| | BULGARIA |
| 1539 | Varna 6 |
| 3499 | Varna 20 |
| | CANADA |
| | CT-244 |
| 6706 | Lee 2 x Kenya Farmer |
| 2964 | Marquis |
| 1013 | Red Bobs |
| 3238 | Red Fife |
| | Rescue |
| 6708 | RL 2520 x Th.6 x Kenya F. |
| | CHINA |
| 112 | China 34 |
| | CHILE |
| 2125 | Chilean Wheat |
| 2760 | Klein Grandero |
| 1179 | Santa Catelina |
| | CANARY ISLES |
| 4236 | Canary 1 |
| 4243 | " 5 |
| | COLUMBIA |
| | Bonza |
| 687 | Napo 63 |
| | Narino 59 |

Appendix 1 (Contd.)

| Aus. No. | Cultivar |
|---|---|
| | CRETE |
| 4272 | Crete 1 |
| 4274 | " 2 |
| 4292 | " 13 |
| 4296 | " 14 |
| 4378 | D.E.S. 0080 |
| 4389 | " 0188 |
| 4385 | " 367 |
| | " 399 |
| | CZECHOSLOVAKIA |
| 2278 | Dioseg No. 2 |
| 2279 | Dioseg No. 200 |
| | CYPRUS |
| 4311 | Cyprus 2 |
| 4321 | " 4 |
| 4327 | " 9 |
| 4329 | " 12 |
| | EGYPT |
| 1744 | Abou Fashi |
| 4469 | Egypt 2 |
| 4473 | " 6 |
| 4490 | " 21 |
| 4501 | " 39 |
| 4513 | " 49 |
| 4528 | " 59 |
| 4533 | " 65 |
| 2325 | Egyptian Wheat |
| 4552 | Giza |
| 4559 | Giza 14 |
| 4563 | " 28 |
| 4566 | " 36 |
| | " 150 |
| | " 144 |
| 1230 | Sinai 2 |
| 1238 | " 8 |
| 1245 | " 13 |

| Aus. No. | Cultivar |
|---|---|
| | FRANCE |
| 1772 | Alter De Gembloux |
| 1576 | Ble Vilmorin 27 |
| 2113 | Chante clair |
| 3190 | Professeur Delos |
| 3563 | Yga Blondeau |
| | JAPAN |
| 351 | Igachikogo |
| | Oregon |
| | GERMANY |
| 2559 | Heines Kolben |
| 3936 | Var-Lutescens Spring |
| | GREECE |
| 4372 | D.E.S. 43 |
| 4575 | Greece 1 |
| 4578 | " 2 |
| 4591 | " 16 |
| 4599 | " 19 |
| 4605 | " 24 |
| 4611 | " G 38290 |
| 4613 | " G 46025 |
| 4614 | " G 58383 |
| 4612 | " G 61450 |
| 5609 | Salonica 1 |
| 5621 | " 11 |
| 5622 | " 14 |
| | HUNGARY |
| 33 | Bankuti |
| 2551 | Hatvani 1140 |
| | Szekacs 164 |
| | HOLLAND |
| 3498 | Van Hoek |

| Aus. No. | Cultivar |
|---|---|
| | INDIA |
| | Binjawar B4 |
| | C-518 |
| 2570 | Hindi 12 |
| 2572 | " 62 |
| 4640 | India 4 |
| 4652 | " 9 |
| 4669 | " 35 |
| 4684 | " 53 |
| 4691 | " 61 |
| 4694 | " 64 |
| 4702 | " 74 |
| 4712 | " 86 |
| | " 96 |
| 4721 | " 100 |
| 4725 | " 110 |
| 4729 | " 113 |
| 4733 | " 115 |
| 4736 | " 117 |
| 4741 | " 120 |
| 4746 | " 134 |
| 4754 | " 146 |
| 4763 | " 180 |
| 4773 | " 193 |
| 4778 | " 195 |
| 4788 | " 207 |
| 4798 | " 210 |
| 6049 | " 213 |
| 6054 | " 220 |
| 4805 | " 224 |
| | " 227 |
| 4819 | " 236 |
| 4824 | " 237 |
| 4829 | " 246 |
| 4834 | " 252 |
| 4840 | " 261 |
| 4847 | " 276 |
| 4850 | " 318 |
| 4855 | " 322 |
| 4859 | " 325 |
| 4873 | Indore E2 |
| 4875 | " E98 |
| 4877 | " P6 |
| 4879 | " P11 |

| Aus. No. | Cultivar |
|---|---|
| 3882 | Indore P34 |
| 4969 | Kashmir 1 |
| 698 | Narsingarh N45 |
| 697 | " N121 |
| 10440 | Pusa 4 |
| 905 | " 12 |
| 921 | " 90 |
| 12114 | " 111 |
| 3208 | Pusa 114 Imperial |
| 5548 | Rewa R12 |
| 1068 | " R36 |
| 5546 | " R53 |
| 5549 | " R67 |
| 5553 | " R76 |
| 5556 | " R101 |
| 1731 | Zonk 1 |
| | **ITALY** |
| 1938 | Biancuccia |
| 2040 | Cairdelenze |
| 2069 | Capelli T.D. |
| 151 | Dante |
| 4392 | D.E.S. 1062 |
| 4397 | " 1069 |
| 4401 | " 1077 |
| | Farro Lungo T.D. |
| 2498 | Giùstalisa |
| 3342 | Scorsonera |
| 1507 | Urria |
| | Villa Ilori |
| | **KENYA** |
| 6040 | Kenya 4 |
| 6045 | " 9 |
| 6046 | Kenya wheat |
| | **MALTA** |
| 2941 | Malta 3 |
| 2946 | Malta yellow |

| Aus. No. | Cultivar |
|---|---|
| | **MOROCCO** |
| 4983 | Morocco 2 |
| 4989 | " 8 |
| 4993 | " 10 |
| 5009 | " 19 |
| 5014 | " 20 |
| 5024 | " 25 |
| 5039 | " 35 |
| 5064 | " 52 |
| 5066 | " 53 |
| | **MEXICO** |
| 1790 | Andes 3 |
| 2201 | Crespo 63 |
| 473 | Lerma Rujo |
| 478 | Lerma Rojo 64A |
| 527 | Mayo 64 |
| 556 | Mexico 23 |
| 558 | " 24 |
| 563 | " 27 |
| | Nadadores 63 |
| | Nainari 60 |
| 770 | Penjamo 62 |
| | Pitic |
| 801 | Pitic 62 |
| 3384 | Sonora 63 |
| 1264 | " 64 |
| 1266 | " 64A |
| 1401 | Tota 63 |
| 1700 | Yagui 50 |
| 1707 | " 54A |
| | 8156 (White grain) |
| | **NEW ZEALAND** |
| 2744 | Aotea |
| 1811 | Arawa |
| 10884 | Solid straw Tuscin |
| 3425 | Tainui |
| 10452 | Zealand |
| 2478 | 140014 |

| Aus. No. | Cultivar |
|---|---|
| | **PALESTINE** |
| 5162 | Palestine 1 |
| 5165 | " 2 |
| 5168 | " 3 |
| 5172 | " 5 |
| 5178 | " 10 |
| 1228 | Sinai 1 |
| | " 12 |
| | **PERSIA** |
| 6291 | C.P.I. 2681 |
| 5184 | Persia 1 |
| 5187 | " 6 |
| 5197 | " 11 |
| 5202 | " 16 |
| 5201 | " 22 |
| 5218 | " 40 |
| 5234 | " 56 |
| 5238 | " 59 |
| 5250 | " 78 |
| 5265 | " 101 |
| 5279 | " 131 |
| 5283 | " 136 |
| | **POLAND** |
| 3850 | T. persicum |
| 3816 | T. polonicum |
| | **PORTUGAL** |
| 1868 | Barbela 0248 |
| 140 | Condestavel |
| 485 | Lusitano |
| 756 | Padeira |
| 800 | Pirana |
| 5295 | Portugal 2 |
| 5298 | " 3 |
| 5313 | " 16 |
| 5314 | " 18 |
| 5326 | " 25 |
| 5333 | " 26 |
| 5347 | " 33 |

| Aus. No. | Cultivar |
|---|---|
| 5355 | Portugal 43 |
| 5374 | " 60 |
| 5378 | " 62 |
| 5404 | " 90 |
| 5412 | " 100 |
| 5428 | " 120 |
| 5438 | " 125 |
| 5449 | " 131 |
| 5461 | " 137 |
| 5472 | " 143 |
| 5492 | " 153 |
| 5499 | " 157 |
| 5522 | " 170 |
| 1067 | Restauracao |
| 3283 | Ribeiro |
| | Toviero |
| | PAKISTAN |
| | C 271 |
| | C 273 |
| | IRAQ |
| 4886 | Iraq 1 |
| 4891 | " 6 |
| 4894 | " 12 |
| 4898 | " 16 |
| 4903 | " 22 |
| 4912 | " 30 |
| 4924 | " 40 |
| 4931 | " 50 |
| 4932 | " 52 |
| 4934 | " 54 |
| | ROUMANIA |
| 2845 | Laza 4 |
| 3299 | Roumanian Autumn |
| 1135 | Rovini |
| | RUSSIA |
| 6301 | C.P.I. 6739 |
| 6313 | C.P.I. 6756 |
| 2312 | Dymchatka |
| 10841 | Erinaceum 29706 |
| 2349 | Erythrospermum 29666 |
| 290 | Graecum 6034 |
| 5572 | Russia 8 Belosiornaia |
| 5578 | Russia 30 Novinka |
| 1185 | Sarrubra |
| 1405 | Transcaucasian |
| | SOUTH AFRICA |
| 1947 | Bird proof |
| 2805 | Kruger |
| 1126 | Rooi kleinkoren |
| | SWEDEN |
| 1830 | Atle |
| 2009 | Brons |
| 2343 | Eroica |
| 2705 | Karn 2 |
| 3527 | Weibulls Atson |
| 2705 | Wis Karn 2 |
| | SYRIA |
| 4115 | Aleppo 1 |
| 4121 | " 5 |
| 4126 | " 10 |
| 4132 | " 21 |
| 4138 | " 26 |
| 4144 | " 30 |
| 4148 | " 31 |
| 4154 | " 33 |
| 4203 | Beyrouth 1 |
| 4206 | " 4 |
| 4346 | Damascus 1 |
| 4350 | " 3 |
| 4355 | " 4 |
| 4357 | " 6 |
| 4359 | " 7 |
| 4367 | " 13 |
| | SPAIN |
| 4157 | Alicante 1 |
| 4160 | " 3 |
| 4165 | " 7 |
| 1870 | Barcelona 4 |
| 2088 | Castellon 1 |
| 10862 | Leon 15 |
| 2923 | Mahon 1 |
| 5108 | Navarra 3 |
| 5119 | " 17 |
| 5127 | " 26 |
| 5137 | " 50 |
| 5149 | " 64 |
| 3305 | Salamanca 7 |
| 3310 | " 12 |
| 5635 | Sevilla 19 |
| 5638 | " 20 |
| | " 27 |
| 3377 | Solina |
| 5726 | Valencia 1 |
| 5740 | " 13 |
| 5753 | " 23 |
| 12097 | Valladolid 1 |
| | TURKEY |
| 5646 | Smyrna 2 |
| 5650 | " 4 |
| 5655 | " 7 |
| 5662 | " 11 |
| 5668 | " 14 |
| | TUNISIA |
| 1 | |
| 1079 | Richelle Tres Hative |
| 5669 | Tunis 1 |
| 5672 | " 2 |
| 5679 | " 8 |
| 5696 | " 21 |
| 5697 | " 23 |

| Aus. No. | Cultivar |
|---|---|
| | UNITED KINGDOM |
| 3242 | Red Marvel |
| | T.vulgare x Rye |
| | U.S.A. |
| 1844 | Baart |
| | Big Club |
| 2123 | Cheyenne |
| | Crim |
| 2255 | Defiance |
| 10846 | Genesee |
| 10851 | Harvest Queen |
| 339 | Huron |
| 348 | Idaed |
| | Iowin |
| | Justin |
| 2782 | Knox |
| 2869 | Lemhi |
| 2870 | Lemhi 53 |
| 2961 | Marquillo |
| 3012 | Michigan Amber |
| 3018 | Mida |
| 3029 | Mindum |
| 3024 | Minn No. 2776 |
| 3145 | Pawnee |
| 3345 | Selkirk |
| | Thatcher |
| 1386 | Thorne |
| 1394 | Timstein |
| 1555 | Vermillon |
| | YUGOSLAVIA |
| 4195 | Belgrade 1 |
| 4198 | " 7 |
| 4202 | " 9 |
| 4298 | Crotia 2 |
| 4305 | " 18 |
| 4340 | Dalmatia |
| 4342 | Dalmatia 2 |
| 2876 | Licka Jara Psenica |
| 3366 | Serajevo 18 |

| Aus. No. | Cultivar |
|---|---|
| | UNKNOWN ORIGIN |
| 1754 | Akathiotico |
| 1760 | Alaska |
| 1801 | Apex |
| 4180 | Argentine C9656 |
| 1824 | Asprov Roullous |
| 1830 | Atle |
| 10831 | Avis |
| 1974 | Babin |
| | Baflo |
| 1875 | Barleta |
| 1905 | Bearded Velvet Node |
| 38 | Beaver Lodge |
| 1956 | Black Hull |
| 3138 | Ble De La Paix |
| 1973 | Boa Boa |
| 1992 | Bonzo 63 |
| 6229 | C591 |
| 2053 | Candeal |
| 2064 | Canus |
| 2086 | Cascade |
| 11413 | Clar.x Kenya Baringa |
| 2146 | Clark No. 40 E.G. |
| 6292 | C.P.I. 6729 |
| 6296 | C.P.I. 6733 |
| 135 | Colonias |
| 2183 | Converse |
| 2189 | Correll's No.8 |
| 154 | Daylight |
| 4439 | D.E.S. 421 |
| 4418 | " 571 |
| 4452 | " 796 |
| 4427 | " 2261 |
| 4432 | " 2963 |
| 2290 | Doubbi |
| 4461 | D.P.I. 31 2 |
| 4460 | D.P. Mezcla |
| 4463 | D.Q. 3 150 2 |
| 2292 | Dread nought |
| 6356 | E. 220 |
| 2316 | Early Russian |

| Aus. No. | Cultivar |
|---|---|
| 2324 | Egyptian 16 |
| 2338 | Enrique Matte |
| 12071 | Erie Sel.255811 |
| 201 | Escondido 41 |
| | Essex Conqueror |
| 204 | Falaria |
| 209 | Family 115 |
| | Favorito x 3815 |
| 2405 | Ferrugineum 14335 |
| 6376 | FL |
| | Florida |
| 2422 | Foffre |
| 236 | Fontana |
| 2460 | Fulcaster |
| 2451 | Frontana |
| 2454 | Frontiera |
| 2472 | Galgalos |
| 11406 | Garra x Khapli |
| 2491 | Gharflor 1611 |
| 10848 | Goldberry 32 |
| 2509 | Golden King |
| 291 | Granadero Klein |
| 4616 | Greek 10 C7135 |
| 11408 | H44 x Minhardi C9669 |
| 319 | Hellas |
| 2563 | Henry |
| 2565 | Heps |
| 2567 | Hilgendorf |
| 2576 | Hochzucht |
| 2580 | Hokuku |
| 331 | Hopea |
| 2597 | Hostianum |
| 2616 | Hybrid 10038 |
| 345 | " RL 607 |
| 2623 | " " 723 |
| | " " 724 |
| 2625 | " " 730 |
| 2629 | Ideal |
| 10856 | Imperial Amber |
| 4647 | Indian 6 |
| | Joffrette |
| 2685 | Juljuli |
| 2690 | Kahala |

| Aus. No. | | Aus. No. | Cultivar | Aus. No. | Cultivar |
|---|---|---|---|---|---|
| 2697 | Kambourico | 5385 | Portugal 65 C7921 | 11596 | Texas Sel'n |
| 2698 | Kambourigo | | | 6703 | Thatcher x Trimeo 630 |
| | Kyperounda | 846 | Poso 41 | | |
| 6704 | Kanred x 38279 | 3791 | Poulard | 1388 | Tiba 63 |
| 6033 | Kenya Crossbred | 1053 | Purple Kernel | 1426 | Trintanu |
| 5789 | Kenya C9906 | 3180 | Precoce | | Tripolirico |
| 5808 | " C10857 | 3185 | Preston | 1431 | Tripolitico |
| 5814 | " C10860 | 881 | Psathas | 3851 | T.compactum |
| 6020 | " RL1373 | 10966 | Ramona | | T.dicoccum |
| 6018 | " RL1375 | 11603 | Ramona 44 | 3879 | T.pyramidale |
| 6016 | " RL1377 | 1029 | Redilla | 3860 | T.sphaerococcum |
| 3585 | Khapl 1 | 3252 | Regent RL9756 | 1434 | Triumfo |
| 2740 | Kharkov | 1013 | Red Bobs 222 | 1442 | T.S.Tunisienne |
| 2750 | Kitchener | 3243 | Red May | | Tufyi |
| 2761 | Klein Lucero | 3245 | Red Rock | 3462 | Turkey |
| | Kloka | 3274 | Reward | 1477 | Turkey 10015 |
| | Koga | 1071 | Rhodesian | 3474 | Tuscan |
| 2784 | Koga 2 | 1076 | Rialle | 10904 | Ukrainka |
| 2804 | Kruger | 1078 | Richelle Hative | 3480 | Ulka |
| 2817 | Kubanka | 1077 | Richelle 374 | 1488 | Universal |
| 2852 | Lawrence | 3287 | Ridit | 1508 | Uruquay C10835 |
| 2894 | Loombah | 3292 | Rio | 5700 | V 39 |
| | N 151 3 | 1105 | RL 975 | 5703 | V 217 |
| 2910 | McMurachy | 1124 | Rooie Lamma | 5712 | V 12 672 |
| 500 | Malvi Local | 1140 | Rural | 5714 | V 12 700 |
| 2983 | Mavrov Roullous | 1151 | Rust Resister | 5723 | V 41 17 |
| 532 | Mentana Aristato | 3321 | San Giorgio | 3502 | Varonne C6146 |
| 662 | Moreno | 3326 | San Martin 1643 | 1551 | Vencedor x Lin Calel |
| | Motia | 1179 | Santa Catalina | | |
| 12083 | Mummy | 1188 | Schultz | 1552 | Vencedor x Kanred |
| 3088 | Niphad 4 | 3960 | Secalotricum | | |
| 722 | Norin 21 | 3354 | Sensation | 1561 | Vesta |
| 3097 | Norka | 10400 | Sonora | 1564 | Vete |
| | Normandie | 1268 | South African Median | 1573 | Vijay |
| 934 | NP 710 | | | 1579 | Villa Gloria White odessa |
| | Opal | 1311 | Steinwedel | | |
| 3133 | Orlandi | | Steinwedel Timopheevi | 3565 | Yielder |
| | Orfed | | | 3574 | Zenati x Booteille |
| 3137 | Pacific Bluestem | 1326 | Sturgeon CI11703 | | |
| 755 | Pacific Bluestem 37 | 1331 | Subtropical Hard White | 1816 | 38 Ardito 21 0 12 |
| 3142 | Parker's sel'n | 3403 | Super hard | 11591 | 38 San Martin 137 |
| 3149 | Pelissier | 3405 | Supreza | | |
| 10871 | Pesterboden | | Svenno | 2713 | 113 Yellow Grain |
| 3162 | Pilot | 1375 | Tarrubra | | |
| 3175 | Polish | 3428 | Tassilo | 11364 | 2780 E |

APPENDIX 2 Wheat cultivars selected to test for resistance to H. avenae at Watchman during 1969.

| Cultivar | Origin | Cultivar | Source |
|---|---|---|---|
| Arawa | New Zealand | Daphne | Dr. A.J. Rathjen |
| India 261 | India | Ford 617 | " |
| Knox | U.S.A. | Joppa | " |
| Morocco 19 | Morocco | Medeah | " |
| Negroz 1145 | Brazil | Waratah | " |
| Norin 21 | Unknown | Yanward | " |
| Portugal 120 | Portugal | | |
| Portugal 131 | Portugal | Loros | Dr. A.J. Rathjen |
| Portugal 143 | Portugal | | |
| Salonica 14 | Greece | Glaive | R.A.C. |
| Spring Wheat 12698 | Afghanistan | Halberd | R.A.C. |
| Turkey | Unknown | | |
| Van Hoek | Holland | | |

APPENDIX 3. Barley and Oat cultivars from the R.A.C. collection which were tested for resistance to H. avenae at R.A.C. during 1967.

| Barley Cultivars | Oat Cultivars | Oat Cultivars |
|---|---|---|
| Anabee | Aberystwyth | Hagera |
| Arabian Blue | Aberystwyth 5147 | Hancock |
| Atlas | Acacia | Ideal |
| Bald Skinless | Adios | Iogold |
| Barbless | Advocate | Irwin |
| Bevan's Special | Advocate x Victoria | Kanota |
| Beecher | Algerian | Kareela |
| Cape | Algeribee | Kelvin |
| Carlsburg | Amery | Kendel |
| Chevalier | Avon | Kent |
| F 78 Jerusalem | Bathurst 4 | Kerson |
| Flynn | Baxter | Kiah |
| Freja | Belar | Kurrajong W2408 |
| Greenough | Blythe | Kurri |
| Kenia | Bombo | Lachlan |
| Lenta | Boone | Kaggan |
| Maga | Boppy | Markton |
| Nepal | Borran | Mindag |
| Noyep | Bradley | Mortgage Lifter |
| Palestine 2 | Buddah | Mulga |
| Palestine E x Yala | Budgery | Myal |
| Prior | Bundy R1558 | N.Z. Cape |
| Prior x Maltworthy | Bunya | Orient |
| Research | Burdette | Pen Rhyn |
| Resibee | Burke | Powys 5226 |
| Titan | Calcutta | Quondong |
| Trabut | Cocker Fulgrain | Richland |
| Trabut N36 | Cooba | R.S.L. |
| Trabut N38 | Coolibah | Rua kura |
| Trebli | Dale | Smyrna |
| Ymer | Dawn | Sunrise |
| | Early Burr | Starks 2 |
| | Early Kherson | Swan |
| | Eaton | Tas Algerian |
| | Frazier | Victoria |
| | Fulmark | Victory |
| | Fulton | Warrigal |
| | Ferguson Nevarra | Weston |
| | Gidgee | Wongan |
| | Guyra | Woodford |

APPENDIX 4. Barley and Oat cultivars selected to test for resistance to H. avenae at Watchman during 1969.

| BARLEY | | OATS | |
|---|---|---|---|
| Cultivar | Source | Cultivar | Cultivar |
| Barbless | R.A.C. | Aberystwyth | Gidgee |
| Bevan's Special | R.A.C. | Adios | Guyra |
| Bussell | W.A.R.I. | Algerian | Irwin |
| CI 3576 | W.A.R.I. | Avon | Kent |
| Clipper | W.A.R.I. | Bathurst 4 | Mortgage Lifter |
| Esperance | W.A.R.I. | Blythe | Mulga |
| Freja | R.A.C. | Boone | N.Z. Cape |
| Palestine 2 | R.A.C. | Boppy | Saia |
| Palestine E x Yala | R.A.C. | Cocker Fulgrain | Smyrna |
| Trabut | R.A.C. | Dale | |
| Trabut 38 | R.A.C. | Fulmark | Sunrise |
| Trebli | R.A.C. | Fulton | Swan |
| WI 2137 | W.A.R.I. | | |

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